



Rapid monitoring of ecological persistence

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Effective conservation of ecological communities requires accurate and up-to-date information about whether species are persisting or declining to extinction. The persistence of an ecological community is supported by its underlying network of species interactions. While the persistence of the network supporting the whole community is the most relevant scale for conservation, in practice, only small subsets of these networks can be monitored. There is therefore an urgent need to establish links between the small snapshots of data conservationists can collect, and the “big picture” conclusions about ecosystem health demanded by policymakers, scientists, and societies. Here, we show that the persistence of small subnetworks (motifs) in isolation—that is, their persistence when considered separately from the larger network of which they are a part—is a reliable probabilistic indicator of the persistence of the network as a whole. Our methods show that it is easier to detect if an ecological community is not persistent than if it is persistent, allowing for rapid detection of extinction risk in endangered systems. Our results also justify the common practice of predicting ecological persistence from incomplete surveys by simulating the population dynamics of sampled subnetworks. Empirically, we show that our theoretical predictions are supported by data on invaded networks in restored and unrestored areas, even in the presence of environmental variability. Our work suggests that coordinated action to aggregate information from incomplete sampling can provide a means to rapidly assess the persistence of entire ecological networks and the expected success of restoration strategies.

ecological networks | biomonitoring | structural stability | mutualism | pollination

To assess progress toward local, national, and international biodiversity conservation targets, it is crucial to understand how ecological communities are being impacted by global change and how well they are responding to conservation interventions (1, 2). Biomonitoring—the process of regularly measuring ecosystems to track changes in different indicators over time—therefore has a critical role to play in guiding conservation policy and practice.

Perhaps, the most fundamental indicator of ecosystem health is the composition and stability of communities. This can be assessed by monitoring communities and whether any of their component species are declining to extinction (3). Thus, for conservation scientists and decision makers, community persistence—the probability that a community can sustain positive abundances of all its constituent populations over time—is one of the most important properties to know about a community (4, 5).

One widespread approach to measure community persistence relies on species interaction networks, where nodes, representing species, are joined by links, representing biotic interactions, such as predation or pollination (6). These networks are then used as a “skeleton” for simulating population dynamics, from which persistence is then measured. While this approach is powerful, collecting interaction network data using fieldwork is expensive and time consuming, often requiring huge investments to approach sampling completeness (7–10). For example, studies have shown that even with exhaustive sampling efforts that covered 80% of pollinator fauna, it was possible to capture only 55% of the interactions in a plant–pollinator network, and it was estimated that sampling effort would need to increase by five times to record 90% of the interactions (11). Similarly, while DNA barcoding and metabarcoding approaches offer the prospect of achieving complete sampling of networks more easily, at present, these methods are far from the norm (12), requiring significant technical expertise, sampling protocols, and infrastructure with costs that can be comparable to traditional field approaches (12).

The expense and time involved in collecting community-level data, such as sampling interaction networks, are in direct contrast to the needs of biomonitoring and the frugal realities of conservation practice (7). Biomonitoring relies on indicators that are sufficiently quick and cheap to sample that regular “snapshots” of ecosystem status can be taken. Thus, although persistence is a fundamental property of communities

Significance

Monitoring progress toward the UN Convention on Biological Diversity's Goals and Targets depends on up-to-date, repeatable, and comparable measures of ecosystem health. Fieldwork remains the primary way that ecosystems are monitored. However, fieldwork is expensive and time-consuming, meaning that, in practice, only small subsets of ecosystems can be monitored. Here, we establish a major bridge from network theory to conservation. We show, through a theoretical lens, statistical framework, and empirical validation, that small amounts of incomplete field data can be “scaled up” to rapidly assess the persistence of whole ecological communities. Our work suggests that ecosystem health can be rapidly and repeatedly assessed using minimal resources, which could substantially improve our ability to monitor progress toward biodiversity policy targets.

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that we wish to monitor, time and cost constraints mean that sampling the required interaction network data with sufficient temporal, spatial, and taxonomic resolution is impractical in all but the most well-resourced contexts.

It has been suggested that interaction networks can be monitored cost-efficiently if only a small subset of interactions—a subnetwork—is sampled (7, 13). A common practice is to predict persistence by simulating the population dynamics of the sampled subnetwork. However, it is unclear whether this practice provides reliable conclusions about the persistence of the wider network. Thus, it is important to assess whether there is any consistent relationship between the persistence of a subnetwork and the persistence of the larger network that the subnetwork comes from. If such a relationship could be established, then whole-network persistence could be inferred from subnetworks that require much less effort to sample. In turn, the prospect of rapid and affordable biomonitoring of network persistence would become feasible.

Here, we provide a solution to diagnosing the persistence of ecological networks without the need for extensive sampling. Specifically, we show that the persistence of a network as a whole is linked to the persistence of small-scale subnetwork structures (network motifs) that require much less sampling effort to monitor (Fig. 1). We use coexistence theory to show that mutualistic and antagonistic interaction networks that are persistent as a whole are composed of subnetworks that would persist in isolation. That is, they are composed of subnetworks that would persist even if they were not embedded within the larger network of interactions. We term these subnetworks persistent in isolation. We show that reliable conclusions about the persistence or nonpersistence of a whole network can be made from sampling the interactions of a small proportion of species. We corroborate our results using empirical data on invaded mutualistic interaction networks (14). We show that persistent ecological networks, despite their spatiotemporal variability, contain more persistent subnetworks in isolation in areas where

invasive species have been removed through restoration action than in areas where there has been no restoration. Finally, we discuss our results in light of opportunities for the rapid biomonitoring of network persistence. By providing an approach for a rapid assessment of the status of a community, our approach could comprise the detection stage of a detection and attribution framework for biodiversity monitoring. This rapid detection step would support local planning and prioritization of action for communities that are not persistent. If integrated into a large-scale monitoring network, our approach could help provide a national or global picture of the persistence of ecological systems.

Linking Network and Subnetwork Persistence

The challenge we face is knowing whether the persistence of a large species interaction network can be inferred by only observing the structure of one or more subnetworks (also known as interaction motifs). The structural approach in ecology (15, 16) provides a theoretical solution to this problem by connecting the persistence of the network as a whole with that of its subnetworks. The central concept in the structural approach is the coexistence domain (D)—the full range of conditions (parameter space) under which all species in a network can coexist, given a particular network structure (17). In other words, species coexist when the network parameter is inside the coexistence domain and do not coexist when the network parameter is outside the coexistence domain. Hence, the persistence of a network as a whole can be studied using the coexistence domain of its underlying network structure (D_{whole}). Similarly, to understand the persistence of a subnetwork, we can study the coexistence domain of its underlying subnetwork. This can be done in two ways, as illustrated in Fig. 2 and *SI Appendix, Fig. S1*. First, we can study the subnetwork as part of the larger network in which it is embedded; formally, this is the projection of the coexistence domain of the network onto the subnetwork ($D_{\text{sub}}^{\text{Embedded}}$) (18).

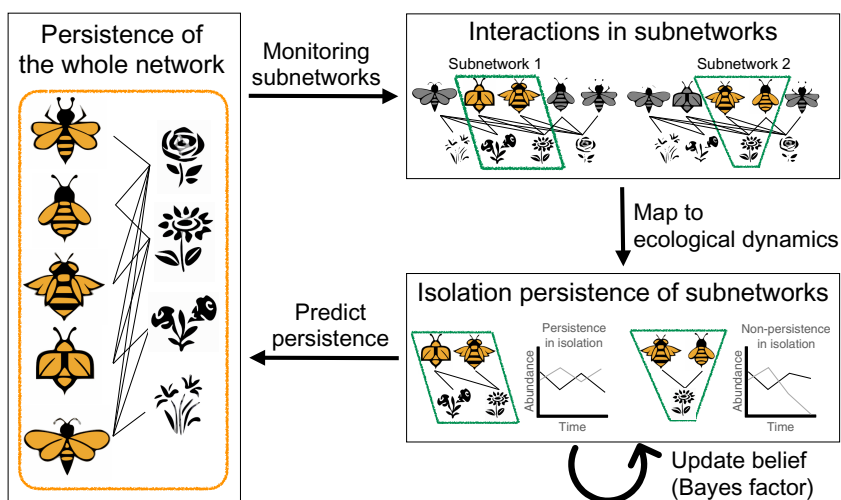


Fig. 1. Illustrated scheme to detect network persistence from monitoring subnetworks. For illustrative purposes, we consider a hypothetical network structure of a bipartite mutualistic network consisting of five pollinator species and four plant species (orange box). Persistence is a network-level property, which makes the network scale the most relevant scale for measuring persistence. However, time and cost constraints and sampling biases limit our knowledge of the network structure. Thus, we most often observe small-scale subnetworks called motifs (two green boxes) that are embedded into the larger network. “Embedded persistence” refers to persistence of these motifs that are part of larger networks. However, given that the whole network is unobservable, we can instead study whether the subnetworks can persist in isolation, removed from the wider network context, which we call the “persistence in isolation” of a subnetwork. This property of “persistence in isolation” is widely used in empirical studies, where researchers predict species persistence by simulating the population dynamics of the sampled subnetwork. While it is clear that the persistence of the network determines the embedded persistence of subnetworks, here, we show that the persistence in isolation of subnetworks is linked to the persistence of the network as a whole, and we can update our belief on the persistence of the whole network from observing the persistence in isolation of the subnetworks.

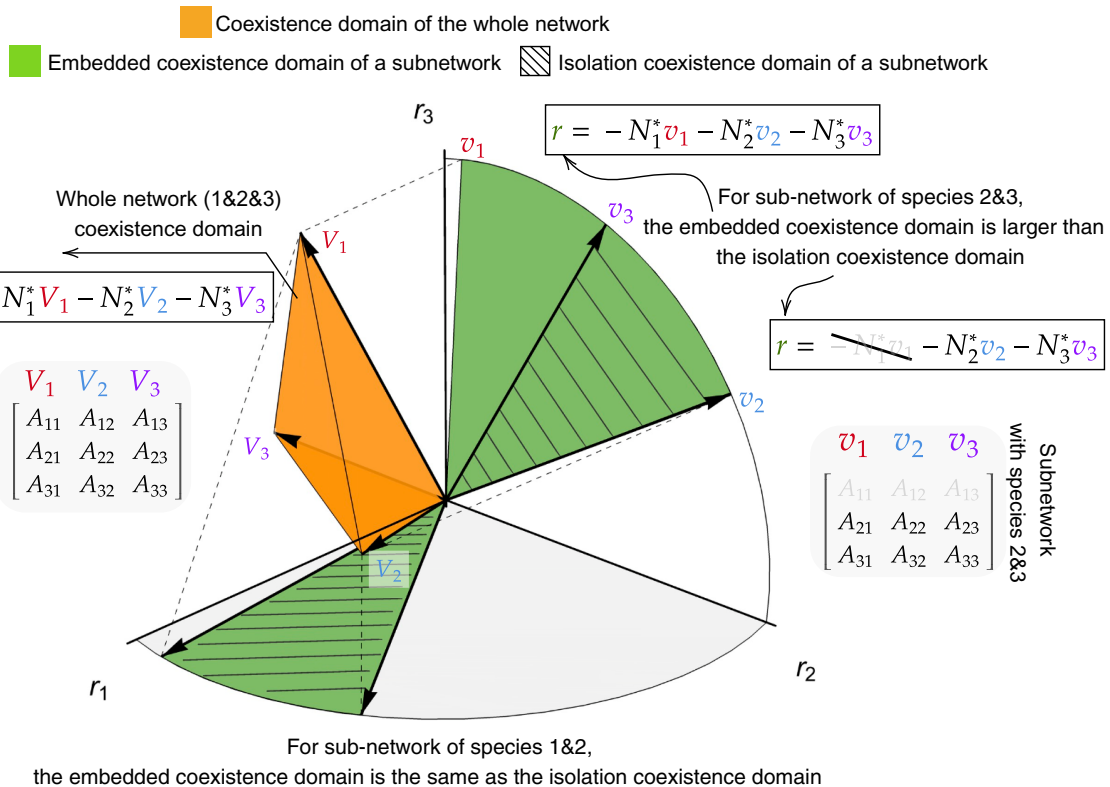


Fig. 2. A structural approach to link persistence across scales. We establish the link between the network and the subnetwork scales via the concept of the coexistence domain: the region of all parameters in which a given set of species coexists. For illustrative purposes, we consider a hypothetical 3-species network. If we want to understand persistence of the network as a whole, we should study the coexistence domain of the network where all species coexist (orange region). If we want to understand the isolation persistence of a subnetwork, we should study the coexistence domain of the subnetwork in isolation i.e., removed from the larger network of interactions in which it is embedded (hashed region). If we then want to understand the persistence of the network as a whole, but we can observe only a subnetwork (embedded persistence), then the observed coexistence domain for the subnetwork is the projection of the network's coexistence domain into the subnetwork's (light green region). The projection of the network's coexistence domain is always larger than (e.g., subnetwork with species 2 and 3) or equal to (e.g., subnetwork with species 1 and 2) the subnetwork's coexistence domain.

Second, we can study the coexistence domain of the subnetwork in isolation, removed from the larger network of which it is a part ($D_{\text{sub}}^{\text{isolation}}$).

In field surveys, where only a subset of a network can be sampled, the network in which that subset is embedded is not observed—only $D_{\text{sub}}^{\text{isolation}}$ is known. Thus, the question is whether the true unobservable coexistence domain of the subnetwork ($D_{\text{sub}}^{\text{embedded}}$) is equivalent to the observed coexistence domain of the subnetwork in isolation ($D_{\text{sub}}^{\text{isolation}}$) and whether $D_{\text{sub}}^{\text{isolation}}$ can be used to infer the persistence of an unobservable network as a whole (D_{whole}).

We formalize $D_{\text{sub}}^{\text{embedded}}$ and $D_{\text{sub}}^{\text{isolation}}$ using the structural approach. The structural approach applies to any population dynamics that are topologically equivalent to Lotka–Volterra dynamics (5, 19). Note that any quasi-polynomial dynamics, which include a large class of ecological models, can be equivalently mapped into Lotka–Volterra dynamics (20). Here, we calculate persistence using a population dynamics model. We assume that a network has S -interacting species in total and is governed by the Lotka–Volterra dynamics (21):

$$\frac{d\mathbf{N}}{dt} = \text{diag}(\mathbf{N}) (\mathbf{r} + \mathbf{A}\mathbf{N}), \quad [1]$$

where \mathbf{N} is the vector of species densities, and \mathbf{A} is the matrix of species interactions. Under the governing population dynamics, the coexistence domain of a network is given by ref. 17:

$$D_{\text{whole}} = \{\mathbf{r} \mid \mathbf{r} = -\sum_{j=1}^S N_j^* \mathbf{A}_j, \text{ with } N_j^* > 0\}, \quad [2]$$

where \mathbf{A}_j denotes the j -th column of the interaction matrix \mathbf{A} . The coexistence domain of a subnetwork with the set of species \mathcal{S} in isolation is given by

$$D_{\text{sub}}^{\text{isolation}} = \{\mathbf{r} \mid \mathbf{r} = -\sum_{j \in \mathcal{S}} N_j^* \mathbf{A}_j^{\mathcal{S} \times \mathcal{S}}, \text{ with } N_i^* > 0\}, \quad [3]$$

where $\mathbf{A}^{\mathcal{S} \times \mathcal{S}}$ is the submatrix of \mathbf{A} that only has species in the set of species \mathcal{S} . In turn, the coexistence domain of a subnetwork with the set of species \mathcal{S} when embedded in the larger network is given by

$$D_{\text{sub}}^{\text{embedded}} = \{\mathbf{r} \mid \mathbf{r} = -\sum_{j=1}^S N_j^* \mathbf{A}_j^{\mathcal{S} \times \mathcal{S}}, \text{ with } N_i^* > 0\}. \quad [4]$$

It is important to note that $D_{\text{sub}}^{\text{embedded}}$ (Eq. 4) is always greater than or equal to $D_{\text{sub}}^{\text{isolation}}$ (Eq. 3). This is because the summation in Eq. 4 is done across all columns, while the summation in Eq. 3 is only done across a subset of all the columns. For example, in Fig. 2, $D_{\text{sub}}^{\text{embedded}} = D_{\text{sub}}^{\text{isolation}}$ for the subnetwork with species 1 and 2, while $D_{\text{sub}}^{\text{embedded}} \supset D_{\text{sub}}^{\text{isolation}}$ for the subnetwork with species 2 and 3. This result implies that observing only a subset

of species without its wider network context (i.e., $D_{\text{sub}}^{\text{Isolation}}$) never overestimates the true coexistence potential of this subset when embedded into the larger network of interactions (i.e., $D_{\text{sub}}^{\text{Embedded}}$). This result is general and does not depend on types of species interactions or the number of species.

Mesoscopic Organizational Principles Behind Macroscopic Persistence

To study the relationship between subnetwork persistence in isolation and network persistence as a whole, we borrow concepts from statistical physics and test whether a macroscopic (whole-network) phase transition is reflected in drastic changes of mesoscopic (subnetwork) properties (22). At the macroscopic scale, the network as a whole exhibits only two phases: persistence or nonpersistence. At the mesoscopic scale, a subnetwork has an additional key property: whether the persistence of the subnetwork is identical in isolation and when embedded in the larger network. An embedded subnetwork is persistent if, and only if, the network as a whole is persistent. Thus, if the persistence of a subnetwork is identical in isolation and when embedded in the larger network, then the subnetwork's persistence (or not) in isolation also indicates whether the network as a whole persists (or not). This property is always true for the subnetworks with $D_{\text{sub}}^{\text{Embedded}} = D_{\text{sub}}^{\text{Isolation}}$, and is true with probability $\text{vol}(D_{\text{sub}}^{\text{Isolation}} \cap D_{\text{sub}}^{\text{Embedded}}) / \text{vol}(D_{\text{sub}}^{\text{Embedded}}) = \text{vol}(D_{\text{sub}}^{\text{Isolation}}) / \text{vol}(D_{\text{sub}}^{\text{Embedded}})$ for all subnetworks, where "vol" denotes the hypervolume of the corresponding geometric domain. This relationship between $D_{\text{sub}}^{\text{Embedded}}$ and $D_{\text{sub}}^{\text{Isolation}}$ suggests the possibility that the persistence of one subnetwork can be a probabilistic indicator of the persistence of the network as a whole. Furthermore, the persistence of many subnetworks can

be an almost-deterministic indicator of the persistence of the network as a whole.

From the above, we hypothesize that the proportion of subnetworks that are persistent in isolation is different between persistent and nonpersistent networks. To formally test this hypothesis, we simulate theoretical networks and analyze the persistence in isolation of their constituent subnetworks as the network is moved along a gradient from persistence to nonpersistence.

We systematically sample inside and outside the coexistence domain of simulated networks (i.e., across two macroscopic phases: persistence and nonpersistence) and check the persistence in isolation of all constituent subnetworks at each sampling point (Fig. 3A). We adopt the normalized distance of the sampled point from the centroid of the coexistence domain as the tuning parameter of the phase transition. Specifically, the centroid has a normalized distance 0, all points on the border of the coexistence domain have normalized distance 0.5, and all points inside (respectively, outside) have normalized distances less (respectively, greater) than 0.5 (Fig. 3A).

We characterize subnetworks using bipartite motifs (23, 24). Bipartite motifs are small subnetworks containing between two and six species, with all species having at least one link (23, 24). Bipartite motifs describe all possible unique subnetwork topologies up to six species. As described above, we enumerate all the motifs present in each network along the gradient of persistent and nonpersistent networks (Fig. 3A) and calculate both the persistence in isolation and embedded persistence of each motif. Although the number of motifs scales exponentially with network size, we expect to see a smooth, rather than sharp, phase transition in the persistence of motifs along the gradient, given the network size in our simulations (22).

Corroborating our hypothesis, as networks were moved along a gradient from network persistence to nonpersistence (Fig. 3A),

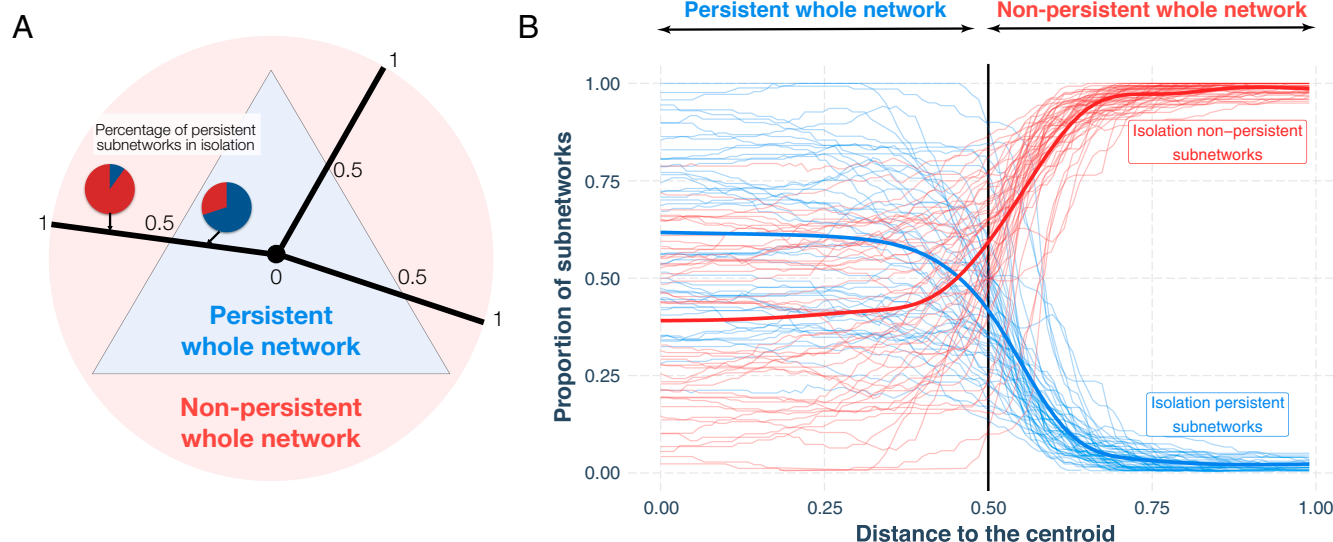


Fig. 3. Generic phase transition across scales. (A) Schematic illustration of the structure of our experiment. For a given network, we measure the proportion of subnetworks (motifs) that are persistent along "transects" that span inside and outside the coexistence domain of the network. Within the coexistence domain, the network is persistent; outside the coexistence domain, the network is nonpersistent. The transects span a tuning parameter that ranges from 0 to 1, with 0 being at the center of the coexistence domain and 0.5 being at the boundary of the coexistence domain. (B) Subnetwork mechanisms driving network persistence as a whole. The x-axis denotes a tuning parameter moving the network from noncoexistent (nonpersistent) to coexistent (persistent). The y-axis denotes the proportion of subnetworks (motifs) in the network that persist (blue) and do not persist (red) in isolation. The whole network is persistent in the left half and nonpersistent in the right half. Each thin line represents one simulation along a "transect," as shown by the black line in panel A (50 are shown here), and the thick lines denote the average. We see a transition in the proportions of persistent and nonpersistent subnetworks as the network transitions from persistence into nonpersistence. This transition shows that a persistent network is primarily composed of persistent subnetworks, and vice versa. This phase transition is generic in almost all simulations (SI Appendix, Appendix B).

we identified a phase transition of persistence across scales of networks and subnetworks (Fig. 3B). That is, when a network as a whole is persistent, a high proportion of its constituent subnetworks (motifs) must themselves be persistent in isolation. Conversely, when the network as a whole is not persistent, the majority of its constituent subnetworks are not persistent in isolation. Importantly, the qualitative pattern was consistent across different community richnesses, interaction types (mutualistic or antagonistic), and network structures (*SI Appendix, Appendix B*). This result is consistent with empirical observations in microbial communities (25). We also provide a heuristic explanation of the emergence of the phase transition (*Methods*).

A Bayesian Framework to Monitor Network Persistence from Subnetwork Persistence

These theoretical findings additionally show that the presence of a single persistent subnetwork in isolation is a probabilistic indicator of the persistence of the network as a whole, while the presence of many persistent subnetworks in isolation is a nearly deterministic indicator (with exponentially decreasing error) of the persistence of the network. In other words, the generic phase transition (Fig. 3) tells us about the probability of subnetwork persistence in isolation when we know whether the whole network is persistent or not. We now ask the inverse question: How we can infer the persistence of the whole network, when we know only whether subnetworks are persistent in isolation.

To formalize this idea, we provide a Bayesian approach to update our beliefs about the persistence of the network from whether subnetworks are persistent in isolation. Specifically, we compute the Bayes factor: the ratio of the posterior likelihood of

the network being persistent as a whole over being nonpersistent, given the observed persistence in isolation of sampled subnetworks. The value of the Bayes factor can be used as evidence of whole-network persistence. In the convention of Bayesian statistics, a Bayes factor larger than 10^2 can be considered decisive evidence that the network is persistent; between 10 and 10^2 is strong, between $10^{1/2}$ and 10 is substantial, and less than $10^{1/2}$ is not worth considering as evidence. The reciprocal thresholds operate to statistically determine whether the network is nonpersistent (26, 27). Note that these thresholds should be considered as a guide, and individual decision-makers may interpret Bayes factors differently, depending on their own attitudes to risk and other contextual factors. The details of our statistical framework can be found in *Methods*.

Fig. 4 shows the proportion of species we need to monitor to reach statistical evidence about whole-network persistence. We find that, regardless of whether the network as a whole is persistent or not, the proportion of species which require monitoring to achieve higher confidence about network persistence/nonpersistence decreases with increasing network size. This is because the Bayes factor generally increases exponentially with the number of sampled networks. Thus, the required monitoring effort increases only slowly with increasing biodiversity in the community.

We also find that the proportion of species which require monitoring is lower, and the statistical confidence is higher when the network as a whole is not persistent (Fig. 4 A-C) compared to when the network is persistent (Fig. 4 D-F). This is because, as our samples are from a binomial distribution, the variance is highest when the network is persistent (i.e., binomial distribution with roughly half of subnetworks persistent in isolation). This suggests that it is easier to detect if a whole network is not

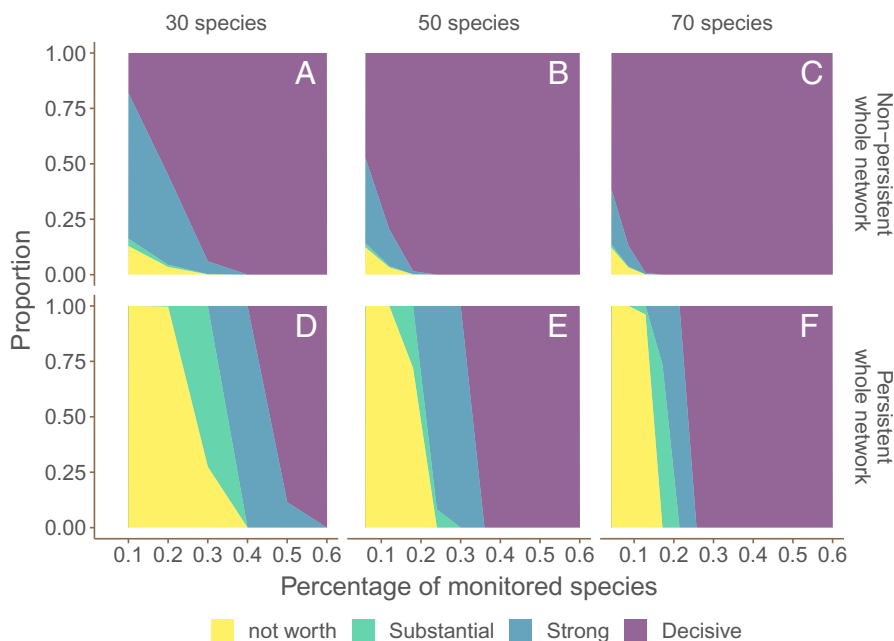


Fig. 4. Bayesian inference of network persistence from subnetwork persistence. The *Upper* panels (A)–(C) show the case when the whole network is not persistent, while the *Lower* panels (D)–(F) show the case when the whole network is persistent. The vertical panels show different network sizes (30, 50, and 70 species, respectively). The x-axis shows the percentage of monitored species out of all present species. The y-axis shows the proportion of samples with different evidence strengths that supports that the network is persistent (*Lower* panels) or nonpersistent (*Upper* panels). We follow the convention in Bayes statistics to classify evidence strength based on Bayes factor K : $K > 10^2$ is considered decisive, $10 < K < 10^2$ is considered strong, $10^{1/2} < K < 10$ is considered substantial, and $1 < K < 10^{1/2}$ is considered not worth considering as evidence. Note that these thresholds should be considered as a guide, and individual decision-makers may interpret Bayes factors differently, depending on their own attitudes to risk and other contextual factors. We find that the proportion of species we need to monitor would decrease with increasing species richness. We also find that it is generally easier to statistically determine whether the network as a whole is not persistent from monitoring subnetworks.

persistent than persistent. Overall, the results in Fig. 4 show that, by monitoring only a small proportion of species, we can be reasonably confident about the persistence or nonpersistence of a whole network.

Empirical Analysis

While it is difficult to directly empirically test the phase transition resulting from the theoretical analysis above, a testable prediction from our result is that a network as a whole is more likely to persist if it contains more persistent in isolation subnetworks. To test this, we analyzed a temporal dataset of eight plant–pollinator networks from Seychelles, each sampled over eight consecutive months (144 pollinator species and 38 plant species in total) (14). In this dataset, half of the networks are subject to disturbance in the form of invasive plants, while the other half have had invasive plant species removed through restoration action (14). Following earlier work that showed that restored sites had higher diversity, function, and resilience (14), we expect restored sites to have higher persistence than unrestored invaded networks. As a consequence, following our theoretical results above, we in turn expect restored networks to contain more persistent-in-isolation subnetworks (motifs) than invaded networks. Details in comparing motif persistence can be found in *Methods*.

Fig. 5A shows that the restored (undisturbed) networks have a higher overrepresentation of persistent in isolation subnetworks (motifs) compared to the unrestored (disturbed) networks. This pattern is robust through the whole sampling period, despite the reorganization of species interactions in the network. Importantly, Fig. 5B shows that these patterns remain qualitatively true

even if we can monitor the interactions of only a small subset of all locally present species. This shows that we can gain insights about the network as a whole using information from only a subset of that network that is much quicker to sample.

Our approach could greatly reduce the sampling cost. The analysis in *SI Appendix, Fig. S17* shows that the community could be effectively monitored for persistence with five plant species. We therefore calculated the reduction in costs that would result from having to sample only five plant species per network. We found that the cost of plant observation would be reduced by 31%, and the cost of insect identification would be reduced by 74%. Combined, this represents a cost reduction of 42%. The details of sampling cost estimates can be found in *SI Appendix, Appendix E*. It is important to note that although monitoring a subset of species reduces costs, monitoring costs can be strongly influenced by the species involved, the types of interaction, and the target metric of interest. All these features must be considered by decision makers when designing monitoring strategies.

Discussion

We have uncovered a generic probabilistic link across organizational scales of ecological networks: An ecological network is more likely to be persistent when a majority of its subnetworks are persistent in isolation, and vice versa. This establishes a theoretical foundation to rapidly monitor the persistence of communities by sampling only small numbers of interactions in subnetworks. Given cost and time constraints common to much conservation work, it is only practical to have high quality data on a small fraction of all locally present species and interactions. Our results

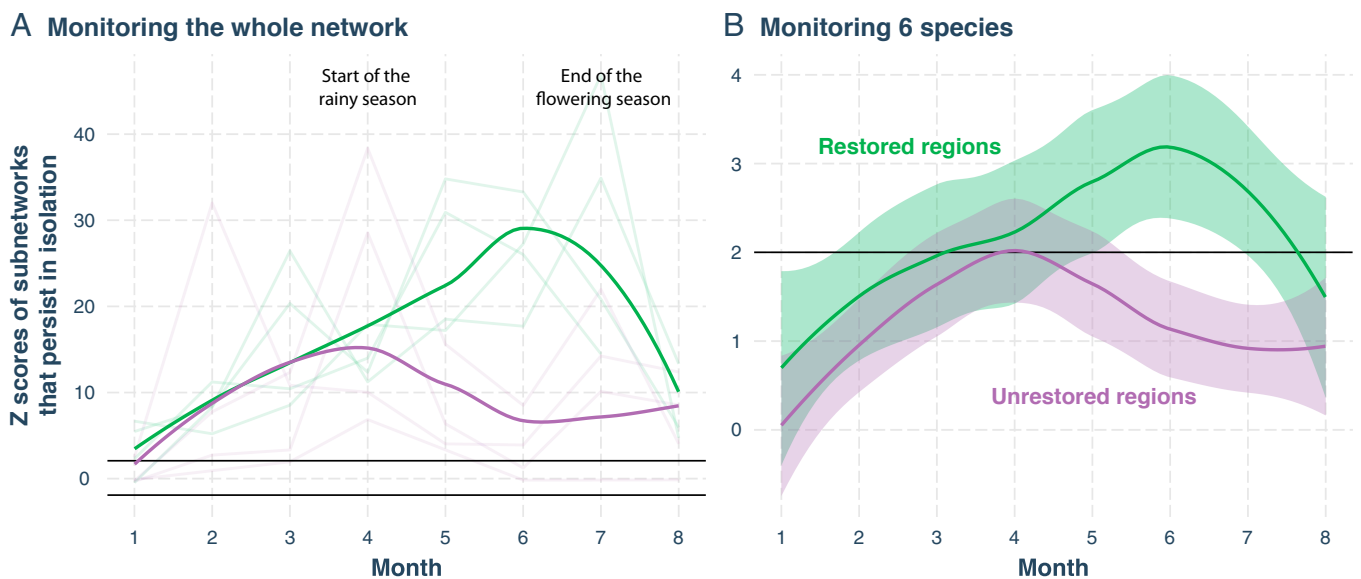


Fig. 5. Restored mutualistic networks contain more subnetworks with a higher likelihood of persistence in isolation than unrestored disturbed networks. We use a temporal dataset with 64 networks (eight networks sampled over eight months) located on the granitic island of Mahé and Seychelles (14). The x-axis denotes the eight consecutive months between September 2012 and April 2013. The y denotes the z-scores of a given subnetwork (overrepresentation or underrepresentation of empirical motif frequency compared to motif frequency in randomized networks). The black horizontal line corresponds to the threshold above or below which a subnetwork (motif) occurs significantly more than random (z -score = 2). The green lines correspond to the restored networks, while the purple lines correspond to the disturbed and unrestored networks. The thick lines correspond to the average across four different networks. The persistent-in-isolation subnetworks are significantly overrepresented in the larger networks, and the overrepresentation is stronger in restored networks than in disturbed networks. These patterns are consistent with the natural history of these plant–pollinator networks. (B) Monitoring a subset of the network. Suppose that we cannot monitor the whole network but only a subset of it. Here, we show the case for monitoring six species (*SI Appendix, Appendix D* for other numbers of monitored species). We find that all the qualitative patterns linking subnetworks and the network in Panel (A) remain. This shows that we can monitor a subnetwork (six species of the whole network) and then study the persistence in isolation of its subnetworks (three to five species in the monitored six species), which would provide useful information of the network as a whole.

have shown that determining the persistence in isolation of a few subnetworks can lead to robust conclusions about the persistence of the network as a whole: If few randomly sampled subnetworks are persistent, then the network as a whole is likely persistent. Our monitoring scheme is insensitive to the size of the whole network, which is in direct contrast to prohibitively expensive sampling of the whole network estimated to be exponential efforts with the size of the whole network (11).

Our results help with a common but fundamental challenge in biodiversity conservation—to make predictions and provide guidance with limited observations (28, 29). The methods presented here could be deployed by a monitoring team to make a decision about community persistence as fast and as cost-effectively as possible. If the team concluded that the focal community was not persistent, it would then have to determine the cause (attribution to drivers) and then act on those causes. Guidance on attribution is beyond the scope of this work; what we provide is an approach to provide a rapid assessment of the status of the community. This is the detection stage of a detection and attribution framework for biodiversity monitoring (30). This rapid detection step would support local planning and prioritization of action for communities classified with high confidence as not being in a persistent state.

The monitoring discussed above is only a first step in the broader goal of monitoring many ecosystems across a country to establish whether regional or national progress is being made to increase the number (or proportion) of systems that are in a persistent state and then deploy resources in response to policy targets to recover those (or some fraction of them) not in a persistent state. In this case, the national monitoring network would work to assess progress toward a general persistence target (with a relevant simple indicator—the proportion of sample communities in a persistent state) across many communities/ecosystems.

Besides the application to rapid biomonitoring, our work also connects two separate schools of thought on ecological networks defined by distinct ecological scales. One school has focused on the mesoscopic scale, providing a more mechanistic understanding through the study of specific small subnetworks or motifs (often called “trophic modules”), such as apparent competition (31–35). In contrast, the other school has focused on the macroscopic scale, studying the interaction networks of entire networks to provide an ecologically more relevant link, but suffering from being coarse-grained and highly phenomenological (36–39). Unfortunately, these two schools have little cross talk. The few theoretical studies on this topic suggest that there is no deterministic, one-to-one link that maps results across the two schools (40–42). We confirm that such a deterministic link does not exist. However, we found that a generic probabilistic link does exist (Figs. 2 and 3). This generic link provides an opportunity to take advantage of both schools. For example, we have taken a phenomenological approach with the trophic constraints to explain why some subnetworks are more persistent in isolation. However, a rich literature has cataloged and explained why some subnetworks are more persistent in isolation, ranging from sign stability (43, 44) to consumer–resource relationships (35, 45), and then applied it to explain observed patterns of species-rich ecological networks (34, 46, 47). Our results have justified that such practice is probably approximately correct (48).

We have provided a Bayesian approach to update our belief on the persistence of ecological networks (Fig. 1). Our belief is quantified by the Bayes factor—the ratio of the posterior probability of the monitored network being persistent over not being persistent. The Bayes factor is consistently updated

by our knowledge of species’ life history (as priors) together with persistence-in-isolation criteria of the observed subnetworks (as evidence). We have followed the convention of Bayesian statistics to set the threshold of statistical evidence (Fig. 4); however, in applied monitoring design, which threshold to use should be subject to indigenous and expert knowledge (49, 50). We have found that conclusions about whole network persistence or nonpersistence can be made from only a handful of subnetworks (Fig. 3).

Our key theoretical prediction—that subnetworks with a higher probability of persistence in isolation are overrepresented in more persistent networks—is supported by empirical temporal mutualistic networks. These empirical results agree with the natural history details of these systems. For example, Fig. 5 shows how restored networks have only slightly higher frequencies of persistent subnetworks than unrestored networks until month four, when the two treatments diverge, and persistent subnetworks substantially increase in number in restored sites relative to unrestored (disturbed) sites. Networks in the two treatments then converge at the end of the flowering season. This divergence in month four corresponds to the start of the rainy season in Seychelles. Rains create a patchy distribution of resources. In the unrestored sites, free movement of pollinators between patches is hindered because invasive species grow densely, disrupting the ability of pollinators to forage effectively (14). If pollinators cannot find resources, or cannot move freely between individuals and species, this increases competition and reduces niche complementarity, which likely causes reduced persistence.

While this study has focused on advancing our theoretical and empirical understanding of persistence, it is important to outline how our approach could be applied in practice. In terms of the required data collection, our approach needs only a small amount of binary (bipartite) species interaction network data. This could be achieved by observing a certain number of randomly selected focal species and recording their interactions, as in the empirical analysis shown in Fig. 5. Our approach does not rely on randomly sampling subnetworks, but rather randomly sampling interactions of a certain number of species, from which network (and thus subnetwork) structures emerge. The number of species sampled depends on the strength of evidence about whole-network persistence required by the practitioner, as shown in Fig. 4 (e.g., sampling interactions of ~40% of species in communities containing 30 to 70 species is required to be reasonably confident). There is no set time period these interaction data should be collected for: The method does not dictate any required length, and so the sampling duration would depend on the question being asked (the temporal scale over which the practitioner is interested in the community’s persistence). The same is true for spatial scale. Networks are a spatial snapshot of species and their interactions; defining the spatial limits of a network (or the edge of a community) remains an outstanding question for community ecology. Therefore, the area being sampled should be decided by the practitioner, using their local knowledge and depending on the questions being asked. Our approach does not demand any particular spatial scale or extent. No specific information is needed about the full community, other than an estimate of the total species richness to estimate how many species should be sampled based on the proportions in Fig. 4. Once this subset of network data has been collected, all downstream analyses to calculate subnetwork persistence, and thus whole-network persistence, rely on modeling. Details of appropriate parameterizations for these models are given in *Materials and Methods*.

A limitation of our approach is that we assume that the subnetworks are random samples from the whole network. However, in practice, sampling bias is pervasive (51, 52). For example, more abundant species are more likely to be sampled. Accounting for sampling bias is a key next step to make our framework more applicable to conservation monitoring and management (53, 54). A related issue is that, for the purpose of monitoring persistence, some species are more important than others (*SI Appendix*, Figs. S18 and S19). Future work can explore how to predict species importance from available species attributes to identify species that should be a priority for monitoring effort.

Another limitation is that we focus on the persistence of all species. However, as turnover is ubiquitous (55), conservation often focuses on the persistence of some keystone species. One possible direction is to link our theoretical framework with other theories studying the persistence of a subset of all species (56–58). A similar limitation is that we focus on local ecological dynamics and do not consider the effects of dispersal. To address this, future research could try to link our theoretical framework with other theories on the persistence of metapopulations (59) and metacommunities (60).

Overall, the match between theoretical predictions and empirical observations shows that information about the persistence of a species-rich ecological network is encoded in its small subnetworks and can be recovered through an appropriate theoretical lens and statistical analysis. This finding has significant application to biodiversity monitoring as indicators of ecological persistence and biodiversity intactness are key foci of monitoring networks around the world. The method we have provided here has the potential to save time and effort and accelerate our ability to detect and mitigate unwanted change to the structure and function of ecological networks.

Supporting Information Appendix (SI). Authors should submit a single separate *SI Appendix* PDF file, combining all text, figures, tables, movie legends, and SI references. *SI Appendix* will be published as provided by the authors; it will not be edited or composed. Additional details can be found in the PNAS Author Center. The PNAS Overleaf SI template can be found here. Refer *SI Appendix* in the manuscript at an appropriate point in the text. Number supporting figures and tables starting with *SI Appendix*, S1 and S2, etc.

Authors who place detailed *Materials and Methods* in an *SI Appendix* must provide sufficient detail in the main text methods to enable a reader to follow the logic of the procedures and results and also must reference SI methods. If a paper is fundamentally a study of a new method or technique, then the methods must be described completely in the main text.

Materials and Methods

Parametrizing Interaction Networks. For brevity, we focus on mutualistic interaction networks here, but our approach can equally be applied to antagonistic interaction networks, such as predation and parasitism (*SI Appendix*, Appendix B)(6, 57). First, we generate theoretical mutualistic networks with ten pollinators and eight plants (*SI Appendix*, Appendix B for the robustness of our results to different network sizes). For illustrative purposes, we present here Erdős–Rényi structures, however, our results apply and are consistent for other network structures, such as nested networks (*SI Appendix*, Appendix B). We then follow an ecologically motivated parameterization that has been widely adopted in the literature (38, 61–63). The interaction matrix of a mutualistic network can then be partitioned as

$$\mathbf{A} = \begin{bmatrix} \text{intraguild competition} & \text{mutualistic benefit} \\ \text{among plants} & \text{for plants} \\ \text{mutualistic benefit} & \text{intraguild competition} \\ \text{for animals} & \text{among animals} \end{bmatrix} = \begin{bmatrix} \mathbf{C}^{(P)} & \mathbf{M}^{(P)} \\ \mathbf{M}^{(A)} & \mathbf{C}^{(A)} \end{bmatrix}.$$

The mutualistic benefit ($\mathbf{M}^{(P)}$ and $\mathbf{M}^{(A)}$) between species i and j is parameterized as $m_{ij} = m_0 b_{ij}/d_i^\delta$, where $b_{ij} = 1$ if species i and j directly interact and $b_{ij} = 0$ otherwise, m_0 represents the overall strength of mutualistic interaction, d_i represents the number of interaction partners, and δ represents the mutualistic trade-off. The intraguild competition ($\mathbf{C}^{(P)}$ and $\mathbf{C}^{(A)}$) between species is parameterized using a mean-field approach where we set the intraspecific competition $c_{ii}^{(P)} = c_{ii}^{(A)} = -1$ and interspecific competition $c_{ij}^{(P)} = c_{ij}^{(A)} = -\rho$.

A Mean-Field Explanation of the Generic Phase Transition. A rigorous explanation of the emergence of the generic phase transition is not trivial. Here, we take a heuristic mean-field approach to explain its emergence. We use S_{whole} to denote the larger network, where $S_{\text{whole}} = 1$ indicates that the network is persistent as a whole, while $S_{\text{whole}} = 0$ indicates that the network is not persistent. We use $S_{\text{sub}_j}^{\text{isolation}}$ to denote the persistence in isolation of subnetwork j and $S_{\text{sub}_j}^{\text{Embedded}}$ to denote its embedded persistence.

Given that the network is persistent as a whole, the conditional probability distribution of persistence in isolation of subnetworks is

$$\begin{aligned} \mathbb{P}(S_{\text{sub}}^{\text{isolation}} | S_{\text{whole}} = 1) &= \prod_j \mathbb{P}(S_{\text{sub}_j}^{\text{isolation}} | S_{\text{whole}} = 1) \\ &\approx \prod_j \left(\frac{\text{vol}(D_{\text{sub}_j}^{\text{isolation}})}{\text{vol}(D_{\text{sub}_j}^{\text{Embedded}})} \right)^{S_{\text{sub}_j}^{\text{isolation}}} \left(1 - \frac{\text{vol}(D_{\text{sub}_j}^{\text{isolation}})}{\text{vol}(D_{\text{sub}_j}^{\text{Embedded}})} \right)^{1 - S_{\text{sub}_j}^{\text{isolation}}}. \end{aligned}$$

Given the linearity of expectation, the expected number of persistent subnetworks is

$$\mathbb{E}(S_{\text{sub}}^{\text{isolation}} | S_{\text{whole}} = 1) = \sum_j \frac{\text{vol}(D_{\text{sub}_j}^{\text{isolation}})}{\text{vol}(D_{\text{sub}_j}^{\text{Embedded}})}.$$

In contrast, given that the network as a whole is not persistent, the conditional probability distribution of persistence in isolation of subnetworks is

$$\begin{aligned} \mathbb{P}(S_{\text{sub}}^{\text{isolation}} | S_{\text{whole}} = 0) &= \prod_j \mathbb{P}(S_{\text{sub}_j}^{\text{isolation}} | S_{\text{whole}} = 0) \\ &\approx \prod_j \left(\text{vol}(D_{\text{sub}_j}^{\text{isolation}}) \right)^{S_{\text{sub}_j}^{\text{isolation}}} \left(1 - \text{vol}(D_{\text{sub}_j}^{\text{isolation}}) \right)^{1 - S_{\text{sub}_j}^{\text{isolation}}}. \end{aligned}$$

Consequently, its expected number of persistent subnetworks is

$$\mathbb{E}(S_{\text{sub}}^{\text{isolation}} | S_{\text{whole}} = 0) = \sum_j \text{vol}(D_{\text{sub}_j}^{\text{isolation}}).$$

Importantly, the vol generally decreases exponentially with network size (17, 64). Thus, $\mathbb{E}(S_{\text{sub}}^{\text{isolation}} | S_{\text{whole}} = 0)$ is exponentially small. In contrast, the ratio $\text{vol}(D_{\text{sub}_j}^{\text{isolation}})/\text{vol}(D_{\text{sub}_j}^{\text{Embedded}})$ does not decrease exponentially (17, 38), thus $\mathbb{E}(S_{\text{sub}}^{\text{isolation}} | S_{\text{whole}} = 1)$ is large. These comparisons confirm what we observe in the phase transition.

Bayesian Inference of Network Persistence from Subnetworks. We take a heuristic Bayesian approach to infer the persistence of the network as a whole from subnetworks. We use S_{whole} to denote the larger network, where $S_{\text{whole}} = 1$ indicates that the network as a whole is persistent, while $S_{\text{whole}} = 0$ indicates that the network is not persistent. We use $S_{\text{sub}_j}^{\text{isolation}}$ to denote the persistence in isolation of subnetwork j and $S_{\text{sub}_j}^{\text{Embedded}}$ to denote its embedded persistence. Note that $S_{\text{sub}_j}^{\text{Embedded}} = S_{\text{whole}}$ by definition.

Given the observations of persistence in isolation of subnetworks, the conditional probability of the network persistence as a whole is

$$\mathbb{P}(S_{\text{whole}} | S_{\text{sub}}^{\text{isolation}}) = \prod_j \frac{\mathbb{P}(S_{\text{whole}}) \mathbb{P}(S_{\text{sub}_j}^{\text{isolation}} | S_{\text{whole}})}{\mathbb{P}(S_{\text{sub}_j}^{\text{isolation}})},$$

where the first equality comes from the assumption of independence: whether a subnetwork persists is independent of one another. Thus, our updated belief in the persistence of the whole network is

$$\begin{aligned} & \frac{\mathbb{P}(S_{\text{whole}}=1 | S_{\text{sub}}^{\text{isolation}})}{\mathbb{P}(S_{\text{whole}}=0 | S_{\text{sub}}^{\text{isolation}})} \\ & \approx \frac{\mathbb{P}(S_{\text{whole}}=1)}{\mathbb{P}(S_{\text{whole}}=0)} \prod_j \left(\frac{1}{\text{vol}(D_{\text{sub}_j}^{\text{Embedded}})} \right)^{S_{\text{sub}_j}^{\text{isolation}}} \\ & \times \left(1 - \frac{\text{vol}(D_{\text{sub}_j}^{\text{isolation}})}{\text{vol}(D_{\text{sub}_j}^{\text{Embedded}})} \right)^{1-S_{\text{sub}_j}^{\text{isolation}}}. \end{aligned}$$

Comparing Motif Persistence in Empirical Networks. We measure the persistence in isolation of subnetworks as the size of their coexistence domains. Importantly, comparing which subnetworks are more persistent can easily be confounded by different parameterizations. That is, small changes in parameters used to calculate the coexistence of different subnetworks can significantly influence conclusions (65, 66). To ensure a fair comparison, we focus on subnetwork pairs that are the transpose of each other because we can parameterize both subnetworks in the pair identically (SI Appendix, Fig. S10). For example, we compare the subnetwork with two top nodes connected to a single bottom node, with the subnetwork containing two bottom nodes connected to a single top node. In ecological terms, this might be comparing the subnetwork describing two pollinators visiting one plant to the subnetwork with one pollinator visiting two plants. In total, we have seven pairs of subnetworks

that range from three species to five species each, and 10 pairs of subnetworks with six species each (SI Appendix, Fig. S10). Note that despite the interaction matrices for each pair of subnetworks being the transpose of each other, the coexistence domains of the two subnetworks are different because of, and only because of, their trophic constraints (17, 67): Plants always have positive intrinsic growth rates in our bipartite networks. For each different subnetwork, we compute the size of its coexistence domain by systematically exploring the parameter space, defined by three parameters: the mutualistic trade-off δ , the overall strength of mutualistic interactions m_0 , and the intraguild competition strength ρ . SI Appendix, Fig. S11 shows that which motif type in a pair has a higher coexistence domain is consistent across almost all parameterization.

We then applied the theoretical results and examined the empirical frequency of each subnetwork (motif) in the observed mutualistic networks. We first computed the raw number of subnetworks present in each empirical mutualistic network using the `bmotif` R package (24). Next, we compute the z-score of the empirical subnetwork frequencies relative to the Erdős-Rényi null model (68, 69). Next, we compare the patterns of these null-corrected subnetwork frequencies between un-restored (invasive species present) and restored (invasive species removed) sites (14). Lastly, we investigate whether these patterns remain if we can monitor only a subset of all species; this tests whether conclusions about whole-network persistence can be made from easy-to-sample subnetworks.

Data, Materials, and Software Availability. Data of empirical plant-pollinator networks is available from <https://www.nature.com/articles/nature21071> (70). The source code to produce the results is available on GitHub at <https://github.com/clsong/ReproduceRapidMonitoring> (71).

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