

A new centrality index designed for multilayer networks

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Abstract

1. Since its inception, the keystone species concept has become a central theoretical framework in ecology. Among many approaches, keystones have been operationalized in natural and human environments using centrality metrics applied to monolayer networks. Despite the great success of this approach, as species make several types of interactions, recent studies on keystones moved from monolayer to multilayer networks.
2. To help fulfil the need for a centrality metric designed for multilayer networks, here we introduce *Gnorm*. We tested the performance of our new metric using in silico data in addition to an empirical data set of frugivory and nectarivory interactions between bats and plants in the Neotropics. A comparison between the results obtained with different random and scale-free networks demonstrates the performance of our new metric.
3. First, a modularity analysis based on the multilayer version of the Louvain algorithm enables the modules to be composed of nodes from different layers. Second, by setting the coupling parameter (ω) and the resolution parameter (γ), module identity changes gradually, from single- to multiple-node modules and from mono- to multilayer composition. Third, we check the number of modules from different layers to which a node belongs (G) at different levels of ω and γ . Finally, by observing how average G decreases with ω and γ , it is possible to calculate *Gnorm* and detect which nodes are most resistant to change in these two parameters. Those resistant nodes are identified as central in the multilayer structure. After applying this new analysis to the bat–plant network, we observed that it identified a different set of potential keystone species compared to previous analyses performed separately for each layer or the aggregated network.
4. In conclusion, our new metric opens a new way of operationalizing the keystone species concept in multilayer networks. It may help identify keystone species involved in different interaction types.

KEYWORDS

centrality, ecological networks, interaction networks, keystone species, modularity, multilayer networks

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1 | INTRODUCTION

The keystone species concept is one of the most successful theoretical frameworks in ecology (Mello, 2019). Since its inception in the mid-20th century (Paine, 1966, 1969), it has opened many avenues for research. It allowed us to better understand what makes some species more important than others for holding together the ecological systems to which they belong (Lafferty & Suchanek, 2016). Despite its great popularity and widespread use, it has always been quite a challenge to operationalize and identify keystones in real environments (Cottee-Jones & Whittaker, 2012; Davic, 2003).

Overcoming this challenge became much more feasible thanks to network science, whose tools have been imported to Ecology for the first time in the 19th century (Ings & Hawes, 2018). Among those tools stand out the concept of centrality and several metrics used to measure it in complex networks (Cirtwill et al., 2018; Costa et al., 2019; Power et al., 1996). As a natural consequence, node properties such as betweenness, closeness and eigenvector have been used solo or in combination to capture different aspects of a species' contribution to network structure and dynamics (González et al., 2010; Mello et al., 2015).

Those node properties are usually calculated based on a modularity analysis, which is an efficient way to operationalize the guilds and functional groups involved in the interactions (Mello et al., 2011; Olesen et al., 2007). So far, virtually only monolayer networks have been assessed in keystone studies (but see an alternative approach in Timóteo et al., 2022), although species live in a 'tangled bank' in Darwin's words (Bascompte, 2009) or in a 'web of life' in Humboldt's words (Lewinsohn & Cagnolo, 2012): that is, systems made of multiple interaction types (Genrich et al., 2017). To disentangle those systems as they really are, ecologists have started to move from monolayer to multilayer networks (Pilosof et al., 2017). Only a few studies have aimed to identify keystone species in multilayer networks, but mostly by assessing centrality in separate layers or in the aggregated network (Mello et al., 2019). Consequently, we need to develop better centrality metrics that really take into account different layers, as well as the weights of the interlayer links.

To help fill this gap, we propose *Gnorm*, a new centrality index based on multilayer modularity. In addition, we test the performance of *Gnorm* using both in silico data and a continent-wide data set of frugivory and nectarivory interactions between bats and plants in the Neotropics. We compare the results obtained with *Gnorm* with those obtained with other commonly used centrality indices. Finally, we comment on how our new index might help us go further in the study of keystone species by proving a way to operationalize the concept in networks that contain two or more interaction types.

2 | METHODS

2.1 | Data set

For testing our new centrality metric, we used an updated version of the bat–plant multilayer network analysed in a previous study on keystone species involved in multiple interaction types (Mello

et al., 2019). The complete data set was made available in a recent data paper (Florez-Montero et al., 2022). The multilayer network comprises 79 bat species and 410 plant species and includes 1346 links of frugivory and 494 links of nectarivory, representing its two layers. The data came from studies carried out in the entire Neotropics (as delimited by Holt et al., 2013), from northern Mexico to southern Argentina. As explained in the following sections, in the present study, we worked only with the giant component of this network in order to be able to calculate all centrality metrics.

2.2 | Monolayer modularity

Among different approaches used to analyse the relative importance of each node to the structure and dynamics of a complex network, assessing community structure is usually the first step (Fortunato, 2010; Girvan & Newman, 2002). Communities are subgroups of nodes that are more densely connected to one another than to other nodes of the same network. Those cohesive subgroups affect how the links are distributed in the network, consequently affecting the relative importance of different nodes. The modular organization of a network can be quantified by the modularity metric (Dormann & Strauss, 2014; Mello et al., 2011; Montoya et al., 2015; Olesen et al., 2007), which evaluates the quality of the division of nodes into communities (Newman & Girvan, 2004), that is,

$$Q = \sum_{i=1}^k (e_{ii} - a_i^2) \quad (1)$$

in which e_{ii} is the fraction of links observed inside the module i to the total links within the network, and a_i^2 is the total number of possible links in module i . We use the adjacency matrix to obtain the proportion of links for node i inside the module C_i as the following:

$$\frac{\sum_{ij} A_{ij} \delta(c_i, c_j)}{\sum_{ij} A_{ij}} = \frac{1}{2m} \sum_{ij} A_{ij} \delta(c_i, c_j), \quad (2)$$

where δ is the Kronecker delta (1 if $c_i = c_j$ and zero otherwise), and m is the total number of network links. Considering the possibility of having a connection between two nodes i and j proportional to their degrees $k_i k_j / 2m$, the modularity index is defined as (Blondel et al., 2008):

$$Q = \frac{1}{2m} \sum_{ij} \left(A_{ij} - \frac{k_i k_j}{2m} \right) \delta(c_i, c_j). \quad (3)$$

Positive modularity values indicate a modular organization of a network—usually for $Q > 0.3$ (Fortunato & Barthelemy, 2007). To identify the communities in a network, here we consider the algorithm proposed by (Blondel et al., 2008). This heuristic method considers a greedy optimization, and community identification is performed in two steps. Initially, the algorithm identifies small communities by optimizing modularity locally. Next, the method aggregates nodes belonging to the same community and builds a new network whose nodes represent the communities. These

two steps are repeated iteratively until maximum modularity is obtained.

2.3 | Multilayer networks

In most complex systems, there are several means of linkage between nodes, which points to a widespread multilayer nature (De Domenico et al., 2013). Following this view, multilayer networks have received growing attention in Ecology and other disciplines (Pilosof et al., 2017), because ecological systems are sets of organisms of different species that interact with one another through multiple interaction types. Those intricate systems have been called a 'tangled bank' in Darwin's words (Lewinsohn & Cagnolo, 2012) and also a 'web of life' in Humboldt's words (Wulf, 2016). Therefore, a multilayer approach helps disentangle this complexity in a more realistic way. Among other advantages, a multilayer approach facilitates studying interactions between interactions, that is, how the outcome of one interaction type affects the outcome of another interaction type. It also helps assess dual interactions, for instance when animals play different roles for the same plants, such as antagonist–mutualist or seed disperser–pollinator (Genrich et al., 2017; Marques Draxler & Kissling, 2022). It should be said, though, that species interactions also occur in gradients, for instance with varying positive to negative outcomes, but gradients fall outside the scope of our study.

Two main types of links exist in a multilayer network: intralayer, connecting different nodes within a layer, and interlayer, connecting the same node between layers (Mucha et al., 2010). In the multilayer network analysed here, each layer presents one type of interaction between bats and plants, and all nodes are represented in all layers. In Figure 1, both types of links are illustrated, and all bat and plant species are present in both layers, even if they have no links in a given layer.

In each layer, a bat species is connected to a plant species by a link if there is at least one record of frugivory or nectarivory interaction between them in our data set (intralayer link). While there are bats that consume only fruits or nectar, many bats consume both kinds of food. These bats are named bridge species (Mello et al., 2019) or state nodes (Boccaletti et al., 2014; Kivelä et al., 2014). Besides, in some cases, the same bat and plant species are connected to one another in both layers, as the bat is both a pollinator and seed disperser of the plant, and this is named a dual interaction (Mello et al., 2019) or multilink (Boccaletti et al., 2014; Kivelä et al., 2014).

2.4 | Multilayer modularity

Considering that the studied multilayer network fits into the category 'node-aligned multiplex network' (Pilosof et al., 2017), each species (of either bats or plants) gets a connection to itself between layers (interlayer link), and all species are represented on all layers.

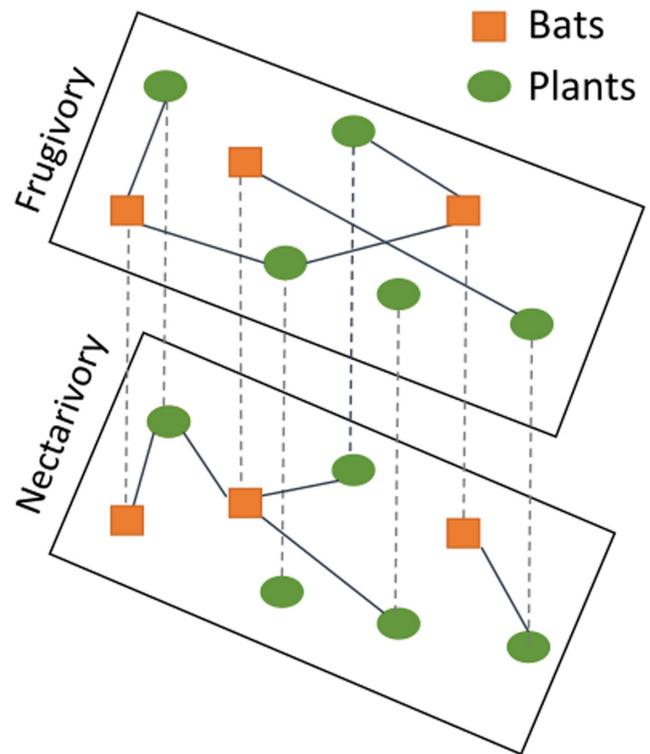


FIGURE 1 Simplified representation of the studied multilayer network, representing interactions of frugivory and nectarivory between bats (orange circles) and plants (green circles). All nodes are represented in both layers, always in the same position in the graph. Intralayer links are represented as solid lines, while interlayer links are represented as dashed lines.

If we pool both layers as one single aggregated network, we verify that the graph is disconnected, which hinders analysing most centrality metrics. To overcome this problem and to be able to calculate all centrality metrics, we need a connected network. Our solution was to select only the maximum connected component (a.k.a., the giant component) of the original network and discard all minor components and isolated dyads. The maximum component contains 74 bat species and 405 plant species and includes 1345 links of frugivory and 488 links of nectarivory, as shown in Figure 2.

The next step was to adapt the Louvain algorithm for multiplex networks. First, we need to modify the modularity function itself (Mucha et al., 2010):

$$Q^M = \frac{1}{\mu} \sum_{ij\alpha\beta} \left[\left(A_{i\alpha,j\alpha} - \gamma \frac{k_{i\alpha} k_{j\alpha}}{2m_\alpha} \right) \delta_{\alpha,\beta} + \omega A_{i\alpha,j\beta} \delta_{ij} \right] \delta(c_{i\alpha}, c_{j\beta}) \quad (4)$$

in which ω (coupling parameter) controls the coupling between the layers of the network, γ (resolution parameter) controls the algorithm's tendency to find smaller or larger modules, δ is the Kronecker delta (1 if $c_{i\alpha} = c_{j\beta}$ and zero otherwise), m is the sum of the degree of each node in the α layer, $A_{i\alpha,j\alpha}$ is the adjacency matrix in layer α , $A_{i\alpha,j\beta}$ is the adjacency matrix between layers, $k_{i\alpha}$ is the degree of node i in layer α and $\mu = \sum_{j,\alpha} A_{i\alpha,j\alpha} + \omega \sum_{i,\alpha,\beta} A_{i\alpha,j\beta}$.

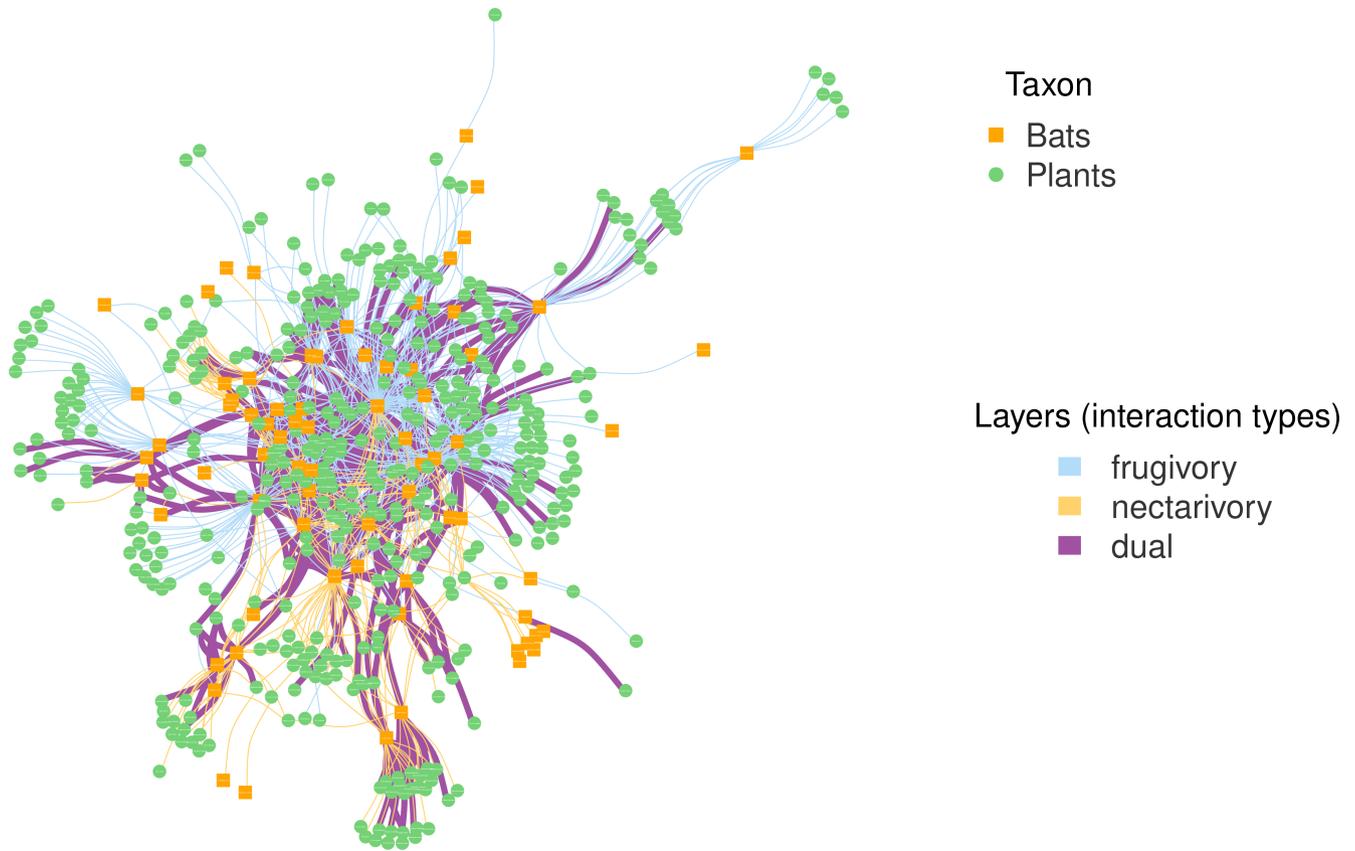


FIGURE 2 The empirical network is made of two layers, representing interactions of frugivory (blue) and nectarivory (yellow) between bats and plants in the entire Neotropics. Dual interactions (purple) between the same bat and plant species are also included. All nodes are represented in both layers, always in the same position in the graph.

In Equation (4), the coupling parameter ω can vary between zero and one. When $\omega = 0$, each layer is considered separately, with no connection to the other layers. In this case, the overall modularity of the network is calculated as the average modularity of its layers. Having $\omega = 1$ represents the maximum coupling, which makes the multiplex network turn into a monolayer network (a.k.a., an aggregated network). In other words, increasing ω from zero to one results in increasing the weights of the interlayer edges (Mucha et al., 2010).

The resolution parameter (γ) was designed for monolayer networks to evaluate modularity (Reichardt & Bornholdt, 2006) and later adapted for using with multilayer networks (Mucha et al., 2010). If γ is high, there will be more modules in the network and they will contain fewer nodes (small modules). Although γ may vary within the range $0 \leq \gamma \leq \infty$, for higher values of γ the modules become so small that each module contains a single node. Then, the range of γ is restricted to smaller than γ_l , in which γ_l is the maximum value of γ before all modules have a single node. If the values of ω and γ are 0 and 1, respectively, the generalized modularity equation (Equation 4) is proportional to the average modularity of the layers of the monolayer network (Newman, 2004; Newman & Girvan, 2004). We represented the table of variation in the number of modules and modularity with ω and γ , in Supporting Information A.

2.5 | Our new centrality metric: Gnorm

As defined by the Louvain algorithm, nodes are not allowed to belong to more than one module on the same layer. We, thus, define G as a discrete integer varying between 1 and the total number of layers in the network. In other words, G represents the number of modules that a given node belongs to. Considering the variation in G as a function of ω and γ , $Gnorm$ is defined as follows:

$$Gnorm = \frac{\sum_{j=1}^{P_2} \sum_{i=1}^{P_1} \bar{G}_{ij}}{\frac{1}{N} \sum_{k=1}^N \sum_{j=1}^{P_2} \sum_{i=1}^{P_1} \bar{G}_{ij,k}} \tag{5}$$

in which P_1 and P_2 are the number of the partitions of ω and γ , N is the number of nodes in the network, i and j are the indices of \bar{G} within ω and γ and k is the node index in the network.

3 | RESULTS

3.1 | Gnorm centrality in the bat–plant multilayer network

We tested how $Gnorm$ performs using the bat–plant multilayer network. After calculating $Gnorm$ for each species, we plotted its

frequency distribution, [Figure 3](#). While many species stayed on average in a single module, a few stayed in two modules. Then, we compared this empirical distribution to the distribution obtained with the randomized version of the network. It was possible to see that, in the original network, there is much more variation in *Gnorm*, and that the empirical distribution is more left-skewed than in the randomized network.

To validate the utility of our new metric, *Gnorm*, we constructed *in silico* bipartite random (i.e. Erdős–Rényi model (1959)) and scale-free (i.e. Barabasi–Albert model (1999)) multilayer networks (with two layers) and calculated the distribution of *Gnorm* in them. The simulated networks have 100, 500 and 1000 nodes, with an average degree of 5, 10 and 15. [Figure 4a](#) represents the results obtained for random bipartite networks. In each network, half of the nodes belong to group A and half to group B. Each node randomly selects its neighbours by keeping the mean degree of the network as defined. Constructing the scale-free bipartite multilayer networks, in each time step, one new node enters the network connecting to the others with their degree probability. The higher the degree of the nodes, the higher the chance of getting linked with new nodes. The *Gnorm* distribution of these networks is plotted in [Figure 4b](#). *Gnorm* behaviour under different levels of resampling also considered in [Supporting Information B](#).

Checking how *Gnorm* varies with γ and ω ([Supporting Information C](#)), and how it is distributed in the bat–plant multilayer network, we then checked how it varies with commonly used monolayer centralities used to identify keystone species in interaction networks (Cirtwill et al., 2018; González et al., 2010; Mello et al., 2015). For this comparison, we considered only bats, as the network was built from animal-centric data, and focused on the nodes with the highest centrality.

Degree centrality, the simplest metric, is defined as the number of links that a node has in the network (Costa, 2004). It is used as a proxy for the niche breadth of a species in an interaction network (González et al., 2010; Mello et al., 2015). Closeness centrality is calculated as the average distance between a node and all other nodes in the network, and each distance is measured as the number of links between two bat species, considering geodesics, a.k.a.

short paths (Sabidussi, 1966). It is used as a proxy for the uniqueness of a species' niche (González et al., 2010; Mello et al., 2015). Betweenness centrality represents the node's role in allowing information to pass from one part of the network to the other and is calculated as the number of the short paths that pass through the node (Freeman, 1977). It is used as a proxy for the role of a species in connecting different guilds and functional groups (González et al., 2010; Mello et al., 2015). Eigenvector, the last centrality, quantifies the node's structural importance while considering the importance of its neighbours, and is calculated as the contribution of a given node to the main eigenvector of the network (Bonacich, 1972; Taylor et al., 2017). It is used as a proxy for the overall importance of a species to the ecological function or ecosystem service delivered by the network (Mello et al., 2019).

3.2 | *Gnorm* and other centralities

There was an intermediate to low correlation (Pearson correlation) between *Gnorm* and the monolayer centralities, [Figure 5](#). Therefore, our new centrality metric points out a different set of potential keystone species.

Gnorm as a new proposed centrality measure, among the other centralities (such as eigenvector centrality, degree centrality, closeness centrality and betweenness centrality) displays a localization effect, [Supporting Information D](#). To compare the rankings of the top 10 most central nodes obtained with *Gnorm* and the monolayer centralities, we used two metrics, binary similarity and distance similarity. Binary similarity is calculated as follows:

$$Sim_{bin} = \frac{\sum_j \sum_i \delta(c_j, g_i)}{N} \quad (6)$$

in which $\delta(c_j, g_i)$ is the Kronecker delta, N is the chosen cut ranking (we assume the 10 best-ranked nodes of each metric to evaluate), c_j and g_i are the vectors ordered by the ranking of the most central nodes and with the highest values of *Gnorm* respectively.

In addition to binary similarity, we can assess similarity by the node's ranking within the chosen cut-off set. To do this, we add a

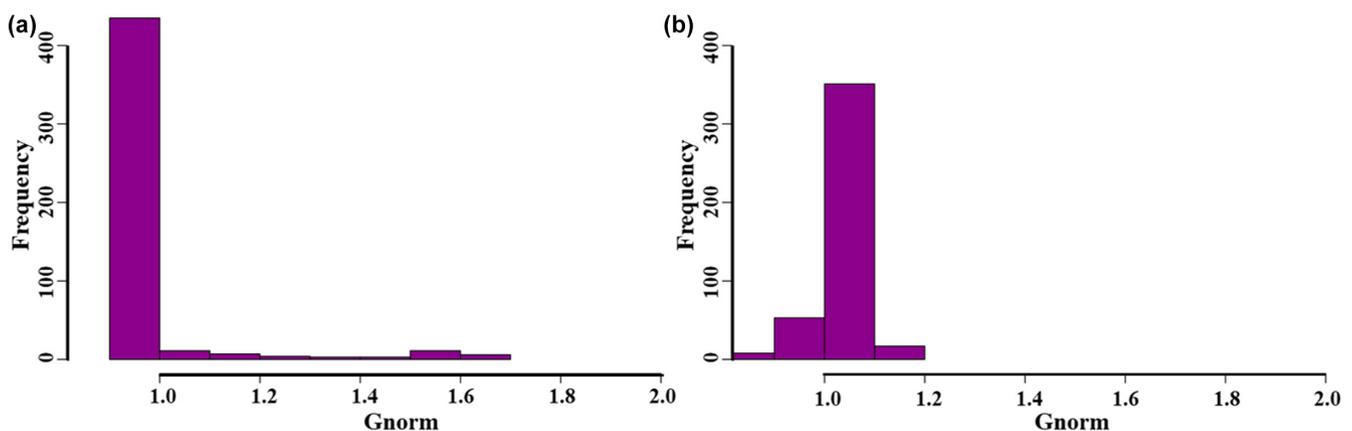


FIGURE 3 Distribution of *Gnorm* for all species in (a) the bat–plant network and (b) the randomized version of the same network.

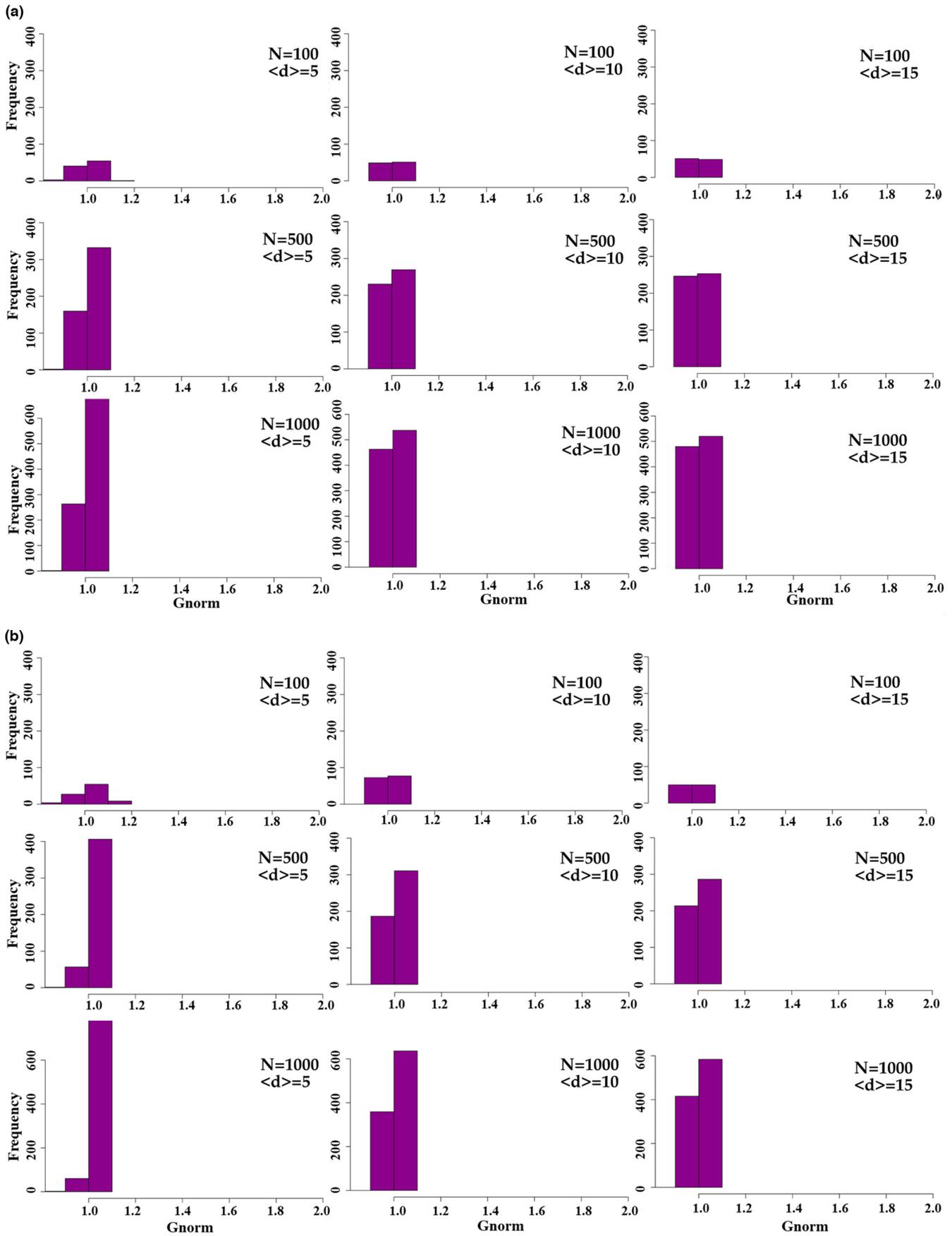


FIGURE 4 (a) Distribution of G_{norm} for random bipartite multilayer networks with different numbers of nodes and average degrees, (b) Distribution of G_{norm} for scale-free bipartite multilayer networks with different numbers of nodes and average degrees.

weight factor proportional to the inverse of the distance between nodes within the Equation (6).

$$Sim_{dist} = \frac{\sum_j^N \sum_i^N \frac{1}{1+|i-j|} \delta(c_j, g_i)}{N}, \quad (7)$$

where the absolute value of $i - j$ is equivalent to the distance between the ranks of nodes g_i and c_j . Needs to remind that both similarity values range from 0 (no nodes in common) to 1 (all nodes in common). Table 1 presents the results of the similarities of the centralities in comparison with *Gnorm*.

4 | DISCUSSION

In the present study, we propose a new centrality metric developed for multilayer networks. First, the resolution parameter (γ) and the coupling parameter (ω), used to calculate the multilayer version of the Louvain modularity, open up new possibilities for operationalizing the keystone species concept in interaction networks. Second, by changing the levels of resolution and coupling, we can identify different configurations of modules, which vary in terms of module size and layer identity. Third, by gradually increasing both parameters, especially coupling, we can also identify highly central nodes that remain in different modules on different layers, resisting growing layer coupling. Finally, based on those

adjustments, we have created a new metric that operationalizes this resistance: *Gnorm*.

It is important to think about the properties of *Gnorm* in comparison to monolayer centrality metrics, so we can understand how it might help us go further in the operationalization of the keystone species concept. On the one hand, the distribution of *Gnorm* is consistent with those of other monolayer centrality metrics. That is, only a few central nodes reach high values, and there is a long tail of peripheral nodes (a.k.a., a localization effect). On the other hand, the ranking of species with highest *Gnorm* differs from those observed for other monolayer centrality metrics, which are widely used in the literature. Therefore, by using *Gnorm* we are able to identify potential keystone species that connect different interaction types and otherwise would pass unnoticed with a monolayer approach.

Another interesting property is that a change in resolution, despite having an effect, does not seem to influence module composition and structure as strongly as a change in coupling. Therefore, it is safe to point out nodes with high *Gnorm* as potential keystone species, considering large changes in coupling but not in resolution. This way, we reduce the probability to observe an exception within a broad range of resolutions, while identifying the most important species in an efficient way. Naturally, for a species to be more comprehensively identified as a keystone, further analyses are needed, including field experiments. Nevertheless, *Gnorm* focuses in steps

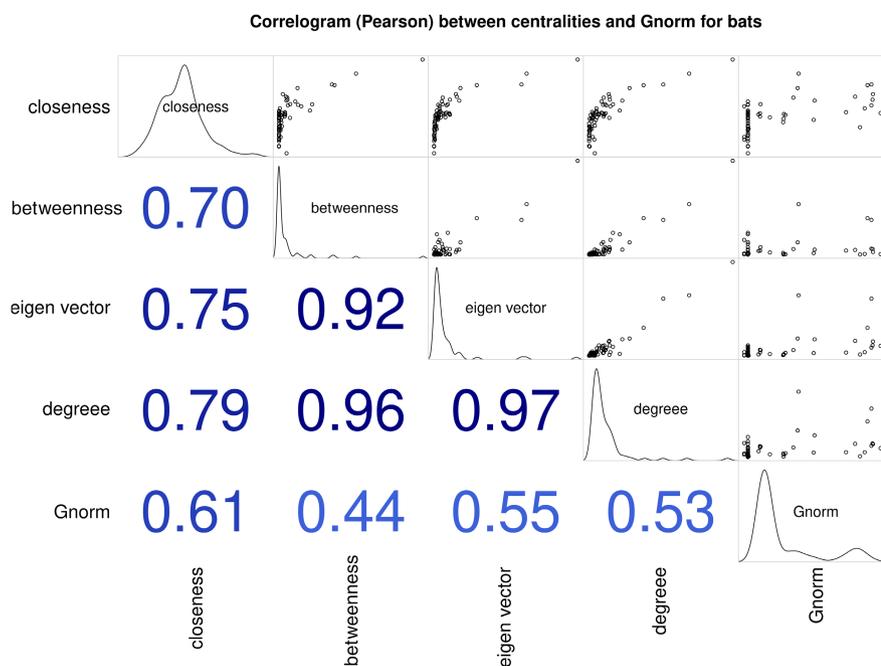


FIGURE 5 Pearson correlation between *Gnorm* centrality and other centralities obtained for Bats species.

TABLE 1 Binary and distance similarity values were calculated for the top 10 species in each centrality in relation to their *Gnorm* values.

Similarity values					
	Closeness	Betweenness	Eigenvector	Degree	<i>Gnorm</i>
Binary Sim	0.6	0.3	0.6	0.4	1.0
Distance Sim	0.25	0.22	0.24	0.20	1.0

related to operationalizing the keystone species concept in multilayer networks.

In the few cases where *Gnorm* varies more strongly with resolution, we can conclude that species with high *Gnorm* may have smaller or larger relative importance if we are biologically interested in focusing on smaller or larger guilds or functional groups. This can happen since the structural importance operationalized by *Gnorm* is based on module configuration. In this case, an expert in the interaction types that define a given multilayer network will be able to choose the proper resolution based on the biological properties of the system or phenomenon under scrutiny.

The expert eye can also see great value in *Gnorm* when interpreting centrality rankings. When we evaluated the top 10 most central species in the bat–plant network, we saw a moderate overlap with monolayer centrality metrics. This is quite interesting, as the *Gnorm* ranking was made taking into account the resistance of each species to coupling. This is a very different criterion from those adopted by monolayer centrality metrics. The Spearman and Pearson correlations also returned positive values, but not very high, reinforcing that the monolayer centralities and *Gnorm* overlap in some ways, but tell different stories about node importance. Something even more interesting than species similarities between the centrality rankings are fine differences in terms of which nodes appear in these rankings. The species that are better ranked only by the values of *Gnorm* and that were not ranked well by the monolayer centralities may be important in a different way within a multilayer network. This importance eludes identification by monolayer metrics, which reinforces the value of studying multilayer networks using metrics that respect their original structure, without aggregating interaction types. Therefore, when analysing multilayer networks, we should focus on *Gnorm* and future metrics that really consider the layered structure, so we do not overlook potential keystone species.

For example, in the case of interactions between bats and plants, it has already been pointed out, based on analyses of monolayer (Castaño et al., 2020; Mello et al., 2015; Queiroz et al., 2021) and multilayer networks (Mello et al., 2019), that bat species such as *Artibeus jamaicensis* (Artjam) and *Anoura caudifer* (Anocau) are usually hubs or connectors. These bats focus more on fruits or flowers, respectively, but are capable of consuming both resources. Therefore, in addition to reaching high values of monolayer centrality, they also reach high values of multilayer centrality. Furthermore, we saw that, taking into account coupling and resolution in the multilayer network, other species, such as *Artibeus concolor* (Artcon) and *Platyrrhinus helleri* (Plahel) may be even more important as bridges between layers. That is so due to their high resistance to coupling, biologically translated as permanence in different modules on different layers. This permanence means that species with high *Gnorm* might be very reliable mutualistic partners for plants of different genera and families, which continue delivering the service under a range of conditions that alter layer coupling in nature.

These properties lead us to suggest that our new centrality metric *Gnorm* is a good tool to help identify keystone species in

interaction networks. Species identified as central by this multilayer metric, even if also identified by monolayer metrics, are very important for the transfer of information through direct and indirect routes in ecological systems formed by multiple interaction types. In the empirical network used as a case study, these pathways unite different groups of plants, from different genera and families, which produce different types of resources vital to maintaining animal populations.

In conclusion, we suggest *Gnorm* as a promising tool to operationalize the keystone species concept in networks formed by multiple interaction types. This new tool might be particularly interesting for researchers who want to assess ‘interactions between interactions’. Conditional outcomes have been receiving growing attention, especially in disease ecology, as reservoir species act like bridges that connect different interaction types between pathogens, hosts and vectors (Alcantara et al., 2022). *Gnorm* might help, for instance, to identify keystone reservoirs responsible for spillover events, among many other applications.

AUTHOR CONTRIBUTIONS

Henrique S. Requejo and Marco A. R. Mello conceived the original project, which was originally presented and publicly defended as the Bachelor's monograph of Henrique S. Requejo. Nastaran Lotfi, Marco A. R. Mello, and Francisco A. Rodrigues further developed the original ideas, improved the methods, and gave new interpretations to the results. Nastaran Lotfi and Henrique S. Requejo designed the new models, wrote the code, and analyzed the data, under the supervision of Marco A. R. Mello and Francisco A. Rodrigues. Nastaran Lotfi, Marco A. R. Mello, and Francisco A. Rodrigues led the writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors certify that they have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14257>.

DATA AVAILABILITY STATEMENT

The data set of bat–plant interactions used to test Gnorm is available as a data paper (Florez-Montero et al., 2022). In silico data and code are available on GitHub via Zenodo, together with tutorials that allow full reproducibility of our analyses (<https://doi.org/10.5281/zenodo.10219625>).

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REFERENCES

- Alcantara, D., de Souza, C., de Mello, V., Torres, J., Lourenço, E., Bassini-Silva, R., Herrera, H., Machado, R., & André, M. (2022). Multilayer networks assisting to untangle direct and indirect pathogen transmission in bats. *Microbial Ecology*, 3, 1292–1306. <https://doi.org/10.1007/s00248-022-02108-3>
- Barabasi, A.-L., & Albert, R. (2023). Emergence of scaling in random networks. *Science*, 286, 509–512. <https://doi.org/10.1126/science.286.5439.509>
- Bascompte, J. (2009). Disentangling the web of life. *Science*, 325(5939), 416–419. <https://doi.org/10.1126/science.1170749>
- Blondel, V. D., Guillaume, J.-L., Lambiotte, R., & Lefebvre, E. (2008). Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment*, 2008(10), P10008. <https://doi.org/10.1088/1742-5468/2008/10/p10008>
- Boccaletti, S., Bianconi, G., Criado, R., Del Genio, C. I., Gómez-Gardenes, J., Romance, M., Sendina-Nadal, I., Wang, Z., & Zanin, M. (2014). The structure and dynamics of multilayer networks. *Physics Reports*, 544(1), 1–122. <https://doi.org/10.1016/j.physrep.2014.07.001>
- Bonacich, P. (1972). Factoring and weighting approaches to status scores and clique identification. *Journal of Mathematical Sociology*, 2(1), 113–120. <https://doi.org/10.1080/0022250x.1972.9989806>
- Castaño, J. H., Carranza-Quiceno, J. A., & Jairo Pérez-Torres, Y. (2020). Bat-fruit networks structure resist habitat modification but species roles change in the most transformed habitats. *Acta Oecologica*, 105, 103550. <https://doi.org/10.1016/j.actao.2020.103550>
- Cirtwill, A. R., Riva, G. V. D., Gaiarsa, M. P., Bimler, M. D., Fernando Cagua, E., Coux, C., & Matthias Dehling, D. (2018). A review of species role concepts in food webs. *Food Webs*, 16, e00093. <https://doi.org/10.1016/j.fooweb.2018.e00093>
- Costa, A., González, A. M. M., Guizien, K., Doglioli, A. M., Gómez, J. M., Petrenko, A. A., & Allesina, S. (2019). Ecological networks: Pursuing the shortest path, however narrow and crooked. *Scientific Reports*, 9, 17826. <https://doi.org/10.1038/s41598-019-54206-x>
- Cottee-Jones, H. E. W., & Whittaker, R. J. (2012). Perspective: The keystone species concept: a critical appraisal. *Frontiers of Biogeography*, 4, 117–127. <https://doi.org/10.21425/F5FBG12533>
- Costa, L. F. (2004). The hierarchical backbone of complex networks. *Physical Review Letters*, 93(9), 098702. <https://doi.org/10.1103/PhysRevLett.93.098702>
- Davic, R. D. (2003). Linking keystone species and functional groups: A new operational definition of the keystone species concept. *Conservation Ecology*, 7, resp11. <https://doi.org/10.5751/ES-00502-0701r11>
- De Domenico, M., Solé-Ribalta, A., Cozzo, E., Kivelä, M., Moreno, Y., Porter, M. A., Gómez, S., & Arenas, A. (2013). Mathematical formulation of multilayer networks. *Physical Review X*, 3, 041022. <https://doi.org/10.1103/PhysRevX.3.041022>
- Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, 5, 90–98. <https://doi.org/10.1111/2041-210X.12139>
- Erdős, P., & Rényi, A. (1959). On random graphs. *Publicaciones Mathematicae*, 6, 290–297.
- Florez-Montero, G. L., Muylaert, R. L., Nogueira, M. R., Geiselman, C., Santana, S. E., Stevens, R. D., Tschapka, M., Rodrigues, F. A., & Mello, M. A. R. (2022). NeoBat interactions: A data set of bat–plant interactions in the neotropics. *Ecology*, 103, e3640. <https://doi.org/10.1002/ecy.3640>
- Fortunato, S. (2010). Community detection in graphs. *Physics Reports*, 486(3–5), 75–174. <https://doi.org/10.1016/j.physrep.2009.11.002>
- Fortunato, S., & Barthelemy, M. (2007). Resolution limit in community detection. *Proceedings of the National Academy of Sciences of the United States of America*, 104(1), 36–41.
- Freeman, L. C. (1977). A set of measures of centrality based on betweenness. *Sociometry*, 40, 35–41. <https://doi.org/10.2307/3033543>
- Genrich, C. M., Mello, M. A. R., Silveira, F. A. O., Bronstein, J. L., & Paglia, A. P. (2017). Duality of interaction outcomes in a plant–frugivore multilayer network. *Oikos*, 126, 361–368. <https://doi.org/10.1111/oik.03825>
- Girvan, M., & Newman, M. E. J. (2002). Community structure in social and biological networks. *Proceedings of the National Academy of Sciences of the United States of America*, 99(12), 7821–7826. <https://doi.org/10.1073/pnas.122653799>
- González, A. M. M., Dalsgaard, B., & Olesen, J. M. (2010). Centrality measures and the importance of generalist species in pollination networks. *Ecological Complexity*, 7(1), 36–43. <https://doi.org/10.1016/j.ecocom.2009.03.008>
- Holt, B., Lessard, J.-P., Borregaard, M., Fritz, S., Araújo, M., Dimitrov, D., Fabre, P.-H., Graham, C., Graves, G. R., Jønsson, K., Nogués-Bravo, D., Wang, Z., Whittaker, R., Fjeldså, J., & Rahbek, C. (2013). An update of wallace's zoogeographic regions of the world. *Science*, 339, 74–78. <https://doi.org/10.1126/science.1228282>
- Ings, T. C., & Hawes, J. E. (2018). The history of ecological networks. In *Ecological networks in the tropics* (pp. 15–28). Springer. https://doi.org/10.1007/978-3-319-68228-0_2
- Kivelä, M., Arenas, A., Barthelemy, M., Gleeson, J. P., Moreno, Y., & Porter, M. A. (2014). Multilayer networks. *Journal of Complex Networks*, 2(3), 203–271. <https://doi.org/10.1093/comnet/cnu016>
- Lafferty, K. D., & Suchanek, T. H. (2016). Revisiting paine's 1966 sea star removal experiment, the most-cited empirical article in the American Naturalist. *The American Naturalist*, 188, 365–378. <https://doi.org/10.1086/688045>
- Lewinsohn, T. M., & Cagnolo, L. (2012). Keystones in a tangled bank. *Science*, 335, 1449–1451. <https://doi.org/10.1126/science.1220138>
- Marques Draxler, C., & Kissling, W. D. (2022). The mutualism–antagonism continuum in neotropical palm–frugivore interactions: From interaction outcomes to ecosystem dynamics. *Biological Reviews*, 97(2), 527–553. <https://doi.org/10.1111/brv.12809>
- Mello, M. A. R. (2019). *Keystone species* (Vol. 1). Oxford University Press. <https://doi.org/10.1093/obo/9780199830060-0213>
- Mello, M. A. R., Felix, G. M., Pinheiro, R. B. P., Muylaert, R. L., Geiselman, C., Santana, S. E., Tschapka, M., Lotfi, N., Rodrigues, F. A., & Stevens, R. D. (2019). Insights into the assembly rules of a continent-wide multilayer network. *Nature Ecology & Evolution*, 3, 1525–1532. <https://doi.org/10.1038/s41559-019-1002-3>
- Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Kalko, E. K. V., Jordano, P., & Martínez de Aguiar, M. A. (2011). The modularity of seed dispersal: Differences in structure and robustness between bat– and bird–fruit networks. *Oecologia*, 167(1), 131–140. <https://doi.org/10.1007/s00442-011-1984-2>
- Mello, M. A. R., Rodrigues, F. A., da Fontoura, L., Costa, W. D., Kissling, Ç. H., Şekerioğlu, F. M., Marquitti, D., & Kalko, E. K. V. (2015). Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos*, 124(8), 1031–1039. <https://doi.org/10.1111/oik.01613>

- Montoya, D., Yallop, M. L., & Memmott, J. (2015). Functional group diversity increases with modularity in complex food webs. *Nature Communications*, 6, 7379. <https://doi.org/10.1038/ncomms8379>
- Mucha, P. J., Richardson, T., Macon, K., Porter, M. A., & Onnela, J.-P. (2010). Community structure in time-dependent, multiscale, and multiplex networks. *Science*, 328(5980), 876–878. <https://doi.org/10.1126/science.1184819>
- Newman, M. E. J. (2004). Analysis of weighted networks. *Physical Review E*, 70(5), 056131. <https://doi.org/10.1103/physreve.70.056131>
- Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E*, 69(2), 026113. <https://doi.org/10.1103/PhysRevE.69.026113>
- Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, 104(50), 19891–19896. <https://doi.org/10.1073/pnas.0706375104>
- Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100, 65–75.
- Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103, 91–93.
- Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1(4), 1–9. <https://doi.org/10.1038/s41559-017-0101>
- Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the quest for keystones. *BioScience*, 46, 609–620. <https://doi.org/10.2307/1312990>
- Queiroz, J. A., Diniz, U. M., Vázquez, D. P., Quirino, Z. M., Santos, F. A. R., Mello, M. A. R., & Machado, I. C. (2021). Bats and hawkmoths form mixed modules with flowering plants in a nocturnal interaction network. *Biotropica*, 53, 596–607. <https://doi.org/10.1111/btp.12902>
- Reichardt, J., & Bornholdt, S. (2006). Statistical mechanics of community detection. *Physical Review E*, 74(1), 016110. <https://doi.org/10.1103/physreve.74.016110>
- Sabidussi, G. (1966). The centrality index of a graph. *Psychometrika*, 31(4), 581–603. <https://doi.org/10.1007/BF02289527>
- Taylor, D., Myers, S. A., Clauset, A., Porter, M. A., & Mucha, P. J. (2017). Eigenvector-based centrality measures for temporal networks. *Multiscale Modeling and Simulation*, 15(1), 537–574. <https://doi.org/10.1137/16M1066142>
- Timóteo, S., Albrecht, J., Rumeu, B., Norte, A. C., Traveset, A., Frost, C. M., Marchante, E., López-Núñez, F. A., Peralta, G., Memmott, J., Olesen, J. M., Costa, J. M., da Silva, L. P., Carvalheiro, L. G., Correia, M., Staab, M., Blüthgen, N., Farwig, N., Parejo, S. H., ... Heleno, R. (2022). Tripartite networks show that keystone species can multitask. *Functional Ecology*, 10, 274–286. <https://doi.org/10.1111/1365-2435.14206>
- Wulf, A. (2016). *The invention of nature: Alexander von Humboldt's new world* (1st ed.). Vintage. ISBN: 978-0345806291.

SUPPORTING INFORMATION

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

Data S1: Additional analyses that explain the rationale and demonstrate the performance of our new centrality metric, *G_{norm}*.

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