

## Opinion

# Ecological Networks over the Edge: Hypergraph Trait-Mediated Indirect Interaction (TMII) Structure

Antonio J. Golubski,<sup>1,\*</sup> Erik E. Westlund,<sup>2</sup> John Vandermeer,<sup>3</sup> and Mercedes Pascual<sup>4,5</sup>

**Analyses of ecological network structure have yielded important insights into the functioning of complex ecological systems. However, such analyses almost universally omit non-pairwise interactions, many classes of which are crucial for system structure, function, and resilience. Hypergraphs are mathematical constructs capable of considering such interactions: we discuss their utility for studying ecological networks containing diverse interaction types, and associated challenges and strategies. We demonstrate the approach using a real-world coffee agroecosystem in which resistance to agricultural pests depends upon a large number of TMII. A hypergraph representation successfully reflects both the importance of species imposing such effects and the context-dependency of that importance in terms of how it is affected by removal of other species from the system.**

## Ecological Complexity and Network Topology

There has been, and still is, great interest in understanding what determines the stability and resilience of ecological systems. What allows one system to bounce back from a disturbance when another does not? Why do some systems contain higher diversity of coexisting species than others? What determines the efficient provisioning of ecosystem services, or the severity of the response of a system to loss or invasion of a given species? The tremendous complexity of ecological systems makes the search for generalizable answers to these questions, based on fundamental system properties, extremely challenging.

Ecologists have gained insight into such questions by conceptualizing complex ecological systems as networks (mathematically described as **graphs**; see [Glossary](#)). An important benefit of this approach is the ability to quantify various aspects of network structure (or **topology**): patterns in how interactions between actors, typically species, are arranged. The ability to dissect the complexity of a system by examining the effects of its structure separately from other elements is a valuable tool in the search for general and/or fundamental patterns and properties [1–3]. A detailed review of such results for ecological systems is beyond the scope of this paper, but to give a few examples: prior work has suggested that communities might be more sensitive to the loss of species with high **degree** [4], **in-degree** or **out-degree** [5,6], or **eigenvector centrality** [7]. Global network metrics including connectedness, clustering, degree distribution, average shortest **path** distance between species [4,8–10], network nestedness and/or compartmentalization [11–14], ‘generalization’ [15], and the relative frequencies of various

### Trends

Hypergraphs allow quantitative analysis of TMII structure in ecological networks.

Hypergraph metrics of species importance reflect influence via nontrophic effects.

Hypergraph topology captures context-dependency of TMII.

Hypergraphs offer new avenues for understanding the roles of TMII in large communities.

<sup>1</sup>Department of Ecology, Evolution, and Organismal Biology, Kennesaw State University, Science Building, 370 Paulding Ave NW, Kennesaw, GA 30144, USA

<sup>2</sup>Department of Mathematics, Kennesaw State University, Math Building, 1100 South Marietta Parkway, Marietta, GA 30060, USA

<sup>3</sup>Department of Ecology and Evolutionary Biology, University of Michigan, Kraus Natural Science Building, 830 North University, Ann Arbor, MI 48109-1048, USA

<sup>4</sup>Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, IL 60637, USA

<sup>5</sup>The Santa Fe Institute, Santa Fe, NM 87501, USA

\*Correspondence: [agolubsk@kennesaw.edu](mailto:agolubsk@kennesaw.edu) (A.J. Golubski).

'motifs' [16,17] have been proposed to influence the sensitivity of a system to perturbations, as measured by different stability measures including persistence. Grouping models based on interaction patterns [18–20] have been suggested as ways to identify species playing unique roles in a system, or to discern organizational elements such as multiple 'channels' of energy flow. Space constraints preclude detailed description of the network quantities referenced in the preceding list, but our point is simply that such works demonstrate that quantitative descriptions of ecological network structure are meaningful. Importantly, analyses of network structure allow insight even in systems for which limited information is available: many of the results cited above for example are based on **unweighted graphs** and/or **undirected graphs** (i.e., representations lacking information on interaction magnitudes and/or directions).

We do not mean to suggest that these approaches are superior to others: merely complementary. Indeed, several of the above examples evaluate the relevance of network metrics via their power to predict the behaviors of dynamic models with specified functional forms.

### Prevalence and Importance of TMIs

Almost universally, studies of ecological network topology have considered only pairwise interactions. This approach is inadequate for considering many important ecological phenomena which are fundamentally properties of more than two species. **Trait-mediated indirect interactions** (TMIs) or **interaction modifications** (IMs) associated with adaptive behaviors [21,22] provide key examples. Consider a forager which drops an unprofitable prey item from its diet when an alternative and more profitable prey species is sufficiently abundant. In that scenario, the latter prey species affects the former via forager behavior: an inherently tripartite interaction. Similarly, when foragers reduce their activity (and thus their rate of prey consumption) in response to fear of a predator, that predator affects the prey via changes in forager behavior. We will use the shorthand TMI to refer to non-pairwise ecological interactions in which a direct interaction between two species is modified by one or more others, even though some important examples do not involve clear changes in traits (such as effects of cover provided by vegetation).

The importance of TMIs is widely appreciated [23–25]. They have repeatedly been shown to be crucial for the structure and function of ecological systems [26–29], including the provision of key system services [30–32] and recovery of systems from disturbance [33]. They have also been implicated as mediators of major unforeseen consequences of anthropogenic impacts on ecological systems. For example, fishing is suspected to have contributed to sea otter declines in the 1990s via effects on killer whale behavior [34], and TMIs have been implicated in multiple important changes in Yellowstone ecosystems following the reintroduction of wolves [35]. Understanding how TMIs influence large and complex ecological systems in a more general and mechanistic way is necessary for predicting how such systems will respond to perturbations, and requires conceptual and analytical frameworks better able to consider the structure of interactive effects in large systems.

There is clear need to develop common theoretical frameworks capable of accommodating diverse interaction types including TMIs [36–40]. TMIs are generally highly structured, and there is reason to expect that interactions among them are central to their community-wide implications [39,41]. However, the complexity introduced by such effects has hindered study of that structure. Some models explore the effects of one [41–43] or more [44] specific adaptive behaviors, effectively containing IMs and structure in them, but only implicitly. Others introduce IMs randomly, without the structural constraints implied by many TMI-generating mechanisms [45–47]. Most models that consider TMIs in great detail (i.e., using differential equations) consider relatively few species. Even then, fully characterizing TMIs can be challenging, and signs of effects can change depending on functional forms and parameter values [48,49]. Quantitative analyses of ecological network structure which include TMIs would represent

### Glossary

**Adjacency:** any nodes which share incidence to at least one common edge or hyperedge are said to be adjacent to one another, as are any edges or hyperedges which share incidence to at least one common node.

**Adjacency matrix:** a square matrix  $A = [a_{ij}]$ , whose rows and columns are indexed by nodes. In an unweighted and undirected graph, multigraph, or hypergraph,  $a_{ij} = k$  if node  $i$  and node  $j$  appear in exactly  $k$  edges or hyperedges together. In the graph case all entries will equal either 0 or 1 because any pair of nodes may share at most one edge.

**Betweenness centrality:** a potential indicator of node importance based on how often the node appears on the shortest path(s) between two others, reflecting its potential role in the rapid and/or efficient transmission of information and/or effects between pairs of other nodes.

**Closeness centrality:** a potential indicator of node importance which is maximized by a low average shortest-path distance (i.e., low 'degrees of separation') to other nodes.

**Degree:** the degree of a node equals the number of edges that it is incident to (the number of interactions in which it participates). In an unweighted graph, this also equals the degree centrality of that node.

**Edge:** an element in a network which typically represents some interaction between two nodes: in this case an ecological interaction between members of different populations.

**Eigenvector centrality:** a potential indicator of node importance which is maximized by participating in many interactions with other high-scoring nodes.

**Graph:** a mathematical description of a network.

**Hyperedge:** the equivalent of an edge in a hypergraph: a hyperedge may represent an interaction which involves any number of nodes.

**Hypergraph:** a generalization of a graph in which the equivalents of edges (termed hyperedges) may each contain (be incident to – 'link') any number of nodes.

**Hyperpath:** the analog of a path in a hypergraph.

**Incidence:** a node and any edge or hyperedge involving that node

valuable tools for dissecting their complex effects and roles in large communities. However, conventional approaches must approximate TMIs with pairwise **edges** [20,49], and fail to reflect their inherently non-pairwise nature.

## Hypergraphs

**Hypergraphs** [50,51] are mathematical constructs capable of representing non-dyadic interactions such as TMIs: we argue here that they hold great promise for considering diverse classes of ecological interactions within a common theoretical framework. The key distinction between a graph and a hypergraph is that, in the former, each edge is associated with precisely two **nodes**, while the equivalent of an edge in the latter – a **hyperedge** – can connect any number of nodes, and thus represent an interaction involving any number of species. Hypergraphs are increasingly being used to study interactive effects in social [52–54] and biomolecular [55,56] networks. We have found only two applications of hypergraphs to community ecology [53,57]. Each of these considers ‘competition hypergraphs’ which, while offering new insights, were derived from directed food web graphs, that is from information on only pairwise trophic interactions. We discuss and illustrate some of the potential hypergraphs hold for considering new and inherently non-pairwise types of interactions which graphs alone cannot satisfactorily represent.

As a starting point in investigating the value of hypergraph representations of ecological communities, we construct a hypergraph based on a real-world coffee agroecosystem (Figure 1 in Box 1). This illustrative example facilitates discussion of some general factors and open areas to be considered when constructing and analyzing ecological hypergraphs containing TMIs. Box 2 presents some technical details of hypergraph representations which help to illustrate: (i) the straightforward way in which hyperedges can represent TMIs, (ii) how hypergraph topology captures the context-dependency of TMIs, and (iii) reasons that network metrics differ in the hypergraph case. This facilitates the biological interpretation of key elements of hypergraph structure.

One common way to extract insight from a network representation of a system is to calculate node properties – namely centrality metrics – as potential indicators of node importance. Hypergraph analogs of such centralities, which incorporate information regarding participation in non-pairwise interactions, have yielded new insights across diverse types of systems [52–57]. We ask how four such indicators of relative node importance in the hypergraph of the coffee agroecosystem differ from those reached via two other representations: a graph containing only direct effects, and a ‘clique multigraph’ in which non-pairwise interactions are approximated by the insertion of additional pairwise edges (Box 2). We compare centralities of each species in each representation, both in the full system and when Azteca ants are deleted. Calculation of these centrality metrics in the hypergraph and clique multigraph cases generally involved applying traditional graph algorithms to the hypergraph and clique multigraph matrices (see code in the supplemental information online), although there are added considerations (see below).

## Species Centralities in Our Illustrative Example

We focus on eigenvector and **betweenness centrality** results (Figure 1 and Tables S4 and S5 in the supplementary material online). Degree and **closeness centrality** showed generally similar patterns, and are presented in Figures S1–S3 and Tables S1–S3 in the supplementary material online. It is intuitive that the graph representation we consider, which omits any representation of TMIs, might inadequately describe a system containing many such effects. We therefore focus on comparisons between the hypergraph and clique multigraph because the latter does model the TMIs of a system, albeit using pairwise interactions.

(formally ‘containing’ it) are said to be incident to one another.

**Incidence matrix:** a binary matrix  $E = [e_{ij}]$  whose rows and columns are indexed by nodes and edges or hyperedges, respectively, and having  $e_{ij} = 1$  if and only if node  $i$  is incident to edge or hyperedge  $j$ .

**Interaction modification (IM):** a modification of an interaction by a species (the ‘modifier’) not involved in that interaction.

**In-degree:** in a directed graph, the number of edges directed into a node.

**Node or vertex:** an object or actor in a network: in this case a population in an ecological community.

**Out-degree:** in a directed graph, the number of edges directed out of a node.

**Path:** a path between two nodes  $v_1$  and  $v_{k+1}$  may be defined as an sequence of  $k$  distinct adjacent edges within the sequence,  $v_1, e_1, v_2, e_2, \dots, v_k, e_k, v_{k+1}$ , such that edge  $e_i$  is the edge joining (incident to both) nodes  $v_i$  and  $v_{i+1}$ .

**Topology:** in this context, the pattern of edge or hyperedge and node arrangement defining the structure of a network.

**Trait-mediated indirect interaction or effect (TMII):** an interaction between two species, or effect of one species on another, which is mediated by some trait (often behavior) of a third species.

**Undirected graph:** a graph that does not contain information regarding directions of effects.

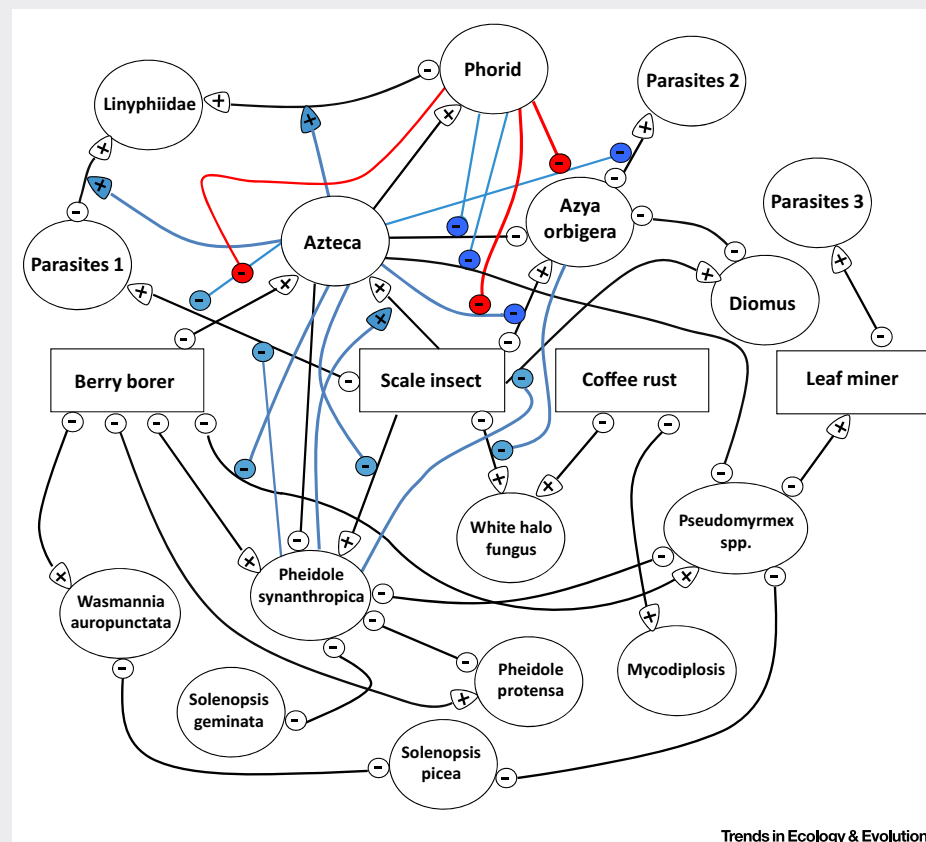
**Unweighted graph:** a graph that does not contain information regarding magnitudes of effects.

### Box 1. An Example: TMIs and Pest Control in a Coffee Agroecosystem

The example interaction network upon which we will focus (Figure 1) was assembled based on field studies spanning 15 years of a 300 hectare organic farm in southern Mexico, which has been in production for nearly 100 years [30–32]. A complex web of interacting trophic and behavioral interactions has been shown to be crucial for controlling agricultural pests (an economically important ecosystem service, which has in recent times received exaggerated attention owing to the coffee rust disease currently devastating coffee production in the Americas). These protective effects are particularly attributable to a large number of IMs imposed by ants of the genus *Azteca*, several of which are further modified by ant-parasitizing phorid flies. See [30–32] and references therein for further descriptions of the system and interactions within it.

Box 2 (and Figure 1 in Box 2) describe how the information within Figure 1 was used to construct a hypergraph representation of this system. The networks we generate are undirected and unweighted; thus information within Figure 1 concerning signs and directions of interactions is ignored. We do this so as to consider as simple a first case as possible for our illustrative example. However, in prior studies metrics calculated from undirected and unweighted network structure have yielded insight into complex systems [4,14,15,52–54]. We do not foresee major conceptual challenges in constructing analogous directed hypergraphs, although this might complicate analyses and interpretations. Challenges in constructing weighted hypergraphs are discussed in the main text.

We construct three representations of this system: a graph which omits TMIs, a hypergraph, and a ‘clique multigraph’ which represents TMIs but utilizing only pairwise interactions (Box 2 for details). We include a graph representation without any TMIs partly because omitting TMIs is exactly what most studies of ecological network structure do, under the implicit assumption that TMIs exist but might not modify the network conclusions, or simply because they cannot be incorporated. However, we focus on comparisons between the hypergraph and clique multigraph representations to evaluate specifically the advantages of the capacity of the former to capture the non-pairwise nature of TMIs.



**Figure 1. Coffee Agroecosystem Web.** Black, blue, and red arrows indicate direct effects, modifications of those direct effects, and modifications of those modifications, respectively. Square nodes indicate agricultural pests. Positive and negative effects (or strengthening and weakening IMs) are respectively indicated by triangular and circular arrowheads: our analyses omit this information to consider the simpler case of an undirected network.

Hypergraph eigenvector centrality clearly flags the importance of *Azteca* ants and phorids, two species at the heart of many of the behavioral interactions previously identified as critical to the structure and function of this system [30–32]. For the full system, hypergraph and clique multigraph eigenvector centralities are identical. However, the hypergraph representation suggests that phorids will be of low importance should *Azteca* ants be lost from the system, which makes biological sense given that most phorid interactions consist of modification of *Azteca* ant behavior. By contrast, clique multigraph eigenvector centrality suggests continued phorid importance when *Azteca* ants are deleted. More-pronounced differences were evident in the path-based metric of betweenness centrality, which in the clique multigraph inappropriately suggests that phorids become important only when *Azteca* ants are removed.

Although we focus on single nodes here, it is worth noting that hypergraph topology can also give a different image of global network properties, and that it is also possible to examine the relative centralities of each hyperedge [52]. The latter provides another promising route for hypergraph representations to contribute unique insights, with centrality metrics potentially serving as indicators of the relative roles and/or importance of specific individual TMIs.

### Challenges and Strategies

Hypergraph frameworks present unique challenges which necessitate substantial biological interpretation at all stages of hypergraph construction and analysis. Multiple reasonable ways to encode a given interaction into a hyperedge will often exist, and TMIs associated with adaptive behaviors present novel challenges for hypergraph construction. Furthermore, graph metrics often have multiple hypergraph analogs. We discuss examples of each of these issues, and suggest some strategies for addressing them, to introduce some of the considerations that arise when constructing and interpreting ecological hypergraphs.

#### Box 2. Representing a Food Web with TMIs as a Hypergraph

Constructing a hypergraph representation of the system from the information contained within Figure 1 in Box 1 is straightforward. We draw one hyperedge for each unique IM, with a node set that contains the modifier plus all species involved in any interactions being modified. Each direct interaction is also included as a hyperedge containing two nodes. The presence of any hyperedge requires the presence of all adjacent nodes, allowing hyperedges to topologically encode the context-dependency of TMIs. For example, removing *Azteca* ants from the system would mean the loss of hyperedge *f* in Figure 1 below, thus removing the link between phorids and either scales or beetles.

Two matrix representations of this hypergraph, from which multiple metrics of interest may be calculated, are depicted below. The hypergraph **adjacency matrix** indicates how many hyperedges a pair of nodes share, but does not contain information regarding how those hyperedges are structured (e.g., how many of the three hyperedges involving scale and beetle in Figure 1 also contain *Azteca*). Because of this, the hypergraph **incidence matrix** is required for many analyses.

The graph representation to which we compare our hypergraph results is obtained by simply omitting any modifications, and encoding only pairwise direct effects. To further investigate the value of the hypergraph representation, we also construct and analyze a 'clique multigraph' representation which represents TMIs by containing one edge between a pair of species for each interaction (pairwise or non-pairwise) in which both species participate, equivalent to one edge for each hyperedge they share. Each hyperedge is thus replaced by a complete sub-multigraph, in other words a clique, consisting of one edge between each pair of nodes it contains. For example, hyperedge *f* in Figure 1 would be approximated by the edges: {phorid, *Azteca*}, {phorid, scale}, {phorid, beetle}, {*Azteca*, scale}, {*Azteca*, beetle}, and {scale, beetle}). The clique multigraph indicates the aggregate participation of each species in non-pairwise interactions, but does not encode how those interactions depend on other species in the network. Adjacency matrices of the hypergraph and 'clique multigraph' representations are identical, but node deletions behave differently between the two: the clique multigraph will retain all edges except those that are incident with the deleted node (i.e., the {phorid, scale}, {phorid, beetle}, and {scale, beetle} edges introduced as part of approximating hyperedge *f* in Figure 1 would persist after the deletion of *Azteca*, even though the interaction represented by hyperedge *f* biologically requires the presence of *Azteca* ants).

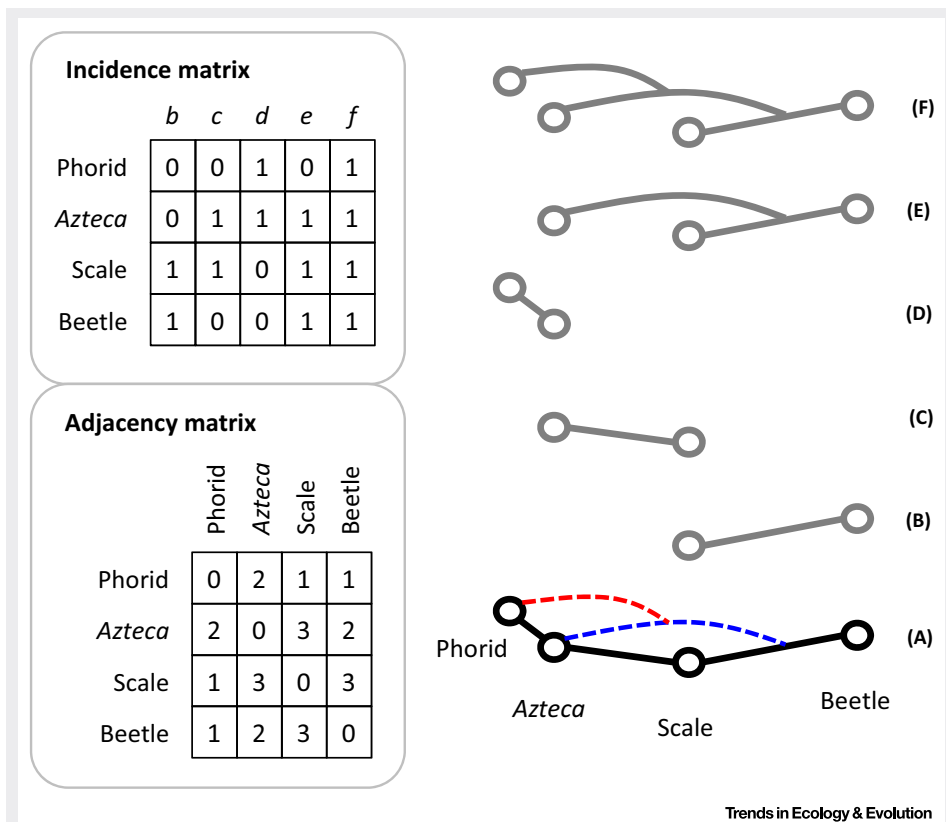
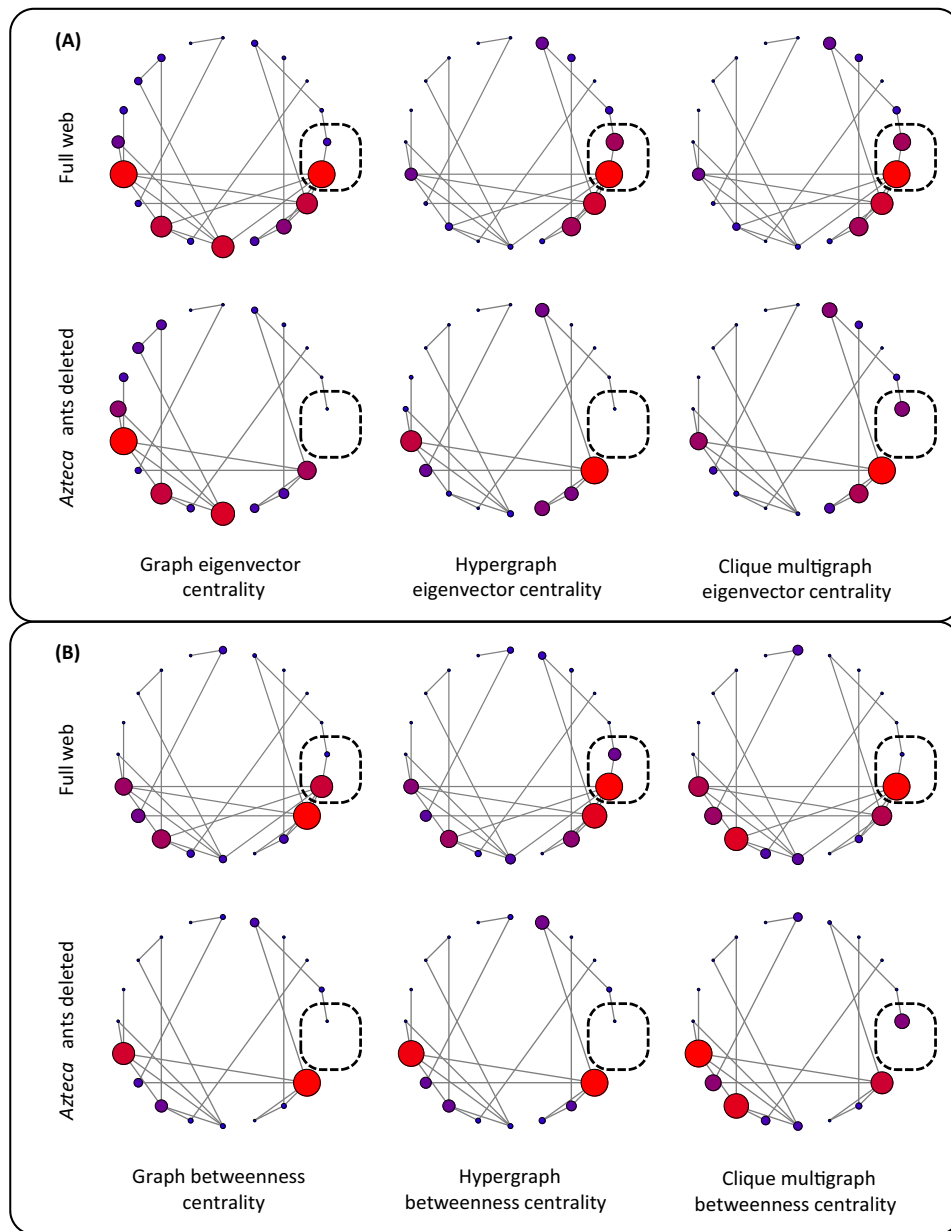


Figure 1. Key Interactions Within the System Depicted in Figure 1 in Box 1 Represented as Edges and Hyperedges, with Corresponding Hypergraph Adjacency and Incidence Matrices. Direct effects, represented by unbroken black lines in (A), include beetles (*Azya orbiger*) preying on scale insects (B), Azteca ants consuming energy from scales (C), and phorid flies parasitizing Azteca ants (D). Indirect effects consist of Azteca ants reducing the magnitude of the scale:beetle interaction by protecting beetles (E, broken blue line in A), and phorid flies reducing the magnitude of the effect of Azteca ants on the scale:beetle interaction by eliciting defensive behavior (F, broken red line in A).

### Encoding Interactions into Hyperedges

Drawing the appropriate hypergraph for a particular system of interest is a nontrivial task which must be informed in light of knowledge about the biology of the system. Consider an herbivore  $N$  which consumes plant  $P$ , and whose activity (and thus feeding rate) is reduced by each of three predators,  $X$ ,  $Y$ , and  $Z$  (we will ignore any potential modifications of the herbivore:predator interactions). Encoding this information as a single hyperedge between all five species would be undesirable because the loss of any one predator would remove that hyperedge, and with it any representation of the effects of the remaining two predators on the  $N:P$  interaction. This is similar to the approach used to construct competition hypergraphs in previous studies [53,57], where the effects of node losses were not a main focus. We suggest that each hyperedge representing a TMII or IM should intuitively include both nodes involved in the basal direct interaction being modified. A second approach would be to draw all hyperedges that are combinatorially possible given this restriction—namely  $\{X,N,P\}$ ,  $\{Y,N,P\}$ ,  $\{Z,N,P\}$ ,  $\{X,Y,N,P\}$ ,  $\{X,Z,N,P\}$ ,  $\{Y,Z,N,P\}$ , and  $\{X,Y,Z,N,P\}$ . This has the merit of reflecting the expected interactive nature of IMs [39]. The hyperedge  $\{X,Y,N,P\}$  for example might reflect reciprocal modifications by species  $X$  and  $Y$  of each other's effects on herbivore behavior. However, at least in the unweighted and undirected case, several of these hyperedges will generally serve to artificially inflate the centralities of nodes  $X$ ,  $Y$ , and  $Z$ : the expected importance of each predator in the system will increase in the presence of additional similar predators, which is precisely the opposite of what is expected in reality [39]. Intermediate





Trends in Ecology &amp; Evolution

**Figure 1. Two Measures of the Centrality of Each Node in the Interaction Network Shown in Figure 1 in Box 1.** This is based on either a graph containing only direct interactions, a hypergraph incorporating interaction modifications (IMs) as non-pairwise interactions, or a 'clique multigraph' which uses pairwise interactions to approximate IMs (see main text and Box 2). Eigenvector centrality (A) increases with the number of interactions in which the focal species participates, as well as the scores of the species with which it interacts. Betweenness centrality (B) reflects the frequency with which a focal node lies on the shortest paths between pairs of other nodes. Larger and redder nodes indicate higher centrality (relative to other nodes within the same web diagram, not across diagrams; data and details regarding the calculation of each metric are presented in Tables S4 and S5 in the supplementary material online). For visual clarity, only edges corresponding to direct interactions in the original graph are drawn. Broken lines encircle and highlight two key players in the system: phorid flies (3:00 clock position) and Azteca ants (3:36 position). In the hypergraph, each centrality metric indicates the relatively high importance of phorids when Azteca ants are present in the web, but not in a web from which Azteca ants have been deleted. Phorid centralities are consistently low in the graph representation. In the clique multigraph, eigenvector centrality inappropriately continues to suggest phorid importance when Azteca ants are deleted; betweenness centrality inappropriately suggests that phorids are relatively unimportant with Azteca ants present, but increase in importance when Azteca ants are removed.

schemes which avoid the pitfalls of each extreme are possible: for example, in this case of combining qualitatively similar TMIs, one could insert only a single hyperedge for each unique combination of a direct interaction and a single species modifying that interaction. In the above example, these would be:  $\{X,N,P\}$ ,  $\{Y,N,P\}$ , and  $\{Z,N,P\}$ . As discussed next, the ideal choice will likely change in weighted and/or directed hypergraphs.

#### Weakening Modifications and Weighted Hypergraphs

The distinction between ‘weakening’ and ‘strengthening’ modifications [39] presents unique challenges for hypergraph construction. In our agroecosystem web example the phorid-mediated hyperedge  $f$  shown in Figure 1 in Box 2 offsets the *Azteca* ant-mediated hyperedge  $e$ , and it could thus be argued that phorids reduce the importance of *Azteca* ants in the system. However, in the undirected and unweighted hypergraph representation we present, the presence of hyperedge  $f$  makes *Azteca* ants more, not less, important in the system based on the centrality metrics we examine. Generally, similar IMs affecting a common direct effect are expected to combine antagonistically [39]. This could suggest the insertion of a large number of hyperedges, corresponding at minimum to each species imposing one second-order modification reducing the first-order modification of the basal direct link by the other species. In an unweighted and undirected hypergraph this would cause each new modifier to (potentially dramatically) increase the relative importance of all other modifiers, whereas in the real world the presence of many similar modifiers would reduce the impact of any one.

Expanding into weighted hypergraphs presents opportunities to accommodate the distinction between weakening and strengthening modifications, via appropriate interpretations of hyperedge weight. For example, with hyperedge weights that combine additively (i.e., the cumulative hyperedge weight experienced by beetles in Figure 1 in Box 2 would be the sum of the weights of hyperedges  $b$ ,  $e$ , and  $f$ ), weakening modifications could be assigned negative weights (which are not uncommon in graph contexts), and strengthening modifications positive weights. Such an approach would preserve the intuitive way in which changes to the web, such as losses of species, could be considered within the hypergraph framework. Representing the weakening versus strengthening aspects of hyperedges in this way will often require the distinction between multiple levels of modifier node within a given hyperedge. The effect represented by hyperedge  $f$  in Figure 1 in Box 2 for example, weakens *Azteca* ant modification of the direct scale:beetle interaction, but in doing so strengthens that underlying direct interaction. If the importance of a species in the system is related to the total effective magnitude of modifications it imposes and direct interactions it participates in, it might thus be appropriate for hyperedge  $f$  to be assigned weights that are positive for phorid (the ultimate modifier), negative for *Azteca* ants (the next-level-down modifier whose effective impact is reduced), and positive again for scale and beetle (the participants in the basal direct interaction whose effective magnitude is increased).

Figure S4 in the supplementary material online presents a preliminary example of this approach, although further development and refinement is required, particularly for cases of pervasive reciprocal weakening modifications as would occur for the antagonistically combining IMs discussed earlier. The potential for weakening modifications to reduce rather than inflate species centrality in a weighted hypergraph suggests that different topologies will be appropriate for representing a given system as an unweighted versus weighted hypergraph. In the latter, the most faithful representation will likely generally contain a large number of hyperedges representing high-order, often weakening, modifications, and developing satisfactory schemes for assigning and combining hyperedge weights in large systems will be a nontrivial task. Interest among ecologists in interaction strengths [58], and the demonstrated relevance of properties of their distribution such as variance and correlation structure [59], further motivates the development of weighted hypergraph models of ecological networks, given that TMIs are one major determinant of these strengths.



### Multiple Hypergraph Analogs of Graph Metrics

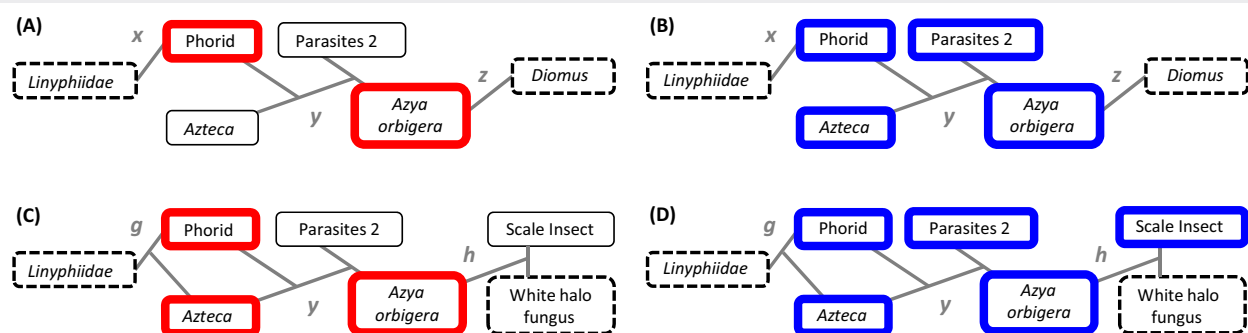
Hypergraphs are extremely general mathematical structures, and even simple fundamental graph objects can have multiple different analogs in a hypergraph. Perhaps the simplest example is that of degree. In a graph, the degree of a node (the number of edges that are incident upon it) coincides exactly with the number of other nodes that it is **adjacent** to; a focal species which participates in  $n$  interactions interacts with  $n$  other species. In a hypergraph, these two numbers can differ greatly. For example, in [Figure I in Box 2](#) every species is adjacent to all three others, while the numbers of hyperedges in which phorids, Azteca, scales, and beetles appear are 2, 4, 4, and 3, respectively. Thus, hypergraph representations allow description of separate **'incidence degree'** and **'adjacency degree'** metrics for each node. Directed hypergraphs containing TMIs also present the possibility of subdividing the out-degree of a node into multiple categories based upon multiple types of effects that a species can impose (e.g., as a prey item, versus directly modifying a direct interaction, versus imposing some higher-order modification of a modification).

The fundamental graph structure of a path provides another example of a concept which must be reinterpreted in the hypergraph context, with alternative interpretations of a **hyperpath** having different biological implications ([Box 3](#)).

#### Box 3. Hyperpaths in an Ecological Hypergraph

It is often of particular interest to determine the distance between a pair of nodes as defined by the shortest path that connects them. Betweenness centrality reflects the frequency with which a given node appears on shortest paths between pairs of other nodes, as an indicator of the degree to which that node might thus facilitate efficient traversal of the graph. In a graph, each pair of adjacent edges along a path is connected by a single node, which makes identifying the nodes that lie on any given shortest path unambiguous. This is not the case in a hypergraph, and several slightly different analogs of a path (known as a hyperpath) exist ([Figure I](#)), with different biological interpretations. One option is to only consider those nodes through which a hyperpath enters and exits each hyperedge (red borders in [Figure I](#)) to be on that hyperpath. Where adjacent hyperedges share multiple incident nodes, as hyperedges  $g$  and  $y$  share incident nodes Phorid and Azteca in [Figure IC](#), this perspective could call for defining a hyperpath as a distinct sequence of nodes and hyperedges, resulting in a greater number of hyperpaths being distinguished (for example, [Figure IC](#) would illustrate two shortest hyperpaths, one passing through Phorid and the other passing through Azteca).

However, consider phorid flies and beetles in the small web illustrated in [Figure I in Box 2](#). If hyperedge  $f$  in [Figure I in Box 2](#) is considered to represent the shortest hyperpath (of length one) between those two nodes, it is reasonable to argue that Azteca ants and scales should be considered part of that hyperpath because the existence of that hyperedge requires their presence. This suggests that it might be most appropriate to quantify betweenness based on which species each shortest hyperpath 'involves' rather than which species it specifically 'passes through': considering any node that is incident with any hyperedge in a hyperpath (blue borders in [Figure I](#) below) to be on that hyperpath. This latter concept of a hyperpath was defined in [60] in the context of directed hypergraphs, and we adopt this perspective for the betweenness centralities we calculate.



Trends in Ecology & Evolution

**Figure I.** Examples of potential shortest hyperpaths from *Linyphiidae* to either *Diomus* (A,B) or white halo fungus (C,D). Paths are taken from [Figure I in Box 1](#): broken borders indicate origin and destination nodes, and each grey letter indicates a single hyperedge. Hyperedge shapes are indicative of the direct interactions and first- and second-order modifications from which each arises. Red and blue borders indicate nodes that would be considered to be 'on' these hyperpaths under the alternative definitions discussed above.

## Concluding Remarks

Currently, few studies of ecological network structure consider TMIs. We suggest that doing so via pairwise interactions alone fails to faithfully represent important aspects of TMI structure, and we argue that hypergraph approaches, which avoid this shortcoming, have the potential to yield valuable new insights complementary to those provided by either dynamic models or graph representations.

As with all models, hypergraph representations of ecological communities constitute an attempt to capture essential features of the system while distilling complexity down to manageable levels. As with any abstraction, there will be unique ways in which hypergraph representations omit or distort important information, leading to unique challenges associated with applying them appropriately and effectively. However, such challenges are offset by equally unique opportunities, and these warrant further development of hypergraph approaches and more extensive comparisons between alternative methods of studying TMI structure. Theoretical advances in this area might also encourage the collection and synthesis of more comprehensive empirical data on TMI structure within and across ecological communities.

## Acknowledgments

This work was supported by a Kennesaw State University IDROP award to A.J.G., E.E.W. and Selena He; and subaward 3002942167 to A.J.G. from National Science Foundation Theory in Biology Program Grant F020952 to M. Pascual and Stefano Allesina.

## Supplemental Information

Supplemental information associated with this article can be found online at <http://dx.doi.org/10.1016/j.tree.2016.02.006>.

## References

1. Strogatz, S.H. (2001) Exploring complex networks. *Nature* 410, 268–276
2. Pascual, M. and Dunne, J.A., eds (2006) *Ecological Networks: Linking Structure to Dynamics in Food Webs*, Oxford University Press
3. Proulx, S.R. *et al.* (2006) Network thinking in ecology and evolution. *Trends Ecol. Evol.* 20, 345–353
4. Solé, R.V. and Montoya, J.M. (2001) Complexity and fragility in ecological networks. *Proc. R. Soc. B* 268, 2039–2045
5. Curtsdotter, A. *et al.* (2011) Robustness to secondary extinctions: comparing trait-based sequential deletions in static and dynamic food webs. *Basic Appl. Ecol.* 12, 571–580
6. Berg, S. *et al.* (2015) Ecological communities are vulnerable to realistic extinction sequences. *Oikos* 124, 486–496
7. Allesina, S. and Pascual, M. (2009) Googling food webs: can an eigenvector measure species' importance for coextinctions? *PLoS Comput. Biol.* 5, e1000494
8. Montoya, J.M. and Solé, R.V. (2002) Small world patterns in food webs. *J. Theor. Biol.* 214, 405–412
9. Williams, R.J. *et al.* (2002) Two degrees of separation in complex food webs. *Proc. Natl. Acad. Sci. U.S.A.* 99, 12913–12916
10. Dunne, J.A. *et al.* (2004) Network structure and robustness of marine food webs. *Mar. Ecol. Prog. Ser.* 273, 291–302
11. Bascompte, J. *et al.* (2003) The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. U.S.A.* 100, 9383–9387
12. Krause, A.E. *et al.* (2003) Compartments revealed in food web structure. *Nature* 426, 282–285
13. Thebault, E. and Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856
14. Stouffer, D.B. and Bascompte, J. (2011) Compartmentalization increases food web persistence. *Proc. Natl. Acad. Sci. U.S.A.* 108, 3648–3652
15. Pocock, M.J.O. *et al.* (2012) The robustness and restoration of a network of ecological networks. *Science* 335, 973–977
16. Bascompte, J. and Stouffer, D.B. (2009) The assembly and disassembly of ecological networks. *Phil. Trans. R. Soc. B* 364, 1781–1787
17. Stouffer, D.B. and Bascompte, J. (2010) Understanding food-web persistence from local to global scales. *Ecol. Lett.* 13, 154–161
18. Allesina, S. and Pascual, M. (2009) Food web models: a plea for groups. *Ecol. Lett.* 12, 652–662
19. Baskerville, E.B. *et al.* (2011) Spatial guilds in the Serengeti food web revealed by a Bayesian group model. *PLoS Comput. Biol.* 7, e1002321
20. Sander, E.L. *et al.* (2015) What can interaction webs tell us about species roles? *PLoS Comput. Biol.* 11, e1004330
21. Wootton, J.T. (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *Am. Nat.* 141, 71–89
22. Abrams, P.A. (1995) Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *Am. Nat.* 146, 112–134
23. Schmitz, O.J. *et al.* (2003) Linking individual-scale trait plasticity to community dynamics. *Ecology* 84, 1081–1082
24. Creel, S. and Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends Ecol. Evol.* 23, 194–201
25. Beckerman, A. *et al.* (2010) Adaptive foragers and community ecology: linking individuals to communities and ecosystems. *Funct. Ecol.* 24, 1–6
26. McNaughton, S.J. (1978) Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. *Science* 199, 806–807
27. Kotler, B.P. *et al.* (1992) Predator facilitation: the combined effects of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.* 29, 199–206
28. Heithaus, M.R. *et al.* (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* 23, 202–210
29. Peacor, S.D. *et al.* (2011) Scaling-up anti-predator phenotypic responses of prey: impacts over multiple generations in a complex aquatic community. *Proc. R. Soc. B* 279, 122–128

30. Vandermeer, J. *et al.* (2010) Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *Bioscience* 60, 527–537
31. Perfecto, I. *et al.* (2014) Complex ecological interactions in the coffee agroecosystem. *Annu. Rev. Ecol. Syst.* 45, 137–158
32. Vandermeer, J. *et al.* (2014) Qualitative dynamics of the coffee rust epidemic: educating the intuition with theoretical ecology. *BioScience* 64, 210–218
33. Dixon, D.L. *et al.* (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science* 345, 892–897
34. Estes, J.A. *et al.* (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282, 473–476
35. Dobson, A.P. (2014) Yellowstone wolves and the forces that structure natural systems. *PLoS Biol.* 12, e1002025
36. Ings, T.C. *et al.* (2009) Ecological networks-beyond food webs. *J. Anim. Ecol.* 78, 253–269
37. Olff, H. *et al.* (2009) Parallel ecological networks in ecosystems. *Phil. Trans. R. Soc. B* 364, 1755–1779
38. Fontaine, C. *et al.* (2011) The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14, 1170–1181
39. Golubski, A.J. and Abrams, P.A. (2011) Modifying modifiers: what happens when interspecific interactions interact? *J. Anim. Ecol.* 80, 1097–1108
40. Kéfi, S. *et al.* (2012) More than a meal.. integrating non-feeding interactions into food webs. *Ecol. Lett.* 15, 291–300
41. Kamran-Disfani, A.R. and Golubski, A.J. (2013) Lateral cascade of indirect effects in food webs with different types of adaptive behavior. *J. Theor. Biol.* 339, 58–69
42. Kondoh, M. (2007) Anti-predator defence and the complexity-stability relationship of food webs. *Proc. R. Soc. B* 274, 1617–1624
43. Kondoh, M. and Ninomiya, K. (2009) Food-chain length and adaptive foraging. *Proc. R. Soc. B* 276, 3113–3121
44. Uchida, S. and Drossel, B. (2007) Relation between complexity and stability in food webs with adaptive behavior. *J. Theor. Biol.* 247, 713–722
45. Arditi, R. *et al.* (2005) Rheagogies: modelling non-trophic effects in food webs. *Ecol. Complex.* 2, 249–258
46. Goudard, A. and Loreau, M. (2008) Nontrophic interactions, biodiversity, and ecosystem functioning: an interaction web model. *Am. Nat.* 171, 91–106
47. Lin, Y. and Sutherland, W.J. (2014) Interaction modification effects on ecological networks are affected by ratio dependence and network topology. *J. Theor. Biol.* 363, 151–157
48. Abrams, P.A. (1992) Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *Am. Nat.* 140, 573–600
49. Dambacher, J.M. and Ramos-Jiliberto, R. (2007) Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. *Q. Rev. Biol.* 82, 227–250
50. Berge, C. (1973) *Graphs and Hypergraphs*, North-Holland Publishing
51. Bretto, A. (2013) *Hypergraph Theory: An Introduction*, Springer International Publishing
52. Bonacich, P. *et al.* (2004) Hyper-edges and multidimensional centrality. *Soc. Networks* 26, 189–203
53. Estrada, E. and Rodríguez-Velázquez, J.A. (2006) Subgraph centrality and clustering in complex hyper-networks. *Physica A* 364, 581–594
54. Cattuto, C. *et al.* (2007) Network properties of folksonomies. *AI Commun.* 20, 245–262
55. Klamt, S. *et al.* (2009) Hypergraphs and cellular networks. *PLoS Comput. Biol.* 5, e1000385
56. Ritz, A. *et al.* (2014) Signaling hypergraphs. *Trends Biotechnol.* 32, 356–362
57. Sonntag, M. and Teichert, H.M. (2004) Competition hypergraphs. *Discrete Appl. Math.* 14, 324–329
58. McCann, K.S. (2012) *Food Webs*, Princeton University Press
59. Allesina, S. *et al.* (2015) Predicting the stability of large structured food webs. *Nat. Commun.* 6, 7842
60. Gallo, G. *et al.* (1993) Directed hypergraphs and applications. *Discrete Appl. Math.* 42, 177–201