# Scaling from Metawebs to Realised Webs: A Hierarchical Approach to Network Ecology

**Tanya Strydom [1*], Alexander M. Dunhill [2], Jennifer A. Dunne [3], Timothée Poisot [4,5], Andrew P. Beckerman [1]**

[1] School of Biosciences, University of Sheffield, Sheffield, UK
[2] School of Earth, Environment and Sustainability, University of Leeds, Leeds, UK
[3] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA
[4] Université de Montréal, Département de Sciences Biologiques, Montréal, QC, Canada
[5] Québec Centre for Biodiversity Sciences, Montréal, QC, Canada

[*]Correspondence: `t.strydom@sheffield.ac.uk`

**Abstract:** Ecological networks provide a critical framework for understanding the architecture of biodiversity and predicting ecosystem responses to environmental change. However, the application of network ecology is often hindered by a lack of clarity regarding the assumptions inherent in different network representations. Here, we present a hierarchical framework that distinguishes between 'metawebs' (representing the fundamental feasibility of interactions) and 'realised webs' (representing interactions expressed in specific spatiotemporal contexts). We contrast our conceptual approach with recent data-centric reviews, focusing instead on the theoretical gradients that govern network construction. We identify five core processes that drive the transition from potential to realised interactions: evolutionary compatibility and co-occurrence, which define the feasibility of links; and abundance, diet choice, and non-trophic interactions, which determine their realisation. Furthermore, we map these processes onto a methodological spectrum of network construction, distinguishing between inductive approaches (*e.g.,* trait-matching and stochastic models) that infer structure from observation, and deductive approaches (*e.g.,* neutral and optimal foraging models) that generate structure from mechanistic first principles. By making explicit the assumptions and scale-dependent processes underpinning these different representations, this framework clarifies the scope of inference possible with each approach, ultimately facilitating more robust predictions of biodiversity dynamics in the anthropocene.

**Keywords:** food web, network construction, biodiversity, scale and process, interaction modelling

# Table of contents

# 1 Introduction

At the heart of modern biodiversity science are a set of concepts and theories about species richness, stability, and function, which have been discussed since the foundational work of Elton (2001), Lindeman (1942), and MacArthur (1955) and more recently Loreau & de Mazancourt (2013). These relate to the abundance, distribution, functions, and services that biodiversity provides. Network representations of interactions among organisms are increasingly argued to be an asset to understanding and predicting the impacts of multiple, simultaneous stress on biodiversity (*e.g.,* foundational studies on food web structure and robustness: Cohen et al. (1990); Martinez & Dunne (1998); Dunne et al. (2002); Simmons et al. (2021)). Documenting interactions between and among taxa is thus one of the fundamental building blocks of community ecology and provides a powerful abstraction and platform for mathematical and statistical modelling of biodiversity to make predictions, and to mitigate and manage threats (Windsor et al., 2023).

However, there is a growing discourse around limitations to the interpretation and applied use of networks, which have been recognised since early discussions of sampling effort and aggregation in food webs (Cohen et al. (1990); Polis (1991); Martinez (1991); recent discussions: Dormann (2023); Blüthgen (2010)). Against this, it is important to evaluate the value and the limitations of the various network conceptualisations and how these relate to biodiversity concepts, such as community structure or ecosystem function (Blüthgen & Staab, 2024). In this perspective we aim to provide an overview of different **food web** representations, particularly how each representation embeds assumptions about the processes that determine interactions (Section 3) about the levels of organization at which this occurs (*i.e.* the biological, ecological, spatial/temporal scales) and the way in which we construct the resulting networks (Section 4).

Fundamentally, we are talking about an intersection of the type of data used to construct a network and the underlying theory as to what drives the resolution and occurrence of interactions among species in those data. We still lack a clear explanation of the different assumptions and scale dependent processes that underpin network construction alongside extensive discussions about the challenges relating to data collection and observation (Blüthgen & Staab, 2024; Brimacombe et al., 2023, 2024; Dunne, 2006; Martinez & Dunne, 1998; Moulatlet et al., 2024; Pimm, 1984; Polis, 1991; Pringle & Hutchinson, 2020; Saberski et al., 2024). Such an understanding should deliver an acceleration in capacity to more effectively predict the impact of multiple stressors on biodiverse communities.

In their recent work, Gauzens et al. (2025) showcased a 2+2 decomposition of networks around aggregated versus species level resolution of nodes and around potential and realised links among the nodes. Their review delivers valuable insight into the methodologies used to collect and manage data among the node and link differentiation. It also delivers an overview of the scale and types of questions that are associated with each category of differentiation.

Here we provide a complementary perspective focused on concepts, models, and theory, in contrast to the data driven breakdown in Gauzens et al. (2025) (*e.g.,* their Tables 1 and 2). Our approach delivers a hierarchical perspective on network construction based on a gradient from feasibility, capturing the concept of metawebs and Gauzen et al's 'potential' webs, through to realised webs as in Gauzens' et al. In contrast to their 2 + 2 decomposition (their Fig 1), our perspective showcases nested ecological scales and processes that derive from shifts in the assumptions and theories embedded along this gradient. This includes classic ecological 'aggregations' such as functional/phylogenetic groups through to species, populations and individuals, unique perspective on how space and time intersect with node and link resolution, refined insight into which networks are derived by induction vs. deduction and a revealing of a core transition between assumptions about how links are derived based on evolutionary vs. ecological theories.

In the following sections we provide a scene-setting review of nodes and edges (links) in networks before aligning various processes that determine interactions with the different network representations. Ultimately, we provide a unique perspective on the nested hierarchy of processes that govern transitions from meta-webs to realised webs. We finish with a refined and nuanced alignment of models/representations and key questions in biodiversity science in the anthropocene.

## 2 Setting the Scene: The Not So Basics of Nodes and Edges

Ecological networks serve multiple uses, representing an 'object' from which inferences can be made. While many aspects of community structure can be analysed without networks (*e.g.,* through trait distributions or abundance patterns) networks provide a formal framework for capturing the organisation of interactions among species. The study of network structure and topology has a long history in ecology, rooted in early theory on energy flow (Lindeman, 1942; Odum, 1968), and later extended to questions of robustness, stability, and complexity (Brose et al., 2006; Dunne et al., 2002; May, 1972; Montoya et al., 2006; *e.g.,* Pimm, 1984). More recent work has built on this foundation to link network structure to ecosystem functioning, persistence, and dynamical behaviour (Danet et al., 2024; Pilosof et al., 2017; *e.g.,* Schneider et al., 2016). Networks are therefore commonly treated as response variables in tests of ecological theory and statistical models of the generative processes that give rise to observed structure, and are widely used to compare communities across environmental gradients or through time (*e.g.,* Hao et al., 2025; Pecuchet et al., 2020). They also provide a platform for evaluating downstream responses to perturbations, including secondary extinctions and robustness to species loss (*e.g.,* Dunne et al., 2002; Keyes et al., 2021, 2024; Staniczenko et al., 2010), as well as for implementing dynamical process that inference about stability, ecosystem function, invasions, climate change, contaminants, and extinction cascades (Curtsdotter et al., 2019; *e.g.,* Delmas et al., 2017; Terry et al., 2025). Against this backdrop of multiple research agendas, the definition of 'edges' and 'nodes', and the levels of organisation at which they are defined, take many forms (Moulatlet et al., 2024; Poisot, Stouffer, et al., 2016), each of which encode a series of assumptions within a network. Here we introduce a perspective on these baseline assumptions.

## 2.1 How do we define a node?

While nodes are conventionally described as representing species, in practice they may correspond to a range of taxonomic and non-taxonomic units, including sub-species, genera, or families, as well as trophic species (*e.g.,* Yodzis (1982); Williams & Martinez (2000)), feeding guilds (*e.g.,* García-Callejas et al., 2023), or life-stage–specific subsets of species (*e.g.,* Clegg et al., 2018). These choices reflect differences in the level, type, and consistency of resolution at which networks are constructed, rather than aggregation per se. In many cases, aggregation is applied explicitly on top of more highly resolved—or unevenly resolved—data to address particular questions, as in the construction of trophic species, and the underlying data may remain available for alternative analyses. Nevertheless, representing nodes at coarser or mixed resolutions can limit taxon-specific inference (*e.g.,* whether species *a* consumes species *b*), bias estimates of degree distributions—particularly generality and vulnerability—and complicate downstream analyses such as extinction or invasion dynamics, where species identity and the consequences of loss may be obscured (Beckerman et al., 2006; Clegg et al., 2018). At the same time, there are clear justifications for using aggregated representations when the distribution of interactions among functional or trophic units is more informative than species-level detail, for example when analysing extinction patterns across feeding guilds (Dunhill et al., 2024). More broadly, issues of resolution, scale, and sampling have long been recognised as central to the construction and interpretation of food webs (Dunne, 2006; *e.g.,* Martinez & Dunne, 1998).

## 2.2 What is captured by an edge?

In order to break down the definitions of an edge, it is important to introduce the concept of *potential* versus *realised* links: potential links reflect feasibility while realised links are connected to flux of some currency (typically energy; see below for more detail). Links within food webs are thus a representation of either potential links between species Pringle (2020) or fluxes within a system *e.g.,* energy transfer or material flow as the result of the feeding links between species (Lindeman, 1942; Proulx et al., 2005). Edges can thus correspond to different ‘currencies’ (Gauzens et al., 2025). There are also a myriad of ways in which the links themselves can be specified. Links between species can be treated as present or absent (*i.e.,* binary), may be defined as probabilities (Banville et al., 2025; Poisot, Cirtwill, et al., 2016) or by continuous functions which further quantify the strength of an interaction (Berlow et al., 2004). How links are specified thus requires intersecting both the currency being modelled and their specification. For example, feasibility is unlikely to accommodate flux, but does align with binary or probability representations. Taking a food web that consists of links representing feasible interactions among a collection of species will be meaningless if one is interested in understanding the flow of energy through the network as the links are not environmentally/energetically constrained.

## 2.3 Network representations

Against these definitions of nodes and edges, networks fall into two major 'types': metawebs, traditionally defined as all the *potential* interactions for a specific species pool (Dunne, 2006); and realised networks, which is the subset of interactions in a metaweb that are *realised* for a specific community at a given time and place. The fundamental differences between these two network representations are the spatial and temporal scale at which they are constructed, and the associated processes that are assumed to drive patterns at these scales.

A metaweb is, at its core, a list of *feasible* interactions between pairs of species. The feasibility for a given pair is derived from the complementarity of their traits, typically aligned with feeding. Feasibility can be further refined by *co-occurrence* leading to the transition from a *global* to *regional metaweb*. Metawebs thus provide a means to identify evolutionary plausible links, regionally plausible interactions, the set of ecologically impossible, *i.e.,* forbidden, links (Jordano, 2016b), and ultimately a definition of the plausible *complete* diet of a species (Strydom et al., 2023).

In contrast, realised networks are typically localised in space and time, with links contingent on species co-occurrence, environmental conditions, and mechanisms of diet choice. As a result, the presence or absence of a link reflects species behaviour, such that even when a realised network is represented as a binary matrix, each edge implies an underlying function describing interaction strength. A realised network is therefore not a simple downscaling of a metaweb based on finer spatial or temporal resolution. Rather than being obtained by filtering feasible interactions through co-occurrence alone, realised webs capture the processes that govern whether interactions are expressed and how energy flows through a community. In this sense, the definition of an edge shifts from one of feasibility to one of realised choice and consequence, centred on energy acquisition and transfer. Consequently, a metaweb and a realised network constructed from the same set of species may share node composition yet differ structurally, because they are constrained by fundamentally different rules governing link presence. This distinction has important implications for interpretation: links absent from a metaweb can be treated as truly absent in terms of feasibility, whereas links absent from a realised network should instead be interpreted as context-dependent absences arising from environmental, behavioural, or community-level constraints.

# 3 From Nodes and Edges to Process and Constraints

In the previous section we discussed how the definition of nodes and edges, representing different scales and processes, lead to the concept of a metaweb and a realised web. The fundamental take-homes are that nodes vary in their resolution, edges vary in what kind of process they represent and the intersection of these, defined by meta- vs. realised webs, underpins distinct lines of inquiry and constraints on the type of inference we can make with networks. Here we reveal five core constraints across evolutionary and ecological scales that further delineate the transition from meta- to realised webs, exposing processes that determine the nature of links among nodes: evolutionary compatibility, co-occurrence, abundance, diet choice, and non-trophic interactions Figure 1.

[Figure 1 about here.]

## 3.1 Processes that determine the feasibility of an interaction

Evolutionary compatibility and co-occurrence are the two principal processes that ‘act’ at the species pair of interest and define feasibility. The scale of inference and set of processes embodied in these two constraints typically combine to define a ‘list’ of interactions that are viable/feasible and defined strictly as present/absent. Reflecting on the previous section, nodes are typically species and rules defining edges are defined by trait complementarity (phylogenetic) and/or co-occurrence. Here we provide more insight into each process.

**Evolutionary compatibility**

This constraint is defined by shared (co)evolutionary history between consumers and resources (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Rossberg et al., 2006; Segar et al., 2020) which is manifested as ‘trait complementarity’ between two species (Benadi et al., 2022). In this body of theory, the consumer has the 'correct' set of traits that allow it to acquire and consume the resource. Interactions that are not compatible are defined as forbidden links (Jordano, 2016b); *i.e.,* they are not physically possible and will *always* be absent within a network.

Networks do not properly arise from models based on this constraint. Instead, interacting species pairs are defined and these are represented as binary (possible vs forbidden) or probabilistic (Banville et al., 2025). For example, in the metaweb constructed by Strydom et al. (2022) probabilities are quantified as the confidence of a specific interaction being *possible* between two species. A network constructed on the basis of evolutionary compatibility is conceptually aligned with a 'global metaweb', and gives us information as to the global feasibility of links between species pairs despite the fact that they do not co-occur (see Figure 1).

**(Co)occurrence**

The co-occurrence of species in both time and space is a fundamental requirement for an interaction between two species to occur (at least in terms of feeding links). Although co-occurrence data alone is insufficient for building an accurate and ecologically meaningful representation of *feeding links* (Blanchet et al., 2020), it is still a critical process that determines the possible realisation of a feeding. Knowledge on the co-occurrence of species allows us to spatially constrain a global metaweb to reflect regional metawebs (Dansereau, Barros, et al., 2024). In the context of Figure 1 this would be the metawebs for regions one and two.

We reinforce that these two constraints don't deliver a network *per se,* but a list of feasible species pairs. Although it is possible to build a network from the list of interactions generated by these constraints, it is important to be aware that the structure of this network is not constrained by any community context: just because species are able to interact does not mean that they will (Caron et al., 2024; Poisot et al., 2015).

## 3.2 Processes that realise networks

In contrast to the above, here we highlight three processes that influence the *realisation* of an interaction between species and thus form the conceptual basis for realised networks. As we show in Figure 1, a 'truly realised' network is the product of properties of the community (**abundance** and **non-trophic interactions**) and the individual (**diet choice**). This represents a conceptual shift from considering the feasibility for species pairwise interactions to considering the edge as a representation of energy flow. Such a transition requires information about how the community, the environment and the individual *constrains* network topology as defined by consumer choice (Quintero et al. (2024), Section 2.3)

### Abundance

Abundance as a realising process emerges from a null model for energy acquisition: organisms feeding randomly will consume resources in proportion to their abundance (Stephens & Krebs, 1986). Here, abundance of different prey species influences the distribution of links in a network (Vázquez et al., 2009) by defining a preference linked to individuals among species meeting (Banville et al., 2025; Poisot et al., 2015). Abundance data (linked to a derived metaweb) delivers a foundation ruleset that can define the distribution and strength of links. Of note, however, is that such abundance constrained interactions are not necessarily contingent on there being any compatibility between species (E. Canard et al., 2012; Momal et al., 2020; Pomeranz et al., 2019).

### Diet choice

It is well established that consumers make more active decisions than eating items in proportion to their abundance (Stephens & Krebs, 1986). Ultimately, consumer choice is underpinned by an energetic cost-benefit framework centered around profitability and defined by traits associated with acquisition and consumption of a resource (Smith et al., 2021; Wootton et al., 2023). Energetic constraints are invoked to construct networks in a myriad of ways (*e.g.,* Beckerman et al., 2006; Cherif et al., 2024; Pawar et al., 2012; Portalier et al., 2019).

In contrast to metaweb 'construction' from a list of pairwise interactions, these methods deliver a realised web directly and as an emergent property of node behaviour. We also here make a distinction, developed below, with models like the Niche Model (Williams & Martinez, 2000), where diet choice is implicit in its probabilistic network generating function, but it is working to replicate the *expected* structure of the network, and this structure does not emerge from node-based rules. Note that we select diet choice as a term to capture rules linked to optimal foraging (Pyke, 1984) and metabolic theory (Brown et al., 2004); it is a sensible 'umbrella concept' for capturing the energetic constraint on of the distribution and strength of interactions.

### Non-trophic interactions

We include non-trophic interactions (see Miele et al., 2019) here not as a determinant of links, but a modifier of them - they are the community context above and beyond co-occurrence and abundance. Non-trophic interactions include competition for space, predator interference, refuge provisioning, recruitment facilitation as well as non-trophic effects that increase or decrease mortality. These interactions specifically modify either the realisation or strength of trophic interactions (Golubski & Abrams, 2011; Ings et al., 2009; Kamaru et al., 2024; Pilosof et al., 2017; Staniczenko et al., 2010) and represent direct (e.g., predator $a$ outcompetes predator $b$) and indirect (e.g., mutualistic/facilitative interactions) mechanisms.

Some interactions, such as pollination, occupy an intermediate position in this framework, as they combine trophic components (e.g. resource consumption) with non-trophic effects that influence reproduction, recruitment, and population persistence (Bascompte & Jordano, 2007; Holland et al., 2002; Sauve et al., 2016). They operate on the realisation of a network by altering the fine-scale distribution and abundance of species and relative contributions of direct and indirect effects to biomass, persistence, stability and the functioning of the communities (Buche et al., 2024; Kéfi et al., 2012, 2015; Miele et al., 2019).

# 4 Network construction

The above five processes are central to understanding the assumptions inherent in building different types of networks. Each of the processes, or combinations thereof, deliver a unique set of boundary conditions on what a network represents and can be used for. Here we build on the introduction of these five processes to further categorise the approaches to constructing networks. In doing so also introduce more detail on a variety of methodologies used to construct networks.

## 4.1 Why construct networks?

Networks are a representation of biodiversity. In a perfect world, we might know about all interactions. However, the empirical collection of interaction data is both costly and challenging to execute (Jordano, 2016a, 2016b; Poisot et al., 2021). In the absence of robust empirical data, we construct models that facilitate interpolation and gap-filling of existing empirical datasets (*e.g.,* Biton et al., 2024; Dallas et al., 2017; Poisot et al., 2023; Stock et al., 2017), predict the feasibility of interaction among pairs of species, or directly predict network structure (see Strydom et al., 2021 for a broader discussion).

They are unique in delivering more than just estimates of species richness. As noted in the introduction, a network embodies the organising structure of biodiversity and allows numerous opportunities for ‘downstream’ analysis, including the comparison of structures, estimation of energy flux or extinction dynamics and ultimately form the structural inputs to dynamical systems models that facilitate ecological and conservation relevant inference about productivity-diversity-stability-function relationships (Danet et al., 2024) in space and time. But making such inferences requires careful attention to one or more of the processes discussed in Section 3.

## 4.2 Construction through induction

Constructing feasible or realised networks can be framed as an ‘inductive reasoning’ process where insight and generalisation arises from a set of observations and relationships. Inductive reasoning as a foundation for network construction is implemented at node and network levels. When applied at the node level, species-specific networks are created and judged by their association with expected feeding interactions. When applied at the network level, networks are judged by their structural properties.

### 4.2.1 Species specific networks: construction through node level induction

Constructing feasible networks and facilitating the interpolation or gap-filling of existing empirical datasets on sets of species interactions can be framed as an ‘inductive reasoning’ process where insight and generalisation arises from a set of observations and relationships about feeding. All methods in this inference space rest on a set of three assumptions: there are a set of ‘feeding rules’ that underpin interaction feasibility (Morales-Castilla et al., 2015); these rules are phylogenetically conserved (Bramon Mora et al., 2018; Dalla Riva & Stouffer, 2016); and they can be specified by matching the traits between consumer and resource.

Evolutionary compatibility and co-occurrence constraints have been critical to the construction of ‘first draft’ networks for communities for which we have no interaction data (Strydom et al., 2022). They are also central to interpolation in data poor regions and predicting interactions for ‘unobservable’ communities *e.g.,* prehistoric networks (Dunhill et al., 2024; Fricke et al., 2022; Yeakel et al., 2014) or future, novel community assemblages (Van der Putten et al., 2010). Furthermore, they have the capacity to evaluate a role of interactions among species relative to their distribution by accounting for the role of the environment and the role of species interactions (Albouy et al., 2014; Gravel et al., 2019; Higino et al., 2023; Pollock et al., 2014). There are substantial data requirements for these approaches including expert knowledge, species traits and phylogenetic relationships and/or interaction data on related species or communities.

Feeding rules are defined in multiple ways. The determination of the feeding rules can be defined *a priori* based on expert knowledge opinions. Typically this is done on a 'trait matching' basis. An example are the paleo food web models of Shaw et al. (2024) and Roopnarine (2017) that specify a series of rules for a set of traits and interactions deemed feasible if all conditions are met. Alternatively the body size ratio between the consumer and resource is often used (*e.g.,* Gravel et al., 2013; Rohr et al., 2010), with the idea that consumers will only utilise a resource with a body size is less than or equal to their own (Brose et al., 2019; Yodzis & Innes, 1992), although it is broadly acknowledged that many herbivores (such as insects) violate these assumptions (Valdovinos et al., 2023). However, work from Van De Walle et al. (2023) seems to suggest that adding morphological traits in addition to body size ratio improves model performance.

Rules are also defined by correlating real world interaction data with suitable ecological proxies for which data is more widely available (*e.g.,* traits) using some sort of binary classifier (see Pichler et al. (2020) for an overview). These include generalised linear models (*e.g.,* Caron et al., 2022), random forest (*e.g.,* Llewelyn et al., 2023), trait-based k-NN (*e.g.,* Desjardins-Proulx et al., 2017), and Bayesian models (Cirtwill et al., 2019; *e.g.,* Eklöf et al., 2013).

Finally, graph embedding uses the structural features of a known network to infer the position of species in an unknown network through the decomposition of the interaction onto the embedding space. This decomposition relies on a combination of ecological proxies (*e.g.,* traits) in conjunction with known interactions to infer the latent values of species, which can then be mapped onto decomposition of a known network. See Strydom et al. (2023) for a detailed review of methods and Strydom et al. (2022) for a specific example.

### 4.2.2 Species agnostic networks: construction through structure induction

Networks in this category are generated using rules that create non-random networks that reflect some minimal empirical knowledge of ecological networks. These can be used in a variety of ways, for example comparing the structure of realised networks to quantify relative deviations from the model structure. They are also used as a way to generate 'realistic' food web structures that are used for dynamical or other analyses. The determination of links between species is only implicitly linked to properties of the nodes. This means these networks are usually not species specific. Although these models are data input light, often requiring only species richness and an estimate of the number of expected links, they make clear assumptions regarding what the expectations are for network structure. These are some of the most commonly used network generation tools (*e.g.,* the Niche model; Williams & Martinez (2000)). There are two sub-categories of these species agnostic networks.

Stochastic network models use a probabilistic rule-set about diet choice and niche breadth to reflect fundamental ideas of foraging biology. These models that are based on the compartmentalisation and acquisition of energy for species at different trophic levels (Allesina & Pascual, 2009; Krause et al., 2003) and that network structure can be determined by distributing interactions along single dimension [the 'niche axis'; Allesina et al. (2008)]. Typically these models parametrise some aspect of the network structure (although see Allesina & Pascual, 2009 for a parameter-free model). These models include the most commonly used network generator, the Niche model (Williams & Martinez, 2000), as well as the original Cascade model (Cohen et al., 1990) and the derived Nested hierarchy model (Cattin et al., 2004). These models often form the basis for dynamic models *e.g.,* the allometric trophic network (Brose et al., 2006; Schneider et al., 2016) and bioenergetic food web models (Delmas et al., 2017).

## 4.3 Construction through deduction

In contrast to the above approaches centred on feasibility, realised networks via methods reflecting abundance and diet choice typically rely on deductive reasoning and have a unique agenda to those above. In contrast to the inductive methods, inference about a realised network follows from a set of premises defining generative processes, often referred to as mechanisms. Typically, models that embed abundance and diet choice constraints reference theory that allows inference about the distribution and strength of interactions. Such models are 'network topology generators' and have a strong representation in research comparing network structures along environmental gradients and delivering inference about extinctions and energy flux. They also provide the structural backbone for dynamical systems modelling to address questions about stability-structure-productivity-function relationships, secondary extinction dynamics, species invasion and climate change. There are two broad groups of models in this deductive category.

### 4.3.1 Species-specific networks

These models capture the behaviour of the nodes by explicitly taking into account the properties of the different species in the community. Which means that there is a degree of variance in which links are predicted between species unlike the more 'static' predictions made by inductive models. However, these networks are 'costly' to construct in real world settings (requiring data about the entire community, as it is the behaviour of the system that determines the behaviour of the part) and also lack the larger diet niche context afforded by metawebs.

Neutral networks are built on the assumption that foraging decisions are tied *only* to the abundance of species within the community (E. F. Canard et al., 2014; Krishna et al., 2008). Here links are solely determined by the relative abundance of the different species in the community. Although it is highly unlikely that abundance is the only determinant of interactions work by Pomeranz et al. (2019) showcases how these neutral processes can be used in conjunction with inductive models to construct more refined/localised networks.

There is a broader group of models that focus on determining interactions in terms of energetic constraints on diet breadth, often using the ratio of consumer-resource bodysize as a proxy for capturing the energetic constraints of feeding. Models such as those developed by Portalier et al. (2019) and Wootton et al. (2023) are similar to the mechanistic approaches discussed in Section 4.2, however instead of determining interactions based on mechanistic feasibility it is rather constrained by the energetic cost of predation. Note that although these models do not place any explicit constraints on the expected structure of the network, the links should still be considered as 'realised' owing to the energetic constraint placed on links. A different subset of diet models (*e.g.,* Beckerman et al., 2006; Petchey et al., 2008) use a diet choice approach, however similar to the stochastic network models they also embed assumptions on network structure. Thus these models predict both interactions and network structure simultaneously, although they would benefit in being refined by more explicitly accounting for trait-based (*i.e.,* feasibility) parameterisation (Curtsdotter et al., 2019).

# 5 Making Progress with Networks

The motivation to leverage network ecology in conservation ecology, environmental risk assessment and natural resource management stems from a shift away from species/population specific measures of the effects of stress and disturbance to community level metrics of these impacts. These metrics, such as resilience and more generally stability, ecosystem function and biodiversity *per se*, are natural properties of networks. This suggests that modern conservation, risk assessment and resource management requires robust network tools to support decision making.

This is also true in the disciplines of ecology and environmental science and their focus on abundance, distribution, functions and services that biodiversity provides (Loreau & de Mazancourt, 2013). Major questions remain, for example, about stability-diversity-productivity relationships, the impacts of extinctions and invasions and the impacts of multiple stressors operating at multiple ecological scales. A network approach to answering these types of questions specifically allows us to evaluate how environmental gradients and anthropogenic stress map through direct and indirect effects among species in a complex community and reveal fundamental patterns and understanding of processes in the natural world.

In order to effectively use networks to aid us in answering questions about conservation/risk assessment/management and core ecological theory, we need to be mindful that we are mapping the *correct* network representation to the question of interest (Gauzens et al., 2025). Notably, there are certain questions that cannot be answered using specific network representations as the scale of the question of interest is fundamentally misaligned with either the process captured by a specific network representation Section 3.1, the underlying data that is used to construct it Section 4 or both of these factors.

Here we discuss and map the different network representations shown in Figure 1 to ‘appropriate’ research questions and agendas see also 1. We also highlight some of the key methodological challenges that currently limit our conceptualisation of a ‘network’ and thus impact their effective practical application in real world settings.

Table 1: Showcasing some of the broader avenues of inquiry, specifically how they map to the different network representations. Additionally we highlight some studies that address or present opening discussions around each research question. Superscripts at the research question indicate the strength of the current literature in addressing that research question: $^{\checkmark}$ indicates area with strong foundational research, $^{\triangle}$ partial/emerging areas of research, and $^{\times}$ areas where research is weak/largely absent

| Network Representation | Example Research Question | Representative Studies |
|---|---|---|
| Global Metaweb | How will novel communities respond to *e.g.,* extinction, turnover, invasion and rewilding $^{\checkmark}$ | Gravel, Albouy, et al. (2016); Dunne et al. (2002) |
| | Diet-based conservation focusing not only on the target species but the species it might depend on for food resources $^{\triangle}$ | Rooney & McCann (2012); Curtsdotter et al. (2011) |
| | Rewiring capacity/potential of species by looking at the *entire* diets of species $^{\triangle}$ | Gilljam et al. (2015); Staniczenko et al. (2010); Su et al. (2024); Marjakangas et al. (2025) |
| | Eco-Evolutionary dynamics and how they relate to the conservation and origination of feeding strategies $^{\times}$ | Poisot et al. (2015); Baskerville et al. (2011) |
| Regional Metawebs | Applied use potential of questions highlighted for global metawebs at the management scale *e.g.,* a protected area $^{\triangle}$ | Albouy et al. (2014); Pellissier et al. (2018) |
| | Refinement/extension of species distribution models by incorporating co-occurrence and species associations *e.g.,* predator and prey $^{\checkmark}$ | Araújo & Luoto (2007); Kissling et al. (2012) |

| Network Representation | Example Research Question | Representative Studies |
|---|---|---|
| Realised webs | The allocation of multiple stressors across networks $^{\Delta}$ | Crain et al. (2008); Beauchesne et al. (2021) |
| | Temperature threshold to community collapse $^{\Delta}$ | O'Gorman et al. (2019); Petchey et al. (2010) |
| | Extinction and persistence after harvesting/invasion/extinction $^{\checkmark}$ | Allesina & Tang (2012); Yodzis (2001) |
| | Stability-diversity-productivity-function $^{\checkmark}$ | Thébault & Fontaine (2010); Rooney & McCann (2012) |
| | Explicilty tying ecosystem level processes and nutrient flows to networks $^{\times}$ | Moore et al. (2004) |
| | Meta communities and the idea of meta-network-communities $^{\Delta}$ | Gravel, Massol, et al. (2016); Gilarranz et al. (2017) |

## 5.1 Key Eco-Evo-Conservation Questions

### 5.1.1 Global Metawebs

The interactions in global metawebs are not constrained by the realisation of specific community assemblages (or species co-occurrence). These networks provide a platform for answering questions that assume interactions *could* occur between species (feasibility) or where the potential diet breadth of species is required. Examples of appropriate research questions at this scale includes those about *hypothetical* or *novel* communities and interactions under future climate change scenarios, or the potential 'position' of an invasive (or re-introduced) species within a network (Hui & Richardson, 2019). This scale is also appropriate for a particular class of questions related to the potential (eco-evolutionary) rewiring capacity of species, and how this may help inform on the opportunities for persistence of species within new community assemblages (Marjakangas et al., 2025). The implicit focus on feasibility in these examples highlights that global metawebs are linked to strong proxies for targets and mechanisms of evolutionary change. This offers a network scale for modelling ecological-evolutionary dynamics and the role that both evolutionary history, natural selection, and phenotypic plasticity shapes the diet breadth of species.

### 5.1.2 Regional Metawebs

Regional metawebs are conceptually a spatially constrained global metaweb. They make explicit the co-occurence between species. Against this backdrop, they are conceptually aligned with similar questions to those posed above, with the added focus on a community facing, real-world, challenge. Additionally, regional metawebs can and have been used to refine and constrain species distribution model predictions, giving us more refined range maps (García-Callejas et al., 2023) or community composition under climate change scenarios, even at global scales (Hao et al., 2025).

However we must exercise a high degree of caution when comparing structures among regional metwebs, whether discrete collections or along environmental gradients. At this scale, where the network embeds the assumptions of feasibility, the link distribution is not meaningfully constrained by environmental factors (see Section 2.2) and it is vital to disentangle structural change *per se* from the multiple processes that might determine species turnover (*e.g.,* $\beta$ - diversity).

### 5.1.3 Realised networks

Realised network are the most representative of what comes to mind when people think of networks, and more specifically how we can use them to help inform on larger biogeographic processes (Thuiller et al., 2024). This is partially because of the popularity and legacy of generative network models (like the Cascade and Niche model) which produce realised network representations, and represent the ideal ‘currency’ for which to understand the constraints placed on interactions/network structure by the broader community and environmental context. This change in currency and context affords us the opportunity to ask questions that revolve around major ecological theory - *e.g.,* community stability and resilience, biodiversity dynamics, ecosystem function, structure-function relationships - and around major conservation and climate change global challenges - *e.g.,* temperature change, extinction dynamics, invasion impacts and reintroductions/rewilding.

Realised networks embody an explicit focus on the link between network structure to ecosystem function. Because the structure of realised webs are isolated from turnover processes they allow us to think about the propagation of change (across both time and space) which allows us to ask questions about the persistence of communities and how they respond to perturbations or stressors (at both the level of the node as well as the modification of links). For example in Section 5.1.1 we discuss how global metawebs can inform as to the rewiring *capacity* of a species, a realised network however would be better suited to capture the rewiring of networks over time as a response to changes in the environment or community.

Although the recent boom in the availability of long-term observation data is allowing us to unpack decades of insights for stability-diversity-productivity relationships for more complex communities (Danet et al., 2024) or to evaluate the impacts and efficacy of re-introductions (Wooster et al., 2024), we need to be mindful that empirical interaction data is typically accumulated over time and so it compresses the transient nature of the interactions between species (Polis, 1991). Thus we need to apply a degree of caution when using empirical data to construct realised networks - although there is scope to think about developing methods that will allow us to modify metawebs in such a way that their structures become more aligned with realised webs (see the next section).

## 5.2 Key methodological challenges

As noted above, the three types of networks help highlight longstanding methodological challenges that affect our ability to increase both precision and accuracy of inference derived from the questions we highlight above. Here we review some of these challenges and opportunities that are arising to mitigate them.

**Understanding what empirical data represents:** Ultimately, knowing what is right/precise/correct in an ecological network requires robust data. What does it mean when we ‘observe’ an interaction be that directly (predator actively feeding on prey) or indirectly via *e.g.,* gut or isotope analysis. A network constructed with empirical data will most likely still represent an ‘accumulation’ of feeding data making it conceptually more closely aligned with the idea of a metaweb.

**The validation of network structure:** Progress has been made in the development of tools and approaches of assessing how well a model recovers pairwise interactions (Poisot, 2023; Strydom et al., 2021), but we still lack a clear set of guidelines for benchmarking the ability of models to recover structure (Allesina et al., 2008; Tylianakis et al., 2010). This makes it challenging to assess if models are capturing network structure accurately, especially if one wants to use empirical data as the 'testing set'. Specifically, can we use a network constructed using long-term interaction observation data (*i.e.,* conceptually a metaweb) to assess the accuracy of a modelled (*I don't know how I feel about this word*), realised network? Additionally one needs to think about *what* aspect of accurate/precise network construction is the most important - is it the structure or ability to correctly predict pairwise links? In the case of attempting to construct a metaweb it is important that one is accurately recovering both links that are truly present and absent, however in the case of realised webs it is perhaps not that clear. Is it sufficient to correctly recover structure *e.g.,* connectance or do the pairwise links also need to be correct?

**Transitioning between metawebs and realised webs:** Currently most approaches to modelling realised networks fail to explicitly account for any form of evolutionary constraint (although see Van De Walle et al. (2023) and Wootton et al. (2023)) and we need to develop either an ensemble modelling approach (Becker et al., 2022; Terry & Lewis, 2020) or tools that will allow for the downsampling of metawebs into realised networks, (*e.g.,* Roopnarine, 2006).

Importantly we need to think critically how the creation of either an 'ensemble network' or downsampled metaweb might change the underlying 'currency' of a network and thus the underlying definition of the edge *e.g.* the downsampling approach developed by Roopnarine (2006) structurally constrains the network to structurally look like a realised web, but the links do not represent prey choice *per se.*

Having a well developed framework as well as 'fluidity' to allow us to scale up between meta- and realised food webs lays the groundwork for us to actively begin the integration of food webs into the classical metacommunity-metaecosystem space (Massol et al., 2011) as well as ecosystem level processes (Liu et al., 2025). That being said developments in the community-ecosystem space should be intentional about articulating a firm distinction as to what defines a 'network' as a unit, as well as defining the logical (spatial and temporal) boundaries between networks (Fortin et al., 2021).

**Making networks more tractable in applied spaces:** There is a disconnect when it comes to effectively using networks in applied spaces. This is probably at least in part related to the challenges with delineating 'boundaries' between networks, and how these relate to 'management units' and scales in addition to a limited interpretability of network metrics, specifically how this can be applied to conservation targets/indices (Dansereau, Braga, et al., 2024). In order to address these shortcomings we need to make an effort to more efficiently map the form (structure) of a network to its function in order to identify how this can effectively be integrated into policy to make it meaningful and actionable (O'Connor et al., 2025), all while remaining mindful to ensure that we identify the appropriate analytical tools and network representation (Pellissier et al., 2018).

Taken together, these challenges highlight three overarching messages. (i) Network representations are inseparable from the data and assumptions used to construct them; (ii) validation and benchmarking must be explicitly aligned with the intended network type and question; (iii) greater conceptual clarity is needed when transitioning between metawebs and realised networks, particularly in applied contexts. Explicitly articulating these distinctions is essential if networks are to be used both rigorously and transparently across scales.

# 6 Conclusion

Having a clear understanding of the interplay between network representations and the processes that they are capable of encoding is critical if we are to understand exactly which networks can be used to answer which questions. A central message of this synthesis is that network representations are not interchangeable, and that their utility depends explicitly on the assumptions, data, and processes they are intended to capture. As we highlight in Section 5 the different network representations have different potential uses and it should be clear that there is no 'best' network representation but rather a network representation that is best suited to its intended purpose. By formalising the assumptions and mechanisms underlying different network constructions, we provide a framework for evaluating when and how particular representations are appropriate. This framework aims to prevent the unintentional misuse or misinterpretation of networks. It also offers a starting point for developing improved approaches to the applied use of networks in addressing questions that are pressing both within the field and across broader biodiversity science.

*Acknowledgements*: TS, APB, and AMD received funding from NERC/NSF grant number NE/X015025/1.

# References

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., & Gravel, D. (2014). From projected species distribution to food-web structure under climate change. *Global Change Biology*, *20*(3), 730–741. https://doi.org/10.1111/gcb.12467

Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, *320*(5876), 658–661. https://doi.org/10.1126/science.1156269

Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, *12*(7), 652–662. https://doi.org/10.1111/j.1461-0248.2009.01321.x

Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, *483*(7388, 7388), 205–208. https://doi.org/10.1038/nature10832

Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, *16*(6), 743–753. https://doi.org/10.1111/j.1466-8238.2007.00359.x

Banville, F., Strydom, T., Blyth, P. S. A., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2025). Deciphering Probabilistic Species Interaction Networks. *Ecology Letters*, *28*(6), e70161. https://doi.org/10.1111/ele.70161

Bascompte, J., & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Baskerville, E. B., Dobson, A. P., Bedford, T., Allesina, S., Anderson, T. M., & Pascual, M. (2011). Spatial Guilds in the Serengeti Food Web Revealed by a Bayesian Group Model. *PLOS Computational Biology*, *7*(12), e1002321. https://doi.org/10.1371/journal.pcbi.1002321

Beauchesne, D., Cazelles, K., Archambault, P., Dee, L. E., & Gravel, D. (2021). On the sensitivity of food webs to multiple stressors. *Ecology Letters*, *24*(10), 2219–2237. https://doi.org/10.1111/ele.13841

Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T. A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling, E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic reservoirs. *The Lancet Microbe*, *3*(8), e625–e637. https://doi.org/10.1016/S2666-5247(21)00245-7

Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, *103*(37), 13745–13749. https://doi.org/10.1073/pnas.0603039103

Benadi, G., Dormann, C. F., Fründ, J., Stephan, R., & Vázquez, D. P. (2022). Quantitative Prediction of Interactions in Bipartite Networks Based on Traits, Abundances, and Phylogeny. *The American Naturalist*, *199*(6), 841–854. https://doi.org/10.1086/714420

Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, *73*(3), 585–598. https://doi.org/10.1111/j.0021-8790.2004.00833.x

Biton, B., Puzis, R., & Pilosof, S. (2024, August 2). *Inductive link prediction boosts data availability and enables cross-community link prediction in ecological networks.* https://ecoevorxiv.org/repository/view/7492/

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, *23*(7), 1050–1063. https://doi.org/10.1111/ele.13525

Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology*, *11*(3), 185–195. https://doi.org/10.1016/j.baae.2010.01.001

Blüthgen, N., & Staab, M. (2024). A Critical Evaluation of Network Approaches for Studying Species Interactions. *Annual Review of Ecology, Evolution, and Systematics*, *55*(1), 65–88. https://doi.org/10.1146/annurev-ecolsys-102722-021904

Bramon Mora, B., Gravel, D., Gilarranz, L. J., Poisot, T., & Stouffer, D. B. (2018). Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nature Communications*, *9*(1), 2603. https://doi.org/10.1038/s41467-018-05056-0

Brimacombe, C., Bodner, K., Gravel, D., Leroux, S. J., Poisot, T., & Fortin, M.-J. (2024). Publication-driven consistency in food web structures: Implications for comparative ecology. *Ecology*, *n/a*(n/a), e4467. https://doi.org/10.1002/ecy.4467

Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, *21*(4), e3002068. https://doi.org/10.1371/journal.pbio.3002068

Brose, U., Archambault, P., Barnes, A. D., Bersier, L.-F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., … Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, *3*(6), 919–927. https://doi.org/10.1038/s41559-019-0899-x

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, *9*(11), 1228–1236. https://doi.org/10.1111/j.1461-0248.2006.00978.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Buche, L., Bartomeus, I., & Godoy, O. (2024). Multitrophic Higher-Order Interactions Modulate Species Persistence. *The American Naturalist*, *203*(4), 458–472. https://doi.org/10.1086/729222

Canard, E. F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D., & Gravel, D. (2014). Empirical Evaluation of Neutral Interactions in Host-Parasite Networks. *The American Naturalist*, *183*(4), 468–479. https://doi.org/10.1086/675363

Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, *7*(8), e38295. https://doi.org/10.1371/journal.pone.0038295

Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*, *33*(4), e13807. https://doi.org/10.1111/geb.13807

Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with trait-based interaction models. *Ecology Letters*, *25*(4), 889–899. https://doi.org/10.1111/ele.13966

Cattin, M.-F., Bersier, L.-F., Banašek-Richter, C., Baltensperger, R., & Gabriel, J.-P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, *427*(6977, 6977), 835–839. https://doi.org/10.1038/nature02327

Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A., Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*, *138*(1). https://doi.org/10.1111/brv.13105

Cirtwill, A. R., Eklöf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for investigating the reliability of empirical network construction. *Methods* *in Ecology and Evolution*, *10*(6), 902–911. https://doi.org/10.1111/2041-210X.13180

Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure. *Ecology*, *99*(12), 2712–2720. https://doi.org/10.1002/ecy.2523

Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag. https://www.springer.com/gp/book/9783642837869

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., & Bommarco, R. (2019). Ecosystem function in predator–prey food webs—confronting dynamic models with empirical data. *Journal of Animal Ecology*, *88*(2), 196–210. https://doi.org/10.1111/1365-2656.12892

Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall, B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs. *Basic and Applied Ecology*, *12*(7), 571–580. https://doi.org/10.1016/j.baae.2011.09.008

Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones using functional traits. *Oikos*, *125*(4), 446–456. https://doi.org/10.1111/oik.02305

Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. *PLOS Computational Biology*, *13*(5), e1005557. https://doi.org/10.1371/journal.pcbi.1005557

Danet, A., Kéfi, S., Johnson, T. F., & Beckerman, A. P. (2024, August 30). *Response diversity is a major driver of temporal stability in complex food webs*. https://doi.org/10.1101/2024.08.29.610288 (Pre-published)

Dansereau, G., Barros, C., & Poisot, T. (2024). Spatially explicit predictions of food web structure from regional-level data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1909). https://doi.org/10.1098/rstb.2023.0166

Dansereau, G., Braga, J., Ficetola, G. F., Galiana, N., Gravel, D., Maiorano, L., Montoya, J. M., O'Connor, L., Pollock, L. J., Thuiller, W., Poisot, T., & Barros, C. (2024). *Overcoming the disconnect between interaction networks and biodiversity conservation and management*. https://ecoevorxiv.org/repository/view/8134/

Delmas, E., Brose, U., Gravel, D., Stouffer, D. B., & Poisot, T. (2017). Simulations of biomass dynamics in community food webs. *Methods in Ecology and Evolution*, *8*(7), 881–886. https://doi.org/10.1111/2041-210X.12713

Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix problem. *PeerJ*, *5*, e3644. https://doi.org/10.7717/peerj.3644

Dormann, C. F. (2023). The rise, and possible fall, of network ecology. In *Defining Agroecology – A Festschrift for Teja Tscharntke* (pp. 143–159.). Tredition.

Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024). Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature Communications*, *15*(1), 8599. https://doi.org/10.1038/s41467-024-53000-2

Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach. *Methods in Ecology and Evolution*, *4*(8), 760–770. https://doi.org/10.1111/2041-210X.12062

Elton, C. S. (2001). *Animal Ecology* (M. A. Leibold & T. J. Wootton, Eds.). University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/A/bo25281897.html

Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1949), rspb.2020.1889, 20201889. https://doi.org/10.1098/rspb.2020.1889

Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning, J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene. *Science*, *377*(6609), 1008–1011. https://doi.org/10.1126/science.abn4012

García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J. B., Allen-Perkins, A., & Bartomeus, I. (2023). Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. *Ecology Letters*, *26*(6), 831–842. https://doi.org/10.1111/ele.14206

Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O'Gorman, E. J., González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U., Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different ecological questions. *Nature Reviews Biodiversity*, 1–10. https://doi.org/10.1038/s44358-025-00056-7

Gilarranz, L. J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J., & Gonzalez, A. (2017). Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science (New York, N.Y.)*, *357*(6347), 199–201. https://doi.org/10.1126/science.aal4122

Gilljam, D., Curtsdotter, A., & Ebenman, B. (2015). Adaptive rewiring aggravates the effects of species loss in ecosystems. *Nature Communications*, *6*(1), 8412. https://doi.org/10.1038/ncomms9412

Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions interact? *Journal of Animal Ecology*, *80*(5), 1097–1108. https://doi.org/10.1111/j.1365-2656.2011.01852.x

Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, *465*(7300, 7300), 918–921. https://doi.org/10.1038/nature09113

Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions: Biological Sciences*, *371*(1694), 1–14. http://www.jstor.org/stable/24768743

Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B., Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, *42*(3), 401–415. https://doi.org/10.1111/ecog.04006

Gravel, D., Massol, F., & Leibold, M. A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, *7*, 12457. https://doi.org/10.1038/ncomms12457

Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator–prey body size relationships. *Methods in Ecology and Evolution*, *4*(11), 1083–1090. https://doi.org/10.1111/2041-210X.12103

Hao, X., Holyoak, M., Zhang, Z., & Yan, C. (2025). Global Projection of Terrestrial Vertebrate Food Webs Under Future Climate and Land-Use Changes. *Global Change Biology*, *31*(2), e70061. https://doi.org/10.1111/gcb.70061

Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*, *11*, e14620. https://doi.org/10.7717/peerj.14620

Holland, J. N., DeAngelis, D. L., & Bronstein, J. L. (2002). Population Dynamics and Mutualism: Functional Responses of Benefits and Costs. *The American Naturalist*, *159*(3), 231–244. https://doi.org/10.1086/338510

Hui, C., & Richardson, D. M. (2019). How to Invade an Ecological Network. *Trends in Ecology & Evolution*, *34*(2), 121–131. https://doi.org/10.1016/j.tree.2018.11.003

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., van Veen, F. J. F., Warren, P. H., & Woodward, G. (2009). Ecological networks–beyond food webs. *The Journal of Animal Ecology*, *78*(1), 253–269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, *14*(9), e1002559. https://doi.org/10.1371/journal.pbio.1002559

Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. https://doi.org/10.1111/1365-2435.12763

Kamaru, D. N., Palmer, T. M., Riginos, C., Ford, A. T., Belnap, J., Chira, R. M., Githaiga, J. M., Gituku, B. C., Hays, B. R., Kavwele, C. M., Kibungei, A. K., Lamb, C. T., Maiyo, N. J., Milligan, P. D., Mutisya, S., Ng'weno, C. C., Ogutu, M., Pietrek, A. G., Wildt, B. T., & Goheen, J. R. (2024). Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. *Science*, *383*(6681), 433–438. https://doi.org/10.1126/science.adg1464

Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015). Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, *96*(1), 291–303. https://doi.org/10.1890/13-1424.1

Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N., Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose, U. (2012). More than a meal… integrating non-feeding interactions into food webs. *Ecology Letters*, *15*(4), 291–300. https://doi.org/10.1111/j.1461-0248.2011.01732.x

Keyes, A. A., Barner, A. K., & Dee, L. E. (2024). Synthesising the Relationships Between Food Web Structure and Robustness. *Ecology Letters*, *27*(10), e14533. https://doi.org/10.1111/ele.14533

Keyes, A. A., McLaughlin, J. P., Barner, A. K., & Dee, L. E. (2021). An ecological network approach to predict ecosystem service vulnerability to species losses. *Nature*

*Communications*, *12*(1), 1586. https://doi.org/10.1038/s41467-021-21824-x

Kissling, W. D., Dormann, C. F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G. J., Montoya, J. M., Römermann, C., Schiffers, K., Schurr, F. M., Singer, A., Svenning, J.-C., Zimmermann, N. E., & O'Hara, R. B. (2012). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, *39*(12), 2163–2178. https://doi.org/10.1111/j.1365-2699.2011.02663.x

Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments revealed in food-web structure. *Nature*, *426*(6964), 282–285. https://doi.org/10.1038/nature02115

Krishna, A., Guimarães Jr, P. R., Jordano, P., & Bascompte, J. (2008). A neutral-niche theory of nestedness in mutualistic networks. *Oikos*, *117*(11), 1609–1618. https://doi.org/10.1111/j.1600-0706.2008.16540.x

Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, *23*(4), 399–417. https://doi.org/10.2307/1930126

Liu, J., Liu, M., Yin, J., Zhang, Y., Guo, Y., Yu, T., Yu, H., & Ming, X. (2025). Harnessing food webs as a framework for enhancing ecosystem multifunctionality. *Biological Conservation*, *310*, 111383. https://doi.org/10.1016/j.biocon.2025.111383

Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S., Shabani, F., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator–prey interactions in terrestrial endotherms using random forest. *Ecography*, *2023*(9), e06619. https://doi.org/10.1111/ecog.06619

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, *16*(s1), 106–115. https://doi.org/10.1111/ele.12073

MacArthur, R. (1955). Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology*, *36*(3), 533–536. https://doi.org/10.2307/1929601

Marjakangas, E.-L., Dalsgaard, B., & Ordonez, A. (2025). Fundamental Interaction Niches: Towards a Functional Understanding of Ecological Networks' Resilience. *Ecology Letters*, *28*(6), e70146. https://doi.org/10.1111/ele.70146

Martinez, N. D. (1991). Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web. *Ecological Monographs*, *61*(4), 367–392. https://doi.org/10.2307/2937047

Martinez, N. D., & Dunne, J. A. (1998). Time, space, and beyond: Scale issues in food-web research. In *Ecological Scale: Theory and Applications* (pp. 207–226). Columbia University Press.

Massol, F., Gravel, D., Mouquet, N., Cadotte, M. W., Fukami, T., & Leibold, M. A. (2011). Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*, *14*(3), 313–323. https://doi.org/10.1111/j.1461-0248.2011.01588.x

May, R. M. (1972). Will a large complex system be stable? *Nature*, *238*(5364), 413–414. https://doi.org/10.1038/238413a0

Miele, V., Guill, C., Ramos-Jiliberto, R., & Kéfi, S. (2019). Non-trophic interactions strengthen the diversity—functioning relationship in an ecological bioenergetic network model. *PLOS Computational Biology*, *15*(8), e1007269. https://doi.org/10.1371/journal.pcbi.1007269

Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from abundance data. *Methods in Ecology and Evolution*, *11*(5), 621–632. https://doi.org/10.1111/2041-210X.13380

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*(7100, 7100), 259–264. https://doi.org/10.1038/nature04927

Moore, J. C., Berlow, E. L., Coleman, D. C., de Ruiter, P. C., Dong, Q., Hastings, A., Johnson, N. C., McCann, K. S., Melville, K., Morin, P. J., Nadelhoffer, K., Rosemond, A. D., Post, D. M., Sabo, J. L., Scow, K. M., Vanni, M. J., & Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, *7*(7), 584–600. https://doi.org/10.1111/j.1461-0248.2004.00606.x

Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, *30*(6), 347–356. https://doi.org/10.1016/j.tree.2015.03.014

Moulatlet, G., Luna, P., Dattilo, W., & Villalobos, F. (2024). *The scaling of trophic specialization in interaction networks across levels of organization*. https://doi.org/10.22541/au.172977303.33335171/v1

O'Connor, L. M. J., Thuiller, W., Brose, U., Chenevois, É., Freund, C., Gauzens, B., Gaüzere, P., Graham, C., Harfoot, M., Hirt, M. R., Lavergne, S., Maiorano, L., Moilanen, A., Verburg, P. H., Visconti, P., & Pollock, L. J. (2025). *The untapped potential of food webs in systematic conservation planning*. https://hal.science/hal-05331872

O'Gorman, E. J., Petchey, O. L., Faulkner, K. J., Gallo, B., Gordon, T. A. C., Neto-Cerejeira, J., Ólafsson, J. S., Pichler, D. E., Thompson, M. S. A., & Woodward, G.

(2019). A simple model predicts how warming simplifies wild food webs. *Nature Climate Change*, *9*(8, 8), 611–616. https://doi.org/10.1038/s41558-019-0513-x

Odum, E. P. (1968). Energy Flow in Ecosystems: A Historical Review. *American Zoologist*, *8*(1), 11–18. https://doi.org/10.1093/icb/8.1.11

Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, *486*(7404), 485–489. https://doi.org/10.1038/nature11131

Pecuchet, L., Blanchet, M.-A., Frainer, A., Husson, B., Jørgensen, L. L., Kortsch, S., & Primicerio, R. (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Global Change Biology*, *26*(9), 4894–4906. https://doi.org/10.1111/gcb.15196

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E., & Gravel, D. (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, *93*(2), 785–800. https://doi.org/10.1111/brv.12366

Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*, *105*(11), 4191–4196. https://doi.org/10.1073/pnas.0710672105

Petchey, O. L., Brose, U., & Rall, B. C. (2010). Predicting the effects of temperature on food web connectance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2081–2091. https://doi.org/10.1098/rstb.2010.0011

Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and Evolution*, *11*(2), 281–293. https://doi.org/10.1111/2041-210X.13329

Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, *1*(4), 101. https://doi.org/10.1038/s41559-017-0101

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, *307*(5949), 321–326. https://doi.org/10.1038/307321a0

Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods in Ecology and Evolution*, *14*(5), 1333–1345. https://doi.org/10.1111/2041-210X.14071

Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., & Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*, *48*(7), 1552–1563. https://doi.org/10.1111/jbi.14127

Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*, *7*(3), 303–312. https://doi.org/10

Poisot, T., Ouellet, M.-A., Mollentze, N., Farrell, M. J., Becker, D. J., Brierley, L., Albery, G. F., Gibb, R. J., Seifert, S. N., & Carlson, C. J. (2023). Network embedding unveils the hidden interactions in the mammalian virome. *Patterns*, *4*(6), 100738. https://doi.org/10.1016/j.patter.2023.100738

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, *124*(3), 243–251. https://doi.org/10.1111/oik.01719

Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks in ecology? *Functional Ecology*, *30*(12), 1878–1882. https://www.jstor.org/stable/48582345

Polis, G. A. (1991). Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory. *The American Naturalist*, *138*(1), 123–155. https://www.jstor.org/stable/2462536

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., & McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*(5), 397–406. https://doi.org/10.1111/2041-210X.12180

Pomeranz, J. P. F., Thompson, R. M., Poisot, T., & Harding, J. S. (2019). Inferring predator–prey interactions in food webs. *Methods in Ecology and Evolution*, *10*(3), 356–367. https://doi.org/10.1111/2041-210X.13125

Portalier, S. M. J., Fussmann, G. F., Loreau, M., & Cherif, M. (2019). The mechanics of predator–prey interactions: First principles of physics predict predator–prey size ratios. *Functional Ecology*, *33*(2), 323–334. https://doi.org/10.1111/1365-2435.13254

Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton University Press. https://doi.org/10.1515/9780691195322-020

Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology, Evolution and Systematics*, *51*, 55–80. https://doi.org/10.1146/annurev-ecolsys-110218-024908

Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, *20*(6), 345–353. https://doi.org/10.1016/j.tree.2005.04.004

Pyke, G. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and Systematic*, *15*, 523–575. https://doi.org/10.1146/annurev.ecolsys.15.1.523

Quintero, E., Arroyo-Correa, B., Isla, J., Rodríguez-Sánchez, F., & Jordano, P. (2024, July 16). *Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations*. https://doi.org/10.1101/2024.02.02.578595 (Pre-published)

Rohr, R. P., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L. (2010). Modeling Food Webs: Exploring Unexplained Structure Using Latent Traits. *The American Naturalist*, *176*(2), 170–177. https://doi.org/10.1086/653667

Rooney, N., & McCann, K. S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution*, *27*(1), 40–46. https://doi.org/10.1016/j.tree.2011.09.001

Roopnarine, P. D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs. *Paleobiology*, *32*(1), 1–19. https://www.jstor.org/stable/4096814

Roopnarine, P. D. (2017). Ecological Modelling of Paleocommunity Food Webs. In *Conservation Paleobiology: Using the Past to Manage for the Future* (pp. 201–226). University of Chicago Press.

Rossberg, A. G., Matsuda, H., Amemiya, T., & Itoh, K. (2006). Food webs: Experts consuming families of experts. *Journal of Theoretical Biology*, *241*(3), 552–563. https://doi.org/10.1016/j.jtbi.2005.12.021

Saberski, E., Lorimer, T., Carpenter, D., Deyle, E., Merz, E., Park, J., Pao, G. M., & Sugihara, G. (2024). The impact of data resolution on dynamic causal inference in multiscale ecological networks. *Communications Biology*, *7*(1), 1–10. https://doi.org/10.1038/s42003-024-07054-z

Sauve, A. M. C., Thébault, E., Pocock, M. J. O., & Fontaine, C. (2016). How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology*, *97*(4), 908–917. https://doi.org/10.1890/15-0132.1

Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, *7*(1), 12718. https://doi.org/10.1038/ncomms12718

Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinsohn, T. M., Lewis, O. T., Novotny, V., Kitching, R. L., & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology & Evolution*, *35*(5), 454–466. https://doi.org/10.1016/j.tree.2020.01.004

Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024, January 30). *A framework for reconstructing ancient food webs using functional trait data.* https://doi.org/10.1101/2024.01.30.578036 (Pre-published)

Simmons, B. I., Blyth, P. S. A., Blanchard, J. L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C. A., Jacob, U., Pennekamp, F., Petchey, O. L., Poisot, T., Webb, T. J., & Beckerman, A. P. (2021). Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nature Ecology & Evolution*, *5*(11), 1478–1489. https://doi.org/10.1038/s41559-021-01547-4

Smith, J. G., Tomoleoni, J., Staedler, M., Lyon, S., Fujii, J., & Tinker, M. T. (2021). Behavioral responses across a mosaic of ecosystem states restructure a sea otter–urchin trophic cascade. *Proceedings of the National Academy of Sciences*, *118*(11), e2012493118. https://doi.org/10.1073/pnas.2012493118

Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, *13*(7), 891–899. https://doi.org/10.1111/j.1461-0248.2010.01485.x

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory* (Vol. 1). Princeton University Press. https://doi.org/10.2307/j.ctvs32s6b

Stock, M., Poisot, T., Waegeman, W., & Baets, B. D. (2017). Linear filtering reveals false negatives in species interaction data. *Scientific Reports*, *7*, 45908. https://doi.org/10.1038/srep45908

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, *13*(12), 2838–2849. https://doi.org/10.1111/2041-210X.13835

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations. *Methods in Ecology and Evolution*, *14*(12), 2917–2930. https://doi.org/10.1111/2041-210X.14228

Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1837), 20210063. https://doi.org/10.1098/rstb.2021.0063

Su, M., Ma, Q., & Hui, C. (2024). Adaptive rewiring shapes structure and stability in a three-guild herbivore-plant-pollinator network. *Communications Biology*, *7*(1), 103. https://doi.org/10.1038/s42003-024-05784-8

Terry, J. C. D., Bonsall, M. B., & Morris, R. J. (2025). The impact of structured higher-order interactions on ecological network stability. *Theoretical Ecology*, *18*(1), 9. https://doi.org/10.1007/s12080-025-00603-0

Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, *101*(7), e03047. https://doi.org/10.1002/ecy.3047

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science (New York, N.Y.)*, *329*(5993), 853–856. https://doi.org/10.1126/science.1188321

Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L. M. J., Ohlmann, M., Poggiato, G., & Münkemüller, T. (2024). Navigating the integration of biotic interactions in biogeography. *Journal of Biogeography*, *51*(4), 550–559. https://doi.org/10.1111/jbi.14734

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*(10), 2270–2279. https://doi.org/10.1016/j.biocon.2009.12.004

Valdovinos, F. S., Hale, K. R. S., Dritz, S., Glaum, P. R., McCann, K. S., Simon, S. M., Thébault, E., Wetzel, W. C., Wootton, K. L., & Yeakel, J. D. (2023). A bioenergetic framework for aboveground terrestrial food webs. *Trends in Ecology & Evolution*, *38*(3), 301–312. https://doi.org/10.1016/j.tree.2022.11.004

Van De Walle, R., Logghe, G., Haas, N., Massol, F., Vandegehuchte, M. L., & Bonte, D. (2023). Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties. *Journal of Animal Ecology*, *92*(4), 913–924. https://doi.org/10.1111/1365-2656.13905

Van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B:*

*Biological Sciences*, *365*(1549), 2025–2034. https://doi.org/10.1098/rstb.2010.0037

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant–animal mutualistic networks: A review. *Annals of Botany*, *103*(9), 1445–1457. https://doi.org/10.1093/aob/mcp057

Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, *404*(6774, 6774), 180–183. https://doi.org/10.1038/35004572

Windsor, F. M., van den Hoogen, J., Crowther, T. W., & Evans, D. M. (2023). Using ecological networks to answer questions in global biogeography and ecology. *Journal of Biogeography*, *50*(1), 57–69. https://doi.org/10.1111/jbi.14447

Wooster, E. I. F., Middleton, O. S., Wallach, A. D., Ramp, D., Sanisidro, O., Harris, V. K., Rowan, J., Schowanek, S. D., Gordon, C. E., Svenning, J.-C., Davis, M., Scharlemann, J. P. W., Nimmo, D. G., Lundgren, E. J., & Sandom, C. J. (2024). Australia's recently established predators restore complexity to food webs simplified by extinction. *Current Biology*, *34*(22), 5164–5172.e2. https://doi.org/10.1016/j.cub.2024.09.049

Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology*, *37*(1), 26–43. https://doi.org/10.1111/1365-2435.13954

Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014). Collapse of an ecological network in Ancient Egypt. *PNAS*, *111*(40), 14472–14477. https://doi.org/10.1073/pnas.1408471111

Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*, *120*(5), 551–570. https://doi.org/10.1086/284013

Yodzis, P. (2001). Must top predators be culled for the sake of fisheries? *Trends in Ecology & Evolution*, *16*(2), 78–84. https://doi.org/10.1016/S0169-5347(00)02062-0

Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*, *139*(6), 1151–1175. https://doi.org/10.1086/285380

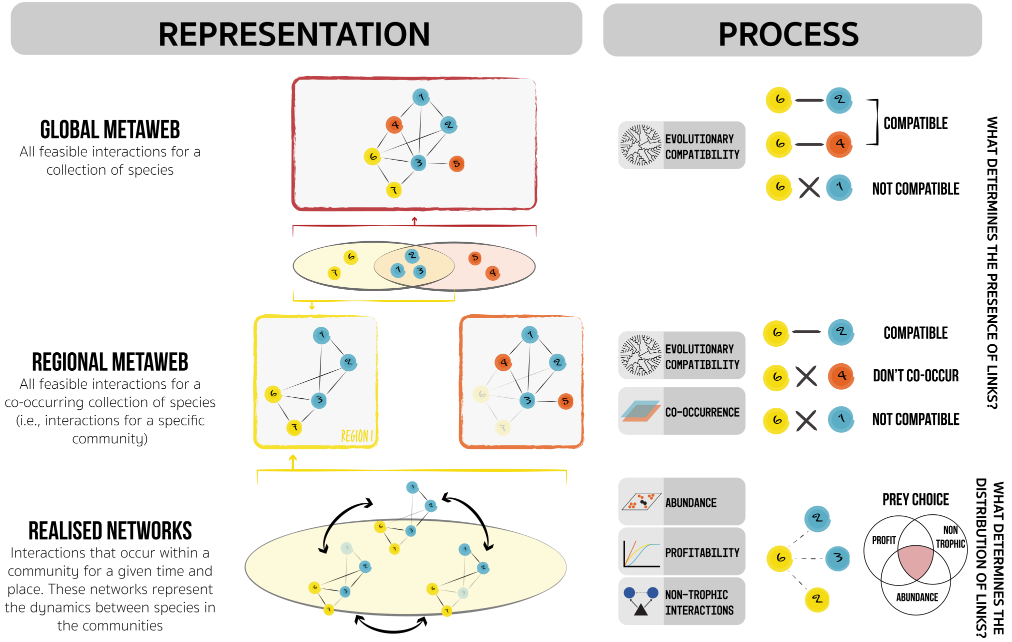

Figure 1: Aligning the various processes that determine interactions (right column) with the different network representations (left column). First, we start with a **global metaweb** this network captures all possible interactions for a collection of species in the global context. However, within the global environment different species occur in different regions (region one = yellow and region 2 = orange), and it is possible to construct two different metawebs (**regional metawebs**) for each region by taking accounting for the co-occurrence of the difference species - as shown here we have two regions with some species that are found in both regions (blue) and others endemic to either region one (yellow) or region two (orange). However, even within a region we do not expect all interactions to be realised but rather that there are multiple configurations of the regional metaweb over both space and time. The 'state' of the different **realised networks** is ultimately influenced not just by the co-occurrence of a species pair but rather the larger community context such as the abundance of different species, maximisation of energy gain, or indirect/higher order interactions.