From Metawebs to Realised Food Webs: A Process-Based Framework for Network Representation

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, S10 2TN
[2] School of Earth, Environment and Sustainability, University of Leeds, Leeds, UK, LS2 9JT
[3] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA
[4] Université de Montréal, Département de Sciences Biologiques, 1375 Avenue Thérèse-Lavoie-Roux, Montréal, QC H2V 0B3, Canada
[5] Québec Centre for Biodiversity Sciences, 1205 Docteur Penfield Avenue, Montreal, Quebec, H3A 1B1, Canada

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

Abstract: Ecological networks are widely used to understand biodiversity and predict ecosystem responses to environmental change, yet different food web representations encode different assumptions about how feeding interactions arise. We develop a process-based framework that links global metawebs of evolutionarily feasible interactions to regional metawebs constrained by spatiotemporal overlap, and ultimately to realised food webs shaped by local ecological conditions. Five processes govern these transitions: evolutionary compatibility and spatiotemporal co-occurrence constrain which interactions are possible and available, while species abundance, consumer diet choice, and non-trophic interactions influence which interactions are realised. We connect these processes to four approaches to network construction (empirical, feasibility-based, process-based, and structure-based) and derive testable hypotheses for evaluating when incorporating ecological processes improves predictions beyond those based on co-occurrence or aggregate network structure. By distinguishing the assumptions underlying each representation, the framework clarifies what different food webs can reveal, where their inferences are limited, and how these limitations can be tested using independent interaction records, trait and distribution data, and repeated observations across sites or time. Ultimately, it provides a basis for matching food web representations to ecological questions and for testing whether explicitly accounting for the processes that generate interactions improves our ability to anticipate ecological change.

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

Table of contents

1 Introduction **2**

2 Setting the Scene: The Not So Basics of Nodes and Edges **4**
2.1 How do we define a node? 4
2.2 What is captured by an edge? 5
2.3 Network representations 5

3 From Nodes and Edges to Process and Constraints **6**
3.1 Processes that determine the feasibility of an interaction 6
3.2 Processes that realise interactions 8

4 Network construction **11**
4.1 Reconstruction from empirical evidence 12
4.2 Inference of Interactions 13
4.3 Specification based on process 15
4.3.1 Abundance-based models 15
4.3.2 Energetic and behavioural models 16
4.4 Structure-based construction 16
4.5 Construction choices shape ecological inference 18

5 Making Progress with Networks **18**
5.1 Matching network representations to ecological questions 21
5.1.1 Global Metawebs 23
5.1.2 Regional Metawebs 24
5.1.3 Realised networks 24
5.2 Key methodological challenges 25

6 Concluding Remarks **26**

References **27**

1 Introduction

At the heart of biodiversity science are theories linking species richness, stability, and ecosystem functioning, from the foundational work of Elton (2001), Lindeman (1942), and MacArthur (1955) to contemporary questions about biodiversity loss and ecosystem resilience. Trophic networks are central to these questions because they capture the feeding interactions underpinning energy flow, community structure, and ecosystem functioning (Cohen *et al.* 1990; Dunne *et al.* 2002; Martinez & Dunne 1998; Simmons *et al.* 2021). Documenting these interactions provides a foundation for understanding biodiversity and anticipating the consequences of environmental change (Galiana & Araújo 2026; Windsor *et al.* 2023).

Yet food webs do more than a description of feeding interactions – their construction embeds assumptions about the ecological processes that generate and constrain those interactions. These assumptions have been discussed in relation to sampling effort (Polis

1991), aggregation (Martinez 1991), and scale (Martinez & Dunne 1998; Moulatlet *et al.* 2024), as well as general interpretation and application (Blüthgen 2010; Blüthgen & Staab 2024; Dormann 2023). Challenges in collecting and observing interactions are also well documented (Polis 1991; Pringle & Hutchinson 2020; Saberski *et al.* 2024). However, these discussions have yet to provide a clear process-based account of how the data and assumptions used to construct a food web shape its representation, what ecological processes it captures, and which questions it can answer. Recent work by Gauzens *et al.* (2025) has synthesised trophic network representations by node resolution and link type, here we address a complementary question: how do ecological processes generate different representations, and what can each representation legitimately tell us?

We propose a process-based hierarchy distinguishing between global metawebs (representing evolutionarily feasible feeding interactions), regional metawebs (constrained by spatiotemporal overlap), and realised food webs (shaped by local ecological processes). The central contribution is to contrast these representations through the processes that constrain or realise their links, clarifying how their assumptions differ, and where their ecological inferences may diverge. This framework provides a basis for choosing network representations to match the correct ecological question, and for assessing when incorporating process information improves ecological prediction.

We focus on trophic networks (food webs), which provide a well-developed foundation for distinguishing evolutionarily feasible interactions from those realised through spatiotemporal overlap, abundance, and consumer diet choice. Although communities are also structured by mutualistic, competitive, parasitic, and facilitative interactions, we lean on the extensive work done in the food web space. However, there is potential for some of the ideas discussed here to transfer to non-trophic interactions. In this perspective we examine how nodes and edges define alternative representations (Section 2), then consider the processes (Section 3) and construction approaches (Section 4) that generate them, before discussing how the framework can guide network choice and ecological inference (Section 5).

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

Ecological networks represent an 'object' from which inferences can be made and serve multiple purposes. While many aspects of community structure can be analysed without networks (*e.g.,* trait distributions or abundance patterns) networks provide a formal framework for capturing the organisation of interactions among species. These are used to study emergent properties of the community such as energy flow (Lindeman 1942; Odum 1968), complexity (Montoya *et al.* 2006), and stability (Pimm 1984; Schneider *et al.* 2016). They allow researchers to examine how interactions among species shape communities (Pecuchet *et al.* 2020), influence their response to environmental change (Hao *et al.* 2025), and determine community robustness (Dunne *et al.* 2002; Staniczenko *et al.* 2010).

But a network is not a neutral description of a community. Its structure depends on what is represented as a node, what counts as an edge, and the spatial, temporal, and biological scales at which these are defined (Poisot *et al.* 2016b). These choices affect which features of a community the network captures and what can be inferred from it (Moulatlet *et al.* 2024). To understand what different food webs represent, we therefore begin with how their nodes and edges are defined.

2.1 How do we define a node?

Although nodes are conventionally described as representing species, they can correspond to a range of taxonomic and non-taxonomic units, including trophic species (Williams & Martinez 2000; Yodzis 1982), feeding guilds (García-Callejas *et al.* 2023), or species-specific life stages (Clegg *et al.* 2018). These choices reflect differences in the level and consistency of resolution at which networks are constructed, rather than aggregation *per se*. Coarser or mixed-resolution nodes can limit taxon-specific inference (*e.g.,* whether species a consumes species b), bias estimates of degree distributions, particularly generality and vulnerability, and complicate analyses of extinction or invasion dynamics by obscuring species identities and the consequences of their loss (Clegg *et al.* 2018). Yet aggregation can also be appropriate when interactions among functional or trophic units are more informative than species-level detail, *e.g.,* analysing extinction patterns across feeding guilds (Dunhill *et al.* 2024). Node definition is therefore not merely a methodological choice: it determines which ecological entities a network represents, which processes can be captured, and which questions can be addressed (Gauzens *et al.* 2025).

2.2 What is captured by an edge?

Understanding how edge assumptions shape ecological process representation requires distinguishing between potential and realised links. Potential links represent feasible interactions between species (Dunne 2006; Pringle 2020), whereas realised links represent interactions expressed within a system, or the transfer of energy or materials through feeding (Lindeman 1942; Proulx *et al.* 2005). Edges can therefore represent different ecological 'currencies' (Gauzens *et al.* 2025). They can also differ in how interactions are quantified: links may be binary (present or absent), probabilistic (Banville *et al.* 2025; Poisot *et al.* 2016a), or represented by continuous measures of interaction strength (Berlow *et al.* 2004). Edge definition thus depends on both the ecological currency being represented and how interactions are quantified. These choices determine the processes a network can capture and the inferences it can support. For example, a network of feasible interactions can characterise potential trophic links but cannot, on its own, establish the magnitude or distribution of energy flow, because its links are not constrained by the environmental conditions or energetic processes governing realised interactions.

2.3 Network representations

Node and edge definitions, together with the assumptions they encode, give rise to two well-established types of ecological network: **metawebs**, which represent potential interactions within a species pool (Dunne 2006), and **realised networks**, which represent interactions expressed within a particular community, place, and time. These representations differ not only in spatial and temporal scope but also in the processes assumed to generate their structure.

A metaweb is fundamentally a list of feasible interactions between species. It identifies evolutionarily and regionally plausible links, excludes ecologically impossible (*i.e.,* forbidden) interactions (Jordano 2016b), and characterises the potential diet breadth of species (Strydom *et al.* 2023). Feasibility is determined primarily by trait complementarity, particularly traits associated with feeding, and can be further constrained by species co-occurrence.

Realised networks, by contrast, are localised in space and time, with links shaped by co-occurrence, environmental conditions, and consumer diet choice. Even when represented as binary matrices, their links reflect interactions that have passed through these ecological filters and may therefore imply energy transfer. Realised networks are not simply spatial

or temporal subsets of metawebs; they emerge from the processes governing whether, and to what extent, interactions occur within a particular community context. Consequently, a metaweb and a realised network containing the same species may differ substantially in structure because their links are subject to different constraints (Strydom *et al.* 2026). Critically, a link absent from a metaweb represents an interaction deemed infeasible under the assumptions used to construct it, whereas a link absent from a realised network may reflect context-dependent ecological constraints, limited observation, or both.

3 From Nodes and Edges to Process and Constraints

The definitions of nodes and edges establish what a food web represents; the distinction between metawebs and realised networks clarifies which processes and inferences each representation supports. We frame these representations as stages in a hierarchy governed by different processes: evolutionary compatibility, spatiotemporal overlap, abundance, consumer diet choice, and non-trophic interaction modification (Figure 1). Each transition imposes a distinct ecological process, making differences between representations testable in terms of process rather than data format alone. The framework is not exhaustive, rather it reflects the current body of theory and evidence that underpins the way in which we construct networks Section 4. The framework also generates testable predictions about the transitions between network representations. In Box 1 we outline how these processes can be evaluated using comparative, experimental, and time-resolved interaction data, but treat these as ways to assess the framework rather than as its primary contribution.

[Figure 1 about here.]

3.1 Processes that determine the feasibility of an interaction

In order to be feasible between two species they must have some degree of evolutionary compatibility and need to have some degree of spatiotemporal overlap. The first reflects trait complementarity; the second limits potential interactions to species able to encounter one another. However, it is worth noting that species need no co-occur for an interaction to be feasible, but rather co-occurrence reflects a means to identify interactions that *could* occur in the local context.

Evolutionary compatibility

Interaction feasibility is constrained by functional compatibility between consumers and

resources. Traits associated with resource acquisition and defence determine whether a feeding interaction is physically and biologically possible, defining the feasible interaction space represented by a metaweb (Dunne 2006). Evolutionary history and co-evolution shape these traits, making phylogenetic relationships and trait complementarity useful predictors of interaction feasibility.

This constraint reflects the evolutionary history of consumers and resources (Dalla Riva & Stouffer 2016; Gómez *et al.* 2010; Rossberg *et al.* 2006; Segar *et al.* 2020), expressed through trait complementarity between species (Benadi *et al.* 2022). Consumers must possess traits that permit them to acquire and consume particular resources, while resource traits may enable or prevent consumption. Interactions lacking this compatibility are defined as forbidden links (Jordano 2016b), these are interactions that are physically or biologically impossible and therefore excluded from the feasible interaction space.

Feasibility need not be viewed as a binary outcome, and it is possible to represent these interactions as probabilities (Banville *et al.* 2025). For example, Strydom *et al.* (2022) used. probabilities to express confidence that a feeding interaction is possible. Webs built based on evolutionary compatibility are aligned with the global metaweb in Figure 1 in that they evaluate the presence of an interaction between species regardless of if they are co-occurring or not.

Spatiotemporal overlap (encounter opportunity)

Even when consumers and resources are evolutionarily compatible, a feeding interaction can only occur if they overlap in space and time. This of course excludes feed on by-products *e.g.,* dung beetles, however even in these circumstances there is still a degree of 'co-occurrence'. We therefore distinguish spatiotemporal overlap, which provides the opportunity for species to encounter one another, from observed co-occurrence patterns, a statistical pattern that can arise for reasons unrelated to direct interactions (Blanchet *et al.* 2020).

Spatiotemporal overlap restricts the feasible interactions in a global metaweb to those that could occur within a particular region or community, providing the transition from global to regional metawebs (Dansereau *et al.* 2024a). In Figure 1, this transition is illustrated by the metawebs for regions one and two, which differ in species composition and therefore in the set of feasible interactions.

Importantly just because species co-occur it does not mean that they will interact (Poisot

et al. 2015) and we should not interpret the structure of regional webs as being an absolute reflection of network structure (Caron *et al.* 2024). This distinction matters because co-occurrence treated as evidence of realised feeding blurs the distinction between regional metawebs and realised food webs, potentially giving similar network structures very different ecological interpretations.

3.2 Processes that realise interactions

Within the feasible interaction space (defined by evolutionary compatibility and spatiotemporal overlap), we identify three processes (abundance, consumer diet choice, and non-trophic interactions) that shape which and how strongly links occur, affecting energy transfer within communities. This is shown Figure 1, although note here it is no longer a question of capturing link compatibility but rather a quantification of the distributions of links within a given community. Unlike metawebs, realised webs are the outcome of consumer behaviour.

Abundance

Abundance provides a baseline modifier of interaction realisation. Under a null model, consumers feed randomly among feasible resources in proportion to prey abundance (Stephens & Krebs 1986; Vázquez *et al.* 2009). Within the context of a regional metaweb, abundance influences encounter frequency and the probability of feeding (Banville *et al.* 2025; Poisot *et al.* 2015), serving as a link modifier. It can therefore help predict the distribution and strength of realised links but does not explicitly establish feasibility or capture selective behaviour and other constraints on feeding.

Diet choice

Here, we use diet choice as an umbrella term for processes derived from optimal foraging theory (Pyke 1984) and metabolic theory (Brown *et al.* 2004) that determine the distribution and strength of realised trophic interactions. Consumers do not necessarily feed in proportion to resource abundance; they can select resources according to the energetic return and the cost of acquiring and consuming them (Stephens & Krebs 1986). Consumer diet choice thus reflects energetic cost–benefit trade-offs centred on prey profitability and constrained by traits associated with resource acquisition and consumption (Smith *et al.* 2021; Wootton *et al.* 2023). These energetic constraints underpin a range of approaches to constructing realised food webs (Beckerman *et al.* 2006; Cherif *et al.* 2024; Pawar *et al.* 2012; Portalier *et al.* 2019).

Non-trophic interactions

Non-trophic interactions are included here not as trophic links, but as processes that modify the occurrence or strength of trophic interactions within realised food webs (Buche *et al.* 2024; Ings *et al.* 2009; Kéfi *et al.* 2012, 2015; Miele *et al.* 2019). They extend the ecological context beyond evolutionary compatibility, spatiotemporal overlap, and abundance by altering encounter rates, feeding success, mortality, or access to resources (Golubski & Abrams 2011; Pilosof *et al.* 2017).

Such effects can arise through direct interactions among consumers, including predator interference or competition for space, or through indirect interactions, such as refuge provisioning, habitat modification, and facilitation, that alter the probability or strength of feeding interactions (Golubski & Abrams 2011; Ings *et al.* 2009; Kamaru *et al.* 2024; Staniczenko *et al.* 2010).

With the caveat that trophic and non-trophic processes are not always cleanly separable. Pollinators, for example, consume floral resources through trophic interactions while also influencing plant reproduction, recruitment, and population persistence through non-trophic processes (Bascompte & Jordano 2007; Holland *et al.* 2002; Sauve *et al.* 2016). However in the context presented here we focus on how non-trophic processes modify trophic network realisation, rather than extending the framework to mutualistic networks in general.

> **Testing the transition from feasible to realised food webs**
>
> Although recent work from Strydom *et al.* (2026) has shown that different network representations do indeed result in different inferences about changes in communities and networks across time it remains to be seen if these differences can be ascribed to specific processes. The framework we present here generates predictions that distinguish it from a purely descriptive classification of network types. Below we present a series of hypotheses that would allow us to explicitly test the framework presented Section 3, but also serves as guidance for thinking about the validation of constructed networks (see Section 4)
>
> **Feasibility constraint.** After accounting for uncertainty in interaction records, a model that represents evolutionary and trait compatibility will exclude more biologically impossible links than a model based only on species occurrence, and its predicted feasible links will transfer better to independent species combinations.

This hypothesis can be tested by comparing trait- or phylogeny-informed metaweb predictions with independent feeding records, including both confirmed interactions and credible forbidden links. Work linking evolutionary history and trait complementarity to interactions provides a mechanistic basis for the prediction (Benadi *et al.* 2022; Dalla Riva & Stouffer 2016; Gómez *et al.* 2010; Segar *et al.* 2020). However, prediction remains sensitive to the traits measured, and apparent forbidden links may reflect insufficient observation rather than true incompatibility. The hypothesis would be weakened if compatibility-informed models did not improve discrimination of feasible and forbidden links in independent data.

Regional filtering. For a fixed global metaweb, restricting links to species with spatiotemporal overlap will reduce the predicted interaction set, but overlap alone will overpredict realised feeding relative to observations from the same region for a restricted time window. This can be tested by comparing regional metawebs with observed local realised food webs constructed across a limited temporal period. Here the expectation is that the regional metaweb would overpredict interactions relative to the local realised web, importantly they would not recover forbidden links

Context-dependent realisation. Within a regional metaweb, models that incorporate consumer and resource abundance, and where relevant consumer diet choice, will predict realised interactions more accurately than models based on spatiotemporal co-occurrence alone. The improvement should depend on the extent to which abundance and feeding preferences constrain interaction realisation, and should be greatest where these processes explain substantial variation in observed feeding. This hypothesis can be tested using repeated interaction observations and abundance data, evaluating predictions against held-out sites or time periods. Abundance-based models provide a baseline for testing how much predictive information is gained by moving beyond co-occurrence, while deviations from abundance-based expectations can reveal the importance of consumer preferences and other ecological constraints (Stephens & Krebs 1986; Vázquez *et al.* 2009; Wootton *et al.* 2023). The hypothesis would be weakened if abundance- and diet-informed models failed to improve predictions over co-occurrence-based models, or if improvements did not generalise to independent observations.

Process-informed prediction. Models that represent the relevant processes governing interaction realisation, including non-trophic effects where these are important,

will predict context-specific food web structure and its responses to environmental change or species turnover more accurately than models based only on aggregate network structure. This hypothesis can be tested by comparing process-based and structure-based models using the same training data and evaluating their predictions against independent observations, at both the level of individual interactions and network properties. Non-trophic interactions may improve predictions where interference, facilitation, or habitat modification alters encounters or feeding success, but their contribution should vary among systems (Golubski & Abrams 2011; Miele *et al.* 2019). Structure-based models may remain competitive for questions concerned only with aggregate topology, while process-based models may perform poorly when relevant mechanisms are inadequately measured or misspecified. The hypothesis would therefore be supported by improvements that generalise to held-out conditions and capture ecological changes not represented in the calibration data.

Across all scenarios, evaluation should distinguish uncertainty in biological feasibility from uncertainty caused by missing observations. Non-detection is not equivalent to a forbidden interaction, and predictive performance should be reported for links and for the structural or ecological quantities relevant to the stated question. Where possible, tests should use independent sites, time periods, or taxa to avoid evaluating a framework against the same evidence used to construct it, or embed phenomena relative to the specific system.

4 Network construction

Above we showcase how network representations embed a specific set of assumptions, thus not only are they representations of biodiversity but they are also models of ecological systems. This is reflected in the way we choose to infer (construct) networks. Ideally, every trophic interaction could be observed directly. In practice, interaction data are costly to collect, incomplete, and often impossible to obtain across entire communities (Jordano 2016a, b; Poisot *et al.* 2021). Food webs must therefore be constructed from empirical observations, ecological inference, or models of network structure, each of which embeds different assumptions about how interactions arise.

The choice of construction approach should be dictated by what the desired network is intended to represent. Is the objective to document an interaction that occurred, infer

whether an interaction is feasible, predict which interactions will be realised under specified ecological conditions, or generate a network with specific structural properties? Each approach imposes distinct constraints on what a network represents and which inferences it supports. Here, we map these processes to the different ways in which food webs can be inferred. Focusing on the information used to assign interactions and the ecological meaning of the resulting links. We distinguish four broad approaches: empirical, which records observed interactions; feasibility-based, which infers potential interactions; process-based, which models how feasible interactions become realised; and structure-based, which generates networks according to structural rules. Importantly these approaches map onto different network representations (Figure 2) owing to the differences in the assumptions they make about how interactions arise.

[Figure 2 about here.]

These approaches are not mutually exclusive in their implementation. Process-based models may use feasibility networks as their starting point, feasibility models may be parameterised using empirical interaction data, and random network generators may be fitted to structural properties observed in empirical food webs. The distinction instead concerns the basis on which links are assigned and the ecological interpretation given to the resulting network.

This distinction matters because food web topology underpins analyses of community structure, energy flux, extinction cascades, ecosystem functioning, and dynamical stability (Danet *et al.* 2024). Differences in topology can reflect genuine ecological variation among communities, but can also arise from differences in sampling strategy, taxonomic resolution, and construction methodology (Brimacombe *et al.* 2023, 2024b). Understanding how a network was constructed is therefore essential for interpreting what it represents and which ecological questions it can legitimately address. Fundamentally, network construction should be treated as an explicit modelling decision: it determines what information an edge encodes, which ecological processes are represented, and what inferences can be drawn.

4.1 Reconstruction from empirical evidence

Empirical food webs are constructed from observations or proxies/evidence of realised trophic interactions. However, different methods capture different aspects of feeding and vary in their temporal and taxonomic resolution, uncertainty, and the ecological meaning

of the resulting links.

Direct observations record feeding events in the field or laboratory and provide direct evidence that an interaction occurred under sampled conditions (Jordano 2016b). However, because interactions are difficult to monitor continuously across entire communities such observations are typically incomplete. Consequently, an unobserved interaction should not necessarily be interpreted as one that cannot occur.

Gut, stomach, and scat analyses identify recently consumed prey, either through manual identification or DNA metabarcoding. These methods provide empirical evidence of feeding by capturing snapshots of recent diet and are subject to biases associated with digestion, detection, and sampling effort (Pompanon *et al.* 2012; Sousa *et al.* 2019). The resulting network represents interactions detectable by the method over its relevant temporal window, rather than necessarily capturing each consumer's complete diet.

Stable isotope analyses provide evidence of assimilated energy pathways and trophic position over longer temporal windows, offering indirect evidence of trophic relationships rather than direct observations of feeding events (Post 2002). Similarly, molecular approaches, including environmental DNA and interaction metabarcoding, can reveal trophic relationships that are otherwise difficult to observe, although the certainty with which they establish specific feeding interactions varies.

Although these empirical sources are observations of realised processes the temporal scale at which this data needs to be collated to ensure sufficient coverage or sampling effort means that a web constructed from these data may therefore function more appropriately as metawebs (Brimacombe *et al.* 2024a). However, empirical metawebs should not be assumed to be complete (Polis 1991), and inferred interactions may be needed to supplement observations (see Section 4.2 on gap-filling).

4.2 Inference of Interactions

Feasibility-based approaches infer trophic interactions from the properties of consumers and resources, drawing on the evolutionary compatibility processes described in Section 3.1. Rather than establishing whether feeding was observed or predicting whether it will occur under specific ecological conditions, these approaches use ecological rules, species traits, and phylogenetic relationships to identify potentially feasible interactions.

Species-specific approaches infer potential interactions between specific consumer–resource

pairs and are therefore conceptually aligned with metawebs. They typically rely on a combination of the following assumptions: that ecological rules constrain interaction feasibility (Morales-Castilla *et al.* 2015); that some of these rules are conserved across species or phylogenetic lineages (Bramon Mora *et al.* 2018; Dalla Riva & Stouffer 2016); and that the properties of consumers and resources can be used to infer their compatibility.

These approaches are central to constructing first-draft networks for communities for which interaction data are unavailable (Strydom *et al.* 2022), supporting the reconstruction of networks in data-poor regions and for unobservable communities, such as paleo-communities (Dunhill *et al.* 2024; Fricke *et al.* 2022; Yeakel *et al.* 2014), or novel future assemblages (Van der Putten *et al.* 2010). These approaches can also help evaluate how species interactions shape distributions by accounting for both environmental conditions and biotic relationships (Albouy *et al.* 2014; Gravel *et al.* 2019; Higino *et al.* 2023; Pollock *et al.* 2014).

Feeding rules can either be explicitly specified or inferred. Expert-based approaches identify feasible interactions using trait matching (Albouy *et al.* 2019; Roopnarine 2017; Shaw *et al.* 2024), while mechanistic approaches use trait-based relationships between consumers and resources (Gravel *et al.* 2013; Rohr *et al.* 2010). Rules can also be inferred using observed interaction data to train classifiers based on ecological proxies that are more widely available, such as species traits (Pichler *et al.* 2020). These include generalised linear models (Caron *et al.* 2022), random forests (Llewelyn *et al.* 2023), trait-based (k)-nearest-neighbour methods (Desjardins-Proulx *et al.* 2017), and Bayesian models (Cirtwill *et al.* 2019; Eklöf *et al.* 2013). Depending on their formulation and training data, these methods may estimate interaction feasibility or the probability of observing an interaction under the conditions represented in the data. These interpretations should not be treated as equivalent. Interactions can also be inferred from the structure of known networks. Graph-embedding uses the structure of a known network to infer the positions of species in a latent representation, combining network information with ecological proxies such as phylogenetic relatedness (Strydom *et al.* 2022, 2023).

These types of approaches can be particularly useful to interpolate missing interactions within observed networks (Beauchesne *et al.* 2016; Biton *et al.* 2025; Dallas *et al.* 2017; Habedank *et al.* 2025; Poisot *et al.* 2023; Stock *et al.* 2017). These gap-filling methods infer links from existing interactions and network structure, sometimes incorporating additional ecological information. An inferred link, however, is not equivalent to an

observed interaction, rather it represents a prediction supported by the information and assumptions used in the inference procedure. Thus, should one use these gap-filling approaches to supplement empirical observations, it is noted in both the metadata, and ideally codified in such a way that it captures this uncertainty.

At the core the approaches discussed above are closely aligned with constructing metawebs (global or regional) as they are (directly or indirectly) built on the assumption that the evolutionary history of species determines who they can interact with.

4.3 Specification based on process

Process-based approaches predict realised food webs by modelling the ecological processes that determine whether feasible trophic interactions occur within communities. Rather than inferring feasibility alone, they operationalise the abundance, diet-choice, and non-trophic processes introduced in Section 3.2 to predict which interactions are realised and in (some cases) the resulting distribution of energy transfer. These networks are used to investigate energy flux, extinction dynamics, ecosystem functioning, and relationships between network structure, stability, productivity, and ecosystem function. They also provide the structural basis for dynamical models examining secondary extinctions, species invasions, and climate change.

Because these approaches represent species properties and feeding processes explicitly, network structure emerges from modelled consumer–resource dynamics rather than from feasibility rules alone. The same species assemblage can therefore yield different networks under different conditions. This detail comes at a cost: models often require extensive community and environmental data, depend on their behavioural assumptions, and do not necessarily represent all feasible interactions beyond the conditions modelled. Note here we explicitly refer to these approaches as models as they aim to describe the behaviour of the system (community) as opposed to outright inference.

4.3.1 Abundance-based models

Abundance-based models provide a simple way to represent the transition from feasible to realised interactions. Neutral models assume that consumers feed randomly among feasible resources, with interaction probabilities related to prey abundance (Canard *et al.* 2014; Krishna *et al.* 2008). Under this formulation, feasibility defines the pool of potential interactions, while abundance influences which interactions are likely to occur.

These models illustrate how two communities can share the same feasible interaction space yet produce different realised networks because their species abundances differ. They are not necessarily intended as complete explanations of trophic interactions; rather, they provide a baseline process through which feasible links are filtered into community-specific predictions. They can therefore be combined with feasibility-based approaches to generate localised food webs (Pomeranz *et al.* 2019).

4.3.2 Energetic and behavioural models

A broader class of process-based approaches predicts realised interactions through energetic and behavioural constraints on feeding. These models often use consumer–resource body-size relationships as proxies for the energetic costs and benefits of prey capture, handling, and consumption. Rather than identifying feasibility alone, they use energetic constraints to determine which interactions are likely to be realised.

For example, models developed by Portalier *et al.* (2019) and Wootton *et al.* (2023) incorporate energetic constraints on predator–prey relationships. Their resulting links represent predicted feeding interactions under the assumptions and conditions of the model, rather than simply identifying biologically compatible species pairs.

Diet-choice models provide a related approach by representing how consumers allocate feeding effort among available resources. Models such as the diet breadth (Beckerman *et al.* 2006) and allometric diet breadth (Petchey *et al.* 2008) models determine interactions through assumptions about consumer foraging behaviour. Because diet choice affects both which interactions occur and how feeding is distributed across resources, these models can generate realised links and emergent network structure. Their process-based interpretation can be strengthened by explicitly incorporating trait-based constraints on feasible interactions (Curtsdotter *et al.* 2019) or complemented by more explicit representations of nutrient dynamics (Cuff *et al.* 2024).

These models allow the same species assemblage to generate different realised networks as abundance, environmental conditions, energetic constraints, or behavioural rules change.

4.4 Structure-based construction

Structure-based approaches generate edges according to probabilistic rules governing network structure, rather than evidence for or predictions about specific species interactions. An edge in such a network does not necessarily indicate that two species are ecologically

compatible or that feeding is expected to occur. Instead, it represents a relationship generated under a model of network structure.

Random and structural models are commonly used to establish null expectations, provide comparative baselines, and generate synthetic networks for dynamical modelling. Their primary purpose is generally not to reconstruct the trophic relationships of a particular community, but to test whether observed or predicted patterns differ from those expected under specified structural rules.

Alongside random graph models such as the Erdős–Rényi model (Erdős & Rényi 1959), approaches have been developed that take existing networks and randomise their interactions to generate alternative configurations while preserving selected structural properties (Banville *et al.* 2023; Bascompte *et al.* 2003; Fortuna & Bascompte 2006). Although such models do not directly reconstruct the ecological processes governing real-world interactions (Bascompte 2007), they provide useful null hypotheses for evaluating the significance of observed network structure.

Stochastic food web models commonly impose probabilistic rules governing properties such as connectance, diet breadth, trophic position, or the distribution of interactions along a niche axis. The Niche Model, for example, generates trophic interactions according to species' positions along a one-dimensional niche axis (Williams & Martinez 2000). The Cascade Model similarly generates networks using rules concerning trophic ordering (Cohen *et al.* 1990), while the Nested Hierarchy Model incorporates assumptions about nested structure and phylogenetic constraints (Cattin *et al.* 2004). These models can reproduce emerging properties of empirical food webs (Stouffer *et al.* 2005) without explicitly representing the identity-specific mechanisms responsible for specific feeding interactions.

The resulting networks are best regarded as structural or synthetic representations that most closely represent realised networks. Their edges are generated under a network-level model rather than established through observations or predictions of realised feeding. This makes them valuable for distinguishing structural expectations from empirical patterns (Strydom *et al.* 2021b) and for providing inputs to dynamical models, including allometric trophic networks (Brose *et al.* 2006; Delmas *et al.* 2017; Schneider *et al.* 2016).

However, the ability of a structural model to reproduce properties of empirical food webs does not establish that it has recovered the ecological mechanisms generating those interactions. It demonstrates instead that the specified structural rules are sufficient to

reproduce the properties being evaluated. The interpretation of such networks therefore depends on whether the objective is to establish a structural null expectation, generate a synthetic network for simulation, or investigate the mechanisms underlying particular trophic relationships.

4.5 Construction choices shape ecological inference

Food web construction determines not only network structure but also the ecological meaning of its interactions and the scope of inference it supports. Empirical links provide evidence of feeding under sampled conditions; feasibility-based links represent biologically plausible interactions; process-based links predict interactions under specified ecological conditions; and structure-based models generate networks against which observed or predicted patterns can be compared without necessarily identifying the interactions occurring in a particular community.

These distinctions are especially important when networks are used to investigate ecological responses to environmental change. A network representing potential interactions within a regional species pool can inform questions about alternative feeding relationships, community assembly, and the potential for interaction rewiring. However, it cannot (without additional assumptions) establish which interactions will be realised at a particular place and time. Conversely, an observed network provides evidence of interactions detected under specific sampling conditions but may not capture the full set of feasible interactions or the distribution of feeding across different environmental contexts.

Network construction should therefore be treated as an explicit modelling decision (Strydom *et al.* 2026). Its inferential value depends on the alignment between the assumptions used to construct the network and the ecological quantity of interest. These assumptions should be made explicit when networks are constructed, compared, or used to predict ecological change (Brimacombe *et al.* 2024b). Three questions should guide their interpretation: What quantity or process is being inferred? What evidence and assumptions support that inference? And what independent evidence can be used to evaluate the resulting network or its predictions?

5 Making Progress with Networks

Ecological networks are increasingly used as the first step in a broader ecosystem-level analysis pipeline (Loreau & de Mazancourt 2013; Thuiller *et al.* 2024), and having access

to networks is relevant to unresolved questions about stability–diversity–productivity relationships, the drivers and consequences of extinctions and invasions, and the impacts of multiple stressors across ecological scales (Simmons *et al.* 2021). However, the inferences that networks support depend on what their links represent, how they were constructed, and the spatial and temporal scales at which they apply (Gauzens *et al.* 2025).

We therefore argue that network applications should begin with three explicit decisions: what do we want to infer, which network representation can support that inference, and how will the inference be evaluated? These decisions connect the ecological processes discussed in Section 3.1 with the construction approaches described in Section 4 and are expanded on in Box 2. In Table 1 we explicitly map common network-driven research questions to the appropriate network representations.

Table 1: Mapping research questions to network representations and highlighting studies that address these questions or identify emerging research directions. This mapping is indicative rather than exhaustive; the appropriate representation depends on the specific inference and the evidence available.

Network Representation	Common Inferential Pitfall	Principal questions and applications	Representative Studies
Global Metaweb	Treating feasible links as evidence of realised feeding or energy flow.	How will novel communities respond to *e.g.,* extinction, turnover, invasion and rewilding ✓	Gravel *et al.* (2016a); Dunne *et al.* (2002)
		Diet-based conservation focusing not only on the target species but the species it might depend on for food resources △	Rooney & McCann (2012); Curtsdotter *et al.* (2011); McDonald-Madden *et al.* (2016)

Network Representation	Common Inferential Pitfall	Principal questions and applications	Representative Studies
		Rewiring capacity/potential of species by looking at the *entire* diets of species $^{\Delta}$	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	Assuming co-occurrence implies trophic interaction	Applied use potential of questions highlighted for global metawebs at the management scale *e.g.,* a protected area $^{\Delta}$	Albouy *et al.* (2014); Pellissier *et al.* (2018); Estrada & Bodin (2008)
		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	Common Inferential Pitfall	Principal questions and applications	Representative Studies
Realised Webs	Assuming observed binary links quantify interaction strength or complete diets.	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)
		Explicitly 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 *et al.* (2016b); Gilarranz *et al.* (2017)

5.1 Matching network representations to ecological questions

The choice of network representation should follow the ecological unit of interest, rather than simply the availability of a dataset or analytical method. The distinctions provided in Box 2 serve as a practical guidance for selecting, constructing, and evaluating networks.

Below we discuss this in more detail for each type of network reconstruction.

Question mapping

Global metawebs

Primary question: Which feeding interactions are biologically feasible within a broader species pool?

Use when: Investigating potential diet breadth, evolutionary constraints on feeding, novel communities, species introductions, or the potential for interaction rewiring under future environmental conditions.

You need: A defined species pool and evidence or assumptions about interaction compatibility, typically based on traits, phylogeny, or documented interactions. Spatial co-occurrence need not be imposed if the aim is to represent the broader feasible interaction space.

It lets you infer: Which interactions are plausible, which appear incompatible, and which potential feeding relationships could become relevant as species distributions or environmental conditions change.

Check it by: Testing predictions against independent interaction records where possible, including evidence for both feasible and forbidden links. Assess sensitivity to the species pool, trait definitions, and rules used to infer compatibility.

Do not infer: That every feasible interaction occurs, that all listed interactions can occur simultaneously, or that the network structure describes energy flow in any specific community.

Regional metawebs

Primary question: Which feasible interactions are possible among species that occur, or are expected to occur, within a region?

Use when: Examining potential interactions within a regional species pool, anticipating community changes following range shifts, or assessing possible feeding relationships involving introduced or reintroduced species.

You need: A regional species pool, distribution or co-occurrence information at an appropriate scale, and rules for identifying feasible feeding relationships.

It lets you infer: How regional species availability constrains the feasible interaction space, and how that space may change as species distributions shift.

Check it by: Comparing predicted species occurrence and feasible interactions with independent distribution and interaction data. When comparing regions, separate

changes due to species turnover from changes in interaction constraints.

Do not infer: That co-occurring species necessarily interact, or that differences between regional networks necessarily reflect changes in feeding behaviour or interaction processes.

Realised networks

Primary question: Which interactions occur, and how are they distributed or expressed, under specific ecological conditions?

Use when: Investigating community responses to environmental change, temporal rewiring, trophic dynamics, or the consequences of altered interactions for ecosystem functioning.

You need: Interaction observations or a predictive model that represents relevant ecological conditions, such as species abundance, environmental context, and diet choice. The temporal window and sampling process should be explicit.

It lets you infer: Which interactions are supported under the sampled or modelled conditions, and (where the data permit) how interaction frequencies or strengths change through space or time.

Check it by: Evaluating predictions against independent observations, accounting for imperfect detection and sampling effort, and assessing whether the network captures the properties relevant to the ecological question.

Do not infer: That unobserved links are impossible, or that a network aggregated across many places or times represents a single community state.

5.1.1 Global Metawebs

Global metawebs are most appropriate for questions about interaction feasibility and potential diet breadth (Adhurya & Park 2025; Mestre & Bastazini 2026). They provide a framework for exploring hypothetical or novel communities under climate change (Hui & Richardson 2019), species invasions, reintroductions, and rewilding, including the potential for species to rewire their interactions (Marjakangas *et al.* 2025). Because global metawebs represent a broad pool of feasible links, they can also support investigations of eco-evolutionary dynamics and how evolutionary history, natural selection, and phenotypic plasticity shape interaction niches.

However, a global metaweb describes potential interactions, not the ecological conditions under which they occur. Its usefulness therefore depends on how well the inferred feasible

interaction space represents biological compatibility and on how that space is translated into a specific community or ecological scenario. In conservation applications, for example, a species' potential diet can help identify the resources it may depend on but cannot establish which resources sustain it in a particular location (Curtsdotter *et al.* 2011; McDonald-Madden *et al.* 2016; Rooney & McCann 2012). Similarly, the presence of a potential link may indicate an opportunity for rewiring but does not demonstrate that a consumer will adopt that interaction (Gilljam *et al.* 2015; Staniczenko *et al.* 2010; Su *et al.* 2024).

5.1.2 Regional Metawebs

Regional metawebs constrain the potential interaction space to species occurring, or expected to occur, within a defined region. This makes them particularly relevant to management questions involving protected areas, changing species distributions, and anticipated shifts in community composition. They can also help refine species distribution models by incorporating information about biotic associations (Albouy *et al.* 2014; Araújo & Luoto 2007; Estrada & Bodin 2008; Kissling *et al.* 2012; Pellissier *et al.* 2018).

The key challenge is distinguishing constraints imposed by regional species availability from constraints on feeding compatibility. Co-occurrence can restrict which interactions are possible but is not sufficient evidence that trophic interactions occur. Likewise, differences in regional metawebs across space or environmental gradients may arise from species turnover (*e.g.,* (β)-diversity), differences in inferred interaction feasibility, or both. Comparisons should therefore separate changes in the species pool from changes in the rules or evidence used to infer interactions.

5.1.3 Realised networks

Realised networks are best suited to questions about which interactions occur under specific ecological conditions and how their expression shapes community dynamics and ecosystem functioning (Thuiller *et al.* 2024). They provide the appropriate starting point for investigating the propagation of multiple stressors (Beauchesne *et al.* 2021; Crain *et al.* 2008), temperature-related thresholds in community collapse (O'Gorman *et al.* 2019; Petchey *et al.* 2010), persistence following harvesting or species loss (Allesina & Tang 2012; Yodzis 2001), and relationships between stability, diversity, productivity, and ecosystem function (Rooney & McCann 2012; Thébault & Fontaine 2010). They can also support investigations of metacommunity dynamics when interactions are considered

across multiple local communities (Gilarranz *et al.* 2017; Gravel *et al.* 2016b).

These inferences depend on how closely the network corresponds to the community state and process of interest. A binary interaction record indicates that an interaction was detected or documented, but does not necessarily quantify its strength, frequency, or contribution to energy transfer. Furthermore, empirical datasets often accumulate observations across extended periods or multiple locations, potentially obscuring temporal and spatial variation in interaction structure (Polis 1991). The increasing availability of long-term interaction datasets offers new opportunities to study these dynamics (Danet *et al.* 2024; Wooster *et al.* 2024), but requires methods that account for sampling effort, imperfect detection, and the spatiotemporal boundaries that need to be applied to ensure that one is operating in the 'realised space'.

5.2 Key methodological challenges

Below we highlight some of the key challenges that currently limit the precision, accuracy, and applied value of ecological network inference.

Validating interactions and network structure. Although ideas presented in Box 1 are presented as potential means of validation it is worth being explicit about the need to validate network structure and pairwise interactions independently. Considerable progress has been made in evaluating the recovery of pairwise interactions (Abramov *et al.* 2026; Poisot 2023; Strydom *et al.* 2021a), but there is less agreement on how to evaluate the recovery of network structure (Allesina *et al.* 2008; Tylianakis *et al.* 2010). The appropriate benchmark depends on the intended representation. For metawebs, evaluation should consider the recovery of both feasible and forbidden links. For realised networks, it remains important to establish when the priority is recovering individual interactions, aggregate properties (*e.g.,* connectance), or both. These objectives are related but not interchangeable: a model may reproduce a network's aggregate structure while misidentifying many of its constituent links, or recover links without accurately representing the structural properties relevant to the ecological question. For example, Strydom *et al.* (2026) showcase how structurally similar networks can disagree as to the specific pairwise interactions.

Connecting metawebs to realised networks. Many approaches for modelling realised networks do not explicitly incorporate evolutionary constraints, although exceptions exist (Van De Walle *et al.* 2023; Wootton *et al.* 2023). Bridging this gap may require ensemble

approaches (Becker *et al.* 2022; Terry & Lewis 2020) or methods that downscale metawebs into context-specific networks (*e.g.,* Roopnarine 2006). Such transitions must account for the ecological filters that determine which feasible links are expressed, including species abundance, diet choice, and relevant environmental conditions. Structural realism alone does not establish that a model captures realised prey choice or energy flow.

More explicit links between metawebs and realised networks could also support integration with metacommunity, metaecosystem, and ecosystem-level theory (Liu *et al.* 2025; Massol *et al.* 2011). Achieving this requires greater clarity about the spatial and temporal scales at which networks should be constructed and interpreted, and how those scales relate to the ecological question (Fortin *et al.* 2021).

Making networks useful in conservation and management. Applied use remains constrained by difficulties in defining network boundaries, aligning networks with management units, and translating network metrics into policy-relevant conclusions (Dansereau *et al.* 2024b). Addressing these challenges requires stronger links between network structure and ecosystem function, alongside careful matching of network representations and analytical methods to management objectives (O'Connor *et al.* 2025; Pellissier *et al.* 2018). Managers need to know whether an analysis identifies potential interactions, predicts interactions under specified conditions, or evaluates consequences for interaction strength and ecosystem processes. These are distinct objectives and require different evidence.

Together, these challenges yield three principles: make construction data and assumptions explicit; align validation with the intended representation and inference; and model the processes that filter feasible links into context-dependent interactions. These principles support more transparent and robust inference across ecological scales.

6 Concluding Remarks

Ecological networks provide powerful abstractions for understanding biodiversity and ecosystem functioning, but their inferential value depends on what their nodes and edges represent, and which ecological processes underpin their construction. Distinguishing interaction feasibility from realisation clarifies why global and regional metawebs, realised networks, and structure-based models support different questions and should not be treated as interchangeable descriptions of ecological systems.

The central implication is that network construction should begin with the intended

inference, aligning representation, available evidence, and evaluation criteria. Assumptions about interaction feasibility, realisation, and spatial and temporal scales should be explicit, as should the objectives against which a network is evaluated. Recovering individual interactions, reproducing network structure, and predicting ecological outcomes are distinct goals, and success in one does not guarantee success in another. Potential interactions should not be mistaken for realised feeding, just as structural similarity should not be taken as evidence of the ecological mechanisms that generate a network.

Ultimately, the value of a food web lies not in how closely it resembles a real-world network, but in whether it captures the ecological relationships needed to answer a particular question. By making the transitions from evolutionary feasibility to spatiotemporal availability and local realisation explicit, our framework provides a basis for testing when and why different network representations lead to different conclusions. The challenge now is to move beyond asking whether a network reproduces observed patterns towards establishing which processes those patterns reflect, and whether representing those processes improves predictions of ecological change. Doing so will help turn food webs from useful descriptions of biodiversity into more transparent, testable tools for understanding and anticipating how ecological communities respond to a changing world.

References

Abramov, K., Nehoray, S.M., Puzis, R., Mucha, P. & Pilosof, S. (2026). Contextual evidence for categorising interactions and guiding their discovery.

Adhurya, S. & Park, Y.-S. (2025). Metaweb approaches for understanding complex ecological interactions: A review. *Ecological Informatics*, 91, 103367.

Albouy, C., Archambault, P., Appeltans, W., Araújo, M.B., Beauchesne, D., Cazelles, K., *et al.* (2019). The marine fish food web is globally connected. *Nature Ecology & Evolution*, 3, 1153–1161.

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., *et al.* (2014). From projected species distribution to food-web structure under climate change. *Global Change Biology*, 20, 730–741.

Allesina, S., Alonso, D. & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320, 658–661.

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

Araújo, M.B. & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol Biogeography*, 16, 743–753.

Banville, F., Gravel, D. & Poisot, T. (2023). What constrains food webs? A maximum entropy framework for predicting their structure with minimal biases. *PLOS Computational Biology*, 19, e1011458.

Banville, F., Strydom, T., Blyth, P.S.A., Brimacombe, C., Catchen, M.D., Dansereau, G., *et al.* (2025). Deciphering Probabilistic Species Interaction Networks. *Ecology Letters*, 28, e70161.

Bascompte, J. (2007). Networks in ecology. *Basic and Applied Ecology*, 8, 485–490.

Bascompte, J. & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38, 567–593.

Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *PNAS*, 100, 9383–9387.

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, e1002321.

Beauchesne, D., Cazelles, K., Archambault, P., Dee, L.E. & Gravel, D. (2021). On the sensitivity of food webs to multiple stressors. *Ecol Lett*, 24, 2219–2237.

Beauchesne, D., Desjardins-Proulx, P., Archambault, P. & Gravel, D. (2016). Thinking outside the box - Predicting biotic interactions in data-poor environments. *Vie et Milieu*, 66, 333–342.

Becker, D.J., Albery, G.F., Sjodin, A.R., Poisot, T., Bergner, L.M., Chen, B., *et al.* (2022). Optimising predictive models to prioritise viral discovery in zoonotic reservoirs. *The Lancet Microbe*, 3, e625–e637.

Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006). Foraging biology predicts food web complexity. *Proc. Natl. Acad. Sci. U.S.A.*, 103, 13745–13749.

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, 841–854.

Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004). Interaction strengths in food webs: Issues and opportunities. *J Anim Ecology*, 73, 585–598.

Biton, B., Puzis, R. & Pilosof, S. (2025). Inductive link prediction facilitates the discovery of missing links and enables cross-community inference in ecological networks. *Nat*

Ecol Evol, 9, 1214–1223.

Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23, 1050–1063.

Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology*, 11, 185–195.

Blüthgen, N. & Staab, M. (2024). A Critical Evaluation of Network Approaches for Studying Species Interactions. *Annual Review of Ecology, Evolution, and Systematics*, 55, 65–88.

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. *Nat Commun*, 9, 2603.

Brimacombe, C., Bodner, K. & Fortin, M.-J. (2024a). Applying a method before its proof of concept: A cautionary tale using inferred food webs. *Global Change Biology*, 30, e17360.

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

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, e3002068.

Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228–1236.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, 85, 1771–1789.

Buche, L., Bartomeus, I. & Godoy, O. (2024). Multitrophic Higher-Order Interactions Modulate Species Persistence. *The American Naturalist*, 203, 458–472.

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, 468–479.

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, e13807.

Caron, D., Maiorano, L., Thuiller, W. & Pollock, L.J. (2022). Addressing the Eltonian shortfall with trait-based interaction models. *Ecology Letters*, 25, 889–899.

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, 835–839.

Cherif, M., Brose, U., Hirt, M.R., Ryser, R., Silve, V., Albert, G., *et al.* (2024). The environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*, 138.

Cirtwill, A.R., Ekl f, 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, 902–911.

Clegg, T., Ali, M. & Beckerman, A.P. (2018). The impact of intraspecific variation on food web structure. *Ecology*, 99, 2712–2720.

Cohen, J.E., Briand, F. & Newman, C. (1990). *Community Food Webs: Data and Theory*. Biomathematics. Springer-Verlag, Berlin Heidelberg.

Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol Lett*, 11, 1304–1315.

Cuff, J.P., Evans, D.M., Vaughan, I.P., Wilder, S.M., Tercel, M.P.T.G. & Windsor, F.M. (2024). Networking nutrients: How nutrition determines the structure of ecological networks. *Journal of Animal Ecology*, 93, 974–988.

Curtsdotter, A., Banks, H.T., Banks, J.E., Jonsson, M., Jonsson, T., Laubmeier, A.N., *et al.* (2019). Ecosystem function in predator–prey food webs—confronting dynamic models with empirical data. *Journal of Animal Ecology*, 88, 196–210.

Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., *et al.* (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs. *Basic and Applied Ecology*, 12, 571–580.

Dalla Riva, G.V. & Stouffer, D.B. (2016). Exploring the evolutionary signature of food webs' backbones using functional traits. *Oikos*, 125, 446–456.

Dallas, T., Park, A.W. & Drake, J.M. (2017). Predicting cryptic links in host-parasite networks. *PLOS Computational Biology*, 13, e1005557.

Danet, A., Kéfi, S., Johnson, T.F. & Beckerman, A.P. (2024). *Response diversity is a major driver of temporal stability in complex food webs*. Available at: https://www.biorxiv.org/content/10.1101/2024.08.29.610288v1. Last accessed 24 November 2024.

Dansereau, G., Barros, C. & Poisot, T. (2024a). Spatially explicit predictions of food web structure from regional-level data. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, 379.

Dansereau, G., Braga, J., Ficetola, G.F., Galiana, N., Gravel, D., Maiorano, L., *et al.* (2024b). Overcoming the disconnect between interaction networks and biodiversity conservation and management.

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, 881–886.

Desjardins-Proulx, P., Laigle, I., Poisot, T. & Gravel, D. (2017). Ecological interactions and the Netflix problem. *PeerJ*, 5, e3644.

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

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. *Nat Commun*, 15, 8599.

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

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, 558–567.

Eklöf, A., Tang, S. & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach. *Methods Ecol Evol*, 4, 760–770.

Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.

Erdős, P. & Rényi, A. (1959). On Random Graphs I. *Publicationes Mathematicae*.

Estrada, E. & Bodin, Ö. (2008). Using Network Centrality Measures to Manage Landscape Connectivity. *Ecological Applications*, 18, 1810–1825.

Fortin, M.-J., Dale, M.R.T. & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proc. R. Soc. B.*, 288, rspb.2020.1889, 20201889.

Fortuna, M.A. & Bascompte, J. (2006). Habitat loss and the structure of plant-animal mutualistic networks: Mutualistic networks and habitat loss. *Ecology Letters*, 9, 281–286.

Fricke, E.C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C.D., Sanisidro, O., *et al.* (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene. *Science*, 377, 1008–1011.

Galiana, N. & Araújo, M.B. (2026). Biotic interactions biogeography: A framework for

understanding how species interactions shape biodiversity patterns across scales. *PLOS Biology*, 24, e3003813.

García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J.B., Allen-Perkins, A., *et al.* (2023). Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. *Ecology Letters*, 26, 831–842.

Gauzens, B., Thouvenot, L., Srivastava, D.S., Kratina, P., Romero, G.Q., Berti, E., *et al.* (2025). Tailoring interaction network types to answer different ecological questions. *Nat. Rev. Biodivers.*, 1–10.

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*, 357, 199–201.

Gilljam, D., Curtsdotter, A. & Ebenman, B. (2015). Adaptive rewiring aggravates the effects of species loss in ecosystems. *Nat Commun*, 6, 8412.

Golubski, A.J. & Abrams, P.A. (2011). Modifying modifiers: What happens when interspecific interactions interact? *Journal of Animal Ecology*, 80, 1097–1108.

Gómez, J.M., Verdú, M. & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, 465, 918–921.

Gravel, D., Albouy, C. & Thuiller, W. (2016a). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions: Biological Sciences*, 371, 1–14.

Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., *et al.* (2019). Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, 42, 401–415.

Gravel, D., Massol, F. & Leibold, M.A. (2016b). Stability and complexity in model meta-ecosystems. *Nature Communications*, 7, 12457.

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, 1083–1090.

Habedank, J., Horn, S., Lemke, P., Sidorenko, V. & Wiltshire, K.H. (2025). A new perspective for revealing "hidden" interactions in ecological networks. *Methods in Ecology and Evolution*, 16, 1314–1321.

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, e70061.

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.

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

Hui, C. & Richardson, D.M. (2019). How to Invade an Ecological Network. *Trends in Ecology & Evolution*, 34, 121–131.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., *et al.* (2009). Ecological networks–beyond food webs. *J Anim Ecol*, 78, 253–269.

Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14, e1002559.

Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*.

Kamaru, D.N., Palmer, T.M., Riginos, C., Ford, A.T., Belnap, J., Chira, R.M., *et al.* (2024). Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. *Science*, 383, 433–438.

Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., *et al.* (2015). Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, 96, 291–303.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., *et al.* (2012). More than a meal… integrating non-feeding interactions into food webs. *Ecology Letters*, 15, 291–300.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J., *et al.* (2012). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, 39, 2163–2178.

Krishna, A., Guimarães Jr, P.R., Jordano, P. & Bascompte, J. (2008). A neutral-niche theory of nestedness in mutualistic networks. *Oikos*, 117, 1609–1618.

Lindeman, R.L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23, 399–417.

Liu, J., Liu, M., Yin, J., Zhang, Y., Guo, Y., Yu, T., *et al.* (2025). Harnessing food webs as a framework for enhancing ecosystem multifunctionality. *Biological Conservation*, 310, 111383.

Llewelyn, J., Strona, G., Dickman, C.R., Greenville, A.C., Wardle, G.M., Lee, M.S.Y., *et al.* (2023). Predicting predator–prey interactions in terrestrial endotherms using random forest. *Ecography*, 2023, e06619.

Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis

of underlying mechanisms. *Ecology Letters*, 16, 106–115.

MacArthur, R. (1955). Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology*, 36, 533–536.

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

Martinez, N.D. (1991). Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web. *Ecological Monographs*, 61, 367–392.

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

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, 313–323.

McDonald-Madden, E., Sabbadin, R., Game, E.T., Baxter, P.W.J., Chadès, I. & Possingham, H.P. (2016). Using food-web theory to conserve ecosystems. *Nat Commun*, 7, 10245.

Mestre, F. & Bastazini, V.A.G. (2026). Metawebs as a tool to connect ecology and biogeography: A critical review. *Ecological Modelling*, 519, 111674.

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, e1007269.

Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264.

Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., *et al.* (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, 7, 584–600.

Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, 30, 347–356.

Moulatlet, G., Luna, P., Dattilo, W. & Villalobos, F. (2024). *The scaling of trophic specialization in interaction networks across levels of organization*. Available at: https://www.authorea.com/users/847478/articles/1235293-the-scaling-of-trophic-specialization-in-interaction-networks-across-levels-of-organization?commit=b492c8793c4eb5b0992b803ab4b784bd9cc1c4bb. Last accessed 7 November 2024.

O'Connor, L.M.J., Thuiller, W., Brose, U., Chenevois, É., Freund, C., Gauzens, B., *et al.* (2025). The untapped potential of food webs in systematic conservation planning.

O'Gorman, E.J., Petchey, O.L., Faulkner, K.J., Gallo, B., Gordon, T.A.C., Neto-Cerejeira, J., *et al.* (2019). A simple model predicts how warming simplifies wild food webs. *Nat. Clim. Chang.*, 9, 611–616.

Odum, E.P. (1968). Energy Flow in Ecosystems: A Historical Review. *Am Zool*, 8, 11–18.

Pawar, S., Dell, A.I. & Savage, V.M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, 486, 485–489.

Pecuchet, L., Blanchet, M.-A., Frainer, A., Husson, B., Jørgensen, L.L., Kortsch, S., *et al.* (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Global Change Biology*, 26, 4894–4906.

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., *et al.* (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93, 785–800.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web structure. *Proc. Natl. Acad. Sci. U.S.A.*, 105, 4191–4196.

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, 2081–2091.

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, 281–293.

Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nat Ecol Evol*, 1, 101.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods in Ecology and Evolution*, 14, 1333–1345.

Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., *et al.* (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*, 48, 1552–1563.

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

Poisot, T., Ouellet, M.-A., Mollentze, N., Farrell, M.J., Becker, D.J., Brierley, L., *et al.* (2023). Network embedding unveils the hidden interactions in the mammalian virome.

Patterns, 4, 100738.

Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251.

Poisot, T., Stouffer, D.B. & Kéfi, S. (2016b). Describe, understand and predict: Why do we need networks in ecology? *Functional Ecology*, 30, 1878–1882.

Polis, G.A. (1991). Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory. *The American Naturalist*, 138, 123–155.

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., *et al.* (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5, 397–406.

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, 356–367.

Pompanon, F., Deagle, B.E., Symondson, W.O.C., Brown, D.S., Jarman, S.N. & Taberlet, P. (2012). Who is eating what: Diet assessment using next generation sequencing. *Mol Ecol*, 21, 1931–1950.

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, 323–334.

Post, D.M. (2002). Using Stable Isotopes To Estimate Trophic Position: Models, Methods, And Assumptions. *Ecology*, 83, 703–718.

Pringle, R.M. (2020). Untangling Food Webs. In: *Unsolved Problems in Ecology*. Princeton University Press, pp. 225–238.

Pringle, R.M. & Hutchinson, M.C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology, Evolution and Systematics*, 51, 55–80.

Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, 20, 345–353.

Pyke, G. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and Systematic*, 15, 523–575.

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, 170–177.

Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution*, 27, 40–46.

Roopnarine, P.D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs.

Paleobiology, 32, 1–19.

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

Rossberg, A.G., Matsuda, H., Amemiya, T. & Itoh, K. (2006). Food webs: Experts consuming families of experts. *Journal of Theoretical Biology*, 241, 552–563.

Saberski, E., Lorimer, T., Carpenter, D., Deyle, E., Merz, E., Park, J., *et al.* (2024). The impact of data resolution on dynamic causal inference in multiscale ecological networks. *Commun Biol*, 7, 1–10.

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, 908–917.

Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. *Nat Commun*, 7, 12718.

Segar, S.T., Fayle, T.M., Srivastava, D.S., Lewinsohn, T.M., Lewis, O.T., Novotny, V., *et al.* (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology & Evolution*, 35, 454–466.

Shaw, J.O., Dunhill, A.M., Beckerman, A.P., Dunne, J.A. & Hull, P.M. (2024). *A framework for reconstructing ancient food webs using functional trait data*. Available at: https://www.biorxiv.org/content/10.1101/2024.01.30.578036v1. Last accessed 1 February 2024.

Simmons, B.I., Blyth, P.S.A., Blanchard, J.L., Clegg, T., Delmas, E., Garnier, A., *et al.* (2021). Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nat Ecol Evol*, 5, 1478–1489.

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, e2012493118.

Sousa, L., Silva, S. & Xavier, R. (2019). DNA metabarcoding in diet studies: Unveiling ecological aspects in aquatic and terrestrial ecosystems. *Environmental DNA*, 1.

Staniczenko, P.P.A., Lewis, O.T., Jones, N.S. & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, 13, 891–899.

Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory*. Princeton University Press.

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

Stouffer, D.B., Camacho, J., Guimerà, R., Ng, C.A. & Nunes Amaral, L.A. (2005). Quantitative Patterns in the Structure of Model and Empirical Food Webs. *Ecology*, 86, 1301–1311.

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2022). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, 13, 2838–2849.

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2023). Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations. *Methods in Ecology and Evolution*, 14, 2917–2930.

Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021a). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20210063.

Strydom, T., Dalla Riva, G.V. & Poisot, T. (2021b). SVD Entropy Reveals the High Complexity of Ecological Networks. *Front. Ecol. Evol.*, 9.

Strydom, T., Karapunar, B., Dunne, J.A., Hull, P., Little, C.T.S., Pimiento, C., *et al.* (2026). Are We Mapping Ecosystems or Models? Framework Choices Dominate Food Web Topology and Extinction Inferences.

Su, M., Ma, Q. & Hui, C. (2024). Adaptive rewiring shapes structure and stability in a three-guild herbivore-plant-pollinator network. *Commun Biol*, 7, 103.

Terry, J.C.D. & Lewis, O.T. (2020). Finding missing links in interaction networks. *Ecology*, 101, e03047.

Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853–856.

Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L.M.J., Ohlmann, M., *et al.* (2024). Navigating the integration of biotic interactions in biogeography. *Journal of Biogeography*, 51, 550–559.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, Conserving complexity: Global change and community-scale interactions, 143, 2270–2279.

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, 913–924.

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, 2025–2034.

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, 1445–1457.

Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.

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, 57–69.

Wooster, E.I.F., Middleton, O.S., Wallach, A.D., Ramp, D., Sanisidro, O., Harris, V.K., *et al.* (2024). Australia's recently established predators restore complexity to food webs simplified by extinction. *Current Biology*, 34, 5164–5172.e2.

Wootton, K.L., Curtsdotter, A., Roslin, T., Bommarco, R. & Jonsson, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology*, 37, 26–43.

Yeakel, J.D., Pires, M.M., Rudolf, L., Dominy, N.J., Koch, P.L., Guimarães, P.R., *et al.* (2014). Collapse of an ecological network in Ancient Egypt. *PNAS*, 111, 14472–14477.

Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*, 120, 551–570.

Yodzis, P. (2001). Must top predators be culled for the sake of fisheries? *Trends in Ecology & Evolution*, 16, 78–84.

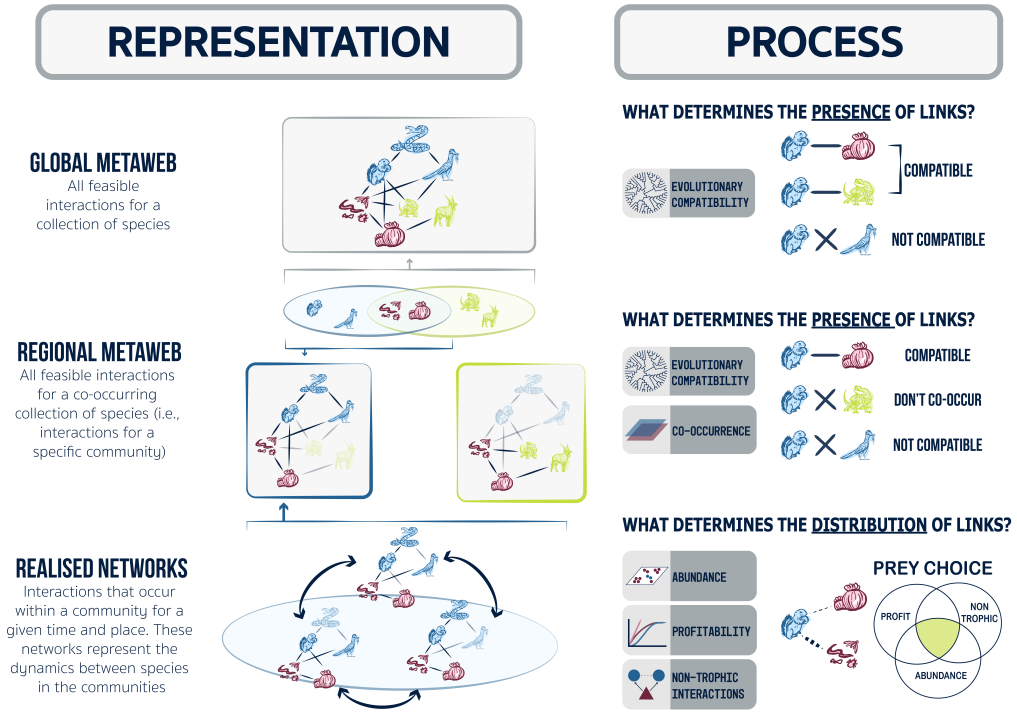


Figure 1: Conceptual summary of the process-based hierarchy linking food web representations to ecological filters. A **global metaweb** represents evolutionarily feasible consumer–resource links across a defined species pool. Restricting this pool by spatiotemporal overlap yields **regional metawebs**, which differ with regional species composition. Species occurring in both regions are shown in red, whereas region-specific species are shown in blue and yellow. **Realised food webs** emerge when abundance, consumer diet choice, and non-trophic interaction modification further filter feasible links under local conditions. The arrows represent transitions that can be tested separately: compatibility constrains the global feasible set; overlap constrains the regional set; and ecological context determines which remaining links occur and how strongly. The framework predicts nested constraints in principle, while allowing empirical estimates to differ because of uncertainty, incomplete sampling, and scale mismatch.

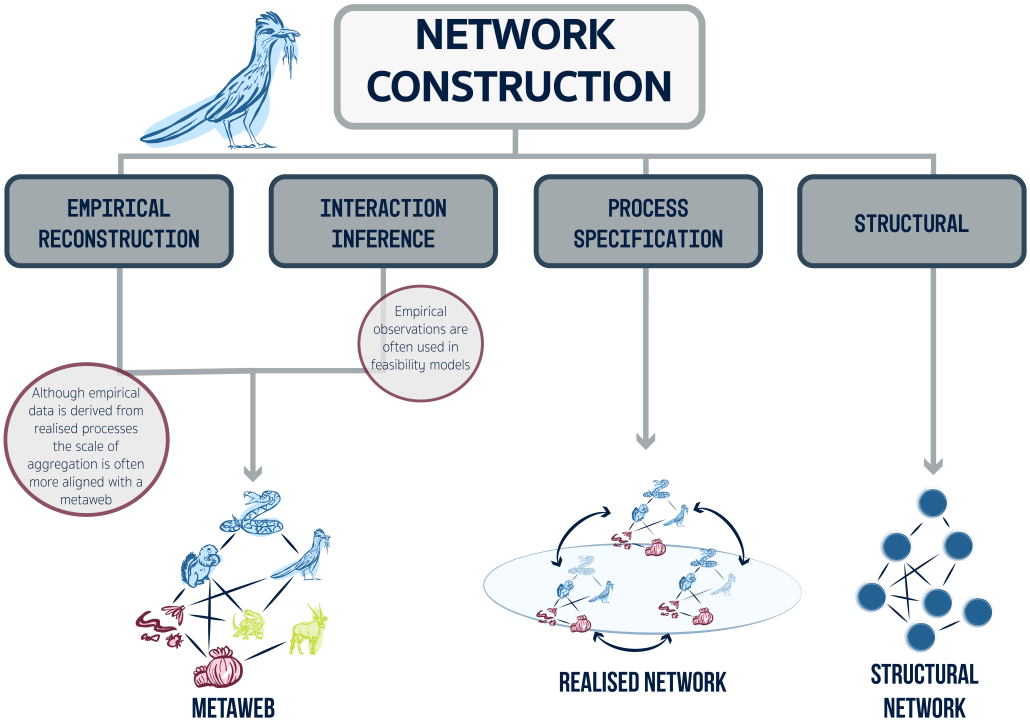


Figure 2: Flow chart showing four approaches to network construction: empirical, feasibility-based, process-based, and structure-based, highlighting the resulting network representation.