

Unveiling the Complexity of Food Webs: A Comprehensive Overview of Definitions, Scales, and Mechanisms

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Abstract: Food webs are a useful abstraction and representation of the feeding links between species in a community and are used to infer many ecosystem level processes. However, the different theories, mechanisms, and criteria that underpin how a food web is defined, and ultimately, constructed means that not all food webs are representing the same ecological process at the same scale. Here we present a synthesis of the different assumptions, scales, and mechanisms that are used to define the different ecological networks, leading to a revision of definitions for different types of networks. Additionally we explicitly link the different network representations to the broader methodological approaches (models) that are used to construct them. In explicitly outlining the assumptions, scales, and mechanisms of network inference allows for a formal categorisation of how to use networks to answer key ecological and conservation questions as well as defining clear guidelines to prevent unintentional misuse or misinterpretation.

Keywords: food web, network construction, scientific ignorance

At the heart of modern biodiversity science are a set of concepts and theories about species richness, stability, and function (Loreau & de Mazancourt, 2013). These relate to the abundance, distribution, and services that biodiversity provides, and how biodiversity (as an interconnected set of species) responds to multiple stressors. Documenting interactions between and among species is thus one of the fundamental building blocks of community ecology, providing a powerful abstraction and platform for mathematical and statistical modelling of biodiversity to make predictions, mitigate threats, and manage services (Windsor et al., 2023). Such network representations of biodiversity are increasingly argued to be an asset to understanding and predicting the abundance, distribution, dynamics, and services provided by multiple species facing multiple stressors (Simmons et al., 2021). However, there is a growing discourse around limitations to the interpretation and applied use of networks (Blüthgen, 2010; Dormann, 2023), primarily as the result of shortcomings regarding their conceptualisation (Blüthgen & Staab, 2024).

We propose that every network embeds assumptions about the process(es) that determine interactions, and about the levels of organization at which this occurs (*i.e.* the biological, ecological, spatial/temporal scale). The differences in these assumptions ultimately influence the nature and scope of inference that can be made from a given network (Proulx et al., 2005). Fundamentally, we are talking about an intersection of the data used to construct the network and the underlying theory as to what drives the occurrence of interactions between species. Although there have been extensive discussions about the challenges relating to data collection and observation (*e.g.*, Blüthgen & Staab, 2024; Brimacombe et al., 2023, 2024; Moulatlet et al., 2024; Polis, 1991; Pringle & Hutchinson, 2020; Saberski et al., 2024) we still lack a clear framework framed by the different assumptions and scale dependent processes.

In this perspective we aim to provide an overview of the different **food web** representations, particularly how these relate to the terminology used to define a food web, and how this is influenced by both the processes that determine interactions Section 2, as well as how this relates to the way in which we construct the resulting networks Section 3. This allows us to deliver an overview of fundamental questions in ecology that we think can benefit from network thinking and a proposal that such thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities. Specifically, we finish this perspective with an overview of fundamental questions in ecology that we think can benefit from network thinking and a proposal that such thinking can accelerate our capacity to predict the impact of change on biodiverse communities.

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

Networks often have multiple uses: an ‘object’ from which inferences are made (*e.g.*, topological inference about biodiversity, interactions among species, and community structure, [REF]); a platform for evaluating ‘downstream’ responses to stressors [REF]; and a platform for evaluating mathematical and statistical models of ‘generative processes’ [REF]. Against this backdrop of multiple research agendas, it should come as no surprise that the definition of ‘edges’ and ‘nodes’, as well as the levels of organisation at which they are collated takes many forms (Moulatlet et al., 2024; Poisot, Stouffer, et al., 2016), while also encoding a series of assumptions within a network.

1.1 How do we define a node?

Although this may seem elementary that a node should represent a (taxonomic) species, the reality is that nodes often represents non-taxonomic units such as a trophic species (*e.g.*, Yodzis (1982); Williams & Martinez (2000)), a feeding guild (*e.g.*, García-Callejas et al., 2023), or a segregation of species by life stages (*e.g.*, Clegg et al., 2018). Such granularity and variation can limit the ability to make (taxonomic) species specific inferences (*e.g.*, does species *a* eat species *b*?), affect inference made from networks, including estimates of complexity and structure (Beckerman et al., 2006; Clegg et al., 2018) and make it challenging to use networks in ‘downstream analyses’, for example, of extinction or invasions. Despite these implications, there may also be value in having nodes that represent an aggregation of species, as the distribution of the links between them may be more meaningful in terms of understanding energy flow and distribution within the system.

1.2 What is captured by an edge?

Links within food webs can be thought of as a representation of either feeding links between species (be that realised or potential (Dunne, 2006; Pringle, 2020), or fluxes within a system *e.g.*, energy transfer or material flow as the result of the feeding links between species (Lindeman, 1942). These correspond to different ‘currencies’ (the feasibility of links or the energy that is moving between nodes). There are also a myriad of ways in which the links themselves can be specified. Links between species can be treated present or absent (*i.e.*, binary), may be defined as probabilities (Banville et al., 2024; Poisot, Cirtwill, et al., 2016) or by continuous functions which further quantify the strength of an interaction (Berlow et al., 2004). How links are specified will influence the structure of the network. For example, taking a food web that consists of links representing all *potential* feeding links in a collection of species will be meaningless if one is interested in understanding the flow of energy through the network as the links are not environmentally/energetically constrained.

1.3 Network representations

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

A metaweb is at its core a list of feasible interactions between pairs of species. The feasibility for a given pair is derived from the complementarity (phylogenetic relationships) of their traits (representing a *global metaweb*), which can be further refined by co-occurrence (representing a *regional metaweb*). By this definition, metawebs provide a means to identify links that are not ecologically plausible, *i.e.*, forbidden links (Jordano, 2016b), or provide an idea of the *complete* diet of a species (Strydom et al., 2023).

In contrast realised networks are relatively localised in space and time, and the links between species are contingent on both the co-occurrence of species, the role of the environment, and mechanisms of diet choice. Fundamentally this means that the presence/absence of a link is the result of the ‘behaviour’ of the species.

This distinction between metawebs and realised webs lead to some further definitions. Links that are absent in a metaweb can conceptually (although not always practically) be treated as being truly absent. However, links that are absent in a realised network cannot be considered as truly absent but rather as absent due to the broader environmental/community context. Furthermore, a realised network is not simply the downscaling of a metaweb to a smaller scale (*e.g.*, moving from the country to the 1x1 km² scale based on fine-scale species co-occurrence). Instead, realised webs capture processes that determine the realisation of an interaction. Specifically, in realised webs, the definition of an edges shifts from being determined by feasibility to that of choices and consequences that centre around energy. Meaning if one were to take the same community of species and constructed both a metaweb and realised network the two networks might have the same species but would be structurally different, owing to the differences in the ‘rules’ constraining the presence of links (Caron et al., 2024).

2 From Nodes and Edges to Process and Constraints

In the previous section we discussed how the definition of nodes and edges at representing different biological and ecological and processes associated with them lead to the concept of a metaweb and a realised web. Here we expand this discussion, introducing five core constraints across these scales that further expose processes that determine the links among species: evolutionary compatibility, co-occurrence, abundance, diet choice,

and non-trophic interactions Figure 1.

[Figure 1 about here.]

2.1 Processes that determine the feasibility of an interaction

Here we introduce evolutionary compatibility and co-occurrence as processes that ‘act’ at the species pair of interest, that is the possibility of an interaction being present/absent is assessed at the pairwise level.

Here we introduce evolutionary compatibility and co-occurrence as processes that ‘act’ at the species pair of interest. The scale of inference and set of processes embodied in these two constraints combine to define a ‘list’ of interactions that are viable/feasible and defined as present/absent. It is however possible to build a network from this information. However, it is important to be aware that the structure of this network is not constrained by any community context and so just because species are able to interact does not mean that they will (Poisot et al., 2015).

Evolutionary compatibility

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

Networks arising from this constraint can be binary (possible vs forbidden) or probabilistic (Banville et al., 2024), *e.g.*, the metaweb constructed by Strydom et al. (2022) uses probabilities to quantify their confidence with regards to the possibility of a specific interaction existing between two species. A network constructed on the basis of evolutionary compatibility is conceptually aligned with a ‘global metaweb’, and gives us information as to the feasibility of links between species despite the fact that they do not co-occur (as shown in Figure 1).

(Co)occurrence

The co-occurrence of species in both time and space is a fundamental requirement for an interaction between two species to occur (at least in terms of feeding links). Although co-occurrence data alone is insufficient for building an accurate and ecologically meaningful representation of *feeding links* (Blanchet et al., 2020), it is still a critical process that determines the realisation of a feeding link and allows us to spatially constrain a

global metaweb based on local communities (Dansereau, Barros, et al., 2024), in the context of Figure 1 this would be the metawebs for regions one and two.

2.2 Processes that modify the behaviour (preference) of species

Here we will showcase three processes that will ultimately influence the realisation of an interaction between species and form the conceptual basis for realised networks. As we show in Figure 1 a ‘truly realised’ network is the product of different facets of both the properties of the community (**abundance** and **non-trophic interactions**) as well as the individual (**profitability**). This represents a contextual shift where the presence (realisation) of an interaction is no longer constrained to evaluating the viability between a *pair* of species but rather takes into consideration information about the community and the individual (Quintero et al., 2024), and as discussed in Section 1.3, links are now *constrained* by consumer choice.

Abundance

The most basic abundance constraint linked to foraging biology is the principle that organisms feeding randomly will consume resources in proportion to their abundance (Stephens & Krebs, 1986), and interactions are not necessarily contingent on there being any compatibility between them (E. Canard et al., 2012; Momal et al., 2020; Pomeranz et al., 2019). However, a more ecologically sound assumption would be that the abundance of different prey species will influence the distribution of links in a network (Vázquez et al., 2009), by influencing which prey are targeted or preferred by the predator, as abundance influences factors such as the likelihood of two species (individuals) meeting (Banville et al., 2024; Poisot et al., 2015). Thus, if abundance data are combined with a derived metaweb, there is a basic ruleset that can define the distribution (*e.g.*, structure) and potentially the strength of links.

Profitability

It is well established that consumers make more active decisions than eating items in proportion to their abundance (Stephens & Krebs, 1986). Ultimately, consumer choice is underpinned by an energetic cost-benefit framework centred around profitability and defined by traits associated with finding, catching, killing, and consuming a resource (Wootton et al., 2023). Although energetic constraints can be invoked in a myriad of ways (Cherif et al., 2024; *e.g.*, Pawar et al., 2012; Portalier et al., 2019) we select profitability as a term to capture rules linked to optimal foraging (Pyke, 1984) and metabolic theory (Brown et al., 2004); it is a sensible ‘umbrella concept’ for capturing the energetic constraint on of the distribution and strength of interactions.

Non-trophic interactions

Perhaps not as intuitive when thinking about the previous constraints, non-trophic interactions (Ings et al., 2009) specifically modify either the realisation or strength of trophic interactions (Golubski & Abrams, 2011; Kamaru et al., 2024; Pilosof et al., 2017; Staniczenko et al., 2010). Non-trophic interactions can modify interactions either ‘directly’ e.g., predator a outcompetes predator b; or ‘indirectly’ e.g., mutualistic/facilitative interactions. Altogether they can alter the fine-scale distribution and abundance of species as well as their persistence (Buche et al., 2024; Kéfi et al., 2012, 2015).

3 Network construction: a case for models

3.1 Why construct networks?

Broadly the desire to construct a network has arisen for two different purposes; building networks that can be used in real-world, applied contexts (have actionable consequences?), and building networks that allow us to interrogate, generate, and reflect upon different ecological theories. The act of constructing a ‘real world’ network through the empirical collection of interaction data is both costly and challenging to execute (Jordano, 2016a, 2016b), which has led to the development of a suite of approaches that allow us to predict the interaction between two species, or network structure (see Strydom, Catchen, et al., 2021 for a broader discussion), or identify missing interactions (gap fill) within existing empirical datasets (*e.g.*, Biton et al., 2024; Dallas et al., 2017; Stock, 2021). However, working with ‘real-world networks’ is data-hungry and cumbersome, and has driven the development of models that construct ecologically plausible networks. These models often explicitly model one or a few of the processes discussed in Section 2 and in doing so allow us to better understand the different constraints determining interactions (Song & Levine, 2024; Stouffer, 2019).

3.2 Construction through induction

Tools developed in the context of constructing networks allow a user to take a collection of species and determine what the interactions between them *could* be. Being able to predict a network is useful for determining all feasible interactions for a specific community, and the tools that have been developed in this context have the potential to allow us to construct first draft networks for communities for which we have no interaction data (Strydom et al., 2022). Making them valuable for interpolation in data poor regions and predicting interactions for ‘unobservable’ communities *e.g.*, prehistoric networks (Dunhill et al., 2024; Fricke et al., 2022; Yeakel et al., 2014) or future, novel community assemblages. Additionally, an understanding of the role of interactions between species has allowed us to better determine the distribution of a species by accounting

not only for the role of the environment but also the role of species interactions (Higino et al., 2023; Pollock et al., 2014).

Owing to the intense amount of data one would need at the community level to make predictions about the realisation of networks Section 2.2 the tools that predict interactions typically only assess the feasibility of interactions and typically focus on capturing some pairwise assessment of the likelihood of an interaction being present between two species. Resting on the assumption that there are a set of ‘feeding rules’ that can be used to make this assessment (Morales-Castilla et al., 2015). The determination of these feeding rules is typically done in a few ways, each with their own constraints and assumptions. Rules can be defined *a priori* based expert knowledge opinions, typically this is done on a trait-based basis *e.g.*, the paleo food web model (Shaw et al., 2024) specifies a series of rules for four different sets of traits and interactions are deemed feasible if all conditions are met. Alternatively rules can be elucidated by correlating real world interaction data with a suitable ecological proxy for which data is more widely available (*e.g.*, traits). These rules can be used by a binary classifier to determine if a link is present (see Pichler et al. (2020) for an overview), including generalised linear models (*e.g.*, Caron et al., 2022), random forest (*e.g.*, Llewelyn et al., 2023), trait-based k-NN (*e.g.*, Desjardins-Proulx et al., 2017), and Bayesian models (Cirtwill et al., 2019; *e.g.*, Eklöf et al., 2013). Finally, graph embedding uses the structural features of a known network to infer the position of species in the network (see Strydom et al. (2022) for a detailed review of methods).

Data implications for these approaches are that they require good datasets from which we can infer the rules, but because they contain real world species it does make it easier to validate them...

3.3 Construction through deduction

(I don’t know how to phrase this better.) As opposed to inferring interactions from known interaction, models are typically more formalised and deduced from a body of theory. SOMETHING ABOUT SYNTHETIC NETWORKS??

3.3.1 Species agnostic networks

These models define networks via an assumption that the interactions between species occurs irrespective of the identity of the species (i.e., species have no agency). Here there some assumption as to the expected structure of a network *i.e.*, the links between the nodes and how they might be distributed, typically constrained by connectance. There are three broad group of models based on some assumption.

First, links are randomly distributed throughout the network (Bascompte et al., 2003; *e.g.*, Fortuna & Bascompte, 2006), these models are often used as a ‘null hypothesis’ to ask questions about network structure (*e.g.*, Banville et al., 2023; Strydom, Dalla Riva, et al., 2021).

Second. Interactions that occur between species are due to the abundance of species within the community (E. F. Canard et al., 2014; Krishna et al., 2008; Pomeranz et al., 2019)

Third. Based on the idea that networks follow a trophic hierarchy and that network structure can be determined by distributing interactions along single dimension (the “niche axis”, Allesina et al. (2008)). Essentially these models can be viewed as being based on the idea of resource partitioning (niches) along a one-dimensional resource which will result in the standard ‘trophic pyramid’ to ensure that all species can ‘fit’ along this resource (which has strong ties back to the idea of intervality) *e.g.*, Cascade model (Cohen et al., 1990), Niche model (Williams & Martinez, 2000), Nested hierarchy model (Cattin et al., 2004).

These models are data light but there are some decisions that need to be made regarding what the expectations are on network structure.

3.3.2 Species-specific networks

In terms predicting interactions current models are rooted in feeding theory and allocate the links between species based on energy *e.g.*, diet models (Beckerman et al., 2006; Petchey et al., 2008) have been used construct networks based on both profitability (as determined by the handling time, energy content, and predator attack rate) as well as abundance (prey density). (Wootton et al., 2023).

At a ‘coarser’, functional level there are models that are based on the compartmentation and acquisition of energy for species at different trophic levels (Allesina & Pascual, 2009; Krause et al., 2003). Models that determine structure are based on the idea that networks follow a trophic hierarchy and that network structure can be determined by distributing interactions along single dimension [the “niche axis”; Allesina et al. (2008)], while parametrising an aspect of the network structure (although see Allesina & Pascual, 2009 for a parameter-free model).

They are ‘costly’ to construct in real world settings (requiring data about the entire community, as it is the behaviour of the system that determines the behaviour of the part) and also lack the larger diet niche context afforded by metawebs.

4 Making Progress with Networks

It is probably both this nuance as well as a lack of clear boundaries and guidelines as to the links between network form and function (although see Delmas et al., 2019) that has stifled the ‘productive use’ of networks beyond the inventorying the interactions between species. Although progress with using networks as a means to address questions within larger bodies of ecological theory *e.g.*, invasion biology (Hui & Richardson, 2019)

and co-existence theory (García-Callejas et al., 2023) has been made we still lack explicit guidelines as to what the appropriate network representation for the task at hand would be, and as highlighted in Box 1, underscores the need to evaluate exactly what process a specific network representation captures as well as its suitability for the question of interest. Below we present a mapping of what we believe are some of the key questions for which interaction networks can be used to the different networks representations that are most suitable, as well as highlight some of the methodological challenges that still need to be improved upon.

4.1 Making use of the different network representations

Methodological challenges

1. Tools that allow us to estimate both the feasibility as well as realisation of links: Currently most approaches to modelling realised networks fail to explicitly account for any form of evolutionary constraint Wootton et al. (2023) and we need to develop either an ensemble modelling approach (Becker et al., 2022; Terry & Lewis, 2020) or tools that will allow for the downsampling of metawebs into realised networks (*e.g.*, Roopnarine, 2006).
2. Is there something in generalisable models that ‘combine’ different processes/aspects (*e.g.*, using body size as a catch all) versus limited models that allow you to unpack things bit-by-bit (*i.e.*, process by process). So Wootton et al. (2023) *may* (TBD) span the gamut but it lacks the ability to unpack... Although maybe the terms do?
3. Modelling interaction strength: Although realised networks are more closely aligned with *explicitly* capturing interaction strength we lack models that allow us to quantify this (Strydom, Catchen, et al., 2021; Wells & O’Hara, 2013).
4. How do we validate our predictions?: Progress has been made to assess how well a model recovers pairwise interactions (Poisot, 2023; Strydom, Catchen, et al., 2021), but we still lack clear set of guidelines for benchmarking the ability of models to recover structure (Allesina et al., 2008)
5. Something about making what we do with networks more tractable in the applied space? *e.g.*, Dansereau, Braga, et al. (2024)

Theory challenges

1. Core Theory Advancement: Do the decades of insights arrived at for stability-diversity-productivity relationships with tri-trophic or diamond shaped models hold for complex communities (10’s-100s) (Danet et al., 2024); How will spatial and temporal variation in climate and productivity drive change in complex ecosystems. Necessary to move to predicting changes in biodiversity per se, ecosystem functions and identifying sensitive and robust species and portions of communities.

2. How will novel communities interact? How will range shifts and invasions result in new/novel community assemblages. And then also the intentional changes of species compositions through rewilding.
3. Does rewiring happen and does it deliver robustness? Specific sub points to consider here is persistence, especially persistence to perturbation. Again, dynamic networks and network/community assembly and finally extinctions (Dunhill et al., 2024).
4. When do invasive species enhance or decimate communities? When do reintroductions work? (Wooster et al., 2024)
5. Are there temperature threshold to community collapse
6. Can socioeconomic networks combined with biological networks drive understanding of externalities?
7. Can paleoecological data from deep time hyperthermal events provide sufficient insight into the targets, pace and recovery times from rapid climate events?

[Figure 2 about here.]

5 Concluding remarks

Having a clear understanding of the interplay between network representations and the processes that they are capable of encoding is critical if we are to understand exactly which networks can be used to answer which questions. As we highlight in Box 1 the different network representations have different potential uses and it should be clear that there is no ‘best’ network representation but rather a network representation that is best suited to its intended purpose. In providing a formalisation regards to the assumptions and mechanisms that need to be explicitly taken into consideration when deciding to use (and construct) networks we hope to prevent the unintentional misuse or misinterpretation of networks as well as provide a starting point from which we can develop a better framework for the applied use of networks to answer questions that are not only pressing within the field but also within broader biodiversity science.

References

- Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320(5876), 658–661. <https://doi.org/10.1126/science.1156269>
- Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, 12(7), 652–662. <https://doi.org/10.1111/j.1461-0248.2009.01321.x>
- 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(9), e1011458. <https://doi.org/10.1371/journal.pcbi.1011458>

[//doi.org/10.1371/journal.pcbi.1011458](https://doi.org/10.1371/journal.pcbi.1011458)

- Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction networks*. *EcoEvoRxiv*. <https://doi.org/10.32942/X28G8Z>
- Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Becker, D. J., Albery, G. F., Sjödin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T. A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling, E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic reservoirs. *The Lancet Microbe*, 3(8), e625–e637. [https://doi.org/10.1016/S2666-5247\(21\)00245-7](https://doi.org/10.1016/S2666-5247(21)00245-7)
- Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- Benadi, G., Dormann, C. F., Fründ, J., Stephan, R., & Vázquez, D. P. (2022). Quantitative Prediction of Interactions in Bipartite Networks Based on Traits, Abundances, and Phylogeny. *The American Naturalist*, 199(6), 841–854. <https://doi.org/10.1086/714420>
- Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3), 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables cross-community link prediction in ecological networks*.
- Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an ecologist’s guide. *Basic and Applied Ecology*, 11(3), 185–195. <https://doi.org/10.1016/j.baae.2010.01.001>
- Blüthgen, N., & Staab, M. (2024). A Critical Evaluation of Network Approaches for Studying Species Interactions. *Annual Review of Ecology, Evolution, and Systematics*, 55(1), 65–88. <https://doi.org/10.1146/annurev-ecolsys-102722-021904>
- Brimacombe, C., Bodner, K., Gravel, D., Leroux, S. J., Poisot, T., & Fortin, M.-J. (2024). Publication-driven consistency in food web structures: Implications for comparative ecology. *Ecology*, n/a(n/a), e4467. <https://doi.org/10.1002/ecy.4467>

- Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4), e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- Buche, L., Bartomeus, I., & Godoy, O. (2024). Multitrophic Higher-Order Interactions Modulate Species Persistence. *The American Naturalist*, 203(4), 458–472. <https://doi.org/10.1086/729222>
- Canard, E. F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D., & Gravel, D. (2014). Empirical Evaluation of Neutral Interactions in Host-Parasite Networks. *The American Naturalist*, 183(4), 468–479. <https://doi.org/10.1086/675363>
- Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*, 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- Cattin, M.-F., Bersier, L.-F., Banašek-Richter, C., Baltensperger, R., & Gabriel, J.-P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427(6977), 835–839. <https://doi.org/10.1038/nature02327>
- Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A., Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*, 138(1). <https://doi.org/10.1111/brv.13105>
- Cirtwill, A. R., Eklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6), 902–911. <https://doi.org/10.1111/2041-210X.13180>
- Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure. *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs’ backbones using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>

- Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. *PLOS Computational Biology*, 13(5), e1005557. <https://doi.org/10.1371/journal.pcbi.1005557>
- Danet, A., Kéfi, S., Johnson, T. F., & Beckerman, A. P. (2024). *Response diversity is a major driver of temporal stability in complex food webs* (p. 2024.08.29.610288). bioRxiv. <https://doi.org/10.1101/2024.08.29.610288>
- Dansereau, G., Barros, C., & Poisot, T. (2024). Spatially explicit predictions of food web structure from regional-level data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 379(1909). <https://doi.org/10.1098/rstb.2023.0166>
- Dansereau, G., Braga, J., Ficetola, G. F., Galiana, N., Gravel, D., Maiorano, L., Montoya, J. M., O'Connor, L., Pollock, L. J., Thuiller, W., Poisot, T., & Barros, C. (2024). *Overcoming the disconnect between interaction networks and biodiversity conservation and management*.
- Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019). Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix problem. *PeerJ*, 5, e3644. <https://doi.org/10.7717/peerj.3644>
- Dormann, C. F. (2023). The rise, and possible fall, of network ecology. In *Defining Agroecology – A Festschrift for Teja Tscharnkte* (pp. 143–159.). Tredition.
- Dunhill, A. M., Zarzychny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024). Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach. *Methods in Ecology and Evolution*, 4(8), 760–770. <https://doi.org/10.1111/2041-210X.12062>
- Fortuna, M. A., & Bascompte, J. (2006). Habitat loss and the structure of plant-animal mutualistic networks: Mutualistic networks and habitat loss. *Ecology Letters*, 9(3), 281–286. <https://doi.org/10.1111/j.1461-0248.2005.00868.x>
- Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning, J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene. *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J. B., Allen-Perkins, A., & Bartomeus, I.

- (2023). Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. *Ecology Letters*, 26(6), 831–842. <https://doi.org/10.1111/ele.14206>
- Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*, 11, e14620. <https://doi.org/10.7717/peerj.14620>
- Hui, C., & Richardson, D. M. (2019). How to Invade an Ecological Network. *Trends in Ecology & Evolution*, 34(2), 121–131. <https://doi.org/10.1016/j.tree.2018.11.003>
- Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., van Veen, F. J. F., Warren, P. H., & Woodward, G. (2009). Ecological networks—beyond food webs. *The Journal of Animal Ecology*, 78(1), 253–269. <https://doi.org/10.1111/j.1365-2656.2008.01460.x>
- Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- Kamaru, D. N., Palmer, T. M., Riginos, C., Ford, A. T., Belnap, J., Chira, R. M., Githaiga, J. M., Gituku, B. C., Hays, B. R., Kavwele, C. M., Kibungei, A. K., Lamb, C. T., Maiyo, N. J., Milligan, P. D., Mutisya, S., Ng’weno, C. C., Ogutu, M., Pietrek, A. G., Wildt, B. T., & Goheen, J. R. (2024). Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. *Science*, 383(6681), 433–438. <https://doi.org/10.1126/science.adg1464>
- Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015). Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>
- Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N., Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose, U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments

revealed in food-web structure. *Nature*, 426(6964), 282–285. <https://doi.org/10.1038/nature02115>

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

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

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

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

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

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

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

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

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

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

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

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

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

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary

through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>

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

Polis, G. A. (1991). Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory. *The American Naturalist*, 138(1), 123–155. <https://doi.org/10.1086/285208>

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

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

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

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

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

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

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

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

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

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

Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinsohn, T. M., Lewis, O. T., Novotny, V., Kitching, R. L.,

- & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology & Evolution*, 35(5), 454–466. <https://doi.org/10.1016/j.tree.2020.01.004>
- Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- Simmons, B. I., Blyth, P. S. A., Blanchard, J. L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C. A., Jacob, U., Pennekamp, F., Petchey, O. L., Poisot, T., Webb, T. J., & Beckerman, A. P. (2021). Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nature Ecology & Evolution*, 5(11), 1478–1489. <https://doi.org/10.1038/s41559-021-01547-4>
- Song, C., & Levine, J. M. (2024). *Rigorous (in)validation of ecological models* (p. 2024.09.19.613075). bioRxiv. <https://doi.org/10.1101/2024.09.19.613075>
- Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, 13(7), 891–899. <https://doi.org/10.1111/j.1461-0248.2010.01485.x>
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory* (Vol. 1). Princeton University Press. <https://doi.org/10.2307/j.ctvs32s6b>
- Stock, M. (2021). Pairwise learning for predicting pollination interactions based on traits and phylogeny. *Ecological Modelling*, 14.
- Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*, 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations. *Methods in Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD Entropy Reveals the High Complexity of Ecological

- 527 Networks. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.623141>
- 528 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.
529 <https://doi.org/10.1002/ecy.3047>
- 530 Van De Walle, R., Logghe, G., Haas, N., Massol, F., Vandegehuchte, M. L., & Bonte, D. (2023). Arthro-
531 pod food webs predicted from body size ratios are improved by incorporating prey defensive properties.
532 *Journal of Animal Ecology*, 92(4), 913–924. <https://doi.org/10.1111/1365-2656.13905>
- 533 Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant–
534 animal mutualistic networks: A review. *Annals of Botany*, 103(9), 1445–1457. [https://doi.org/10.1093/](https://doi.org/10.1093/aob/mcp057)
535 [aob/mcp057](https://doi.org/10.1093/aob/mcp057)
- 536 Wells, K., & O’Hara, R. B. (2013). Species interactions: Estimating per-individual interaction strength and
537 covariates before simplifying data into per-species ecological networks. *Methods in Ecology and Evolution*,
538 4(1), 1–8. <https://doi.org/10.1111/j.2041-210x.2012.00249.x>
- 539 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
540 <https://doi.org/10.1038/35004572>
- 541 Windsor, F. M., van den Hoogen, J., Crowther, T. W., & Evans, D. M. (2023). Using ecological networks
542 to answer questions in global biogeography and ecology. *Journal of Biogeography*, 50(1), 57–69. <https://doi.org/10.1111/jbi.14447>
- 543
- 544 Wooster, E. I. F., Middleton, O. S., Wallach, A. D., Ramp, D., Sanisidro, O., Harris, V. K., Rowan, J.,
545 Schowanek, S. D., Gordon, C. E., Svenning, J.-C., Davis, M., Scharlemann, J. P. W., Nimmo, D. G.,
546 Lundgren, E. J., & Sandom, C. J. (2024). Australia’s recently established predators restore complexity
547 to food webs simplified by extinction. *Current Biology*, 34(22), 5164–5172.e2. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.cub.2024.09.049)
548 [cub.2024.09.049](https://doi.org/10.1016/j.cub.2024.09.049)
- 549 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory
550 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 551 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
552 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. [https://doi.org/10.](https://doi.org/10.1073/pnas.1408471111)
553 [1073/pnas.1408471111](https://doi.org/10.1073/pnas.1408471111)
- 554 Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*,
555 120(5), 551–570. <https://doi.org/10.1086/284013>

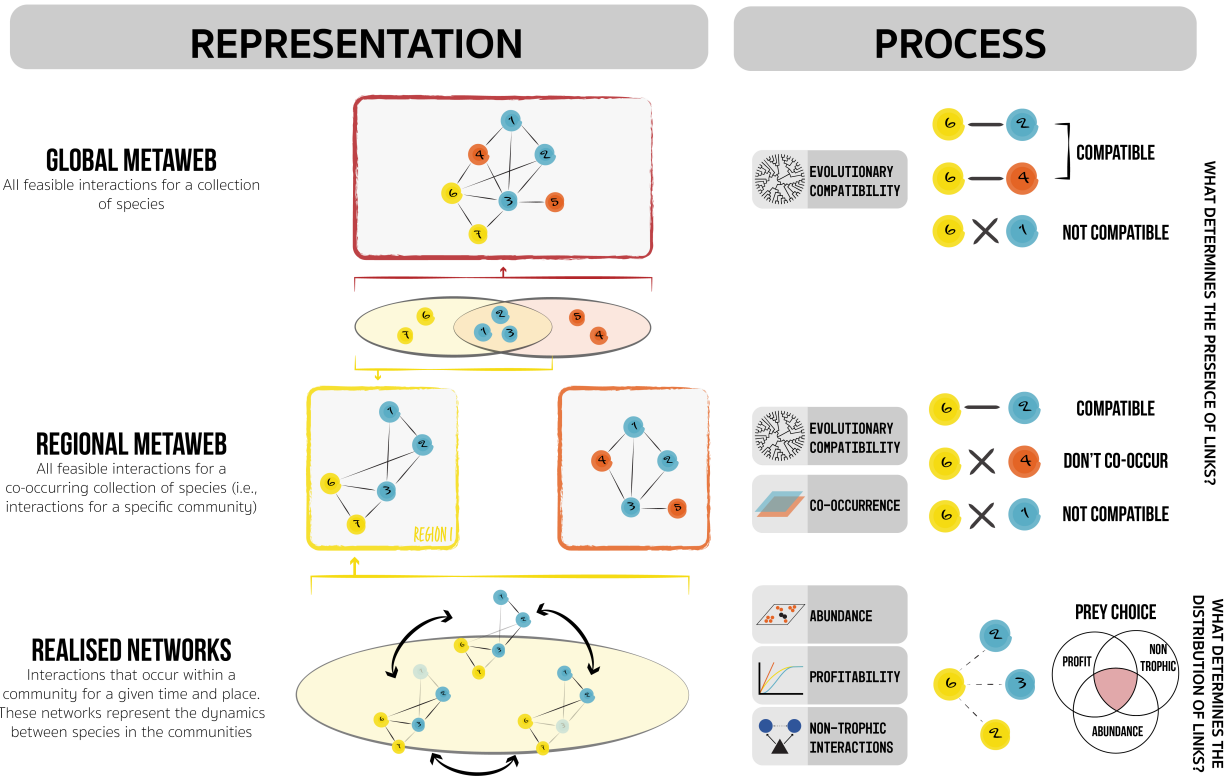


Figure 1: Aligning the various processes that determine interactions (right column) with the different network representations (left column). First, we start with a **global metaweb** this network captures all possible interactions for a collection of species in the global context. However, within the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

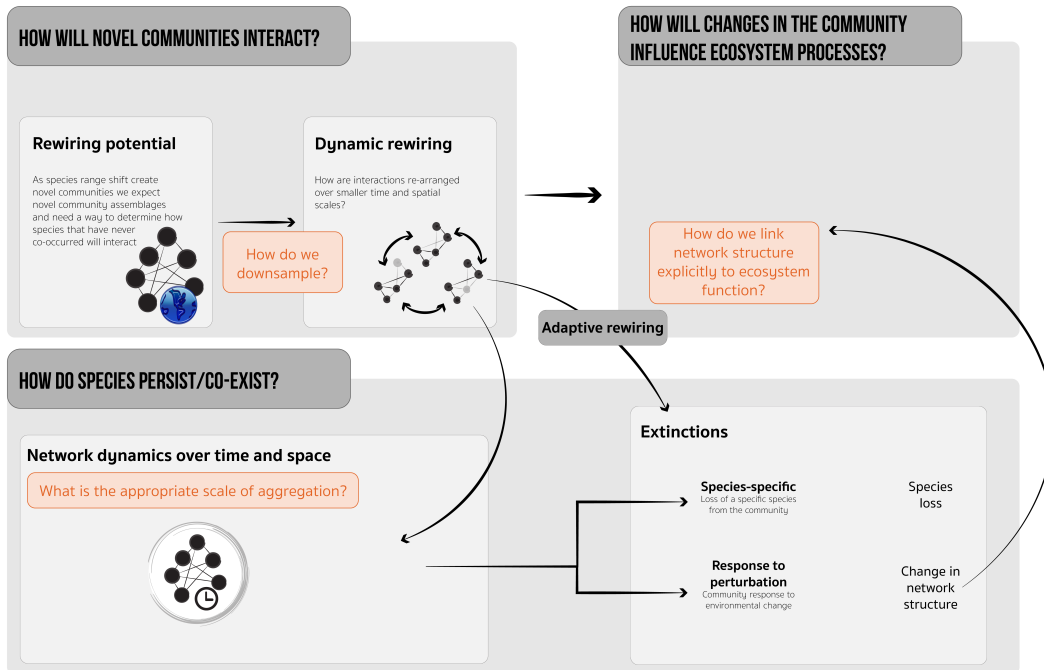


Figure 2: Here we highlight some of the outstanding questions in both network as well as general ecology, as well as some of the outstanding methodological challenges with regards to constructing food webs (shown in orange) that we are faced with.