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. Here we present a synthesis of the different assumptions, scales and mechanisms that are used to define different ecological networks ranging from metawebs (an inventory of all potential interactions) to fully realised networks (interactions that occur within a given community over a certain timescale). Illuminating the assumptions, scales, and mechanisms of network inference allows a formal categorisation of how to use networks to answer key ecological and conservation questions and defines guidelines to prevent unintentional misuse or misinterpretation.

At the heart of modern biodiversity science are a set of concepts and theories about biodiversity, stability and function. These relate to the abundance, distribution and services that biodiversity provides, and how biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction between species is one of the fundamental building blocks of ecological communities, providing a powerful abstraction that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately, make predictions, mitigate change, and manage services (Windsor et al., 2023). Such network representations of biodiversity (including within species diversity) are increasingly argued to be an asset to predictive ecology, climate change mitigation and resource management, with the argument that characterising biodiversity in a network will afford a deeper capacity to understand and predict the abundance, distribution, dynamics and services provided by multiple species facing multiple stressors. 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 the conceptualisation of networks (Blüthgen & Staab, 2024).

An 'interaction network' can be defined and conceptualised in a myriad of ways, which means that different networks will be embedding different processes (or determinants) of interactions, ultimately influencing the patterns and mechanisms that are inferred (Proulx et al., 2005). The different ways in which a network can be represented is the result of *how* the network is constructed, which itself rests on two pillars: the data used to construct the network (of which there has been a plethora of discussions as to the challenges relating to the scale and nature of data collection/observation *e.g.,* Blüthgen & Staab, 2024; Brimacombe et al., 2023; Moulatlet et al., 2024; Polis, 1991; Pringle & Hutchinson, 2020; Saberski et al., 2024) and the underlying theory as to what drives the occurrence of interactions between species. The latter represents an expression of mechanism and process that gives rise to the patterns that emerge from collating interactions among species, and will ultimately inform which data are deemed important in the determination of interactions occurring. Each of these pillars carries with it a set of practical, semantic and conceptual constraints that not only influence progress in making network ecology more valuable and potentially predictive, but help define the spatial, temporal, and evolutionary scale of assumptions we make and the predictions we might generate from different network representations.

In this perspective we aim to provide an overview of the different **food web** representations (*a note on how there has been developments in the 'bipartite space' and it would be flawed to try and view them in tandem as food webs and non-trophic webs are two very different conceptualisations*), particularly how these relate to the terminology used to define a network, and how this influenced by both the processes that determine networks as well as how this relates to the way in which we construct networks. The provision of this detail ultimately leads to a set of insights and conclusions about whether, when. and under what conditions

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network representations of biodiversity can contribute to the advancement of ecological theory and generate value in predictive ecology. 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 multiple stressors on biodiverse communities.

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

Defining a food web seems simple; it is the representation of the interactions (edges) between species (nodes) in the form of a network, however the definition of 'edges' and 'nodes', as well as the levels of organization at which they are aggregated can take many forms Moulatlet et al. (2024), which ultimately encodes a series of assumptions and criteria within a network. An awareness of variance in the way a food web can be defined is critical as a network (or its adjacency matrix) is both the 'object' from which inferences are made (*e.g.,* the interactions between species, or how the structure influences ecosystem level processes) as well as the 'product' of either the data collection (Brimacombe et al., 2023) or prediction process (Banville et al., 2024). One thus needs to be aware of both the criteria that is used to define nodes and edges, and what processes or mechanisms the aggregation of the two represents, as this will determine what the network can be used for.

1.1 How do we define a node?

Although this may seem an elementary question in the context of food webs — a node *should* represent a (taxonomic) species, the reality is that nodes can often represent an aggregation of different species - so called 'trophic species' (Williams & Martinez, 2000; Yodzis, 1982) or segregation of species by life stages (Clegg et al., 2018). Practical implications of how we are aggregating the nodes is that the resolution may not always be 'pixel perfect', which limits the ability to make (taxonomic) species specific inferences *e.g.,* does species a eat species b, however there is value in having nodes that represent an aggregation of species, as the distribution of the links between them are more meaningful in terms of understanding energy flow and distribution within the system.

1.2 What is captured by an edge?

At its core, links within food webs can be thought of as a representation of either feeding links between species - be that realised (Pringle, 2020) or potential (Dunne, 2006), alternative links can represent fluxes within the system *e.g.,* energy transfer or material flow as the result of the feeding links between species (Lindeman, 1942). Fundamentally this means that the links within a network represent different 'currencies' (either the

feasibility of a link existing between two species or the energy that is moving through the system) and how the links within a network are specified will influence the resulting structure of the network. For example taking a food web that consists of links representing all *potential* feeding links for a community (*i.e.,* a metaweb) will be meaningless if one is interested in understanding the flow of energy through the network as the links within a metaweb do not represent environmental/energetic constraints, making them poor representations of which interactions are *realised* in a specific location (Caron et al., 2024). In addition to the various ways of defining the links between species pairs there are also a myriad of ways in which the links themselves can be quantified. Links between species are often treated as being present or absent (*i.e.,* binary) but it is also possible to use probabilities (Banville et al., 2024; which quantifies how likely an interaction is to occur, Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of of an interaction, Berlow et al., 2004).

1.3 Network representations

Broadly, networks can be thought of to fall into two different 'types'; namely metawebs; traditionally defined as all of 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 difference between these two different network representations is that a metaweb provides insight as to the viability of an interaction between two species occurring and is 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 highly localised and the links between species are contingent on both the co-occurrence of species, the role of the environment, and population and community dynamics on predator choice. In the context of definitions and semantics the links that are represented by a metaweb and a realised network are different; links that are absent in a metaweb can be treated as being truly absent, however links that are absent in a realised network cannot be considered to be truly absent but rather as absent due to the broader environmental/community context. Importantly, a realised network is *not* simply the downscaling of a metaweb to a smaller scale (*e.g.,* moving from the country to the 1x1 km^2 scale based on fine-scale species co-occurrence) but represents a shift towards capturing the higher level processes that determine the *realisation* of an interaction, *i.e.,* the definition of an edges shifts from being determined by interaction feasibility to that of energetic choices/consequences. Thus, different network representations are determined and constrained by different sets of assumptions as to what the processes are that determine the presence/absence of an interaction between two species as well as the resulting network structure.

2 From Nodes and Edges to Scale, Context, and Process

The interplay between network representation and network (node and edge) definition is primarily governed by the process(es) that determine the interaction between species, however these processes are also scale and context dependent. Here we start by introducing the five core processes that determine either the feasibility or the realisation of interactions, namely: evolutionary compatibility, co-occurrence, abundance, predator choice, and non-trophic interactions; while simultaneously contextualising them within, and linking them to, the different network representations Figure 1. We can think of the different network representations to be conceptually analogous to the fundamental and realised niche, whereby the metaweb represents the 'fundamental diet niche' of a species and a realised network represents the 'realised diet' of a species. Of course these processes do not function in a vacuum and do interact with/influence one another, but it is still beneficial to present them in a categorical manner as these different processes are often the underpinning logic in the development of prediction/network models, the criteria for data collection in the field, and the scale of organisation for which they are relevant (species, population, or community).

[Figure 1 about here.]

2.1 The processes that determine species interactions

Evolutionary compatibility

There is compelling evidence that an interaction occurring between two species is the result of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Segar et al., 2020) which, in the more proximal sense, is manifested as the 'trait complementarity' between two species (Benadi et al., 2022), whereby one species (the predator) has the 'correct' set of traits that allow it to chase, capture, kill, and consume the other species (the prey). For species pairs where this condition is not met the link is deemed to be *forbidden* (Jordano, 2016b); *i.e.,* not physically possible and will always be absent within a network. A network constructed on the basis of evolutionary compatible links is most closely aligned with a metaweb, although it would not be required that the species co-occur (as shown in Figure 1), and arguably makes for a good approximation of the 'Eltonian niche' of species (Soberón, 2007). Finally, one should be aware that it is possible to represent evolutionary compatible interactions as either binary (possible vs forbidden) or as a probability (Banville et al., 2024), where the probability represents how likely the interaction between two species is to be possible.

(Co)occurrence

Although the outright assumption that because two species are co-occurring it must mean that they are

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interacting is flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at least in terms of feeding links) if they are not co-occurring in time and space. Thus, although co-occurrence data alone is insufficient to build an accurate and ecologically meaningful representation of *feeding links* it is still a critical process that determines the realisation of feeding links and allows us to constrain a global metaweb to only consider 'realised' communities (Dansereau et al., 2024) and an understanding of the intersection of species interactions and their co-occurrence (*sensu* a fusion of the the Grinnellian and Eltonian niches niche, Gravel et al. (2019)) is meaningful when one is operating in the space of trying to determine the distribution of a species (Higino et al., 2023; Pollock et al., 2014).

Abundance

The abundance of the different species within the community is thought to influence the realisation of feeding links primarily in two ways. Firstly there is the argument that the structure of networks (and the interactions that they are composed of) are driven *only* by the abundance of the different species and that interactions are not contingent on there being any compatibility (trait matching) between them, *sensu* neutral processes (Canard et al., 2012; Momal et al., 2020). 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), or in the dynamic sense will influence the persistence of viable populations.

Profitability (energetics)

Ultimately, predator choice is underpinned by the energetic cost-benefit (profitability) of trying to catch, kill, and consume prey (where a predator will optimise energy intake while minimising handling and search time (energy cost)), and is well described within both optimal foraging (Pyke, 1984) and metabolic theory (Brown et al., 2004). The energetic cost of feeding is determined by both the energy content as well as the density (abundance) of prey (as this influences search time), and a predator will opt to select the prey type that will be most profitable. Additional work on on understanding the energetic cost that the environment imposes on an individual (Cherif et al., 2024) as well as the way a predator uses the landscape to search for prey (Pawar et al., 2012) brings us closer to accounting for the energetic cost of realising feeding links.

Non-trophic interactions

Perhaps not as intuitive when thinking about the processes that determine feeding links is accounting for the ability of non-trophic interactions (such as competition) to modify either the realisation or strength of trophic interactions (Golubski & Abrams, 2011; Pilosof et al., 2017). Non-trophic interactions can modify in-

teractions either 'directly' *e.g.,* predator *a* outcompetes predator *b* or 'indirectly' *e.g.,* mutualistic/facilitative interactions will alter the fine-scale distribution and abundance of species as well as their persistence (Buche et al., 2024; Kéfi et al., 2012, 2015). The 'unobservable' nature of non-trophic interactions makes them a challenge to quantify, however their importance in network dynamics (Staniczenko et al., 2010) as well as cascading effects (*e.g.,* Kamaru et al., 2024) should not be overlooked.

2.2 Contextualising the processes that determine species interactions

It should be self evident that the different processes discussed above will ultimately influence the realisation of interactions as well as the structure of a network, however they are acting at different scales of organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of the species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise level and one is left with a 'list' of interactions that are present/absent. Although it is possible to build a network (*i.e.,* metaweb) from this information it is important to be aware that the structure of this network is not constrained by real-world dynamics or conditions (*i.e.,* the community context), and so just because species are able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who's structure is a closer approximation of reality (localised interactions) one needs to take into consideration the properties of the community as a whole and information about the individuals it is comprised of (Quintero et al., 2024), which requires more data at the community scale, such as the abundance of species.

3 Network construction is nuanced

The act of constructing a 'real world' network will ultimately be delimited by its intended use, however the reality is that the empirical collection of interaction data is both costly and challenging to execute (Jordano, 2016a, 2016b), especially if one wants to capture *all* aspects of the processes discussed in Section 2 (owing to the different time and spatial scales they may be operating at). Thus we often turn to models to either predict networks (be that the interaction between two species, or network structure (Strydom et al., 2021)), or as a means to identify missing interactions (gap fill) within an existing empirical dataset (Biton et al., 2024; Dallas et al., 2017; Stock, 2021), and so for the purpose of this discussion network construction will be synonymous with using a model as a means to represent or predict a network. That is not to say that there is no need for empirical data collection, but rather that using a model for food web prediction (or reconstruction) is a more feasible approach as it allows us to make inferences about interactions that are not happening in the 'observable now' (Strydom et al., 2021), and has the added benefit that one is able to explicitly account for uncertainty within the network construction process (Banville et al., 2024). Most

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importantly different models have different underlying philosophies, this allows isolate and operate within one (or a few) of the processes discussed in Section 2, and better sets us up to understand how different processes determine interactions (Song & Levine, 2024; Stouffer, 2019). Here we will introduce the three different types of network representations (metawebs, realised networks, and structural networks), how they link back to (and encode) the different processes determining interactions Figure 1, and broadly discuss some of the modelling approaches that are used to construct these different network types. This is paralleled by a hypothetical case study (Box 1) where we showcase the utility/applicability of the different network representations in the context of trying to understand the feeding dynamics of a seasonal community.

ⓘ Box 1 - Why we need to aggregate networks at different scales: A hypothetical case study

Although it might seem most prudent to be predicting, constructing, and defining networks that are the closest representation of reality there are pros and cons of constructing both realised networks as well as metawebs. Let us take for example a community that experiences a degree of species turnover between seasons. In this community we expect species to be either present or absent depending on the season (*i.e.,* changes in co-occurrence) as well as some species exhibiting seasonal shifts in their diets (be that due to changes in species occurrence or predator choice). If one were to construct a metaweb that disregards these season shifts (*i.e.,* a global metaweb) it is clear that these finer nuances would be lost. It is of course possible to construct either smaller metawebs for the different seasonal communities (thereby capturing the changes in community diversity), or realised networks for each season (to capture diet or ecosystem process shifts *e.g.,* Schwarz et al. (2020)). However, these small-scale networks lack the context of the bigger picture that is available at the metaweb - that is it gives us a more holistic idea of the entire diet range of a specific species, which is important when one needs to make conservation-based/applied decisions (*e.g.,* conserving the entire diet of a species and not just seasonal prey items) as well as providing information on interactions that may be possible regardless of the environmental/community context (species may have the capacity to consume certain prey items but do not do so due to local conditions). With this is mind let us see how the different network aggregations can be used: *not3 that for now I am using Figure 2 for layout experimentation purposes*

[Figure 2 about here.]

3.1 Models that predict metawebs (feasible interactions)

This is perhaps the most developed group of models; with a variety of approaches having been developed that typically determine the feasibility of an interaction using the trait compatibility between predator and

prey (*i.e.* their evolutionary compatibility) to determine 'feeding rules' (Morales-Castilla et al., 2015). These feeding rules are broadly elucidated in two different ways; mechanistic feeding rules can be explicitly defined and applied to a community (Dunne et al., 2008; Roopnarine, 2017; *e.g.,* Shaw et al., 2024) or they are inferred from a community for which there are interaction data and the 'rules' are then applied to a different community (Caron et al., 2022; Cirtwill et al., 2019; Desjardins-Proulx et al., 2017; Eklöf et al., 2013; Llewelyn et al., 2023; Pichler et al., 2020; Strydom et al., 2022; *e.g.,* Strydom et al., 2023). The fundamental difference between these two model groups is that 'mechanistic models' rely on expert knowledge and make explicit assumptions on trait-feeding relationships, whereas the 'pattern finding' models are dependent on existing datasets from which to elucidate feeding rules. These models are useful for determining all feasible interactions for a specific community, and owing to the availability of empirical interaction datasets (Gray et al., 2015; *e.g.,* Poelen et al., 2014; Poisot, Baiser, et al., 2016), as well as the development of model testing/benchmarking tools (Poisot, 2023), means that these models can be validated and (with relative confidence) be used to construct first draft networks for communities for which we have no interaction data (Strydom et al., 2022), and are valuable not only in data poor regions but also for 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. Importantly metawebs are inherently 'static' in the sense that they are *not* able to capture dynamic processes (since the notion of feasibility is all or nothing), however they provide a bigger picture context (*e.g.,* understanding the *entire* diet breadth of a species) and often require little data to construct.

3.2 Models that predict realised networks (realised interactions)

In order to construct realised networks models need to incorporate *both* the feasibility of interactions (*i.e.,* determine the entire diet breadth of a species) as well as then determine which interactions are realised (*i.e.,* incorporate the 'cost' of interactions). As far as we are aware there is no model that explicitly accounts for both of these 'rules' (although see Olivier et al. (2019)) and rather *only* account for processes that determine the realisation of an interaction (*i.e.,* abundance, predator choice, or non-trophic interactions). Although the use of allometry *i.e.,* body size (Beckerman et al., 2006; *e.g.,* Valdovinos et al., 2023; White et al., 2007; Yodzis & Innes, 1992) may represent a first step in capturing 'evolutionary compatibility' alongside more energy (predator choice) driven processes we still need to account for other traits that determine feeding compatibility (*e.g.,* Van De Walle et al., 2023 show how incorporating prey defensive properties alongside body size improves predictions). In terms of constructing realised networks, diet models (Beckerman et al., 2006; Petchey et al., 2008) have been used construct networks based on both predator choice (as determined

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by the handling time, energy content, and predator attack rate) as well as abundance (prey density) and progress has also been made in understanding the compartmentation of energy in networks and how this influences energy acquisition (Krause et al., 2003; Wootton et al., 2023). As realised networks are are build on the concept of dynamic processes (the abundance of species will always be in flux) these networks are valuable for understanding the behaviour of networks over time or their response to change (Curtsdotter et al., 2019; Delmas et al., 2017; Lajaaiti et al., 2024). However, they are 'costly' to construct (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.

3.3 Models that predict structure (interaction agnostic)

Although we identify mechanisms that determine species interactions in Section 2 not all models that are used to predict networks explicitly operate at the 'process' level, but rather represent the *structure* of a network based on a series of *a priori* assumptions as to the distribution of links between (typically trophic not taxonomic) species. These models operate by parametrising an aspect of the network structure, (*e.g.,* the niche model (Williams & Martinez, 2000) makes an assumption as to the expected connectance of the network,although see Allesina & Pascual (2009) for a parameter-free model) or alternatively uses structural features of an exiting *realised* network (*e.g.,* stochastic block model, Xie et al. (2017)). Importantly these structural models do not make species specific predictions (they are usually species agnostic and treat nodes as trophic species) and so cannot be used to determine if an interaction is either possible *or* realised between two species (*i.e.,* one cannot use these models to determine if species a eats species b). Although this means this suite of models are unsuitable as tools for predicting species-specific interactions, they have been shown to be sufficient tools to predict the structure of networks (Williams & Martinez, 2008), and provide a data-light (the models often only require species richness) but assumption heavy (the resulting network structure is determined by an assumption of network structure) way to construct a network.

4 Making Progress with Networks

4.1 Further development of models and tools

There has been a suite of models that have been developed to predict feeding links, however we are lacking in tools that are explicitly taking into consideration estimating both the feasibility as well as realisation of links, *i.e.,* both interactions and structure simultaneously (Strydom et al., 2021). This could be addressed either through the development of tools that do both (predict both interactions and structure), or to develop

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). Additionally, although realised networks are more closely aligned with capturing interaction strength we lack models that allow us to quantify this (Strydom et al., 2021; Wells & O'Hara, 2013). In addition to the more intentional development of models we also need to consider the validation of these models, there have been developments and discussions for assessing how well a model recovers pairwise interactions (Poisot, 2023; Strydom et al., 2021), although their are still challenges related to the completeness of the datasets that are to be used for validation, specifically the challenge of dealing with false-negatives (Catchen et al., 2023). In terms of validating the predicted structure of networks, we still lack clear set of guidelines for benchmarking the ability of models to recover structure (Allesina et al., 2008).

4.2 At what scale should we be predicting and using networks?

The appropriate level of aggregation for a 'network' is an emerging discussion within the field (Estay et al., 2023; Moulatlet et al., 2024; Saberski et al., 2024), and perhaps presents the biggest challenge if we want to understand how different processes determine interactions (Saravia et al., 2022), as well as identify the appropraite networks for different research questions Figure 3. Thus we need an understanding of not only how time and scale influence the interpretation of networks (Blüthgen & Staab, 2021; Morales & Vázquez, 2008), but how this is in turn influenced by the type of network representations used. Space influences both network properties (Galiana et al., 2018), as well as dynamics (Fortin et al., 2021; Rooney et al., 2008), and time has implications when it comes to accounting for seasonal turnover in communities (Brimacombe et al., 2021; Laender et al., 2010) as well as thinking about co-occurrence, particularly the records that are used to determine co-occurence (Brimacombe et al., 2024). Although multilayer networks may allow us to encode the nuances of space and time (Hutchinson et al., 2019) we still need to understand the implications of *e.g.,* constructing networks that are not at ecologically but rather politically relevant scales (Strydom et al., 2022) and what the implications of this disconnect may be.

4.3 Making use of the different network representations

It should be clear that there is a high degree of interrelatedness and overlap between the way in which a network is constructed (modelled or predicted) and the process(es) that it captures Figure 1, these are encoded (embedded) within the network representation and ultimately influences how the network can and should be used (Berlow et al., 2008; Petchey et al., 2011), with different network representations yielding different interpretations of processes (Keyes et al., 2024). 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. In
Figure 3 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.

[Figure 3 about here.]

Table 1: This table representis an alternative approach to try and think about mapping quations to network
representations.

Question (broad)	Question (specific)	Network representation
Species invasions	What species will the invading species interact with?	Regional metaweb but need to derive information from a global metaweb since these are interactions that are 'novel'
Species invasions	How does the invading species alter network dynamics and function?	Realised network (after having moved through the global metaweb to understand which interactions are feasible)
Range shifts and novel communities	Under global change how will novel community assemblages interact?	Global metaweb, need context of broader community
Extinctions	Cascading effect of the loss of a species from the network	Regional metaweb - need to account for entire diet, a realised network will exclude the entire diet but will allow to elucidate the final structure
Species/community persistence	Dynamics over time. Stability/resilience. How does a change in pop *A* affect pop *B*?	Realised networks - but dynamic!

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Question (broad)	Question (specific)	Network representation
Synthetic networks	Creating ecologically plausible communities for synthetic analyses	Structural networks - data light!
Practical use	What is both attainable (data constraints) but also of practical use to 'real world' decision making. So moving from theory to applied	??Regional metawebs??

5   Concluding remarks

Having a clear understanding of the interplay between network representations and the processes that they are capapble 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, scales, 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., 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

Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T. A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling, E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic

318   reservoirs. *The Lancet Microbe*, *3*(8), e625–e637. https://doi.org/10.1016/S2666-5247(21)00245-7

319 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.
320   *Proceedings of the National Academy of Sciences*, *103*(37), 13745–13749. https://doi.org/10.1073/pnas.
321   0603039103

322 Benadi, G., Dormann, C. F., Fründ, J., Stephan, R., & Vázquez, D. P. (2022). Quantitative Prediction of
323   Interactions in Bipartite Networks Based on Traits, Abundances, and Phylogeny. *The American Naturalist*,
324   *199*(6), 841–854. https://doi.org/10.1086/714420

325 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The "Goldilocks factor" in food webs. *Proceedings of*
326   *the National Academy of Sciences*, *105*(11), 4079–4080. https://doi.org/10.1073/pnas.0800967105

327 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
328   V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
329   (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, *73*(3),
330   585–598. https://doi.org/10.1111/j.0021-8790.2004.00833.x

331 Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables*
332   *cross-community link prediction in ecological networks*.

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

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

337 Blüthgen, N., & Staab, M. (2021). Ecology: Mammals, interaction networks and the relevance of scale.
338   *Current Biology*, *31*(13), R850–R853. https://doi.org/10.1016/j.cub.2021.05.032

339 Blüthgen, N., & Staab, M. (2024). A Critical Evaluation of Network Approaches for Studying Species
340   Interactions. *Annual Review of Ecology, Evolution, and Systematics*, *55*(1), 65–88. https://doi.org/10.
341   1146/annurev-ecolsys-102722-021904

342 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2021). Inferred seasonal interaction rewiring of a freshwater
343   stream fish network. *Ecography*, *44*(2), 219–230. https://doi.org/10.1111/ecog.05452

344 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A*
345   *cautionary tale using inferred food webs*. https://doi.org/10.13140/RG.2.2.22076.65927

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

349 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory
350   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., 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

Catchen, M. D., Poisot, T., Pollock, L. J., & Gonzalez, A. (2023). *The missing link: Discerning true from false negatives when sampling species interaction networks.*

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*(n/a). 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

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

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

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

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

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

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

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

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

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

Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and Network Analyses of Cambrian Food Webs. *PLOS Biology*, *6*(4), e102. https://doi.org/10.1371/journal.pbio.0060102

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

Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks over space. *Frontiers in Ecology and Evolution*, *11*.

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

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

Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya, J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, *2*(5), 782–790. https://doi.org/10.1038/s41559-018-0517-3

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

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

Gray, C., Figueroa, D. H., Hudson, L. N., Ma, A., Perkins, D., & Woodward, G. (2015). Joining the dots: An automated method for constructing food webs from compendia of published interactions. *Food Webs*, *5*, 11–20. https://doi.org/10.1016/j.fooweb.2015.09.001

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

Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., & Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community ecology. *Functional Ecology*, *33*(2), 206–217. https://doi.org/10.1111/1365-2435.13237

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

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

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

Laender, F. D., Oevelen, D. V., Soetaert, K., & Middelburg, J. J. (2010). Carbon transfer in a herbivore- and microbial loop-dominated pelagic food webs in the southern Barents Sea during spring and summer. *Marine Ecology Progress Series*, *398*, 93–107. https://doi.org/10.3354/meps08335

Lajaaiti, I., Bonnici, I., Kéfi, S., Mayall, H., Danet, A., Beckerman, A. P., Malpas, T., & Delmas, E. (2024). *EcologicalNetworksDynamics.jl A Julia package to simulate the temporal dynamics of complex ecological networks* (p. 2024.03.20.585899). bioRxiv. https://doi.org/10.1101/2024.03.20.585899

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., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator–prey interactions in terrestrial endotherms using random forest. *Ecography*, *2023*(9), e06619. https://doi.org/10.1111/ecog.06619

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, J. M., & Vázquez, D. P. (2008). The effect of space in plant–animal mutualistic networks: Insights from a simulation study. *Oikos*, *117*(9), 1362–1370. https://doi.org/10.1111/j.0030-1299.2008.16737.x

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

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

Olivier, P., Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A. F., & Nordström, M. C. (2019). Exploring the temporal variability of a food web using long-term biomonitoring data. *Ecography*, *42*(12), 2107–2121. https://doi.org/10.1111/ecog.04461

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

Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some thoughts on judging food web models. *Journal of Theoretical Biology*, *279*(1), 169–171. https://doi.org/10.1016/j.jtbi.2011.03.019

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

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

Poelen, J. H., Simons, J. D., & Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to share and analyze species-interaction datasets. *Ecological Informatics*, *24*, 148–159. https://doi.org/10.1016/j.ecoinf.2014.08.005

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., Baiser, B., Dunne, J., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S. A., & Gravel, D. (2016). Mangal – making ecological network analysis simple. *Ecography*, *39*(4), 384–390. https://doi.org/10.1111/ecog.00976

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

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 Systematic*, *15*, 523–575. https://doi.org/10.1146/annurev.ecolsys.15.1.523

Quintero, E., Arroyo-Correa, B., Isla, J., Rodríguez-Sánchez, F., & Jordano, P. (2024). *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

Rooney, N., McCann, K. S., & Moore, J. C. (2008). A landscape theory for food web architecture. *Ecology Letters*, *11*(8), 867–881. https://doi.org/10.1111/j.1461-0248.2008.01193.x

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

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

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

Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, *91*(3), 630–642. https://doi.org/10.1111/1365-2656.13652

Schwarz, B., Vázquez, D. P., CaraDonna, P. J., Knight, T. M., Benadi, G., Dormann, C. F., Gauzens, B., Motivans, E., Resasco, J., Blüthgen, N., Burkle, L. A., Fang, Q., Kaiser-Bunbury, C. N., Alarcón, R., Bain, J. A., Chacoff, N. P., Huang, S.-Q., LeBuhn, G., MacLeod, M., … Fründ, J. (2020). Temporal scale-dependence of plant–pollinator networks. *Oikos*, *129*(9), 1289–1302. https://doi.org/10.1111/oik.07303

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

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*,

10(12), 1115–1123. https://doi.org/10.1111/j.1461-0248.2007.01107.x

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

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

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

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

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

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

Wells, K., & O'Hara, R. B. (2013). Species interactions: Estimating per-individual interaction strength and covariates before simplifying data into per-species ecological networks. *Methods in Ecology and Evolution*, *4*(1), 1–8. https://doi.org/10.1111/j.2041-210x.2012.00249.x

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, *22*(6), 323–330. https://doi.org/10.1016/j.tree.2007.03.007

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

Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, *77*(3), 512–519. https://doi.org/10.1111/j.1365-2656.2008.01362.x

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

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

Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in Networks. *Scientific Reports*, *7*(1), 5269. https://doi.org/10.1038/s41598-017-05585-6

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

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

Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*, *139*(6), 1151–1175. https://doi.org/10.1086/285380
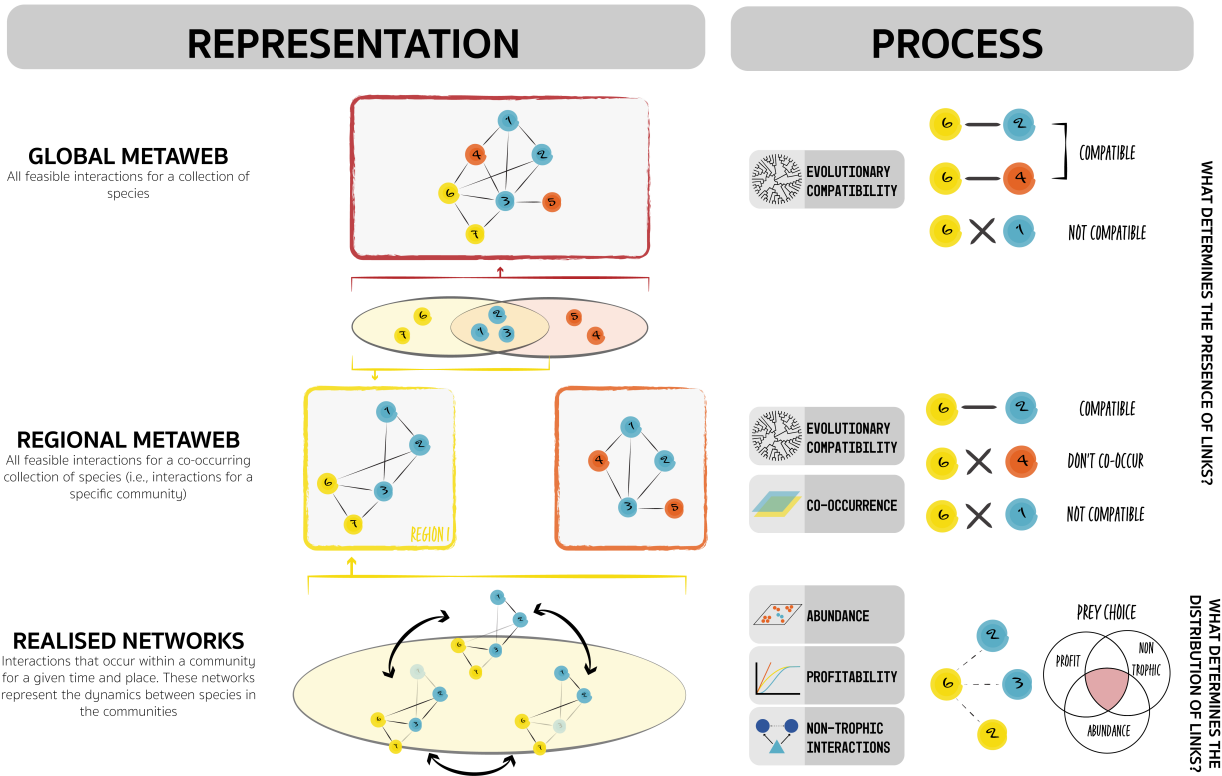
Figure 1: Aligning the various processes that determine interactions (right column) with the different network representations (left column). First we start with a **global metaweb** this network captures all possible interactions for a collection of species in the global context. However within the global environment different species occur in different regions (region one = yellow and region 2 = orange), and it is possible to construct two different metawebs (**regional metawebs**) for each region by taking accounting for the co-occurrence 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** are 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.

1. A 'global' metaweb

Knowledge of the entire diet breadth of a species is valuable
especially in terms of
understanding how a species will respond to changes
in the community - *e.g.,* invasions/rewilding exercises
(where does the new species 'fit' within the network?)
as well as potential capacity to shift its diet.
ALthough this might make sense across space and
not time but certain
species act as links across the landscape.

2. Seasonal metawebs

○ Knowledge at the finer scale is also
valuable to understand/identify that there
are in fact differences
between the seasons

○ Information of seasonal diet
of species
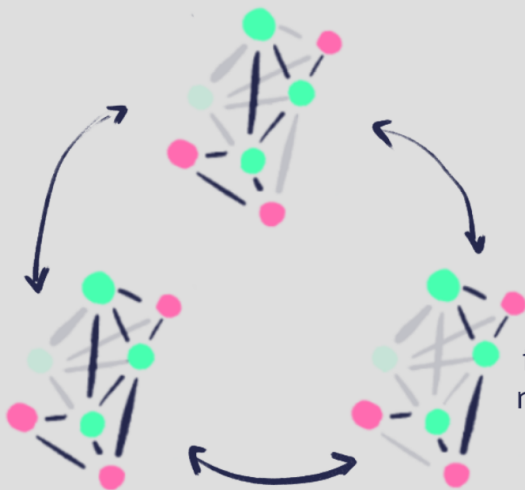
3. Seasonal realised network(s)

Dynamics are useful because they
are a representation
of the different configurations/energy
flows/ecosystem processes. Also to detect more
nuanced shifts in diet - *e.g.,* seasonal diet shifts.

○ Structurally informative
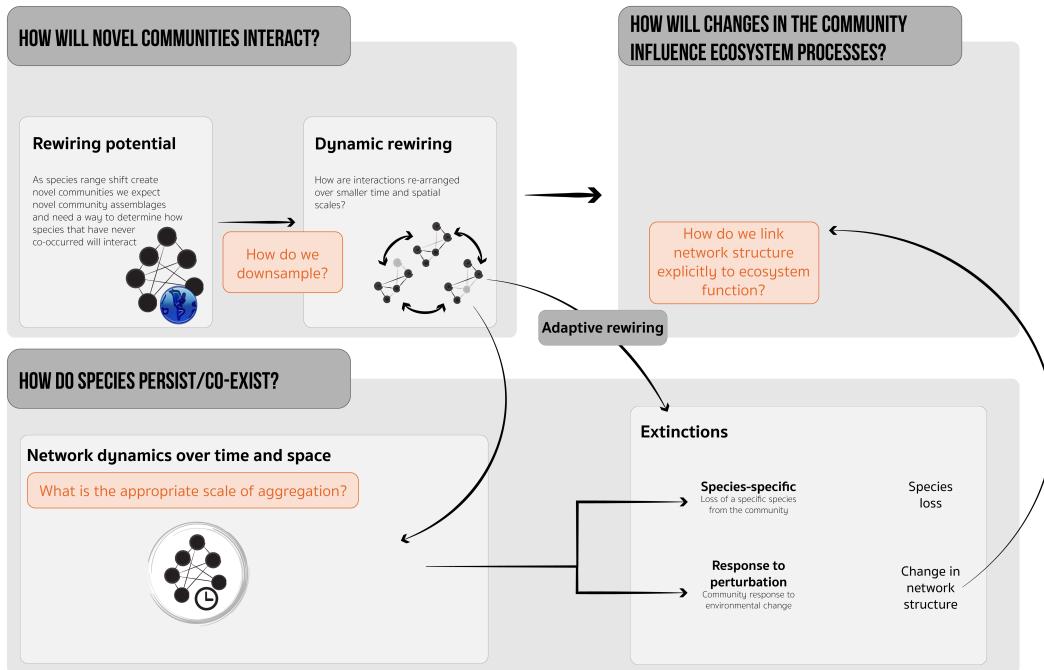○ can be @ ever finer scale of time/space

Figure 2

Figure 3: Here we highlight som of the outstanding questions in both network as well as general ecology, as well as some of the outstadning methodological challenges we face.