# Unveiling the Complexity of Food Webs: A Comprehensive Overview of **Definitions, Scales, and Mechanisms** Tanya Strydom <sup>1</sup>; Jennifer A. Dunne <sup>2</sup>; Timothée Poisot <sup>3,4</sup>; Andrew P. Beckerman <sup>1</sup> 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.

Keywords: food web, network construction, scientific ignorance

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 14 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 23 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

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.

# <sub>37</sub> 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.

### 48 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.

### <sub>7</sub> 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 an interaction,
Berlow et al., 2004).

# 73 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, 81 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 83 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. 85 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<sup>2</sup> 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 88 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.

# <sup>2</sup> 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 100 'fundamental diet niche' of a species and a realised network represents the 'realised diet' of a species. Of 101 course these processes do not function in a vacuum and do interact with/influence one another, but it is still 102 beneficial to present them in a categorical manner as these different processes are often the underpinning 103 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). 105

[Figure 1 about here.]

# 2.1 The processes that determine species interactions

# Evolutionary compatibility

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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 110 more proximal sense, is manifested as the 'trait complementarity' between two species (Benadi et al., 2022), 111 whereby one species (the predator) has the 'correct' set of traits that allow it to chase, capture, kill, and 112 consume the other species (the prey). For species pairs where this condition is not met the link is deemed 113 to be forbidden (Jordano, 2016b); i.e., not physically possible and will always be absent within a network. 114 A network constructed on the basis of evolutionary compatible links is most closely aligned with a metaweb, 115 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 117 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 119 species is to be possible.

#### (Co)occurrence

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

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).

#### 131 Abundance

The abundance of the different species within the community is thought to influence the realisation of feeding 132 links primarily in two ways. Firstly there is the argument that the structure of networks (and the interactions 133 that they are composed of) are driven only by the abundance of the different species and that interactions 134 are not contingent on there being any compatibility (trait matching) between them, sensu neutral processes 135 (Canard et al., 2012; Momal et al., 2020). However, a more ecologically sound assumption would be that 136 the abundance of different prey species will influence the distribution of links in a network (Vázquez et al., 137 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 139 the dynamic sense will influence the persistence of viable populations.

#### 141 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 interactions 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 160 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 162 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 164 (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 166 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 169 et al., 2024), which requires more data at the community scale, such as the abundance of species.

# 3 Network construction is nuanced

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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, 173 2016a, 2016b), especially if one wants to capture all aspects of the processes discussed in Section 2 (owing 174 to the different time and spatial scales they may be operating at). Thus we often turn to models to either 175 predict networks (be that the interaction between two species, or network structure (Strydom et al., 2021)), 176 or as a means to identify missing interactions (gap fill) within an existing empirical dataset (Biton et al., 177 2024; Dallas et al., 2017; Stock, 2021), and so for the purpose of this discussion network construction will 178 be synonymous with using a model as a means to represent or predict a network. That is not to say that 179 there is no need for empirical data collection, but rather that using a model for food web prediction (or 180 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 182 to explicitly account for uncertainty within the network construction process (Banville et al., 2024). Most

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

note I am using a figure for layout experimentation purposes

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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 ('global metaweb') these details would be lost and it would be valuable 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.q., conserving the entire diet of a species and not just seasonal previtems) 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

[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 197 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 199 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 201 difference between these two model groups is that 'mechanistic models' rely on expert knowledge and make 202 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 204 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 206 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 208 (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 210 al., 2014) or future, novel community assemblages. Importantly metawebs are inherently 'static' in the sense 211 that they are not able to capture dynamic processes (since the notion of feasibility is all or nothing), however 212 they provide a bigger picture context (e.g., understanding the entire diet breadth of a species) and often 213 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., 217 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 219 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; 221 Yodzis & Innes, 1992) may represent a first step in capturing 'evolutionary compatibility' alongside more 222 energy (predator choice) driven processes we still need to account for other traits that determine feeding 223 compatibility (e.g., Van De Walle et al., 2023 show how incorporating prey defensive properties alongside 224 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

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.

# 5 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 237 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., 239 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 241 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 246 to be sufficient tools to predict the structure of networks (Williams & Martinez, 2008), and provide a datalight (the models often only require species richness) but assumption heavy (the resulting network structure 248 is determined by an assumption of network structure) way to construct a network.

# $_{50}$ 4 Making Progress with Networks

# <sup>251</sup> 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 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 appropriate networks for different research questions Figure 3. Thus we need an understanding of not only 270 how time and scale influence the interpretation of networks (Blüthgen & Staab, 2021; Morales & Vázquez, 271 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 273 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 275 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., 277 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. 279

#### 4.3 Making use of the different network representations

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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.

### 96 4.4 How will novel communities interact?

Here we can talk about the effects of range shifts and invasions and how this will result in new/novel community assemblages. And then also the intentional changes of species compositions through rewilding.

# 99 4.5 How will changes in the community influence ecosystem processes?

Linking to dynamic networks and how this lets us build spatially/temporally explicit networks which can be used to infer form and function. Also bring in the discussion on the suitable aggregation (and the fact that we don't know)

# 4.6 How do species persist/co-exist?

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).

[Figure 3 about here.]

Table 1: This table represent is 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	Regional metaweb but need to derive
	species interact with?	information from a global metaweb since
		these are interactions that are 'novel'

Question (broad)	Question (specific)	Network representation
Species invasions	How does the invading species alter	Realised network (after having moved
	network dynamics and function?	through the global metaweb to
		understand which interactions are
		feasible)
Range shifts and	Under global change how will novel	Global metaweb, need context of broader
novel communities	community assemblages interact?	community
Extinctions	Cascading effect of the loss of a	Regional metaweb - need to account for
	species from the network	entire diet, a realised network will exclude
		the entire diet but will allow to elucidate
		the final structure
Species/community	Dynamics over time.	Realised networks - but dynamic!
persistence	Stability/resilience. How does a	
	change in pop $A$ affect pop $B$ ?	
Synthetic networks	Creating ecologically plausible	Structural networks - data light!
	communities for synthetic analyses	
Practical use	What is both attainable (data	??Regional metawebs??
	constraints) but also of practical use	
	to 'real world' decision making. So	
	moving from theory to applied	

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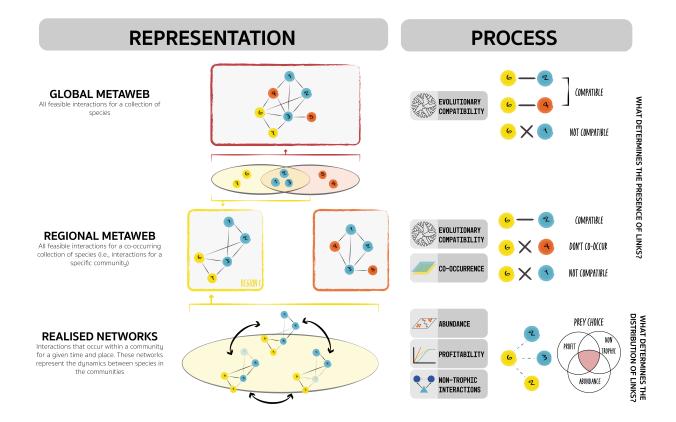
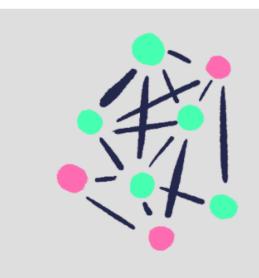


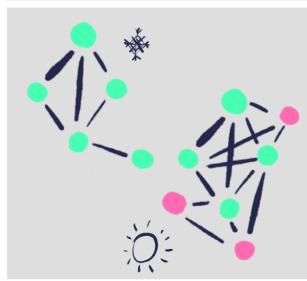
Figure 1: Aligning the various processes that determine interactions (right column) with the different network representations (left column). First we start with a **global metaweb** this network captures all possible interactions for a collection of species in the global context. However within the 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 Metawe

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.

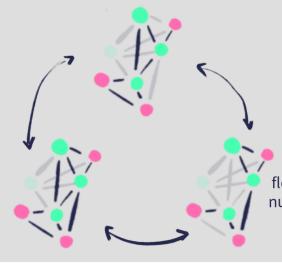
Although this might make sense across space and not time but certain species act as links across the landscape.



# 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



# 3. Seasonal reulised

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 · con be @ ever fine scale of time / space

Figure 2

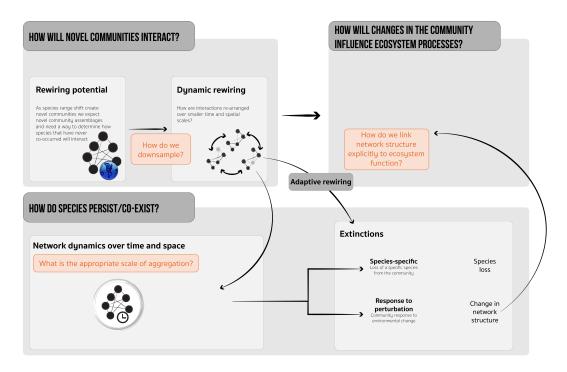


Figure 3: Here we highlight som of the outstanding questions in both network as well as general ecology, as well as some of the outstanding methodological challenges we face.