

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.

Keywords: food web, network construction, scientific ignorance

1 At the heart of modern biodiversity science are a set of concepts and theories about biodiversity, stability
2 and function. These relate to the abundance, distribution and services that biodiversity provides, and how
3 biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction between
4 species (or individuals) is one of the fundamental building blocks of ecological communities provide a powerful
5 abstraction that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately,
6 one hopes, make prediction, mitigate change and manage services [ref]. Such network representations of
7 biodiversity (including within species diversity) are increasingly argued to be an asset to predictive ecology,
8 climate change mitigation and resource management. Here, it is argued that characterising biodiversity in
9 a network will allow deeper capacity to understand and predict the abundance, distribution, dynamics and
10 services provided by multiple species facing multiple stressors.

11 However, the way that a network is constructed (encoded) defines an epistemology of the network concept
12 which, we argue, can influence the resulting observations and conclusions about pattern and mechanisms
13 that are made (Brimacombe et al., 2023; Proulx et al., 2005). This process of constructing networks has two
14 major pillars: the data and theory, the latter representing an expression of mechanism and process giving
15 rise to patterns that emerge from collating interactions among species. Each of these pillars carries with it
16 a set of practical, semantic and conceptual constraints that not only influence progress in making network
17 ecology more valuable and potentially predictive, but help define the spatial, temporal and evolutionary scale
18 of assumptions we make and predictions we might generate from the networks.

19 With respect to data, it is extremely challenging to actually record species interactions in the field (Jordano,
20 2016a, 2016b). Despite notable herculean efforts (**Woodward? Benguela?** Maiorano et al. (2020)), actual
21 coverage of ‘real world’ interaction data remains sparse (Poisot et al., 2021). Against this practical challenge,
22 there is additionally high variance in the terminology we use to define networks. Finally, the mathematical
23 and statistical tools we use to construct, conceptualise, analyse and predict with these networks are also
24 highly variable.

25 1. what are the underlying assumptions about nodes, edges, scale and process that are made when we
26 attempt to delimit and describe a food webs;

27 2. are there families of commonly used tools that map onto assumptions about scales and processes;

28 The provision of this detail ultimately leads to a set of insights and conclusions about whether, when and
29 under what conditions network representations of biodiversity can contribute to the advancement of ecological
30 theory and generate value in predictive ecology. Specifically, we finish this perspective with an overview of
31 fundamental questions in ecology that we think can benefit from network thinking and a proposal that such

32 thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities.

33 1 Setting the Scene: The Not So Basics of Nodes and Edges

34 Defining a food web seems simple; it is the representation of the interactions (edges) between species (nodes),
35 however the definition of ‘edges’ and ‘nodes’, as well as the scale at which they are aggregated can take
36 many forms (Poisot, Stouffer, et al., 2016). Networks can be constructed at the population (the links among
37 individuals), community (the links between species), or metacommunity (changes between locations) level.
38 Even if one were to limit their scope to thinking of interaction networks only in terms of food webs at the
39 community-level there are still many ways to define the various components of the network Panel A of [1](#),
40 one needs to understand the different intentions/assumptions that are made when a food web is constructed.
41 Although the main goal of constructing a food web is to capture and represent the feeding links between
42 species there are many ways to define the nodes (*e.g.*, species or taxonomic group), edges (*e.g.*, *potential* or
43 *realised* feeding links), the magnitude of the edges (*e.g.*, binary vs probabilistic), and even how the network
44 itself is delimited (does it represent an aggregation of interactions over time?).

45 [Figure 1 about here.]

46 1.0.1 How do we define a node?

47 Although this may seem an elementary question in the context of food webs — a node *should* represent a
48 (taxonomic) species, the reality is that nodes can often represent an aggregation of different species - so called
49 ‘trophic species’ or segregation of species by life stages. Representing nodes as non-taxonomic species can be
50 useful in certain contexts (Williams & Martinez, 2000; Yodzis, 1982) and in cases where the adult and larval
51 stages of a species have different diets it may make ecological sense (Clegg et al., 2018) meaning that it is
52 not uncommon that networks often have nodes that have different definitions of a ‘species’ *e.g.* consisting
53 of both taxonomic and trophic species. Practical implications of how we are aggregating the nodes is that
54 the resolution may not always be ‘pixel perfect’ *i.e.*, we may be unable to assess the co-extinction risk of a
55 species pair, however there is value in having nodes that represent an aggregation of species, as these convey
56 a much more general overview of how the links are distributed within the community.

57 1.0.2 What is meant by an edge?

58 At its core, links within food webs can be thought of as a representation of either feeding links between
59 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within
60 the community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will

influence the resulting structure of the network - and the inferences we will make thereof. 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. 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).

1.0.3 Putting the parts together

The ingredients one uses to construct networks generates a unique representation of the mechanisms (see Section 2) that allow inference and reasoning about the structure, aspects of dynamics (*e.g.*, stability), and potentially the function of communities (*e.g.*, flux). It is thus important to keep in mind that different networks are going to be representing different processes and that can only be used for inference of some but not all aspects of the community at large. Here it may be meaningful to contextualise the different ‘types’ of food webs within the larger research programmes (or even practical needs) that have been driving the construction of them.

Before thinking about the ways in which we can predict networks it is perhaps meaningful to take a step back and think about the different criteria that must be met in order for an interaction to be able to occur between two species, specifically thinking of this in terms of distinguishing between the feasibility versus realisation of an interaction and how these are determined (and defined by) different ‘rules’/mechanisms. If we look at this feasibility-reality continuum (Figure 2) it is clear how the different predictive approaches (methods) tend to fall within one of the broader categories identified (distinguished) in the triangle. This is not to say that this shortcoming should be viewed as a ‘bug’ but rather a ‘feature’ of the field as it allows one to engage with, as well as construct networks at different scales, which is particularly valuable if one takes into consideration the considerable ‘data cost’ of predicting well resolved, realised networks in comparison to constructing high-level metawebs. However, it is important that there is an awareness and acknowledgement of where within this feasibility-reality one is working at and how this will impact and limit the contexts in which the resulting network can be used and applied within.

90 2 From Nodes and Edges to Scales, Context, and Processes

91 Armed with these basics, it is now possible to review the scales and assumptions that are made by a wide
92 range of tools to assist in constructing networks against poor data with the hope of capturing important
93 processes that underpin accurate prediction. Our thesis centres on a four-tier conceptualization of networks:
94 evolutionary compatibility, co-occurrence, feasibility, abundance, predator choice, and non-trophic interac-
95 tions. In the following sections we review each of these and then provide a synthesis among them.

96 2.1 Understanding the processes that determine species interactions

97 Processes that are all-or-nothing (possibility) vs processes that are context dependent (likelihood). Processes
98 form the underlying logic of models (and *arguably*, no, for sure even empirical data) capture. This means
99 also the interplay of the two, *i.e.*, the use of models to ‘gap fill’ within existing empirical dataset (Biton et
100 al., 2024; Stock, 2021). Ultimately when we put this all together it will influence how we can (and should)
101 use the resulting network. Here we present Figure 2 some of the processes that have been shown to influence
102 either/or the feasibility (possibility) of an interaction occurring between two species or if a feasible interaction
103 is realised (likelihood of realisation) within the specific environmental/community context. Of course these
104 processes do not function in a vacuum and do interact with/influence one another but it is still beneficial
105 to present them as such as these are often the underlying processes that influence model development, the
106 criteria for data collection in the field, and the scale of organisation for which they are relevant (species,
107 population, community).

108 [Figure 2 about here.]

109 Evolutionary compatibility

110 There is compelling evidence that the possibility of an interaction occurring between two species is the result
111 of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Segar et al., 2020).
112 In the more proximal sense this is manifested as the ‘trait complementarity’ between two species, whereby
113 one species (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume
114 the other species (the prey). For species pairs where this condition is not met the link is deemed to be
115 forbidden (Jordano, 2016b); *i.e.*, not physically possible and will always be absent within the network. In the
116 context of trying to determine the feasibility (*i.e.*, the *possibility*) of an interaction, phylogeny is an excellent
117 predictor (Fricke et al., 2022; Strydom et al., 2022) and allows one to construct what can be considered to
118 be a metaweb. In terms of thinking about the anatomy of an ‘feasibility network’ one should be aware that
119 it is possible to represent interactions as either binary (feasible/forbidden; *i.e.*, the traditional definition of a

120 metaweb Dunne (2006)) or as a probability (Banville et al., 2024), where the probability represents how likely
121 that the interaction between two species is feasible (what is the possibility of this interaction occurring?).

122 (Co)occurrence

123 Although the outright assumption that because two species are co-occurring it must mean that they are
124 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at
125 least in terms of feeding links) if they are not co-occurring in time and space. Thus co-occurrence data alone is
126 insufficient to build an accurate and ecologically meaningful representation of a food web having information
127 on the co-occurrence of species can further aid us in refining metawebs by allowing us to downsample the
128 network based on the species found in a specific location, or even add additional uncertainty based in how
129 likely species are to co-occur (Dansereau et al., 2023). Additionally the interplay between the interaction
130 between a species pair and their co-occurrence is meaningful when one is operating in the space of trying to
131 determine the distribution of a species (Higino et al., 2023), and forms a key component of some of the next
132 generation species distribution models *e.g.*, joint SDMs (Pollock et al., 2014).

133 Abundance

134 The abundance of the different species within the community can influence the likelihood of an interaction
135 occurring in a myriad of ways. There is the argument that networks (and the interactions that make them up)
136 are driven by only the abundance of the different species and not the characteristics (traits), *sensu* neutral
137 processes and have been formalised with the neutral model (Canard et al., 2012), as well as statistical tools
138 (Momal et al., 2020). Alternatively the abundance of species in a community can influence which interactions
139 are ultimately realised (Banville et al., 2024; Poisot et al., 2015).

140 Predator choice (energetic cost)

141 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume
142 prey, and is well described within optimal foraging theory [ref] and rests on the idea that the prey a predator
143 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. There are
144 additional bodies of work that attempt to include the cost of movement that the environment imposes on an
145 individual (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012). In terms of formalising
146 these processes in the context of predicting networks using diet models (Beckerman et al., 2006; Petchey et al.,
147 2008) that have predator choice determined by the handling time, energy content, prey density, and predator
148 attack rate. Wootton et al. (2023) developed a model that moves the energy of the system into different
149 modules related to the process of the predator acquiring energy from the prey *i.e.*, compartmentation in food
150 webs (Krause et al., 2003).

151 **Indirect interactions**

152 The realisation (presence/absence) or strength of trophic interactions themselves can also be modified by
153 other, indirect (non-trophic), interactions (Golubski & Abrams, 2011; Pilosof et al., 2017), this can be either
154 ‘directly’ through *e.g.*, competition or ‘indirectly’ *e.g.*, mutualistic/facilitative interactions will alter the fine-
155 scale distribution and abundance of some species (Kéfi et al., 2012, 2015).

156 It should be self evident that the different processes discussed above are all ultimately going to influence the
157 realisation of interactions as well as the structure of a network, however they are acting at different scales of
158 organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of the
159 species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise
160 level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a
161 network (*i.e.*, metaweb) from this information it is important to be aware that the structure of this network
162 is not constrained by real-world dynamics or conditions (*i.e.*, community context), just because species are
163 able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who’s
164 structure is a closer approximation of reality (localised interactions) one needs to take into consideration
165 properties of the community as a whole and not just the two species of interest.

166 **downsampling paragraph??**

167 **3 Network prediction is nuanced**

168 The different models that are used to either predict or construct networks have an underlying philosophy
169 that often only captures one or a few of the processes discussed in Section 2.1, has implications for how the
170 resulting network is defined Section 1, which will ultimately delimit and define what inferences can be made
171 from the resulting network. Selecting a model for the task of network prediction should come down to two
172 things; what *aspect* of a food web one is interested in predicting, and what data are available, necessary,
173 and sufficient, and what is the purpose of wanting to predict a network? It is important that a researcher
174 is aware of this to ensure that the appropriate model is selected. Broadly researchers will be interested in
175 predicting/constructing two different types of networks; *metawebs*, which is essentially a list of all interactions
176 that are *possible* for a specific community (*i.e.*, at the scale of the species pairs), or being able to predict
177 location specific, *realised*, networks for the community (*i.e.*, at the scale of the community). The nature
178 of metawebs means that they are unable to capture the structural metrics of realised/‘real-world’ networks
179 (Caron et al., 2024). The researcher is also constrained by the data needs of both the model as well as the
180 network type; for example in order to predict a realised network one needs additional community/population

181 level data (*e.g.*, abundance), making metawebs a more feasible choice in data-poor contexts (*e.g.*, Strydom et
182 al. (2023) construct a metaweb using a species list and a phylogenetic tree). The final question is assessing
183 the purpose of predicting a network - is it to create a series of simulated, species agnostic but still ecologically
184 plausible, networks [*e.g.*,] or to predict a network for a specific community at a specific location. It is these
185 three points that will ultimately dictate which model is going to best allow one to predict the appropriate
186 network.

187 **3.1 Models that predict structure**

188 Although we identify mechanisms that determine species interactions in Section 2.1 not all models that are
189 used to predict networks operate at this ‘mechanistic’ level (at least in absolute terms), but rather represent
190 the *structure* of a network based on a series of *a priori* assumptions of network connectance (*e.g.*, the niche
191 model Williams & Martinez (2000); although see Allesina & Pascual (2009) for a parameter-free model) or
192 other structural features of a *realised* network (*e.g.*, stochastic block model, Xie et al. (2017)). Importantly
193 these structural models do not make species specific predictions (they are usually species agnostic and treat
194 nodes as trophic species) and so cannot be used to determine if an interaction is either possible *or* realised
195 between two species (*i.e.*, one cannot use these models to determine if species *a* eats species *b*). Although this
196 means this suite of models are unsuitable as tools for predicting interactions, they have been shown to be
197 sufficient tools to predict the structure of networks (Williams & Martinez, 2008).

198 **3.2 How do we predict food webs?**

199 There as many ways to predict networks as what there is to define them and along with taking into con-
200 sideration the points raised in the previous section it is also beneficial to think about the context in which
201 the different models were developed - and how this will influence the networks that they produce... Also it
202 is not feasibly possible to list every single approach that has been developed to predict networks and so we
203 will present what we believe to be the broad families that represent the different approaches to predicting
204 networks Table 1, particularly how these relate to the processes identified in Section 2.1, as well as models
205 that predict network structure (see Section 3.1). A more extensive overview of the different models that fall
206 with in the different model families can be found in SuppMat 1 and for a more detailed breakdown of the
207 different ‘traits’ of the model families refer to SuppMat 2.

Table 1: A summary of the different families of tools that can be used to generate food webs.

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
null	Links are randomly distributed within a network		parameter assumptions, species agnostic	structural network	
neutral	Network structure is random, but species abundance determines links between nodes	abundance	parameter assumptions	structural network	Canard et al. (2012)
resource	Networks are interval, species can be ordered on a 'niche axis'		parameter assumptions, species agnostic	structural network	Williams & Martinez (2008)
generative	Networks are determined by their structural features		need real world networks	structural network	
energetic	Interactions are determined by energetic costs	abundance + energy	does not account for forbidden links in terms of evolutionary compatibility	'energy' network	
graph embedding	Interactions can be predicted from the latent traits of networks	evolutionary compatibility	need real world networks	metaweb	Strydom et al. (2023)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
trait matching	Interactions can be inferred by a mechanistic frame-work/relationships	evolutionary compatibility	well studied species/communities	metaweb	Morales-Castilla et al. (2015)
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	evolutionary compatibility	need real world networks	metaweb	Pichler et al. (2020)
expert knowledge	'Boots on the ground'	evolutionary compatibility	well studied species/communities	metaweb	
data scavenging	Webscraping to create networks from online databases		need real world networks	metaweb	Poisot, Gravel, et al. (2016) (if you squint?)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
co-occurrence	co-occurrence patterns arise from interactions so we can use these patterns to reverse engineer the interactions	co-occurrence	does not account for forbidden links in terms of evolutionary compatibility or account for energy constraints	co-occurrence network	

²⁰⁸ There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle,
²⁰⁹ 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible
²¹⁰ *representations* (*sensu* structural networks). This represents two challenges; one is that models that repre-
²¹¹ sent generalisations of networks often lack the ability to retrieve any species/community specificity which
²¹² limits their utility for real world, species-driven scenarios *e.g.*, species driven conservation efforts (Dunn et
²¹³ al., 2009), however networks that are constructed through either (most) empirical observations or through
²¹⁴ predictive means are fundamentally going to represent metawebs, *i.e.*, lack constrained links, a representation
²¹⁵ of structure, or energy flow...

²¹⁶ 4 Making Progress with Networks

²¹⁷ 4.1 Further development of models and tools

²¹⁸ As we show in Table 1 there has been a suite of models that have been developed to predict trophic links,
²¹⁹ however we are lacking in tools that are explicitly taking into consideration estimating both the feasibility
²²⁰ as well as realisation of links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021).
²²¹ This could be addressed either through the development of tools that do both (predict both interactions and
²²² structure), or it might be possible to do a ensemble modelling approach (Becker et al., 2022). Alternatively
²²³ the development of tools that will allow for the downsampling of metawebs into realised networks (*e.g.*,
²²⁴ Roopnarine, 2006), although deciding exactly what is driving differences between local networks and the
²²⁵ regional metaweb might not be that simple (Saravia et al., 2022). Probably also something that aligns with
²²⁶ trying to predict interaction strength - because that would be the gold standard. Probably also worth just

227 plainly stating that feasibility of developing a model that is both broadly generalisable, but also has local
228 specificity is probably not attainable (Stouffer, 2019)

229 **4.2 At what scale should we be predicting/using networks?**

230 Look at Hutchinson et al. (2019)

231 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a
232 ‘network’. Realistically most empirical networks are more aligned with metawebs as opposed to realised
233 networks as they are often the result of some sort of aggregation of observations across time, this creates a
234 two-fold problem. Firstly, we need to think about how this affects any sort of development of theory that sits
235 closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer questions
236 about realised networks using feasible networks? The second is that this lack of ‘direction’ as to how we
237 should define a network is (actually) probably one of the biggest barriers that is affecting the use of networks
238 in applied settings... By define I mean both delimiting the time and geographic scale at which a network is
239 aggregated at (Estay et al., 2023). This is important because it can influence the inferences made, *e.g.*, the
240 large body of work (landscape theory for food web architecture) that showcases how different species use the
241 landscape will influence network dynamics (Rooney et al., 2008). There is also a bit of an interplay with
242 time and data and the different scales that they may be integrated at - co-occurrence may span decades and
243 just because two species have been recorded in the same space does not mean it was at the same timescale
244 (Brimacombe et al., 2024)

245 **4.3 How should we use different networks?**

246 What for and how we can use networks is perhaps one of the biggest ‘gaps’ we have in network ecology
247 (Tim’s EBV ms), and there is a serious need to start drawing clear, ecological links between network form
248 and function (although see Delmas et al., 2019). That being said one of the most important things we can
249 do is to be aware of the parameter space that is possible given a specific definition of a network and operate
250 within those parameters. And we should use this in how we also evaluate/benchmark the performance of the
251 different models as well; Poisot (2023) presents a set of guidelines for assessing how well a model recovers
252 pairwise interactions but we lack any clear strategies for benchmarking structure.

253 **4.4 Feasible, realised, or sustainable?**

254 When do we determine a link to be ‘real’... In the context of feasible networks this is perhaps clearer - if all
255 things were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the prey.

256 However in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction
257 - just because an interaction is possible in the now is it able to sustain a population in the long term. And
258 what is the scale for that long term - are we thinking at the generational scale? Because ultimately when we
259 are constructing a network we are aggregating not only across space but also across time... This is probably
260 again a Lokta-Volterra space question and something that the dynamic foodweb model (BEFW, Curtsdotter
261 et al. (2019)) is addressing, but again it is integrating this with the feasible/realised axis.

262 5 Concluding remarks

263 I think a big take home will (hopefully) be how different approaches do better in different situations and so
264 you as an end user need to take this into consideration and pick accordingly. I think Petchey et al. (2011)
265 might have (and share) some thoughts on this. I feel like I need to look at Berlow et al. (2008) but maybe
266 not exactly in this context but vaguely adjacent. This is sort of the crux of the argument presented in
267 Brimacombe et al. (2024) as well.

268 Do we expect there to be differences when thinking about unipartite vs bipartite networks? Is there underlying
269 ecology/theory that would assume that different mechanisms (and thus models) are relevant in these two
270 ‘systems’.

- 271 • The Terry & Lewis (2020) paper looks at some methods but is specifically looking at a bipartite world...

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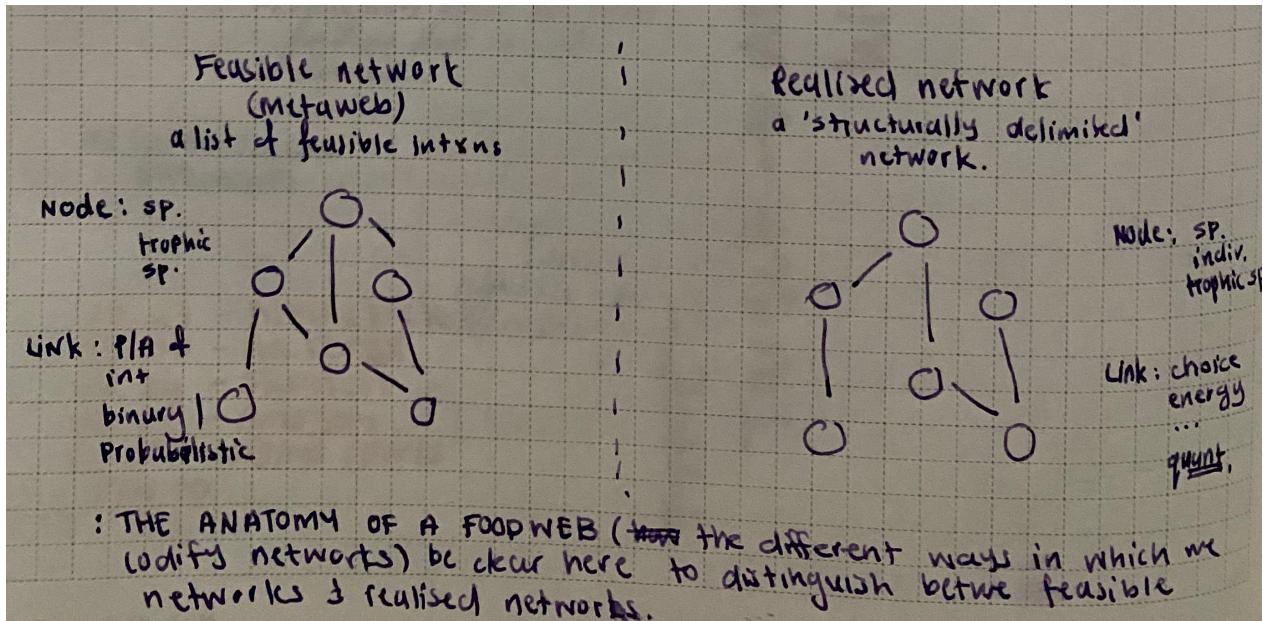


Figure 1: The many ways in which a food web can be defined and described at the node, edge, and even network level.

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		木	179	
level of obj.		(mechanisms) what determines direct interaction		the "driver" of the interaction ≠ the underlying theory (l:1) & the way we get to the answer is diff e.g. co-occurrence is about sharing space/time but we use niche theory env. filtering as the means to determine co-occurrence.
6	Species	fund. niches (inv. filter)	co- occurrence	
15		buckbones (mora) truit-match	"capacity"	
21	Pop.	neutral. funct. resp.	pop size/ dynamics	
0	indiv.	"physics" 2D 3D prey choice	energy	
3		?? allometric scaling??		
		: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES		

Figure 2: TODO.