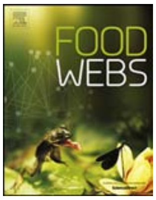
Food Webs xxx (2018) e00093

Contents lists available at ScienceDirect

Food Webs

journal homepage: fooweb



# A review of species role concepts in food webs

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## ARTICLE INFO

*Article history:*
Received 16 July 2017
Received in revised form 22 May 2018
Accepted 4 July 2018
Available online xxxx

*Keywords:*
Eltonian niche
Network structure

## ABSTRACT

Many different concepts have been used to describe species' roles in food webs (i.e., the ways in which species participate in their communities as consumers and resources). As each concept focuses on a different aspect of food-web structure, it can be difficult to relate these concepts to each other and to other aspects of ecology. Here we use the Eltonian niche as an overarching framework, within which we summarize several commonly-used role concepts (degree, trophic level, motif roles, and centrality). We focus mainly on the topological versions of these concepts but, where dynamical versions of a role concept exist, we acknowledge these as well. Our aim is to highlight areas of overlap and ambiguity between different role concepts and to describe how these roles can be used to group species according to different strategies (i.e., equivalence and functional roles). The existence of "gray areas" between role concepts make it essential for authors to carefully consider both which role concept(s) are most appropriate for the analyses they wish to conduct and what aspect of species' niches (if any) they wish to address. The ecological meaning of differences between species' roles can change dramatically depending on which role concept(s) are used.

**Contents**

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https://doi.org/10.1016/j.fooweb.2018.e00093

Please cite this article as: A. Cirtwill et al., A review of species role concepts in food webs, Food Webs (2018), https://doi.org/10.1016/j.fooweb.2018.e00093

## 1. Introduction

Ecologists often wish to understand a species' "place in the biotic environment, its relations to food and enemies" (Elton, 1927 in Johnson and Steiner, 2000) or, in short, its *Eltonian niche* (see Box 1). Eltonian niches provide a conceptual framework with which to relate species sharing the same environment. Species can be arranged along a hypothetical "niche axis" indicating their degree of similarity to each other (Godoy et al., 2018). Species with overlapping niches compete for whatever resource(s) are associated with the niche axis and therefore may be less likely to coexist (Godoy et al., 2018). When a single limiting resource can be used as the niche axis, this is a straightforward framework with which to analyze ecological communities. In many cases, however, species require (and compete for) a wide variety of abiotic and biotic resources that may not all be known. In such cases, it may not be possible to specify the Eltonian niches of all species in a community.

It is possible, however, to describe the biotic component of species' Eltonian niches using food webs — networks of species' trophic interactions (Pimm et al., 1991). These networks often describe antagonistic interactions such as predation and parasitism, but can also include mutualisms (such as pollination and seed-dispersal) where one species feeds on another while providing a reproductive service. Food webs describe energy and biomass flows through a community (Lindeman, 1942; Wootton, 1997), represent ecosystem functions (Memmott et al., 2007; Reiss et al., 2009; Thompson et al., 2012), and can offer insights into the community's overall *stability* (Neutel et al., 2002; Thébault and Fontaine, 2010). Thus, describing species' *roles* in food webs (i.e., how each species participates in its community) provides a toolbox with which to assess species' Eltonian niches both in terms of their requirements for survival and their impacts on their communities (Chase and Leibold, 2003).

Note, however, that roles and Eltonian niches are related but not equivalent. A species' role in a network (e.g., a food web describing interactions between species at a single site) describes only part of the Eltonian niche. This is true even when we completely ignore species' abiotic requirements (Peterson, 2011). First and foremost, food webs generally only include one type of interaction (e.g., predation or pollination but not both Fontaine et al., 2011). Some researchers are attempting to rectify this limitation (e.g., Fontaine et al., 2011), but published webs including multiple interaction types remain rare (but see Pocock et al., 2012; Albrecht et al., 2014). A species' role in a food web therefore describes only the portion of its niche that relates to the kind of interaction being described in the food web. For example, the roles of a species of Lepidoptera will be quite different in networks describing pollination, herbivory, or predation. Moreover, the Eltonian niche aims to identify the biotic conditions that a species requires in order to persist for moderate timescales (i.e., from individual lifespans up to thousands of years Peterson, 2011) while food webs describe communities at a particular point in time with no guarantee that the species present during sampling will persist. Food webs thus provide a representation of species' niches that are narrowly focused on a single interaction type and may include a broader set of conditions than would allow moderate-term persistence.

As well as these difficulties with selecting appropriate spatial and temporal scales at which to define species' niches based on their food-web roles, there is also the question of which role concept to use. Some of these role concepts offer clearer analogues to the Eltonian niche than others, which can limit the applicability of network studies to other branches of ecology that apply the Eltonian niche concept more directly. Moreover, this plethora of definitions can lead to confusion when considering different studies of species' roles. This is similar to the confusion that has arisen in the *keystone species* literature, where an intuitive concept has been associated with many, sometimes mutually exclusive, precise definitions (Cottee-Jones and Whittaker, 2012). To tackle these problems, here we review several commonly-used concepts of species' roles in food webs. For each definition, we summarize the methodology used to obtain the role and highlight its connection to the species' Eltonian niche. Where multiple role concepts describe similar aspects of species' Eltonian niches, we take care to point these connections out. As well as reviewing role definitions, we outline ways in which species with similar roles may be grouped. Finally, we conclude with an outline of current limitations to the idea of species' roles, and how researchers are working to overcome these limitations. Terms in italics are defined in Box 1.

## 2. Concepts of species' roles in networks

### 2.1. Degree

One of the mathematically simplest definitions of a species' role is it's *degree*: the number of interaction partners (or feeding links in which the species participates; Fig. 1; Jordán et al., 2007). Degree depends only on the focal species' *local* neighborhood within the network — those species which directly interact with the focal species. Thus, degree provides a measure of species' participation in a food web without requiring any knowledge of the *global* (i.e., overall) structure of the web (Jordán et al., 2007). Degree can also be used to investigate particular subsets of a species' local neighborhood. If the focal species' role as a predator specifically (for example) is of greater interest than its overall role, degree can be divided into in-degree — the number of incoming links — and out-degree — the number of outgoing links (Fig. 1B). In food web terms, in-degree corresponds to generality — number of prey — and out-degree to vulnerability — number of predators (Jordán et al., 2006). Note that this is only applicable in *unipartite* networks because each group of species in a *bipartite* network has only in-links or only out-links. In any of these forms, degree describes a species' place in the biotic environment in terms of how strongly the species interacts with its community.

Degree has often been equated with importance to the structure and functioning of a community. Species with high degrees are believed to be particularly important because changes to the abundances of such species directly affect many other species (Lai et al., 2012). Perturbations to high-degree species may therefore have larger effects on the food web than perturbations to low-degree species. Moreover, it is more likely that high-degree species in mutualistic networks will have interaction partners that depend very strongly upon them and could go extinct if the high-degree species becomes rare (Bascompte et al., 2006; Aizen et al., 2008). In antagonistic networks, this may also be true of species with high vulnerabilities (out-degrees) but not necessarily those with high generalities (in-degrees; (Curtsdotter et al., 2011). In both antagonistic

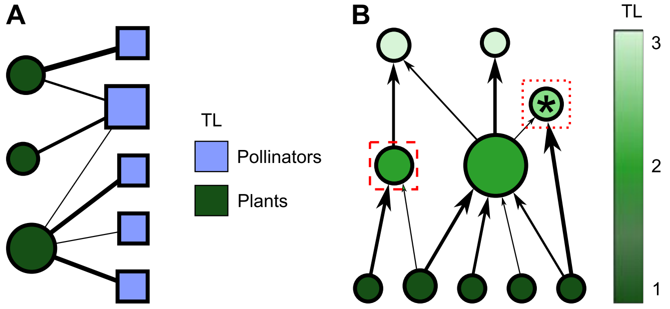

**Fig. 1.** Each of the two food webs below contain species with different degrees and trophic levels. A) In this bipartite food web, pale blue squares represent pollinators and dark green circles represent plants. Note that species in one group only interact with species in the other group (i.e., plants do not pollinate other plants). B) In a unipartite food web, any two species (circles) could potentially interact and all nodes belong to a single group. It is possible (though rare) for plants to consume animals, and animals may consume plants, animals, or both. The species marked with '*' illustrates this by consuming both a basal resource and another consumer. In a unipartite web, a focal species' degree (number of interaction partners) can also be subdivided into in- and out-degrees based on numbers of prey and predators, respectively. For example, the species highlighted in the red, dashed box has an in-degree of 2 and an out-degree of 1, giving an overall degree of 3. In both networks, node size increases with degree while fill represents trophic level (TL; height in food chains). In A), the two groups of species are at different trophic levels. In B), trophic levels increase from primary producers (TL=1; dark green) to predators (TL=3, very light green). Most of the species in this food web have integer trophic levels. The species marked with '*', however, is an omnivore with both plant and animal resources. Its trophic level therefore depends on the exact definition of trophic level used. Short-weighted trophic level considers only the most direct path from the focal species to a primary producer; under this definition, the focal species has a trophic level of 2. Prey-averaged trophic level (PATL), in contrast, considers the trophic levels of all the focal species' prey. If interaction strengths (indicated by line weights) are not considered, the focal species has a trophic level of 2.5. If interaction strengths are accounted for, however, the focal species' PATL will be closer to 2 because the omnivore has a stronger link to the basal resource than to its herbivore prey.

and mutualistic networks, the removal of a high-degree or high-vulnerability species is more likely to cause secondary extinctions than the removal of a low-degree species (Dunne et al., 2002; Memmott et al., 2004; Eklöf and Ebenman, 2006; Kaiser-Bunbury et al., 2010; Curtsdotter et al., 2011). This suggests that species with many interactions may be keystone or dominant species in ecological networks because they are generalists with many interaction partners (Dunne et al., 2002). Degree can also have implications for understanding the impacts of introduced species. For example, specialist pollinators that are weak contributors to nestedness (i.e., that tend not to interact with a subset of plants that interact with generalist pollinators) are more likely than generalists to interact with exotic plants (Stouffer et al., 2014) while generalist introduced species tend to interact with partners that are strongly dependent upon them (Aizen et al., 2008). This suggests that introduced plants may be valuable resources for specialist pollinators that have lost native interaction partners and that efforts to control these plants may have adverse effects on some pollinator species. In predator-prey food webs, generalists may also be more likely to become successful invaders and drive native specialists extinct, leading to "biological homogenization" (Olden et al., 2004; Layman and Allgeier, 2012). Although it seems intuitively likely that species with broader diets (higher degrees) are more likely to become invasive, this does not appear to be the case for birds (Kolar and Lodge, 2001). The relationship between invasiveness and degree in other taxa remains to be seen.

As well as predicting species' effects on their communities, degrees can also be used to predict which species are most likely to go extinct after the loss of an interaction partner. Specialist consumers (those with low in-degrees) are particularly vulnerable to the loss of prey (Allesina, 2012). This is because, with fewer prey to begin with, it is more likely that the lost prey would constitute a critical proportion of the consumer's diet than would a single lost prey in the diet of a generalist with many resources to draw from. This difference in vulnerability to secondary extinction in turn has implications for biogeography. As specialists are more likely to go extinct following the loss of a prey species, they should appear in fewer habitat patches than generalists at the landscape level (Holt, 2010; Gravel et al., 2011) and have smaller geographic ranges overall (Holt, 2010). This means that specialists make a particularly large contribution to *beta diversity* (Ødegaard, 2006).

Despite its utility, some have argued that the *qualitative* degree described above, which is calculated based only on the presence or absence of links between species, does not accurately reflect species' specialization or importance to the community (e.g., Blüthgen et al., 2006). To address this problem, several *quantitative* extensions of degree have been formulated. These extensions all weight interactions to reflect the importance of the focal species to each of its interaction partners rather than assuming all interactions have the same importance (Blüthgen et al., 2007; Dormann, 2011; Nilsson and McCann, 2016). Weighted measures may thus provide a more realistic measure of a species' effect on its interaction partners than qualitative degree (Wootton, 2005; Vázquez et al., 2005). However, calculating weighted degrees requires more detailed data than those used to determine qualitative degree. As these data are more costly and time-intensive to collect, datasets that include interaction weights are much rarer than food webs that include only the presence or absence of interactions, limiting their use to date.

Both quantitative and qualitative degree describe the breadth of a species' Eltonian niche (how many resources and enemies it has) but neither reveals *what* the species' niche is. As described above, this can still be useful when ranking species' risk of extinction or their potential to cause adverse effects if lost. For studies which aim to compare other aspects of species' Eltonian niches, however, other role concepts are necessary.

### 2.2. Trophic level

Besides describing the potential for a species to affect the rest of its community, degree can also be used to give an idea of a species' vertical position in a food web — i.e., its *trophic level* (Thompson et al., 2007). This role concept refers to a species' place in the *food chains* that make up a food web, relative to the primary producers that support the community. Species that do not consume any other species in the web (i.e., those with an in-degree of zero) are primary producers or other basal resources (Williams and Martinez, 2000). At the other extreme, species with no predators (i.e., those with an out-degree of zero) are top predators (Fig. 1B). Those with both predators and prey (i.e., non-zero in- and out-degrees) are intermediate consumers. In most cases, this also includes cannibalistic species (Williams and Martinez, 2000). In Eltonian niche terms, trophic levels tell us whether a focal species relates to its biotic environment as a predator, prey, or both. This has implications for, among other areas, island biogeography and studies of invasive species. In both cases, species with lower trophic levels are more likely to successfully colonize a novel site as they are less likely to require prey that may or may not be present (Holt, 2010).

For species other than primary producers and top predators, degree alone is not enough to calculate trophic levels. Instead, it is necessary to consider the network structure beyond the focal species' local neighborhood. Specifically, trophic levels can be calculated by following food chains from primary producers to the focal species (Lindeman, 1942). Each step up the food chain is a new trophic level, with strict herbivores (that consume only basal resources) assigned a trophic level of two and consumers occupying ever higher values based on their sets of prey species (Lindeman, 1942; Darnell, 1961; Baird and Ulanowicz, 1989; Christian and Luczkovich, 1999). This

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simple definition was developed under the assumption that species feed on sets of prey with the same trophic level (Lindeman, 1942). As the prevalence and importance of omnivory in food webs has become clear (Holt, 1997; Emmerson and Yearsley, 2004; Thompson et al., 2007), however, non-integer trophic levels based on the average lengths of food chains leading to the focal species have become the norm (Cousins, 1987; Vander Zanden and Rasmussen, 1996; Williams and Martinez, 2004; Thompson et al., 2007). To emphasize this shift, some researchers prefer the term "trophic position" (e.g., Levine, 1980; Cohen et al., 2003). As the two terms refer to the same property, we will continue to use trophic level to refer to a species' vertical position in a food web.

A variety of methods have been developed to account for species that feed on prey at different trophic levels (Fig. 1B). Each approach emphasizes different interactions. "Shortest trophic level", for example, assumes that because losses occur during the transfer of energy between trophic levels, species obtain most of their energy along the shortest food chain in which they participate (Hairston, N.G., Jr and Hairson, N.G., Sr, 1993; Williams and Martinez, 2004). Under this concept, therefore, a species' trophic level is one greater than the lowest trophic level among its prey (Hairston, N.G., Jr and Hairson, N.G., Sr, 1993; Williams and Martinez, 2004). Other methods such as prey-averaged trophic level take all food chains in which the focal species participates into account (Williams and Martinez, 2004). These measures can also incorporate dynamical information by weighting each prey species according to the proportion of the predator's diet it makes up. Regardless of the precise methodology, however, trophic levels always rank species based on their vertical position in food webs, with primary producers setting the baseline.

Trophic levels can also be calculated independent of food-web topology by using stable isotopes (Peterson and Fry, 1987; Vander Zanden and Rasmussen, 1996; Post, 2002). This approach uses the different rates of bioaccumulation of carbon and nitrogen isotopes to measure species' average trophic levels without requiring knowledge of specific interactions between species. Because they are calculated based on tissue samples, stable isotope-based trophic levels are always weighted averages that depend upon the proportions of each prey in the predator's diet and on the digestability of each prey. While the stable isotopes approach is therefore useful in cases where the structure of the food web is not known or where researchers desire a dynamical version of trophic level, there are also a number of methodological issues that limit its applicability. Stable isotope ratios vary between taxa and tissue types depending on their particular biochemistries (Vander Zanden et al., 2015) and between study sites, requiring the use of baseline species in each food web under study (Kling et al., 1992; Cabana and Rasmussen, 1994; O'Reilly et al., 2002; Boecklen et al., 2011). Moreover, $n$ isotopes can only be used to distinguish among $n + 1$ potential sources (Phillips and Gregg, 2003) — and then only when the isotope values of the sources are distinct (Newsome et al., 2012). For species with many sources of prey — especially where those prey represent different taxa and/or feed in different habitats — the range of possible diets for a consumer may be too broad to obtain a good estimate of its trophic level (Phillips and Gregg, 2003). Improved statistical methods can help to solve this problem, but ideally stable isotopes data should be combined with direct observations of feeding interactions or of scat (Newsome et al., 2012). All of the above caveats for both topological and stable-isotopes methods notwithstanding, different measures of trophic level tend to be strongly correlated (Williams and Martinez, 2004; Carscallen et al., 2012). This supports the idea that topological definitions of trophic levels are grounded in sound ecological characteristics and suggests that trophic levels may be comparable across studies even if different methodologies are used. That is, different definitions of trophic level capture similar information about a species' Eltonian niche.

Similar to degree, trophic level can be used to predict which species may have large effects on their communities — for example by causing a *trophic cascade* (Dyer and Letourneau, 2003; Eklöf and Ebenman, 2006; Boersma et al., 2014; Estes et al., 2015) after a change in abundance. Top predators and primary producers are expected to have particularly large effects on the rest of their communities through top-down and bottom-up control, respectively (Power, 1992; Dyer and Letourneau, 2003; Gratton and Denno, 2003). Both groups tend to have strong direct effects on the trophic level immediately below/above them (Gratton and Denno, 2003; Polishchuk et al., 2013); these direct effects can have cascading indirect effects by leading to alternately higher and lower abundances at each level (Power, 1992). Whether or not a trophic cascade occurs also depends on the degree of omnivory in the web (Thompson et al., 2007) as well as the type of web (Dyer and Letourneau, 2003), such that trophic level is not always a strong predictor of cascades. Nevertheless, where omnivory is low (Thompson et al., 2007), species at risk of causing trophic cascades following a change in abundance may be high priorities for conservation action because of the risk that they might negatively impact the rest of their community. Like degree, therefore, trophic level offers information about how important a species is to its biotic community. Unlike degree, which is related to the breadth of the Eltonian niche but not what the niche might be, trophic level gives information about the position of a species' niche along an axis from producer to top predator, but not the breadth of the Eltonian niche.

### 2.3. Motif roles

A major limitation to both trophic level and degree is that they give little information on species' indirect interactions (except for those involved in trophic cascades) — interactions that can have major impacts on the focal species despite not involving it directly (Wootton, 1994; Jordán et al., 2006). The ability of these role concepts to describe species' Eltonian niches is therefore limited because indirect effects can modulate the relationships between the focal species and their interaction partners. For example, if a predator of the focal species has other prey and the focal species becomes rare, the predator might seek out the alternative prey (McCann et al., 2005). The interaction between the predator and its alternate prey might thereby provide the focal species with relief from predation pressure (Hammill et al., 2015). Similarly, removal of a predator might allow its prey to increase in abundance which in turn could affect the abundance of other predators (Sanders et al., 2013). In either case, indirect interactions can modulate the effect of a focal species' biotic environment and shape its Eltonian niche.

More generally, each unique arrangement of interacting species (i.e., each *motif*) has different consequences for the flow of energy and biomass through a network. Some of these *meso-scale* structures have been shown to affect the focal species' population size and dynamics (Polis et al., 1989; Holt, 1997; Zabalo, 2012), suggesting that participation in certain motifs can also affect species' Eltonian niches. To test for such effects, one can define species' *motif roles* within a food web. These roles extend the concept of network structural motifs — unique patterns of $n$ interacting species (Milo et al., 2002) — to the species level by tracking the frequency with which each species occupies each position within each motif (Fig. 2; Stouffer et al., 2012; Cirtwill and Stouffer, 2015). This role definition aims to provide a more holistic picture of species' Eltonian niches by explicitly including direct and indirect interactions

To determine the motif role of a focal species, the network is first decomposed into a set of motifs (Milo et al., 2002; Stouffer et al., 2007). In unipartite food webs (i.e., those where the species are not divided into groups such as plants and pollinators), there are 13 unique three-species motif structures (Stouffer et al., 2007). Some of these motifs have clear biological meanings and have been studied in isolation, including “three-species food chains” (Fig. 2; Hastings and Powell, 1991; Bascompte and Melián, 2005; Laws and Joern, 2013), “apparent competition” (two prey sharing a predator Holt and Kotler, 1987; Bascompte and Melián, 2005; Lefèvre et al., 2009; McKinnon et al., 2013), and “intraguild predation” (two predators sharing a prey, where one predator also consumes the other Polis et al., 1989; Holt, 1997; Kondoh, 2008; Zabalo, 2012). Others, including many of the motifs involving two-way interactions (i.e., A eats B and B eats A), have not yet been interpreted to our knowledge. This is also true for most motifs that contain more than three species. These large motifs are necessary when describing species' roles in bipartite food webs, which contain only two three-species motifs (Baker et al., 2015). Where possible, however, it is best to use relatively small motifs. This is partly because of computational limitations and the difficulty in interpreting large motifs but also because the impact of indirect effects is expected to decrease moving farther from the focal species (Jordán et al., 2006; Jordán and Scheuring, 2002).

Regardless of the size of motifs being used, each motif contains one or more unique positions. In a three-species food chain motif, each species occupies a unique position as the top, bottom, and middle species all have different biological meanings (Stouffer et al., 2012; Cirtwill and Stouffer, 2015). In an apparent competition motif, in contrast, there are only two unique positions as the two prey are indistinguishable in the context of that motif. Once a network has been broken down into its component motifs, the motif roles of each species can be calculated by counting the number of times the focal species occurs in each position within each motif (Stouffer et al., 2012; Baker et al., 2015; Cirtwill and Stouffer, 2015). This yields a vector of frequencies which describes the focal species' role in terms of its direct and indirect interactions, providing a detailed picture of the way in which the species is embedded in its community (Fig. 2; Stouffer et al., 2012; Baker et al., 2015; Cirtwill and Stouffer, 2015). Because a motif role provides a detailed picture of a focal species' relationships to other species in the community (as a competitor as well as predator and prey), the motif role can be seen as a holistic description of the species' niche from the perspective of the interaction described in the food web. Note that this description is more nuanced than that given by degree as motifs also describe the relationships between the focal species' interaction partners, revealing the presence of trophic loops, intraguild predation, and other ecologically important patterns. To our knowledge, there are not yet any published studies combining interaction strengths with motifs. However, a Python package which calculates weighted (or unweighted) motif roles is currently in production (Bramon Mora et al., 2018). With the upcoming release of this tool, we expect that quantitative studies of motif roles will soon be available.

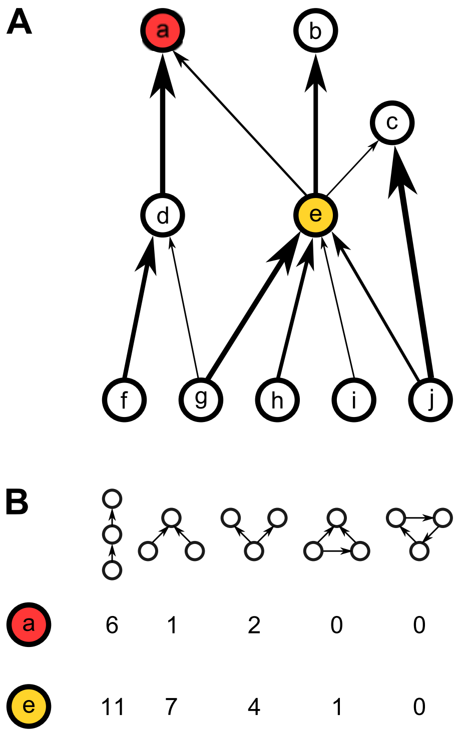

**Fig. 2.** Motif roles describe the way in which each species is embedded in a food web. They are defined by decomposing the web into its component motifs (unique configurations of *n* interacting species) and counting the number of times that each species appears in each motif. In A), we highlight two focal species. In B), we show the roles of these two species, defined based on three-species motifs. Note that while there are 13 different three-species motifs, this simple food web contains only one-way interactions and therefore is made up of the five motifs which contain one-way interactions exclusively. These five motifs are shown above the roles of species ‘a’ and ‘e’; note that the three-species loop motif does not occur in the roles of either species. Also note that each set of 3 interacting species represents only one motif: the motif which includes all interactions among those three species. For example, the set [c, e, j] represents the omnivory motif (second from right in the lower panel) but does not represent a three-species chain or direct competition motif (left and second from left) as these motifs do not capture all of the interactions within this set of species.

Despite being a relatively new development, motif roles have already been used to compare the ways in which free-living species and parasites fit into food webs (Cirtwill and Stouffer, 2015), to measure variation in species' roles over space and time (Baker et al., 2015), and to test whether species' roles are phylogenetically conserved (Stouffer et al., 2012). As motif roles are summaries of the biotic components of species' Eltonian niches, these studies analogously test whether free-living species and parasites have similar Eltonian niches; whether Eltonian niches vary over space and time; and whether related species have similar Eltonian niches, respectively. Motifs can also be used to define the roles of each interaction within a food web (Cirtwill and Stouffer, 2015). Shifting perspective from species to the interactions between them can illustrate how different subtypes of interactions (e.g., concomitant predation on parasites inside their hosts) can shape species' Eltonian niches (Cirtwill and Stouffer, 2015).

Apart from motif roles, the frequencies with which motifs appear in networks have also been linked to community stability, with some motifs appearing much more commonly in stable than unstable networks (Stouffer, 2010; Borrelli et al., 2015). This approach has been extended to predict which species contribute most to the stability of their communities (Stouffer et al., 2012). To the extent that species' motif roles provide a holistic summary of the biotic component of species' Eltonian niches, this is a particularly exciting development. It suggests that the filling of some niches within a community gives a greater boost to the stability of that community than does filling other niches. If this finding is repeated, motif roles could therefore provide a means of prioritizing species for conservation or restoration on the basis of their ability to stabilize a community under threat.

### 2.4. Centrality

Motif roles incorporate meso-scale structures to describe species' direct and indirect interactions. Some measures of *centrality* also incorporate meso-scale (i.e., direct and indirect interactions) and global network structures to describe a species' ability to influence the rest of the food web (Estrada, 2007; Lai et al., 2012). These measures extend the thinking behind degree (which considers only the focal species' local neighborhood) and also consider the focal species' impact through indirect interactions (Jordán et al., 2006; Lai et al., 2012). This extension means that the straightforward association between degree and Eltonian niche breadth is blurred for other measures of centrality.

Please cite this article as: A. Cirtwill et al., A review of species role concepts in food webs, Food Webs (2018), https://doi.org/10.1016/j.fooweb.2018.e00093

Measures of centrality that incorporate meso-scale network structures are usually calculated by identifying the set of food chains in which the focal species participates and then summarizing the species' participation in these chains, just as with prey-averaged trophic level. Unlike trophic levels, however, measures of centrality also consider the food chains that do not involve the focal species and also consider species "above" the focal species as well as those at lower trophic levels. Two such measures, "betweenness centrality" and "information centrality" (Fig. 3), both quantify the frequency with which the focal species appears on paths between pairs of other species (White and Borgatti, 1994; Jordán et al., 2006; Estrada, 2007). The main difference between the two is that betweenness centrality includes only the shortest paths between species while information centrality includes all paths (Jordán et al., 2006; Estrada, 2007). Both measures assess the importance of species as "bridges" for energy transfer (Poulin et al., 2013). A species with high betweenness or information centrality takes part in more food chains and therefore affects more energy flows than a species with low centrality. Both measures can also be calculated incorporating interaction strength (Dormann et al., 2008).

While betweenness and information centrality are based on food chains (meso-scale structures), other definitions of centrality are based on the global structure of the food web. One such measure, eigenvector centrality, is based on the defining eigenvector — the eigenvector associated with the largest eigenvalue — of the food web matrix (Bonacich, 1972; Allesina and Pascual, 2009). Eigenvectors are used to decompose matrices into orthogonal (completely uncorrelated) axes — this is exactly the process underlying principal components analyses (PCA) and other ordination methods (Jolliffe, 2002). The defining eigenvector of a food web is analogous to the first axis of variation in a PCA. In this formulation, the centrality of species $i$ is the $i$th entry in the defining eigenvector (Bonacich, 1972; Allesina and Pascual, 2009; Lai et al., 2012). Keeping with the PCA analogy, a species' eigenvector centrality is its position on the first axis of variation in the structure of the network. Eigenvector centrality can be understood as a distributed version of degree, where each neighbor $j$ contributes to the degree of species $i$ in proportion to $j$'s centrality (Lai et al., 2012).

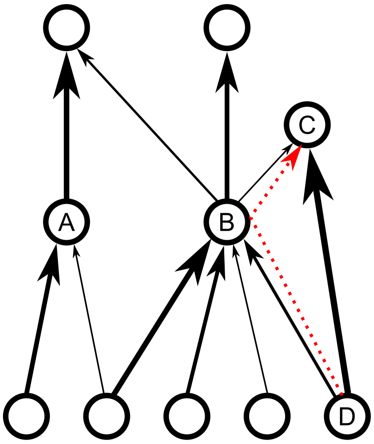

**Fig. 3.** Betweenness centrality measures the number of times a focal species appears on the shortest path between pairs of other species. This measure is often used to infer a species' ability to affect the rest of the food web. Species A appears on two such paths while species B appears on 11. Species B is therefore more likely to have a large effect on its community than is species A. Note that because only the shortest path between a pair of species is considered, the path D-B-C (traced by the dotted arrow) does not contribute to the betweenness centrality of species B. Information centrality is similar to betweenness centrality but includes all paths passing through a species; not only the shortest path. Thus, the path D-B-C would be included when calculating information centrality.

Like other centrality measures, eigenvector centrality aims to describe a species' importance in the network. In this case, a species that interacts with highly-connected partners will have high eigenvector centrality and is likely to be important because any variation in the focal species' abundance will affect its highly-connected partners and, via these partners, the rest of the web (Poulin et al., 2013). This logic is similar to that used when ranking species' importance by their degree, except that eigenvector centrality incorporates the structure of the whole network. Eigenvector centrality can also be related to network stability. The leading eigenvalue (the value associated with the first eigenvector; analogous to the amount of variance explained by the first PCA axis) determines whether a network is locally stable (Neubert and Caswell, 1997; Estrada, 2007; Plank and Law, 2011; Donohue et al., 2013; Rohr et al., 2014). Species with extreme values of eigenvector centrality can therefore be viewed as strong contributors to the stability (or instability) of a food web.

At least nine other centrality measures have been proposed (Jordán et al., 2007). Comparative studies have generally found strong correlations between different centrality measures (Jordán et al., 2006; Estrada, 2007), suggesting that the various centrality measures capture equivalent information about species' roles. We therefore will not describe the other measures in detail here (detailed descriptions are given in Jordán et al., 2007, 2006; Estrada, 2007).

The logic behind all of these centrality measures draws heavily on the keystone species concept — the notion that certain species will have a much larger effect on their community than would be expected based on the species' biomass alone (Paine, 1966; Jordán et al., 2006). Indeed, because highly-central species are expected to affect many other species, centrality has been used to identify potential keystone species in several studies (Jordán et al., 2006; Estrada, 2007; Lai et al., 2012; Mello et al., 2015). Like the keystone species concept, centrality does not tell us so much what a species' Eltonian niche is, but rather suggests which species might have niches that are particularly important for the structure or functioning of the food web. A central species is likely to have a strong effect on the rest of the food web, but we cannot tell whether two central species interact with similar sets of partners or otherwise fit into the web in similar ways. To relate centrality to the Eltonian niche it may be necessary to use several role concepts in the same study.

## 3. Grouping species with similar roles

### 3.1. *Structural and regular equivalence*

Having completed a brief outline of methods for describing species' roles within networks, we now introduce *equivalence* methods for identifying species with similar roles. There are several ways to group species based on their level of equivalence within a network, but all aim to identify sets of species with similar Eltonian niches. These approaches differ from the previous definitions of role by focusing explicitly on the identities of species' interaction partners (Yodzis and Winemiller, 1999). For instance, two species with the same degree may or may not interact with the same partners, but two species are only *structurally equivalent* if they share identical sets of interaction partners (Fig. 3; Borgatti, 2002). In fact, two structurally-equivalent species will have the same roles under any of the definitions above and, by interacting with the same predators and prey, have the same Eltonian niches.

The strict definition of structural equivalence can be relaxed slightly to quantify the degree of structural equivalence on a continuous scale by using a distance metric such as Jaccard dissimilarity (number of common interaction partners divided by the number of partners interacting with either species) to compare the overlap in species' interaction partners (Yodzis and Winemiller, 1999). It would also be possible to calculate a continuous version of structural equivalence using a distance metric such as Bray-Curtis dissimilarity that could accommodate interaction strengths as well as sets of interactions, but to our knowledge this has not yet been done. While such quantitative measures provide more information by placing species on a continuous scale from fully equivalent to completely distinct, they are still restrictive in that species interacting with ecologically similar, but not taxonomically identical, partners will not be considered equivalent. For example, consider two species of herbivorous insects, each of which consumes a different plant from the same genus and which are preyed upon by similar spider species. Intuitively, we understand that these two insects have similar roles in their community (and Eltonian niches) despite having low structural equivalence. To capture this intuitive similarity, another technique is evidently necessary.

One proposed solution to this problem is to adapt the concept of *regular equivalence* from the study of social networks (White and Reitz, 1983) to ecological networks (Johnson et al., 2001; Luczkovich et al., 2003). In this framework, *nodes* (or species) within a network are equivalent if they interact with the same "types" of partners (Fig. 4). For example, in a network of several corporations, company presidents are equivalent because they each interact with boards of directors, venture capitalists, etc. (Johnson et al., 2001). Even though each company president may interact with different individuals, company presidents nevertheless form a recognizable "type" or "group" of people that interact with people who belong to a set of other recognizable groups (e.g., boards of directors and venture capitalists). In ecological networks, researchers often wish to avoid defining such groups *a priori* in order to avoid biasing analyses towards collections of species that are appealing to humans but may not be ecologically relevant. To do this, several algorithms have been developed that iteratively assign species to groups until the best-fitting arrangement of groups has been reached (Borgatti and Everett, 1993; Johnson et al., 2001; Luczkovich et al., 2003). Fortunately, the groups determined by such algorithms (e.g., predatory insects, scavengers, and aquatic larvae) usually tend to be intuitive and biologically meaningful (Johnson et al., 2001; Luczkovich et al., 2003). Thus, by identifying species with similar roles, regular equivalence groups can point to elements of Eltonian niches that are shared by the species in a group. Some of these groups also include information about abiotic requirements such as habitat requirements and thus begin to address the non-biotic components of species' Eltonian niches. As with structural equivalence, regular equivalence could be calculated using quantitative food webs. This appears to be uncommon at present but may be a useful approach in future work.

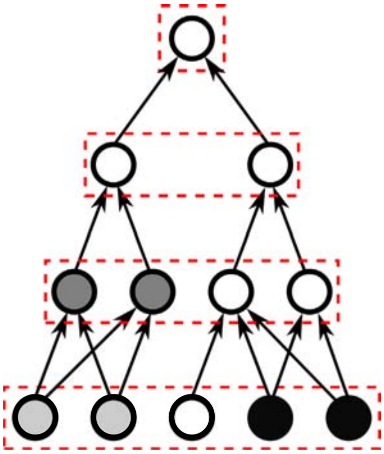

**Fig. 4.** Sets of *structurally* equivalent species (nodes with the same gray fill; nodes with white fill are not structurally equivalent to any other node) interact with exactly the same *sets of partners* while sets of *regularly* equivalent species (enclosed in red, dashed boxes) interact with partners from the same *sets of groups*. In this web, regular equivalence groups correspond to trophic levels such that primary producers (bottom group) only interact with herbivores (second group from bottom), herbivores interact with primary producers and consumers (second group from top), and so on. Note that structurally-equivalent species are also regularly-equivalent, but the reverse is not necessarily true (e.g., the two groups of herbivores in this food web are regularly but not structurally equivalent).

Structural and regular equivalence groups are being used increasingly often in food web research, with structural equivalence having the longer history. Structurally equivalent species are often collapsed into *trophospecies* in order to reduce bias in the resolution of unipartite food webs (e.g., Martinez, 1991; Vermaat et al., 2009). Larger, higher-trophic level species are often easier to identify than smaller, lower-trophic level, or cryptic species, leading to better resolution at the top of the food web than among basal species. This greater detail at the top of the food web can then bias estimates of food-web structural properties such as the number of links per species or proportions of species in different trophic groups (e.g., top predators, basal resources), hindering efforts to understand the true structure and function of communities (Martinez, 1991; Thompson and Townsend, 2000). To reduce this bias and facilitate comparisons between food webs, structurally equivalent species are often collapsed into a single node, or trophospecies (Martinez, 1991). Each node then represents a unique Eltonian niche within the food web.

Regular equivalence, on the other hand, has much in common with the concept of functional redundancy in which species with similar "functions" in a community are grouped together. This redundancy is believed to be important because species with similar Eltonian niches may be able to compensate if one species becomes rare or goes extinct (Naeem, 1998; Rosenfeld, 2002; Aizen et al., 2012). The loss of a species with a redundant role in a community will therefore have little effect on the rest of the community (Naeem, 1998; Rosenfeld, 2002; Aizen et al., 2012). As well as identifying groups of species with redundant roles, simulated food webs constructed using models based on regular equivalence groups capture many of the characteristics of empirical webs (Allesina and Pascual, 2009). This has lead to the suggestion that groups might be the appropriate level of analysis in future studies of food webs, particularly as larger and more detailed data become available (Allesina and Pascual, 2009). Despite the usefulness of groups for identifying redundant or similar species, approaches based on lumping species into groups share a common drawback with describing networks based on summary statistics. Specifically, focusing on groups of similar species necessarily obscures the differences between the species within a group. These differences may be relevant for ecological functions other than those involving predator-prey interactions (e.g., habitat construction) and it is important to recognize that focusing on different types of interactions or ecological functions will lead to different groups. Nevertheless, group-based approaches to analyzing food webs hold great promise, especially as more techniques are developed to incorporate more ecological information into regular equivalence groups (Gauzens et al., 2015). These increasingly detailed groups should lower the risk of masking important differences between species.

### 3.2. Module-based roles

Another way to group species according to their types of interaction partners is through *module* roles, which measure the extent to which species interact with different modules (tightly-knit groups) within a network. Module-based roles are similar to centrality in that they measure the importance of a species' Eltonian niche to the community rather than describing the niche directly. Unlike centrality, however, module-based roles depend more explicitly on the meso-scale structure of the network. That is, the size and arrangement of modules within a network is critical to the definition of module-based roles. Modules are defined as a group of species that interact more frequently among themselves than with species that are not members of the module (Kirkpatrick et al., 1982; Guimerà and Amaral, 2005a,b). They are usually detected algorithmically using techniques such as simulated annealing that aim to find the set of modules that minimizes the number of links between different modules (Guimerà and Amaral, 2005a).

Once modules have been defined, species can be classified based first on the focal species' importance to its own module and second on the extent to which the focal species' interactions are distributed across modules (Guimerà and Amaral, 2005a). The focal species' importance within its module is determined by on its "within-module degree", a Z-score testing whether the focal species has significantly more interactions with other species in the same module than the average number of within-module links (Guimerà and Amaral, 2005a). Note that within-module degree only involves information about the module to which the focal species belongs and does not depend on the number of links the focal species has to species in other modules. Species with a within-module degree of at least 2.5 are designated "hubs" and have significantly more interactions within their module than the average ($p \ll 0.005$; Guimerà and Amaral, 2005a).

Both hub and non-hub species can be further divided based on the participation coefficient, which measures the evenness of the distribution of the focal species' interactions. Values near 0 indicate species that interact almost exclusively within their own modules, whereas values near 1 indicate species who interact with species in all modules equally (Fig. 5). Participation coefficient, like degree, focuses on direct interactions among species. Longer paths, i.e., those used to calculate trophic level or centrality, are not considered. Unlike degree, however, participation coefficient takes the modular structure of the network into account. By distinguishing between interaction partners in different modules, module-based roles are conceptually similar to motif roles. Both include some information about indirect interactions as well as direct interaction: strength of association with a particular group of species for module-based roles, and participation in different configurations of interactions for motif roles.

Using these two parameters (within-module degree and participation coefficient), species can be divided into varying numbers of roles. In general, however, module hubs have low participation coefficients and are important to the cohesion of their modules but have few interactions with other modules. Network hubs have high participation coefficients and are important to the coherence of the network as a whole as well as the cohesion of their module (Guimerà and Amaral, 2005a; Olesen et al., 2007; Poulin et al., 2013). In non-hub species, low participation coefficients indicate peripheral species while high participation coefficients indicate connector species that "glue" different modules together (Guimerà and Amaral, 2005a; Olesen et al., 2007; Poulin et al., 2013).

As with motif roles, module-based roles are relatively new and their potential is only beginning to be explored. So far it has been shown that plants' and pollinators' module-based roles are conserved between their native and exotic ranges (Olesen et al., 2007), and that the module-based roles of parasites and free-living species are phylogenetically conserved (Poulin et al., 2013). This suggests that module roles may be highly consistent in both mutualistic and antagonistic networks; that a species that has many interactions concentrated within its module at one site is likely to also be a module hub at another site (Olesen et al., 2007) and a species that is closely related to a connector species is also likely to interact with species in several modules (Poulin et al., 2013). This potential for consistent module-based roles is intriguing but still requires more empirical support. Connecting module-based roles to traits such as body size can also reveal groups of species which fulfill similar functions in a community. For example, large-bodied frugivores tend to be module hubs but, because of their tendency to consume only the largest fruits, do not connect different modules. Instead, these between-module links tend to be supplied by medium-bodied frugivores which act as connectors (Donatti et al., 2011). Identifying species' module roles can therefore highlight an ecologically important group of species that might otherwise be missed (Donatti et al., 2011). The taxonomic diversity of species within a module may also be an indicator of how robust the module, and the network as a whole, is likely to be to species loss (Donatti et al., 2011; Mello et al., 2011).

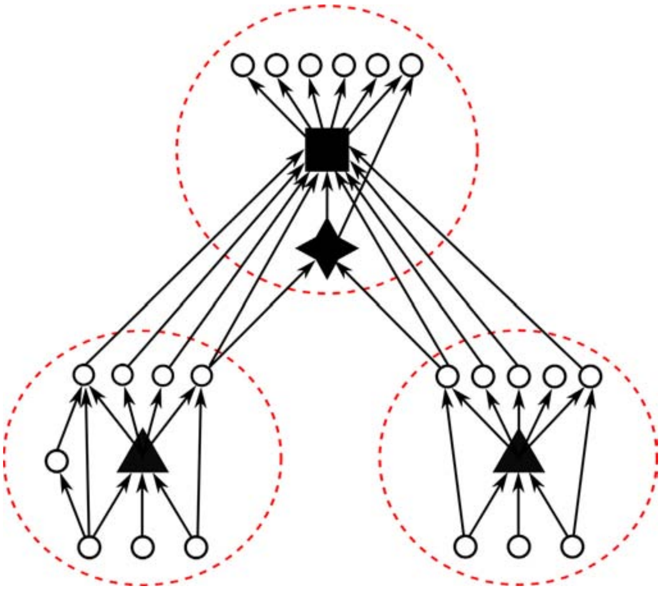

**Fig. 5.** This unipartite food web contains three modules (circled in red, dashed lines). It is possible to group species with similar roles based on how often they interact with species within their module and with species in other modules. Hub species have significantly more interactions within their module than the average (i.e., high "within-module degree"; Z-score>2.5). Different types of hubs can be distinguished based on the evenness of their interactions across modules (their "participation coefficients"). Both network and module hubs have significantly more partners within their own module than other species. The network hub (black square) has many interactions with other modules (participation coefficient close to 1) while module hubs (black triangles) rarely interact with species from other modules (participation coefficient close to 0). Non-hub species (connectors and peripherals) do not have significantly more links within their module than the average (Z-score<2.5) and, again, can be distinguished by the distribution of their interactions among modules. The connector (black star) has interactions spread evenly among modules ( participation coefficient close to 1). Finally, peripheral species (white circles) have few interaction partners within their modules and few links to other modules (participation coefficient close to 0).

### 3.3. Functional roles

Instead of grouping species with similar structural roles, we may wish to group species with similar ecological functions. Regular equivalence offers one way to identify groups of functionally redundant species (e.g., Gauzens et al., 2015). Another approach is to group species based on traits that are expected to affect an ecological function such as seed dispersal or pollination. Species with similar traits are believed to make similar contributions to the function in question, and can therefore be said to have similar *functional roles* (Tilman, 2001; Petchey and Gaston, 2002; Dehling et al., 2016). As a species' function in a community is intimately related to the way it interacts with resources and enemies, a species' functional role also describes part of a species' Eltonian niche.

Traits that describe species' functional roles influence the set of interactions in which they participate (Thompson and Townsend, 2005; Dehling et al., 2016). One trait that has been found to explain

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a great deal of variation in predator-prey interactions is body mass, as many taxa feed on smaller prey (e.g., Williams and Martinez, 2000; Stouffer et al., 2006; Petchey et al., 2008; Williams, 2008; Stouffer, 2010; Williams et al., 2010; Gravel et al., 2011; Stouffer et al., 2011; Zook et al., 2011). In most cases, however, more than one trait is necessary to describe all of the interactions in a community (Cattin Blandenier, 2004; Allesina, 2011, Allesina et al., 2008; Eklöf et al., 2013). Moreover, while using empirical traits to create model food webs can reproduce general structural properties, such approaches often fail to predict specific interactions (Petchey et al., 2008; Bartomeus et al., 2016). In an attempt to address both of these shortcomings, some studies have used artificial traits based on the properties of the observed network (Rohr et al., 2010; Dalla Riva and Stouffer, 2015; Rohr et al., 2016). These abstract traits are generally derived from the network itself and are based on the idea that predators' "foraging traits" must match the "vulnerability traits" of their prey (Rohr et al., 2010; Dalla Riva and Stouffer, 2015) or that mutualist interaction partners must have well-matched traits (Rohr et al., 2016). Artificial traits are conceptually similar to ordination axes in that they reduce the variation in species' interaction partners to a minimal set of dimensions that may or may not be easy to interpret. Species with similar artificial traits (and similar interactions) are likely to share real traits as well; looking for the traits that unite species with overlapping functional roles could guide the choice of traits to include in future models of ecological networks. In this way, artificial traits can reveal similarities between species that are not obvious based on easily-observed traits such as body mass. Moreover, species with similar artificial traits are likely to be functionally redundant (Rosenfeld, 2002) or strongly compete with each other. Functional roles can thus be used to identify species with similar Eltonian niches as well as highlighting traits that shape interactions.

An alternative way to identify species with similar functional roles is to analyze the traits of the focal species' interaction partners rather than the traits of the focal species itself (Fig. 6; Dehling et al., 2016). This approach is common in studies of plant-pollinator communities, where pollination syndromes are often used to predict which species will interact (Waser et al., 1996; Fenster et al., 2004; Ollerton et al., 2009). Pollinators vary in their adherence to classical syndromes (Fenster et al., 2004; Ollerton et al., 2009), but in general species tend to interact with partners whose traits are relatively similar and match some limiting trait of the focal species (Stiles, 1975; Wolf et al., 1976; Dalsgaard et al., 2009; Stang et al., 2009; Junker et al., 2013; Dehling et al., 2014). By grouping species that interact with partners that have similar traits, we can infer sets of species that have similar functional roles in their community.

Functional roles have been used to demonstrate co-adaptation between interaction partners, as mutualists are expected to converge on compatible traits (Blüthgen et al., 2007; Hutchinson et al., 2018). Species with unique functional roles interact with partners that have extreme or unusual values of the traits that affect the interaction being studied (Dehling et al., 2016). Because of this, they tend to interact with fewer partners (Junker et al., 2013; Maglianesi et al., 2014; Coux et al., 2016) and, as specialists, may then be more vulnerable to extinction (Allesina, 2012). Species with similar functional roles, meanwhile, may indicate functional redundancy and a more robust community (Rosenfeld, 2002; Aizen et al., 2012).

Grouping species based on functional traits is somewhat analogous to grouping regularly-equivalent species based on the types of species with which they interact. The major distinction is that regular-equivalence groups are emergent properties of a network's topology whereas functional roles are linked at least implicitly to a functional mechanism. These mechanisms could be, for example, fruit size (Dehling et al., 2016, 2014) or flower characteristics that limit the set of interaction partners (Fenster et al., 2004; Ollerton et al., 2009; Hutchinson et al., 2018). As well as physical traits, behavioral traits such as diurnal or nocturnal activity (Knop et al., 2017) strongly shape the sets of interaction partners available to each species and could be used to define species' functional roles. This focus on biologically-explicit groups means that functional roles provide a convenient summary of species' Eltonian niches in the type of network being studied and that functional roles are among the easiest role concepts to relate to species' natural histories.

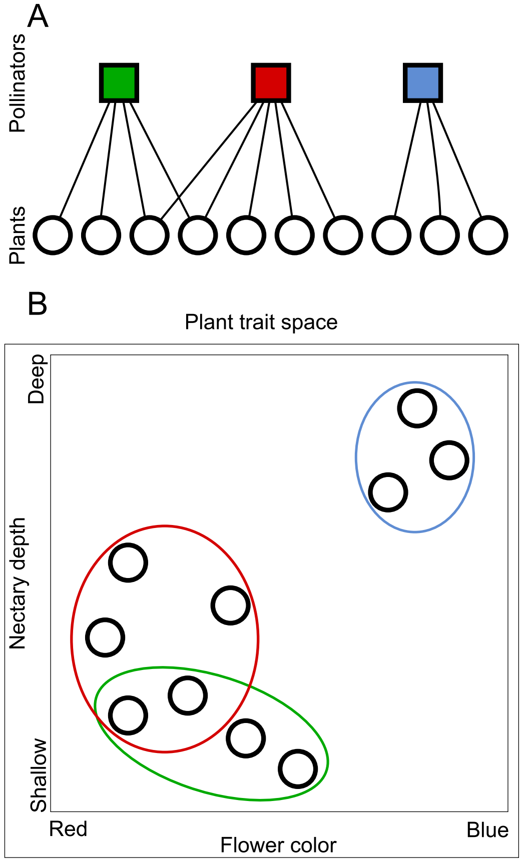

**Fig. 6.** The functional roles framework uses the traits of interaction partners to group species with similar roles. A) In this plant-pollinator network, we are interested in comparing the roles of the three pollinators (colored squares). B) The functional role of each pollinator is characterized by the area of trait space that includes all plants visited by the pollinator. In this community, the red and green pollinators' roles (lower left) overlap while the blue pollinator has a unique role (upper right). Note that the axes used to describe the trait space may be concrete traits, as shown here, or abstractions such as PCA axes that describe variation in many traits.

## 4. Limitations to role concepts and future directions

As described above, one of the main limitations of species roles is that while they do offer insight into a species' Eltonian niche — its "place in the biotic environment, its relations to food and enemies" (Elton, 1927 in Johnson and Steiner, 2000) — a role will only capture one aspect of that niche. In particular, most of the role concepts described above focus on identifying species with more 'important' niches based on their likelihood of having substantial effects on the rest of the web. Some concepts such as motif roles and functional roles are more flexible, as they describe all of a species' interactions rather than providing a single summary statistic. These roles give a better picture of species' Eltonian niches from the perspective of food webs, but the fact remains that roles defined in a food web describing only one type of interaction will overlook components of species' niches that do not involve that interaction (Fontaine et al., 2011; Kéfi et al., 2016). Combining different network types has the potential to improve this by integrating distinct aspects of species' niches (e.g., as pollinators and as prey Fontaine et al., 2011). One way forward is to identify species' module roles in a network which includes trophic interactions and positive and negative non-trophic interactions (Kéfi et al., 2016). The role concepts described in Kéfi et al. (2016) provide a more comprehensive picture of species' Eltonian niches than do roles in webs which describe a single interaction.

Another important limitation in studies of species' roles is the point-sample nature of most ecological networks. Species' Eltonian niches encompass their relationships to the biotic and abiotic environment as a whole, but networks provide a spatially and temporally limited snapshot of communities. As more networks that include replication over time and/or space are published (e.g., Olesen et al., 2011, 2008; Leong et al., 2015; Ponisio et al., 2017), we will obtain more thorough descriptions of species' roles. As information about the spatial and temporal variability of species' roles becomes available, we may be able to better understand the differences between species' "fundamental" Eltonian niches (all of the interactions in which a focal species could reasonably participate) and the Eltonian niches that they actually realize in a particular community (i.e., species' realized niches). This is especially intriguing with respect to species which have moved outside of their historical ranges (e.g., introduced species or those whose ranges have shifted due to climate change). It is possible that a species' role in its native community could be used to predict the way in which it will interact with a novel set of potential partners (Aizen et al., 2008; Emer et al., 2016). For example, the traits of an introduced species' interaction partners in its native habitat could be used to identify a plausible set of interaction partners in a novel setting. The species' degree in its native range, meanwhile, could indicate it's dietary flexibility. A species which interacts with only a single partner in its native range is less likely to find suitable interaction partners in a novel setting than one which interacts with many partners that have a variety of traits. Supporting these possibilities, in plant-pollinator networks degree and closeness centrality are highly conserved across locations (Emer et al., 2016) and high-degree pollinators tend to have relatively flexible sets of interaction partners (Ponisio et al., 2017). If species' roles in their native and introduced communities are generally related, then species' roles will be a powerful tool for conservation biologists.

Besides exploring the spatial and temporal variation of species' roles, an increasing number of studies have connected species' roles to their phylogenies. Related species tend to have similar roles for several of the role concepts we describe above (Stouffer et al., 2012; Poulin et al., 2013; Rohr and Bascompte, 2014). Species' phylogenies are believed to shape their roles because *phylogenetically-conserved* traits affect interactions between species (Gómez et al., 2010; Dalla Riva and Stouffer, 2015). Thus, conserved traits lead to conserved interactions which lead to conserved roles. As well as explaining similarities between the roles of related species, incorporating evolutionary processes into studies of ecological networks can provide insights into the historical drivers of the structure of current communities (Rezende et al., 2009; Chamberlain et al., 2014; Schleuning et al., 2014; Peralta, 2016; Hutchinson et al., 2018).

Most contemporary studies attempt to explain trends in network structure using species' traits (Woodward et al., 2005; Brose, 2010) or neutral processes (Siepielski et al., 2010; Canard et al., 2014; Poisot et al., 2015). These approaches have been valuable, but evolutionary explanations may be more parsimonious (in terms of modelling) when there are many traits that are likely to affect interactions. If important traits are phylogenetically conserved, it may be possible to predict interactions using a simple model that contains only phylogenetic information rather than a complex model including a large number of traits. Evolutionary explanations may also be useful as a proxy for traits that are unknown, difficult to measure, or are not the main research focus.

Explanations based on species' evolutionary histories may also explain species that seem to lack appropriate interaction partners in modern networks. This is most obvious in the case of "evolutionary anachronisms" such as the large-seeded plants of South America that are believed to have been dispersed by large mammals that are now extinct (Janzen and Martin, 1982). Adaptations to extinct interaction partners can also explain species' interactions with introduced species, such as when these large-seeded South American plants are dispersed by introduced cattle and horses (Barlow, 2000).

Perhaps the most important factor limiting the usefulness of species roles to ecologists is that role concepts are often abstract. This abstraction can be beneficial as, for example, it allows us to identify groups of species when we are not confident that any particular taxonomic level or ecosystem function is the appropriate basis for categories (Luczkovich et al., 2003). Nevertheless, roles that are not clearly tied to some aspect of species' natural histories can make network studies less accessible to non-specialist readers. Eltonian niches provide a common ground between species roles and other ecological concepts; we therefore propose that future researchers could emphasise this connection to integrate species roles into the ecological literature in a more intuitive way.

One step in this direction is to use ecological concepts to guide the choice of network measures (Mello et al., 2015) that define a species' role. For example, we may be concerned about an invasive species competing with native species. To measure the likelihood of competition, we might choose degree as our role concept on the basis that a generalist invader will likely compete with many native species. Alternatively, we could use functional roles to predict which native species' roles overlap most with the invader. The choice of role concept will also depend on the data that are available (e.g., trait data, interaction strengths, or only presence/absence of interactions). We may, for instance, wish to order species according to their impact on the rest of the community to set conservation priorities. If interaction strengths are known, then a weighted measure of centrality will be useful. If only unweighted interactions are known, it may be more useful to use module-based roles to track species' ability to affect their local neighbourhoods and the network as a whole. When using weighted versions of role concepts, it is important to note that rare or weak interactions may still be important for community stability because of their potential for dissipating perturbations (Emmerson and Yearsley, 2004; Allesina and Tang, 2012; Wootton and Stouffer, 2016). After selecting network measures that specifically address the ecological question at hand, we also suggest that researchers bear in mind the part of a species' Eltonian niche that they are analyzing (e.g., a species' importance or its vertical position in food chains, or a more holistic summary such as motif roles) and use this niche framework to place their results in the context of the focal species' ecology.

## 5. Conclusions

Throughout this review we have outlined some of the questions that have been asked using some of the most commonly-used species role concepts. To conclude, we return to the question of why species roles, in general, are useful. Networks allow us to place the focal species in its community context but the network as a whole is difficult to interpret. By reducing a complex network to a single value or vector, species' roles compress the network into a tractable form. If we consider food webs as maps of ecological communities (Pimm et al., 1991), roles provide the topographic lines, borders, and roadways that simplify a map and provide meaning. Just as different types of maps have different themes (e.g., political maps, terrain maps, geological maps), different role concepts provide different perspectives on a food web. Our task as researchers working with species' roles is to make our choice of role concept, and the aspect of species' Eltonian niches that it is meant to capture, as clear as cartographers make their maps.

## Acknowledgments

We would like to acknowledge the support of the National Science and Engineering Research Council of Canada (to ARC), the São Paulo Research Foundation (FAPESP grants 2013/13319-5 and 2014/20572-1; to MPG), a University of Canterbury Masters Scholarship, the Miss E. L. Hellaby Indigenous Grasslands Research Trust, and an Australian Higher Degree Scholarship (to MDB), a University of Canterbury Doctoral Scholarship, Meadow Mushrooms Postgraduate Scholarship, and a New Zealand International Doctoral Research Scholarship (to EFC), support from the 2013-2014 BiodivERsA/FACCE-JPI joint call for research proposals, with the national funders ANR, BMBF, FORMAS, MINECO, NWO, and PT-DLR (to CC), and a Marsden Fast-start Grant administered by the Royal Society of New Zealand and a grant from the German Research Foundation (DE 2754/1-1; to DMD). We would also like to thank Daniel B. Stouffer and Ross M. Thompson for the conversation and comments that greatly strengthened this review.

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Please cite this article as: A. Cirtwill et al., A review of species role concepts in food webs, Food Webs (2018), https://doi.org/10.1016/j.fooweb.2018.e00093

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## Glossary

*Eltonian niche:* A species' interactions with food sources and natural enemies.

*Stability:* The ability of a food web to withstand perturbations.

*Role:* A species' relationship to others in its food web. May be summarized in many ways depending on which aspects of the species' niche or network structure are of most interest.

*Keystone:* A species with larger effects on its community than would be expected based on its biomass.

*Degree:* The number of direct interactions in which a species participates.

*Local:* The portion of the food web that directly affects the focal species.

*Global:* The entire food web.

*Unipartite web:* A web containing one group of species that interact amongst themselves.

*Bipartite web:* A web containing two groups of species where all interactions occur between groups.

*Beta diversity:* Change in community composition (turnover) between sites. Calculated as the ratio (Whittaker's beta) or difference (absolute turnover) between local and regional diversity.

*Qualitative web:* A web in which links are present or absent (i.e., not weighted). Also called a *binary* or *topological* web.

*Quantitative web:* A web where links are weighted by frequency, biomass transfer, or some other property. Also called a *weighted* web.

*Trophic level:* A species' vertical position in a food web or height in a food chain.

*Food chain:* A path from a primary producer to a top predator, where each step up the chain corresponds to an increase in trophic level.

*Trophic cascade:* Significant changes in the abundance of species at a higher or lower trophic level following a change in the abundance of a focal species.

*Motifs:* Unique patterns of $n$ interacting species; building blocks of networks.

*Meso-scale:* The structure of the network including the focal species' local neighborhood and some indirect interactions, but not the entire network.

*Motif role:* The vector describing a species' frequency of participating in each position within each motif of a given size class

*Centrality:* A species' ability to affect the rest of the network by participating in many food chains.

*Structural equivalence:* When a set of species all interact with exactly the same set of partners.

*Regular equivalence:* When a set of species all interact with partners from the same groups, but not necessarily with the same sets of partners.

*Node:* A component of a network. In food webs, usually a species.

*Trophospecies:* A set of structurally equivalent species, collapsed into a single node.

*Module:* A group of species that interact more often amongst themselves than with other species.

*Functional roles:* Roles defined by traits of the focal species' interaction partners that are relevant for a particular ecological process.

*Phylogenetic conservation:* The tendency for related species to have more similar traits because of their shared common ancestry.

Please cite this article as: A. Cirtwill et al., A review of species role concepts in food webs, Food Webs (2018), https://doi.org/10.1016/j.fooweb.2018.e00093