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CONCEPT

Networking nutrients: How nutrition determines the structure of ecological networks

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Abstract

1. Nutrients can shape ecological interactions but remain poorly integrated into ecological networks. Concepts such as nutrient-specific foraging nevertheless have the potential to expose the mechanisms structuring complex ecological systems. Nutrients also present an opportunity to predict dynamic processes, such as interaction rewiring and extinction cascades, and increase the accuracy of network analyses.
2. Here, we propose the concept of nutritional networks. By integrating nutritional data into ecological networks, we envisage significant advances to our understanding of ecological processes from individual to ecosystem scales.
3. We show that networks can be constructed with nutritional data to illuminate how nutrients structure ecological interactions in natural systems through an empirical example. Throughout, we identify fundamental ecological hypotheses that can be explored in a nutritional network context, alongside methods for resolving those networks.
4. Nutrients influence the structure and complexity of ecological networks through mechanistic processes and concepts including nutritional niche differentiation, functional responses, landscape diversity, ecological invasions and ecosystem robustness. Future research on ecological networks should consider nutrients when investigating the drivers of network structure and function.

KEYWORDS
food webs, functional responses, macronutrients, network ecology, nutritional network, trophic interactions

1 | INTRODUCTION

Nutrients, represented as elemental (e.g., carbon and nitrogen) or biochemical (e.g., protein and carbohydrate, lipid) macronutrients (Kaspari, 2020) and micronutrients (e.g., iodine, copper and zinc; Kaspari, 2021), underpin many biological processes (Simpson & Raubenheimer, 2012). This view has been evidenced across decades of research (Slansky, 1982), from host–parasite interactions (Sequeira & Mackauer, 1992; Slansky, 1986) to trophic cascades through entire ecosystems (Persson, 1999) and, most notably, trophic interactions (Belovsky, 1984; Mayntz et al., 2005; Scriber & Slansky, 1981). The study of trophic interactions in nutritional contexts has underpinned ongoing development of existing fundamental ecological theories such as optimal foraging theory (Jensen et al., 2012; Raubenheimer & Simpson, 2018; Schoener, 1987; Stephens & Krebs, 1986). To identify the mechanisms driving ecosystem function, the flow of nutrients through complex systems must be examined (Loreau & Holt, 2004) from individual and population to community and superorganismal scales (Lihoreau et al., 2014). To date, however, system-level research has focussed on coarse chemical balances, usually in the context of ecological stoichiometry (Liu & Sun, 2013; Sterner & Elser, 2008), largely neglecting how nutrients structure food webs. Despite nutrients appearing to have a significant role in driving ecological interactions (Hutchinson et al., 2019; Kohl et al., 2015; Mayntz et al., 2005), they are scarcely integrated into ecological network analyses. Network analyses can be used to investigate the identity and structure of ecological interactions, and their contribution to ecosystem functioning (Montoya et al., 2006) or robustness—the resilience of a network to disturbance or environmental change (Pocock et al., 2012). Network ecology can integrate different nutritional data to overcome the separation of elemental and macromolecular approaches between plant and animal nutrition, effectively linking trophic levels.

The few examples of network analyses incorporating nutritional data focus on energy transfer (Gauzens et al., 2019), social networks (Senior et al., 2016) or human nutrition (Timberlake et al., 2022). Network-like diagrams have represented elemental nutrient transfer, usually in freshwater or soil (De Ruiter et al., 1993; Sterner et al., 1996), and network-based models have been used to assess ecosystem function (Cherif & Loreau, 2013; Thébault & Loreau, 2003) and nutrient cycling (Quévreux et al., 2021). The methodological complexities of interdisciplinary research have likely stifled this subfield; however, streamlined nutritional assays (Cuff et al., 2021) and methods for increased integration of trait data into networks (Eklöf et al., 2013; Junker et al., 2013; Woodward et al., 2005) now present an opportunity to incorporate nutrition into ecological networks. Here, we describe the mechanisms by which nutrients drive interactions, how these structure networks and the benefits of integrating nutrients into ecological network analyses. We focus on biochemical macronutrients in trophic interactions, but the concepts and ideas presented here apply to a broader range of interaction types and networks, and other currencies such as energy and elements. Throughout, we contend that integrating nutrients and networks can identify mechanisms driving ecological interactions and illuminate determinants of network robustness.

2 | HOW NUTRIENTS INFLUENCE INTERACTIONS

2.1 | Specialist versus generalist foragers and nutritional deficiencies

Networks form at all scales of biological organisation (Guimarães, 2020) and nutrients impact different scales through a range of mechanisms (Figure 1). Individual generalist foragers alter their interactions to redress nutritional deficiencies, termed nutrient-specific foraging (Kohl et al., 2015; Mayntz et al., 2005), but this is dependent on the availability of suitable resources. Generalists may therefore consume a large quantity and range of resources to balance suboptimal nutrition (Cuff, Tercel, Vaughan, et al., 2022; Pompozzi et al., 2019; Rendon et al., 2019), increasing their degree (i.e., number of connections), and overall linkage density and interaction evenness of trophic networks (Figure 1). Specialists, however, often do not exhibit or exhibit less compensatory feeding when nutritionally deficient (Despland & Noseworthy, 2006; Simpson & Raubenheimer, 2012). Specialists can, however, forage more efficiently (Pompozzi et al., 2019), including on resources suboptimal for generalists; this could increase modularity (the distribution of links within rather than between sets of nodes; Lau et al., 2017) of networks through niche differentiation (Behmer & Joern, 2008; Figure 1). The interactions of specialists may also comprise a subset of those of their generalist counterparts if they specialise on nutritionally favourable resources, increasing nestedness (interactions of individuals forming subsets of wider interactions; Lau et al., 2017; Figure 1). Nutritionally favourable resources might include those rich in a nutrient otherwise limited in that system. Such resources might therefore have a higher degree and centrality (the relative importance of a node, often based on the number of ‘walks’ that pass through it; Lau et al., 2017). This would also potentially reduce the robustness of networks and increase linkage density as consumers forage randomly, seeking that nutrient (Figure 1). Foragers naïve to their systems (i.e., recent immigrants) may similarly forage randomly as they determine optimal sources of nutrition, initially increasing their degree (Figure 1). Many of these concepts are discussed in greater detail below.

2.2 | Nutrients and functional responses

The determination of consumer interaction frequencies by resource abundances, linked to functional responses (Holling, 1966), is affected by resource nutrient contents and preceding consumer interactions (Schmidt et al., 2012). Functional responses can therefore rationalise responses to nutritional conditions; for example, a ‘Type IV’ relationship may indicate overabundance of a particular nutrient (Bressendorff & Toft, 2011), whereas a ‘Type I’ functional response could indicate an optimally balanced resource nutrient profile (Figure 2). This likely extends to other functional response types, ultimately driving nutrient-specific foraging. Although the exact responses will depend upon factors including defences, toxins and ease-of-capture (see Section 5 below), the nutritional context could underpin a mechanistic link between resource abundance and trophic interaction strength (Vaughan et al., 2018).

Much of the evidence surrounding functional responses is, however, based on laboratory studies, which constrain the sources of variation being assessed (Coblentz et al., 2022) and therefore the relevance of these data to complex interaction networks. Further research is therefore required to determine the role of nutrition in

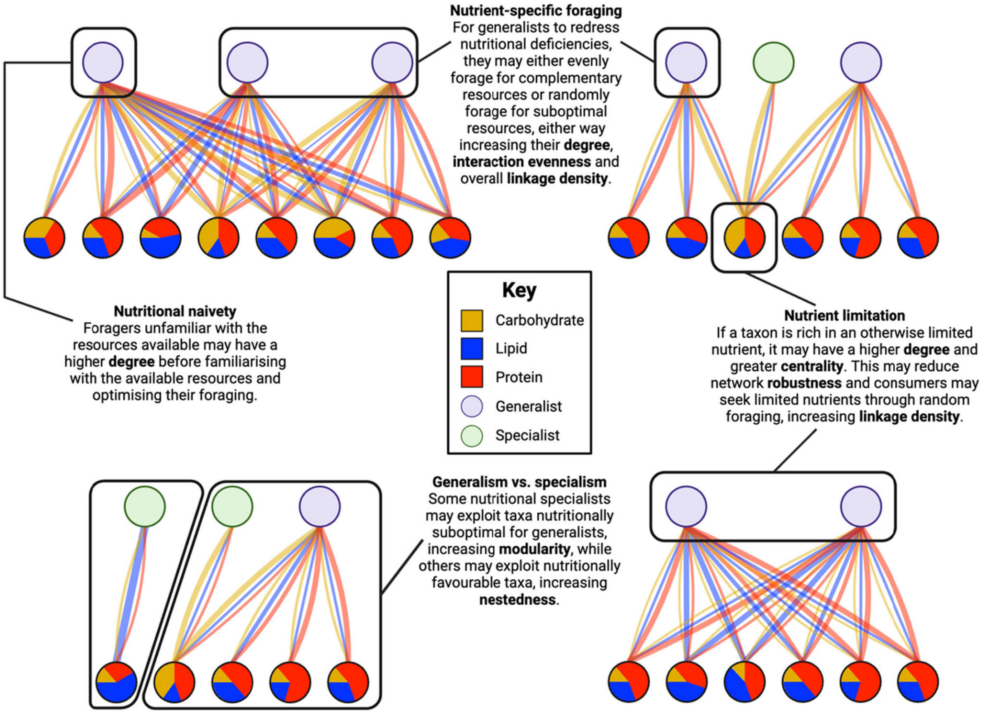

FIGURE 1 Examples of nutrient-mediated ecological processes and their potential effects on the structure of ecological networks. Yellow, blue and read denote carbohydrate, lipid and protein, respectively, with link weights representing the amount of that nutrient exchanged in interactions. Upper nodes represent consumers (purple and green denoting generalists and specialists, respectively) and lower nodes are resources, with the ratio of their colours representing their proportional content of the three macronutrients. The outcome of any analyses of such networks will depend on whether interactions are weighted or not. The hypotheses presented within the figure refer to metrics of traditional networks (i.e., not nutrient-weighted; a preliminary analysis of nutrient-weighted networks is presented below).

driving functional responses in field-based systems and network contexts. Nevertheless, some hypotheses can still be drawn: (i) nutritionally balanced resources may be linearly exploited by consumers since they provide all of the nutrients required; (ii) if a resource contains more of a particular nutrient that is critical to the development or survival of the consumer, it may be disproportionately consumed until the consumer is saturated with that nutrient; (iii) if a nutrient is less critical but still important for survival, this may similarly experience focussed exploitation and saturation, but only once resource density reaches a point at which adjusted foraging becomes a valid investment; and (iv) if a resource is rich in toxins or contains a concentration of a nutrient that may become toxic with focused feeding (e.g., carbohydrate in sap-feeding insects), exploitation may increase until experience of the toxicity or saturation with that nutrient drives the consumer to seek alternative sources. Importantly, the impact of different balances of nutrient contents will differ depending on the consumer, their optimal nutrient intake and the system they are in.

3 | NUTRIENTS INFLUENCE ECOLOGICAL INTERACTIONS AND NETWORK STRUCTURE

The influence of nutrient-driven ecological processes on interactions across trophic levels can manifest in cascades from basal resources to apex predators (Elser et al., 1998; Raubenheimer et al., 2009; Wilder et al., 2013). The structure of ecological networks may therefore influence and be influenced by nutrition, particularly driven by ecological processes such as nutrient-specific foraging and nutrient limitation, as described above (Figure 1).

3.1 | Nutritional variation over time and space determines network structure

Patterns of nutritional redundancy and complementarity, and their implications for network structure will vary between ecosystems. Deserts, caves and systems with scarce photosynthetic flora, for example, are likely to be carbohydrate-poor (Peterson et al., 2016). This could drive consumers to seek carbohydrate-rich resources disproportionately (Figure 1). Native fauna may, however, be physiologically adapted to rely less on scarce nutrients or efficiently extract them from suboptimal sources. In a nutritionally balanced system, however, the same consumer may interact evenly with resources. Importantly, nutritional requirements and contents vary at an intraspecific level with development and seasonality (e.g., in relation to reproduction or diapause; Raubenheimer et al., 2007), leading to individual-level responses, which may be better represented by individual-level networks.

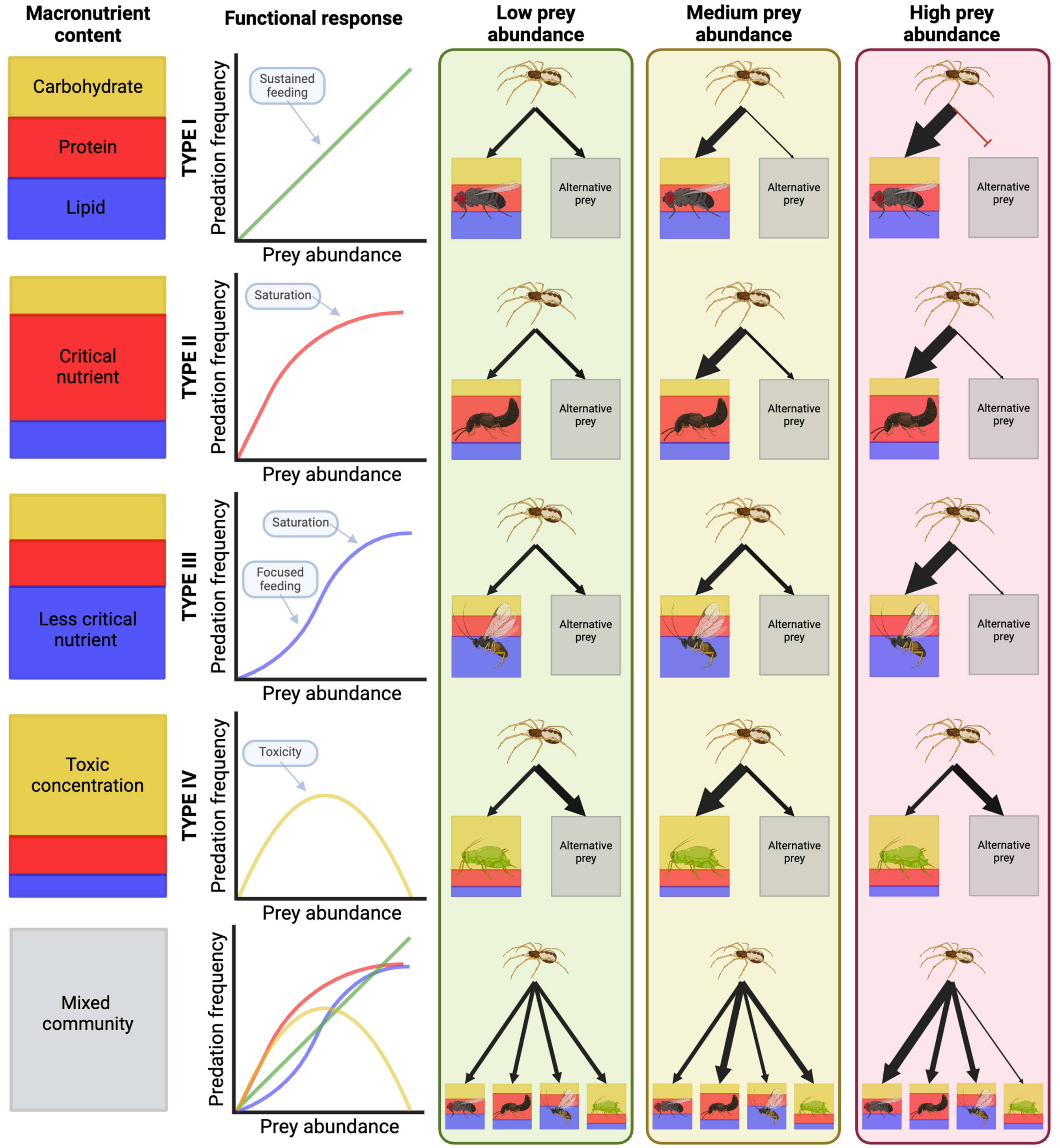

FIGURE 2 How functional responses might reflect different nutrient contents and how this may manifest in network topologies. Example networks are given in which spiders are consuming nutritionally dissimilar prey.

The dissimilarity of nutritional networks across time and space may be most pronounced for species translocated to novel environments, such as invasive species. Unfamiliar nutritional landscapes are evolutionarily mismatched to a forager's innate nutrient-seeking behaviours (Al Shareefi & Cotter, 2019; Simpson & Raubenheimer, 2005). Animals in novel habitats may therefore forage inefficiently, at least initially, and their proliferation may be predicated on their nutritional or behavioural plasticity (Shik & Dussutour, 2020). This evolutionary mismatch imposes fitness consequences (Al Shareefi & Cotter, 2019; Simpson & Raubenheimer, 2005) and an introduced consumer's naivety to native resources, alongside phenological mismatches, requires adaptability to forage optimally.

The demonstrable success of invasive species in adapting to novel nutritional landscapes may reflect the prevalence of dietary generalism in many highly invasive species (Coogan et al., 2018; Krabbe et al., 2019; Saveanu et al., 2017; Shik & Dussutour, 2020), indicating their potential for adaptive foraging and better nutritional exploitation. This is usually explained by outperformance of native competitors or a lack of native predators, but it stands to reason that nutrition may play an important role. Moreover, the impacts of invasive species may increase with the nutritional complementarity of the system being invaded since fewer fitness costs will be initially incurred. This will act as a positive feedback loop that ultimately leads to increasingly severe effects on native communities (Kaplan & Eubanks, 2005; Zhang et al., 2012). Invasive species can also alter the nutritional environment by acting as a novel resource to native or other non-native consumers, or through mutualisms (e.g., food-for-protection mutualisms between honeydew-producing hemipterans and ants; Helms & Vinson, 2002; Wilder et al., 2011). This invasive nutritional niche hypothesis could be assessed just as climatic niches have been for invasive species (Broennimann et al., 2007), although integration of these interactions into nutritional networks could highlight how nutrients structure the interactions of invasives, and how nutrients drive these relationships.

Nutrients can similarly explain long-distance foraging, and migration choices and behaviours (Shaw, 2016), which ultimately underpin how regional species pools translate to local ecological networks. Variation in the nutritional content of bamboo, for example, can drive seasonal migration of pandas (Nie et al., 2015). The extension of the nutritional naivety concept to the migration of birds, butterflies, whales and other migrants further broadens its relevance across ecological contexts. These populations can show high fidelity towards migration sites despite passing unfamiliar but suitable sites *en route*, thought to confer the advantage of consistent foraging (Greenberg, 1984; Shimada et al., 2020). This aversion to unfamiliar sites aligns with the notion that foragers (with the exceptions of extreme generalists, and physiologically or behaviourally plastic taxa) benefit from prior experience of resources in order to optimise nutrient acquisition. Other than adaptation and generalism, migrants can succeed by sheer abundance based on the likelihood that some individuals forage optimally by chance. Ballooning spiders may subscribe to this since they can travel hundreds of kilometres before arriving stochastically in nutritionally novel environments (Bell et al., 2005; Greenstone, 1990; Weyman, 1993). Migrants can also act as nutritional reservoirs between spatially distinct, local networks (Bauer & Hoye, 2014; Gresh et al., 2000; Schmitz et al., 2010) and may provide consistent or seasonal nutritional subsidies to local consumers (Ando et al., 2013; Tercel et al., 2022), altering the nutritional landscape and, ultimately, nutritional networks. The import of locally scarce nutrients by migrants could have particularly profound effects on the foraging decisions of local species, resulting in rapid rewiring.

3.2 | Nutrients rationalise network assembly, rewiring and robustness

The nutrients most important in structuring networks will vary based on the resources available and the requirements of consumers. Lipid limitation in higher trophic levels, for example, may predispose consumers to seek lipid-rich resources disproportionately, whereas many herbivores and omnivores tend towards protein-rich resources (Al Shareefi & Cotter, 2019; Margalida, 2008; Raubenheimer et al., 2009; Wilder et al., 2013). Animal bodies are typically protein-rich and carbohydrate-poor (Cuff et al., 2021). Whilst some consumers tolerate carbohydrate-rich diets (Hawley et al., 2016; Wiggins & Wilder, 2022; Wilder et al., 2011), non-structural carbohydrate-rich diets can be detrimental or toxic to other species (Alcántar-Fernández et al., 2019; Hewson-Hughes et al., 2011; Schlotterer et al., 2009). This suggests that nutritional surplus, not just limitation, could structure networks. Even protein-rich diets can reduce fitness (Anderson et al., 2020), and Bertrand's rule would suggest that this is upheld for most chemicals (Raubenheimer et al., 2005). Similar patterns have been observed in the responses of organisms to elemental content of food (e.g., knife-edge responses; Meunier et al., 2023).

Integrating nutrition into ecological networks will identify sources of nutrients for consumers, in turn determining secondary extinction risk by assessing the nutritional redundancy of its available resources (i.e., availability of alternative sources of nutrients). This could facilitate assessments of resource availability for species of conservation concern or the likelihood of biocontrol of pests by assessing the nutritional complementarity of available resources. These dynamic effects are essentially network rewiring (i.e., interaction switching) and robustness, in which primary extinctions drive the formation of new interactions and/or a series of cascading secondary extinctions (Kaiser-Bunbury et al., 2010). Nutrition ultimately determines the resilience of consumers to change (Ponton et al., 2020) and will therefore regulate network assembly and structure, determine network robustness and drive responses of individuals and networks to dynamic processes.

Resources rich in otherwise scarce nutrients may be more central to networks, potentially overlooked by conventional analyses as simply rare interactions despite their ecological importance. This nutrient limitation may also rationalise new nodes connecting to existing nodes with high degrees, as is the case in preferential attachment models of network assembly (Barabási et al., 1999; Olesen et al., 2008; see the hypothesis about centrality as a result of nutrient limitation in Figure 1). Such mechanistic rules could be incorporated into adaptive network models to guide predictions or provide testable hypotheses in contexts including conservation, restoration, invasion and perturbation (Kaiser-Bunbury et al., 2010; Maia et al., 2021; Raimundo et al., 2018). Ultimately though, nutritional diversity and resource nutrition evenness will influence the robustness of networks; for example, if higher trophic levels are lipid-limited (Wilder et al., 2013), apex predators may be more likely to succumb to secondary extinction if lipid-rich resources are removed. Greater nutritional redundancy (i.e., resources having similar nutrient contents) will thus increase network connectance as consumers exploit more resources for each nutrient. If alternative sources of a given nutrient are not available when one such resource is removed, its consumers may fail to meet their nutritional requirements and become extinct. Some robustness analyses redistribute interactions based on variables such as node centrality (i.e., preferential attachment; Olesen et al., 2008), previously known interactions (Kaiser-Bunbury et al., 2010) or not at all. Consumers are often considered to persist if they are connected to at least one extant resource, neglecting the nutritional consequences of these interactions. By integrating nutritional data into robustness analyses, it may be possible to generate more realistic robustness analyses that better account for population fitness.

4 | NUTRITIONAL NETWORKS IN PRACTICE

4.1 | Constructing and analysing nutritional networks

Constructing a nutritional network requires interaction data (i.e., an edge list or matrix of nodes, representing species or other ecological units, interacting with other nodes), nutritional data (i.e., nutrient contents of the nodes or nutritional values transferred between nodes) and the application of graph theory. For nutritional ecologists, the application of graph theory will likely be a novel (inexpensive but possibly time-consuming) addition to their workflow. Adopting network ecology will require some familiarity with network concepts and terminology. Network ecologists, however, will need nutritional data (e.g., from biochemical analysis), which will increase experimental costs and labour. Research at interdisciplinary boundaries such as this will often require additional labour and expense, but such approaches also generate novel research directions that address otherwise unanswerable questions. Through collaborative approaches between researchers across these disciplines, the additional inputs can be minimised whilst making use of existing expertise in each respective field.

Nutritional networks could be constructed from a few different perspectives, which will in turn affect how network properties can be assessed: (i) representing each nutrient in a distinct network layer with the same interactions weighted differently based on the exchange of nutrients in interactions (see next section, Figure 3), (ii) clustering taxa based on their nutrient contents and representing these groups as nodes or otherwise integrating nutritional data as node trait data (akin to the incorporation of trait data into networks in many cases) and (iii) treating nutrients as nodes and representing the interaction of consumers with each nutrient. In the case of (ii), network properties can be assessed based on interactions between nodes in the same way as traditional approaches to network analysis, where nodes usually represent species; this can shift focus onto the traits (in this case, nutrients) used to cluster taxa, but care must be taken not to distort interpretation or emergent properties, especially across trophic levels (Buchkowski & Lindo, 2021). In (iii), only information regarding the relative frequency of nutrient transfer irrespective of ecological context is available, facilitating analyses focussed on nutrient provision; Timberlake et al. (2022) demonstrate this approach very effectively. By constructing separate network layers for each nutrient in method (i), the interaction identities remain the same between networks but link weights change, facilitating comparison of network properties between nutrients using weighted metrics, essentially adding a contextual dimension to commonplace assessments of network dissimilarity across space and time (Fründ, 2021). This could similarly be incorporated into other existing frameworks, such as parallel networks, the inclusion of nutrients into which has already been proposed (Olff et al., 2009).

The integration of trait data into analyses of trophic interactions has gained increasing traction over the last decade given its power in predicting and rationalising interactions (Brose et al., 2019; Green & Côté, 2014; Spitz et al., 2014). Treating nutrients as quantitative traits is a viable alternative strategy for the integration of nutritional data into networks, especially if alongside other trait information. The nutritional redundancy of different taxa is an important consideration in this depending on the method of integrating trait data; for example, if node identities are based on trait similarity, nutritionally similar prey that can be ecologically distinct may be confounded (e.g., ichneumonid wasps and linyphiid spiders are nutritionally similar despite being behaviourally, taxonomically and ecologically disparate). Regardless, this integration of nutrients could facilitate streamlined analysis of the joint impacts of nutrients alongside other traits (e.g., morphological traits such as gape width or body size, genetic traits, environmental traits), even ignoring 'Linnean' taxonomy in favour of function. Each approach to integrating nutritional data into networks could be used to answer different questions within the remit of nutritional and network ecology, but we focus here on the first example, the representation of nutrition in link weights.

4.2 | An empirical example of a predator–prey nutritional network

To demonstrate the process and benefits of constructing and analysing nutritional networks, we provide here an empirical example. Nutritional data are underrepresented in ecological networks, but the data set presented by Cuff, Tercel, Vaughan, et al. (2022) is sufficient to explore nutritional network construction and analysis preliminarily. These interaction data have been used to explore the density dependence of foraging (Cuff, Tercel, Drake, et al., 2022), the impact of weather on trophic networks (Cuff, Windsor, et al., 2023), the impact of prey availability data sources on null network analyses (Cuff et al., 2024) and, most relevantly, the relationship between foraging and nutrition (Cuff, Tercel, Vaughan, et al., 2022). This latter study, the only one using these interaction data to integrate nutritional data, aimed to investigate the nutritional dynamics of field-collected spiders using molecular dietary analysis, micro-scale macronutrient analysis and network-based null models. This study did not, however, conduct any network-level analyses nor did it attempt to integrate nutritional data into networks. Binary interaction data were generated via dietary metabarcoding (Cuff, Tercel, Drake, et al., 2022), and nutritional data were determined via the

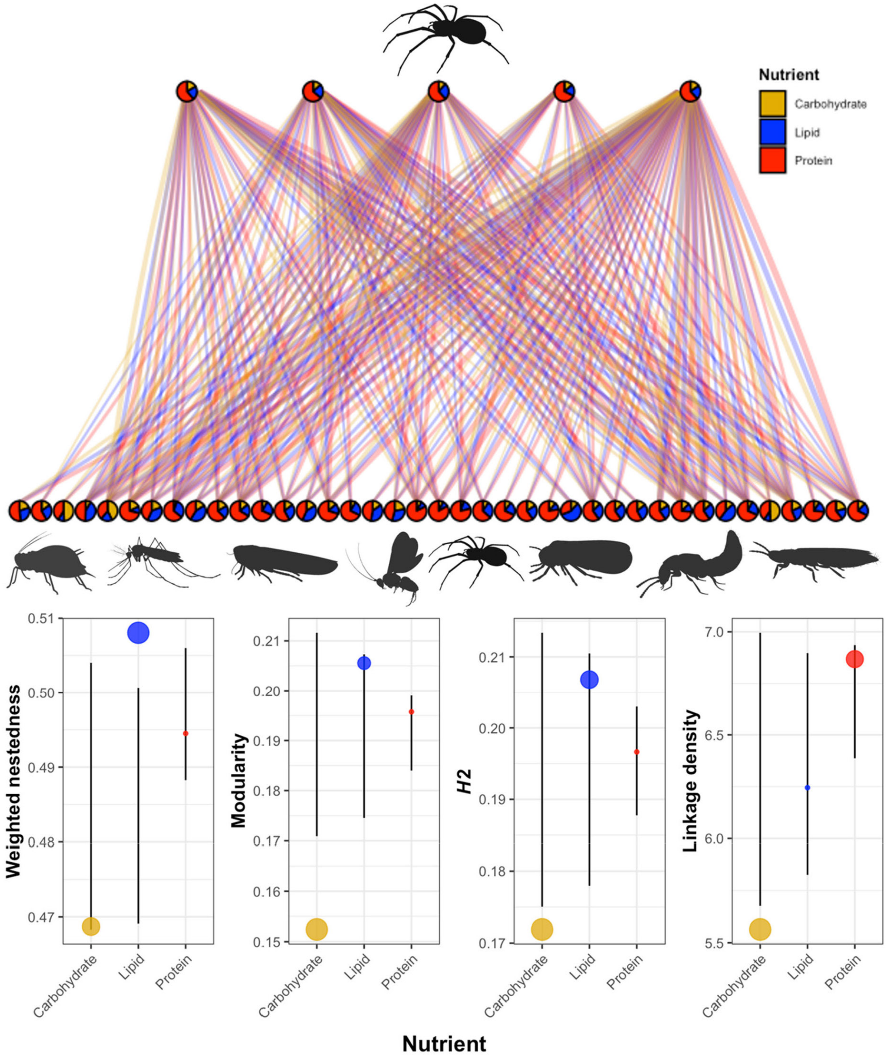

FIGURE 3 By assessing network structure with interactions weighted based on the transfer of each individual nutrient, it is possible to visualise how nutrients transfer through ecological networks, the importance of each nutrient for different consumers and how rich the resources exploited by each consumer are in each nutrient. This network represents the exchange of three macronutrients (yellow, blue and red representing carbohydrate, lipid and protein, respectively) between spiders (top level; each a different genus, their mean macronutrient intakes represented by the pie chart proportions of each colour) and their prey (bottom level; their mean macronutrient content represented by the pie chart proportions of each colour). Link weights represent nutrient transfer (proportional nutrient content multiplied by observed interactions). Four network properties are compared between macronutrients and between observed and null networks in the lower panel: weighted nestedness (a measure of the extent to which interactions of individuals form subsets of wider interactions), quantitative modularity (the extent to which links are distributed within rather than between sets of nodes), H_2' (the degree of specialisation or partitioning of interactions) and linkage density (the average number of links per node). Points represent observed network metrics, and lines represent standard deviation of null network metrics. Point sizes represent the standardised *Z*-score value. By constructing weighted networks based on the proportional nutrient contents and frequencies of interactions for each nutrient separately, network properties can be compared between nutrients and with null networks. The properties of the networks constructed using data from each of the three macronutrients quantified varied in their values and deviation from null networks, indicating how each nutrient may structure interactions differently, or how network structure influences nutrient acquisition.

MEDI protocol (Cuff et al., 2021). These data were integrated into a bipartite network of predator–prey interactions between spiders and their prey. The methods used to generate these data are given in full by Cuff, Tercel, Vaughan, et al. (2022) and described briefly in the Supporting Information. By bringing these data together, it is possible to investigate how nutrients affected interactions between spiders and their prey.

We incorporated these interaction and nutritional data into three overlapping networks, conceptually similar to a multilayer network (Hutchinson et al., 2019; Pilosof et al., 2017), by representing the transfer of each nutrient between resource and consumer as interaction weights (Figure 3; Supporting Information). In this way, it is possible to compare weighted network properties across the three networks to ascertain how nutrients may distinctly contribute to or be affected by the structure of interactions. This could be expanded into a true multilayer network, but it would require careful consideration of the meaning of interlayer links (although some clear options prevail; e.g., ratios of nutrients). The link identities are consistent across the three networks, but the link weights differ depending on the transfer of the different nutrients, facilitating comparison of network properties via weighted metrics (Figure 3).

The nutritional network was subsequently compared with null networks. The type of null model used in such comparisons is crucial for determining the parameters being assessed and their constraints (Cantor et al., 2017; Cuff et al., 2024; Gotelli & Graves, 1996). Here, we used a null model that randomly switched nutrient contents between prey (across 1000 iterations). These nutrient contents were used to generate new link weights (nutrient contents multiplied by the number of interactions with each spider genus based on the observed data). Network-level metrics were generated for these null networks to represent the nutritional network metrics if resource nutrient contents were random. We focussed on weighted nestedness, modularity, specialisation (H_2'; Blüthgen et al., 2006) and linkage density based on the hypotheses presented above (Figure 1). By comparing the observed network metrics for each nutrient with these null nutritional networks (via *Z*-score standardisation), it is possible to test hypotheses related to nutrients as a driver of network structure explicitly.

In this example, several of the nutrition-related network properties hypothesised above can arguably be observed (Figure 1). The carbohydrate network had lower nestedness (observed = 0.467, expected = 0.486 ± 0.018 SD, standardised *Z*-score = −1.014), linkage density (obs = 5.563, exp = 6.334 ± 0.664, *Z* = −1.160) specialisation (obs = 0.172, exp = 0.194 ± 0.018, *Z* = −1.226) and modularity (obs = 0.152, exp = 0.192 ± 0.019, *Z* = −2.047) than expected. The lipid network had higher nestedness (obs = 0.517, exp = 0.485 ± 0.016, *Z* = 2.023), modularity (obs = 0.204, exp = 0.190 ± 0.016, *Z* = 0.859) and specialisation (obs = 0.207, exp = 0.193 ± 0.016, *Z* = 0.848) than expected, but lower linkage density (obs = 6.245, exp = 6.368 ± 0.528, *Z* = −0.234). The protein network had higher linkage density (obs = 6.868, exp = 6.660 ± 0.267, *Z* = 0.780), modularity (obs = 0.194, exp = 0.192 ± 0.007, *Z* = 0.301) and specialisation (obs = 0.197, exp = 0.196 ± 0.007, *Z* = 0.125) than expected, but lower nestedness (obs = 0.485, exp = 0.497 ± 0.009, *Z* = −1.457).

The relatively low linkage density for carbohydrate, when considered alongside the low modularity and specialisation, indicates generalist foraging for the few prey rich in carbohydrate, and uneven feeding on those few carbohydrate-rich resources. That linkage density was not so low for the protein nor lipid networks is indicative of the higher concentrations of protein and lipid across the network. Whilst binary networks or those weighted solely based on interaction frequency might show a higher-than-expected linkage density for nutrient-limited networks (Figure 1), these nutritional networks will show a lower linkage density for the most limited nutrient (because less of it is exploited in the network, resulting in smaller link weights), together allowing the identification of nutrient limitation and the nutrient that is limited. The most limited nutrient is not, however, necessarily the most sought-after by the consumers. Despite some consumers tolerating carbohydrate-rich diets (Hawley et al., 2016; Wiggins & Wilder, 2022; Wilder et al., 2011), non-structural carbohydrate-rich diets can be detrimental or toxic (Alcántar-Fernández et al., 2019; Hewson-Hughes et al., 2011; Schlotterer et al., 2009). Lipids are, however, known to be important and more limited in higher trophic levels of arthropod networks (Wilder et al., 2013).

The higher-than-expected nestedness in the lipid network and the relatively high modularity and specialisation could indicate that the spiders are obtaining most of their lipid intake from a few lipid-rich species, the identity of which may differ between spider groups (as hypothesised for specialism in Figure 1). This nutritional partitioning would have important consequences for network robustness. Such insights from nutritional networks could guide the management of ecosystems for conservation, biocontrol and various other contexts. Importantly, networks replicated in space and/or time would allow quantitative comparison of observed networks that might elucidate other nutrient-driven processes. In any case, nutritional network properties such as these can provide ecological context to complex nutritional systems and can be used to test various system-level questions regarding the structuring of interactions by nutrients.

5 | CONSIDERATIONS FOR NUTRITIONAL NETWORKS AND THEIR LIMITATIONS

5.1 | Auxiliary hypotheses underpinning nutritional networks

Whilst nutrients may be an important driver of interactions, they are not an outright determinant of them. Nutrients are likely to provide a great deal of predictive or explanatory power for network analysis (Hutchinson et al., 2019), and some networks can arguably be rationalised by relatively few variables (Eklöf et al., 2013). No single dimension is likely to explain entirely the structure of an ecological network though. Other drivers and constraints of foraging should be considered alongside nutrition, especially considering that the nutrient dependence of interactions could be overridden by predator hunger state (Lang & Gsödl, 2001), gape limitation (Arim et al., 2010), biomechanics (Cuff, Labonte, et al., 2023), prey abundance, or prey traits including dispersal (Pastorok, 1981), camouflage (Skelhorn & Rowe, 2016), defences (Provost et al., 2006), escape capability (Lang & Gsödl, 2001; Provost et al., 2006) or size (Bence & Murdoch, 1986; Downes, 2002; Turesson et al., 2002). Nutritional dynamics can also be determined by traits such as sex, life stage (Al Shareefi & Cotter, 2019; Cuff, Tercel, Vaughan, et al., 2022) and phenology (Raubenheimer et al., 2007), incentivising the parallel integration of such traits into networks (Poisot et al., 2015). This can be achieved by considering nutrition in the context of trait matching. By representing a consumer's nutritional needs and a resource's nutrient content, nutritional trait matching could present an incredibly valuable means for predicting and inferring links in networks. Through this framework, other traits can also be incorporated, or nutrients can be integrated into existing networks to enhance predictive power. In the case of the spider–prey example above, for example, the size of prey that make contact with webs may determine the ability of linyphiid spiders to subdue and consume them, whereas spiders with adhesive webs, such as araneids, might not be constrained by this trait.

Nutrients can affect trophic interactions at different stages of the foraging process too, from prey choice, through consumption of different quantities of different prey, to extraction of specific nutrients (Kohl et al., 2015; Pekár et al., 2010), which may be challenging to represent in networks. Wootton et al. (2023) define eight stages of trophic interactions, each with different relevant traits: (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) subjugation, (6) ingestion, (7) digestion and (8) nutrient allocation. This last step is the most intuitively linked to nutrition given that it directly links resource nutrient content to fitness, but nutrients may influence each of the other stages variably across different consumers. Search may be adjusted to redress nutritional deficiencies, detection may depend on the ability to sense different nutrients, attack decision will be driven by prey choice, pursuit may be limited by the consumer's current nutritional state, and digestion may depend on the presence of endosymbionts able to metabolise or uptake nutrient sources. Considering this framework and particularly how the interaction data within a study pertain to these stages may influence whether to include nutritional data and the form that these may take. In the empirical example above, for example, the metabarcoding detections pertain primarily to the latter stages (e.g., ingestion) given that the prey have already been consumed, but the earlier stages (i.e., search, detection, decision and pursuit) can only be inferred without further analysis. Direct observation of interactions, however, may not account for Stages 6–8. Such context needs careful consideration in the context of nutritional networks.

There are various indicators of nutritional deficits within consumers that may alter their ecology (Wagner et al., 2013), yet, whilst there is evidence of resource nutrient content influencing consumer choices (Cuff, Tercel, Vaughan, et al., 2022; Kohl et al., 2015; Mayntz et al., 2005; Rendon et al., 2019; Schmidt et al., 2012), this is predicated on the notion that consumers are aware of or able to sense differences in nutrient contents between different resources. Some generalists are thought to remain in a suboptimal nutritional state (Symondson et al., 2002) and may forage randomly to redress nutritional deficiencies, essentially relying on generalism to acquire randomly the required nutrients and not necessarily requiring the capacity to sense nutrients. Similarly, specialists can be adapted to the specific nutrients provided by their resource (Despland & Noseworthy, 2006; Simpson & Raubenheimer, 2012). Evidence suggests that some consumers can sense nutrient contents though, through olfaction (Julliard et al., 2017; Nevo et al., 2019), taste (Peneaux et al., 2017; Ruedenauer et al., 2015) and possibly other senses. Through this, many consumers may be able to differentiate between the nutrient contents of not only prey taxa or individuals, but also different tissues within an individual organism. Nutritional variation between tissues can be pronounced in animals (Kohl et al., 2015; Pekár et al., 2010) and plants (e.g., between stems, leaves, fruit and nectaries). Nutrient regulation through targeted consumption of specific tissues (Mayntz et al., 2005; Pekár et al., 2010) could lead to increased superfluous killing and abandonment of non-target tissues, which could manifest unconventionally in functional responses (Maupin, 2001; Samu & Biro, 1993). If the tissue types consumed are known a priori (e.g., plant–pollinator and seed dispersal concern nectaries and fruit, respectively), it is straightforward to account for this, but otherwise, observations, records or feeding trials may provide this context.

5.2 | Constructing nutritional networks from disparate data sources

To construct nutritional networks, nutritional and interaction data must be collected in parallel. We provide an empirical example above, including several ways of visualising and analysing nutritional networks. Streamlined and cost-effective protocols for nutrient quantification are available (Cuff et al., 2021), but many alternative methods exist, each with different advantages (Zaguri et al., 2021, 2022). The most affordable and rapid nutrient analysis methods tend to be colorimetric assays, but these often neglect the complexity and diversity of broad nutrient classes. Spectrometry-based methods and techniques such as hydrolysed amino acid analysis can identify better-resolved nutritional constituents (e.g., individual amino acids), but are markedly more expensive (Cuff et al., 2021; Zaguri et al., 2021, 2022). Ultimately, whichever method is used, these data become attributes of the nodes or links identified in the interaction data. Direct observation of interactions is the most straightforward method for collecting interaction data, but newer techniques such as DNA metabarcoding can facilitate construction of highly resolved and data-rich networks (Cuff, Windsor, et al., 2022). There are, however, no protocols currently available for parallel macronutrient and nucleic acid extraction from the same individual, precluding individual-level networks constructed using these methods together. Node-level averages can, however, be determined for coarser networks (Cuff, Tercel, Vaughan, et al., 2022). Metabarcoding-based networks neglect the life stage and sex of their nodes (Nestel et al., 2016), preclude detection of cannibalism. These methods also often fail to differentiate between direct consumption and nutritionally distinct interactions such as scavenging, secondary predation, accidental consumption, parasitism and symbiosis (Cuff, Kitson, et al., 2023; Greenstone et al., 2007; Miller et al., 2021; Neidel et al., 2022; Paula et al., 2015; Tercel et al., 2021). Solutions to these problems are, however, increasingly emerging with methodological innovation.

Network construction and analysis are also susceptible to various limitations (McLeod et al., 2021), although the nature and impact of these is determined by the hypothesis tested (Cuff et al., 2024) and can often be overcome with good experimental design. These limitations can be compounded when combining data from different methodologies (Cuff, Windsor, et al., 2022) and nutritional networks will inherit these problems. Detectability biases are a critical consideration in networks, ultimately determining completeness (Quintero et al., 2022) and network properties (Macgregor et al., 2017; McLeod et al., 2021). Network completeness can be determined by assessing the accumulation of novel pairwise interactions detected or observed (Chacoff et al., 2012; Jordano, 2016; Macgregor et al., 2017; Traveset et al., 2015); nutritional networks will only differ in needing to account for nutritional variation within and between nodes. The number of samples from which node-level nutritional data need to be collected will vary depending on ontogeny, habitat and myriad other factors. Individual networks will circumvent these challenges if individual resource and consumer nutritional data can be collected in parallel, but care must be taken to ensure that nutritional data are accurate and representative. It is crucial as well that researchers remain vigilant to the underlying assumptions (i.e., auxiliary hypotheses) involved in nutritional network construction and analysis. The acquisition of nutrients, for example, might not perfectly reflect the nutrient content of the resource consumed according to whole-body nutrient quantification if the consumer selects specific tissues. Ultimately, how nutritional data are collected and integrated into networks will be critical in determining how they affect network properties.

6 | BROADER CONTEXT AND CONCLUSIONS

Nutrients are likely to be a dominant structuring force in ecological networks but are poorly integrated into them despite their potential to rationalise network properties, predict rewiring and determine robustness. This transcends bipartite trophic interactions; mutualisms often rely on nutritional rewards, the attractiveness of which may depend on nutritional complementarity and quality. Equally, the viability of host–parasitoid interactions is constrained by the nutrition of developing parasitoids. Even within social and sexual interactions (e.g., trophallaxis in ants, nuptial gifts between nursery web spiders, *Pisaura mirabilis*) nutrients may determine interaction outcomes. Whilst we have focussed on the implications of nutrients for direct interactions, particularly predator–prey, these concepts are much more broadly applicable. Indeed, nutrients are likely to be a significant effector of indirect interactions via nutritional cascades throughout whole networks or by driving competition between consumers and/or resources. By investigating motifs within networks, these indirect interactions can be identified (Simmons et al., 2019; Tavella et al., 2022) and nutritional drivers elucidated. Other chemical constituents of resources including toxins may also modify nutritional effects but could similarly and simultaneously be integrated into networks.

To represent complex interdependent systems, multilayer networks offer a significant advance, linking discrete networks across space and time (Pilosof et al., 2017). Our example of a nutritional network conceptually overlaps with this by presenting different nutrients as effective network layers, but this lacks interlayer links between nodes, which typically represent differences in abundance over space and/or time (Fortin et al., 2021; Hervías-Parejo et al., 2023). By integrating these nutritional layers into a multilayer framework, it would be possible to investigate nutritional networks more cohesively, bridging gaps between nutrients, which are inherently linked biologically. Equally, more standard-practice multilayer approaches could link single nutrients over time and/or space. Nutritional networks ultimately present an opportunity to apply current best practices and state-of-the-art of network ecology to resolve fundamental ecological hypotheses and significantly extend our understanding of the mechanisms driving natural systems. By integrating nutrients into ecological network analyses, their impact on network structure, dynamics and function can be elucidated. Characterising nutrients as a fundamental driver of ecological processes will help to explain the mechanisms underpinning interactions and network structures across a broad range of contexts, ultimately unlocking the potential to extend our understanding of complex natural systems.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data presented in this manuscript are available online via Zenodo: https://zenodo.org/doi/10.5281/zenodo.6516934 (Cuff, Evans, et al., 2022).

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REFERENCES

Al Shareefi, E., & Cotter, S. C. (2019). The nutritional ecology of maturation in a carnivorous insect. *Behavioral Ecology*, *30*(1), 256–266. https://doi.org/10.1093/beheco/ary142

Alcántar-Fernández, J., González-Maciel, A., Reynoso-Robles, R., Pérez Andrade, M. E., Hernández-Vázquez, A. D. J., Velázquez-Arellano, A., & Miranda-Ríos, J. (2019). High-glucose diets induce mitochondrial dysfunction in *Caenorhabditis elegans*. *PLoS One*, *14*(12), e0226652. https://doi.org/10.1371/journal.pone.0226652

Anderson, T. R., Raubenheimer, D., Hessen, D. O., Jensen, K., Gentleman, W. C., & Mayor, D. J. (2020). Geometric stoichiometry: Unifying concepts of animal nutrition to understand how protein-rich diets can be "too much of a good thing". *Frontiers in Ecology and Evolution*, *8*, 196. https://doi.org/10.3389/fevo.2020.00196

Ando, H., Setsuko, S., Horikoshi, K., Suzuki, H., Umehara, S., Inoue-Murayama, M., & Isagi, Y. (2013). Diet analysis by next-generation sequencing indicates the frequent consumption of introduced plants by the critically endangered red-headed wood pigeon (*Columba janthina nitens*) in oceanic island habitats. *Ecology and Evolution*, *3*(12), 4057–4069. https://doi.org/10.1002/ece3.773

Arim, M., Abades, S. R., Laufer, G., Loureiro, M., & Marquet, P. A. (2010). Food web structure and body size: Trophic position and resource acquisition. *Oikos*, *119*(1), 147–153. https://doi.org/10.1111/j.1600-0706.2009.17768.x

Barabási, A.-L., Albert, R., & Jeong, H. (1999). Mean-field theory for scale-free random networks. *Physica A: Statistical Mechanics and its Applications*, *272*(1–2), 173–187. https://doi.org/10.1016/S0378-4371(99)00291-5

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, *344*(6179), 1242552. https://doi.org/10.1126/science.1242552

Behmer, S. T., & Joern, A. (2008). Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(6), 1977–1982. https://doi.org/10.1073/pnas.0711870105

Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, *95*(2), 69–114. https://doi.org/10.1079/BER2004350

Belovsky, G. E. (1984). Herbivore optimal foraging: A comparative test of three models. *The American Naturalist*, *124*(1), 97–115. https://doi.org/10.1086/284254

Bence, J. R., & Murdoch, W. W. (1986). Prey size selection by the mosquitofish: Relation to optimal diet theory. *Ecology*, *67*(2), 324–336. https://doi.org/10.2307/1938576

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 9. https://doi.org/10.1186/1472-6785-6-9

Bressendorff, B. B., & Toft, S. (2011). Dome-shaped functional response induced by nutrient imbalance of the prey. *Biology Letters*, *7*(4), 517–520. https://doi.org/10.1098/rsbl.2011.0103

Broennimann, O., Treier, U. A., Müller-Schärer, H., Thuiller, W., Peterson, A. T., & Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters*, *10*(8), 701–709. https://doi.org/10.1111/j.1461-0248.2007.01060.x

Brose, U., Archambault, P., Barnes, A. D., Bersier, L.-F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., … Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, *3*(6), 919–927. https://doi.org/10.1038/s41559-019-0899-x

Buchkowski, R. W., & Lindo, Z. (2021). Stoichiometric and structural uncertainty in soil food web models. *Functional Ecology*, *35*(1), 288–300. https://doi.org/10.1111/1365-2435.13706

Cantor, M., Pires, M. M., Marquitti, F. M. D., Raimundo, R. L. G., Sebastián-González, E., Coltri, P. P., Perez, S. I., Barneche, D. R., Brandt, D. Y. C., Nunes, K., Daura-Jorge, F. G., Floeter, S. R., & Guimarães, P. R. (2017). Nestedness across biological scales. *PLoS One*, *12*(2), e0171691. https://doi.org/10.1371/journal.pone.0171691

Chacoff, N. P., Vázquez, D. P., Lomáscolo, S. B., Stevani, E. L., Dorado, J., & Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network: Sampling a plant-pollinator network. *Journal of Animal Ecology*, *81*(1), 190–200. https://doi.org/10.1111/j.1365-2656.2011.01883.x

Cherif, M., & Loreau, M. (2013). Plant–herbivore–decomposer stoichiometric mismatches and nutrient cycling in ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754), 20122453. https://doi.org/10.1098/rspb.2012.2453

Coblentz, K. E., Squires, A., Uiterwaal, S., & Delong, J. P. (2022). Quantifying predator functional responses under field conditions reveals interactive effects of temperature and interference with sex and stage. *Journal of Animal Ecology*, *91*(7), 1431–1443. https://doi.org/10.1111/1365-2656.13703

Coogan, S. C. P., Raubenheimer, D., Zantis, S. P., & Machovsky-Capuska, G. E. (2018). Multidimensional nutritional ecology and urban birds. *Ecosphere*, *9*(4), e02177. https://doi.org/10.1002/ecs2.2177

Cuff, J. P., Evans, D. M., Vaughan, I. P., Wilder, S. M., Tercel, M. P., & Windsor, F. M. (2022). Networking nutrients: How nutrition determines the structure of ecological networks—Dataset. *Zenodo*. https://doi.org/10.5281/ZENODO.6516934

Cuff, J. P., Kitson, J. J. N., Hemprich-Bennett, D., Tercel, M. P. T. G., Browett, S. S., & Evans, D. M. (2023). The predator problem and PCR primers in molecular dietary analysis: Swamped or silenced; depth or breadth? *Molecular Ecology Resources*, *23*(1), 41–51. https://doi.org/10.1111/1755-0998.13705

Cuff, J. P., Labonte, D., & Windsor, F. M. (2023). *Understanding trophic interactions in a warming world by bridging foraging ecology and biomechanics with network science*. Open Science Framework. https://doi.org/10.31219/osf.io/78rkp

Cuff, J. P., Tercel, M. P. T. G., Drake, L. E., Vaughan, I. P., Bell, J. R., Orozco-terWengel, P., Müller, C. T., & Symondson, W. O. C. (2022). Density-independent prey choice, taxonomy, life history, and web characteristics determine the diet and biocontrol potential of spiders (Linyphiidae and Lycosidae) in cereal crops. *Environmental DNA*, *4*(3), 549–564. https://doi.org/10.1002/edn3.272

Cuff, J. P., Tercel, M. P. T. G., Vaughan, I., Drake, L. E., Wilder, S., Bell, J. R., Müller, C. T., Orozco-terWengel, P., & Symondson, W. O. C. (2022). *Evidence for nutrient-specific foraging of invertebrate predators under field conditions*. https://doi.org/10.22541/au.164908092.21266343/v1

Cuff, J. P., Tercel, M. P. T. G., Windsor, F. M., Hawthorne, B. S. J., Hambäck, P. A., Bell, J. R., Symondson, W. O. C., & Vaughan, I. P. (2024). Sources of prey availability data alter interpretation of outputs from prey choice null networks. *Ecological Entomology*, *49*, 418–432. https://doi.org/10.1111/een.13315

Cuff, J. P., Wilder, S. M., Tercel, M. P. T. G., Hunt, R., Oluwaseun, S., Morley, P. S., Badell-Grau, R. A., Vaughan, I. P., Bell, J. R., Orozco-terWengel, P., Symondson, W. O. C., & Müller, C. T. (2021). MEDI: Macronutrient Extraction and Determination from Invertebrates, a rapid, cheap and streamlined protocol. *Methods in Ecology and*

Evolution, *12*(4), 593–601. https://doi.org/10.1111/2041-210X.13551

Cuff, J. P., Windsor, F. M., Tercel, M. P. T. G., Bell, J. R., Symondson, W. O. C., & Vaughan, I. P. (2023). Temporal variation in spider trophic interactions is explained by the influence of weather on prey communities, web building and prey choice. *Ecography*, *2023*, e06737. https://doi.org/10.1111/ecog.06737

Cuff, J. P., Windsor, F. M., Tercel, M. P. T. G., Kitson, J. J. N., & Evans, D. M. (2022). Overcoming the pitfalls of merging dietary metabarcoding into ecological networks. *Methods in Ecology and Evolution*, *13*(3), 545–559. https://doi.org/10.1111/2041-210X.13796

De Ruiter, P. C., Van Veen, J. A., Moore, J. C., Brussaard, L., & Hunt, H. W. (1993). Calculation of nitrogen mineralization in soil food webs. *Plant and Soil*, *157*(2), 263–273. https://doi.org/10.1007/BF00011055

Despland, E., & Noseworthy, M. (2006). How well do specialist feeders regulate nutrient intake? Evidence from a gregarious tree-feeding caterpillar. *Journal of Experimental Biology*, *209*(7), 1301–1309. https://doi.org/10.1242/jeb.02130

Downes, S. J. (2002). Size-dependent predation by snakes: Selective foraging or differential prey vulnerability? *Behavioral Ecology*, *13*(4), 551–560. https://doi.org/10.1093/beheco/13.4.551

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., Dalsgaard, B., De Sassi, C., Galetti, M., Guimarães, P. R., Lomáscolo, S. B., Martín González, A. M., Pizo, M. A., Rader, R., Rodrigo, A., Tylianakis, J. M., Vázquez, D. P., & Allesina, S. (2013). The dimensionality of ecological networks. *Ecology Letters*, *16*(5), 577–583. https://doi.org/10.1111/ele.12081

Elser, J. J., Chrzanowski, T. H., Sterner, R. W., & Mills, K. H. (1998). Stoichiometric constraints on food-web dynamics: A whole-lake experiment on the Canadian Shield. *Ecosystems*, *1*(1), 120–136. https://doi.org/10.1007/s100219900009

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

Fründ, J. (2021). Dissimilarity of species interaction networks: How to partition rewiring and species turnover components. *Ecosphere*, *12*(7), e03653. https://doi.org/10.1002/ecs2.3653

Gauzens, B., Barnes, A., Giling, D. P., Hines, J., Jochum, M., Lefcheck, J. S., Rosenbaum, B., Wang, S., & Brose, U. (2019). fluxweb: An R package to easily estimate energy fluxes in food webs. *Methods in Ecology and Evolution*, *10*(2), 270–279. https://doi.org/10.1111/2041-210X.13109

Gotelli, N. J., & Graves, G. R. (1996). *Null models in ecology*. Smithsonian Institution Press.

Green, S. J., & Côté, I. M. (2014). Trait-based diet selection: Prey behaviour and morphology predict vulnerability to predation in reef fish communities. *Journal of Animal Ecology*, *83*(6), 1451–1460. https://doi.org/10.1111/1365-2656.12250

Greenberg, R. (1984). Neophobia in the foraging-site selection of a neotropical migrant bird: An experimental study. *Proceedings of the National Academy of Sciences of the United States of America*, *81*(12), 3778–3780. https://doi.org/10.1073/pnas.81.12.3778

Greenstone, M. H. (1990). Meteorological determinants of spider ballooning: The roles of thermals vs. the vertical windspeed gradient in becoming airborne. *Oecologia*, *84*, 164–168.

Greenstone, M. H., Rowley, D. L., Weber, D. C., Payton, M. E., & Hawthorne, D. J. (2007). Feeding mode and prey detectability half-lives in molecular gut-content analysis: An example with two predators of the Colorado potato beetle. *Bulletin of Entomological Research*, *97*(2), 201–209. https://doi.org/10.1017/S000748530700497X

Gresh, T., Lichatowich, J., & Schoonmaker, P. (2000). An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: Evidence of a nutrient deficit in the freshwater systems of the Pacific Northwes. *Fisheries*, *25*, 15–21. https://doi.org/10.1577/1548-8446(2000)025%3C0015:AEOHAC%3E2.0.CO;2

Guimarães, P. R. (2020). The structure of ecological networks across levels of organization. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 433–460. https://doi.org/10.1146/annurev-ecolsys-012220-120819

Hawley, J., Simpson, S. J., & Wilder, S. M. (2016). Flesh flies regulate the consumption of 3 macronutrients to maximize lifespan and egg production. *Behavioral Ecology*, *27*(1), 245–251. https://doi.org/10.1093/beheco/arv151

Helms, K. R., & Vinson, S. B. (2002). Widespread association of the invasive ant *Solenopsis invicta* with an invasive mealybug. *Ecology*, *83*(9), 2425–2438. https://doi.org/10.1890/0012-9658(2002)083[2425:WAOTIA]2.0.CO;2

Hervías-Parejo, S., Colom, P., Beltran Mas, R., Serra, E., Pons, S., Mesquida, V., & Traveset, A. (2023). Spatio-temporal variation in plant–pollinator interactions: A multilayer network approach. *Oikos*, *2023*(8), e09818. https://doi.org/10.1111/oik.09818

Hewson-Hughes, A. K., Hewson-Hughes, V. L., Miller, A. T., Hall, S. R., Simpson, S. J., & Raubenheimer, D. (2011). Geometric analysis of macronutrient selection in the adult domestic cat, *Felis catus*. *Journal of Experimental Biology*, *214*(6), 1039–1051. https://doi.org/10.1242/jeb.049429

Holling, C. S. (1966). The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada*, *98*(S48), 5–86. https://doi.org/10.4039/entm9848fv

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

Jensen, K., Mayntz, D., Toft, S., Clissold, F. J., Hunt, J., Raubenheimer, D., & Simpson, S. J. (2012). Optimal foraging for specific nutrients in predatory beetles. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1736), 2212–2218. https://doi.org/10.1098/rspb.2011.2410

Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, *30*(12), 1883–1893. https://doi.org/10.1111/1365-2435.12763

Julliard, A.-K., Al Koborssy, D., Fadool, D. A., & Palouzier-Paulignan, B. (2017). Nutrient sensing: Another chemosensitivity of the olfactory system. *Frontiers in Physiology*, *8*, 468. https://doi.org/10.3389/fphys.2017.00468

Junker, R. R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H., & Stang, M. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional Ecology*, *27*(2), 329–341. https://doi.org/10.1111/1365-2435.12005

Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B., & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecology Letters*, *13*(4), 442–452. https://doi.org/10.1111/j.1461-0248.2009.01437.x

Kaplan, I., & Eubanks, M. D. (2005). Aphids alter the community-wide impact of fire ants. *Ecology*, *86*(6), 1640–1649. https://doi.org/10.1890/04-0016

Kaspari, M. (2020). The seventh macronutrient: How sodium shortfall ramifies through populations, food webs and ecosystems. *Ecology Letters*, *23*(7), 1153–1168. https://doi.org/10.1111/ele.13517

Kaspari, M. (2021). The invisible hand of the periodic table: How micronutrients shape ecology. *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 199–219. https://doi.org/10.1146/annurev-ecolsys-012021-090118

Kohl, K. D., Coogan, S. C. P., & Raubenheimer, D. (2015). Do wild carnivores forage for prey or for nutrients?: Evidence for nutrient-specific foraging in vertebrate predators. *BioEssays*, *37*(6), 701–709. https://doi.org/10.1002/bies.201400171

Krabbe, B. A., Arnan, X., Lannes, P., Bergstedt, C. E., Larsen, R. S., Pedersen, J. S., & Shik, J. Z. (2019). Using nutritional geometry to define the fundamental macronutrient niche of the widespread invasive ant *Monomorium pharaonis*. *PLoS One*, *14*(6), e0218764. https://doi.org/10.1371/journal.pone.0218764

Lang, A., & Gsödl, S. (2001). Prey vulnerability and active predator choice as determinants of prey selection: A carabid beetle and its aphid prey. *Journal of Applied Entomology*, *125*(1–2), 53–61. https://doi.org/10.1111/j.1439-0418.2001.00511.x

Lau, M. K., Borrett, S. R., Baiser, B., Gotelli, N. J., & Ellison, A. M. (2017). Ecological network metrics: Opportunities for synthesis. *Ecosphere*, *8*(8), e01900. https://doi.org/10.1002/ecs2.1900

Lihoreau, M., Buhl, J., Charleston, M. A., Sword, G. A., Raubenheimer, D., & Simpson, S. J. (2014). Modelling nutrition across organizational levels: From individuals to superorganisms. *Journal of Insect Physiology*, *69*, 2–11. https://doi.org/10.1016/j.jinsphys.2014.03.004

Liu, C., & Sun, X. (2013). A review of ecological stoichiometry: Basic knowledge and advances. In *Reference module in earth systems and environmental sciences*. Elsevier. ISBN: 9780124095489. https://doi.org/10.1016/B978-0-12-409548-9.05519-6

Loreau, M., & Holt, R. D. (2004). Spatial flows and the regulation of ecosystems. *The American Naturalist*, *163*(4), 606–615. https://doi.org/10.1086/382600

Macgregor, C. J., Evans, D. M., & Pocock, M. J. O. (2017). Estimating sampling completeness of interactions in quantitative bipartite ecological networks: Incorporating variation in species' specialisation. *bioRxiv*. https://doi.org/10.1101/195917

Maia, K. P., Marquitti, F. M. D., Vaughan, I. P., Memmott, J., & Raimundo, R. L. G. (2021). Interaction generalisation and demographic feedbacks drive the resilience of plant–insect networks to extinctions. *Journal of Animal Ecology*, *90*(9), 2109–2121. https://doi.org/10.1111/1365-2656.13547

Margalida, A. (2008). Bearded vultures (*Gypaetus barbatus*) prefer fatty bones. *Behavioral Ecology and Sociobiology*, *63*(2), 187–193. https://doi.org/10.1007/s00265-008-0649-6

Maupin, J. L. (2001). Superfluous killing in spiders: A consequence of adaptation to food-limited environments? *Behavioral Ecology*, *12*(5), 569–576. https://doi.org/10.1093/beheco/12.5.569

Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S., & Simpson, S. J. (2005). Nutrient-specific foraging in invertebrate predators. *Science*, *307*(5706), 111–113. https://doi.org/10.1126/science.1105493

McLeod, A., Leroux, S. J., Gravel, D., Chu, C., Cirtwill, A. R., Fortin, M., Galiana, N., Poisot, T., & Wood, S. A. (2021). Sampling and asymptotic network properties of spatial multi-trophic networks. *Oikos*, *130*(12), 2250–2259. https://doi.org/10.1111/oik.08650

Meunier, C. L., Boersma, M., Declerck, S. A. J., & Laspoumaderes, C. (2023). How sharp is the knife? Herbivore and carnivore sensitivity to resource stoichiometric quality. *Oikos*, *2023*(9), e09898. https://doi.org/10.1111/oik.09898

Miller, K. E., Polaszek, A., & Evans, D. M. (2021). A dearth of data: Fitting parasitoids into ecological networks. *Trends in Parasitology*, *37*(10), 863–874. https://doi.org/10.1016/j.pt.2021.04.012

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*(7100), 259–264. https://doi.org/10.1038/nature04927

Neidel, V., Sint, D., Wallinger, C., & Traugott, M. (2022). RNA allows identifying the consumption of carrion prey. *Molecular Ecology Resources*, *22*(7), 2662–2671. https://doi.org/10.1111/1755-0998.13659

Nestel, D., Papadopoulos, N. T., Pascacio-Villafán, C., Righini, N., Altuzar-Molina, A. R., & Aluja, M. (2016). Resource allocation and compensation during development in holometabolous insects. *Journal of Insect Physiology*, *95*, 78–88. https://doi.org/10.1016/j.jinsphys.2016.09.010

Nevo, O., Razafimandimby, D., Valenta, K., Jeffrey, J. A. J., Reisdorff, C., Chapman, C. A., Ganzhorn, J. U., & Ayasse, M. (2019). Signal and reward in wild fleshy fruits: Does fruit scent predict nutrient content? *Ecology and Evolution*, *9*(18), 10534–10543. https://doi.org/10.1002/ece3.5573

Nie, Y., Zhang, Z., Raubenheimer, D., Elser, J. J., Wei, W., & Wei, F. (2015). Obligate herbivory in an ancestrally carnivorous lineage: The giant panda and bamboo from the perspective of nutritional geometry. *Functional Ecology*, *29*(1), 26–34. https://doi.org/10.1111/1365-2435.12302

Olesen, J. M., Bascompte, J., Elberling, H., & Jordano, P. (2008). Temporal dynamics in a pollination network. *Ecology*, *89*(6), 1573–1582. https://doi.org/10.1890/07-0451.1

Olff, H., Alonso, D., Berg, M. P., Eriksson, B. K., Loreau, M., Piersma, T., & Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *364*(1524), 1755–1779. https://doi.org/10.1098/rstb.2008.0222

Pastorok, R. A. (1981). Prey vulnerability and size selection by Chaoborus larvae. *Ecology*, *62*(5), 1311–1324. https://doi.org/10.2307/1937295

Paula, D. P., Linard, B., Andow, D. A., Sujii, E. R., Pires, C. S. S., & Vogler, A. P. (2015). Detection and decay rates of prey and prey symbionts in the gut of a predator through metagenomics. *Molecular Ecology Resources*, *15*(4), 880–892. https://doi.org/10.1111/1755-0998.12364

Pekár, S., Mayntz, D., Ribeiro, T., & Herberstein, M. E. (2010). Specialist ant-eating spiders selectively feed on different body parts to balance nutrient intake. *Animal Behaviour*, *79*(6), 1301–1306. https://doi.org/10.1016/j.anbehav.2010.03.002

Peneaux, C., Machovsky-Capuska, G. E., Raubenheimer, D., Lermite, F., Rousseau, C., Ruhan, T., Rodger, J. C., & Griffin, A. S. (2017). Tasting novel foods and selecting nutrient content in a highly successful ecological invader, the common myna. *Journal of Avian Biology*, *48*(11), 1432–1440. https://doi.org/10.1111/jav.01456

Persson, L. (1999). Trophic cascades: Abiding heterogeneity and the trophic level concept at the end of the road. *Oikos*, *85*(3), 385. https://doi.org/10.2307/3546688

Peterson, J. A., Ode, P. J., Oliveira-Hofman, C., & Harwood, J. D. (2016). Integration of plant defense traits with biological control of arthropod pests: Challenges and opportunities. *Frontiers in Plant Science*, *7*, 1794. https://doi.org/10.3389/fpls.2016.01794

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

Pocock, M. J. O., Evans, D. M., & Memmott, J. (2012). The robustness and restoration of a network of ecological networks. *Science*, *335*(6071), 973–977. https://doi.org/10.1126/science.1214915

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, *124*(3), 243–251. https://doi.org/10.1111/oik.01719

Pompozzi, G., García, L. F., Petráková, L., & Pekár, S. (2019). Distinct feeding strategies of generalist and specialist spiders. *Ecological Entomology*, *44*(1), 129–139. https://doi.org/10.1111/een.12683

Ponton, F., Morimoto, J., Robinson, K., Kumar, S. S., Cotter, S. C., Wilson, K., & Simpson, S. J. (2020). Macronutrients modulate survival to infection and immunity in *Drosophila*. *Journal of Animal Ecology*, *89*(2), 460–470. https://doi.org/10.1111/1365-2656.13126

Provost, C., Lucas, É., & Coderre, D. (2006). Prey preference of *Hyaliodes vitripennis* as an intraguild predator: Active predator choice or passive selection? *Biological Control*, *37*(2), 148–154. https://doi.org/10.1016/j.biocontrol.2006.01.005

Quévreux, P., Barot, S., & Thébault, É. (2021). Interplay between the paradox of enrichment and nutrient cycling in food webs. *Oikos*, *130*(1), 95–109. https://doi.org/10.1111/oik.07937

Quintero, E., Isla, J., & Jordano, P. (2022). Methodological overview and data-merging approaches in the study of plant–frugivore interactions. *Oikos*, *2022*(2), oik.08379. https://doi.org/10.1111/oik.08379

Raimundo, R. L. G., Guimarães, P. R., & Evans, D. M. (2018). Adaptive networks for restoration ecology. *Trends in Ecology & Evolution*, *33*(9), 664–675. https://doi.org/10.1016/j.tree.2018.06.002

Raubenheimer, D., Lee, K. P., & Simpson, S. J. (2005). Does Bertrand's rule apply to macronutrients? *Proceedings of the Royal Society B: Biological Sciences*, *272*(1579), 2429–2434. https://doi.org/10.1098/rspb.2005.3271

Raubenheimer, D., Mayntz, D., Simpson, S. J., & Tøft, S. (2007). Nutrient-specific compensation following diapause in a predator: Implications for intraguild predation. *Ecology*, *88*(10), 2598–2608. https://doi.org/10.1890/07-0012.1

Raubenheimer, D., & Simpson, S. J. (2018). Nutritional ecology and foraging theory. *Current Opinion in Insect Science*, *27*, 38–45. https://doi.org/10.1016/j.cois.2018.02.002

Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: Toward an integrated framework. *Functional Ecology*, *23*(1), 4–16. https://doi.org/10.1111/j.1365-2435.2009.01522.x

Rendon, D., Taylor, P. W., Wilder, S. M., & Whitehouse, M. E. A. (2019). Does prey encounter and nutrient content affect prey selection in wolf spiders inhabiting Bt cotton fields? *PLoS One*, *14*(1), e0210296. https://doi.org/10.1371/journal.pone.0210296

Ruedenauer, F. A., Spaethe, J., & Leonhardt, S. D. (2015). How to know which food is good for you: Bumblebees use taste to discriminate between different concentrations of food differing in nutrient content. *Journal of Experimental Biology*, *218*(14), 2233–2240. https://doi.org/10.1242/jeb.118554

Samu, F., & Biro, Z. (1993). Functional response, multiple feeding and wasteful killing in a wolf spider (Araneae: Lycosidae). *European Journal of Entomology*, *90*, 471–476.

Saveanu, L., Manara, E., & Martín, P. R. (2017). Carrion consumption and its importance in a freshwater trophic generalist: The invasive apple snail *Pomacea canaliculata*. *Marine and Freshwater Research*, *68*(4), 752. https://doi.org/10.1071/MF15304

Schlotterer, A., Kukudov, G., Bozorgmehr, F., Hutter, H., Du, X., Oikonomou, D., Ibrahim, Y., Pfisterer, F., Rabbani, N., Thornalley, P., Sayed, A., Fleming, T., Humpert, P., Schwenger, V., Zeier, M., Hamann, A., Stern, D., Brownlee, M., Bierhaus, A., … Morcos, M. (2009). *C. elegans* as model for the study of high glucose—Mediated life span reduction. *Diabetes*, *58*(11), 2450–2456. https://doi.org/10.2337/db09-0567

Schmidt, J. M., Sebastian, P., Wilder, S. M., & Rypstra, A. L. (2012). The nutritional content of prey affects the foraging of a generalist arthropod predator. *PLoS One*, *7*(11), e49223. https://doi.org/10.1371/journal.pone.0049223

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics: Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Schoener, T. W. (1987). A brief history of optimal foraging ecology. In A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), *Foraging behavior* (pp. 5–67). Springer US. https://doi.org/10.1007/978-1-4613-1839-2_1

Scriber, J. M., & Slansky, F. (1981). The nutritional ecology of immature insects. *Annual Review of Entomology*, *26*(1), 183–211. https://doi.org/10.1146/annurev.en.26.010181.001151

Senior, A. M., Lihoreau, M., Buhl, J., Raubenheimer, D., & Simpson, S. J. (2016). Social network analysis and nutritional behavior: An integrated modeling approach. *Frontiers in Psychology*, *7*, 18. https://doi.org/10.3389/fpsyg.2016.00018

Sequeira, R., & Mackauer, M. (1992). Nutritional ecology of an insect host-parasitoid association: The pea aphid-*Aphidius ervi* system. *Ecology*, *73*(1), 183–189. https://doi.org/10.2307/1938730

Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, *30*(6), 991–1007. https://doi.org/10.1007/s10682-016-9860-5

Shik, J. Z., & Dussutour, A. (2020). Nutritional dimensions of invasive success. *Trends in Ecology & Evolution*, *35*(8), 691–703. https://doi.org/10.1016/j.tree.2020.03.009

Shimada, T., Limpus, C. J., Hamann, M., Bell, I., Esteban, N., Groom, R., & Hays, G. C. (2020). Fidelity to foraging sites after long migrations. *Journal of Animal Ecology*, *89*(4), 1008–1016. https://doi.org/10.1111/1365-2656.13157

Simmons, B. I., Cirtwill, A. R., Baker, N. J., Wauchope, H. S., Dicks, L. V., Stouffer, D. B., & Sutherland, W. J. (2019). Motifs in bipartite ecological networks: Uncovering indirect interactions. *Oikos*, *128*(2), 154–170. https://doi.org/10.1111/oik.05670

Simpson, S. J., & Raubenheimer, D. (2005). Obesity: The protein leverage hypothesis. *Obesity Reviews*, *6*(2), 133–142. https://doi.org/10.1111/j.1467-789X.2005.00178.x

Simpson, S. J., & Raubenheimer, D. (2012). *The nature of nutrition: A unifying framework from animal adaptation to human obesity*. Princeton University Press.

Skelhorn, J., & Rowe, C. (2016). Cognition and the evolution of camouflage. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1825), 20152890. https://doi.org/10.1098/rspb.2015.2890

Slansky, F. (1982). Insect nutrition: An adaptationist's perspective. *The Florida Entomologist*, *65*(1), 45. https://doi.org/10.2307/3494145

Slansky, F. (1986). Nutritional ecology of endoparasitic insects and their hosts: An overview. *Journal of Insect Physiology*, *32*(4), 255–261. https://doi.org/10.1016/0022-1910(86)90036-3

Spitz, J., Ridoux, V., & Brind'Amour, A. (2014). Let's go beyond taxonomy in diet description: Testing a trait-based approach to prey-predator relationships. *Journal of Animal Ecology*, *83*(5), 1137–1148. https://doi.org/10.1111/1365-2656.12218

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Sterner, R. W., & Elser, J. J. (2008). Ecological stoichiometry: Overview. In S. E. Jørgensen & B. D. Fath (Eds.), *Encyclopedia of ecology* (pp. 1101–1116). Academic Press.

Sterner, R. W., Elser, J. J., Chrzanowski, T. H., Schampel, J. H., & George, N. B. (1996). Biogeochemistry and trophic ecology: A new food web diagram. In G. A. Polis & K. O. Winemiller (Eds.), *Food webs* (pp. 72–80). Springer.

Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, *47*(1), 561–594. https://doi.org/10.1146/annurev.ento.47.091201.145240

Tavella, J., Windsor, F. M., Rother, D. C., Evans, D. M., Guimarães, P. R., Palacios, T. P., Lois, M., & Devoto, M. (2022). Using motifs in ecological networks to identify the role of plants in crop margins for multiple agriculture functions. *Agriculture, Ecosystems & Environment*, *331*, 107912. https://doi.org/10.1016/j.agee.2022.107912

Tercel, M. P. T. G., Moorhouse-Gann, R. J., Cuff, J. P., Drake, L. E., Cole, N. C., Goder, M., Mootoocurpen, R., & Symondson, W. O. C. (2022). DNA metabarcoding reveals introduced species predominate in the diet of a threatened endemic omnivore, Telfair's skink (*Leiolopisma telfairii*). *Ecology and Evolution*, *12*(1), e8484. https://doi.org/10.1002/ece3.8484

Tercel, M. P. T. G., Symondson, W. O. C., & Cuff, J. P. (2021). The problem of omnivory: A synthesis on omnivory and DNA metabarcoding. *Molecular Ecology*, *30*(10), 2199–2206. https://doi.org/10.1111/mec.15903

Thébault, E., & Loreau, M. (2003). Food-web constraints on biodiversity–ecosystem functioning relationships. *Proceedings of the National*

Academy of Sciences of the United States of America, *100*(25), 14949–14954. https://doi.org/10.1073/pnas.2434847100

Timberlake, T. P., Cirtwill, A. R., Baral, S. C., Bhusal, D. R., Devkota, K., Harris-Fry, H. A., Kortsch, S., Myers, S. S., Roslin, T., Saville, N. M., Smith, M. R., Strona, G., & Memmott, J. (2022). A network approach for managing ecosystem services and improving food and nutrition security on smallholder farms. *People and Nature*, *4*(2), 563–575. https://doi.org/10.1002/pan3.10295

Traveset, A., Olesen, J. M., Nogales, M., Vargas, P., Jaramillo, P., Antolín, E., Trigo, M. M., & Heleno, R. (2015). Bird–flower visitation networks in the Galápagos unveil a widespread interaction release. *Nature Communications*, *6*(1), 6376. https://doi.org/10.1038/ncomms7376

Turesson, H., Persson, A., & Brönmark, C. (2002). Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. *Ecology of Freshwater Fish*, *11*(4), 223–233. https://doi.org/10.1034/j.1600-0633.2002.00019.x

Vaughan, I. P., Gotelli, N. J., Memmott, J., Pearson, C. E., Woodward, G., & Symondson, W. O. C. (2018). econullnetr: An R package using null models to analyse the structure of ecological networks and identify resource selection. *Methods in Ecology and Evolution*, *9*(3), 728–733. https://doi.org/10.1111/2041-210X.12907

Wagner, N. D., Hillebrand, H., Wacker, A., & Frost, P. C. (2013). Nutritional indicators and their uses in ecology. *Ecology Letters*, *16*(4), 535–544. https://doi.org/10.1111/ele.12067

Weyman, G. S. (1993). A review of the possible causative factors and significance of ballooning in spiders. *Ethology Ecology & Evolution*, *5*(3), 279–291. https://doi.org/10.1080/08927014.1993.9523016

Wiggins, W. D., & Wilder, S. M. (2022). Carbohydrates complement high-protein diets to maximize the growth of an actively hunting predator. *Ecology and Evolution*, *12*(8), e9150. https://doi.org/10.1002/ece3.9150

Wilder, S. M., Holway, D. A., Suarez, A. V., LeBrun, E. G., & Eubanks, M. D. (2011). Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(51), 20639–20644. https://doi.org/10.1073/pnas.1115263108

Wilder, S. M., Norris, M., Lee, R. W., Raubenheimer, D., & Simpson, S. J. (2013). Arthropod food webs become increasingly lipid-limited at higher trophic levels. *Ecology Letters*, *16*(7), 895–902. https://doi.org/10.1111/ele.12116

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A., & Warren, P. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*(7), 402–409. https://doi.org/10.1016/j.tree.2005.04.005

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

Zaguri, M., Kandel, S., Lavie, N., & Hawlena, D. (2022). Methodological limitations and conceptual implications of nutritional estimations. *Oikos*, *2022*(7), oik.08467. https://doi.org/10.1111/oik.08467

Zaguri, M., Kandel, S., Rinehart, S. A., Torsekar, V. R., & Hawlena, D. (2021). Protein quantification in ecological studies: A literature review and empirical comparisons of standard methodologies. *Methods in Ecology and Evolution*, *12*(7), 1240–1251. https://doi.org/10.1111/2041-210X.13601

Zhang, S., Zhang, Y., & Ma, K. (2012). Disruption of ant-aphid mutualism in canopy enhances the abundance of beetles on the forest floor. *PLoS One*, *7*(4), e35468. https://doi.org/10.1371/journal.pone.0035468

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Detailed description of the empirical data.

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