Bridging nutritional geometry and network ecology to quantify the robustness of nutritional networks

Jordan P. Cuff[1+], Raul Costa-Pereira[2], Maximilian P.T.G. Tercel[3,4], Brooke Zanco[5], Juliano Morimoto[6,7], Finlay Ryder[8], Colin M. Lynch[9], Ian P. Vaughan[8], Sheena Cotter[10], Beatrice Dale[11], Rosy Christopher[1], Fredric M. Windsor[8]

[1]School of Natural and Environmental Sciences, Newcastle University, Newcastle-upon-Tyne, United Kingdom

[2]Universidade Estadual de Campinas, Campinas, São Paulo, Brazil

[3]CEFE, University of Montpellier, CNRS, EPHE, IRD, Montpellier, France

[4]CIBIO-InBIO, Universidade do Porto, Vairão, Portugal

[5]Pollinator Futures Research Centre, Macquarie University, Australia

[6]Institute of Mathematics, University of Aberdeen, Aberdeen, United Kingdom

[7]Universidade Federal do Paraná, Curitiba, Brazil

[8]School of Biosciences, Cardiff University, Cardiff, United Kingdom

[9]School of Complex Adaptive Systems, Arizona State University, Tempe, AZ, USA

[10]School of Natural Sciences, University of Lincoln, Lincoln, United Kingdom

[11]School of Geography and Natural Sciences, Northumbria University, Newcastle-upon-Tyne, United Kingdom

[+]Corresponding author at jordancuff@gmail.com

Abstract

Understanding the robustness and resilience of ecological networks is key to managing ecosystems and mitigating biodiversity loss. Simple models of network robustness simulate species losses across ecological networks but lack physiological realism, asserting that species persist if they interact with another organism. This neglects the nutritional consequences of resource loss and nutrition as a key driver of interactions. Defining how nutrition drives the robustness of ecological networks requires a fundamental understanding of how nutrition drives fitness, which nutritional geometry offers.

Here, we discuss the potential for bridging nutritional geometry and network ecology to define the thresholds for nutrition-mediated secondary extinctions in networks and, subsequently, nutritional network robustness. Through this integration, nutritional status can be quantified across scales, from individuals to ecosystems. Network rewiring in this context provides a mechanistic basis for predicting shifts in trophic interactions and their subsequent implications for energy and nutrient flow. We present a framework that integrates nutritional geometry and network ecology by combining individual-based geometric approaches with broader network-based analyses, which is currently underexplored. Our hope is that this can advance collaboration across nutritional geometry and network ecology to enhance our understanding of how nutrition drives the structure and health of ecosystems.

Keywords: biodiversity loss, ecosystem stability, food web, geometric framework of nutrition, resilience, rewiring

Introduction

Network ecology can characterise complex biological systems by employing graph theory and other mathematical concepts to quantify the structural properties of biotic interactions across space and time (May, 1972; Montoya et al., 2006). Ecological networks are usually constructed based on empirical field data describing ecological interactions such as predation, collected using methods ranging from direct observation to DNA-based detection (Bascompte, 2007; Cuff et al., 2022). In these ecological networks, nodes, which can represent a diversity of ecological elements (e.g., individuals, species, functional groups, ecosystem services; Dee et al., 2017; Lau et al., 2017; Proulx et al., 2005), are connected by links which represent the ecological interactions themselves (e.g., herbivory, mutualism, predation, parasitism and competition). These networks typically represent species, with the links between them most often indicating the flow of resources via feeding (Montoya et al., 2006). The aim of constructing these networks is to represent the complexity of interactions underway in an ecosystem and how they are structured, with an expectation that this representation is accurate, but rarely if ever totally complete (Jordano, 2016).

A key property of networks is their ‘robustness’ to the loss of species, quantified as the number of ‘secondary’ extinctions that an initial, ‘primary’ loss incurs (i.e., nodes lost as a result of losing their resources; Bascompte, 2009; Kaiser-Bunbury et al., 2010; Staniczenko et al., 2010). Predicting how ecological networks respond to loss, particularly through trophic cascades and eventual ecosystem collapse, is particularly valuable for prioritising conservation actions and managing ecosystem functions (Canning & Death, 2017; Petsopoulos et al., 2021). Classic models of robustness have, however, been based solely on whether affected species retain any observed interactions with any other resource node in the network (Dunne et al., 2002; Kaiser-

Bunbury et al., 2010; Memmott et al., 2004; Olesen et al., 2008). The loss of a resource could result in its consumers switching resources, represented in networks through 'rewiring', which is the capacity for consumer nodes to connect to novel resources to mitigate their loss of interactions and to persist within the ecological network. Consumers may otherwise simply lose that resource interaction, with potentially negative physiological consequences. Current robustness analyses neglect these consequences, therefore lacking physiological realism and neglecting the prevalent nutritional and, ultimately, fitness consequences of resource changes, potentially overestimating network robustness (Cuff, Evans, et al., 2024). It is vital that we can understand and predict rapidly changing ecological networks under multiple stressors, including climate change and biodiversity loss, which threaten the stability of ecosystems (Ward et al., 2026; Woodward et al., 2010).

A nutritional perspective on ecological networks considers how nutrients flow through ecosystems and how these nutrients structure interaction networks (Cuff, Evans, et al., 2024). By weighting links in a network according to the relative transfer of nutrients between resources and consumers (i.e., nutrient intake), the structure of networks can be viewed through the lens of nutrient flow. This can elucidate mechanisms that structure ecological interactions across levels of biological organisation, from organism-level processes like nutrient-specific foraging (Cuff, Tercel, et al., 2024; Mayntz et al., 2005) to ecosystem-level properties like nutrient limitation and/or dilution (Kaspari & Welti, 2024; Kearney et al., 2010). Importantly, revealing how nutrition could determine network robustness requires a basic understanding of how nutrition drives the fitness of individuals within those networks, which is not available from ecological nor nutritional networks themselves. Other analytical frameworks, including nutritional geometry, can offer this information (Krabbe et al., 2019; Moatt et al., 2019; Raubenheimer et al., 2009).

The geometric framework of nutrition (GFN) is a quantitative multidimensional framework for understanding how animals balance their intake of multiple nutrients simultaneously, extending beyond traditional single-nutrient studies (Raubenheimer & Simpson, 1993; Simpson et al., 2004; Simpson & Raubenheimer, 1993, 2012). Nutritional geometry studies often assess how the performance of populations is affected by specific nutritional conditions or how those populations navigate nutritional choices and trade-offs, directly linking nutrition to fitness (Harrison et al., 2014; Simpson & Raubenheimer, 2012). The disparity between ecological interaction studies, which typically concern communities, and nutritional geometry, which typically concerns populations, has been acknowledged. Frameworks based on agent-based, state-space and multi-scale modelling of nutrition have been proposed to overcome this (Simpson et al., 2010), but these are complex and computationally demanding, and progress has been slow. Senior et al. (2016) used a similar approach to demonstrate the importance of nutrition for the structure of social interactions, for example. Ultimately though, the integration of nutritional geometry into ecological and nutritional networks for the analysis of nutritional network robustness requires the development of a bespoke approach.

Here, we propose a novel framework to quantify nutritional network robustness across dimensions of nutritional variation and scales of biological organisation. We highlight the methodological process required to bridge nutritional networks and nutritional geometry, the data requirements and the constraints imposed by this approach, alongside future pathways to addressing these constraints. Moreover, we outline how this can be extended through the inclusion of network rewiring, here determined based on the nutritional feasibility of those interactions (i.e., fulfilment of consumer nutritional niches). We also discuss the need for increased collaboration between nutritional ecologists and network scientists to unlock the full potential of nutritional network robustness analysis. We focus on bipartite networks in which the simulated removal of resources can trigger consumer secondary extinctions, but the concept could also be applied to more complex networks without strict consumer and resource groups. By quantifying nutritional network robustness, we offer a physiologically grounded framework for predicting future ecological interactions and identifying ecosystems vulnerable to collapse that may benefit from conservation management.

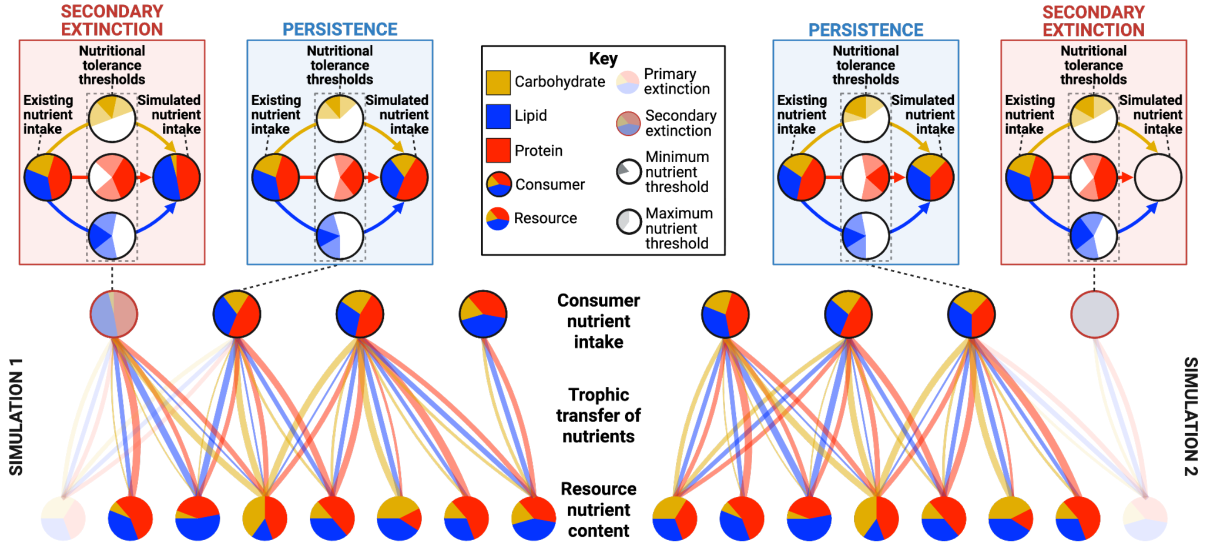

Figure 1: The mechanism by which nutritional network robustness can be determined. With the simulated removal of a node in the network, the proportional nutrient intake of its consumers will change. If nutrient intake proportions, represented by the interactions that consumer is observed engaging in, exceed the minimum and maximum proportion of any one nutrient, the fitness or survival of that node is considered to be compromised, resulting in its secondary extinction. Through iterative simulated removal of different nodes, and different numbers of nodes, the vulnerability of the network to secondary extinctions can be quantified. Created in BioRender. https://BioRender.com/gl8ywts

The conceptual underpinnings of nutritional network robustness

At its core, our concept of nutritional network robustness describes the resilience of nutritional balancing in an ecosystem following the loss of its organisms (species, taxa or individuals, depending on the network). Following the simulated loss of resources in a network, two scenarios are possible: i) a consumer maintains interactions with resources that fall within its nutritional niche and persists in the network; or ii) where the loss of resources cause a consumer's nutritional intake to fall outside its nutritional niche (i.e., the long-term fitness of that consumer is compromised), the consumer is considered a secondary extinction and is lost from the network (Figure 1; but see section on ‘rewiring’ below). The rate of secondary extinctions proportional to the primary removal of nodes in the network determines the robustness of the nutritional network (as in existing measures of ecological network robustness; Ávila-Thieme et al., 2023; Keyes et al., 2024). In essence, using this framework, we can predict how resilient the flow of nutrients through an ecosystem is to perturbation and biodiversity loss based on the ability of its consumers to meet their nutritional needs following resource loss.

Whilst the concept is relatively intuitive, the analysis is more complex. In order to assess the robustness of a nutritional network, we need three datasets: (i) the interaction network of organisms within the focal system; (ii) the nutrients transferred in those interactions (for which resource nutrient content and the frequency of interactions can be used as a proxy); and (iii) the consumer’s nutritional niche (i.e., the optimal proportion of nutrient intake that maximises fitness and therefore persistence in the network). The nutritional network concept has so far successfully integrated components (i) and (ii) (Cuff, Evans, et al., 2024), but (iii) is somewhat more insidious within the context of field ecology, where these networks are most useful. The consumer’s optimal nutritional niche can, however, be derived from experimental work undertaken within various frameworks, among which nutritional geometry is arguably the most developed and applicable (Raubenheimer et al., 2009; Simpson & Raubenheimer, 2012).

By quantifying shifts and trends in the balance of nutrients animals seek, the GFN allows exploration of the behavioural, physiological and broader ecological drivers of this balance, but also how animals navigate trade-offs and translate nutrition into performance (e.g., fitness, growth, reproduction; Fanson et al., 2009; Lee et al., 2008; Morimoto & Lihoreau, 2019; Rapkin et al., 2018; Simpson et al., 2004). Central to GFN is the ‘intake target’ of a consumer, which is the balance of nutrients required to optimise fitness or an alternative performance metric (Simpson & Raubenheimer, 1993, 1995), and the ‘rules of compromise’, which determine how organisms will prioritise intake when their intake target cannot be reached. Together, these measurements comprise the optimal nutritional niche and the fitness consequences of falling outside of it.

The intake target of a given species may change drastically depending on life stage (Boggs, 2009), reproductive cycle (Ashworth et al., 2009), seasonality (Irwin et al., 2015), locality (Zanco et al., 2025), metabolic rate (Huey & Kingsolver, 2019), developmental environment (Zanco et al., 2026) and other factors which impact the nutritional needs of individuals. Surrounding this is the wider nutritional niche, which defines the limits beyond which dietary intake may deleteriously compromise long-term fitness or survival of the consumer and therefore their persistence (Machovsky-Capuska et al., 2016). Within nutritional geometry, this nutritional niche is often represented as a ‘performance landscape’ in which a ‘response surface’ represents the multidimensional nutritional space within which a consumer’s fitness varies with nutrient intake (Simpson et al., 2004). These data crucially provide the information necessary to define the nutritional proportions a consumer would require in order to remain in an ecological network (Shik et al., 2018, 2020).

Animals rarely achieve their optimal intake target in natural systems (indeed, there is no singular ‘global’ optimal intake target since it can be defined based on different components of fitness that prioritise different nutrients). Nutritional deficiencies are continuously redressed through nutrient-specific foraging (Kohl et al., 2015; Mayntz et al., 2005), especially in generalist consumers, which are thought to remain in a nutritionally suboptimal state (Symondson et al., 2002). Nutritional geometry studies are typically conducted in controlled *ex situ* feeding trials, where a range of artificial food mixes can be formulated and their intake can be directly observed (Simpson & Raubenheimer, 1995). The focus on the quantities consumed in such feeding trials has, however, focused nutritional geometry particularly on lab-based studies, whereas direct translation of these workflows and their results to field-based studies is difficult, particularly due to difficulties in measuring the quantities of nutrients consumed (Raubenheimer, 2011; Raubenheimer & Simpson, 2020). The development of analytical approaches which allow diets and resources to be represented as proportional nutrient mixtures irrespective of amounts when absolute nutrient intakes cannot be measured directly (Raubenheimer, 2011; Lynch et al. submitted) arguably provide a bridge between the estimation of nutritional niches and their maintenance in field-based ecological networks.

By assessing the flow of nutrients between resources and consumers, our conceptual framework for nutritional network robustness builds upon the existing nutritional network concept. To assess alignment of nutrient intake with optimal nutritional niches, nutritional network robustness analyses will likely be most easily implemented by comparing the nutritional proportions of observed intake relative to the optima, rather than absolute quantities. The use of absolute quantities of nutrients could be integrated to assess the ability of consumers to meet their nutritional needs, but would require significant effort and data quality not typically possible for field studies. Direct observation of feeding in the field can miss cryptic interactions, and even molecular methods for detecting interactions (e.g., dietary metabarcoding) neglect nutritionally important contexts, like the life stages, tissue types and biomass of resources post-consumption (Cuff et al., 2022). This, paired with difficulties inferring the nutrient content of the tissue consumed, and the lack of continuous data on interactions in the field (Lynch et al., 2025), can heavily skew estimation of the amounts consumed. Nutritional network robustness analysis would therefore most simply represent nutrient intake as 0-1 bounded proportions of the nutrients obtained from resources.

A methodological framework for nutritional network robustness analysis

We propose a multi-stage workflow that can be used to achieve our vision of nutritional network robustness analysis, split into four discrete phases: (i) field surveys (Figure 2A); (ii) post-hoc laboratory analyses (Figure 2C); (iii) *ex situ* experimentation (Figure 2D); and (iv) data integration and analysis (Figure 2B, E, F).

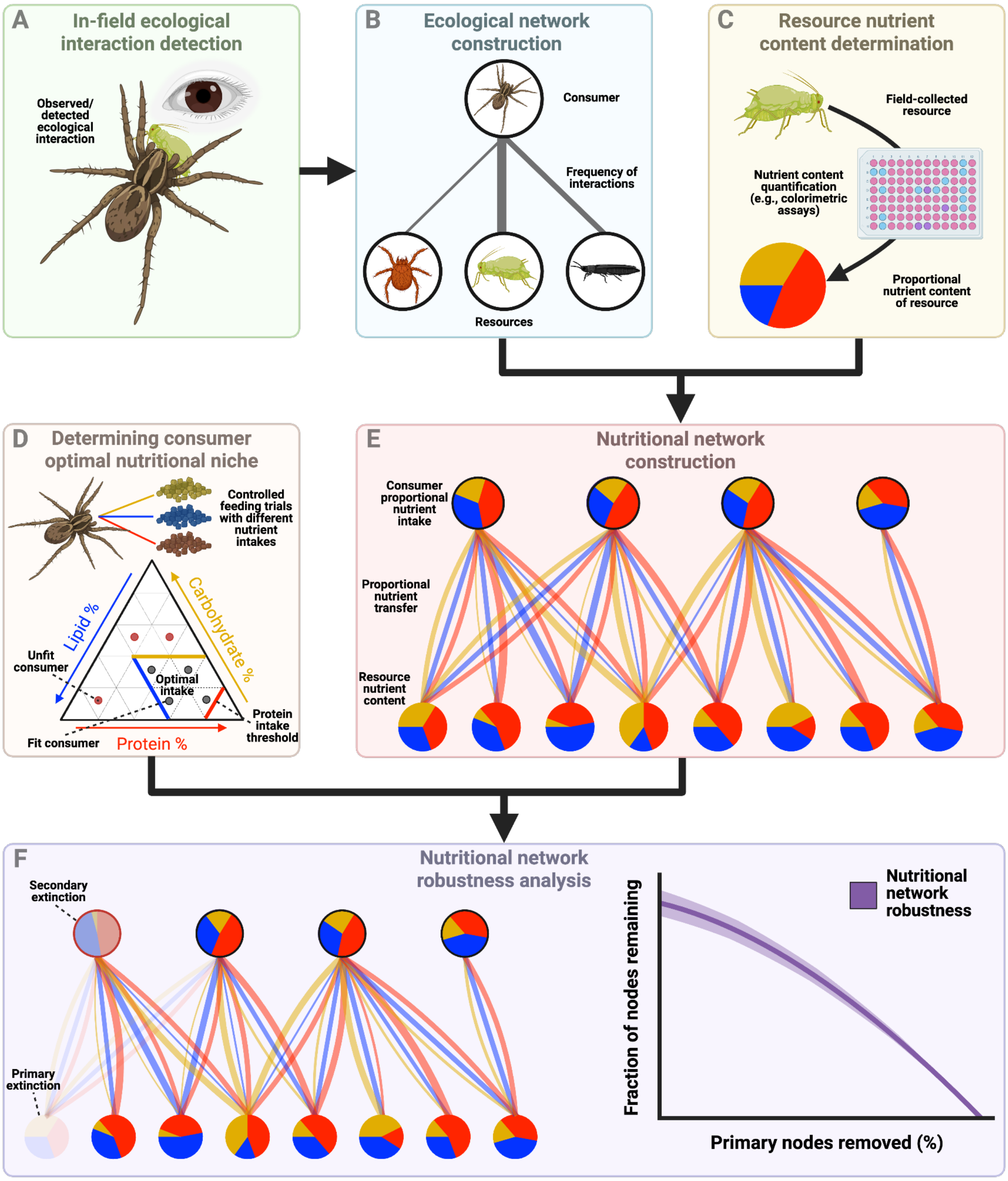

Figure 2: A proposed workflow for quantifying nutritional network robustness. Ecological interactions must first be detected or observed (A) in order to construct an ecological network (B). The resource nutrient content can then be determined (or, ideally, consumer nutrient intake/uptake; C) to construct a nutritional network in which interactions are modulated by nutritional proportions (E). Optimal nutritional niche thresholds can then be determined for each consumer based on the effects of different proportional nutrient intakes on fitness or survival (and thus their persistence in the network; here, represented by a constrained equilateral mixture triangle; D). These thresholds can be used to determine secondary extinctions following simulated removal of nodes within the network (Figure 1; F). It is expected that this will present a less conservative measure of network robustness given that research quality as well

as loss will drive secondary extinctions. Created in BioRender. https://BioRender.com/gl8ywts

The field survey component of this workflow can largely mirror any existing approach to ecological network construction, often involving direct observation or remote sensing of ecological interactions (Cuff et al., 2022; Dawson et al., 2026), or post-hoc molecular or isotopic analyses (Mata et al., 2021; Wise et al., 2006). To complete nutritional network construction, the transfer of nutrients between resources and consumers must be quantified. Resource nutrient content can closely align with consumer nutrient intake (Wilder et al., 2019) and may be much more convenient to determine in most field contexts (Cuff et al., 2021), especially when interactions are cryptic. This, so far, mirrors the workflow required for nutritional network analysis (Cuff, Evans, et al., 2024).

The extension of the nutritional network concept to address robustness then requires integration of optimal nutritional niches based on the proportions of nutrients that a consumer requires to achieve optimal fitness (i.e., through which they can persist within the network). These optimal nutritional niches are multidimensional (i.e., dimensions = nutrients) and can be derived from nutritional geometry (Machovsky-Capuska et al., 2016). Using empirical no-choice *ex situ* feeding trials for each consumer in the network, it is possible to determine the intake target of each consumer, and the nutritional niche breadth that they can occupy without encountering deleterious fitness effects that would impact their ability to persist in the network long-term (Simpson et al., 2004; Simpson & Raubenheimer, 1995; Shik et al., in press). The observed nutrient intake of consumers in the field (their realised nutritional niche) will usually represent different proportions within this fundamental nutritional niche (i.e., the range of nutrient balances a consumer can persist on). Where it is difficult or impossible to conduct these feeding trials for all consumer nodes in a network, it is likely that some inferences can be made based on phylogenetic relationships (Morimoto, 2024). This phylogenetic approach does, however, demand caution since physiology and phylogeny can diverge (Shik & Dussutour, 2020), and changes in resource nutrient content and consumer requirements (e.g., under climate change) might decouple historical associations based on relatedness, resource quality, consumer traits and performance (Zanco et al., under review).

Once the nutritional niches of consumers are known, their estimated nutrient intake in the field can be compared to their niches to ascertain whether the baseline network satisfies the nutritional niches of the consumers. It is expected that the nutrient intake of most consumers will already exist within their nutritional niche. If consumers fall outside their nutritional niches in the empirical network, this may indicate that the consumers sampled were redressing nutritional deficits (which may be addressed through more sampling of individuals with different recent feeding histories), that they are already in a suboptimal state of fitness (which could indicate an ‘extinction debt’) or that there are limiting nutrients that they are unable to sense or access, all of which may reduce nutritional network robustness sharply. Many of these problems may be common in individual-level networks, but less prevalent when aggregating interactions across individuals within populations, which is likely to generate a more holistic and stable interpretation of realised niche.

Before any robustness analyses, the difference between the consumer’s intake target and the nutrients available to them can be used to quantify their ‘nutritional fit’ (i.e., the likelihood of the consumer meeting its intake target by chance within the studied network) and their ‘nutritional vulnerability’ (i.e., the inverse of nutritional fit - the likelihood of the consumer failing to satisfy their nutritional niche within the studied network), both of which could be estimated through integration with prey availability-based null network models (e.g., ‘econullnetr’; Vaughan et al., 2018). At its simplest, this would require several assumptions to be made, including that all resources are accessible (e.g., biomechanically) and findable (e.g., recognisable cues), although constraints could be imposed on simulations based on empirical or theoretical compatibility data. Complementarity analyses could be used alongside robustness analyses to compare the nutritional landscape (i.e., the breadth and relative abundance of available resources) to consumer nutritional niches across extinction simulations for each consumer. A dissimilarity metric (e.g., Euclidean distance) comparing nutritional landscapes and niches might highlight how easily compromised a consumer’s complementarity to the nutritional landscape is. Similarly, inspecting how the removal of each resource taxon impacts these metrics may identify which taxa disproportionately shape the nutritional landscape. This is most likely for those resources with proportional nutrient contents at the periphery of the nutritional landscape, the loss of which may prevent consumers reaching some nutrient intake proportions (C. Lynch et al., 2025).

Nutritional network robustness can be quantified by randomly (or non-randomly; e.g., by order of connectance to establish ‘best’ and ‘worst’ case scenarios) simulating the removal of nodes (beginning with one, but increasing the number of nodes lost iteratively until all nodes are removed). With each simulated removal, the nutrient intake of each consumer will be updated, and this simulated nutrient intake can be compared against that consumer’s nutritional niche to determine whether they would maintain fitness and persist in the network. Where a consumer is unable to maintain optimal fitness, it would be considered a secondary extinction, and would therefore be removed from the network. The number of secondary extinctions relative to primary extinctions across iterative permutations of different resource loss sequences can then be used to determine nutritional network robustness based on the normalised area under the extinction curve (i.e., how readily secondary extinctions occur following primary extinctions). This comparison of primary and secondary extinctions is standard for other ecological network robustness analyses. In most cases, a robustness value of 1 is considered a highly robust network, whereas a value of 0 is deemed highly fragile (although value ranges will differ across approaches).

Extending nutritional network robustness through rewiring

Whilst understanding the robustness of nutritional networks will be key in highlighting the capacity of ecosystems to support the persistence of their extant fauna, foraging processes are not static (Bartley et al., 2019; Marjakangas et al., 2025; Vizentin-Bugoni et al., 2020). Some consumers may respond to nutritional change reproductively; for example, social bees may produce more workers in response to nutritional changes (Kaluza et al., 2018; Zheng et al., 2014). Others may extend their foraging ranges to seek alternative resources (Covich, 1976; Owen-Smith et al., 2010). Many consumers will, however, redress nutritional deficits through compensatory feeding (i.e., nutrient-specific foraging; Kohl et al., 2015; Mayntz et al., 2005), prey switching is an expected outcome of the loss of species within a network (Bergerud, 1983). Networks will therefore ‘rewire’ (i.e., change structure through redistribution of interactions) in response to perturbation (Ward et al., 2026). Importantly, this may not solely be the redistribution of interactions to novel resources (i.e., expansion of their trophic niche), but also the more intensive use of existing resources (i.e., ‘re-weighting’ of links within the network), especially if those resources are readily available and generally nutritionally balanced or complementary to most of the consumer’s other resources. This may, however, incur deleterious effects, such as excessive consumption of plant secondary compounds, which could limit the potential for re-weighting, or, alternatively, lead to increased specialisation towards specific resources and/or selective pressure on key detoxification pathways (Zanco et al., under review).

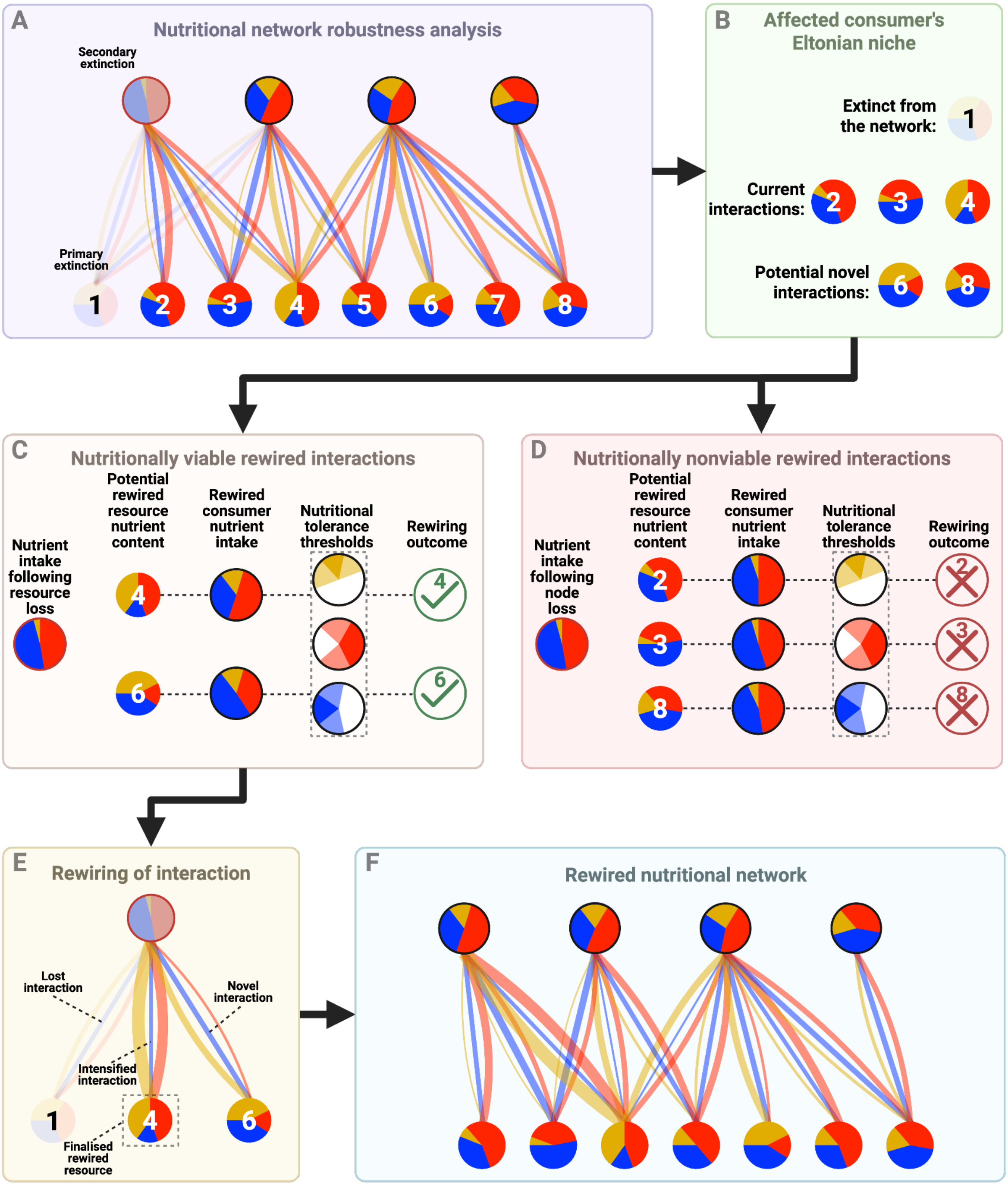

Figure 3: A proposed workflow for the simulation of nutritional network rewiring following resource loss in robustness analyses. Following identification of potential secondary extinctions during the first phase of nutritional network robustness analysis (Figure 1, Figure 2; A), all of the resources available and accessible to consumers facing secondary extinction should be identified (i.e., its fundamental Eltonian niche, defined by the probability of interaction based on morphological and ecological traits or known interactions; B). Based on whether these resources can rebalance the consumer's nutrient intake to a range within its nutritional niche, these resources can be considered viable for rewiring (C, D). If sufficiently available, it is intuitive that consumers will intensify use of resources they already interact with (E), unless there are potential associated deleterious effects (e.g., toxins). This will more dynamically represent the robustness of nutritional networks by accounting for resource switching through a physiologically-grounded approach (F). Created in BioRender. https://BioRender.com/gl8ywts

Rewiring provides a more conservative measure of network robustness, leading to greater-than-expected robustness by accounting for interaction switching (Timóteo et al., 2016). In the context of nutritional networks, rewiring could be incorporated into robustness estimates by allowing each ecological interaction with an extinct resource to be redistributed to an alternative resource (i.e., mechanistically, a standard approach to rewiring), ideally based on the availability of resources to the consumer. By fixing the degree of each consumer based on the empirical network, the number of interactions should remain realistic, although more open-ended approaches may represent more dynamic changes to ecological networks. The resources to which interactions can be redistributed should be based on the broader fundamental Eltonian niche of the consumer, taking into account not only nutrition, but also the broader feasibility of the interaction based on foraging behaviour (Michalko et al., 2021; Semenyuk & Tiunov, 2019), morphology (Brose et al., 2005, 2019), biomechanics (Cuff, Labonte, et al., 2024) and other potential interaction constraints. Such data are readily available from some open-source databases (e.g., Pekár et al., 2021; Ridgway & Wesner, 2025), but may otherwise require additional study to parameterise. By filtering potential interactions to those resources that would maintain a nutrient intake within the consumer's nutritional niche (and randomly assigning interactions if multiple resources satisfy these criteria), physiologically-informed network rewiring could be used to generate a potentially more realistic measure of nutritional network robustness. Crucially, this could be used to predict likely interactions following perturbation, with significant value in conservation and biodiversity management. Similarly, and separately, these rewiring rules could be used to predict the interactions of consumers in entirely new environments, such as invasive species upon first arriving at a new location, or the reintroduction of a taxon to a region where it has become locally extinct.

Rewiring of nutritional networks will likely reflect the nutritional redundancy of resources within a network. If many resources overlap in their nutrient content, the loss of one or few such resources is unlikely to result in many secondary extinctions if those interactions can be rewired to nutritionally similar resources. This may align with the phylogenetic relationship between resources in the network, with closely related taxa likely sharing similar ecologies, nutritional profiles, and, indeed, optimal intakes (Burns & Strauss, 2011; Morimoto, 2024; Simpson & Raubenheimer, 1993; although life stage differences will also introduce variation; Raubenheimer et al., 2022; Wilder & Eubanks, 2010), but also possibly being similarly vulnerable to extinction (González-del-Pliego et al., 2019; Verde Arregoitia et al., 2013).

If there are few resources particularly rich in specific nutrients, their loss may be difficult, if not impossible, to substitute nutritionally through redistribution of that interaction to alternative resources; for example, if the only lipid-rich resource in the network is lost, a consumer may not be able to redress this balance through feeding on the otherwise lipid-poor resources available. This could be used to identify nodes with significant leverage over the robustness of nutritional networks (and therefore potential conservation or management targets). In such cases, interaction with a greater number of resources could redress the incurred nutritional imbalance, but this may create unrealistically high node degrees for consumers. More complex models of network rewiring could, in such cases, allow for redistribution of interactions with extant resources to redress any imbalances, leading to more widespread rewiring of networks and potentially cascading impacts to competition and predation pressure; for example, following the loss of a protein-rich resource, a consumer's existing interactions with protein-poor resources may be rewired to more balanced resources. This would potentially enhance our understanding of complex community-wide nutritional dynamics and their interactions with fitness and physiology.

Conclusions

Understanding how nutrition determines the stability of ecological networks and wider ecosystems would represent a significant advance to our understanding of community ecology, biodiversity loss and ecosystem collapse. The framework we have suggested could provide this insight, but crucially requires the bridging of network science and nutritional geometry. Through this integration, the fitness and physiology of individual organisms can be related to the structure of interaction networks to determine the capacity of ecosystems to support the persistence of their extant fauna. Importantly, this same framework could be used to assess how the changing prevalence of antinutrients (i.e., toxins such as plant secondary metabolites; Zanco et al., under review) similarly impacts the persistence of nodes and the robustness of ecological networks. Through increased collaboration between network ecologists and nutritional geometrists, but also increased accessible and open sharing of data within these domains (Morimoto & Lihoreau, 2020), this framework can be readily implemented to a range of contexts and systems, offering valuable insight into the resilience of ecosystems to biodiversity loss and wider perturbations.

Author contributions

Jordan P. Cuff: Conceptualisation; visualisation; writing – original draft; writing – review and editing. Raul Costa-Pereira: Writing – review and editing. Maximilian P.T.G. Tercel: Writing – review and editing. Brooke Zanco: Writing – review and editing. Juliano Morimoto: Writing – review and editing. Finlay Ryder: Writing – review and editing. Colin M. Lynch: Writing – review and editing. Ian P. Vaughan: Writing – review and editing. Sheena Cotter: Writing – review and editing. Beatrice Dale: Writing – review and editing. Rosy Christopher: Writing – review and editing. Fredric M. Windsor: Conceptualisation; writing – review and editing.

Acknowledgments

JPC and RCP were funded by a NERC Global Partnerships Seedcorn Fund (NE/C003246/1), co-funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP). JPC was also funded by a Newcastle University Academic Track Fellowship. MPTGT received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 857251 - BIOPOLIS Fellowship. FR was funded by the James Pantyfedwen Foundation. For the purpose of open access, the author has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

Data availability

No data were generated nor used for this manuscript.

References

Ashworth, C. J., Toma, L. M., & Hunter, M. G. (2009). Nutritional effects on oocyte and embryo development in mammals: Implications for reproductive efficiency and environmental sustainability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1534), 3351–3361. https://doi.org/10.1098/rstb.2009.0184

Ávila-Thieme, M. I., Kusch, E., Corcoran, D., Castillo, S. P., Valdovinos, F. S., Navarrete, S. A., & Marquet, P. A. (2023). NETWORKEXTINCTION: An R package to simulate extinction propagation and rewiring potential in ecological networks. *Methods in Ecology and Evolution*, *14*(8), 1952–1966. https://doi.org/10.1111/2041-210X.14126

Bartley, T. J., McCann, K. S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M. M., MacDougall, A. S., Tunney, T. D., & McMeans, B. C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, *3*(3), 345–354. https://doi.org/10.1038/s41559-018-0772-3

Bascompte, J. (2007). Networks in ecology. *Basic and Applied Ecology*, *8*(6), 485–490. https://doi.org/10.1016/j.baae.2007.06.003

Bascompte, J. (2009). Disentangling the Web of Life. *Science*, *325*(5939), 416–419. https://doi.org/10.1126/science.1170749

Bergerud, A. T. (1983). Prey Switching in a Simple Ecosystem. *Scientific American*, *249*(6), 130–141.

Boggs, C. L. (2009). Understanding insect life histories and senescence through a resource allocation lens. *Functional Ecology*, *23*(1), 27–37. https://doi.org/10.1111/j.1365-2435.2009.01527.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

Brose, U., Cushing, L., Berlow, E. L., Jonsson, T., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cohen, J. E., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Knapp, R. A., Ledger, M. E., Memmott, J., … Martinez, N. D. (2005). BODY SIZES OF CONSUMERS AND THEIR RESOURCES: *Ecological Archives E086-135*. *Ecology*, *86*(9), 2545–2545. https://doi.org/10.1890/05-0379

Burns, J. H., & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences*, *108*(13), 5302–5307. https://doi.org/10.1073/pnas.1013003108

Canning, A. D., & Death, R. G. (2017). Trophic cascade direction and flow determine network flow stability. *Ecological Modelling*, *355*, 18–23. https://doi.org/10.1016/j.ecolmodel.2017.03.020

Covich, A. P. (1976). Analyzing Shapes of Foraging Areas: Some Ecological and Economic Theories. *Annual Review of Ecology and Systematics*, *7*, 235–257.

Cuff, J. P., Evans, D., Vaughan, I., Wilder, S., Tercel, M., & Windsor, F. (2024). Networking nutrients: How nutrition determines the structure of ecological networks. *Journal of Animal Ecology*, *93*(8), 974–988. https://doi.org/10.1111/1365-2656.14124

Cuff, J. P., Labonte, D., & Windsor, F. M. (2024). Understanding Trophic Interactions in a Warming World by Bridging Foraging Ecology and Biomechanics with Network Science. *Integrative And Comparative Biology*, *64*(2), 306–321. https://doi.org/10.1093/icb/icae070

Cuff, J. P., Tercel, M. P. T. G., Vaughan, I. P., Drake, L. E., Wilder, S. M., Bell, J. R., Müller, C. T., Orozco-terWengel, P., & Symondson, W. O. C. (2024). Prey nutrient content is associated with the trophic interactions of spiders and their prey selection under field conditions. *Oikos*, e10712. https://doi.org/10.1111/oik.10712

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., 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

Dawson, W., Evans, D. M., Abrahams, C., Kitson, J. J. N., Collins, L., & Cuff, J. P. (2026). Ecoacoustics for context-rich direct and indirect trophic interaction data and ecological network construction. *Methods in Ecology and Evolution*, 2041-210x.70288. https://doi.org/10.1111/2041-210x.70288

Dee, L. E., Allesina, S., Bonn, A., Eklöf, A., Gaines, S. D., Hines, J., Jacob, U., McDonald-Madden, E., Possingham, H., Schröter, M., & Thompson, R. M. (2017). Operationalizing Network Theory for Ecosystem Service Assessments. *Trends in Ecology & Evolution*, *32*(2), 118–130. https://doi.org/10.1016/j.tree.2016.10.011

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Fanson, B. G., Weldon, C. W., Pérez-Staples, D., Simpson, S. J., & Taylor, P. W. (2009). Nutrients, not caloric restriction, extend lifespan in Queensland fruit flies (*Bactrocera tryoni*). *Aging Cell*, *8*(5), 514–523. https://doi.org/10.1111/j.1474-9726.2009.00497.x

González-del-Pliego, P., Freckleton, R. P., Edwards, D. P., Koo, M. S., Scheffers, B. R., Pyron, R. A., & Jetz, W. (2019). Phylogenetic and Trait-Based Prediction of Extinction Risk for Data-Deficient Amphibians. *Current Biology*, *29*(9), 1557-1563.e3. https://doi.org/10.1016/j.cub.2019.04.005

Harrison, S. J., Raubenheimer, D., Simpson, S. J., Godin, J.-G. J., & Bertram, S. M. (2014). Towards a synthesis of frameworks in nutritional ecology: Interacting effects of protein, carbohydrate and phosphorus on field cricket fitness. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1792), 20140539. https://doi.org/10.1098/rspb.2014.0539

Huey, R. B., & Kingsolver, J. G. (2019). Climate Warming, Resource Availability, and the Metabolic Meltdown of Ectotherms. *The American Naturalist*, *194*(6), E140–E150. https://doi.org/10.1086/705679

Irwin, M. T., Raharison, J.-L., Raubenheimer, D. R., Chapman, C. A., & Rothman, J. M. (2015). The Nutritional Geometry of Resource Scarcity: Effects of Lean Seasons and Habitat Disturbance on Nutrient Intakes and Balancing in Wild Sifakas. *PLOS ONE*, *10*(6), e0128046. https://doi.org/10.1371/journal.pone.0128046

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

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

Kaluza, B. F., Wallace, H. M., Heard, T. A., Minden, V., Klein, A., & Leonhardt, S. D. (2018). Social bees are fitter in more biodiverse environments. *Scientific Reports*, *8*(1), 12353. https://doi.org/10.1038/s41598-018-30126-0

Kaspari, M., & Welti, E. A. R. (2024). Nutrient dilution and the future of herbivore populations. *Trends in Ecology & Evolution*, *39*(9), 809–820. https://doi.org/10.1016/j.tree.2024.05.001

Kearney, M., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1557), 3469–3483. https://doi.org/10.1098/rstb.2010.0034

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

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

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

Lee, K. P., Simpson, S. J., Clissold, F. J., Brooks, R., Ballard, J. W. O., Taylor, P. W., Soran, N., & Raubenheimer, D. (2008). Lifespan and reproduction in *Drosophila*: New insights from nutritional geometry. *Proceedings of the National Academy of Sciences*, *105*(7), 2498–2503. https://doi.org/10.1073/pnas.0710787105

Lynch, C., Baudier, K., Montgomery, D., & Barrett, M. (2025). *Minimizing inferential bias in the theory and design of nutritional experiments through the application of the equilateral mixture triangle*. https://doi.org/10.64898/2025.12.06.692245

Lynch, C. M., Bespalova, I., Harrison, J. F., Pratt, S. C., Pavlic, T. P., & Fewell, J. H. (2025). Piecewise-Continuous Sampling: A Method for Minimizing Bias and Sampling Effort for Estimated Metrics of Animal Behavior. *Ethology*, *131*(12), 290–302. https://doi.org/10.1111/eth.70021

Machovsky-Capuska, G. E., Senior, A. M., Simpson, S. J., & Raubenheimer, D. (2016). The Multidimensional Nutritional Niche. *Trends in Ecology & Evolution*, *31*(5), 355–365. https://doi.org/10.1016/j.tree.2016.02.009

Marjakangas, E., Dalsgaard, B., & Ordonez, A. (2025). Fundamental Interaction Niches: Towards a Functional Understanding of Ecological Networks' Resilience. *Ecology Letters*, *28*(6), e70146. https://doi.org/10.1111/ele.70146

Mata, V. A., Silva, L. P., Veríssimo, J., Horta, P., Raposeira, H., McCracken, G. F., Rebelo, H., & Beja, P. (2021). Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators. *Ecological Applications*, *31*(8). https://doi.org/10.1002/eap.2457

May, R. M. (1972). Will a Large Complex System be Stable? *Nature*, *238*(5364), 413–414. https://doi.org/10.1038/238413a0

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

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1557), 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Michalko, R., Gibbons, A. T., Goodacre, S. L., & Pekár, S. (2021). Foraging aggressiveness determines trophic niche in a generalist biological control species. *Behavioral Ecology*, *32*(2), 257–264. https://doi.org/10.1093/beheco/araa123

Moatt, J. P., Fyfe, M. A., Heap, E., Mitchell, L. J. M., Moon, F., & Walling, C. A. (2019). Reconciling nutritional geometry with classical dietary restriction: Effects of nutrient intake, not calories, on survival and reproduction. *Aging Cell*, *18*(1), e12868. https://doi.org/10.1111/acel.12868

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

Morimoto, J. (2024). Optimum ratio of dietary protein and carbohydrate that maximises lifespan is shared among related insect species. *Aging Cell*, *23*(3), e14067. https://doi.org/10.1111/acel.14067

Morimoto, J., & Lihoreau, M. (2019). Quantifying Nutritional Trade-Offs across Multidimensional Performance Landscapes. *The American Naturalist*, *193*(6), E168–E181. https://doi.org/10.1086/701898

Morimoto, J., & Lihoreau, M. (2020). Open Data for Open Questions in Comparative Nutrition. *Insects*, *11*(4), 236. https://doi.org/10.3390/insects11040236

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

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2267–2278. https://doi.org/10.1098/rstb.2010.0095

Pekár, S., Wolff, J. O., Černecká, Ľ., Birkhofer, K., Mammola, S., Lowe, E. C., Fukushima, C. S., Herberstein, M. E., Kučera, A., Buzatto, B. A., Djoudi, E. A., Domenech, M., Enciso, A. V., Piñanez Espejo, Y. M. G., Febles, S., García, L.

F., Gonçalves-Souza, T., Isaia, M., Lafage, D., … Cardoso, P. (2021). The World Spider Trait database: A centralized global open repository for curated data on spider traits. *Database*, *2021*, baab064. https://doi.org/10.1093/database/baab064

Petsopoulos, D., Lunt, D. H., Bell, J. R., Kitson, J. J. N., Collins, L., Boonham, N., Morales-Hojas, R., & Evans, D. M. (2021). Using network ecology to understand and mitigate long-term insect declines. *Ecological Entomology*, *46*(4), 693–698. https://doi.org/10.1111/een.13035

Proulx, S., Promislow, D., & Phillips, P. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, *20*(6), 345–353. https://doi.org/10.1016/j.tree.2005.04.004

Rapkin, J., Jensen, K., Archer, C. R., House, C. M., Sakaluk, S. K., Castillo, E. D., & Hunt, J. (2018). The Geometry of Nutrient Space–Based Life-History Trade-Offs: Sex-Specific Effects of Macronutrient Intake on the Trade-Off between Encapsulation Ability and Reproductive Effort in Decorated Crickets. *The American Naturalist*, *191*(4), 452–474. https://doi.org/10.1086/696147

Raubenheimer, D. (2011). Toward a quantitative nutritional ecology: The right-angled mixture triangle. *Ecological Monographs*, *81*(3), 407–427. https://doi.org/10.1890/10-1707.1

Raubenheimer, D., Senior, A. M., Mirth, C., Cui, Z., Hou, R., Le Couteur, D. G., Solon-Biet, S. M., Léopold, P., & Simpson, S. J. (2022). An integrative approach to dietary balance across the life course. *iScience*, *25*(5), 104315. https://doi.org/10.1016/j.isci.2022.104315

Raubenheimer, D., & Simpson, S. J. (1993). The geometry of compensatory feeding in the locust. *Animal Behaviour*, *45*(5), 953–964. https://doi.org/10.1006/anbe.1993.1114

Raubenheimer, D., & Simpson, S. J. (2020). *Eat Like the Animals: What Nature Teaches Us About the Science of Healthy Eating*. Houghton Mifflin Harcourt.

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

Ridgway, J., & Wesner, J. (2025). A global dataset of freshwater fish trophic interactions. *Scientific Data*, *12*(1), 160. https://doi.org/10.1038/s41597-024-04211-1

Semenyuk, I. I., & Tiunov, A. V. (2019). Foraging behaviour as a mechanism for trophic niche separation in a millipede community of southern Vietnam. *European Journal of Soil Biology*, *90*, 36–43. https://doi.org/10.1016/j.ejsobi.2018.12.001

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*. https://doi.org/10.3389/fpsyg.2016.00018

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

Shik, J. Z., Kooij, P. W., Donoso, D. A., Santos, J. C., Gomez, E. B., Franco, M., Crumière, A. J. J., Arnan, X., Howe, J., Wcislo, W. T., & Boomsma, J. J. (2020). Nutritional niches reveal fundamental domestication trade-offs in fungus-farming ants. *Nature Ecology & Evolution*, *5*(1), 122–134. https://doi.org/10.1038/s41559-020-01314-x

Shik, J. Z., Rytter, W., Arnan, X., & Michelsen, A. (2018). Disentangling nutritional pathways linking leafcutter ants and their co-evolved fungal symbionts using stable isotopes. *Ecology*, *99*(9), 1999–2009. https://doi.org/10.1002/ecy.2431

Simpson, S. J., & Raubenheimer, D. (1993). A multi-level analysis of feeding behaviour: The geometry of nutritional decisions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *342*(1302), 381–402. https://doi.org/10.1098/rstb.1993.0166

Simpson, S. J., & Raubenheimer, D. (1995). The geometric analysis of feeding and nutrition: A user's guide. *Journal of Insect Physiology*, *41*(7), 545–553. https://doi.org/10.1016/0022-1910(95)00006-G

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

Simpson, S. J., Raubenheimer, D., Charleston, M. A., & Clissold, F. J. (2010). Modelling nutritional interactions: From individuals to communities. *Trends in Ecology & Evolution*, *25*(1), 53–60. https://doi.org/10.1016/j.tree.2009.06.012

Simpson, S. J., Sibly, R. M., Lee, K. P., Behmer, S. T., & Raubenheimer, D. (2004). Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour*, *68*(6), 1299–1311. https://doi.org/10.1016/j.anbehav.2004.03.003

Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs: Structural dynamics and robustness of food webs. *Ecology Letters*, *13*(7), 891–899. https://doi.org/10.1111/j.1461-0248.2010.01485.x

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

Timóteo, S., Ramos, J. A., Vaughan, I. P., & Memmott, J. (2016). High Resilience of Seed Dispersal Webs Highlighted by the Experimental Removal of the Dominant Disperser. *Current Biology*, *26*(7), 910–915. https://doi.org/10.1016/j.cub.2016.01.046

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

Verde Arregoitia, L. D., Blomberg, S. P., & Fisher, D. O. (2013). Phylogenetic correlates of extinction risk in mammals: Species in older lineages are not at greater risk. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20131092. https://doi.org/10.1098/rspb.2013.1092

Vizentin-Bugoni, J., Debastiani, V. J., Bastazini, V. A. G., Maruyama, P. K., & Sperry, J. H. (2020). Including rewiring in the estimation of the robustness of mutualistic networks. *Methods in Ecology and Evolution*, *11*(1), 106–116. https://doi.org/10.1111/2041-210X.13306

Ward, C. A., Tunney, T. D., Hale, K. R. S., O'Connor, R. F., & McCann, K. S. (2026). The rewiring of ecological networks in a variable world. *Nature Reviews Biodiversity*, *2*(6), 355–369. https://doi.org/10.1038/s44358-026-00159-9

Wilder, S. M., Barnes, C. L., & Hawlena, D. (2019). Predicting Predator Nutrient Intake From Prey Body Contents. *Frontiers in Ecology and Evolution*, *7*, 42. https://doi.org/10.3389/fevo.2019.00042

Wilder, S. M., & Eubanks, M. D. (2010). Might nitrogen limitation promote omnivory among carnivorous arthropods? Comment. *Ecology*, *91*(10), 3114–3117. https://doi.org/10.1890/09-2080.1

Wise, D. H., Moldenhauer, D. M., & Halaj, J. (2006). Using Stable Isotopes To Reveal Shifts In Prey Consumption By Generalist Predators. *Ecological Applications*, *16*(3), 865–876. https://doi.org/10.1890/1051-0761(2006)016[0865:USITRS]2.0.CO;2

Woodward, G., Benstead, J. P., Beveridge, O. S., Blanchard, J., Brey, T., Brown, L. E., Cross, W. F., Friberg, N., Ings, T. C., Jacob, U., Jennings, S., Ledger, M. E., Milner, A. M., Montoya, J. M., O'Gorman, E., Olesen, J. M., Petchey, O. L., Pichler, D. E., Reuman, D. C., … Yvon-Durocher, G. (2010). Ecological Networks in a Changing Climate. In *Advances in Ecological Research* (Vol. 42, pp. 71–138). Elsevier. https://doi.org/10.1016/B978-0-12-381363-3.00002-2

Zanco, B., Bridle, J., Cuff, J. P., da Silva, C. R. B., Diamond, S. E., Lynch, C. M., Mirth, C. K., & Morimoto, J. (submitted). *Nutritional geometry as a foundation for predicting the evolution of plant–consumer interactions under climate change*.

Zanco, B., Morimoto, J., Cockerell, F., Mirth, C., & Sgrò, C. M. (2025). Nutritional optima for life-history traits vary with temperature and across locally-adapted populations. *Journal of Insect Physiology*, *163*, 104815. https://doi.org/10.1016/j.jinsphys.2025.104815

Zanco, B., Widman, E., Fulton, T. L., Diamond, S. E., Da Silva, C. R., & Ponton, F. (2026). Bee vulnerability to climate change in a shifting nutritional landscape: Why sociality and life-history strategy matter. *Current Opinion in Insect Science*, *77*, 101556. https://doi.org/10.1016/j.cois.2026.101556

Zheng, B., Wu, Z., & Xu, B. (2014). The Effects of Dietary Protein Levels on the Population Growth, Performance, and Physiology of Honey Bee Workers During Early Spring. *Journal of Insect Science*, *14*(1). https://doi.org/10.1093/jisesa/ieu053