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Research Article

Integrating network and stable isotope approaches to reveal food web structures

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Progress in food web ecology relies on assessing the strengths, limitations and complementarity of different approaches to characterize food web structures. We determined whether the network approach, depicting the detailed architectures of nodes connected by trophic links, and the stable isotope approach, providing a biochemical representation of food webs using ecological tracers, deliver similar view of food web structures. We synthesized candidate metrics that characterize the vertical structure, clustering, complexity and trophic diversity of food webs in both approaches. We then combined databases of empirical freshwater stable isotope values and a niche model to simulate diverse but realistic networks and convert them into isotopic spaces. Finally, we evaluated the associations between metrics computed on networks and stable isotopes using redundancy analysis (RDA) and their variability depending on initial characteristics of food webs. Network and isotopic metrics were well associated ($R^2 = 0.62$), especially those describing vertical food web structure (e.g. food chain length). Network clustering metrics (e.g. number of modules) were associated with isotopic clustering (e.g. nearest neighbour distance) and isotopic diversity metrics (e.g. standard ellipse area). There were poor associations between complexity metrics in the network approach (e.g. connectance) and other isotopic metrics. Increasing node richness and food web compartmentalisation altered the associations between network and isotopic metrics by modifying delineation of energy pathways and trophic clusters. Our study highlights the conditions where network and stable isotope metrics are similar or bring

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complementary information to characterizing food web structures. We encourage continued exploration of the complementarity of both approaches under different environmental constraints and propose that isotopic data can represent biodiversity structure to test long-standing hypotheses about food web structure complexity, including those related to ecosystem function.

Keywords: food web dimensions, stable isotopes, trophic structure, network

Introduction

Understanding trophic interactions among species is a cornerstone of the long-standing effort to understand ecosystem functioning in a changing world (Thompson et al. 2012, Moore et al. 2018, Pringle and Hutchinson 2020). One central framework for estimating food web architecture is the network approach which represents species or trophic groups as nodes linked by feeding interactions, thereby enabling the analysis of emergent structural properties such as connectivity, compartmentalization and trophic hierarchy in food webs. By combining multiple analytical methods (e.g. gut-content analysis and modeling), this framework can yield highly resolved food webs and has driven major advances in relating food web complexity to the stability of ecological dynamics (Landi et al. 2018). However, network approaches often represent a snapshot of trophic interactions if not included in a dynamic modeling context.

A second framework for studying food webs has emerged from stable isotope analysis, which uses isotopes as tracers to focus on the movement of material and energy through biomass pools rather than on explicit exhaustive dietary links among trophic units (Lindeman 1942, Paine 1980, Layman et al. 2015). This approach provides time-integrated estimates of consumer resource use and offers insight into energy pathways. Although network and stable isotope frameworks thus provide distinct and potentially complementary perspectives on food web structure, they remain only weakly integrated. Even studies that combine both approaches (e.g. hierarchical isotopic mixing models; Phillips et al. 2014) often treat them separately because they rely on different metrics. This disconnect reflects enduring differences in definitions (dietary links among nodes versus energy/ elemental pathways among biomass pools) and in the resolution of trophic units, which are constrained by the methodological nuances of each approach (Dunne 2006, Majdi et al. 2018, Nielsen et al. 2018).

Advances in network sciences have inspired the development of metrics describing food web structures according to trophic units and their interconnected linkages (Newman 2006, Rezende et al. 2009). In parallel, metrics describing the dimensionality of isotopic spaces (i.e. multidimensional coordinate space in which each axis represents a stable isotope ratio and where points are plotted according to their isotopic values) have been developed to help describe isotopic niches of trophic units (Layman et al. 2007). While these two sets of metrics have been largely studied in isolation, complementarity between them is expected since they both aim to assess common properties of food webs. For instance, metrics based on the measurement of stable nitrogen isotopes ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) are widely used to reveal vertical trophic structure as defined in network approaches (Post 2002b, Layman et al. 2012). In addition, network metrics quantifying the number of trophic groups in networks and the mean nearest neighbour distance describing clustering in isotopic spaces may both reveal functional groups related to resource exploitation. Yet, the former indicates the number of expected trophic groups based on clearly defined interactions between trophic units while the latter quantifies how much the trophic units in the groups are aggregated in isotopic space.

Despite being crucial in unifying food web ecology, surprisingly few studies have attempted to integrate the descriptions of food web structures based on network metrics (defined here as metrics derived from the architecture of nodes and edges) with descriptions based on isotopic metrics (defined here as metrics derived from the position of stable isotope values in isotopic space). In one rare example, Brind'Amour and Dubois (2013) showed that isotopic diversity indices depended on species diversity and specialization by modeling simplified food webs. Following this approach in more complex food webs, Jabot et al. (2017) subsequently showed that distances between trophic units in isotopic spaces were only weakly correlated to trophic dissimilarities between nodes in networks, and that the strength of these correlations depended on species richness, level of omnivory and complexity of interactions in the food webs. These two studies suggest that isotopic and network metrics may be poorly correlated; however, they were limited to simulations not bounded by empirical data and they investigated a small number of metrics. For this reason, the complementarity, or lack thereof, between isotope- and network-based approaches to characterizing food web structure remains unclear.

This study explores the complementarity of network and stable isotope approaches to better characterize food web structure in a changing world. We tested for associations between network and isotopic metrics using a globally distributed dataset of freshwater stream and lake food webs. We synthesized candidate metrics from network and isotopic research that describe the vertical structure, the amount of clustering, and the complexity and diversity in food web structures. We then built on the approach introduced by Jabot et al. (2017) to 1) simulate a wide diversity of food web structures by combining theoretical models with three global empirical datasets; 2) transform networks into isotopic spaces; 3) select only simulated isotopic spaces (and associated networks) reflecting empirical patterns observed at the global scale; and 4) assess the relationships between network and isotopic metrics computed from these selected simulations. Our investigation is motivated by a series of hypotheses. First, there should be a strong association between network and isotopic metrics that describe the vertical structure of food webs because they are quantified similarly in both approaches. Second, metrics describing clustering of trophic groups and energy pathways should also be similar between approaches because of parallels in their characterization (i.e. clustering methods based either on networks or isotopic spaces). Third, because links are resolved only in the network approach and not in the stable isotope approach, network metrics related to complexity may be relatively less associated with isotopic metrics. Fourth, aligned with past, we expected associations between metrics to be modulated by species richness and connection between the different food web compartments.

Material and methods

Synthesis of network and isotopic metrics

To analyse food web structures, we synthetized ten network metrics and nine potential isotope-based analogues into three general structure categories that apply to both approaches: 1) vertical structure, the number of trophic transfers from basal resource to the focal organism, 2) clustering, the tendency for sub groups versus uniform distribution of trophic units and 3) complexity and diversity, the identity, quantity and patterning of food web components. For consistency and clarity of presentation we assign a short identifier for each metric and provide a written definition and reference in Table 1 (see the Supporting information for a detailed version with metric illustrations).

There are other notable differences in the way that network and isotope approaches are typically conducted, so we had to make some careful decisions about the best way to represent food webs given our objectives. First, food web studies are conducted at different levels of biological organization depending on the research question. Isotopic metrics are usually computed at the population or community level (e.g. for specific taxa, Layman et al. 2007, Jackson et al. 2011) while the network metrics are commonly calculated at both the node levels and the whole food web scale (i.e. from basal species to top consumers, Bersier et al. 2002, Blondel et al. 2008). To align with network approaches, we computed isotopic metrics on isotopic spaces including primary consumers to apex predators. Second, we computed the network metrics accounting for weighted trophic links to capture differences in feeding intensity or resource use that are central features of isotopic structures (Vander Zanden and Rasmussen 1996, Phillips et al. 2014). We thus adopted this methodology to align with our overall objective of directly comparing metrics across approaches.

Empirical data

We used data from real food webs to parametrize the simulations with initial empirical characteristics and allow for only considering realistic isotopic spaces obtained from the simulated networks in subsequent analyses so that empirically 'realistic' network and isotopic metrics could be compared.

To derive those empirical characteristics, first, we retrieved trophic links for 185 freshwater food webs obtained from the GlobAL daTabasE of traits and food Web Architecture (GATEWAy) from Brose et al. (2019) and the Mangal database from Poisot et al. (2016) (Fig. 1A – Step 1). We only selected data from freshwater food webs to be sure that network structures reflected by our simulations will reflect structures depicted by freshwater isotopes only. The GATEWAy database is a global dataset of food webs (with 222 151 feeding links between 5736 species retrieved from observations and published studies) from which we selected 80 freshwater food webs (streams and lakes) that included on average 235 trophic links (± 244 1 SD). The Mangal database includes 1300 ecological networks distributed worldwide from which we retrieved 105 food webs found in streams, lakes, ponds, reservoirs and rivers, comprising an average of 148 links (± 137 1 SD). These trophic links allow us to compute the empirical connectance values of the 185 food webs used for simulations of networks (Fig. 1A – Step 1).

Second, we used a global database of empirical stable isotope values from lentic and lotic systems (ISOFRESH; Boulêtreau et al. 2025, Fig. 1A – Step 2) to provide a template for essential aspects of the simulated food webs, to bound those simulations to realistic food webs further, and to facilitate comparison of realistic metrics from both approaches. The mean and variability (1 SD) of δ^{13}C and δ^{15}N values for freshwater communities were compiled from peer-reviewed and grey literature. We selected freshwater communities according to two criteria: 1) the community included at least three fish species to allow the calculation of the metrics related to surfaces within the isotopic space computed in the next steps, and 2) the community included primary consumers and primary producers. This led to the selection of 260 freshwater communities located in 39 countries, 44% and 56% of which were from lentic and lotic systems, respectively (Supporting information). The freshwater communities were represented by, on average ± SD, 21 ± 10 taxa (range: 5–60), including an average of 8 ± 5 fish species, 4 ± 3 secondary invertebrate consumers, 4 ± 2 primary consumers and 4 ± 3 primary producers. Thus, this database provided comprehensive and diverse empirical cases to compute the range of initial number of nodes (i.e. species richness) to include in the simulated food webs to represent empirical sampling usually obtained from isotope analyses. It also provided the isotopic values of the basal nodes used to convert networks into isotopic spaces, and it ultimately permitted us to compute the empirical ranges (quantiles at 1% and 99%) for each isotopic metric to select only realistic simulated isotopic spaces. Note that we complementarily conducted supplementary analyses by bounding the empirical range with the minimum and the maximum values computed over all the empirical isotopic spaces and with the quantile regression at 5% and 95% in order to validate the robustness of our results when increasing or reducing the number of isotopic spaces selected to run the analyses of metric associations (Supporting information).

Table 1. Synthesis of network metrics (left) and isotopic metrics (right) commonly used to study food web structure.

	Network			Stable isotopes		
	Metric	Definition	Reference	Metric	Definition	Reference
Vertical structure	**$TP_{network}mean$**	Average trophic position of all consumers weighted by biomass	Levine 1980	**$TP_{iso}mean$**	Average trophic position of all consumers	Post 2002b
	TLmax	Maximum trophic position in the food web	Levine 1980	***FCL***	Food chain length: maximum trophic position among all consumers	Post 2002b
Clusters	***Mod***	Modularity: describes how nodes in subgroups interact with each other compared with nodes outside of their subgroup; increases when nodes in subgroups more often interact with each other than with other nodes	Newman 2006	***IDis***	Isotopic dispersions: weighted-deviation to the average position of points in the isotope biplot divided by the maximal distance to the centre of gravity	Cucherousset and Villeger 2015
	Nmod	Number of modules: number of subgroups of interacting nodes; can include several trophic groups	Blondel et al. 2008	***IDiv***	Isotopic divergence: reflects abundance-weighted deviances between all organisms and the centre of gravity of the convex hull incorporating those organisms in an isotope biplot	Cucherousset and Villeger 2015
	Nsbm	Number of groups from the stochastic block model: the number of trophic groups detected using a stochastic block model	Baskerville et al. 2011, Lee and Wilkinson 2019, O'Connor et al. 2020	***NND***	Mean nearest neighbour distance: a measure of density and clustering of species within the community	Layman et al. 2007
	BenthicPath	Benthic pathway: the mean proportion of energy from the benthic compartment	Inspired from soil ecology Hedde et al. 2024	***BenthicRel***	Benthic reliance: proportion of biomass in secondary consumers derived from the benthic compartment	Vander Zanden and Vadeboncoeur 2002
Complexity and diversity	***C***	Connectance: the number of realized trophic links over the number of all possible links	Martinez 1992	***SEAc***	Standard ellipse area (corrected): core isotope niche of the consumers in the community (here at 95%)	Jackson et al. 2011
	LD	Link diversity: the diversity of weighted trophic links; the higher the number of links and their evenness, the higher it is	Bersier et al. 2002	***TA***	Total area: convex hull area covered by all species in the biplot space (i.e. total amount of niche space occupied); provides an indication of the community niche width	Layman et al. 2007
	TV	Trophic generality: mean number of prey per node	Bersier et al. 2002	***CD***	Mean distance to the centroid: average spacing within the biplot; provides the average degree of trophic diversity	Layman et al. 2007
	TV	Trophic vulnerability: mean number of consumers per node	Bersier et al. 2002			

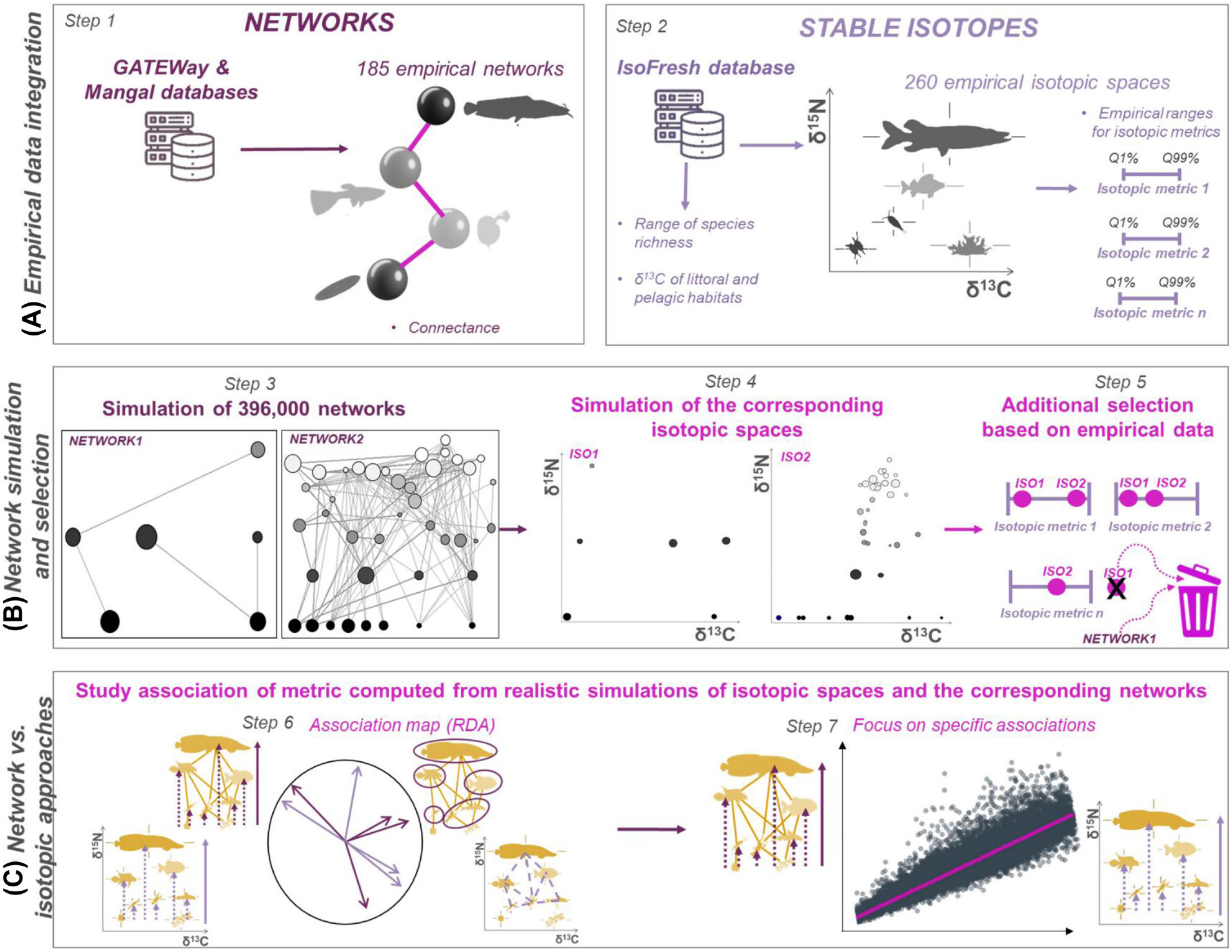

Figure 1. Analytical framework used in this study. (A) Data retrieval for the initial parameters used in the food web simulations and to compute empirical ranges of isotopic metrics for food web selection. (B) Simulations of networks, transformation into isotopic spaces and selection of realistic simulations based on matching empirical ranges and isotopic metrics computed on the simulated isotopic spaces. The shading of nodes delineates their trophic level positions. (C) Assessment of the association between the ten network and nine isotopic metrics using a redundancy analysis (light and dark purple arrows are the isotopic and network metrics, respectively) and linear mixed effect models.

Simulation of food webs

The simulation of networks (Fig. 1B – Step 3) followed the niche model principle (Williams and Martinez 2000), but was adapted to account for the presence of compartments in food webs (see below). The niche model is classically used to simulate realistic food web structures in network approaches (Allesina 2008, Williams and Martinez 2008). It remains one of the most widely used and empirically validated generative models for food webs and was used here as a controlled framework for generating networks with different initial characteristics and so generate the corresponding isotopic spaces. According to this model, a niche position and a feeding range, *r*, whose centre is *c*, in a one-dimensional trophic niche is assigned to each food web node. Each consumer, *i*, consumed a sequence of prey randomly drawn from r_i, which collectively defined the trophic links in the food web. Both loops (prey can also consume their predators) and cannibalism were allowed in the model. Primary producers in the food web were defined as the nodes without trophic links to prey, and consumers were all the remaining nodes. Each food web was simulated with a connectance *C* (i.e. fraction of all possible links that are realized) and was composed of *S* nodes (i.e. node richness).

We expanded on the classical niche model by including two compartments in our simulated food webs, whereby the number of nodes was equally allocated and included at least one primary producer. This model allowed us to simulate more complex aquatic food webs, including the different energy flow origins (here, benthic versus pelagic sources) while keeping the fundamental rules of consumer interactions in the niche model (i.e. feeding range *r* centred on *c*, Supporting information). Taking into account this connection between food web compartments permitted us to reflect more or less connected energy channels that can be met in real ecosystems and so brings more realistic food web structures. The compartments can be more or less connected depending on the probability of node interactions between compartments $\text{Comp}_{\text{prob}}$, which is fixed between

0 (i.e. nodes in compartment 1 are not allowed to interact with nodes in compartment 2) and 1 (i.e. equal probability of interactions among nodes in different compartments as in the same compartment; this corresponds to the classical niche model). Note that varying $\mathrm{Comp}_{\mathrm{prob}}$ can change the initial value of connectance in the simulations so the model is parameterized to ultimately match the initial input connectance.

Next, expanding from Jabot et al. (2017), trophic links in the simulated food webs were weighted depending on the level of trophic specialization, on whether prey and consumers were in the same compartment or not, and prey biomass. First, the preference p_{ij} of a consumer i for one of its prey j is defined by:

$$p_{ij} = \frac{e^{-\frac{(n_j - c_i)^2}{2\sigma^2}}}{\sigma\sqrt{2\pi}} m_{ij} \tag{1}$$

where $\sigma = 1$ – trophic specialization, n_j is the position of species j in the niche dimension, c_i is the centre of the niche of species i, and $m_{ij} = 1$ if both species i and j are in the same compartment and $m_{ij} = \mathrm{Comp}_{\mathrm{prob}}$ otherwise. Thus, preferences are stronger with prey niches close to the feeding range centre of the consumer $ci_,$ and the more specialized the consumers, the narrower the distributions. Fi_j between consumer i and prey j is then defined from the preferences p_{ij} such that the sum of the preferences of consumer i is equal to 1:

$$F_{ij} = \frac{p_{ij}}{\sum_{k \in \, prey\ of\ i} p_{ik}} \tag{2}$$

Finally, following Jabot et al. (2017), the weighted food webs were obtained by multiplying each interaction strength F_{ij} in the food webs by the biomass B_j of prey j. Each node biomass was randomly drawn from a log-normal distribution ($\mu = 0$, $\sigma^2 = 1$) to reflect realistic distributions (Cohen 2020).

We parameterized our food web simulations with the node richness, S, which varied between 5 and 65 (by increments of 5), to correspond to the range of species richness reflected in the empirical isotopic data. We considered initial connectance, C, from 0.05 to 0.30 (by 0.05 steps) based on empirical connectance computed from the GATEWAy and Mangal databases. We considered variations in $\mathrm{Comp}_{\mathrm{prob}}$ from 0 to 1 (increments of 0.1) and in trophic specialization of consumers from 0 to 0.8 (increments of 0.2). We ran 100 simulations of each combination of parameters, resulting in 396 000 simulated networks, and we computed the 10 network metrics (Table 1) for each of these food webs.

Simulation of isotopic spaces

Following the framework of Jabot et al. (2017), we transformed the simulated food webs into isotopic spaces defined by δ^{13}C (x-axis in the space) and δ^{15}N (y-axis; Fig. 1B – Step 4). The objective was to obtain isotopic spaces that correspond to the networks generated by the niche model. One point in the isotopic space is equivalent to one node in the network. The coordinates of the points in the isotopic spaces are computed based on the consumer–resource links identified from the niche model and on rules known from empirical observations detailed below. In this procedure, δ^{13}C and δ^{15}N values were determined for primary producers in the food webs based on empirical ranges (Fig. 1A), and values of consumers were calculated following Eq. 3 and 4. Isotopic values of consumers reflected the weighted average values of their prey, added to a trophic discrimination factor of 3.4‰ for δ^{15}N and 1‰ for δ^{13}C (Zanden and Rasmussen 2001, Post 2002b). Thus, we used the following equations:

$$\delta^{13}\mathrm{C}_{\mathrm{i}} = 1 + \frac{\Sigma j F_{ij} B_i \delta^{13} C_j}{\Sigma j F_{ij} B_i} \tag{3}$$

$$\delta^{15} N_i = 3.4 + \frac{\Sigma j F_{ij} B_i \delta^{15} N_j}{\Sigma j F_{ij} B_i} \tag{4}$$

where i is the consumer, j is the prey, F_{ij} is the interaction strength between i and j weighted by B_j which is the biomass of prey j, and $\delta^{13}\mathrm{C}_j$ and $\delta^{15}\mathrm{N}_j$ are the isotopic values of prey j. While Fij corresponds to a normalized representation of how consumers allocate feeding efforts across available resources, Fij* × Bj provides a proportional measure of realized interaction strength that depends on resource biomasses rather than an absolute estimate of energy flux.

For our simulations, δ^{15}N values for primary producers were assumed to be constant and fixed at 0.0‰. While we recognize that primary producer δ^{15}N values can vary among waterbodies (Cabana and Rasmussen 1996), differences among compartments (major habitats) are relatively small (Vander Zanden et al. 1999), so we avoided overcomplicating our models by holding these values constant. Conversely, δ^{13}C regularly differs among energy source compartments in food webs (e.g. pelagic versus benthic). To address this, we computed the 1% and 99% quantiles of the δ^{13}C values in the isotope database for uniform distributions of pelagic (algae, phytoplankton) and benthic primary producers (phytobenthos, macrophytes). We obtained ranges between −38.7‰ and −19.9‰ for pelagic producers, and between −36.7‰ and −12.6‰ for benthic producers. This allowed us to include variability in the basal isotope ratios in food webs that mirrors the ranges found in real systems, which can differ according to locations and ecosystem types. Finally, we computed the nine isotopic metrics described in Table 1 on each simulated isotopic space.

Selection of realistic isotopic spaces and corresponding networks

We selected realistic isotopic spaces and the corresponding simulated networks based on the empirical ranges computed from the global isotope dataset. A simulated isotopic space was selected only if all the isotopic metrics calculated on the given space fell within the empirical ranges (quantiles at 1% and 99%) computed for each isotopic metric (Fig. 1B – Step

5). This selection process results in 46 822 isotopic spaces (i.e. 13% of the simulations) and the corresponding simulated networks being retained. Further details on the characteristics of the selected isotopic spaces and networks are presented in the Supporting information.

Testing for associations between network and isotopic metrics

To test for associations between metrics computed on the selected networks and isotopic spaces, we initially conducted a redundancy analysis (RDA; Legendre and Legendre 1998), using scaled-centred variables (Fig. 1C – Step 6). We ran two supplementary RDA to validate metric associations when increasing or decreasing the number of simulations selected for identifying metric association (Supporting information). The significance of the RDA was tested using 10 000 permutations.

Then, we independently analysed the strongest associations between isotope-derived and network metrics identified with the RDA. Note that this comparison was possible because metrics were computed for each given network and its corresponding isotopic space that exhibited the same node richness. We assessed how the initial food web characteristics (i.e. node richness, probability of interactions between food web compartments and consumer specialization) could modulate the relationships between variables by fitting mixed effects models (Fig. 1C – Step 7). In those models, the network metrics were considered response variables, and the isotope-derived metrics, their interaction with the node richness *S* and the probability of interactions between food web compartments, $\text{Comp}_{\text{prob,}}$ were fixed effects. This allowed us to quantify how the strength of the relationship varied as a function of these parameters and identify the conditions under which the metric associations could change. The simulation number was included as a random effect, and families of residual distributions were specifically selected depending on the associations between variables (Gaussian for continuous response variables and Poisson for counts). Assumptions of linear mixed-effects models were verified by visual inspection of residual versus fitted plots, normality of residuals and absence of multicollinearity (variance inflation factor < 3).

All the analyses were conducted with R software (www.r-project.org). Food web simulations were performed with home-made functions and modified functions from Jabot et al. (2017). Isotope-based metrics were computed using the package 'SIBER' (Jackson et al. 2011). Network metrics were computed using the packages 'igraph' (Csardi and Nepusz 2006) and 'sbm' (Chiquet et al. 2024). The RDA and the mixed effect models were analysed using the packages 'vegan' (Dixon 2003) and 'lme4' (Bates et al. 2015), respectively.

Results

General map of metric associations

Isotopic and network metrics were generally well associated (RDA: adjusted $R^2 = 0.62$, $F = 8540.1$; Fig. 2), especially the metrics used to describe the vertical structure of food webs (mean and maximum trophic position). The metrics used to describe the amount of clustering through the network approach were grouped with metrics used to describe trophic diversity and clusters in the stable isotope approach (Fig. 2). The modularity (*Mod*) and the number of modules (*Nmod*) in networks were positively associated with the centroid distance (*CD*) and the corrected standard ellipse area (*SEAc*) in isotope spaces. These associations show that subgroups of trophic units interact more often with each other than with those outside of their subgroup, and food webs with a high number of modules were well reflected by a high trophic diversity in isotopic spaces (i.e. large distances of each consumer to the mean isotope ratios of the whole community and widespread core isotopic niche). In addition, the number of clusters identified with *Nsbm* (network) was positively associated with the total area of the convex hull of consumers (*TA*, isotopic), indicating that high isotopic diversity will reflect high numbers of trophic groups in networks. In contrast, *Nsbm* was negatively associated with isotopic dispersion and divergence (*IDis* and *IDiv*). This means that a high number of trophic groups in networks may often be related to isotopic spaces where dominant species (in terms of biomass) are more densely found at the centroid of the occupied isotopic area, and where points (species in our case) are not over-dispersed (i.e. low values of *IDis* and *IDiv*). Such configuration might typically reflect food webs with generalist

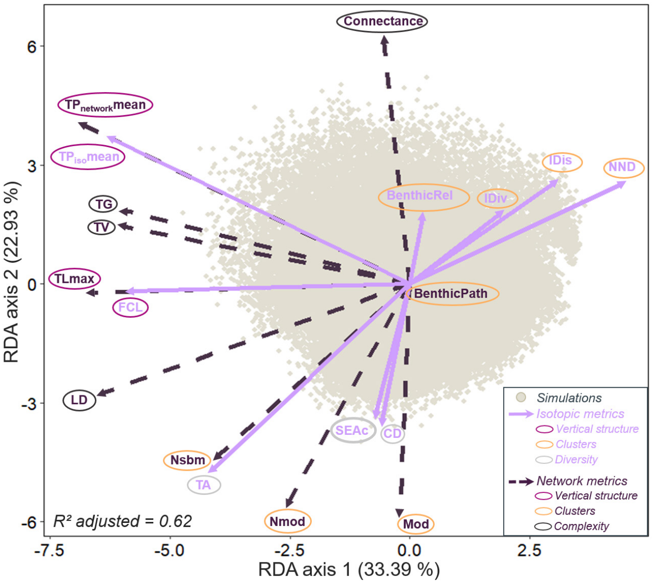

Figure 2. Biplot of the redundancy analysis (RDA) of the association between isotopic metrics computed on simulated isotopic spaces (light purple) and network metrics computed on simulated food webs (dark purple), with the three metric dimensions indicated by oval colour. The relative lengths of the vectors indicate the explanatory power of each variable in the ordination, with longer vectors representing stronger associations with the data structure. Vectors pointing in the same direction are positively correlated, while vectors pointing in opposite directions suggest negative correlations. Metrics are defined in Table 1.

species dominance and/or energy channelled through a few central pathways. The metric describing clustering in energy pathways (*BenthicPath*, network) was not associated with other metrics, including the isotopic metric of benthic reliance (*BenthicRel*), in any of the dimensions examined.

Among the metrics used to describe complexity in the network approach, only the link diversity (*LD*) was negatively associated with the mean nearest neighbour distance (*NND*, isotopic), denoting that diversity in trophic links is low when the trophic redundancy in isotopic niches is high. The connectance (*C*, network), the trophic generality (*TG*, network) and the trophic vulnerability (*TV*, network) were poorly associated with isotopic metrics. However, *C* (network) tended to be opposite the *SEAc* and *CD* isotopic metrics in the second dimension of the RDA.

Strength of associations and their modulation by food web characteristics

For the metrics related to the vertical structure, the association between *TLmax* (network) and *FCL* (isotopic) was a 1:1 relationship and was not influenced by the initial characteristics of simulation parameters. The mean trophic positions calculated from the two approaches (TP_{iso} and TP_{network}) were also strongly positively associated (Fig. 3A, Supporting information: marginal $R^2 = 0.80$), and the association was slightly reinforced when increasing *S* but weakened when increasing $\text{Comp}_{\text{prob}}$ (Supporting information). This means that food webs consisting of numerous species equally exploiting both food web compartments may exhibit slightly different trophic positions from stable isotope and network perspectives although the association between mean trophic positions remains strong regardless of the initial simulation parameters (Supporting information).

For the metrics associating clusters from the network approach to the trophic diversity in the stable isotope approach, the positive association between *Mod* and *CD* or *SEAc* (Fig. 3C and D) exhibited the same marginal R^2 (0.34) in which the associations in both cases were weakened when increasing *S*, but reinforced when increasing $\text{Comp}_{\text{prob}}$. This means that this association may be all the more relevant in the case of a high connection between both compartments in the food webs. *CD* and *SEAc* may help delineate different clusters and so pathways of matter transfer, but increasing the number of species studied from stable isotopes may limit our ability to determine clusters related to energy pathways in the isotopic space. The associations between *Nmod* (network) and *CD* (isotopic) (Fig. 3E; marginal $R^2 = 0.22$) or *SEAc* (isotopic) (Fig. 3F; marginal $R^2 = 0.22$) were weakened when increasing *S* and not affected by $Comp_{prob}$, as found for the strong positive association between *Nsbm* (network) and *TA* (isotopic) (Fig. 3G; marginal $R^2 = 0.44$). These both indicate that increasing the number of species studied in isotopic spaces may limit our ability to identify trophic clusters from large *TA* or *SEAc*, regardless of the connection level between the compartments in the food web.

For the metrics associating clusters from the network approach with clusters in the stable isotope approach, we confirmed the negative association between *Nsbm* and *IDis* (Fig. 3H; marginal $R^2 = 0.43$), and we found that this association was strengthened when increasing $Comp_{prob}$ but substantially weakened and even reversed at high *S* (Supporting information). This means that dispersion among trophic nodes in isotopic spaces better permits discernment of trophic groups at low species richness and when there are not siloed food web compartments. We still tested the strength of the association between metrics describing benthic energy clusters, *BenthicPath* (network) and *BenthicRel* (isotopic), which we had hypothesized to be strong but was very low (Fig. 3J; marginal $R^2 < 0.01$). The association was improved when both *S* and $\text{Comp}_{\text{prob}}$ were increased, but remained weak.

When associating network complexity metrics with metrics in the stable isotope approach, we found that the negative association between *LD* (network) and the mean *NND* (isotopic) was one of the strongest among all studied associations (Fig. 3B; marginal $R^2 = 0.70$), and was weakened when increasing *S* but reinforced when increasing $\text{Comp}_{\text{prob}}$. This reflects that the amount of clustering observed in isotopic spaces using *NND* may (negatively) correlate less clearly with the diversity of energy pathways (measured by *LD*) when food webs are strongly compartmented. Finally, although the relationships accounting for *C* (network) were unclear from the RDA, we still considered the potential negative association between *C* and *CD* (isotopic) (Fig. 4I; marginal $R^2 = 0.05$). We found that this relationship was not influenced by *S* but tended to be reinforced when increasing $\text{Comp}_{\text{prob}}$. This means many clusters with high centroid distances may correspond to a low number of realized trophic links only when the connection between basal food web compartments is high. Overall, much of the variability in the studied associations depended on the number of trophic nodes and the probability of node interactions between compartments.

Discussion

Advances in food web ecology are predicated upon a robust understanding of comparative strengths and weaknesses of different approaches to characterize food web structure (Delmas et al. 2019). By investigating empirically conditioned simulations, we reveal strong congruence between metrics commonly employed in network and stable-isotope approaches to describe vertical food web structure, but only moderate or weak associations between metrics describing the degree of clustering and those related to food web complexity, respectively (Fig. 4). In addition, metric associations were generally weakened when the richness of trophic nodes and the level of food web compartmentalisation increased. Together, this research identifies both opportunities and challenges to unifying stable-isotope and network approaches in the study of food web structure, thereby helping uncover the much sought-after links between biological structure and ecosystem functioning.The idea that ecosystems are vertically structured based on the trophic

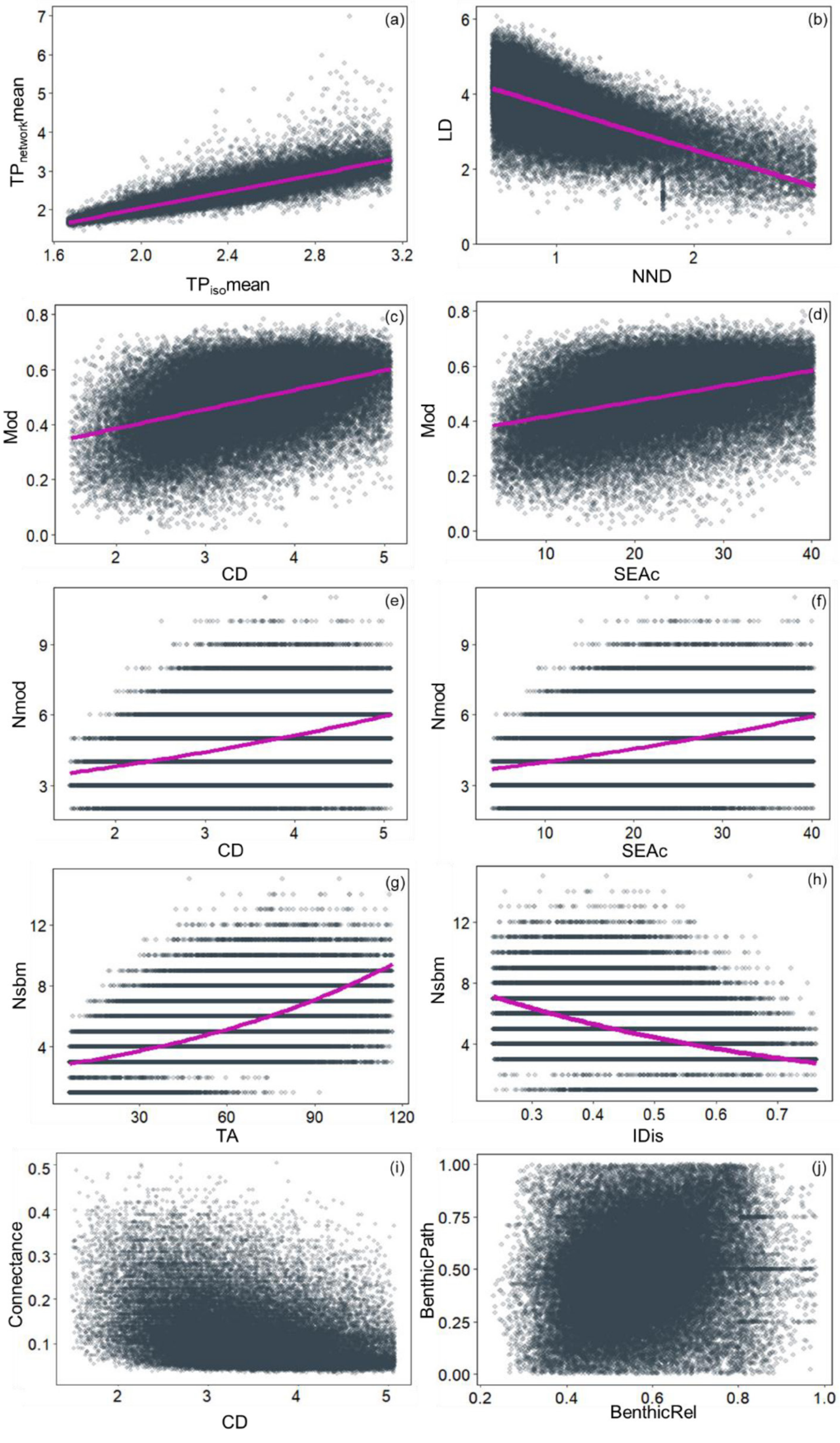

Figure 3. Specific associations between network metrics (y-axis) computed on simulated food webs and isotopic metrics (x-axis) computed on simulated isotopic spaces. Each dot is a simulated food web, and the magenta lines are the fitted relationships between both types of metrics. Metrics are defined in Table 1.

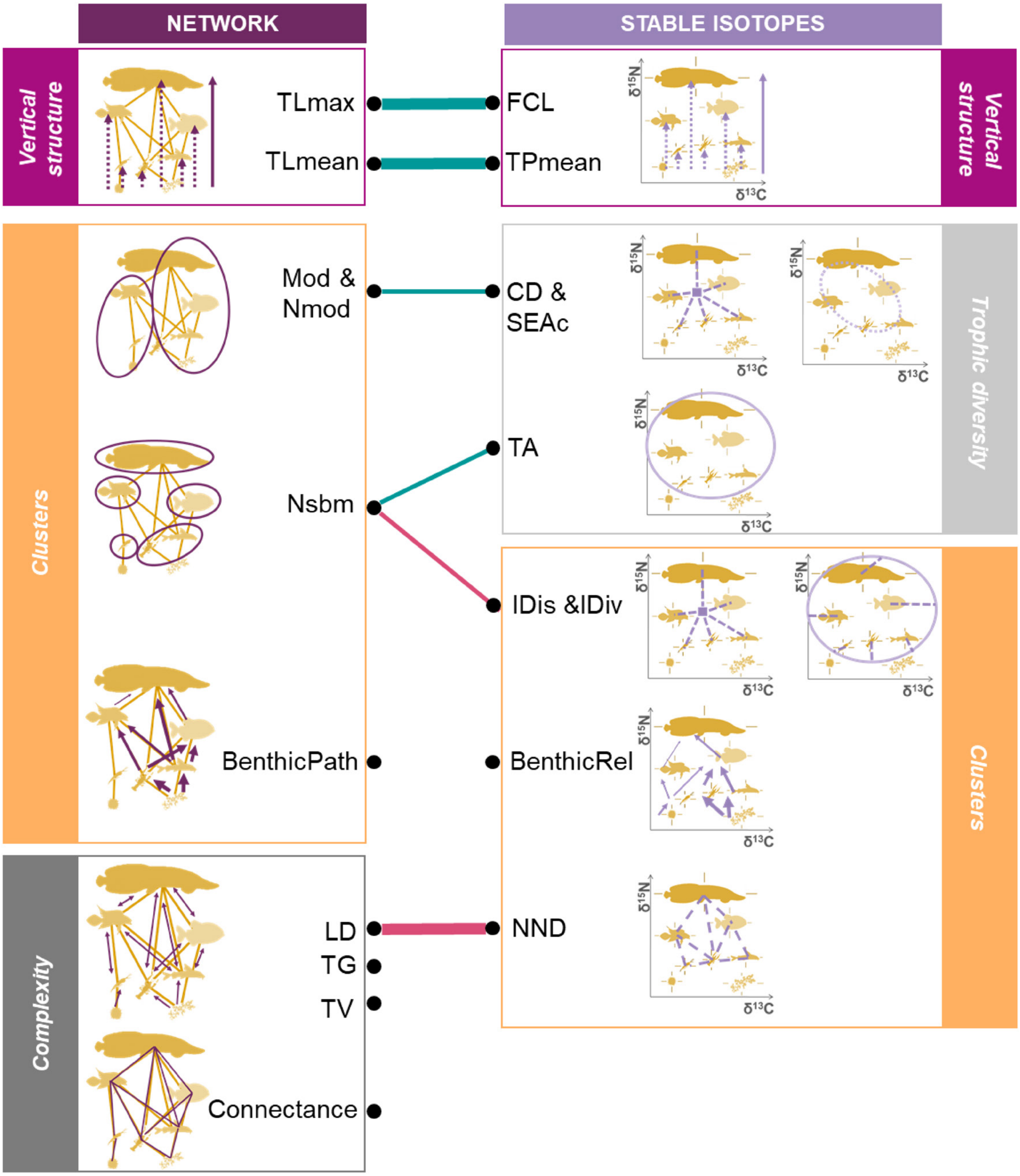

Figure 4. Summary of the associations (links between boxes) between network (left) and isotopic metrics (right) analysed in the present study. The purple rectangle encapsulates metrics describing the vertical structure of food webs, orange boxes correspond to clustering metrics and grey boxes contain metrics describing network complexity and trophic diversity in the network and isotopic approaches, respectively. Strengths of associations are proportional to line widths linking metrics; dark pink lines are negative associations, while cyan lines are positive associations. Metrics are defined in Table 1.

interactions of their constituent species is widely accepted in ecology (Elton 1927). Yet, different interpretations can be drawn depending on how the vertical structure of food webs is measured (Yodzis 1984, Post 2002a). A strictly network approach may characterize the number of trophic links from the base of the food web to an organism based on its diet (Williams and Martinez 2000). By contrast, stable isotopes provide biochemical evidence of those habits by harnessing the trophic enrichment of ^{15}N that occurs from one trophic transfer to the next as prey become consumer biomass (Post 2002b). Here, we demonstrate strong concordance between isotopic metrics and network metrics describing vertical food web structures, specifically the maximum number of trophic levels. The interchangeability of approaches for characterising vertical food web structure is supported by many past investigations of environmental constraints on food chain length, an inherently network construct (Briand and Cohen 1987, Pimm et al. 1991), that have been assessed using stable isotopes (McHugh et al. 2010, Sabo et al. 2010). However, as the baseline values of δ^{15}N used to compute trophic position vary along environmental gradients (Peipoch et al. 2012), cautions must be considered when comparing trophic positions in different real systems (e.g. stable isotope values of consumers need to be standardized). In addition, further syntheses investigating the consequences of variable trophic discrimination factors (an estimate of the magnitude of the shift in isotopic ratios between resources and consumers; Bastos et al. 2017) in stable isotope analyses are needed because trophic discrimination is mainly assumed to be constant across trophic levels, yet can vary as a function of numerous factors (e.g. diet quality; Stephens et al. 2023). This could influence the estimation of trophic positions from stable isotopes (Hussey et al. 2014) and so influence the strength of the relationship between both approaches for describing the vertical food web structure.

Clustering of food web nodes is frequently examined to link ecosystem functioning and stability when analysed through networks (Thebault and Fontaine 2010, Stouffer and Bascompte 2011, Saint-Béat et al. 2015), while clustering measures are mainly used to study functional diversity and resource use variability in the stable isotope approach (Newsome et al. 2007, Rigolet et al. 2015, Newton 2016). Our study reveals positive associations of network clustering metrics with metrics describing clusters and trophic diversity in isotopic spaces. Food webs with many trophic groups in the network approach corresponded to a large convex hull in the isotopic space, likely because both reflect high functional diversity (Layman et al. 2007). This result supports and extends the findings of Jabot et al. (2017) that isotopic functional distances are positively linked with trophic functional distances in networks. New to our study, the modularity and number of modules in food webs, describing energy-source segregation among food web components (Gauzens et al. 2015), were also well associated with large core isotopic niches and centroid distances, which relate to diversity in resource exploitation (Layman et al. 2012). The two approaches can thus be complementary since the indirect quantification of energy flow allowed by stable isotope data can be interpreted to reflect the modularity in food web structure, and vice versa. In contrast, metrics designed to characterise energy pathways derived from benthic compartments were unrelated. This result could stem from the relatively strong overlap between the empirical δ^{13}C values of the two basal compartments that we used in our food web simulations, which likely challenged the ability of stable isotopes approaches to differentiate source use by consumers. Overall, joining these different clustering metrics will advance our understanding of how the clusters and trophic diversity detected through stable isotope analysis relate to ecosystem functioning and stability, patterns usually assessed using the network approach.

The network complexity of links and nodes in food webs has been identified as a key property of ecosystem dynamics (Dunne et al. 2005, Mougi and Kondoh 2016, van Altena et al. 2016). Thus, revealing viable equivalencies in the stable isotope approach could help incorporate an energy flow perspective into this understanding. At the moment, we can only identify that clustering in isotopic niches is associated with a higher trophic pathway diversity in networks. The other metrics describing complexity were difficult to associate with isotopic metrics alone. Finding equivalence for connectance, trophic generality and vulnerability is challenging owing to initial resolution asymmetry between the network approach (with links and nodes) and the pure isotopic approach (based on the isotopic space only, without definition of actual links) (Liew et al. 2018, Nielsen et al. 2018). This limitation generally applies to metrics directly related to the number of nodes or links between nodes in the network approach (Garvey and Whiles 2016, Majdi et al. 2018). Given that connectance is a fundamental attribute of food webs (Martinez 1992), a possible path forward may be to increase the number of sampled species and the number of tracers used in isotope studies (e.g. δ^{34}S or δ^{2}H; Hayden et al. 2021, Raoult et al. 2024) and apply isotopic diet analysis, perform compound-specific stable isotope analyses (Ohkouchi et al. 2017) or use fatty acid analyses (Rubenson et al. 2020). These approaches should increase the resolution of the different prey species contributions to consumer diets. Such developments would allow more refined description of energy flow pathways in a food web that may better reflect the complexity currently measured in network approaches.

The overall characteristics of the food web (richness of trophic nodes and interactions between food web compartments) often modulated the strength of the association between metrics (Brind'Amour and Dubois 2013, Jabot et al. 2017). We report that increasing coupling between energy pathways in food webs (here increasing the connection between the two food web compartments when simulating networks) tended to strengthen the associations between isotopic and network metrics. This suggests that disconnection between the different energy pathways in food webs may blur the association between network structures and isotopic spaces. Empirical food webs are never totally compartmentalized due to the presence of generalists and omnivorous species that couple food web compartments by drawing their energy from various basal resources and feeding at multiple trophic levels (Flaherty and Ben-David 2010, Gauzens et al. 2015). So, as this coupling is the general case in nature, the connections between isotopic and network metrics are expected to be particularly valuable to study empirical cases. By contrast, simulating increases in node richness tended to weaken metric associations because reaching a certain node richness could increase overlap in isotopic niches, and so ultimately reverse the trend of associations. The reshuffling of energy pathways, species richness and diversity is expected to occur as a result of environmental changes (Bartley et al. 2019) and so future studies should seek to identify how metric associations are modulated under these different perturbations, particularly in response to rapid global change.

Limitations and perspectives

Our modeling approach, coupled with global-scale empirical data, enabled the incorporation of realistic food web structures. Interestingly, only a restricted portion of the simulated isotopic spaces met our selection criteria (i.e. fell within the bounds of empirical isotopic metrics). Because simulated isotopic spaces were converted from simulated networks, we can speculate that only a small fraction of networks, among an infinite number of potential food webs, are realized in real ecosystems. In particular, unrealistic food chain lengths led to the highest number of unselected food webs, echoing pioneering works on limiting food chain lengths based on both approaches (Pimm and Lawton 1977, Post 2002a, Williams and Martinez 2004). In addition, further methodological considerations may be a source of variation for the associations between metrics. For instance, we observed slight differences in mean trophic positions that could emerge from the weighting procedure in network metrics (Kortsch et al. 2021). The variability found when focusing on specific metric associations in this study attests to the limited capacity for predicting network metrics from isotopic ones and vice versa. However, this study shows that metrics generally converge between the different approaches. Although we acknowledge that our results apply for networks obtained from the compartment niche model developed here and specific assumptions on interaction strengths, our approach remains general as it can be applied to any directed network model (e.g. cascade, stochastic block and trait-matching models), including more realistic estimations of interaction strengths (e.g. using allometric relations), or to empirical food webs. This opens more opportunities to analyse how different food web structures might affect the relations between network-based and isotopic-based metrics.

Although isotopic baseline variability and energy source overlap may vary among habitats and ecosystems, which could potentially modulate the identified relationships, we expect that our results apply across various terrestrial and aquatic ecosystems because we simulated key general properties of food webs (e.g. energy compartmentalization and modular organization) that are also well documented in terrestrial and marine ecosystems (Rooney et al. 2006, Gauzens et al. 2015). In pursuing a more unified approach to evaluating trophic interactions, the mapping of metric associations we provide may allow scientists to synthesize data and ideas across network and stable isotope approaches. This idea may also promote better integration of tools to study food web structure in diverse ecosystems. Expanding stable isotope data in food web research may also increase opportunities to ground-test many network-driven theories with new data. Similarly, emerging tracer techniques to resolve consumer diets, such as faecal or gut DNA metabarcoding, can be helpful to understand where species linkages may impact biochemical pools and flows. We encourage scientists to continue to test relationships between food web metrics to remove barriers between distinct approaches and learn about the consistency of theories explaining structure and function relationships in food webs, which is critical to advance ecological science.

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Author contributions

Chloé Vagnon: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Tyler Tunney**: Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Timothy Jardine**: Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Julian D. Olden**: Project administration (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Angus R. McIntosh**: Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Marie-Elodie Perga**: Conceptualization (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Michelle Jackson**: Project administration (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Javier Sánchez-Hernández**: Writing – original draft (equal); Writing – review and editing (equal). **Julien Cucherousset**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Elisa Thébault**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

The data used in this study are a subset of the ISOFRESH database available in a Zenodo data repository (doi: 10.5281/zenodo.14982323) and presented in Boulêtreau et al. 2025, the GATEWAy database available at the iDiv data repository https://doi.org/10.25829/iDiv.283-3-756 and the Mangal database available in a Zenodo data repository (doi: 10.5281/zenodo.16998). Data are also available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15349235.

Supporting information

The Supporting information associated with this article is available with the online version.

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