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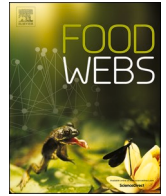
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Review

Food webs speak of human impact: Using stable isotope-based tools to measure ecological consequences of environmental change

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ABSTRACT

Linking their major biotic and abiotic components, food webs form the core of ecosystems, many of which are today exposed to multiple human impacts acting at several spatial and temporal scales. A food web perspective allows for a quantification of environmental change effects on both the structure of biological diversity and the functioning of ecosystems. Food web metrics based on stable isotope analysis (SIA) represent a promising way for an integrative assessment of these responses. While showing high sensitivity to environmental change, they are, however, rarely presented and discussed within a systematic mechanistic and hypothesis-driven framework. Here we first provide a global overview of anthropogenic impact types, their effects on food webs and the associated ecological mechanisms. Based on published studies from terrestrial, freshwater and marine ecosystems, we then demonstrate the versatility of SIA-based metrics, allowing for quantification of several key food web attributes and applicable across a wide range of human-induced impacts such as eutrophication, pollution, introduction of exotic species or connectivity interruption. We finally propose a guiding framework to make SIA application in the studies of anthropogenic impact on food webs more rigorous and enhance its potential for producing novel insights.

1. Introduction

Ecosystems across the globe are exposed to single and cumulative effects of anthropogenic pressures acting simultaneously at several spatial and temporal scales (Vitousek et al., 1997). This poses a major challenge in terms of research, legislation and management, and results in an urgent need of tools for quantifying the response of ecosystems and their components to environmental change. Such tools should ideally: (a) be universally applicable across different types of impacts and ecosystems, different levels of biological organization and a range of temporal and spatial scales; (b) be easily accessible and simple in use, interpretation and communication, and c) allow for retrospective and potentially long-term analysis (e.g. applicable to paleontological, historical and archaeological materials).

Taking an ecological network perspective is crucial for understanding and quantifying the effects of multiple stressors on ecosystems and their components, notably because biotic interactions within networks may modify direct and interactive stressor effects, as well as their

propagation to other groups of organisms (Bruder et al., 2019). Ecosystem resilience to environmental change appears to be intimately linked to the resilience of food webs (Kuiper et al., 2015), the scaffold of ecosystems linking their major biotic and abiotic components and translating the structure of biological diversity into ecosystem functions (Thompson et al., 2012). In their essence, food webs are adaptive networks of nodes (trophic entities) interacting over fluxes of energy and matter within and across ecosystems (Fig. 1a). Their organization is often viewed in the perspective of a vertical and a horizontal dimension: the former reflects the number of trophic levels and covers trophic chain length and omnivory, the latter reflects the number of nodes (diversity) within trophic levels (Duffy et al., 2007).

Metrics based on stable isotopes analysis (SIA) have been widely applied to characterize trophic interactions and energy fluxes in empirical studies. Directly affected by the isotopic composition of assimilated energy sources, stable isotope values of an organism's tissue provide time-integrated insights into its trophic relationships (Grey, 2006). Assessing stable isotope values of food web nodes allows

; SIA, Stable Isotope Analysis.

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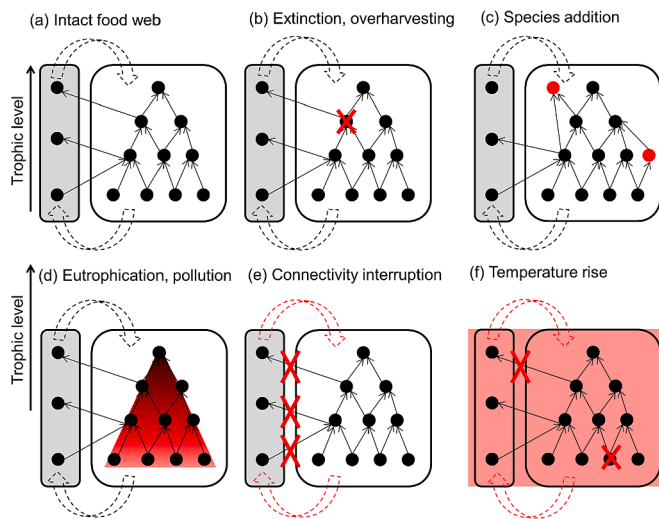


Fig. 1. Schematic representation of the direct effects of different impact types on food webs. Resources or consumers are represented by filled circles, arrows display the fluxes of energy and matter between them. The white- and grey-filled boxes represent two connected adjacent food webs (e.g., terrestrial and marine) and the red symbols represent the impact. The dashed arrows represent reciprocal exchanges (in terms of matter and energy) between adjacent food webs, with potential feedback loops occurring with a spatial or temporal lag. (a) An intact food web; (b) a food web subject to species loss due to extinction or overharvesting; (c) a food web affected by addition of non-native species at different trophic levels; (d) a food web exposed to bottom-up effects of eutrophication or pollution with potential biomagnification up the food chain; (e) a food web subject to the disruption of connectivity with the adjacent ecosystem; (f) a food web exposed to a global environmental effect such as temperature rise with general impacts on metabolism and specific impacts on certain nodes and fluxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

projecting the whole food web or its compartments in the “isotopic space” sensitive to both food web topology and the intensity of fluxes between single nodes. Importantly, advances in statistical analyses have allowed stable isotope ecology to rapidly expand the scope of inference way beyond simple comparisons of raw stable isotope values on biplots (Layman et al., 2012), even though the latter remain highly informative for retrospective studies often limited in possibilities for statistical analysis due to insufficient sample sizes (Szpak et al., 2018). However, as we will discuss further, scientific publications using SIA-based metrics for the assessment of anthropogenic effects on food webs rarely state explicit hypotheses or make links to theoretical concepts of ecology that could provide a better mechanistic understanding of the observed patterns.

Here, building upon existing ecological theory and a selection of published empirical studies covering a high diversity of SIA-based metric applications, we first summarize the types of anthropogenic impacts, their direct effects on food webs and ecological mechanisms they may trigger (e.g., cascading effects, competitive interactions, changes in feeding behavior). Second, we discuss the types of inference on food web attributes which can be derived from SIA with existing analytical tools and their responsiveness to anthropogenic impacts of different nature. Third, we suggest a roadmap for SIA-based food web metric application to studies of environmental change which would support selection of the most pertinent SIA-based response variables and formulation of quantitative predictions, and also increase reliability of SIA-based inference. SIA-based approaches are now being applied in practically all types of environments, from agroecosystems, forests, streams, lakes and coastal ecosystems, to more specific and complex cases, such as deep-sea or arctic environments. Without aiming at being exhaustive, we make an attempt to cover this diversity drawing upon illustrative examples to point out some of the specificities of different ecosystems in the context

of human impact assessment. While many highly interesting retrospective studies inform us on the long-term effects of anthropogenic impacts in both terrestrial and aquatic environments (e.g. Blight et al., 2015; Jacobs et al., 2017; Olden et al., 2019; Guiry et al., 2020), most of them are limited to considering raw stable isotope values of specific organisms. We thus cite only few of them to underline some specific points, choosing to focus this paper on the studies using SIA-based food web metrics.

2. Anthropogenic pressures and the nature of resulting impacts on food webs

Multiple human activities “attack ecosystems from the top to the bottom simultaneously” (McCann, 2011). Their effects on ecosystems in general and food webs in particular may affect different levels of biological organization and propagate further through different mechanisms (Fig. 1). The varying nature of the pressures determines (a) the “initial attack surface”, which may be specific nodes, a whole trophic level, specific fluxes or even the whole food web and (b) the types of possible ecological mechanisms that can be triggered in response. As a consequence, single or several food web attributes may undergo a change resulting in a new topological configuration, a change in the degree of control exerted by higher trophic levels on lower ones (interaction strength) or in the magnitude and direction of fluxes. Importantly, the changes in different food web attributes in response to pressures may occur simultaneously or progressively: for example a topological change may result in modification of fluxes and interaction strength between specific nodes or the other way around.

Removal (e.g., through overharvesting, destruction of habitat, introduction of novel pathogens) or addition (e.g., through deliberate or accidental introduction of non-native species) of specific nodes directly affects food web topology (Fig. 1b and c). This may result in a reorganization of the food web, due to a novel configuration of interspecific interactions (e.g., predation and competition) (Eby et al., 2006). Further propagation of the stressor effects depends on the structure and strength of trophic interactions (Hansson et al., 2013). When involving higher trophic levels in systems with strong top-down control (e.g., through top predators), the effects of topological change may propagate through cascading mechanisms (Estes et al., 2011). Inversely, if taxonomic identity and biomass of primary producers at the base of the food web are affected (due to e.g., eutrophication or exposure to pollutants), secondary effects may spread bottom-up along the food chain to higher trophic levels (Fig. 1d; Fleeger et al., 2003). In the case of contamination or toxic pollution, this may be accompanied by effect reinforcement across trophic levels from the bottom to the top of the food chain (i.e. biomagnification) (Vander Zanden and Rasmussen, 1996) or its attenuation through biodilution (Watanabe et al., 2008). Importantly, food web structure may affect the nature and magnitude of these effects. For instance, elevated trophic positions of predators in a food web exposed to eutrophication can result in higher accumulation of contaminants in their tissues (Kelly et al., 2006; Barst et al., 2020).

Not only single nodes or compartments, but whole fluxes of energy and matter within or across ecosystems may be directly modified by anthropogenic change (e.g. Fig. 1e). Terrestrial and aquatic ecosystems are linked by reciprocal exchanges of organic matter at several trophic levels (leaf litter input, insect emergence, transfers by mobile predators; Polis and Hurd, 1996; Baxter et al., 2005; Baruch et al., 2021). These play an important role in both donor and recipient ecosystem functioning and stability (Huxel and McCann, 1998). Riparian deforestation or introduction of a novel predator or a competitor may block reciprocal exchanges of organic matter, modifying the relative importance of allochthonous and autochthonous energy sources in both food webs (Wallace et al., 1997; Baxter et al., 2004; Middleton et al., 2013). Similar effects may be caused by disruption of longitudinal connectivity in rivers (e.g., dam construction) which impedes migration of diadromous fish and therefore the delivery of marine-derived nutrients to food webs of

Table 1

Examples of stable isotope niche assessment application to different levels of biological organization.

Level of biological organization considered	Species, community, or compartment concerned	Type of question explored	Reference
Population	Brown trout (<i>Salmo trutta</i>)	Trophic niche diversity of trout populations along a gradient of riparian land use management	Evangelista et al. (2014)
Population	Freshwater crab (<i>Potamonautes oveni</i>), red swamp crayfish (<i>Procambarus clarkii</i>)	Trophic niche breadth of a native crab species in the presence of an invasive crayfish	Jackson et al. (2016)
Population	Invasive ant (<i>Formica paralugubris</i>)	Trophic niche breadth of invasive ant populations in the native and introduced part of the species range	Balzani et al. (2021)
Species	Mammoth (<i>Mammuthus primigenius</i>) and other mammoth steppe herbivores	Historical niche breadth of mammoth and its adaptation to changing environmental conditions	Schwartz-Narbonne et al. (2019)
Species/Community	Fish community	Niche overlap between tropical and temperate coastal fish communities and individual species co-occurring under climate change	Kingsbury et al. (2020)
Species/Community	Passerine bird community and single species	Niche expansion of passerine species between natural, rural and urban habitats	Pagani-Núñez et al. (2019)
Community	Stream vertebrate and invertebrate community	Decline in the local trophic niche in response to deforestation and pathogen introduction	Morris et al. (2016)
Food web compartment	Benthic community	Change in the shallow-water benthic community niche following glacier retreat	Pasotti et al. (2015)
Food web	Food web associated with aquaculture farm	Food webs of the fouling community associated with coastal bivalve aquaculture farms compared to analogous non-farm structures	Maurin et al., 2019

upstream habitats (Wipfli and Baxter, 2010). The effects of subsidy disruptions between ecosystems may, in turn, affect feedback loops connecting donor and recipient ecosystems, which allow a part of the resources to be recycled back to the original system (Baruch et al., 2021). Conversely, human activities may also introduce artificial subsidies into ecosystems, such as human food refuse (Jessop et al., 2012), sewage and organic matter derived from agriculture or aquaculture (e.g., White et al., 2017). These affect specific compartments of the recipient food web and, through migratory consumers, may propagate to other ecosystems (Jefferies et al., 2004). Finally, changes in universal drivers of metabolic processes such as temperature may affect all nodes and fluxes of a food web simultaneously and in multiple ways (Fig. 1f; Tylianakis et al., 2008; Woodward et al., 2010). Thus global warming may modify not only the presence and biomass of species (nodes) or magnitude of reciprocal fluxes, but also their phenology and through it the dynamic coupling (topology and fluxes) between compartments of food webs and between food webs (Winder and Schindler, 2004; Larsen et al., 2016). Global change may also act through shifts in regional species distribution which may lead to a re-organization of major food web fluxes locally (Yurkowski et al., 2018).

Importantly, the ultimate food web response to a pressure is largely determined by the influence of anthropogenic pressures on species-level processes such as: competition for resources, shifts to new resources, spatio-temporal optimization of their sharing, and behavioral change (e.g., adaptation to changing predation pressure). Taking these mechanisms into consideration is a prerequisite for formulating hypotheses on the possible effects of specific pressure types on food web attributes, and for selecting the most appropriate response variables to test them.

3. Using stable isotopes to detect the effects of environmental change on food webs

Stable isotope analysis (SIA) has become a key technique in the empirical studies of trophic interactions (Boecklen et al., 2011; Majdi et al., 2018), and has been increasingly applied for quantifying human stressor effects on food webs (Mancinelli and Vizzini, 2015). The widespread use of SIA has been particularly stimulated by the emergence of the concept of the “isotopic niche” (Newsome et al., 2007) basing upon the Hutchinsonian n-dimensional ecological niche (Hutchinson, 1957). The multidimensional isotopic space occupied by the nodes of the food web is thereby viewed as a reflection of the realized ecological niche allowing for quantitative characterization of two major types of food web attributes: its topology, and the magnitude and direction of its fluxes. This perspective is applicable to several levels of biological organization from the stable isotope niche of a population (or a species in its range of distribution), a

community (e.g., fish community), a food web compartment (e.g., pelagic) to the whole food web of an ecosystem (e.g., lake) (Table 1). Importantly, new technical opportunities, such as compound-specific analysis, now allow including the microbial compartment into stable isotope studies with the perspective of getting a view on the “end-to-end food webs” connecting microbial to metazoan food webs (Middelburg, 2014). At present, application of CSIA to the microbial compartment is limited to specific biomarkers (Middelburg, 2014) and has a restricted utility in the field studies being labour intensive and costly and allowing in most cases only to distinguish between large taxonomic groups (e.g. green algae and diatoms versus cyanobacteria, phytoplankton versus bacteria or fungi versus bacteria; e.g. Bontes et al., 2006; Evrard et al., 2010; Pollierer et al., 2019). Future technical improvements are needed to reach a finer discrimination of prokaryotes and microscopic eukaryotes and refine the resolution of the food webs investigated using SIA.

The combination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ defining a 2D isotopic niche is particularly informative as it allows simultaneous examination of the horizontal ($\delta^{13}\text{C}$: variation within trophic levels) and the vertical ($\delta^{15}\text{N}$: variation along the food chain) dimensions of food webs. The variation of $\delta^{13}\text{C}$ values among primary producers of different type (e.g., algae, macrophytes, periphyton in aquatic ecosystems, and C_3 , C_4 and CAM plants in terrestrial environments; O’Leary, 1981) and origin (pelagic versus benthic, autochthonous versus allochthonous, photosynthetic versus methanogenic; Rounick and Winterbourn, 1986; Grey, 2016) allows tracking changes in major energy and matter fluxes in the food web. $\delta^{15}\text{N}$ variation reflects shifts in trophic position at the level of a single consumer (Minagawa and Wada, 1984), translated into trophic chain length variation at a community or food web level (Post, 2002). It may furthermore allow distinguishing between primary producers, as $\delta^{15}\text{N}$ differs, for instance, between plants with and without symbiotic N-fixing bacteria (Schmidt and Stewart, 2003; Höglberg, 1997). In addition, in aquatic ecosystems exposed to eutrophication, $\delta^{15}\text{N}$ variation may also reflect an enrichment in nitrogen due to agricultural or urban runoff (anthropogenic nitrogen sources; Oczkowski et al., 2016; Fry, 2006). The effects of increasing productivity may be particularly complex and span a wide gradient of negative and positive $\delta^{15}\text{N}$ shifts (from -10‰ to $+10\text{‰}$) across different trophic levels (Guiry, 2019).

Stable isotopes of other elements add further pieces of information to food web studies, and can be integrated with carbon and nitrogen into several multidimensional statistical metrics. SIA of sulfur ($\delta^{34}\text{S}$) used in combination with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ allows for a better distinction between multiple primary producers in marine and wetland ecosystems (Connolly et al., 2004). In estuaries and coastal systems, differences in the sources of inorganic sulfur (sea-salt sulfate, sulfate ions from precipitation, sulfide from anoxic sediments) (Kaplan et al., 1963; Nriagu and Coker, 1978; Fry

et al., 1982) result in substantial $\delta^{34}\text{S}$ variations. The latter may, for instance, allow for distinction between marine algae and seaweeds, terrestrial plants and marsh grasses and their contribution to estuarine and coastal food webs (e.g. saltmarsh and seagrass ecosystems) (Peterson et al., 1985). Nonetheless some caution should be taken when using sulfur isotopes with careful consideration of their distribution along the river-sea gradient strongly affected by spatio-temporal patterns of salinity (Fry and Chumchal, 2011). Sea-spraying may also potentially have confounding effects in coastal and island systems, changing the isotopic signature of terrestrial food sources in proximity of the sea (Guiry et al., 2020).

Stable isotope ratios of two further elements, H and O, reflect both diet and drinking water sources for consumers and show consistent patterns of variation e.g., between terrestrial and aquatic primary producers as well as between trophic levels (Vander Zanden et al., 2016). Deuterium (δD) has been successfully used as a tracer of autochthonous and allochthonous organic matter as well as of methane-derived subsidies in aquatic food webs (Doucet et al., 2007; Deines et al., 2009). As the patterns of hydrogen and oxygen isotopes vary geographically, combining $\delta^2\text{H}$ - and $\delta^{15}\text{O}$ -based isotopic niches with $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ -based isotopic niches allows considering resource use at different spatial scales (Rader et al., 2017).

Stable isotopes of bioessential and trace metals (components of earth surface processes, pollutants, and also nutrients for organisms: e.g. Fe, Cu, Zn, Ca, Mg, Hg, Pb) have also been suggested as informative tracers. While their major field of application remains in environmental geochemistry, our knowledge on their involvement in biological cycling and behavior within food webs (e.g., trophic fractionation) has expanded (Wiederhold, 2015). As a consequence, they are currently not only used for tracing pollutants across food webs, but are also starting to be applied for diet reconstruction and for characterizing food web attributes in both modern and ancient environments (e.g., Jaouen et al., 2013; Martin et al., 2017).

Finally, another promising development that allows us to increase the number of tracers and improve the precision of SIA-based estimates is replacing or complementing bulk analysis with compound-specific SIA (fatty and amino acids) mostly of C, N and H. For instance, $\delta^{13}\text{C}$ of essential amino acids is being increasingly used to achieve a finer separation between sources in terrestrial and aquatic ecosystems (O'Brien et al., 2005; Vokhshoori et al., 2014). $\delta^{15}\text{N}$ of certain amino acids allows for a more precise estimation of consumer trophic position (Chikaraishi et al., 2009) and for tracing primary resources (McCarthy et al., 2013).

In the examples brought up below, we focus on the stable isotopes of five elements which are most commonly used in trophic studies: C, N, S, O & H. We structure the following section according to three key types of SIA-based statistical inference: mixing models, circular statistics and niche-based metrics, allowing us to assess different facets of food web change in response to human impacts and their mitigation.

3.1. Mixing models

Based on the stable isotope values of the consumers and their putative sources, mixing models estimate the dietary contribution of each source to a consumer (typically expressed in %; Phillips et al., 2005) and allow quantifying its degree of specialization and omnivory (e.g., Jackson et al., 2017). They are particularly useful for distinguishing between allochthonous and autochthonous sources of energy and thus modification of subsidy fluxes for example due to a change in land use (Jonsson and Stenroth, 2016) or landscape connectivity (e.g., reconnection of terrestrial and freshwater food webs to the marine environments; Tonra et al., 2015). Furthermore, based on the above-mentioned isotopic differences between organic matter sources of different origin, mixing models allow tracking pathways of anthropogenic carbon, nitrogen and sulfur integration into food webs (e.g., agricultural and urban waste, pellet material from fish farms, angling baits; Wayland and Hobson, 2001; Birkhofer et al., 2011; Bašić et al., 2015). They have also been efficient for detecting consumer diets shifts following disruption of allochthonous subsidies (Brauns et al., 2011) or introduction of a novel

species (Kovalenko and Dibble, 2014). When applied to top predators, mixing models produce quantitative estimates of the whole food web or target compartment reliance on specific carbon sources as well as of the degree of coupling between distinct energy channels (Vander Zanden and Vadeboncoeur, 2002) and thus also its modification due to human activities (Evangelista et al., 2014). Mixing model outputs may also be used to parametrize topological food web models (e.g. Calizza et al., 2015) and improve the food web flow estimates of linear inverse models such as Ecopath (Van Oevelen et al., 2010), which provide highly valuable tools for assessing the effects of disturbance in general and anthropogenic impacts in particular.

An important advantage of using mixing models is that formulating specific testable hypotheses and interpreting model outputs is relatively straightforward. For instance, the fact that “contribution of algae to the diet of a consumer increases from X% to Y% in response to deforestation” can be easily communicated both to an expert and a non-expert. Simple metrics expressing proportional diet similarity can be calculated based on mixing model output and expressed in values between 0 (no common food items) and 1 (same food items in the same proportions) (Costantini et al., 2018). One of key limitations for the application of mixing models is their sensitivity to the number and reliable identification of sources. A study system with a high number of potential sources with overlapping isotopic values may render mixing model output uninterpretable, and, at the same time, failing to cover all of the key sources may lead to erroneous results (Phillips et al., 2014). Importantly, the widespread use of mixing models based on Bayesian inference today allows for a more accurate assessment of observed effects and associated uncertainties as well as for an incorporation of multiple sources (Phillips et al., 2014).

3.2. Circular statistics

Vector-based circular statistics quantify directional changes of mean position of an individual (e.g. related to its mobility or ontogenetic change) or of a group (population, species, community) within isotopic space (Schmidt et al., 2007). The direction and the magnitude of change are assessed to compare points in time (e.g., before and after perturbation) or space (e.g., control versus treatment). This approach has been used to detect spatial or temporal shifts of whole food webs and their components in response to eutrophication (Xu et al., 2014), invasive species introduction (Schmidt et al., 2007; Rogosch and Olden, 2020), change in agroecosystem management (Duyck et al., 2011) and massive habitat modification (Freedman et al., 2013). The significance of shifts in vector length and angle relative to the centroid position can be assessed (Turner et al., 2010), and these outputs of circular statistics are often discussed similarly to mixing models in terms of changes in reliance of the food web or its components on specific sources. However, their relation to actual food web attributes and ecological mechanisms is comparably less clear, which makes them less intuitive for interpretation or formulation of specific predictions.

3.3. Niche-based metrics

The toolbox for the statistical analysis of SI data has been considerably enriched by the introduction of metrics quantifying different aspects of food web node distribution in the multidimensional isotopic space which integrates changes of both food web topology and fluxes. A proxy for overall food web diversity, the isotopic niche size (quantified as convex hull, standard ellipse area or kernel utilization density; Jackson et al., 2011; Eckrich et al., 2020) has been frequently applied to assess food web or population response to habitat modification, shrinking or fragmentation (Layman et al., 2007b; Resasco et al., 2018; Pagani-Núñez et al., 2019), forest and riparian vegetation management (Evangelista et al., 2014; Kemp, 2019), pollution (Hogsden and Harding, 2012), and extinction (Barnum et al., 2015). Decrease of a trophic niche size at population or food web level is often interpreted in terms of trophic diversity loss. Kemp (2019), for instance, found a 78% of

reduction in bat diet trophic niche with 26% of tropical forest decline on Borneo and explained it by a reduced diversity of basal resources and insect prey available to bats in degraded forests. An opposite effect was achieved by management efforts aiming to diminish human impact: invasive rat (*Rattus rattus*) eradication on Palmyra Atoll was followed by a pronounced expansion of the isotopic niche of the native land crab (*Geograpsus* spp.) community due to release of several crab species from predation and competition with rats (Nigro et al., 2017).

Metrics quantifying isotopic niche dimensions along a specific axis, such as food chain length, $\delta^{15}\text{N}$ range, $\delta^{15}\text{N}$ -based trophic position and $\delta^{13}\text{C}$ range, have been found particularly responsive to direct topological change such as loss or addition of top predators (Sagouis et al., 2015) or of basal sources (Donazar-Aramendia et al., 2019), but also to general habitat degradation (e.g., Nakagawa et al., 2007). When an anthropogenic impact primarily modifies competition and functional redundancy within the food web, patterns of organism packing in the isotopic space may reveal to be highly informative. Along with statistical methods that allow quantifying the degree of n-dimensional isotopic niche overlap (e.g., Swanson et al., 2015; Eckrich et al., 2020), metrics, such as the nearest neighbor distance and its variance, evenness, uniqueness and mean centroid distance, were proposed for quantifying the degree of trophic redundancy within food webs, several of them applicable to multidimensional isotopic space (Layman et al., 2007a; Cucherousset and Villéger, 2015; Rigolet et al., 2015). Using such metrics allowed detecting a decrease in trophic redundancy (and thus of food web stability) in stream food webs in response to land use change (Price et al., 2019) and in coastal food webs as a consequence of sealing (Saporiti et al., 2014). Finally, any pressures affecting relative biomass distribution between trophic levels and diversity within trophic levels may modify the food web shape, typically characterized by the relation between the horizontal and vertical food web dimensions (e.g., Graham et al., 2017). Such shifts can be easily visualized in isotopic space and quantified using Euclidian distances of isotope values for pairs of species (Fry and Davis, 2015).

3.4. Current limits of SIA application for impact assessment

As evident from the numerous examples mentioned above, SIA-based metrics have already been widely used for detecting the impacts of anthropogenic change on different food web attributes. However, in the majority of published studies, links between ecological mechanisms and the SIA-based metrics selected as response variables are rarely discussed and, even more rarely, are specific hypotheses on environmental change effects on stable isotope values explicitly formulated and tested (but see e.g. Kisse-Machumu et al., 2017; Johnson et al., 2018; Burdon et al., 2019). This is partly due to persisting gaps in our knowledge on the causal relationships between novel pressures and food web attributes and partly due to weak links between stable isotope ecology and ecological theory. In the following sections, we formulate a roadmap for future research (Fig. 2) suggesting several steps that would improve SIA application in the studies of anthropogenic impact on food webs and enhance its potential for producing new insights. We illustrate them with an example taken from the literature (Fig. 3).

4. A roadmap for SIA application in the study of environmental change

4.1. Formulating initial hypotheses (Fig. 2a)

Formulating testable hypotheses is a key tenet of science and an important guide for the planning of experimental work and the selection of the most appropriate response variables to measure and metrics to assess. Our knowledge on the drivers of isotopic patterns within ecosystems is rich but still incomplete, especially in view of the complexity of interacting ecological, biochemical and biogeochemical processes that may be involved at different levels (from isotopic routing within organisms to complex patterns of organic matter transport and cycling

Roadmap for the anthropogenic impact assessment with SIA

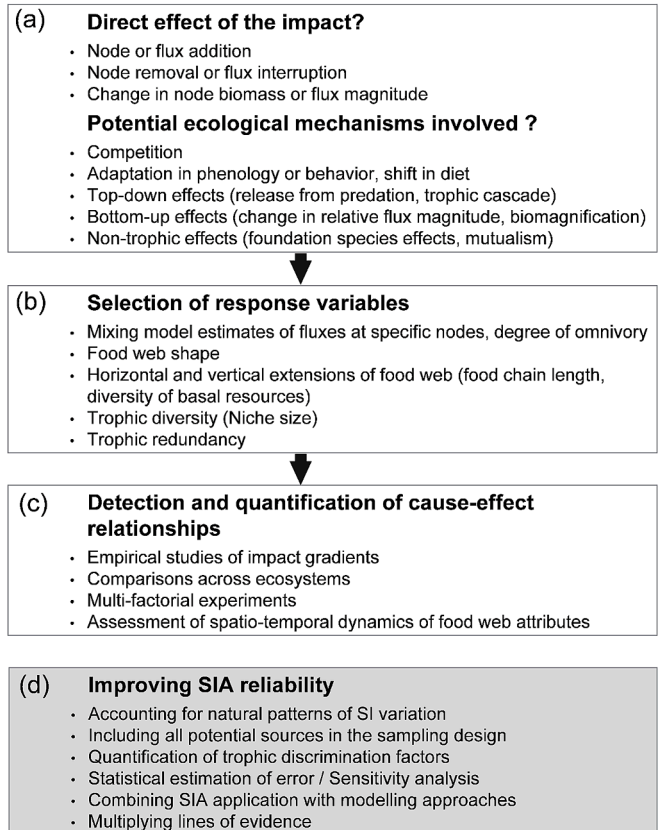


Fig. 2. A roadmap for application of SIA-based approaches in the assessment of anthropogenic impacts on food webs.

within and across ecosystems). The multifactorial nature of potentially interacting human pressures adds to this complexity. Nonetheless we believe that it is important to systematically make the intellectual effort of placing any study aiming to apply SIA-based tools to human impact assessment on food webs in the framework of ecological theory and, when possible, formulating clear testable hypotheses.

To facilitate this task, our suggestion is to start any study involving SIA for environmental impact assessment by considering the following questions:

- What is your degree of knowledge of isotopic patterns in your study system (e.g. whether food web structure and key sources of isotopic variation have been identified)? Are the phenomena you are interested in understanding likely to be associated with a degree of isotopic variation that is analytically meaningful?
- What is the expected direct effect of the considered pressure type on the food web (in terms of Fig. 1): for example node, flux, or basal resource addition or elimination; increase or decrease of their biomass or magnitude?
- What are the possible ecological mechanisms which may be triggered in response to this direct effect: for example competition, shift in diet, top-down or bottom-up propagation of effects? These mechanisms may notably also involve non-trophic interactions (such as foundation species effects; Borst et al., 2018).

When your knowledge of the study system allows for it, considering these questions should help formulate specific hypotheses on the possible food web effects of the anthropogenic stressor in question and select appropriate levels of biological organization for response assessment. For instance, in Johnson et al. (2018), three ecological hypotheses were formulated for the lake Huron food web response to the

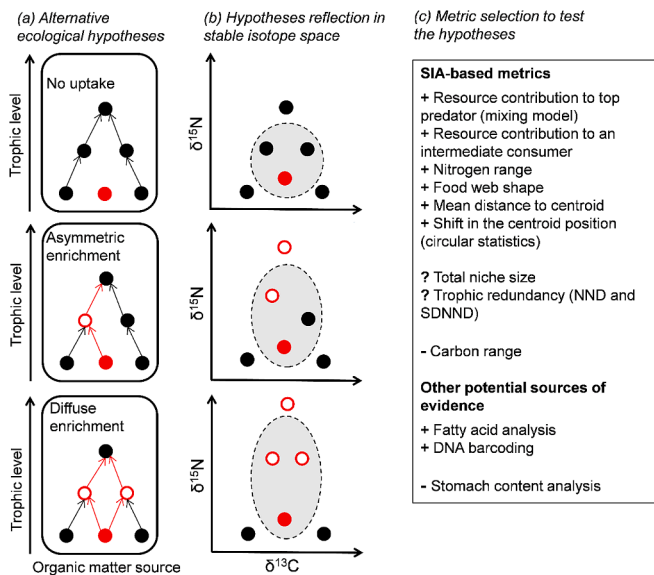


Fig. 3. An example of SIA-metric selection to test alternative ecological hypotheses in the case of anthropogenic subsidy addition to a freshwater food web (based on Johnson et al., 2018). The filled red circle represents the added resource. Red arrows and hollow red circles represent food web pathways integrating novel resource. The shaded circle with the hatched line represents the standard ellipse characterizing the isotopic niche occupied by the food web. a) Schematic representation of a three-level food web with two energy pathways leading to the top-predator; b) hypothetical changes reflected in the isotopic space. c) Potential measures of response with high (+), unknown (?) and no (–) capacity of discriminating between hypotheses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

introduction of aquaculture-derived organic matter: (a) no uptake by the food web, (b) asymmetric uptake through one of the energy flow channels (e.g., pelagic), or (c) symmetric uptake by both pelagic and benthic channels (Fig. 3a).

4.2. Selection of response variables (Fig. 2b)

As a second step, SIA-based variables most appropriate for investigating food web response to the studied pressure type should be identified from the available toolbox of statistical metrics. Different metrics provide complementary pieces of information on the changes undergone by the food web and focusing on single metrics may be inappropriate or even misleading. For example, trophic redundancy within a food web may be increased both through an addition of a novel consumer within the food web, and through the loss of a key basal source. In the first case, the total size of the isotopic niche is expected to stay the same, while, in the second case, it is expected to shrink following a loss of trophic diversity within the food web. When using a combination of several SIA-based metrics, different axes of change may be distinguished and the risk of missing an effect on a particular food web attribute can be avoided.

Importantly, the effects of a stressor on specific food web nodes may be different if not opposite depending on the position of the node considered. For example, disruption of connectivity between marine and brackish habitats in Bahamian tidal creeks strongly reduced potential prey diversity of a mobile marine top predator (*Lutjanus griseus*, or grey snapper) resulting in shrinking of its isotopic niche (Layman et al., 2007b). The same landscape fragmentation released a lower trophic level fish (*Gambusia hubbsi*) from predation and led to diversification of its trophic (and thus isotopic) niche (Araújo et al., 2014). This work illustrates, that, while considering anthropogenic effects on specific food web nodes may help reveal mechanisms of ecological response (e.g.,

competition, resource switching), considering a higher biological level (a food web compartment or the whole food web) may be necessary to capture the overall effects on the food web.

In the lake Huron example (Fig. 3b), a novel introduced resource had a significantly higher $\delta^{15}\text{N}$ values than natural baselines. It could thus be expected, that integration of aquaculture waste would affect most significantly metrics sensitive to the vertical food web axis (nitrogen range and food web shape), as well as mixing model estimates of source contribution to consumers integrating this novel source of organic matter. Other sources of evidence, such as fatty acid analysis or DNA-barcoding could further reinforce the reliability of SIA-based conclusions in this case (Fig. 3c).

4.3. Detection and quantification of cause-effect relationships (Fig. 2c)

A major constraint for formulating ecologically sound hypotheses currently lies in our limited understanding of shape and strength of relationships between SIA-based food web metrics and different types of anthropogenic impacts. Thus, while most studies using SIA-based metrics have been limited to control-impact and/or before-after designs, very few have assessed the response of SIA-based structural metrics along a gradient of disturbance intensity. Importantly, these relationships may also be non-linear or limiting rather than central. For instance, Evangelista et al. (2014) found a hump-shaped relationship between canopy cover and the trophic niche size of brown trout (*Salmo trutta*) populations in headwater streams, pointing at the existence of a forest management optimum at which the fish feed on the broadest range of resources and act as most effective couplers of food web channels based on autochthonous and allochthonous energy. In the above-mentioned study of Layman et al. (2007b), a hyperbolic decay model was best at describing the response of grey snapper niche width to a gradient of tidal creek disconnection from the ocean. Threshold-type relationships may be hypothesized in the food webs of the systems where alternative stable states and regime shifts are possible (Andersen et al., 2009). For instance, drastic shifts between overall reliance on pelagic and benthic energy pathways (estimated using mixing models) have been reported for lakes exposed to eutrophication (Xu et al., 2014). More studies applying SIA-based metrics along impact gradients should clarify the shape of such relationships and enhance our capacity for making quantitative predictions and detecting proximity to tipping points. The real-world complexity with multiple processes shaping stable isotope patterns (not all of them yet fully understood) and multiple stressors affecting ecosystems make such studies particularly challenging and not always possible in the field. In some cases, controlled experiments of multi-factorial design may allow to better disentangle these processes as well as identify potential interactions between the effects of different impact types (O’Gorman et al., 2012).

High spatio-temporal dynamism of food webs remains a clear challenge for application of any empirical food-web based assessment of ecosystem condition. Food webs in most ecosystems are linked by energy and matter fluxes with neighboring ecosystems and experience pronounced temporal dynamics: e.g. both autochthonous and allochthonous prey availability changes throughout the year; consumer requirements for prey change too (McMeans et al., 2015). An increasing body of evidence suggests that taking temporal (seasonal, inter-annual or successional, e.g., Dalu et al., 2017) dynamics of food web interactions into account is indispensable for understanding their structure and resilience to disturbance. Thus, the importance of an allochthonous subsidy for a stream food web differs enormously depending on the moment of the year when it is delivered (Nakano and Murakami, 2001). Consequently, the timing of subsidy disruption due to human impact (e.g., riparian vegetation cutting) will determine the nature of its effect, and whether it will translate into strongly destabilizing or rather neutral consequences for the food web. Mobile consumers likewise play an important stabilizing role allowing for spatio-temporal couplings within and across food webs (McCann and

Rooney, 2009). Their arrival or disappearance due to environmental change may thus have grave consequences for food webs. A single stable isotope sampling in a year reflects only a “snapshot” of such food web dynamics, even though a certain temporal perspective may be added if several types of tissues (Martínez del Río et al., 2009), or several compounds are analyzed (Nielsen et al., 2018). Increasing the number of samplings in space and time taking into account intra- and inter-annual dynamics would allow for a better detection of the potentially coupling or de-coupling effects of environmental change. In some cases, sampling radiocarbon-dated layers of slowly forming tissues such as bones or scales of long-living animals (particularly interesting for top predators) may provide a very exciting historical record of environmental change effects (e.g. Olden et al., 2019).

4.4. Improving SIA reliability (Fig. 2d)

Sources of uncertainty related to stable isotope analyses have already been widely discussed in literature (Martínez del Río et al., 2009; Phillips et al., 2014; Nielsen et al., 2018). Some of them are intrinsic to the choices made for the SIA application (e.g., sampling design, assumptions made on trophic fractionation) and represent a more or less avoidable “noise”. Others originate from true ecological processes (e.g., seasonal or ontogenetic shifts in diet or dispersal processes) or the type of anthropogenic impact, and, if correctly taken into account in the study design, represent an opportunity for a better understanding of the food web structure and its responsiveness to environmental change.

A key prerequisite for making any inference on food webs based on SIA is a good understanding of patterns of variation in SI values of sources. While SIA is usually reliable for distinguishing between sources derived from distinctly different habitats (terrestrial-aquatic, marine-freshwater, pelagic-benthic), source differentiation at a finer scale may be challenging (Jabot et al., 2017). For instance, stable isotope similarity of different prey types may impede SI-based distinction between contributions of these sources and lead to an underestimation of the consumer diet diversity (Phillips et al., 2014). Additional variation may be introduced by the ecosystem-specific spread of isotopic values between the basal sources (Hoeinghaus and Zeug, 2008; Brind’Amour and Dubois, 2013), ecosystem-specific metabolic processes (e.g., in soils Hyodo et al., 2010), regional factors such as climate or circulation (Oczkowski et al., 2020) or by systematic gradients in stable isotope value distribution (e.g., along the upstream-downstream axis, or a salinity gradient; Newsome et al., 2010; Hette-Tronquart et al., 2016). In retrospective studies, the effects of variation in atmospheric CO₂ or surface nitrate (ocean) on the isotopic baselines have to be taken into account (Espinasse et al., 2019). It is thus important to be able to discern the effects of natural sources of variation from the actual effects of the investigated type of environmental change.

A key condition for getting ecologically sound SIA-based estimates of food web structure is sampling all sources relevant for the food web compartment studied (Phillips et al., 2014), including novel anthropogenic sources of energy and matter such as waste inputs, which may be initially unknown. Great care should be taken when defining sampling size (Pearson and Grove, 2013; Rossman et al., 2016) and when considering simplifying sampling design (e.g., aggregation of isotopically similar sources or several life stages of a consumer), as this may lead to averaged values with no ecological meaning (Phillips et al., 2014). Intra-specific or intra-guild variation may play a key role as a basis for population and food web resilience to environmental change (Des Roches et al., 2018) and should be explicitly accounted for (e.g., Semmens et al., 2009). Furthermore, the trophic niche of many organisms changes over their life cycle (e.g., Zhao et al., 2014; Golikov et al., 2018), and they may respond to anthropogenic pressures differently at different ontogenetic stages. To detect such effects, distinct life stages or body size classes should be treated as separate entities in the statistical analysis of stable isotope data or, alternatively, continuous ontogenetic shifts may be modeled (Hertz et al., 2016).

Estimates of mixing models and those of the trophic level number and food chain length are particularly sensitive to trophic discrimination factors (TDFs, the differences in isotopic composition between an animal and its diet) (Phillips et al., 2014). TDFs may vary substantially depending on the environmental context (e.g., temperature or resource limitation), the trophic position and physiological status of the consumer, as well as fat and protein content of the energy source (McCutchan et al., 2003; Florin et al., 2011; McMahon et al., 2015). For hydrogen and oxygen, TDFs also depend on the isotopic mass balance of water and water-tissue fractionation during biosynthesis (Vander Zanden et al., 2016). This source of error may in many cases be reduced by experimental estimation (e.g., Barnes et al., 2008) or conducting compound-specific rather than bulk SI analysis (Hobbie and Werner, 2004; Chikaraishi et al., 2009). Importantly, sources of TDF variation may be themselves intrinsic to human impacts. For instance, sites affected by hydropeaking often have a distinct hydrological and temperature regime. This may induce an additional variation in SIA-based metrics, as already observed in streams naturally differing in temperature regime (Hette-Tronquart et al., 2013) or exposed to different flow conditions (Singer et al., 2005).

Altogether this brings us to the importance of keeping in mind the fact that stable isotope niche never exactly equals the dietary niche, but rather represents its more or less distorted reflection in the isotopic space based on the time-integrated record of the actually assimilated part of the ingested food (Hette-Tronquart, 2019). An optimal use of SIA remains in combination with other approaches such as stomach content analysis, use of other tracers (e.g., fatty acids analysis), behavioral observations, field and laboratory experiments or DNA analyses (Majdi et al., 2018; Nielsen et al., 2018). Use of multiple stable isotopes (Rossman et al., 2016), as well as direct integration of stable isotope data with other types of information, e.g., weighting food web nodes by biomass and abundance (Cucherousset and Villéger, 2015; Rigolet et al., 2015), integrating biomass into trophic position estimates (iTP; Ishikawa et al., 2017) or incorporating prey abundances into mixing models (Yeakel et al., 2011), offer promising ways of increasing quantitative rigor of SIA-based metrics and better distinguishing true cause-effect relationships from noise. Recently developed statistical packages based on Bayesian inference allow for the estimation of uncertainty related to SIA-based metrics, be it source contributions to diet of single or multiple consumers (Kadoya et al., 2012), trophic level and trophic position estimates (Jennings and Van Der Molen, 2015; Quezada-Romegialli et al., 2018) or niche-based metrics (Jackson et al., 2011). Bayesian statistics offer major advantages in comparison to frequentist statistics not only in terms of a more reliable estimation of the magnitude of effects and associated uncertainty, but also in terms of communication of the latter to non-experts. A particularly powerful Bayesian-inference based analysis tool is offered by inclusive modelling frameworks, such as MixSIAR (Stock et al., 2018), allowing for integration of multidimensional data and multiple model comparison. Finally, food web simulations integrating stable isotope data (e.g., Brind’Amour and Dubois, 2013; Jabot et al., 2017) allow us not only to evaluate the reliability of SI proxies of food web properties, but also to explore their relation to other food web attributes such as connectance or interaction strength that are difficult to quantify empirically.

5. Conclusions and outlook

SIA-based food web metrics offer a highly versatile set of tools, promising a multitude of applications in ecological research as well as in ecosystem management, notably assessment of ecosystem condition and its response to restoration. Highly responsive to a very wide range of impacts, they also comply with other requirements expressed in the beginning of this review: applicability across different ecosystems, different levels of biological organization and different spatio-temporal scales (including a possibility for long-term retrospective studies), relative accessibility and easiness of interpretation. Substantial

knowledge has already been accumulated on the potential sources of variation driving stable isotope patterns in ecosystems and a row of methodological tools have been proposed for quantifying them and taking them into account in the SIA-based food web studies.

We aimed here to cover at best the diversity of current SIA applications for the assessment of environmental change effects on different ecosystems. One of key observations this review allowed us to make is the fact that different bodies of literature (terrestrial versus freshwater versus marine ecology, biology of contemporary ecosystems versus paleobiology, biology of macro-organisms versus microbiology) appear rather isolated, which probably slows down the reciprocal transfer of novel concepts and methods emerging in the field of stable isotope ecology. Thus, while stable isotope approaches are rather widely used in terrestrial literature, we found surprisingly fewer studies applying niche-based metrics in these environments compared to aquatic literature, where these metrics have initially been proposed and are very widely used for over a decade. Similarly, while the links between the long-term patterns of environmental change affecting species and ecosystems and their responses to ongoing global change are evident, few studies have yet integrated data sets from modern and historical data sets (but see Guiry and Hunt, 2020). Such studies are clearly a promising venue for advancing the reliability of our interpretation of both historical patterns and of current observations of food web response to change. The last missing connection refers to the frequent absence of the microbial compartment in our view of the food webs in their isotopic reflection. This is largely due to some persisting technical challenges and also knowledge gaps limiting our capacity to work on the same level of precision (population, species) for microbes as for macro-organisms in the wild. Hypothesis-driven laboratory experimentation may allow for some advancements in our knowledge on microbial compartment response to different facets of environmental change.

Declarations of interest

None.

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