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Editorial

Questioning the roles of resources nutritional quality in ecology

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Our understanding of ecosystem functioning is strongly linked to the study of predator–prey relationships and food web structures. However, trophic ecology has often focused on identifying taxonomic relationships and quantifying the biomass or energy ingested by consumers, but has often failed to integrate the importance of the nutritional quality of resources in ecological dynamics. Underlying this gap is the multi-dimensional nature of resource quality which has hampered any consensus on the definition of resource nutritional quality. In this special issue, we aimed at gathering a subset of articles exemplifying the diversity of variables by which resources quality is quantified, the diversity of research topics that can be tackled in ecology – from physiological or evolutionary aspects to ecosystem processes – and propose some perspectives on the integration of nutritional quality within broader ecological concepts. Using a semi-automated literature analysis, we map the current landscape of the 'resources nutritional quality' research of the last 30 years. We depict how it has been quantified through physical, biological or chemical indicators, the use of these parameters being largely dependent on the type of ecosystem studied and on the investigated ecological process. We then position the articles published in this special issue of Oikos within this landscape, showing they cover a small but relatively well representative subset of the domains of resources quality-related issues. Articles in this special issue browse a range of individual and population-level approaches (embracing evolutionary questions) to community related questions, include methodological issues and ecosystem-wide approaches using trophic quality indicators as tracers of resources origin. Based on these studies and on the literature review, we identify a non-exhaustive list of challenges and perspectives of research that we consider of highest priority in the large topic of trophic ecology.

Keywords: ecological stoichiometry, literature analysis, macro and micro-nutrients, nutritional geometry, trophic ecology

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Introduction

The nutrition of consumers has long been proposed as a major determinant of community structures and ecological processes in ecosystems (Elton 1927, Lindeman 1942). Resources availability regulates numerous individual or population parameters such as consumers' physiology, life history traits or some behavioural parameters, while ultimately shaping communities and affecting ecosystem processes. First based on a quantitative approach (e.g. how much biomass/basal resources is/are available in the ecosystem and transferred to upper trophic levels?), it has progressively included more qualitative aspects of resources (e.g. are the resources edible, digestible, bringing essential compounds?; Odum 1953, Boyd and Goodyear 1971, Scriber and Slansky 1981). Thus, in different ecosystems and trophic levels, it appeared that certain dynamics of populations, communities or ecosystems could depend on the sole quantity of available resources but also on the quality of these resources (Boyd and Goodyear 1971, Österblom et al. 2008). While the need to consider the 'resources quality' in ecological questions has been acknowledged, there is however no consensus on how to define this quality as it can refer to a wide range of parameters.

To take into account the importance of resources quality in ecological processes, different frameworks have been developed in the past decades, focusing on distinct physico-chemical or biochemical parameters (Wagner et al. 2013). Nutritional geometry (Simpson and Raubenheimer 2012) focuses on general descriptors of resources biochemical composition, including energetic macronutrients (proteins, carbohydrates and lipids), micronutrients (vitamins) or allelochemicals and fiber contents. In contrast, the Ecological stoichiometry framework (Sterner and Elser 2002) focuses on chemical elements. Those elements of focus are mainly carbon (C), nitrogen (N) and phosphorus (P), but they can also be extended to all other essential and non-essential elements (Karimi and Folt 2006). More specifically, the Ecological stoichiometry framework considers the balance between elemental requirements of consumers and elements availability in their resources, explicitly including the consequences of trophic interactions on elemental cycles. Some authors also considered the importance of some specific biochemical compounds (the 'biochemical view of trophic interactions'; Müller-Navarra 2008). This perspective focuses on important molecules such as long chain poly unsaturated fatty acids – LC PUFAs – sterols, or amino-acids, which, when not present in sufficient amounts in the food resource, are susceptible to limit the consumers' performances or the biological production of ecosystems (Müller-Navarra et al. 2004). Despite the recent attempts to combine these approaches in common conceptual frameworks (Sperfeld et al. 2016, 2017, Anderson et al. 2020, Ruiz et al. 2021), it still appears that the different visions of nutritional quality are rarely integrated.

One question that arises is whether the difference in parameters selected to describe and quantify resource quality between ecosystems, species or trophic levels depends on the cultural and historical artefacts of the researchers (e.g. based on the historical development of the different sub-disciplines in different ecosystem types), or reflects true differences in ecological functioning. We also question whether some resources quality-related parameters are more universal than others.

The aim of this Oikos special issue entitled 'The role of the nutritional quality of resources in ecosystem functioning' was to provide an up-to-date, general overview of how ecologists consider resources quality in their studies, and propose some thoughts on the determinants of resource quality and the importance of its consideration in future studies. The contributions published in this special issue are grounded within an exhaustive mapping of the current state of literature, based on a semi-automated literature analysis. We analyse how food quality has been quantified in ecological research and evaluate how much food quality indicators differ between targeted ecosystems, organisms and ecological questions. For full transparency, we detail the approach by which we built this map. The articles published in this special issue are then positioned on the landscape of nutritional quality revealed by the literature map, opening the discussion on the multifactorial nature of resources quality. Finally, based on some articles of the special issue and the results of our literature analysis, a list of future directions of research is proposed.

Mapping the current landscape of resources quality research

Overall methodology

To analyze the diversity of articles dealing with resource quality, we conducted a bibliometric analysis by semi-automatic text mining, using the litsearch R-package (Grames et al. 2019). The approach included a preliminary Web of Science search (1991–2020) using the terms ('nutrition* quality' OR 'quality prey' OR 'quality food' OR 'quality resource*' OR 'diet quality' OR 'resource* quality' OR 'food quality' OR 'prey* quality') and restricting Web of Science categories to fields related to environmental sciences and Ecology. This research, conducted on 20 November 2020, returned 2624 references (to which the nine articles of this special issue were added). Words or expressions (up to three words) that appeared in either the abstract, title or authors' keywords of at least 10 papers were automatically extracted. This initial list of unique terms (3882 in total) was thereafter manually screened and checked to identify and categorize keywords (1060 in total) into four categories. The first category defined a food quality parameter (i.e. as a structural, elemental or biochemical property of the food source) in which keywords were divided in eight subcategories (Table 1). The second defined endpoints or purposes, i.e. an individual, populational, community or ecosystemic process under focus, and was subcategorized in 10 categories. The third category defined

Table 1. List of categories and sub-categories defining food quality parameters, purposes, organisms and ecosystems.

Categories	Subcategories
Food quality	Amino-acids/proteins; biomechanics; carbohydrates; elemental–stoichiometry; energy; isotopes; lipids; metals; undefined
Purposes	Contamination; development; diversity–evolution; carbon fluxes; fitness (growth, survival); foraging; species interactions (predation, invasion, parasitism, communication, defense); metabolism; physiology; reproduction–recruitment
Organisms	Algae; annelida–nematodes; arthropods; detritus; micro-heterotrophs; molluscs; plants–trees; rotifer; sponge–cnidaria–echinoderms; vertebrate; virus
Ecosystems	Inland waters; marine; terrestrial; ecotone

organisms under focus (11 categories) and the fourth an ecosystem type (marine, terrestrial, inland waters or cross-ecosystem) (Table 1). For instance, the terms 'arachidonic', 'lipid composition' and 'polyunsaturated' were categorized as 'food quality parameters' and pooled within a 'lipids' subcategory of the 'food quality parameters' category (see the Supporting information for the full list of keywords and keywords allocations to categories and subcategories).

In a second step, the literature database was automatically screened again for the presence–absence of the selected keywords in the title, abstract and authors' keywords of each paper. After this step, 72% of papers could be attributed at least one subcategory of food quality. The list of papers (ca 600) for which no matching food quality terms had been detected was manually screened again in order to 1) detect additional keywords for food quality parameters, 2) discard papers which topic was not directly related to food quality aspects, 3) identify papers actually dealing with food quality but in which food quality was not defined by a structural or biochemical property of the food source itself but rather as the effect of a food source on a consumer life-history traits (subcategory 'undefined'). The final dataset contained 2359 papers that were attributed to at least one food quality subcategory.

Binary matrices of keywords presence/absence in the article title, abstracts and authors keywords on the final dataset were automatically computed for each of the four categories. Presence of at least one keyword of a given subcategory was thereafter used to allocate this subcategory to the paper: for instance, the presence of 'arachidonic' would allocate the paper to the subcategory 'lipids' in the food quality matrix. A single paper could be allocated to two subcategories within the category matrix. 97% of papers were allocated at least one purpose subcategory, 94% at least one organism subcategory and 86% at least one ecosystem type subcategory.

Co-occurrences within and between subcategories were mapped using non-metric multidimensional scaling (NMDS, vegan package), and clusters were identified using k-means (stats R-package). The number of clusters was decided from a broken stick approach and their significance was tested using analysis of similarities (vegan package). Whether two subcategories co-occurred more frequently than what could be expected under the hypothesis of a random distribution was detected using X^2 tests, using a Bonferroni's correction.

A map of nutritional quality research

When considering all scientific publications in the ecological and environmental science fields, food quality is mostly mentioned as an elemental or stoichiometric property of the food source (39% of all papers, Fig. 1a), while lipid or amino-acid/protein content or composition, or an energetically-based reference, are present in about 20% of papers. Isotopes and metals contents are the least frequent references of food quality (< 6%). Food quality is not referred as to an explicit parameter of the food source in 23% of papers ('undefined' subcategory). In almost half of the papers (47%), the food quality refers to more than one sub-category. 67% of papers that refer to an elemental–stoichiometric definition also refer to terms from other subcategories (predominantly lipids, amino-acids/proteins and energy). References to carbohydrates, protein compositions and biomechanical properties significantly co-occur as well (Supporting information).

Articles also preferentially refer to species-level fitness terms (> 54%) and foraging (53%) (Fig. 1b), with frequent co-occurrence (foraging is significantly associated to terms related to metabolism and physiology, while fitness terms are significantly associated to contamination and physiology, Supporting information). References to community and ecosystemic processes (diversity–evolution, production, carbon fluxes, species interactions, development and phenology) are less frequent (18–30%). Terms related to contamination occur in 8% of papers.

Research on nutritional quality of food resources overwhelmingly focuses on arthropods (55% of articles), and > 35% of articles include at least one primary producer (algae and/or plants and trees; Fig. 1c). Arthropods co-occur with algae in 30% of articles, and with plants and trees in 18% of articles and for 17% of articles with microheterotrophs (Supporting information). Vertebrates and micro-heterotrophs are focus organisms for ca 20% of articles. Other taxonomic groups are present in < 10% of articles. There is an almost equal share between terrestrial and aquatic ecosystems, but inland waters represent twice more papers than marine ecosystems (Fig. 1d).

There are clear segregations of the terms used to define resources nutritional quality in between ecosystems and endpoints (Fig. 2a) so that articles can be segregated within three clusters (Fig. 2b). Elemental, stoichiometric and lipids descriptors preferentially co-occur in articles focusing on aquatic environments (both marine and continental), where

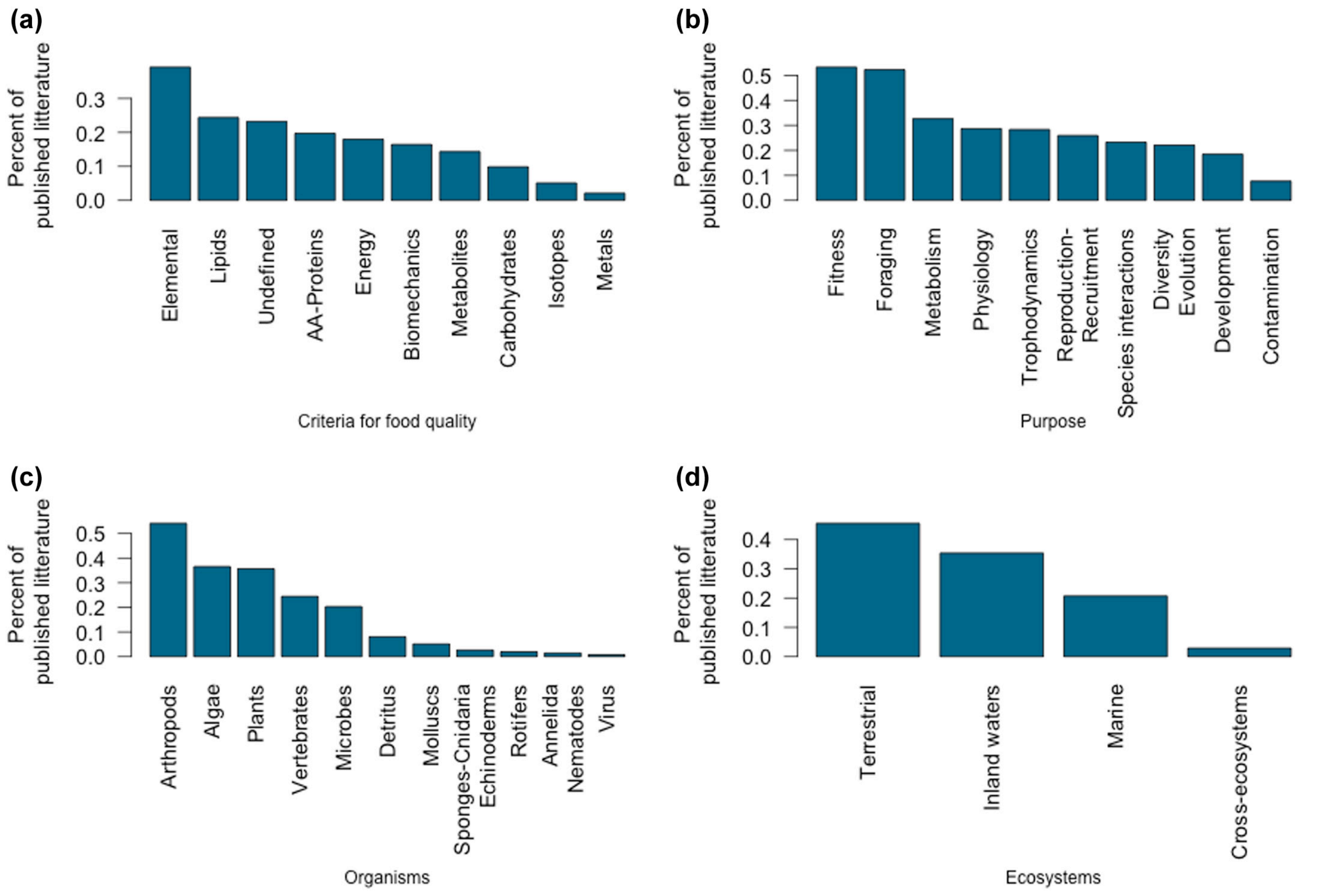

Figure 1. Distribution of published articles between food quality sub-categories (a), purposes (b), studied organisms (c) and ecosystem types (d). Sums of percentages can reach > 100% as articles can be attributed to several subcategories.

they are related to scientific questions related to carbon fluxes and fitness, foraging and metabolism. This cluster, figured in purple in Fig. 2, is also the one with the highest intra-group similarities and the most dissimilar with the two other clusters. Undefined food quality clusters with purposes such as diversity–evolution, reproduction–recruitment and species interactions, which preferentially cooccur with studies on terrestrial environments (in green in Fig. 2). Food quality aspects related to metabolites, overall nutritional geometry (i.e. biochemical composition in amino-acids–proteins and carbohydrates), as well as those addressing energetical aspects, cluster with physiological purposes, and are less dependent of ecosystem type. Articles of the Special issue cover well the spectrum of research about nutritional quality of two of the clusters. Because all of the contributions considered at least one explicit variable to quantify the nutritional quality of the resource, none of them falls within the cluster of 'undefined food quality' (in green). Five of the articles of the Special issue (Chouvelon et al. 2022, Lowman et al. 2022, Mathieu-Resuge et al. 2022, Sentis et al. 2022, van Deurs et al. 2022) fall within the cluster aquatic ecosystem/stoichiometry-lipids/trophodynamics-fitness, a proportion that mirrors well the actual predominance of those themes within the overall research (Fig. 2c). Two more articles of this Special issue (Le Gall et al. 2022, Zaguri et al. 2022) belong to the cluster linking the nutritional geometry to physiological aspects, which is current ranked second in term of contribution to the overall research. Last, two articles of the Special issue lie at the interface of the dominant cluster (i.e. aquatic ecosystem/stoichiometry-lipids/trophodynamics-fitness) and the cluster including evolutionary–reproduction purposes (Hudson et al. 2022, Leal et al. 2022).

Current status and perspectives of the research on nutritional quality

Resources quality: what are we talking about?

Our analysis is able to classify most of the articles according to a restricted set of the most common parameters used for describing resources (Table 1). Only 23% of the articles are attributed to the undefined parameters, which either means that the authors used other quality parameters or – for most cases – did not directly referred to any quality parameter, considering some resources of higher quality than others based on a priori knowledge and non-presented or non-measured parameters. This 'undefined' category is more represented in

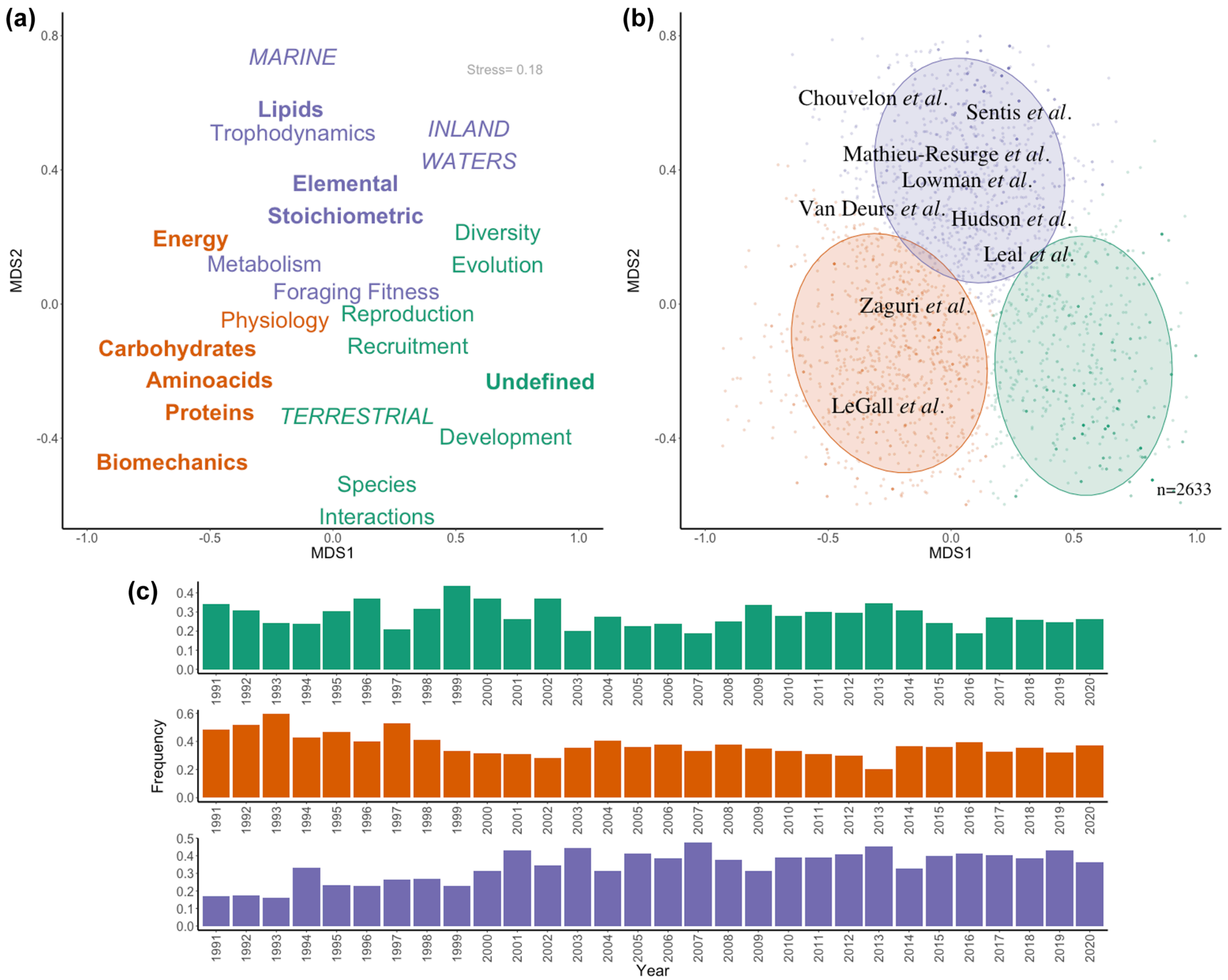

Figure 2. Map describing the nutritional quality research on the 1991–2020 period. Colors figure the significant clusters. (a) NMDS biplot of nutritional quality sub-categories (bold), purposes (in light) and ecosystem types (italics). Colors figure the significant clusters. (b) NMDS biplot of articles with emphasis on the positioning of the articles of this Special issue. (c) Changes in articles distribution within the three clusters over years.

terrestrial than in aquatic ecosystems that might be at least partly explained by the long-lasting knowledge of some plant quality gradients for herbivores in agronomy. Among all the parameters used, those referring to the elemental contents of resources (including the stoichiometric approaches) are the most represented, followed by those focusing lipids, amino-acids/proteins and energy. This dominance may partly arise from the technical simplicity of elemental analyses compared to the analysis of more specific compounds (e.g. macronutrients, requiring more complex methodologies; Zaguri et al. 2022). It could also partly come from the classical use of %N (or the C/N ratio) as an indicator of plant quality for cattle in agronomical studies (Laycock and Price 1970) and the more recent development of the Ecological stoichiometry framework (Sterner and Elser 2002). Biomechanical parameters (including all physical defenses) used to be largely considered in the early 90s but the relative use of this parameter is clearly declining in the recent years. The articles published in this special issue are well representative of these trends since one third of the published articles question resources quality through the consideration of resources elemental content (Chouvelon et al. 2022, Lowman et al. 2022, Sentis et al. 2022), while a second third focuses on resources macro-nutrient contents, alone (Le Gall et al. 2022, Zaguri et al. 2022) or in association with fatty acids (van Deurs et al. 2022). Finally, three articles specifically focus on fatty acids/lipids (Hudson et al. 2022, Leal et al. 2022, Mathieu-Resuge et al. 2022).

Are resources quality indicators used similarly between ecosystems?

Terrestrial and aquatic ecosystems are almost equally represented in our analysis of existing scientific literature, which contrasts with the articles published in the special issue, largely dominated by aquatic studies (only two articles considering terrestrial consumers: Le Gall et al. 2022, Mathieu-Resuge et al. 2022). Interestingly, parameters used for describing resources quality significantly differ between ecosystems. Lipids are mainly investigated in aquatic ecosystems – both in freshwaters and marine ecosystems – while macro-nutrients are more frequently investigated in terrestrial ecosystems. This observation directly questions the origin of this difference: are lipids less important in terrestrial ecosystems or is it simply a cultural bias related to the fact that most of the researchers working on lipids come from aquatic ecology? From a biological viewpoint, there is no reason for lipids to play a less relevant role in terrestrial ecosystems, and for example long chain polyunsaturated fatty acids are known as essential for both terrestrial and aquatic consumers (Hixson et al. 2015). Since some LC-PUFAs are more abundant in aquatic than in terrestrial ecosystems, terrestrial consumers might benefit from the transfer of these compounds from aquatic ecosystems (Hixson et al. 2015). Elemental approaches are certainly the most shared among ecosystem types, even if these ones are a little bit closer to inland waters. This last observation might be related to the historical development of stoichiometric approaches by limnologists in the late 1990s (Sterner and Elser 2002), the transfer to other ecosystems being more recent. Finally, parameters related to biomechanics and metabolites (including preys chemical defenses) are more typically found in terrestrial ecosystem studies. Aquatic plants may indeed contain less physical defenses – or at least are less studied for that – and plant chemical defenses have long been considered in pioneer works as one of the most important parameter of forage quality for the cattle (Laycock and Price 1970).

For which purpose are these quality indicators measured?

As expected, most studies dealing with resources quality consider the consequences of quality parameters on the fitness and/or on the foraging behavior of consumers. Most authors thus investigate the consequences of resource quality on the growth, on the survival and on the reproduction of the consumers (Le Gall et al. 2022), ultimately permitting to question secondary production and population/community dynamics in ecosystems (Rosen and Trites 2000) – even if such studies remain generally limited in the literature. Other studies (Le Gall et al. 2022, van Deurs et al. 2022), question food choices of consumers when exposed to resources of different quality, in more or less close relationship to the so-called optimal foraging theory (Pyke et al. 1977). Both fitness- and foraging-related approaches are quite equally distributed between ecosystem types. In contrast, approaches explicitly dealing with the role of resources quality in species interactions (e.g. competition or parasitism) are more closely related to terrestrial ecosystems. It is also interesting to note that less than 20% of all published studies, explicitly refer to evolutionary issues, while many interactions between species and the quality of their resources have been shaped on an evolutionary time scale. In this special issue, Hudson et al. (2022) tackle such question through the analysis of different fish lineages and their metabolic capacities of PUFA synthesis, showing how divergences between lineages depend on the history of freshwater colonization of the studied species. Finally, since some elements/molecules used for defining resources quality can be typical from some ecosystems or resource types, such resources quality parameters can be consequently used as ecosystem tracers (Majdi et al. 2018). For example, Leal et al. (2022) used fatty acids of land origin to trace the origin of different food subsidized for a targeted marine molluscan species in seashore ecosystems, while documenting the consequences of different nutritional qualities for the larval settlement and dispersion. In contrast, for characterizing the organic matter transfers from aquatic to terrestrial ecosystems, Mathieu-Resuge et al. (2022) analyze LC-PUFAs combined with stable isotopes for determining the origin of trophic resources for spiders in ecosystems more or less close to lakeshores. Out of this special issue, it can be noted that micro-nutrients or pollutants have also been successfully used for tracking the origin of organic matter in ecosystems or determining habitat use by organisms (Ramos and González-Solís 2011). Finally, references linking resources quality to ecosystem functioning parameters (such as carbon-fluxes) account for ca 30% of all published studies, even if we cannot know from the present literature review to what extent such ecosystem-wide parameters have actually been studied.

How to measure and compare resources quality?

A striking observation in our literature analysis is that a large proportion of articles dealing with resource quality does not investigate any parameter related to the response of consumers to resources consumption/ingestion. A lot of published articles thus focuses on 'potential' resource quality parameters and never measures their effective consequences on consumers. Yet, consumer requirements may vary widely depending between taxa (Frost et al. 2006) but also between individuals of a similar taxon (Leal et al. 2017, Le Gall et al. 2022). Evaluation of consumers' requirements might also greatly depend on the purpose of the study. For example, some fatty acids are especially important for reproduction, less for growth (Becker and Boersma 2005, Bec et al. 2006). The nutritional geometry framework also evidences that the relative amounts of macro-nutrients required for consumers largely vary depending on the life history trait considered or on the sex of the consumer (Lee et al. 2008). Consumers' responses to some quality parameters are also not monotonous and some compounds present in excess in resources can be deleterious for consumers upon a definite threshold (Boersma and Elser 2006, Anderson et al. 2020). Finally, environmental stressors are able to significantly change the nutritional requirements of a consumer. For example, temperature is a major factor impacting the lipidic and stoichiometric requirements of consumers (Masclaux et al. 2009, Ruiz et al. 2020). Defining a priori the quality of a resource without evaluating its consequences on consumers' life history traits might thus sometimes lead to large inaccuracies. Another point that deserves attention concerns the way the analyses are conducted, and the discrepancies that arises from methodological differences between studies. In this special issue, Zaguri et al. (2022) elegantly demonstrate the difficulty to compare the macro-nutrient contents of different resources originating from different methodologies. This question is crucial for generalizing the results coming from different studies, and this paper shall be cautiously read before starting any meta-analysis on nutritional quality topics (especially those considering macro-nutrients).

Why should we take resources quality into account for studying ecosystem functioning?

First premises of trophic ecology focused on biomass and/or energetic currencies for defining resources quality (Elton 1927, Lindeman 1942; see Layman et al. 2015 for an historical review). While the total amount of energy contained in basal resources remains important, a large number of studies underlined the importance of taking into account multiple resources quality parameters to improve our understanding of ecosystems functioning (Marcarelli et al. 2011). This is especially true for primary consumers facing the largest imbalances between their requirements and what can be found in their resources, as early underlined by Boyd and Goodyear (1971). Despite the general acknowledgment that food quality largely drives organism performances, numerous studies continue to neglect resources quality as a fundamental parameter ultimately driving the direction and the intensity of numerous ecological processes. In this special issue, Sentis et al. (2022) revisit the predictions of the largely used Rosenzweig–MacArthur consumer–resource model through the introduction of explicit stoichiometric constraints within the model parametrization. The introduction of such resource quality constraints radically changes the predictions of the model in response to nutrient enrichment and temperature increase. Such findings underline the necessity of integrating nutritional quality in theoretical but also experimental approaches to properly understand the response of ecosystems to changes in environmental parameters.

Challenges and future directions

In comparison to our literature review, the articles published in this special issue of Oikos constitute a small but relatively well representative subset of studies dealing with resources quality-related issues. Based on these studies and on the literature review, we identify a non-exhaustive list of challenges and perspectives of research that we consider of the highest priority in the large topic of trophic ecology.

- Both resource quantity and quality matter, but they might not intervene within the same processes, life-stages or even generations of consumers (Le Gall et al. 2022, Leal et al. 2022, van Deurs et al. 2022). There is a crucial need to merge those two nutritional aspects within the study of ecological processes. In that sense, the modelling approach developed from field-based data by van Deurs et al. (2022) is certainly inspiring to fully unfold individual tradeoffs. Besides, studies with resources quality are largely restricted to individual or population levels approaches. Trying to upscale the impacts of consumers' nutritional constraints, both in terms of availability and quantity, to their consequences on ecosystem functioning certainly stands as a key challenge of this research area. The use of models taking explicitly into account resources quality along with abundance (as in Sentis et al. 2022) certainly represents a promising way to achieve this goal.
- A second lesson of this analysis is that some aspects of trophic ecology may still be too much restricted to some scientific sub-disciplines or to some ecosystem types. Cross-ecosystem studies, as those developed by Leal et al. (2022) and Mathieu-Resuge et al. (2022) remain rare. Research in trophic ecology would certainly largely benefit from combining the different frameworks used for characterizing resources quality and their impacts – keeping in mind that methodologies should be harmonized or at least inter-calibrated between studies (Zaguri et al. 2022).
- The resource quality should be understood as a multidimensional property and it is hard to imagine explaining all resources constraints in ecosystems while considering only one kind of quality descriptor (Chouvelon et al. 2022). As underlined in this special issue, different life-history traits of consumers can respond differently to deficiencies in various aspects of resource quality (e.g. specific lipids deficiency might affect consumers' reproduction while not affecting their growth, van Deurs et al. 2022). Taking into account the multidimensional nature of resource quality through the consideration of consumers' responses to the large diversity of diets available for them constitutes a major challenge (Ruiz et al. 2021).
- As generally observed in ecosystem ecology, evolutionary questions are still too rarely explicitly tested in trophic ecology investigations. Despite a large array of studies have observed and discussed the evolutionary tenets at play behind the selection of consumers nutritional requirements (see for example Hudson et al. 2022 in this issue), the inclusion of such research questions in the general understanding of ecosystem functioning remains limited.
- Finally, Lowman et al. (2022) illustrate that the potential nutritional quality of basal producers can be significantly altered by global warming. In the context or the current global changes and considering the multiple stressors organisms are exposed to, understanding the causes and the consequences of changes in basal resource quality in a multistressor context (concomitant changes in temperature, nutrient and water availability, presence of pollutants …) is an urgent need, as much in terms of prediction of future ecosystem trajectories as in terms of goods and services provision by nature for humanity.

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Author contributions

Michael Danger: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing – original draft (equal); Writing – review and editing (equal). **Alexandre Bec**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Jerome Spitz**: Conceptualization (equal); Project administration (equal); Writing – review and editing (equal). **Marie-Elodie Perga**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jsxksn0cd> (Danger et al. 2022).

Supporting information

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

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