Disentangling food-web environment relationships: a review with guidelines

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Abstract

Food webs represent the energy fluxes and the nutrient cycling between interacting species that underpin several ecosystem functions. Whether and how interactions vary across environmental gradients is still largely unknown. We reviewed the literature searching for systematic relationships between structural food-web properties and environmental gradients. Temperature and biotic factors are amongst the most frequently addressed drivers of food web structure. We also assessed the degree to which food web ecology has accomplished a mechanistic understanding of ecosystem functioning. We found that most studies are one-off descriptions of local food webs making it difficult to achieve an understanding of the response to human or environmental gradients. The lack of a consistent theory predicting how food webs change across environmental gradients, the diversity of objectives in food-web studies, and the absence of a standardized methodology for analysing them severely limit progress in the field. Moving forward requires the establishment of a core set of testable predictions, agreed standards for data collection and analysis, and the development of geographically distributed experimental studies of food-webs dynamics.

Keywords: biotic interactions; community ecology; ecological networks; environmental change; trophic interactions.

Introduction

Charles Elton, in the late 1920s, was the first to describe communities as networks of species connected by trophic interactions (Elton, 1927). Research on the topic increased during the 70s and 80s (Layman et al., 2015). Recently, it is gaining new momentum given a renewed interest in understanding how species interactions mediate the effects of environmental change on biodiversity and ecosystem functioning. Food webs depict energy processing and transformation, incorporating information about species composition (nodes in network terminology) and the distribution of trophic interactions (links connecting nodes) (Barnes et al., 2018). By explicitly considering trophic interactions, food webs represent energy and matter fluxes within ecosystems. Such a conceptual approach enables merging the compositionalist and the functionalist approaches to biodiversity science (Jordano, 2016), thus promoting a more comprehensive and integrated understanding of the effects of environmental changes on biodiversity and ecosystem functioning.

Species distributions and their interactions are driven by multiple environmental gradients, such as temperature and precipitation (Peterson et al., 2011; Post, 2013). If emerging functional food-web properties such as trophic regulation (top-down control of lower trophic levels by a higher-level consumer) or energy transfer efficiency (the efficiency with which energy is moved across trophic levels), change consistently along environmental gradients, our ability to predict the consequences of global environmental changes on ecological communities would increase considerably (Bideault et al. 2021).

Broad-scale biogeographical relationships such as the latitudinal diversity gradient, species distribution-environment associations, species-area relationships, temperature-body size rules, or species range-size frequency distributions, are often used to derive predictions about the ecological consequences of global change. The study of biogeographical rules for food webs is relatively recent yet promising. Baiser et al. (2019), for instance, were able to provide evidence relating food web structure to latitudinal diversity gradient (e.g., increasing and decreasing food chain length with latitude) and Rapoport's rule (i.e., inverse relationship between species turnover and latitude). A study by O'Connor et al. (2020), on the tetrapod food webs across Europe, concludes that trophic diversity (the number of trophic roles played by species) varies similarly to species richness, decreasing towards higher latitudes. According to these authors, climate-related factors (such as temperature) and net primary productivity also play a role in the variation of trophic diversity. Work by Mendoza and Araújo (2019) supports the view that global terrestrial trophic structures are linked to climate and simplified by human impact. Finally, Albouy et al. (2019) studying the global marine fish food web, conclude that structural metrics correlate with sea surface temperature, increasing towards lower latitudes.

Previous reviews have addressed the effects of environmental gradients on ecological networks (Pellissier et al., 2017; Tylianakis & Morris, 2017), concluding that these relate mainly to changes in species composition, relative abundances, or coevolutionary processes affecting interactions. These reviews have also suggested ways to improve food web ecology (Cohen et al., 1993; Dunne, 2005; Ings et al., 2009; Thompson et al., 2012), with the most relevant being: 1) describing the network nodes (increased node resolution) and links accurately (reporting all links, preferentially quantitatively, considering that the strength of the trophic interactions may also be relevant to assess food web robustness, and based on direct observations); 2) standardizing data structure; 3) encouraging manipulative experiments or resorting to studying networks on natural gradients (to better understand food web dynamics and improve predictability); 4) strengthening the theoretical framework and mechanistic understanding, improving predictability. Correctly defining the setting (spatial description, sampling temporal span, and effort) and promoting collaborative efforts between researchers with different expertise (e.g. taxonomists, community ecologists specialized in different ecosystems) have also been suggested. These recommendations aim to improve data quality, comparability, and availability and drive the field towards a more mechanistic (and hopefully predictive) view.

We review how these issues have been addressed. Our objectives were twofold: i) to search for relationships between environmental gradients and food-web structural properties and ii) to assess how the description of food webs helped provide a deeper mechanistic understanding of ecosystem functioning at large biogeographical scales. We focus on the description of nodes and links, the standardization of data structures, the use of experimental approaches (either manipulative or natural), and the extent to which the spatial context is described.

Literature review

We reviewed the literature over the last decade (from 2006 to 2017), compiling a comprehensive database with 463 studies conducted worldwide (see Appendix A and Appendix B: Figure 1).

FIGURE 1

Studies were selected through searching the Web of Science (search terms: “food web”, “trophic network”, “trophic AND environmental gradient”, “trophic relations”, “trophic level AND environment” and “trophic level AND climate change”). The search returned 5217 articles that we filtered according to the following criteria (see Appendix B): i) studies included at least three nodes with trophic interactions; ii) studies addressed the relation between food web properties and environmental gradients.

We followed the classification of Garnier et al. (2016) to systematize information and divided the environmental drivers as: direct (those affecting the network nodes directly, e.g., temperature), indirect (proxies of direct drivers e.g., altitude), resource (food/nutrient resource, e.g., nutrients), and disturbance (e.g., urbanization gradient) (see Appendix B: Figure 2). More detailed information on the methods can be found in the Supporting Information (see Appendix B).

Results

Defining the food-web: its elements and interactions

Studies use food webs with varying node resolution, and different methods to determine interactions (see Appendix B: Figures 6-7). Node resolution can vary between and within studies, in which case broader taxonomic classifications are more common at basal trophic levels. Most articles used broad group-assignment criterion, “other taxonomic groups” (47.7% of the total number of articles). The recurrence to coarser taxonomic resolution in studies is a consequence of food-web basal elements being generally more taxonomically or functionally aggregated than higher trophic levels, which more frequently have one-species nodes (see Appendix B: Figure 7). Food web metrics vary in their sensitivity to aggregation: connectance and predator/prey ratio are almost invariant to aggregation, while mean chain length and linkage density are more susceptible (Martinez, 1993). Additionally, metrics are more susceptible to taxonomic aggregation than trophic/functional aggregation since trophic aggregation lumps together functionally similar species, leading to a smaller impact on the overall structure of the network (Sugihara et al. 1997).

Documentation of trophic interactions frequently uses stable isotopes (14.3%, second only to resorting to scientific literature, 46.0%). Other methods include statistical associations between the occurrences/abundances/biomass of the interacting species (5.4%), feeding experiments (4.3%), and gut content analysis (4.1%) (see Appendix B: Figure 6).

Method choice might affect food web structure, with stable isotopes and fatty acids identifying feeding interactions over a long period (producing time-averaged results) while gut content provides greater taxonomic resolution but a more punctual picture (Kolts et al., 2013). The variety of approaches inevitably limits comparability across studies. Further research is needed on how to standardize networks from studies using different sampling methodologies.

Environmental effects on nodes and interactions

Freshwater, marine, and soil studies address mainly both resource-related (e.g., nutrients) and direct drivers (those affecting species directly such as temperature), according to the classification of Garnier et al. (2016). Terrestrial studies address mainly direct and indirect drivers (see Appendix B: Figure 2). Two predictors stand out as having a significant relationship with variation in the food web: temperature and biotic-related variables (e.g., the presence of other species, either predators or prey). The response variable most frequently considered is node abundance/biomass (the abundance/biomass of a food web node) (see Appendix B: Figure 12).

Temperature is the most addressed factor affecting food web structure. It was found to be significant in 35.2% of studies. The most widely reported effects are reduction in body size with increasing temperature in most trophic levels, phenological mismatches affecting interactions, increasing decomposition rate, and primary productivity with increasing temperature (Fig. 2). However, even these observations are not consistent across publications, depending on local conditions, the species considered, and the spatial scale. Additionally, some traits characterizing nodes and interactions are interrelated, such as the body size of interacting species and the interaction strength, with interaction strength being positively related to the predator/prey size ratio (Legagneux et al., 2014).

FIGURE 2

Environmental effects on structural metrics

Structural metrics describing emerging network properties are investigated only in a minority of studies (19.7%, 91 studies); possibly because not all conceptualize trophic interactions as networks, instead focusing on pairwise interactions. Amongst studies that use structural metrics, food chain length, connectance, and link density are the most widely documented (Fig. 3). We discuss in greater detail the first two, considering that link density provides similar information to connectance.

FIGURE 3

Food chain length

Food chain length reports the maximal trophic level in a food web (Post 2002), and is expected to decrease with increasing disturbance, *sensu* Bender (1984), either as a consequence of “pulse” (instantaneous perturbation after which the system returns to the previous equilibrium, e.g., Taylor et al. 2017) or “press” disturbances (a constant perturbation to the system, e.g., Clausen & York 2008). Additionally, food chain length increases with energy availability and ecosystem size (Baiser et al., 2012; Pimm, 1991; Ruhí et al. 2016; Young et al., 2013). These relationships are intrinsically related to energy availability since, all other things being equal, to a greater area corresponds a greater amount of total energy available. Likewise, an increased disturbance corresponds to a decrease in the stability of energy flows available to organisms. Yet studies generally search for the best mutually exclusive explanations, not acknowledging that disturbance, energy availability, and ecosystem size are related.

In addition to energy availability and ecosystem size, other gradients are found to influence food chain length (Fig. 4), particularly in marine food webs: fishing tends to decrease food chain length, while temperature appears to have an ambivalent effect. Increased nutrient availability, on the other hand, has a positive effect on food chain length (Fig. 4). The apparent inconsistency in some of these effects, such as the effects of nutrients and acidification (Fig. 4), is also documented in lake ecosystems (Ward et al. 2017). These authors concluded that the relationship is complex and dependent on local characteristics, with productivity being determinant: ecosystem size has a positive effect on food chain length in regions with lower productivity, while a negative effect on food chain length occurs in higher productivity regions. This is the opposite of what has been commonly accepted, that productivity has a positive effect on food chain length (e.g., Young et al. 2013) and underlines the difficulty of finding general patterns amid such complexity. There might, however, be some differences between terrestrial and aquatic systems, due to different relationships between productivity and species richness (Waide et al. 1999), with the latter affecting food chain length.

FIGURE 4

Albouy et al. (2019), in a study resorting to a metaweb derived from trait-matching based on a database of trophic interactions, concluded that food chain length has a positive relationship with sea surface temperature, in agreement with the hypothesis that, to more energy entering the system corresponds a greater food chain length. Braga et al. (2019), resorting to expert-based food webs, found smaller food chain lengths in higher latitudes for European terrestrial vertebrates and increasing food chain length with climatic variability.

Connectance

Connectance is a metric of network complexity and is computed as the ratio between the number of realized interactions to the total number of all possible interactions. It has been related to community stability (how effectively does the community return to previous equilibriums after a disturbance) (De Angelis, 1975; Dunne et al., 2002), and species richness (Warren, 1990). Despite an earlier debate (De Angelis, 1975; Gardner & Ashby, 1970), there is apparently no relation between connectance and empirical network stability (Jacquet et al. 2016). However, in our review, connectance appears to benefit from ecosystem disturbance and variability. For example, urbanization (Docile et al., 2016) and proximity to river estuaries in coastal food webs (Careddu et al., 2015) have been shown to relate to increased connectance. In both cases, the lower number of species found in the more urbanized sites and near the river estuary might have caused connectance to increase, consistent with a hypothesized inverse relationship between connectance and species richness (May, 1972). Nutrient availability has been shown to increase connectance as has temperature (Fig. 4). This ambivalent relationship between temperature and connectance is supported by past research showing that the effect of temperature on connectance depends on the local species pool (Petchey et al. 2010). Connectance is also constrained by species richness (Poisot & Gravel, 2014), since there are fewer potential species arrangements in species-poor networks. Considering that species richness is constrained by climate, it follows that connectance should be also affected by temperature.

Recent studies on vertebrate food webs in Europe (Braga et al. 2019) have concluded that connectance is positively correlated to temperature, while the inverse is observed for the human footprint. On the other hand, precipitation has a complex effect that changes direction: if we consider low to intermediate precipitation (negative effect) or high precipitations (positive effect). Finally, a study on the global marine food webs (Albouy et al. 2019), concludes that, although connectance is mostly constant between -40º and 40º of latitude, it increases considerably at the poles, which might be explained by the lower species richness.

Food webs in space and time

Food webs more often describe snapshots of trophic interactions at a given place and time than summarise the full set of potential interactions that can exist for any assemblage of species. Additionally, studies tend to vary widely in spatio-temporal resolution and extent (see Appendix B: Figures 8 to 10).

The spatial boundaries delimiting the characterisation of food webs are often contingent on the available data (Baiser et al., 2012), vary with observer perceptions or conveniences (Moore & De Ruiter, 2012) and with traits examined (body size, dispersal ability) (Woodward et al. 2005). Additionally, according to Cohen (1978), food webs can be divided into “source” (one or a few prey species and their consumers), “sink” (one or a few consumers and the species they feed upon), and “community” food webs (depicting the feeding interactions in a community). These different concepts carry differences in the taxonomic and spatial boundaries. Some examples are present in the reviewed literature, such as the detritus-based source food web in Lake Obersee, Germany (Majdi et al, 2016), the sink food web focused on the minke whale in the Barents Sea (Lindstrom et al., 2009), or the freshwater community at the Bere Stream, England (Woodward et al., 2008). Spatial boundaries can be determined based on organismal home ranges or, more generally, the physical limits to movement (Moore & De Ruiter, 2012) (e.g., chalk stream food webs in southern England, Woodward et al. 2008). Food webs investigated across increasingly large extents are more likely to lose precision on trophic interactions, shifting from direct observations to potential interactions instead (e.g., Braga et al. 2019). Comparisons across food web topologies measured at different scales thus need to be conducted with caution.

Food webs are connected to external elements through dispersal and allochthonous subsidies (external sources of nutrients) (Massol et al., 2011; Meunier et al., 2017). They can be interconnected through dispersal if, for instance, a predator with large home ranges connects otherwise unconnected local food webs (e.g., McCann et al. 2005). On the other hand, allochthonous subsidies can constitute major energy sources, having a positive direct effect on particular food web nodes, and through those, impacting the whole network. For instance, in a study conducted in the Baltic Sea to evaluate how light availability and allochthonous dissolved organic matter (ADOM) affected the planktonic food web, researchers concluded that the reduced light had a limited effect on the bacteria/phytoplankton biomass ratio. However, by adding carbon without reducing light, microzooplankton shift from their preferred resource, phytoplankton, to bacteria as a result of increased bacterial/phytoplankton ratio (Meunier et al., 2017). Dispersal, allochthonous subsidies, foraging and migration make the definition of food web boundaries difficult to establish (Guzman et al. 2019).

Spatial scale has two components: extent (the area of the spatial extent of the study site) and resolution (how spatially detailed is the information). As an example, one article evaluating food web richness and composition variability across 39 sites in the United States (Buckley et al., 2010) was classified as having a “continental” spatial extent (the study area extension), but a “local” resolution (the food webs described local trophic interactions in each site). The studies reviewed were mostly local, whether in extent or resolution (see Appendix B: Figures 8 and 9). Most studies dwell on local food webs, on small-sized systems (e.g., microcosms, mesocosms, experimental field sites, lakes) (66.3%), several studies have a regional scale (25.1%), and only a few refer to the global (2.2%) or continental/oceanic scales (1.9%). Spatial resolution is, as expected, even more dominated by local (77.1%) and regional scales (18.8%).

Most studies do not replicate observations, whether spatially or temporally, or resort to temporal and spatial averaging. Environmental variation, changes in abundance, and observation errors can cause variation in pairwise interactions and in characterizations of food web metrics (Cirtwill et al., 2019). Additionally, spatial variability in pairwise interactions can also be caused by intra-specific variability in species traits across populations of the same species (Poisot et al., 2015). Some studies included spatial variability in food web structure (27.4% of the total), generally through multiple sampling sites within the study area, frequently spatially averaging the resulting food web (by creating a metaweb considering all the species and trophic interactions observed in each local food web). Others went a step further and effectively evaluated the spatial heterogeneity along environmental gradients (e.g., Doi et al. 2013).

Around a third of the studies (32.2%) account for temporal variability in food web structure, at least by averaging the sampling at multiple time points (temporal averaging) or considering multiple sampling time points (e.g., seasons). Temporal averaging masks seasonal or inter-annual dynamics, affecting the structural metrics of local food webs (Jordán & Osváth, 2009; López et al., 2018), which is not a problem if the goal is to approximate the “potential” food web rather than the “actual”. In our review, most studies consider periods of less than one year (46.4%) or more than ten years (24.0%) and just a few address periods of one to five (18.8%) or five to ten years (4.1%) (see Appendix B: Figure 10). The relatively short time span of most studies reduces the likelihood of detecting responses to sub-lethal disturbances, which may take decades to express themselves (e.g., Peterson et al. 2003).

There has been an increasing number of articles using inferred networks from other sources of information, such as species co-occurrence or traits (Morales-Castilla et al. 2015). These have been emerging as a response to the lack of spatially replicated networks (e.g., Albouy et al., 2019 and Mendoza & Araújo, 2019).

Studies of approaches and objectives

There is no standardized approach to evaluate the impacts of environmental gradients on food web structure. In most studies, relating food web structure and environmental gradients is not even the primary objective (see Appendix B: Figure 13). Several studies compare food web structures across gradients, like temperature (e.g., Franzè & Lavrentyev 2017) or between sites with different environmental characteristics (e.g., Matias et al. 2017) (observational studies: 38.9%). Often, studies (Pellissier et al. 2017) i) directly compare network properties (e.g., structural metrics) and environmental variables using a variety of statistical methods; ii) evaluate the residual variation (allowing, for instance, to separate the effect of species richness on connectance); iii) develop rarefaction analysis (allowing the comparison of food webs that differ in terms of sampling effort or complexity); iv) implement null models (evaluating to what extent is the variation in any given food web property a result of chance); v) compare food webs with hypothesis-based metawebs (composed of interactions between all the species in the community, for example); vi) align food web motifs evaluating if they present a common core structure; or vii) develop a statistical model joining co-occurrences and interactions such as joint species distribution models.

Other studies use experimental manipulation of environmental drivers in mesocosms (e.g., Özen et al. 2013), microcosms (e.g., Burgmer & Hillebrand 2011), or simulate natural food webs in virtual environments (e.g., Zhang et al. 2017) (controlled experiments: 32.6%; natural experiments: 11.5%; simulations: 5.8%).

Studies also vary in their objectives: marine studies (43.6%) are dominated by fishing-related management problems, such as sustainability (Lindegren et al., 2009), top predator overfishing (Llope et al., 2011), or fish stock evaluation (Kempf et al., 2006).

The objectives of freshwater studies (28.9%) are more diverse, with some addressing issues like the impact of water mixing (Blottière et al., 2017), the effect of temperature (Zander et al., 2017), light availability (Collins et al., 2016), salinity (Cañedo-Argüelles et al., 2016), drought (Lu et al., 2016), flow regulation (Ruhí et al., 2016), or the variation in decomposition rates (Ferreira et al., 2015). Terrestrial studies (12.7%) tend to focus on the effects of environmental factors, such as precipitation (Deguines et al., 2017), temperature (Sentis et al., 2013), CO_2 (Dyer et al., 2013), or multidimensional expressions of climate change (Mortensen et al., 2016). Finally, articles on soil food webs (11.0%) address mainly the relations with plants (Cesarz et al., 2017), allochthonous nutrient input (Hu et al., 2017), elevated CO_2 (Mueller et al., 2016), hydrological changes (Sun et al., 2016) and warming (Schwarz et al., 2017). Despite apparent differences of focus, if we consider keyword frequency in studies across the four main ecosystem types (see Appendix B: Figure 13), it appears that the effects of climate or environmental change have dominated the research in the last decade.

Discussion

While food webs can be clearly defined as ”…the feeding relationships among species or groupings of species” (Moore & De Ruiter, 2012), there is plenty of room for interpretation when researchers seek to quantify or even qualify the trophic relationships among organisms. Detailed information on these relationships is generally lacking. How should interacting nodes be defined? Should nodes have the same taxonomic or functional resolution? How should the links be established, and the strength of interactions measured? Where does a food web begin and end, in other words, how are spatial boundaries of food webs determined? Are snapshots of food webs representative of the potential sets of trophic relationships that can be established among organisms, that is, how should the relevant temporal resolution and extent of the interactions be defined? These questions and their answers can affect the study design, the results, and the interpretations of the observed food web patterns and processes, limiting comparability and preventing generalizations about environmental effects on food web structure and function (e.g., Martinez 1991, Dunne 2005).

Progress made in the last decade

Several recommendations have been made to move food web ecology forward. They often focus on increasing data quality to increase predictability (e.g., Cohen et al. 1993, Dunne 2005, Ings et al. 2009, Thompson et al. 2012). For example, data should be made freely available online, improving not just data access but also standardization and comparability across multiple case studies. Our review shows only modest signs of progress in this regard. Two notable examples are the studies conducted with the software Ecopath with Ecosim, which are stored in the EcoBase (Christensen & Walters, 2004), and those stored in the “mangal” database (Poisot et al. 2016). Nevertheless, both require data and metadata to be strictly standardized.

As for data quality, despite progress in techniques helping to describe food web structure from ecosystem sampling, such as stable isotopes or fatty acids to determine interactions or environmental DNA to identify the species present (Charvet et al., 2014), their use is still not widespread. Researchers are still heavily reliant on published information or expert knowledge to determine interactions and node resolution, which are frequently defined at broader taxonomic resolutions than the species. Manipulative studies (e.g., mesocosms) or natural experiments, allowing researchers to better understand the underlying mechanisms and contribute to a more predictive food web ecology, have become more widely used, but observational studies still dominate (observational: 38.9%; controlled experiment: 32.6%; natural experiments: 11.5%). Previous reviews have also called for a stronger theoretical framework (e.g., Ings et al. 2009), for example by integrating food web ecology with foraging theory or the metabolic theory of ecology. Indeed, some of the reviewed articles seek such an intersection between the metabolic theory of evolution and food web ecology (Eklöf et al., 2012; Sentis et al., 2014), but many articles are still focused on local or regional questions of applied value without connections to ecological theory.

Perspectives

Despite hundreds of empirical and experimental studies in the past decades, food web ecology still lacks general predictions about environmental effects on trophic interactions and the associated effects on ecosystem functioning. Indeed, no ubiquitous relationships between food-web structural properties and environmental gradients emerge from our review (fig. 4), despite recent studies uncovering clear relationships with environmental characteristics (Mendoza & Araújo, 2019) or relating the number of trophic levels to productivity, and temperature (Oksanen et al., 2020). Nevertheless, we identified opportunities for unifying methods and concepts in food web ecology. Specifically, we propose three areas of inquiry to help move the field forward.

Refinement of theory and testable predictions

Research is usually the most efficient when small sets of testable predictions on the most pressing questions are agreed upon and pursued collectively. Food web ecology still lacks such a tight framework. There are pieces in the literature exploring how aspects of food web structure vary over gradients (Pellissier et al., 2017; Tylianakis & Morris, 2017). Recently, a quantitative framework has been proposed to partition the drivers of network change at the biogeographical scales (Gravel et al., 2019; Poisot et al., 2015). The integration of metabolic theory to consumer-resources theory (Brown et al., 2004) also allows investigating how pairwise interactions and trophic regulation scale with temperature (Bideault et al., 2019; Gounand et al., 2016). Another example is the integration of foraging theory to predict food web structure (Petchey et al., 2008). However, akin to empirical observations, the theory is fragmented by the diversity of gradients and models used to study food-web properties. A good example, testing theoretical predictions resorting to foraging and metabolic theory, is the paper by Sentis et al. (2014). Drawing on existing theory, the authors seek a mechanistic understanding of the effects of temperature and nutrient enrichment on interaction strength and food-web structure. It is possible and desirable to derive testable predictions (a few examples in Table 1), thus connecting food web ecology with existing ecological theory.

TABLE 1

A unified theory of food web dynamics across environmental gradients will require a scalable approach, with comparable models to the study of food web modules (to understand mechanisms) up to the study of entire networks (to document emerging properties). From a bottom-up perspective, temperature, solar radiation intensity, and primary productivity are likely the most relevant environmental drivers to focus on, because of their relevance as surrogates of energy availability. Similarly, theory should focus on the set of food web functional properties relevant to understanding ecosystem functioning. A useful path for global change research is to focus on biomass distribution, consumption:production ratio, trophic regulation, and network topology. Lastly, we emphasize that the development of theory should be performed in conjunction with experiments and observations (see below) so that quantitative predictions can be formulated and adequately tested.

The emerging field of food-web biogeography has led to renewed efforts to map variation of food-web structures across continental to global scales (e.g., Albouy et al. 2019; Mendoza & Araújo, 2019; O'Connor et al. 2020) and to develop a set of testable predictions (Baiser et al. 2019). These studies are, nevertheless, mired by the lack of high-quality data on empirical trophic interactions (Gravel et al. 2019), forcing researchers to inferences of interactions rather than observed interactions (Morales-Castilla et al. 2015). Addressing the data gap at biogeographical will unlikely be achieved by increasing data collection. More promising approaches involve improvements in theory and models and better understanding of the dichotomy between actual and potential food webs.

Agreed standards for data collection and analysis

Studies of food webs can address different questions. Although refinement of theories and hypotheses will lead to convergence of methods for data acquisition and analysis, there will always be diversity in the approaches used.

Convergence will benefit from an agreed and consistent definition of “interaction”. Variation in criteria for link determination limits comparability across studies. For example, researchers have cast doubt on the usefulness of binary depictions of food-web interactions (Banašek-Richter et al., 2004). There is a range of direct and indirect approaches for identifying links and/or measuring strengths of interactions and there is no guarantee that conclusions with different methods are comparable (Berlow et al., 2004). Agreement on a core set of procedures for establishing links would help reduce methodological-induced variation in food-web patterns. Furthermore, food webs should be defined by the spatial boundaries constraining the movement of most organisms (akin to the species pool concept, see for review Carstensen et al. 2013). Finally, the taxonomic resolution of nodes should be increased, ideally to species level, and it should be consistent within a single food web. Hopefully, novel molecular methods to process gut contents will help ensure species-level resolution of nodes (Roslin et al., 2016).

Minimum agreed standards are needed for enabling comparability across studies, an effort already attempted in biographical assessments and models of climate change (Araújo et al., 2019; Taheri et al 2021). Attention should be given to robust data specifications to aggregate datasets and perform comparative studies, such as the “mangal” data specification (Poisot et al., 2016). The adoption of such a standard not only requires taking into consideration data acquisition and structure, but also implies that all relevant metadata is collected, making comparative studies over gradients more accessible. The existence of comparable, high-quality data is a pressing issue to further food-web ecology.

Development of geographically distributed experimental studies

Understanding how food webs respond to perturbations, is strongly reliant on the ability to generalize conclusions from local observations. The need for geographical replication of local experiments across environmental gradients is critical (Freestone & Osman, 2011; Pelini et al., 2014). The implementation of multiple-site experiments can help discern if local observations are the product of local contingencies or general mechanisms acting across scales (Borer et al., 2014). Examples of geographically distributed experiments include BIODEPTH, probably the first large-scale coordinated experiments so far, designed to test the relationships between biodiversity and ecosystem functions (Hector et al., 1999), and the Iberian Ponds established to assess aquatic food web dynamics across environmental gradients (Pereira et al. 2021). The development of globally replicated experiments assessing the responses of food webs to environmental gradients can help establish a benchmark for testing predictive food-web models.

Conclusions

The relationship between food webs and the environment is context-dependent, being affected by the species pools, the type of ecosystem and environmental gradients considered, or the types of disturbances. An attempt to generalize observations across environmental gradients is presently weakened by the plethora of approaches used and by the lack of comparable datasets across multiple sites. Advancing food web ecology is poised with several scientific challenges, logistical difficulties, and lack of funding. We encourage researchers to refine theory and better align methods with it. An investment in geographically replicated sampling schemes would help solve long-standing difficulties in discerning environmental drivers of food-web structure.

Appendixes A-C. Supplementary data Supplementary data associated with this article can be found, in the online version, at XXXXX.

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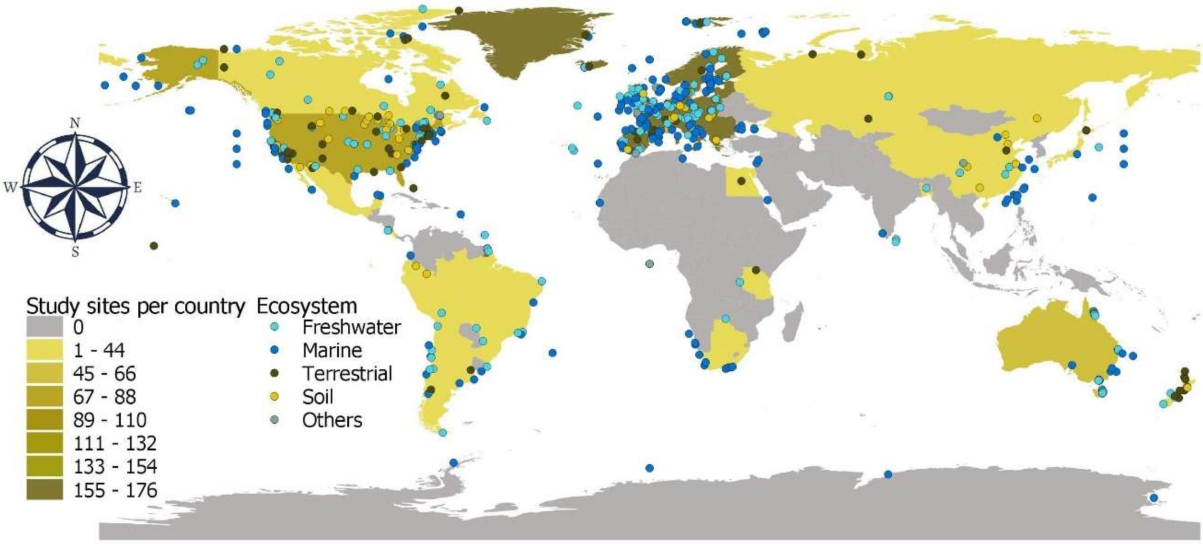
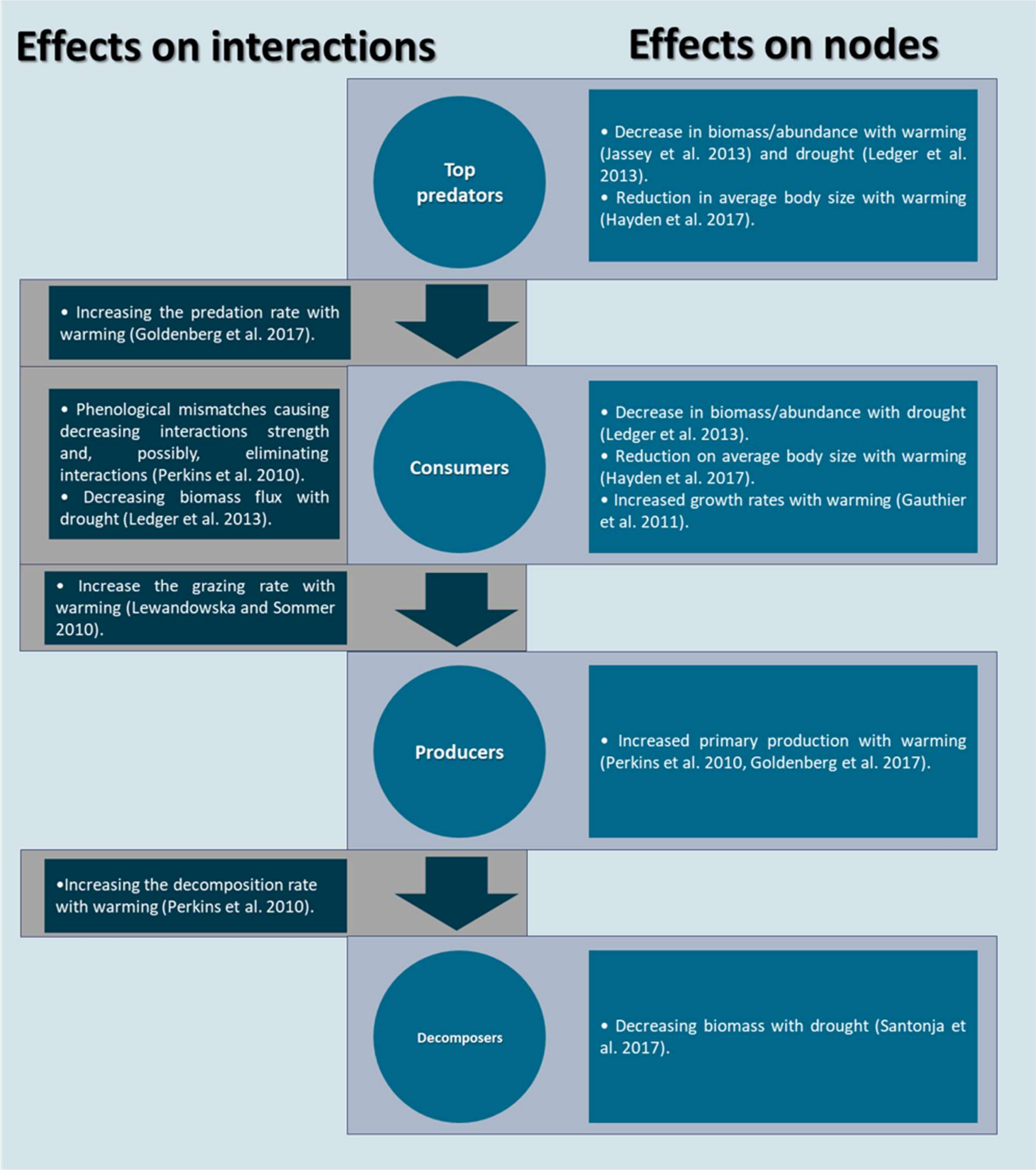

N
W
E
S
Study sites per country
0
1 - 44
45 - 66
67 - 88
89 - 110
111 - 132
133 - 154
155 - 176
Ecosystem
Freshwater
Marine
Terrestrial
Soil
Others



- Decrease in biomass/abundance with warming (Jassey et al. 2013) and drought (Ledger et al. 2013).
- Reduction in average body size with warming (Hayden et al. 2017).

- Increasing the predation rate with warming (Goldenberg et al. 2017).

- Phenological mismatches causing decreasing interactions strength and, possibly, eliminating interactions (Perkins et al. 2010).
- Decreasing biomass flux with drought (Ledger et al. 2013).

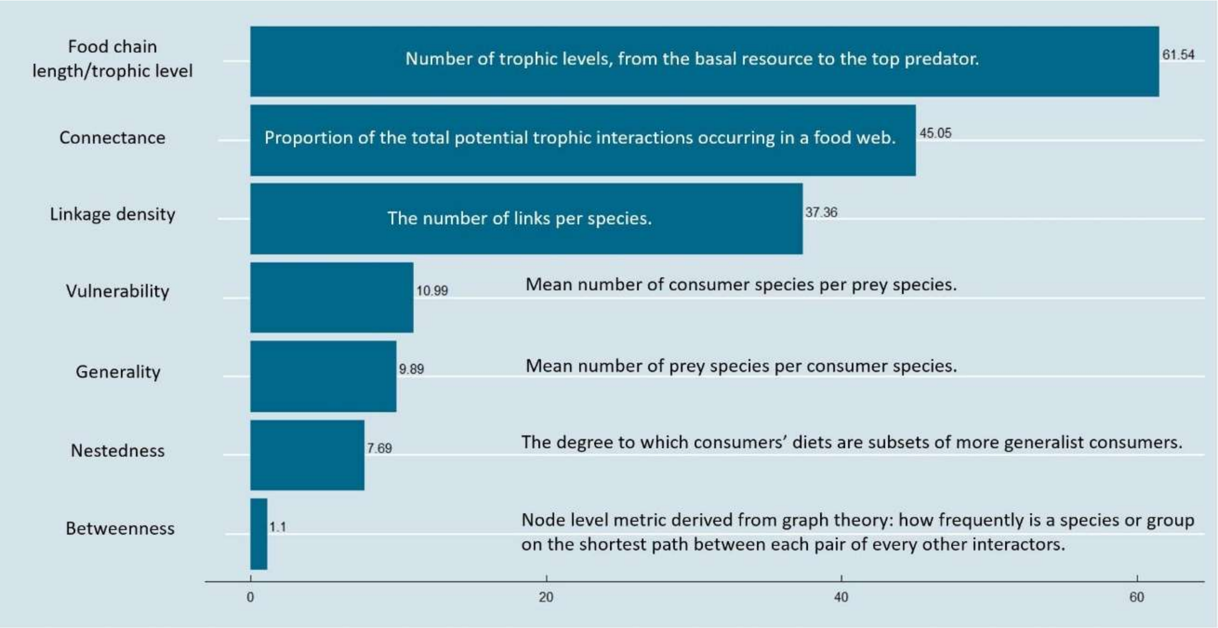
- Decrease in biomass/abundance with drought (Ledger et al. 2013).
- Reduction on average body size with warming (Hayden et al. 2017).
- Increased growth rates with warming (Gauthier et al. 2011).

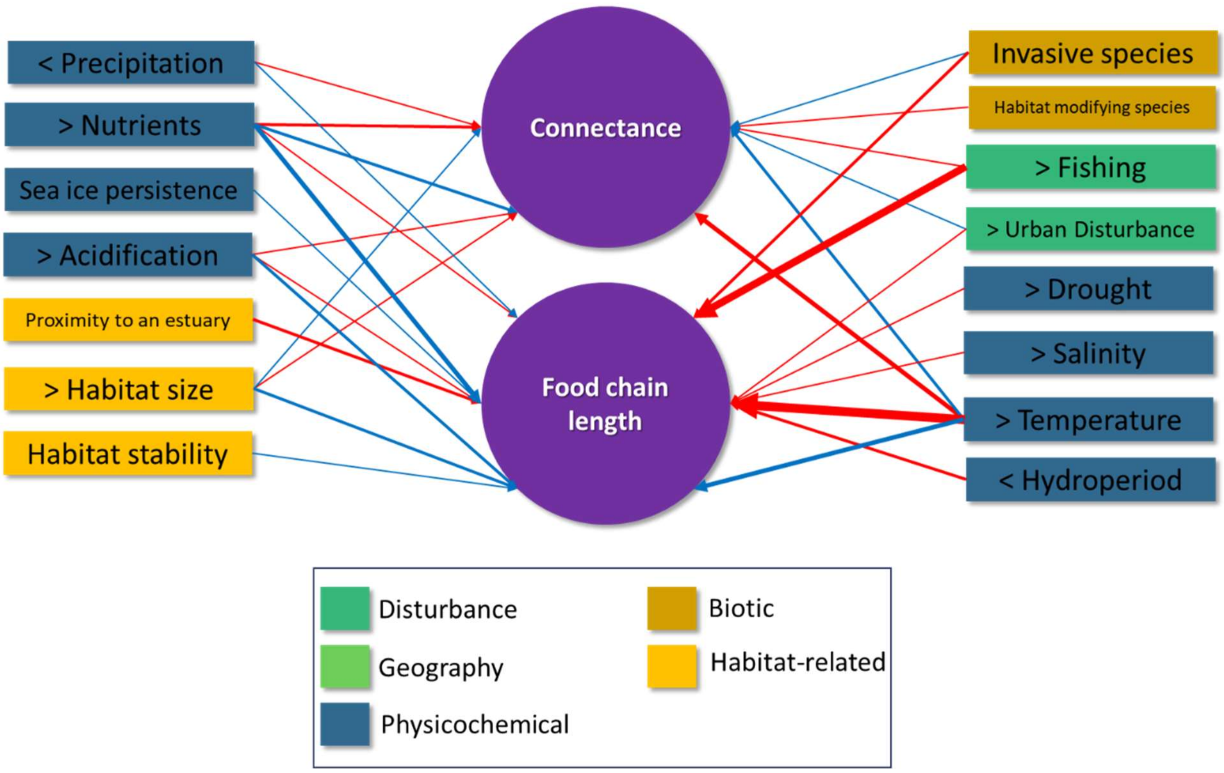
- Increase the grazing rate with warming (Lewandowska and Sommer 2010).

- Increased primary production with warming (Perkins et al. 2010, Goldenberg et al. 2017).

- Increasing the decomposition rate with warming (Perkins et al. 2010).

- Decreasing biomass with drought (Santonja et al. 2017).


Food chain length/trophic level
Number of trophic levels, from the basal resource to the top predator.
61.54
Connectance
Proportion of the total potential trophic interactions occurring in a food web.
45.05
Linkage density
The number of links per species.
37.36
Vulnerability
10.99
Mean number of consumer species per prey species.
Generality
9.89
Mean number of prey species per consumer species.
Nestedness
7.69
The degree to which consumers' diets are subsets of more generalist consumers.
Betweenness
1.1
Node level metric derived from graph theory: how frequently is a species or group on the shortest path between each pair of every other interactors.
0
20
40
60


< Precipitation
> Nutrients
Sea ice persistence
> Acidification
Proximity to an estuary
> Habitat size
Habitat stability
Connectance
Food chain length
Invasive species
Habitat modifying species
> Fishing
> Urban Disturbance
> Drought
> Salinity
> Temperature
< Hydroperiod
Disturbance
Geography
Physicochemical
Biotic
Habitat-related

Supported by (theory)	**Predictions**	**Empirically tested**
MT, FT	Warming (combined with body size) increases predator-prey interaction strength in ectotherms, by increasing foraging velocity (but has no effect on sit-and-wait predators).	Novich et al . (2014)
MT, FT	Connectance decreases with warming (depending on the sensitivity of attack rate and handling time to temperature).	Sentis et al. (2014)
MT, FT	Interaction strength decreases with resource availability.	Sentis et al. (2014)
MT, FT	Interaction strength increases with temperature.	Sentis et al. (2014)
ES	Increased CO2 (elevated C:N and C:P ratios, causing stoichiometric imbalances) decreases primary producers' growth, detritivore rate, herbivore consumption, growth, and reproduction.	Perkins et al. (2010)

Ecological Theories	
Metabolic theory (MT)	Proposes that body size and temperature drive metabolic rate and predicts how metabolic rate controls ecological processes at all levels of organization, from individuals to the biosphere.
Ecological stoichiometry (ES)	Addresses the balance of energy and chemical elements in ecological systems (organisms, ecosystem).
Foraging theory (FT)	Views the predator-prey interaction at the individual level, discussing and even predicting how both, predator and prey species adjust their behaviour to respond to environmental variation.

Fig. 1. Study sites for the articles considered per major biome (Countries and EU + UK, Switzerland and Norway: light yellow to brown: number of studies per country).

Fig. 2. Commonly reported environmental effects on food webs per trophic level and examples of supporting studies. The environmental effects reported in rows with dark blue arrows relate to interactions between adjacent trophic levels.

Fig. 3. Overview of the food web metrics used in the reviewed literature. Percentage of each metric used in the 91 studies resorting to any of the food web metrics (19.7% of the total reviewed).

Fig. 4. Main significant environmental effects on connectance and food chain length found in the literature review. Arrow thickness expresses number of articles. The > and < sign express the directionality in the environmental gradient. Blue arrows - positive effect; red arrows - negative effect (this figure is based upon the values in the Supporting Material, Appendix A).

Table 1. Integrating food web ecology with other fields of ecology to get to a more mechanistic understanding of the relationships of food web with the environment contributes increase predictability while furthering the empirical verification of theory.