Disentangling food-web environment relationships: a review with guidelines

Mestre, F.[1]* (fmestre@uevora.pt); Gravel, D.[2] (dominique.gravel@usherbrooke.ca); García-Callejas, D.[3] (david.garcia.callejas@gmail.com); Pinto-Cruz, C.[4] (ccruz@uevora.pt); Matias, M.G.[1,5] (miguel.matias@mncn.csic.es) & Araújo, M.B.[1,5] (mba@uevora.pt)

*Corresponding author.

ORCID: FM: 0000-0002-7390-1120; **DG**: 0000-0002-4498-7076; **DGC**: 0000-0001-6982-476X; **CPC**: 0000-0002-2818-5700; **MGM**: 0000-0001-9198-2051; **MBA**: 0000-0002-5107-7265.

1 - Rui Nabeiro Biodiversity Chair, MED - Mediterranean Institute for Agriculture, Environment and Development, Universidade de Évora. Casa Cordovil 2ª Andar, Rua Dr. Joaquim Henrique da Fonseca, 7000 – 890 Évora, Portugal.

2 - Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada.

3- Estación Biológica de Doñana, CSIC, Avda. Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla, Spain.

4 - MED - Mediterranean Institute for Agriculture, Environment and Development & Departamento de Biología, Escola de Ciências e Tecnologia. Universidade de Évora, Ap. 94, 7002-554 Évora, Portugal.

5 - Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, CSIC, c/ José Gutiérrez Abascal, 2, 28006 Madrid, Spain.

Acknowledgements: FM, DGC, CPC, MGM, MBA were supported thorough the project StateShifts (ref. PTDC/AAG-MAA/3764/2014) funded by FCT, the Portuguese Foundation for Science and Technology. FM, MGM, MBA were supported thorough the project AQUACOSM.

Author contributions: FM created the database upon which this review is based and co-wrote the manuscript with DG, DGC, CPC, MGM and MBA.

Data availability statement: A file with the database upon which the review was based is made available as Supplementary Information.

Data sources: The review is based upon the review of 463 papers published between 2006 and 2017. References are made available within the database.

Abstract

Food webs represent energy fluxes and nutrient cycling, underpinning ecosystem functioning. Whether and how interactions vary over 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 addressed drivers on determining structural food web properties. Most studies are local, replication is often lacking, and regional generalities are difficult. 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 studying 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; ecosystem services; environmental change; food webs.

1. Introduction

The representation of communities as networks of species connected by trophic relationships was first proposed by Charles Elton in the late 1920s (Elton, 1927). Research on the topic increased during the ’70s-’80s (Layman et al., 2015) and gained new momentum recently, owing to the renewed interest in understanding environmental change effects on biodiversity. Food webs provide a schematic representation of energy processing and transformation while 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 species, interactions, energy and matter fluxes, this framework allows the exploration of the effects of environmental changes on different facets of biodiversity.

Species distributions and their interactions are driven by multiple environmental characteristics, such as temperature and precipitation (Peterson et al., 2011; Post, 2013). Food webs provide the link between community ecology (and its building blocks, individuals, species, and populations) and ecosystem ecology (flows of biomass, energy and nutrients) (Thompson et al., 2012). If emerging functional food-web properties such as trophic regulation, energy transfer efficiency, or primary and secondary productivity, changed predictably along environmental gradients, then our ability to anticipate the consequences of global environmental changes on ecological communities would be considerably simplified.

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 anticipate some of the ecological consequences of global changes. It is less clear, however, if aspects of food-web organization follow consistent changes along gradients (Baiser et al., 2019), such as temperature and productivity (Mendoza & Araújo, 2019).

Previous reviews have addressed the effects of environmental gradients on ecological networks (Pellissier et al., 2017; Tylianakis & Morris, 2017), concluding that these are mainly related with changes on species composition, relative abundances, or coevolutionary processes affecting interactions. Avenues for improvement in food web and network ecology have also been addressed (Cohen et al., 1993; Dunne, 2005; Ings et al., 2009; Thompson et al., 2012), recommending: 1) an accurate description of network nodes, 2) improved information on the links (reporting all links, preferentially quantitatively and based on observations), 3) defining the setting (spatial description, sampling temporal span and effort), 4) standardizing the data structure, 5) promoting collaborative efforts between researchers with different expertise, 6) strengthening the theoretical framework and mechanistic understanding (to improve predictability), 7) resorting to a more individual-based perspective, 8) integrating different types of ecological networks, 9) studying networks on natural gradients, and 10) encouraging manipulative experiments. These recommendations are intended to improve data quality, comparability and availability and drive the field towards a more predictive, mechanistic view.

We comprehensively reviewed the literature over the last decade (2006 to 2017), asking if structural food-web properties change consistently with environmental variation. We compiled a comprehensive database with 463 studies distributed worldwide (Figure 1 and Annex 1, Supporting Information).

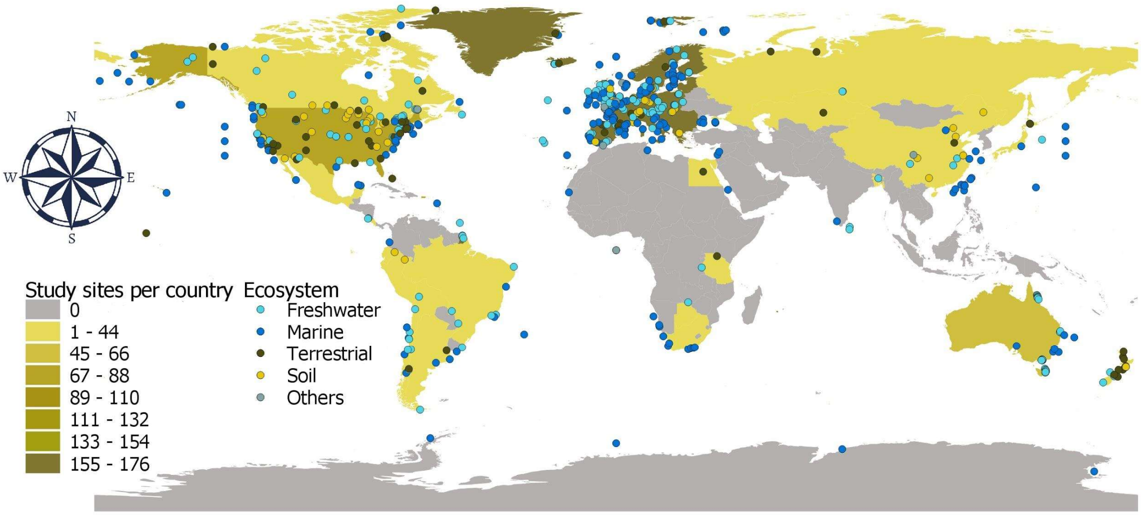


Figure 1 – Study sites for the articles considered per major biome (Countries and EU + UK, Switzerland and Norway: light yellow to brown: number of studies per country).

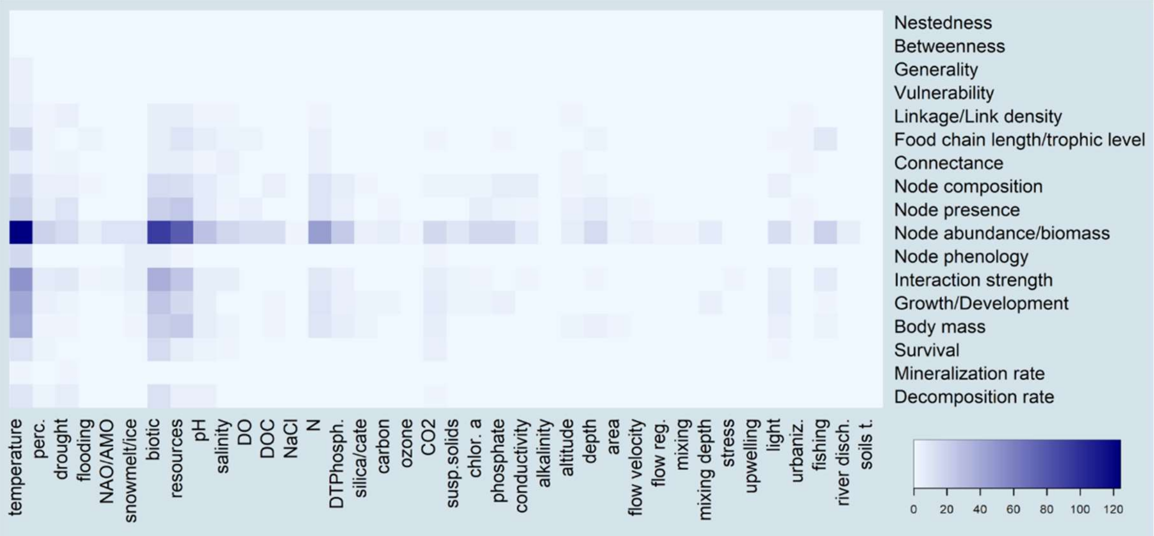
Our objectives were: i) search for the existence of relationships between environmental gradients and food-web structural properties, whether at the node, interaction or food web structural level; ii) assess the state-of-the-art of food web ecology and provide future perspectives.

We analysed the number of articles showing significant relations between predictors and response variables and summarized this information in a database. The inclusion of articles in the database followed a two-step selection process: a) a search in the Web of Science with pre-determined keywords b) retaining those with at least three trophic interactors being related to an environmental gradient.

2. Environmental gradients and food webs

2.1. *Effects on nodes and interactions*

Two predictors stand out as showing significant relations with response variables (Figure 2): temperature and biotic-related variables (e.g. presence of predators). The response variable that was more frequently considered was node abundance/biomass (the abundance/biomass of a species, trophic or functional group).



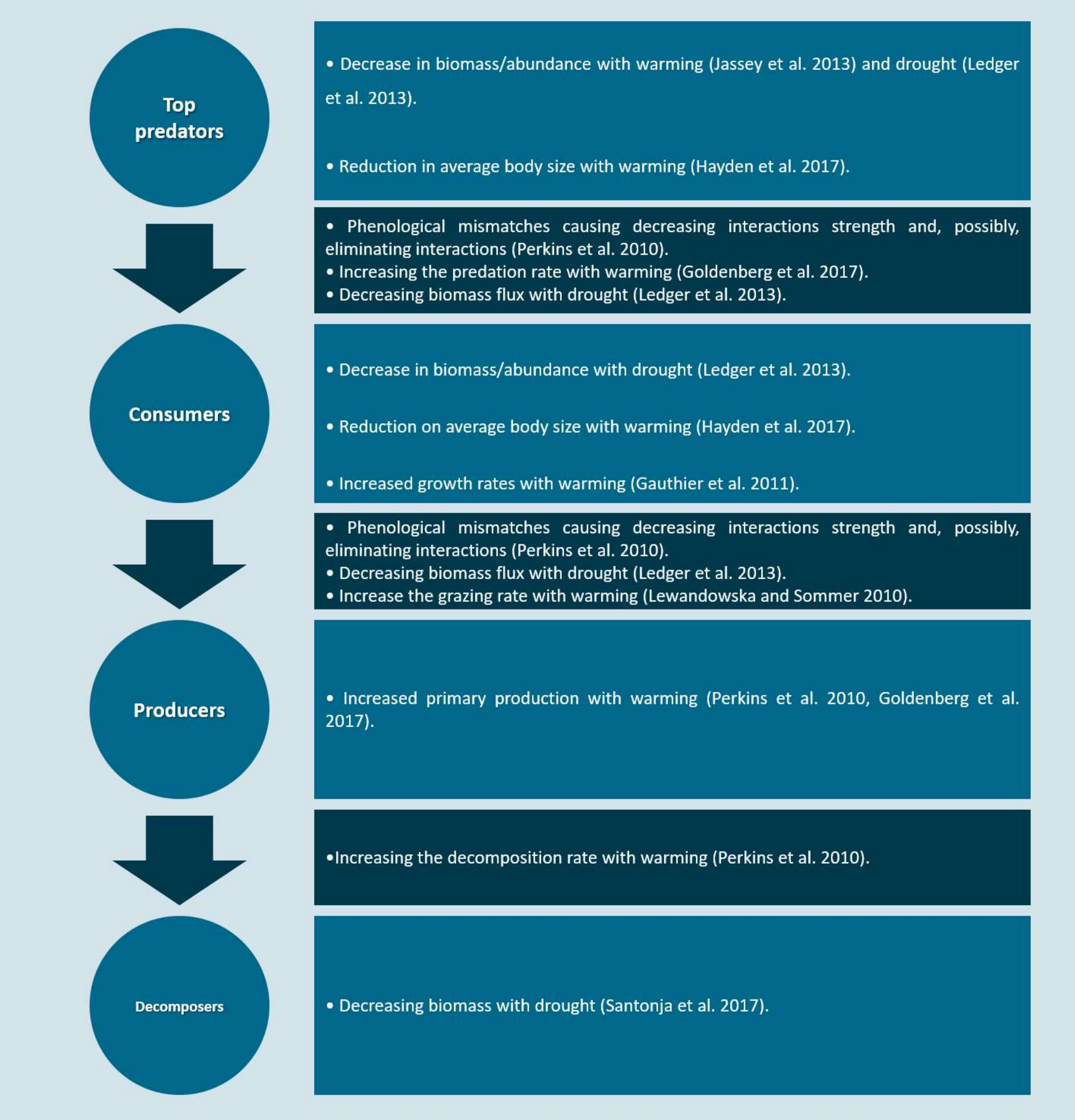
Drivers: temperature: average temperature and temperature variability; perc. - precipitation/irrigation; drought - drought frequency and intensity; flooding - flooding frequency and intensity; NAO/AMO - North Atlantic Oscillation/Atlantic Multidecadal Oscillation; snowmelt/ice - snowmelt date and sea ice persistence; biotic - presence of predator or basal, resource species; resources - nutrients, organic matter and resources; pH - pH and CO2 concentration in some marine studies; salinity - water salinity; DO - Dissolved oxygen; DOC - dissolved organic carbon; NaCl - NaCl concentration; N - dissolved inorganic nitrogen, nitrite (NO3-), nitrate (NO2-) and ammonium (NH4); DTPhosph. - dissolved inorganic and total phosphorus; silica/cate - Silica and silicate; carbon - carbon concentration; ozone - ozone exposure; CO2 - CO2 concentration in soil and atmosphere; susp.solids - suspended solids, soil extract suspended and water turbidity; chlor. a - chlorophyll a; phosphate - phosphate concentration; conductivity - electric conductivity; alkalinity; altitude; depth - water depth; area - region or lake area; flow velocity - water flow velocity; flow regulation - water flow regulation; mixing - water mixing; mixing depth - water mixing depth; stress - environmental stress; upwelling - upwelling events; light - light intensity; urbaniz. - urbanization gradient; fishing - fishing intensity; river disch. - river discharge; soils t. - soil texture.

Figure 2 – The number of articles assessing the significant relations between environmental and human-related drivers (columns) and response variables (rows).

The effects of environmental warming on food webs, and consequently ecosystem functioning, is a concern that is well demonstrated by the frequency with which this variable is addressed in research (35.2% of the articles consider either temperature or temperature variability to be significant predictors).

The presence of other species, such as predators (e.g. Maran & Pelini 2016) or species at the base of the food web (Charvet et al., 2014), another variable gathering attention from researchers in the last decade (26.1% of the articles consider biotic predictors to be significant predictors). With the ongoing environmental change, and the consequent range shifts and local extinctions, communities are expected to undergo compositional changes, triggering the emergence of novel communities (e.g. Lurgi et al. 2012). These changes, a consequence of communities suffering local extinctions or species inputs, will impact food webs (e.g. Seifert et al. 2015) and have been the focus of much attention in the last decade, as demonstrated by the high frequency of articles resorting to biotic predictors.

The most widely reported patterns in the literature are the reduction in body size with increasing temperature in most trophic levels, phenological mismatches affecting interactions, increasing decomposition rate and primary productivity with increasing temperature (Figure 3). However, even these patterns are not widespread and are heavily dependent upon local conditions, species involved, and scale. On the other hand, some of these food-web traits 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 (e.g. Legagneux et al., 2014).



- 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).

- Phenological mismatches causing decreasing interactions strength and, possibly, eliminating interactions (Perkins et al. 2010).
- Increasing the predation rate with warming (Goldenberg et al. 2017).
- 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).

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

Figure 3 – 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.

2.2. *Effects on structural metrics*

Collective properties of food webs can be summarized by network-level metrics. We examined the frequency with which different food web metrics were used in the reviewed articles. Only a few studies resort to network metrics to describe food webs (19.7%, 91 studies). This may be because not all studies describe food webs as networks. Some resort to describing the effects of environmental drivers on interactions and species or trophic/functional groups, without requiring the use of a network structure. Food chain length, link density and connectance were the most used structural metrics (Figure 4), and thus we discuss these in greater detail in the next sections.

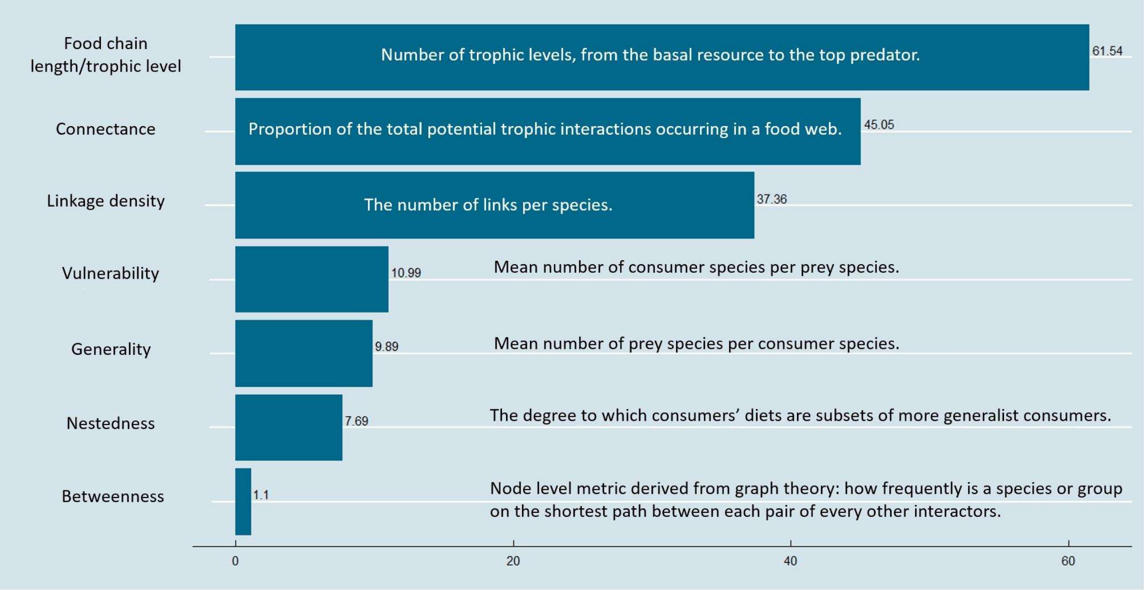


Figure 4 - Overview of the food-web metrics used in the reviewed literature. Percentage of each metric used in the 91 studies resorting to any of the food web metrics (19.65% of the total reviewed).

2.2.1. *Food chain length*

It has been postulated that food chain length decreases with increasing disturbance and increases with increasing energy availability and ecosystem size (Pimm, 1991; Young et al., 2013). The literature shows that flow regulation (Ruhí et al., 2016), increased productivity (Young et al., 2013), and increased habitat size (Baiser et al., 2012) increase food chain length. These proposed relationships are intrinsically related to energy availability since, all other things being equal, a greater area corresponds to a greater amount of energy available. Likewise, an increased disturbance corresponds to a decrease in the constancy with which energy is available to organisms. Yet studies do not treat disturbance, energy availability, and ecosystem size as equivalent, rather searching for the best mutually exclusive correlates. Disturbance has been proposed as a candidate driver for food chain length in systems prone to disturbance (e.g. freshwater systems affected by changes in hydrology, Ruhí et al. (2016)). In systems characterized by greater levels of environmental stability, habitat size is another candidate driver of food chain length (Baiser et al., 2012). In systems with environmental drivers directly limiting primary producers, such as nutrient availability (Doi, 2012), resource availability appears to be the main driver.

2.2.2. *Connectance*

Connectance characterizes food web complexity (Poisot & Gravel, 2014) and has been related to community stability, robustness (De Angelis, 1975; Dunne et al., 2002), and species richness (Warren, 1990). It is still not settled whether increased connectance increases or decreases network resilience (De Angelis, 1975; Dunne et al., 2002; Gardner & Ashby, 1970), or whether species richness covaries with connectance (Warren, 1990; Winemiller, 1989). However, a recent study using 116 empirical food webs concluded that stability might not be related to traditional descriptors of connectivity, such as connectance (Jacquet et al. 2016). In the present review, we found a few examples of studies relating complexity and stability (e.g. Garay-Narvaez et al. 2013, Galiana et al. 2014, Cesarz et al. 2015). For example, in a study performing *in silico* experiments on empirical vertebrate food webs (Galiana et al., 2014), researchers concluded that those with lower connectance were shown to be less resistant to invasions, probably because vacant niches are more likely.

Connectance has also been related to ecosystem disturbance and variability. For example, urbanization (Docile et al., 2016) and proximity to a river estuary 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 the hypothesized inverse relationship between connectance and species richness (May, 1972). Finally, connectance is relatively robust to differences in sampling effort (Martinez et al., 2012), taxonomic resolution (Martinez, 1993), and scale (Martinez & Havens, 1993), which makes it a reliable metric for comparing multiple studies which consider a diversity of node resolutions and spatial and temporal scales.

In our review, the effect of each environmental gradient on the three most common metrics was frequently inconsistent. We identified, for example, both positive and negative effects of increasing temperature on connectance, link density and food chain length (Figure 5).

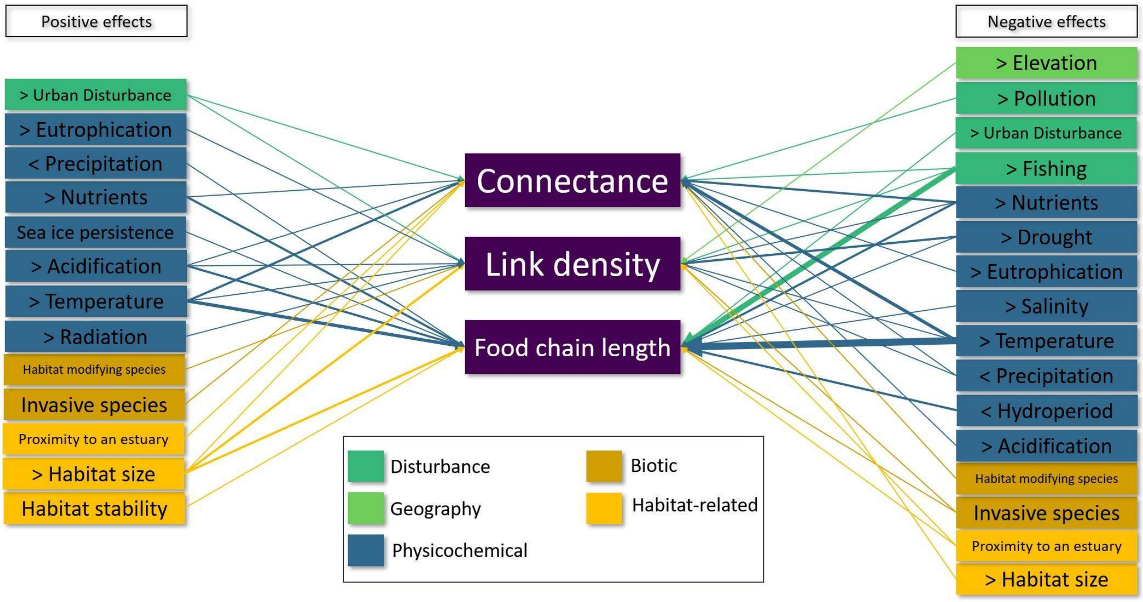


Figure 5 – Main significant environmental effects on connectance, link density, and food chain length found in the literature review. Arrow thickness expresses the number of articles on which it is based. The > and < sign express the directionality in the environmental gradient. Connections are scaled by the number of articles in the database.

As such, one of the most pervasive findings is that studies particularities hinder the emergence of general patterns.

3. The need for a uniform approach

While food webs can be clearly defined as ”… the feeding relationships among species or groupings of species” (Moore & De Ruiter, 2012), there is substantial room for interpretation regarding the specifics of the relationships. How should interacting species or groups of species be defined? Should nodes have the same taxonomic or functional resolution? How should interactions be measured? How are spatial boundaries of food webs determined? How should the relevant temporal resolution and extent of the interactions be defined? Different answers to these questions will affect the study design, results, and interpretations of underlying patterns and processes in food webs. This variability, as we have shown, is hindering the comparability and potential generalizations about environmental effects on food webs structure and function (e.g. Martinez 1991, Dunne 2005).

3.1. *Defining the food-web: its elements and interactions*

Studies use food webs with varying resolutions for nodes and different methods to determine interactions (Supporting Information Figures A5-6). Node resolution (species, taxonomic, trophic, and functional groups) influences structural metrics like connectance, linkage density or complexity, and predator:prey ratios (Thompson & Townsend, 2000). It can vary between and within food web studies, with broader taxonomic classifications being common at basal trophic levels and finer resolutions being common at higher levels. Most of the articles reviewed here use the broadest possible class, “other taxonomic groups” (47.7% of the total number of articles). The recurrence of coarse taxonomic resolutions in food web studies likely is a consequence of the basal elements of the food webs being more taxonomically aggregated (Supporting Information Figures A6). It follows that food web metrics vary in their sensitivity to the aggregation of species into functional or trophic groups. Connectance and predator:prey ratio are almost invariant to aggregation (Martinez, 1993). For instance, one study (Sugihara et al. 1997) concluded that only the proportion of basal species and linkage density are affected by aggregation. This study also suggested that metrics are more susceptible to taxonomic aggregation than trophic aggregation because trophic aggregation lumps together functionally similar species, leading to a smaller impact on the overall structure of the network.

Trophic interactions can be characterized by energy fluxes, frequency of feeding events, impact on growth rates or impact on population sizes (Berlow et al., 2004). Detection of trophic interactions frequently uses stable isotopes (14.3%, second only to using previous references, 46.0%). Other methods of studying interactions include statistical associations between the occurrences/abundances/biomass of the interacting species (5.4%), feeding experiments (4.3%), and gut content analysis (4.1%) (Supporting Information Figure A5).

Method choice can also impact food web structure: stable isotopes and fatty acids identify feeding interactions over a wider period of time (time-averaged results) providing information even if the stomachs are empty (Kolts et al., 2013); stomach contents provide greater taxonomic resolution but are invasive (Kolts et al., 2013).

The variety of approaches in use inevitably limits comparability across studies and compromises generalizations. Further research is needed on how to standardize interaction measurements from networks estimated using different sampling methodologies.

3.2. *Food-webs in space and time*

Food webs typically characterize snapshots of trophic interactions at a given place and time. However, since studies vary in the spatial and temporal resolutions and extents used to characterise them (e.g., spatial scales ranging from “local” to “global”, or temporal scales from “< 1 year” to “> 10 years”), detection of general patterns is most likely impaired (Supporting Information Figure A7-A9).

The spatial boundaries delimiting the sources of data used to construct food webs are often arbitrary (Baiser et al., 2012) and vary with observer perceptions or conveniences (Moore & De Ruiter, 2012). Additionally, according to Cohen (1978), food webs can be divided into source, sink, and community food webs. These differences in determining which species are considered have implications for determining the spatial boundaries of the food web. Some examples are present in the literature reviewed, 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 sampled across increasingly large extents are more likely to lose information regarding the actual trophic interactions, instead of representing potential interactions (e.g. Braga et al. 2019). Comparisons across food web topologies measured at different scales thus need to be done with caution.

Food webs are also not spatially isolated, being connected to external elements through dispersal or allochthonous subsidies (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 disconnected local food-webs (e.g. McCann et al. 2005). On the other hand, allochthonous subsidies (Meunier et al., 2017), whether at the bottom or elsewhere in the food web, can constitute major energy sources, sustaining complex organizations. Both dispersal and allochthonous subsidies make the definition of food web boundaries difficult to establish.

Spatial scale has two main components, namely extent (the area of the study site) and resolution (the resolution of the food webs). 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, but a “local” resolution. The studies reviewed here were mostly local, whether in extent or resolution (Supporting Information Figure A7-8). 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 on food webs do not provide replicates, whether spatial or temporal, 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). It follows that uncertainty in the detection of pairwise interactions scales up to the network level potentially biasing some structural properties more than others (Poisot et al., 2015). Communities are notoriously variable, and it is standard practice to evaluate and consider uncertainty in comparative studies. However, probably owing to difficulties in documenting pairwise interactions and characterising the full spectrum of interactions in a network, attempts to characterise food webs often result in a single characterisation, a snapshot, with no attempts to assess their representativeness. A few studies have some way of including spatial variability in food web structure (27.4% of the total), generally through multiple sampling sites within the study area, although spatially averaging the resulting food web. Some go a step further and effectively evaluate the spatial heterogeneity along environmental gradients. For instance, Doi and colleagues (2013) demonstrated small-scale spatial heterogeneity among planktonic food webs along an environmental gradient of water chemistry and primary productivity. In a study where the spatial scale and extent were varied systematically, the latter was found to have more impact on network metrics considering the relevance of fully encompassing the environmental gradients considered (Vinagre et al, 2017). Around a third of the studies 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) (32.18% of the total). Temporal averaging is likely to mask seasonal or inter-annual dynamics, affecting the structural metrics of local food webs (Jordán & Osváth, 2009; López et al., 2018). The majority of studies on temporal dynamics of networks concern mutualistic interactions (e.g. CaraDonna et al. 2017), with just a few dealing with food webs. A study, conducted at the Åland Islands in the Northern Baltic Sea, evaluated the temporal variability in a benthic food-web (Nordström et al., 2009) and concluded that there is intra-seasonal variation in food web components both within and between trophic levels. Additionally, in this study, interannual variability was limited, demonstrating that the food web was temporally stable. However, seasonal fluctuation of stable isotope values decreased in the higher trophic level which shows that distinct trophic levels respond differently to time, which is certainly a consequence of the fact that lower trophic levels have generally shorter life spans and faster generational times. Consequently, a difference in the food webs' basal resources might be diluted in the upper trophic levels (Kolts et al., 2013; O'Reilly et al., 2002).

Most of the reviewed studies include 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%) and five to ten years (4.1%) (see also Supporting Information Figure A9). The relatively short time span of temporal food-web studies reduces dramatically the likelihood of detecting responses to sub-lethal disturbances, which may take decades to express themselves (e.g. Peterson et al. 2003).

3.3. Diversity of approaches and objectives

There is no standardized approach to evaluate the impacts of environmental variables on food webs and, in most studies, this is not even the primary objective. Several studies resort to the comparison of food web structure 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%). Others use experimental manipulation of environmental characteristics 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%; simulation 5.8%).

Studies also vary in their objectives. Marine studies (43.6%, see Fig.1) 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), CO2 (Dyer et al., 2013), or climate change as a whole (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 CO2 (Mueller et al., 2016), hydrological changes (Sun et al., 2016) and warming (Schwarz et al., 2017).

4. Progresses made in the last decade

Previous authors have made recommendations to advance food web ecology focusing mainly on data quality and the move towards more predictability (e.g. Cohen et al. 1993, Dunne 2005, Ings et al. 2009, Thompson et al. 2012). It is important to reflect on how far we have gone and if we are moving in the right direction.

A positive sign is an emergence of manipulative studies (e.g., mesocosms) or natural experiments, as a more generalized approach. However, observational studies still dominate, representing most of the reviewed literature. Despite progress with techniques allowing better descriptions of food-web structure, 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 heavily reliant on published information as the main source of information to determine interactions and node resolution is still defined in broader taxonomic resolutions than the species.

Another unresolved issue is the lack of data standardization, of which our review only shows modest signs of progress. One notable exception is the many marine models developed with Ecopath with Ecosim (Christensen & Walters, 2004), which require the data and metadata to be standardized and stored in an online database with a strictly defined structure.

Some of the reviewed articles seek a more mechanistic, and thus more predictive approach to understanding the way food webs respond to environmental gradients, as recommended by earlier reviews (e.g. Ings et al. 2009). Understanding the underlying processes explaining food web structural response to gradient is achieved by resorting to experimental manipulation. Many of the reviewed studies are controlled manipulative or natural experiments as mentioned above.

Previous works 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. 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 research questions of applied value for the management of natural resources (e.g., fisheries) without seeking a connection to a broader unifying ecological theory.

Past work (Cohen et al., 1993) has also highlighted the need for collaboration between researchers to tackle the challenge of identifying multiple taxa, bringing in taxonomists to work with food web ecologists. The need for geographically distributed coordinated experimental studies is an additional incentive to collaboration, considering it involves researchers working on multiple regions.

5. 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 function. Indeed, no ubiquitous relationships between food-web structural properties and environmental gradients emerge from our review despite recent studies, building on the concept of meta-webs (Morales-Castilla et al., 2015), uncovering clear relationships with environmental parameters (Mendoza & Araújo, 2019) or relating the number of trophic levels with productivity, and temperature (both, average and seasonality) (Oksanen et al., 2020). Despite progress in sampling techniques (e.g., stable isotopes or environmental DNA), there is substantial scope for improving and unifying methodologies and the conceptual underpinnings of much of the research. Developments in three areas of inquiry could help the field move forward.

5.1. Refinement of theory and testable predictions

Science is usually on the right path when small sets of testable predictions on the most pressing questions are agreed upon and pursued collectively by researchers in the field. 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). For instance, there is a long tradition to study how trophic regulation varies over productivity (e.g., the green world hypothesis, Hairston et al. (1960)). Recently, a quantitative framework has been proposed to partition the drivers of network change at the biogeographical scales (Gravel et al., 2018; 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 optimal foraging theory to predict food web structure (Petchey et al., 2008). However, akin to empirical observations, theory is fragmented by the diversity of gradients and models used to study food-web properties.

A consistent 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). It should focus on a few gradients, and we note that temperature, solar radiation intensity, and primary productivity are likely the best candidates because of their relevance as surrogates of energy availability. These gradients are intimately related, although their effects might differ since temperature directly affects all species in the food-web via physiological effects (Brown et al., 2004), while radiation and productivity affect plants directly and indirectly higher trophic levels (Loreau, 2010). Similarly, theory should focus on the set of food-web functional properties that are measurable in the field and relevant to understand ecosystem functioning. Based on tradition and relevance for global change studies, a useful path 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.

5.2. Minimum sets of agreed standards for data collection and analysis

Studies of food webs can dwell on different questions, and although refinement of theories and hypotheses is expected to reduce variation in the methodologies for data acquisition and analysis (see above), there will always be diversity in the approaches used.

A consistent definition of “interaction” is required. Variation in criteria for link determination could limit comparability with researchers casting doubt on the usefulness or even validity 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 in food-webs and there is no guarantee that the conclusions with different methods are comparable (Berlow et al., 2004). Agreement on a core set of procedures for establishing such links would help reduce variation in food-web patterns associated with variation in the methods used. Furthermore, food webs should be defined by natural spatial boundaries constraining the movement of a majority of organisms. Finally, the taxonomic resolution of the nodes should be increased (ideally at the species level) and minimally it should be consistent within a single food-web. Hopefully, novel molecular methods to process gut contents will solve part of the problem ensuring species-level resolution of the nodes (Roslin et al., 2016).

Nevertheless, minimum agreed standards are needed for enabling comparability across studies (Poisot et al., 2016), an effort already achieved for using data and models of species distributions (Araújo et al., 2019). In particular, attention should be given to robust data specifications to aggregate datasets and perform comparative studies. The "mangal" data specification (Poisot et al., 2016), for instance, is a common language to store and share network data. It is based on a hierarchical collection of ecological objects, from individuals to networks. The adoption of such a standard not only requires taking into consideration data acquisition and structure, it also implies that all relevant metadata is collected, making comparative studies over gradients more accessible.

5.3. Development of geographically distributed experimental studies

Understanding how food webs respond to perturbations relies heavily on the ability to generalize conclusions often derived from observations at single locations. The need for geographical replication of local experiments across environmental gradients is critical for understanding the relationship between biological observations and environmental or evolutionary predictors (Freestone & Osman, 2011; Pelini et al., 2014). The implementation of multiple-site experiments can lend support to the interpretation that local observations are not the product of local contingencies, rather providing meaningful inferences 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). The development of globally replicated experiments assessing the responses of food webs to perturbations across relevant environmental gradients has the potential to establish a benchmark for the future development of predictive food-web models.

6. Conclusions

The analytical tools required and the setting up of manipulative experiments extending across large geographical areas and periods of time is a costly endeavour requiring collaboration between researchers across regions. Advancing food web ecology is poised with several scientific challenges, logistical difficulties, and lack of funding. We encourage researchers to develop theoretical and methodological approaches, as well as geographically replicable sampling schemes, to help solve these long-standing issues concerning the environmental drivers coercing food-web structure.

7. References

Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. Science Advances. https://doi.org/10.1126/sciadv.aat4858

Baiser, B., Gotelli, N.J., Buckley, H.L., Miller, T.E., & Ellison, A.M. (2012). Geographic variation in network structure of a nearctic aquatic food web. Global Ecology and Biogeography, 21(5), 579–591. https://doi.org/10.1111/j.1466-8238.2011.00705.x

Baiser, B., Gravel, D., Cirtwill, A.R., Dunne, J.A., Fahimipour, A.K., Gilarranz, L.J., Grochow, J.A., Li, D., Martinez, N.D., McGrew, A., Poisot, T., Romanuk, T.N., Stouffer, D.B., Trotta, L.B., Valdovinos, F.S., Williams, R.J., Wood, S.A., & Yeakel, J.D. (2019). Ecogeographical rules and the macroecology of food webs. Global Ecology and Biogeography, geb.12925. https://doi.org/10.1111/geb.12925

Banašek-Richter, C., Cattin, M.F., & Bersier, L.F. (2004). Sampling effects and the robustness of quantitative and qualitative food-web descriptors. Journal of Theoretical Biology. https://doi.org/10.1016/S0022-5193(03)00305-9

Barnes, A. D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., de Ruiter, P., & Brose, U. (2018). Energy Flux: The Link between Multitrophic Biodiversity and Ecosystem Functioning. Trends in Ecology and Evolution, 33(3), 186–197. https://doi.org/10.1016/j.tree.2017.12.007

Berlow, E.L., Neutel, A.M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., Mckane, A.J., Montoya, J.M., & Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. In Journal of Animal Ecology. https://doi.org/10.1111/j.0021-8790.2004.00833.x

Bideault, A., Loreau, M., & Gravel, D. (2019). Temperature modifies consumer-resource interaction strength through its effects on biological rates and body mass. Frontiers in Ecology and Evolution. https://doi.org/10.3389/fevo.2019.00045

Blottière, L., Jaffar-Bandjee, M., Jacquet, S., Millot, A., & Hulot, F.D. (2017). Effects of mixing on the pelagic food web in shallow lakes. Freshwater Biology, 62(1), 161–177. https://doi.org/10.1111/fwb.12859

Borer, E.T., Harpole, W.S., Adler, P.B., Lind, E.M., Orrock, J.L., Seabloom, E.W., & Smith, M.D. (2014). Finding generality in ecology: A model for globally distributed experiments. Methods in Ecology and Evolution. https://doi.org/10.1111/2041-210X.12125

Braga, J., Pollock, L.J., Barros, C., Galiana, N., Montoya, J.M., Gravel, D., Maiorano, L., Montemaggiori, A., Ficetola, G.F., Dray, S., & Thuiller, W. (2019). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. Global Ecology and Biogeography. https://doi.org/10.1111/geb.12981

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., & West, G.B. (2004). Toward a metabolic theory of ecology. Ecology, 85(7), 1771–1789. https://doi.org/10.1890/03-9000

Buckley, H.L., Miller, T.E., Ellison, A.M., & Gotelli, N.J. (2010). Local- to continental-scale variation in the richness and composition of an aquatic food web. Global Ecology and Biogeography, 19(5), 711–723. https://doi.org/10.1111/j.1466-8238.2010.00554.x

Burgmer, T., & Hillebrand, H. (2011). Temperature mean and variance alter phytoplankton biomass and biodiversity in a long-term microcosm experiment. Oikos, 120(6), 922–933. https://doi.org/10.1111/j.1600-0706.2010.19301.x

Cañedo-Argüelles, M., Sala, M., Peixoto, G., Prat, N., Faria, M., Soares, A.M.V.M., Barata, C., & Kefford, B. (2016). Can salinity trigger cascade effects on streams? A mesocosm approach. Science of the Total Environment, 540(SI), 3–10. https://doi.org/10.1016/j.scitotenv.2015.03.039

CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., &

Sanders, N.J. (2017). Interaction rewiring and the rapid turnover of plant–pollinator networks. Ecology Letters, 20(3), 385–394. https://doi.org/10.1111/ele.12740

Careddu, G., Costantini, M.L., Calizza, E., Carlino, P., Bentivoglio, F., Orlandi, L., & Rossi, L. (2015). Effects of terrestrial input on macrobenthic food webs of coastal sea are detected by stable isotope analysis in Gaeta Gulf. Estuarine, Coastal and Shelf Science, 154, 158–168. https://doi.org/10.1016/j.ecss.2015.01.013

Cesarz, S., Ciobanu, M., Wright, A.J., Ebeling, A., Vogel, A., Weisser, W.W., & Eisenhauer, N. (2017). Plant species richness sustains higher trophic levels of soil nematode communities after consecutive environmental perturbations. Oecologia, 184(3), 715–728. https://doi.org/10.1007/s00442-017-3893-5

Cesarz, S., Reich, P.B., Scheu, S., Ruess, L., Schaefer, M., & Eisenhauer, N. (2015). Nematode functional guilds, not trophic groups, reflect shifts in soil food webs and processes in response to interacting global change factors. Pedobiologia, 58(1), 23–32. https://doi.org/10.1016/j.pedobi.2015.01.001

Charvet, S., Vincent, W.F., & Lovejoy, C. (2014). Effects of light and prey availability on Arctic freshwater protist communities examined by high-throughput DNA and RNA sequencing. FEMS Microbiology Ecology, 88(3), 550–564. https://doi.org/10.1111/1574-6941.12324

Christensen, V., & Walters, C.J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. Ecological Modelling, 172(2–4), 109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

Cirtwill, A.R., Eklöf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for investigating the reliability of empirical network construction. Methods in Ecology and Evolution, 10(6), 902–911. https://doi.org/10.1111/2041-210X.13180

Cohen, J.E. (1978). Food webs and niche space. Princeton University Press.

Cohen, J.E., Beaver, R.A., Cousins, S.H., DeAngelis, D.L., Goldwasser, L., Heong, K.L., Holt, R.D., Kohn, A.J., Lawton, J.H., Martinez, N., O'Malley, R., Page, L.M., Patten, B.C., Pimm, S.L., Polis, G.A., Rejmánek, M., Schoener, T.W., Schoenly, K., Sprules, W.G., Teal, J.M., Ulanowicz, R.E., Warren, P.H., Wilbur, H.M., Yodzis, P. (1993). Improving food webs. Ecological Society of America, 74(1), 252–258. https://doi.org/10.2307/1939520

Collins, S.M., Sparks, J.P., Thomas, S.A., Wheatley, S.A., & Flecker, A.S. (2016). Increased Light

Availability Reduces the Importance of Bacterial Carbon in Headwater Stream Food Webs. Ecosystems, 19(3), 396–410. https://doi.org/10.1007/s10021-015-9940-3

De Angelis, D.L. (1975). Stability and Connectance in Food Web Models. Ecology, 56(1), 238–243. https://doi.org/10.2307/1935318

Deguines, N., Brashares, J.S., & Prugh, L.R. (2017). Precipitation alters interactions in a grassland ecological community. Journal of Animal Ecology, 86(2), 262–272. https://doi.org/10.1111/1365-2656.12614

Docile, T., Rosa, D.C.O., Figueiró, R., & Nessimian, J. (2016). Urbanisation alters the flow of energy through stream food webs. Insect Conservation and Diversity, 9(5), 416–426. https://doi.org/10.1111/icad.12176

Doi, H. (2012). Resource productivity and availability impacts for food-chain length. Ecological Research, 27(3), 521–527. https://doi.org/10.1007/s11284-012-0941-9

Doi, H., Zuykova, E.I., Shikano, S., Kikuchi, E., Ota, H., Yurlova, N.I., & Yadrenkina, E. (2013). Isotopic evidence for the spatial heterogeneity of the planktonic food webs in the transition zone between river and lake ecosystems. PeerJ, 1, e222. https://doi.org/10.7717/peerj.222

Dunne, J.A. (2005). The Network Structure of Food Webs. In M. Pascual & J. A. Dunne (Eds.), Ecological Networks: Linking Structure to Dynamics in Food Webs (pp. 27–86). Oxford University Press.

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

Dyer, L.A., Richards, L.A., Short, S.A., & Dodson, C.D. (2013). Effects of CO2 and Temperature on Tritrophic Interactions. PLoS ONE, 8(4). https://doi.org/10.1371/journal.pone.0062528

Eklöf, J.S., Alsterberg, C., Havenhand, J.N., Sundbäck, K., Wood, H.L., & Gamfeldt, L. (2012). Experimental climate change weakens the insurance effect of biodiversity. Ecology Letters, 15(8), 864–872. https://doi.org/10.1111/j.1461-0248.2012.01810.x

Elton, C.S. (Charles S. (1927). Animal Ecology. University of Chicago Press.

Ferreira, V., Chauvet, E., & Canhoto, C. (2015). Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. Canadian Journal of Fisheries and Aquatic Sciences, 72(2), 206–216. https://doi.org/10.1139/cjfas-2014-0119

Franzè, G., & Lavrentyev, P. (2017). Microbial food web structure and dynamics across a natural temperature gradient in a productive polar shelf system. Marine Ecology Progress Series, 569, 89–102. https://doi.org/10.3354/meps12072

Freestone, A.L., & Osman, R.W. (2011). Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. Ecology. https://doi.org/10.1890/09-1841.1

Galiana, N., Lurgi, M., Montoya, J.M., & López, B.C. (2014). Invasions cause biodiversity loss and community simplification in vertebrate food webs. Oikos, 123(6), 721–728. https://doi.org/10.1111/j.1600-0706.2013.00859.x

Garay-Narvaez, L., Arim, M., Flores, J.D., & Ramos-Jiliberto, R. (2013). The more polluted the environment, the more important biodiversity is for food web stability. Oikos, 122(8), 1247–1253. https://doi.org/10.1111/j.1600-0706.2012.00218.x

Gardner, M.R., & Ashby, W.R. (1970). Connectance of large dynamic (Cybernetic) systems: Critical values for stability. Nature, 228(5273), 784. https://doi.org/10.1038/228784a0

Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., Legagneux, P., & Cadieux, M.-C. (2011). The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Écoscience, 18(3), 223–235. https://doi.org/10.2980/18-3-3453

Goldenberg, S.U., Nagelkerken, I., Ferreira, C.M., Ullah, H., & Connell, S.D. (2017). Boosted food web productivity through ocean acidification collapses under warming. Global Change Biology, 23(10), 4177–4184. https://doi.org/10.1111/gcb.13699

Gounand, I., Kéfi, S., Mouquet, N., & Gravel, D. (2016). Trait selection during food web assembly: the roles of interactions and temperature. Theoretical Ecology, 9(4), 417–429. https://doi.org/10.1007/s12080-016-0299-7

Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N.D., Nyman, T., Poisot, T., Stouffer, D.B., Tylianakis, J.M., Wood, S.A., & Roslin, T. (2019). Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. Ecography, 42(3), 401–415. https://doi.org/10.1111/ecog.04006

Hairston, N.G., Smith, F.E., & Slobodkin, L.B. (1960). Community Structure, Population Control, and Competition. The American Naturalist, 94(879), 421–425. https://doi.org/10.1086/282146

Hayden, B., Myllykangas, J.P., Rolls, R.J., & Kahilainen, K.K. (2017). Climate and productivity shape fish and invertebrate community structure in subarctic lakes. Freshwater Biology, 62(6), 990–1003. https://doi.org/10.1111/fwb.12919

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H. (1999). Plant diversity and productivity experiments in European grasslands. Science. https://doi.org/10.1126/science.286.5442.1123

Hu, Z., Zhu, C., Chen, X., Bonkowski, M., Griffiths, B., Chen, F., Zhu, J., Hu, S., Hu, F., & Liu, M. (2017). Responses of rice paddy micro-food webs to elevated CO2 are modulated by nitrogen fertilization and crop cultivars. Soil Biology and Biochemistry, 114, 104–113. https://doi.org/10.1016/j.soilbio.2017.07.008

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H., & Woodward, G. (2009). Review: Ecological networks - beyond food webs. Journal of Animal Ecology, 78(1), 253–269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P., & Gravel, D. (2016). No complexity-stability relationship in empirical ecosystems. Nature Communications. https://doi.org/10.1038/ncomms12573

Jassey, V.E., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N., Mitchell, E.A., Toussaint, M.L., Francez, A.J., & Gilbert, D. (2013). Above- and belowground linkages in Sphagnum peatland: Climate warming affects plant-microbial interactions. Global Change Biology, 19(3), 811–823. https://doi.org/10.1111/gcb.12075

Jordán, F., & Osváth, G. (2009). The sensitivity of food web topology to temporal data aggregation. Ecological Modelling, 220(22), 3141–3146. https://doi.org/10.1016/J.ECOLMODEL.2009.05.002

Kempf, A., Floeter, J., & Temming, A. (2006). Decadal changes in the North Sea food web between 1981and 1991 - implications for fish stock assessment. Canadian Journal of Fisheries and Aquatic Sciences [Can. J. Fish. Aquat. Sci.], 63(11), 2586–2602. https://doi.org/10.1139/F06-147

Kolts, J.M., Lovvorn, J.R., North, C.A., Grebmeier, J.M., & Cooper, L.W. (2013). Relative value of stomach contents, stable isotopes, and fatty acids as diet indicators for a dominant invertebrate predator (*Chionoecetes opilio*) in the northern Bering Sea. Journal of Experimental Marine Biology and Ecology, 449, 274–283. https://doi.org/10.1016/j.jembe.2013.10.005

Layman, C.A., Giery, S.T., Buhler, S., Rossi, R., Penland, T., Henson, M.N., Bogdanoff, A.K., Cove, M.V., Irizarry, A.D., Schalk, C.M., & Archer, S.K. (2015). A primer on the history of food web ecology: Fundamental contributions of fourteen researchers. Food Webs, 4, 14–24. https://doi.org/10.1016/j.fooweb.2015.07.001

Ledger, M.E., Brown, L.E., Edwards, F.K., Milner, A.M., & Woodward, G. (2013). Drought alters the structure and functioning of complex food webs. Nature Climate Change, 3(3), 223–227. https://doi.org/10.1038/nclimate1684

Legagneux, P., Gauthier, G., Lecomte, N., Schmidt, N.M., Reid, D., Cadieux, M.-C., Berteaux, D., Bêty, J., Krebs, C.J., Ims, R.A., Yoccoz, N.G., Morrison, R.I.G., Leroux, S.J., Loreau, M., & Gravel, D. (2014). Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nature Climate Change, 4(5), 379–383. https://doi.org/10.1038/nclimate2168

Lewandowska, A., & Sommer, U. (2010). Climate change and the spring bloom: A mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton. Marine Ecology Progress Series, 405, 101–111. https://doi.org/10.3354/meps08520

Lindegren, M., Möllmann, C., Nielsen, A., & Stenseth, N.C. (2009). Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proceedings of the National Academy of Sciences of the United States of America, 106(34), 14722–14727. https://doi.org/10.1073/pnas.0906620106

Lindstrom, U., Smout, S., Howell, D., & Bogstad, B. (2009). Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. Deep-Sea Research Part II-Tropical Studies in Oceanography, 56(21–22), 2068–2079. https://doi.org/10.1016/j.dsr2.2008.11.017

Llope, M., Daskalov, G.M., Rouyer, T.A., Mihneva, V., Chan, K.-S., Grishin, A.N., & Stenseth, N.C. (2011). Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and anthropogenic conditions. Global Change Biology, 17(3), 1251–1265. https://doi.org/10.1111/j.1365-2486.2010.02331.x

López, D.N., Camus, P.A., Valdivia, N., & Estay, S.A. (2018). Food webs over time: evaluating structural differences and variability of degree distributions in food webs. Ecosphere, 9(12), e02539. https://doi.org/10.1002/ecs2.2539

Loreau, M. (2010). Linking biodiversity and ecosystems: towards a unifying ecological theory. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 365(1537), 49–60. https://doi.org/10.1098/rstb.2009.0155

Lu, X., Gray, C., Brown, L.E., Ledger, M.E., Milner, A.M., Mondragón, R.J., Woodward, G., & Ma, A. (2016). Drought rewires the cores of food webs. Nature Climate Change, 6(9), 875–878. https://doi.org/10.1038/nclimate3002

Lurgi, M., Lopez, B.C., & Montoya, J.M. (2012). Novel communities from climate change. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1605), 2913–2922. https://doi.org/10.1098/rstb.2012.0238

Majdi, N., Michiels, I.C., & Traunspurger, W. (2016). Resource depletion affects the structure of an experimental benthic food web. Limnologica, 59, 99–108. https://doi.org/10.1016/j.limno.2016.03.009

Maran, A.M., & Pelini, S.L. (2016). Predator contributions to belowground responses to warming. Ecosphere, 7(9). https://doi.org/10.1002/ecs2.1457

Martinez, N.D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecological Monographs. https://doi.org/10.2307/2937047

Martinez, N.D. (1993). Effects of Resolution on Food Web Structure. Oikos, 66(3), 403. https://doi.org/10.2307/3544934

Martinez, N.D., & Havens, K. (1993). Effect of scale on the food web structure. Science, 260(5105), 242–244.

Martinez, N.D., Hawkins, B.A., Dawah, H.A., Feifarek, B.P., Ecology, S., & Apr, N. (2012). Effects of Sampling Effort on Characterization of Food-Web Structure. Ecology, 80(3), 1044–1055. https://doi.org/10.1890/0012-9658(1999)080[1044:EOSEOC]2.0.CO;2

Massol, F., Gravel, D., Mouquet, N., Cadotte, M.W., Fukami, T., & Leibold, M.A. (2011). Linking community and ecosystem dynamics through spatial ecology. Ecology Letters, 14(3), 313–323. https://doi.org/10.1111/j.1461-0248.2011.01588.x

Matias, M.G., Pereira, C.L., Raposeiro, P.M., Gonçalves, V., Cruz, A.M., Costa, A.C., & Araújo, M.B. (2017). Divergent trophic responses to biogeographic and environmental gradients. Oikos, 126(1), 101–110. https://doi.org/10.1111/oik.02604

May, R.M. (1972). Will a large complex system be stable? Nature, 238(5364), 413–414. https://doi.org/10.1038/238413a0

McCann, K.S., Rasmussen, J.B., & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. Ecology Letters. https://doi.org/10.1111/j.1461-0248.2005.00742.x

Mendoza, M., & Araújo, M.B. (2019). Climate shapes mammal community trophic structures and humans simplify them. Nature Communications. https://doi.org/10.1038/s41467-019-12995-9

Meunier, C.L., Liess, A., Andersson, A., Brugel, S., Paczkowska, J., Rahman, H., Skoglund, B., & Rowe, O.F. (2017). Allochthonous carbon is a major driver of the microbial food web – A mesocosm study simulating elevated terrestrial matter runoff. Marine Environmental Research, 129, 236–244. https://doi.org/10.1016/j.marenvres.2017.06.008

Moore, J.C., & De Ruiter, P.C. (2012). Energetic Food Webs. Oxford Series in Ecology and Evolution. Oxford University Press.

Morales-Castilla, I., Matias, M.G., Gravel, D., & Araújo, M.B. (2015). Inferring biotic interactions from proxies. Trends in Ecology and Evolution, 30(6), 347–356. https://doi.org/10.1016/j.tree.2015.03.014

Mortensen, L.O., Schmidt, N.M., Høye, T.T., Damgaard, C., & Forchhammer, M.C. (2016). Analysis of trophic interactions reveals highly plastic response to climate change in a tri-trophic High-Arctic ecosystem. Polar Biology, 39(8), 1467–1478. https://doi.org/10.1007/s00300-015-1872-z

Mueller, K.E., Blumenthal, D.M., Carrillo, Y., Cesarz, S., Ciobanu, M., Hines, J., Pabst, S., Pendall, E., de Tomasel, C.M., Wall, D.H., & Eisenhauer, N. (2016). Elevated CO2 and warming shift the functional composition of soil nematode communities in a semiarid grassland. Soil Biology and Biochemistry, 103, 46–51. https://doi.org/10.1016/j.soilbio.2016.08.005

Nordström, M., Aarnio, K., & Bonsdorff, E. (2009). Temporal variability of a benthic food web: Patterns and processes in a low-diversity system. Marine Ecology Progress Series, 378, 13–26. https://doi.org/10.3354/meps07872

O'Reilly, C.M., Hecky, R.E., Cohen, A.S., & Plisnier, P.-D. (2002). Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. Limnology and Oceanography, 47(1), 306–309. https://doi.org/10.4319/lo.2002.47.1.0306

Oksanen, T., Oksanen, L., Vuorinen, K.E.M., Wolf, C., Mäkynen, A., Olofsson, J., Ripple, W.J., Virtanen, R., & Utsi, T.A. (2020). The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis. In Ecography. https://doi.org/10.1111/ecog.05076

Özen, A., Šorf, M., Trochine, C., Liboriussen, L., Beklioglu, M., Søndergaard, M., Lauridsen, T.L., Johansson, L.S., & Jeppesen, E. (2013). Long-term effects of warming and nutrients on microbes and other plankton in mesocosms. Freshwater Biology, 58(3), 483–493. https://doi.org/10.1111/j.1365-2427.2012.02824.x

Pelini, S.L., Diamond, S. E., Nichols, L.M., Stuble, K.L., Ellison, A.M., Sanders, N.J., Dunn, R.R., & Gotelli, N.J. (2014). Geographic differences in effects of experimental warming on ant species diversity and community composition. Ecosphere. https://doi.org/10.1890/ES14-00143.1

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M.A., Melián, C.J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N.E., & Gravel, D. (2017). Comparing species interaction networks along environmental gradients. Biological Reviews. https://doi.org/10.1111/brv.12366

Petchey, O.L., Beckerman, A.P., Riede, J.O., & Warren, P.H. (2008). Size, foraging, and food web structure. Proceedings of the National Academy of Sciences, 105(11), 4191–4196. https://doi.org/10.1073/pnas.0710672105

Peterson, C.H., Rice, S.D., Short, J.W., Esler, D., Bodkin, J.L., Ballachey, B.E., & Irons, D.B. (2003). Long-Term Ecosystem Response to the Exxon Valdez Oil Spill. In Science (Vol. 302, Issue 5653, pp. 2082–2086). American Association for the Advancement of Science.

https://doi.org/10.1126/science.1084282

Peterson, T.A., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., & Araújo, M.B. (2011). Ecological Niches and Geographic Distributions. Princeton University Press.

Pimm, S. L. (1991). *The balance of nature? : ecological issues in the conservation of species and communities*. University of Chicago Press.

Poisot, T., Baiser, B., Dunne, J.A., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T.N., Stouffer, D. B., Wood, S.A., & Gravel, D. (2016). Mangal - making ecological network analysis simple. Ecography, 39(4), 384–390. https://doi.org/10.1111/ecog.00976

Poisot, T., & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree distribution and emerging network properties. PeerJ, 2, e251. https://doi.org/10.7717/peerj.251

Poisot, T., Gravel, D., Leroux, S., Wood, S.A., Fortin, M.-J., Baiser, B., Cirtwill, A.R., Araújo, M.B., & Stouffer, D.B. (2016). Synthetic datasets and community tools for the rapid testing of ecological hypotheses. Ecography, 39(4), 402–408. https://doi.org/10.1111/ecog.01941

Poisot, T., Stouffer, D.B., & Gravel, D. (2015). Beyond species: why ecological interaction networks vary through space and time. Oikos, 124(3), 243–251. https://doi.org/10.1111/oik.01719

Post, E. (2013). Ecology of climate Change: The importance of biotic interactions. In *Monographs in Population Biology*. Princeton University Press. https://doi.org/10.2307/j.ctt2jc8jj

Roslin, T., Majaneva, S., & Clare, E. (2016). The use of DNA barcodes in food web construction—terrestrial and aquatic ecologists unite! Genome, 59(9), 603–628. https://doi.org/10.1139/gen-2015-0229

Ruhí, A., Muñoz, I., Tornés, E., Batalla, R.J., Vericat, D., Ponsatí, L., Acuña, V., von Schiller, D., Marcé, R., Bussi, G., Francés, F., & Sabater, S. (2016). Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. Freshwater Biology, 61(9), 1536–1549. https://doi.org/10.1111/fwb.12794

Santonja, M., Fernandez, C., Proffit, M., Gers, C., Gauquelin, T., Reiter, I.M., Cramer, W., & Baldy, V. (2017). Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest. Journal of Ecology, 105(3), 801–815. https://doi.org/10.1111/1365-2745.12711

Schwarz, B., Barnes, A.D., Thakur, M.P., Brose, U., Ciobanu, M., Reich, P.B., Rich, R.L., Rosenbaum, B., Stefanski, A., & Eisenhauer, N. (2017). Warming alters the energetic structure and function but not resilience of soil food webs. Nature Climate Change, accepted(iDiv), 1–9. https://doi.org/10.1038/s41558-017-0002-z

Seifert, L.I., Weithoff, G., Gaedke, U., & Vos, M. (2015). Warming-induced changes in predation, extinction and invasion in an ectotherm food web. Oecologia, 178(2), 485–496. https://doi.org/10.1007/s00442-014-3211-4

Sentis, A., Hemptinne, J.L., & Brodeur, J. (2013). Effects of simulated heat waves on an experimental plant-herbivore-predator food chain. Global Change Biology, 19(3), 833–842. https://doi.org/10.1111/gcb.12094

Sentis, A., Hemptinne, J.L., & Brodeur, J. (2014). Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure. Ecology Letters, 17(7), 785–793. https://doi.org/10.1111/ele.12281

Sugihara, G., Bersier, L.-F., & Schoenly, K. (1997). Effects of taxonomic and trophic aggregation on food web properties. Oecologia, 112(2), 272–284. https://doi.org/10.1007/s004420050310

Sun, F., Pan, K., Tariq, A., Zhang, L., Sun, X., Li, Z., Wang, S., Xiong, Q., Song, D., & Olatunji, O.A. (2016). The response of the soil microbial food web to extreme rainfall under different plant systems. Scientific Reports, 6(1), 37662. https://doi.org/10.1038/srep37662

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., & Tylianakis, J.M. (2012). Food webs: Reconciling the structure and function of biodiversity. In Trends in Ecology and Evolution (Vol. 27, Issue 12, pp. 689–697). Elsevier Current Trends. https://doi.org/10.1016/j.tree.2012.08.005

Thompson, R.M., & Townsend, C.R. (2000). Is resolution the solution?: The effect of taxonomic resolution on the calculated properties of three stream food webs. Freshwater Biology, 44(3), 413–422. https://doi.org/10.1046/j.1365-2427.2000.00579.x

Tylianakis, J.M., & Morris, R.J. (2017). Ecological Networks Across Environmental Gradients.

Annu. Rev. Ecol. Evol. Syst, 48(1), annurev-ecolsys-110316-022821. https://doi.org/10.1146/annurev-ecolsys-110316

Vinagre, C., Costa, M.J., & Dunne, J.A. (2017). Effect of spatial scale on the network properties of estuarine food webs. Ecological Complexity, 29, 87–92. https://doi.org/10.1016/j.ecocom.2017.01.004

Warren, P.H. (1990). Variation in Food-Web Structure: The Determinants of Connectance. The American Naturalist, 136(5), 689–700. https://doi.org/10.1086/285123

Winemiller, K.O. (1989). Must connectance decrease with species richness? American Naturalist, 134(6), 960–968. https://doi.org/10.1086/285024

Woodward, G., Papantoniou, G., Edwards, F., & Lauridsen, R.B. (2008). Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. Oikos, 117(5), 683–692. https://doi.org/10.1111/j.2008.0030-1299.16500.x

Young, H.S., Mccauley, D.J., Dunbar, R.B., Hutson, M.S., Ter-Kuile, A.M., & Dirzo, R. (2013). The roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems. Ecology, 94(3), 692–701. https://doi.org/10.1890/12-0729.1

Zander, A., Bersier, L.-F., & Gray, S.M. (2017). Effects of temperature variability on community structure in a natural microbial food web. Global Change Biology, 23(1), 56–67. https://doi.org/10.1111/gcb.13374

Zhang, L., Takahashi, D., Hartvig, M., & Andersen, K.H. (2017). Food-web dynamics under climate change. Proceedings. Biological Sciences, 284(1867), 20171772. https://doi.org/10.1098/rspb.2017.1772