

SPECIAL REVIEW

Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics

ROSS M. THOMPSON*, JENNIFER DUNNE^{†,‡} AND GUY WOODWARD[§]^{*}*Australian Centre for Biodiversity and School of Biological Sciences, Monash University, Clayton, Vic., Australia*[†]*Santa Fe Institute, Santa Fe, NM, U.S.A.*[‡]*Pacific Ecoinformatics and Computational Ecology Lab, Berkeley, CA, U.S.A.*[§]*School of Biological and Chemical Sciences, Queen Mary University of London, London, U.K.*

SUMMARY

1. Food webs are a powerful whole-system way to represent the patterns of biodiversity and energy flow in a readily quantifiable framework amenable to comparative analyses. Integrated theory and data on complex trophic interactions provide useful and novel ways to study ecosystem structure, dynamics, function and stability.
2. Freshwater ecology has contributed considerably to the advancement of food-web ecology. This has occurred through early application of methodological advances such as stable isotope analysis and description of some of the most detailed food webs, including Little Rock Lake and the Broadstone Stream food webs.
3. Freshwater food webs are often highly resolved, although the inclusion of components such as bacteria continues to be challenging. Characteristics of stream food webs appear to include high rates of omnivory and a strong role for body size as a structuring influence.
4. While freshwater ecology has often included landscape factors, food webs from freshwaters have most often been collected at small spatial scales. There is a need to take a landscape approach to the study of food-web dynamics in freshwater ecosystems.
5. Studies of food webs that take an experimental approach or utilise natural gradients remain rare but will be vital to untangling causative relationships between changing environmental conditions and food-web structure and dynamics.
6. Emerging directions in freshwater food-web research involve integrating individual-level variation and information on traits into food-web studies. This is allowing a growing understanding of the ways in which food webs can be used to integrate community, evolutionary and population processes into studies of biodiversity.
7. A Virtual Issue of *Freshwater Biology* entitled 'Advances in food-web research: a compendium of *Freshwater Biology* papers' brings together papers included in this review that have been published in the journal since 1985. The Virtual Issue can be located at [http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1365-2427/homepage/virtual_issue_advances_in_food-web_research.htm](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-2427/homepage/virtual_issue_advances_in_food-web_research.htm).

Keywords: food webs, lakes, review, streams, trophic network

Freshwater food webs: a brief history

Darwin (1859) described species as being embedded in an 'entangled bank' of interdependent interactions, implicitly recognising the key role of food webs in understanding

the diversity of species. Ecologists have long sought to characterise the complexity of the entangled bank by quantifying food webs and seeking generalities in structure and the factors that underpin them. While early studies described food webs from a range of ecosystems,

Correspondence: Ross M. Thompson, Australian Centre for Biodiversity and School of Biological Sciences, Monash University, Clayton, Vic. 3800, Australia. E-mail: ross.thompson@monash.edu

freshwater systems were at the forefront and have remained so for over a century. The first specific food web published for a freshwater ecosystem was that of Forbes (1887) who described the trophic relationships within Lake Mendota in Wisconsin, just 7 years after the first food web was produced by Camerano (1880). Through the next several decades, food webs were described for a range of freshwater ecosystems, culminating in the seminal work of Lindeman (1942). Lindeman described the food-web structure and flows of energy and nutrients within Cedar Bog Lake in central Minnesota, and in so doing defined the underpinnings of much of modern food-web ecology, particularly within the tradition of ecosystem ecology.

The development of food-web research has been described in numerous reviews (Pimm, Lawton & Cohen, 1991, Cohen *et al.*, 1993; Dunne, 2006, Ings *et al.*, 2009), so we will only touch briefly on historical aspects here, to place freshwater studies in a wider context. Broadly, the discipline moved from an early phase that focussed on understanding the properties of food webs that might confer stability upon ecosystems (e.g. MacArthur, 1955; Hutchinson, 1959; May, 1972; Paine, 1980), through to a search for general structural characteristics (e.g. Pimm *et al.*, 1991), followed by the development of structural (e.g. Cohen & Newman, 1985; Allesina, Alonso & Pascual, 2008) and dynamical (e.g. Law and Blackford, 1992, Yodzis, 1998, Brose, Williams & Martinez, 2006b) food-web models (Fig. 1). Advances in the resolution and types of data available rendered the conclusions of many earlier studies obsolete (Dunne, 2006). For example, mathematical analyses of the relationship between stability and complexity in food webs suggested that simple communities should be more stable (May, 1972), a conclusion that has been shown to be a consequence of the use of random structure and equal interaction strengths. Also, a range of food-web attributes that were proposed to be scale invariant, particularly constant values for the number of links per species and the fraction of taxa that are top, intermediate and basal, were shown to be highly sensitive to data quality and aggregation (Lawton, 1989, Martinez 1993).

Much of the early search for general patterns in food webs was informed by a catalogue of simple food webs that generally included fewer than 50 taxa (see Cohen, 1978, 1989; Pimm, 1982). These webs were characterised by highly variable taxonomic resolution and means of determining trophic links and were criticised for failing to represent the complexity of real communities (Polis, 1991). The highly variable and poor resolution of early food-web data sets and accompanying overly simplistic analyses

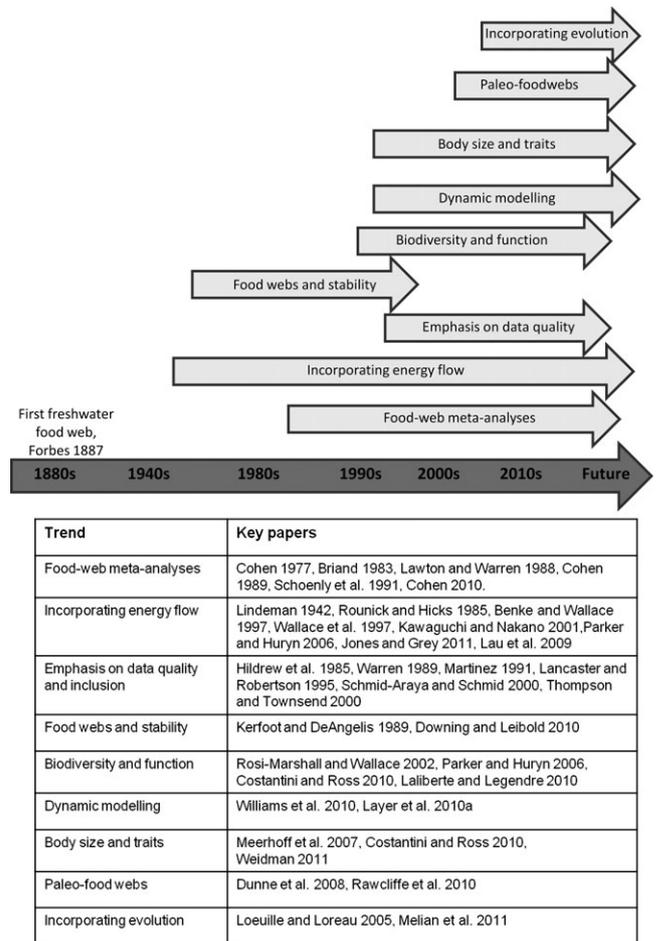


Fig. 1 Trends in the study of freshwater food webs over the last century. Large arrows indicate major research directions historically and in future, with important freshwater papers at the bottom of the diagram.

and models (Dunne, 2006) stimulated a new generation of food-web research starting in the late 1980s. New data sets were more detailed than their predecessors and many included taxa that had been traditionally considered too difficult to incorporate (e.g. chironomids and algae described to species), including microcrustacea and meiofauna (Martinez, 1991; Lancaster & Robertson, 1995; Schmid-Araya & Schmid, 2000; Thompson & Townsend, 2004). Important natural features such as omnivory (feeding at more than one trophic level), feeding cycles (e.g. mutual predation, species *a* eats *b* and *b* eats *a*) and cannibalism were increasingly documented, challenging prior data and models that largely ignored such complexities.

Freshwater systems were prominent among these new, more highly and evenly resolved food-web data sets (Hildrew, Townsend & Hasham, 1985; Warren, 1989, Martinez, 1991). In addition, many advances in empirical methodology emerged in work focussed on freshwater

systems. For example, stable isotope analysis (SIA) allowed the quantification of interaction strengths and energy flows (Rounick & Hicks, 1985). Also, for the first time, a number of studies compiled and analysed replicate food webs along various kinds of gradients related to environmental stress, seasonality, disturbance, climate and resource supply (e.g. Townsend *et al.*, 1998, Rosi-Marshall & Wallace, 2002, Schmid-Araya *et al.*, 2002; Baiser, Russell & Lockwood, 2011, Layer *et al.*, 2011). Recently, system-level responses to experimental perturbations have been examined in highly resolved food webs in freshwater mesocosms (Brown *et al.*, 2011, Ledger, Edwards, Brown *et al.*, 2011). Food-web approaches are now widely recognised for their potential to reconcile observed patterns in biodiversity with evolutionary mechanisms that underpin coexistence, such as adaptive behaviour (Valdovinos *et al.*, 2010) and phylogenetic relatedness (Ives & Godfray, 2006), and the ecosystem processes that emerge from these patterns (Reiss *et al.*, 2009).

Freshwater food webs: where are we now?

Empirical aspects

The trend towards comprehensive, highly resolved food webs was initiated largely by pioneering work in three model freshwater systems: the Broadstone Stream food web (Hildrew *et al.*, 1985; Schmid-Araya & Schmid, 2000), the Skipwith Pond food web (Warren, 1989) and the Little Rock Lake food web (Martinez, 1991). This was followed by later work in a variety of highly resolved stream webs (Thompson & Townsend, 2000; Layer *et al.*, 2010a,b). Many freshwater food webs are far more highly and evenly resolved than their marine and terrestrial counterparts, especially at lower trophic levels (Ings *et al.*, 2009). For instance, among the primary producers, diatoms can be identified and quantified relatively easily, and these are common features of recent freshwater webs (Townsend *et al.*, 1998; Rawcliffe *et al.*, 2010, Layer *et al.*, 2010a,b, Brown *et al.*, 2011; Layer *et al.*, 2011). Invertebrates are also often highly resolved, whereas they tend to be aggregated in other systems.

While food webs such as those for Broadstone Stream (Hildrew *et al.*, 1985; Layer *et al.*, 2011) and Little Rock Lake (Martinez, 1991) are very comprehensive and highly resolved, they still have limitations. For instance, many microbial taxa are ignored or grouped in a 'black box', a shortcoming common to almost all empirical food webs because of the logistic challenges involved (Purdy *et al.*, 2010). Also, they generally lack systematic documentation of parasites (but see Hernandez & Sukhdeo, 2008), which

have been more commonly documented for marine or estuarine food webs (Huxham, Beaney & Raffaelli, 1996, Thompson, Mouritsen & Poulin, 2005, Lafferty, Dobson & Kuris, 2006). In addition, there is no consensus on how to include non-living components such as detritus in food webs. In the case of completeness, the value of relentlessly attempting to catalogue every species and their interactions in a system needs to be weighed against the insights gained (Thompson & Townsend, 2000). The yield–effort relationship starts to decelerate as ever-increasing resources are needed to capture ever rarer and/or difficult to characterise links and species (Ings *et al.*, 2009). For example, many of the soft-bodied freshwater meiofauna, although diverse and often abundant, can only be identified live, by video microscopy requiring enormous commitments of time and money to characterise their specific roles in food webs. The few webs that have included them (including Schmid-Araya & Schmid, 2000) tend to have low connectance, suggesting a trade-off between completeness and resolution. In contrast to the meiofauna problem, the systematic inclusion of parasites, which represent a large part of the diversity and complexity of trophic interactions in any system, clearly is feasible and yields new insights (Lafferty *et al.*, 2008). Also, the current aggregation or exclusion of microbial and other microscopic taxa may change if emerging metagenomic approaches can prise open the microbial black box and provide more data on these groups in future (Purdy *et al.*, 2010). Key, interrelated methodological questions thus appear to be: does extra effort reveal valuable information that would otherwise be hidden by ignoring groups, are efforts at completeness reducing or increasing methodological bias and artefacts in the data, and to what degree are perceived food-web properties sensitive to sampling effort, link and node inclusion thresholds, and sampling consistency?

Network organisation

Much food-web research has been devoted to characterising patterns in catalogues of binary presence-or-absence webs, which has been useful for trying to identify fundamental patterns in the trophic organisation of ecosystems regardless of the habitat (e.g. Dunne, Williams & Martinez, 2002a, Stouffer *et al.*, 2005) and for characterising baseline structural robustness of systems (e.g. Sole & Montoya, 2001; Dunne, Williams & Martinez, 2002b), including work focussed on freshwater systems (Srinivasan *et al.*, 2007). Network structure analyses have moved well beyond an early narrow focus on species richness, linkage density, connectance and fractions of

top, intermediate and basal species. Recent studies have looked at a wide variety of structural characteristics, including the occurrence of types of species such as herbivores, omnivores, cannibals, and species that occur in loops (e.g. Williams & Martinez, 2000, Dunne, Williams & Martinez, 2004; Vermaat, Dunne & Gilbert, 2009); food chain lengths and trophic level (e.g. Post 2002, Williams and Martinez 2004); degree distributions (e.g. Dunne *et al.*, 2002a; Stouffer *et al.*, 2005); small interaction motifs (Stouffer *et al.*, 2007) and compartments (Krause *et al.*, 2003); small-world properties (Dunne *et al.*, 2002b); and intervality (Stouffer, Camacho & Amaral, 2006). Nestedness and modularity have primarily been studied in bipartite networks (e.g. plant-pollinator networks) and only occasionally in food webs. One study showed that the significant nestedness of geographic occurrences of species in 50 Adirondack lakes (Srinivasan *et al.*, 2007) is related to the high robustness of those food webs to likely species losses. A number of simple models of food-web network structure have been proposed and tested against data (Williams & Martinez, 2000; Cattin *et al.*, 2004; Stouffer *et al.*, 2005, Allesina *et al.*, 2008). All of these studies have included the analysis of freshwater food webs, alongside terrestrial, marine and estuarine webs. Although food webs appear to share fundamental organisation that is scale dependent on the number of species and links of the web (e.g. Dunne *et al.*, 2004), it will be interesting to know whether there are fine-grained structural differences between different habitats. This should be possible once more high-quality data sets for various habitat types become available (Hagen *et al.*, 2012).

One aspect of organisation and species roles in food webs important for freshwater studies is omnivory. A common criticism of early food-web data was the failure to include this type of feeding (Polis, 1991), although this was perhaps least true of freshwater food webs (Thompson *et al.*, 2007). Most freshwater predators are omnivorous in the sense that they feed on multiple trophic levels, but some, such as crayfish, are 'true omnivores' in the narrower use of the term whereby they eat both animal and plant material. Omnivorous feeding may occur at a given point in time or over the course of an individual's lifetime (Stouffer & Bascompte, 2011), with ontogenetic shifts in trophic status being especially prevalent in aquatic systems (Woodward *et al.*, 2010b). Omnivory appears to be a defining characteristic of many of the second generation of freshwater food webs (Warren, 1989; Rawcliffe *et al.*, 2010), particularly those described for running waters (Woodward *et al.*, 2010b; c, Woodward, Speirs & Hildrew, 2005a,b).

Omnivory can potentially cause a wide range of effects in ecosystems. Early studies based on simple Lotka-Volterra models suggested that it destabilised dynamics (Pimm and Lawton, 1978), while later studies of non-equilibrium dynamics of small modules concluded the opposite (McCann and Hastings, 1997). More recent studies explore the effects of omnivory in more realistic complex food webs using a variety of empirical and modelling approaches, but have yet to achieve unified understanding. The recognition of the potential importance of omnivory in freshwater food webs was in part driven by descriptions of trophic cascades, and considerations as to what may prevent or permit them (Carpenter & Kitchell, 1993; Brett & Goldman, 1996; Shurin *et al.*, 2002). There is some evidence that omnivory might dampen cascades (Bascompte, Melian, Sala 2005), although this is not always the case. For instance, it is not necessarily the presence of omnivory *per se* that is important, but the particular configuration and strength of the links and how omnivorous modules are connected to the wider network (Okun *et al.*, 2008). While claims have been made that omnivory is so rampant in natural systems that it completely destroys the utility of the trophic-level concept (Polis & Strong, 1996), a study using flow-weighted food-web data showed that about half of a web's species complement can be assigned to discrete trophic levels (Williams and Martinez, 2004).

Because gape-limited predation and handling constraints often determine predator diets in aquatic systems (Brose, Berlow & Martinez, 2005), the potential for omnivory should be determined largely by body size (Woodward *et al.*, 2005a,b, 2010c). Consequently, it should be more prevalent in systems where there are clearer size-delimited trophic 'levels' (phytoplankton-zooplankton-fishes in lakes) relative to those where predators and prey overlap more extensively in body size (e.g. insect larvae in the benthos). This might explain why cascades (and the alternative equilibria they can generate) appear to be generally more common in lakes than in running waters, although this suggestion has yet to be tested rigorously with models and data in a cross-system comparison.

Network quantification

Increasingly, quantitative data for nodes (e.g. body size, abundance) and/or links (e.g. interaction strength) have been used to address new types of questions in food-web research (Cohen, Jonsson & Carpenter, 2003). There are many ways to quantify linkage or interaction strength, one of the key aspects of food-web research (Berlow *et al.*, 2004, Berlow *et al.*, 2009; Wootton & Emmerson, 2005),

and the particular form used will depend on the question being asked. It is therefore important when comparing across studies that like is compared with like, as an important link in one context might not be important in another. For instance, within a given food web, a large biomass flux from a resource to a consumer is an important link in terms of the total transfer of energy, yet it might be trivial in terms of *per capita* interaction strength and dynamical stability if the resource has high biomass production relative to consumer ingestion (Woodward *et al.*, 2005b). Although it is logistically demanding to produce food webs with quantification of links or nodes, these provide richer pictures of the trophic relations in an ecosystem than binary webs (Benke & Wallace, 1997) and allow new types of questions to be answered. Perhaps the easiest quantification increasingly used to annotate binary web data (Brose *et al.*, 2006b), inform network structure analyses (Williams, Anandanadesan & Purves, 2010, Stouffer & Bascompte, 2011) and constrain food-web dynamics models (e.g. Brose *et al.*, 2006b, Berlow *et al.*, 2009) is species body size (see Petchey & Dunne, in press for a review). Increasingly, both stable isotope analysis and gut contents analysis are used to form more complete pictures of biomass flows, mitigating the respective shortcomings of each (Rawcliffe *et al.*, 2010; Layer *et al.*, 2011). Most recently, these approaches have also been used to pick up 'hidden' pathways, such as consumer production based on methane sequestration, which would go undetected by traditional methods such as gut content analysis (Jones & Grey, 2011).

Time and space

Comparative studies of food-web structure across habitats (e.g. Dunne *et al.*, 2002a) use data sets that give 'static' depictions of food webs, by integrating species and links over usually unspecified ecological time and space. However, food webs are dynamic, with taxa, links and aspects of structure changing over time and space, as has been well demonstrated for freshwater systems (Warren, 1989; Closs & Lake, 1994; Tavares-Cromar & Williams, 1996; Thompson & Townsend, 1999; Woodward *et al.*, 2005b). They also vary across spatiotemporal scales (Martinez & Lawton, 1995; Thompson & Townsend, 2005). Recent work has suggested that freshwater food webs possess a degree of 'ergodicity', meaning that changes over temporal and spatial dimensions are to some extent interconnected (Olesen *et al.*, 2010). For example, at small scales, trophic interactions occur between individuals within patches, whereas intergenerational metacommunity dynamics may come into play at

the larger landscape scale. In the latter case, local food webs form subsets of a larger, but less tightly connected, regional network; thus, headwater streams are (re)colonised from neighbouring systems by a diaspora of dispersing terrestrial adult insects during the oviposition period (Hagen *et al.*, 2012). In some cases, it has been shown that large mobile predators act to couple food-web dynamics across spatial scales (Winemiller & Jepsen, 1998; Vander Zanden & Vadeboncoeur, 2002) with potential effects on food-web stability (Kerfoot & Deangelis, 1989; McHugh, McIntosh & Jellyman, 2010). These temporal and spatial aspects are still not well understood in food webs for freshwater systems or other habitats, but they are likely to be extremely important to answer certain questions. For example, freshwater systems are fragmented habitats within a terrestrial landscape and will become more disconnected from one another in future because of human activity (e.g. land-use change, drainage for agriculture, hydropower impoundments in river networks); understanding this in greater detail will be important for conservation and management (Hagen *et al.*, 2012).

The majority of food-web studies have focussed on small spatial scales. Freshwater ecology as a discipline, however, has moved to a broader landscape perspective of aquatic ecosystems, studying them in a landscape (or catchment) context. The importance of cross-ecosystem movements of materials for local food-web structure has been well demonstrated (Polis, Anderson & Holt, 1997), and freshwater studies have confirmed the important role of detrital inputs in shaping food webs (Wallace *et al.*, 1997). Additionally, large-scale manipulative experiments have identified the complex pathways of materials moving between streams and adjacent riparian areas (Kawaguchi & Nakano, 2001). A different approach – stable isotopes along a natural resource gradient – has been used to further emphasise the important role of allochthonous materials in streams (Lau, Leung & Dudgeon, 2009). Freshwater food webs can thus be embedded in more complex landscape-level patterns of energy flows that permeate ecosystem boundaries (Polis *et al.*, 1996; Layer *et al.*, 2010a; Hagen *et al.*, 2012), with stable isotope analysis often key in detecting cross-system subsidies.

Replicate food webs along gradients

The compilation of replicate sets of food webs in particular habitats has provided new ways to study drivers of food-web structure. Gradient approaches are often preferred when the environment shifts along a more continuous scale as it does in most natural systems. This approach has been used effectively to understanding the

role of disturbance and resource supply in driving food-web structure in streams (Townsend *et al.*, 1998). More recent studies have used a gradient approach to assess how freshwater food webs change through time and space (Layer *et al.*, 2010b; Olesen *et al.*, 2010) and in response to resource availability (Rosi-Marshall & Wallace, 2002), climate (Woodward *et al.*, 2010c), pH (Layer *et al.*, 2011, 2010a,b), disturbance (Parker & Huryn, 2006) and eutrophication (Rawcliffe *et al.*, 2010). A common approach here is to use space-for-time substitution, based to a large extent on the ideas related to ergodicity, and this has been used to assess how increased pH is associated with larger but less dynamically stable food webs (Layer *et al.*, 2010b) and how increased temperature is associated with species loss but lengthening of food chains in Icelandic streams (Friberg *et al.*, 2009; Woodward *et al.*, 2010c). The study of changes in food webs along temporal and spatial gradients has been assisted by access to palaeolimnological data (Rawcliffe *et al.*, 2010), although the full potential of the fossil record for constructing hindcast food webs has yet to be realised. This offers the potential for better understanding of very long-term temporal network dynamics. Preliminary work in constructing food webs using a space-for-time substitution in a contemporary palaeolimnological setting provides some clues as to how this might be achieved (Rawcliffe *et al.*, 2010).

Experimental food webs

While gradient studies provide important insights into how the environment can constrain food-web structure, they are often limited by the fact that these systems are effectively in equilibrium in many cases, as their constituent species have had many generations to play out their population and community dynamics. To develop more mechanistic understanding, systems need to be perturbed and responses within the resident community characterised. Replicated experimental manipulations in food-web ecology are still far less common than correlational gradient-based studies, yet they are essential if we are to use network-based approaches to assess the impacts of environmental change as a dynamic stressor. As such, they can complement gradient-based approaches, as illustrated in a recent study of pelagic food webs that used complementary experimentation to determine the processes underlying patterns observed in natural lakes (Weidman, Schindler & Vinebrooke, 2011). Of course, for experimentation, context is important, and we should remember that if the stressor is both large enough and fast enough, new equilibrium conditions might never be reached. Discrete categories can be assigned in many

cases, especially in experimental settings, where mutually exclusive and binary treatments have been used (Brown *et al.*, 2011; Ledger *et al.*, 2011).

One key question that experimental studies can answer is, 'How responsive are food-web properties to perturbations?' Recent work demonstrated that certain food-web properties (e.g. trivariate patterns; connectance; path length) are highly replicable among stream mesocosms, highlighting the potential for experimentation (Brown *et al.*, 2011). Other research using aquatic mesocosms assessed the response of food webs with different levels of species richness to a pulse disturbance (Downing & Leibold, 2010); this showed that species-rich macroinvertebrate communities had higher resilience (recovered more quickly), but were not more resistant to perturbations. Other experimental work showed that streams are affected strongly by intermittent drought, with marked species loss and secondary production declining by about half an order of magnitude (Ledger *et al.*, 2011). Pond mesocosms have also been used widely to explore community and ecosystem responses to environmental perturbations, especially warming (e.g. McKee *et al.*, 2003; Yvon-Durocher *et al.*, 2010; Dossena *et al.*, 2012).

Experimental food-web ecology is one of the most promising pathways for elucidating interactions between biodiversity and ecosystem functioning (Hooper *et al.*, 2005). The majority of studies in this area have concentrated on a single trophic level (e.g. Diaz *et al.*, 2003, see Hooper *et al.*, 2005 for a review). More recent biodiversity-and-ecosystem functioning studies have taken a food-web approach (O'Connor *et al.*, 2009), treating biodiversity as both an independent variable and a dependent variable in terms of an ecosystem's ability to maintain biodiversity. Costantini & Rossi (2010) used experimental mesocosms to investigate the effects of species richness on rates of leaf litter decomposition and found a complex interaction between diversity at different trophic levels and the functional measure. They also found an important role for species traits rather than simply biodiversity *per se*. The integration of information on functional traits into studies of biodiversity and ecosystem function is an important research frontier (Laliberte & Legendre, 2010), and aquatic ecosystems are particularly tractable for this type of work.

Freshwater food webs: future directions

Modelling and testing of dynamics

Freshwater research has produced some of the best-described high-quality food webs, yet the focus has remained largely on empirical rather than modelling

approaches. A better marriage between these two approaches promises to be mutually beneficial, since for many years both have been held back by shortcomings in the other. A few of the more recent studies have included some form of structural or dynamical modelling (Layer *et al.*, 2010b, 2011). We are starting to get to the stage where empirical or experimental studies are being conducted at intergenerational scales (Brown *et al.*, 2011; Ledger *et al.*, 2011), and these have huge potential for informing, testing and validating dynamical food-web models. Freshwater ecology could also make good use of existing time-series biomonitoring data in which the dynamics of main trophic elements of food webs are characterised but not yet connected. By drawing in the feeding links of, for instance, the diatom, invertebrate and fish assemblages that are routinely sampled in many monitoring programmes, we could rapidly generate new food-web data that span large environmental gradients at interannual-to-decadal scales (Woodward *et al.*, 2010a; Friberg *et al.*, 2011). Even longer-term dynamics could be explored in lakes by developing models using data from palaeolimnological subfossil and fossil samples (Rawcliffe *et al.*, 2010) to investigate how food webs have shifted over centennial-to-millennial scales. Although preserved records are unlikely to be complete, as certain taxa will be missing, many representatives from across multiple trophic levels will be detectable and remaining gaps could be filled by inference from contemporary sampling in a space-for-time substitution approach (Rawcliffe *et al.*, 2010).

Food webs – from individuals to ecosystems

The exploration of the effects of resolution and aggregation has recently started to consider the most fundamental level of organisation in food webs: the interactions between individuals (Woodward *et al.*, 2010b, McCoy *et al.*, 2011). This is where trophic transfers actually occur, while higher-level species and network properties are simply emergent manifestations of individual interactions and behaviour. This has been largely overlooked by much of the existing food-web literature, as individual-level data are challenging to collect in many systems. However, the methodology of gut sampling widely used in freshwater food-web studies is very amenable to this type of data compilation and analysis (Woodward *et al.*, 2010b). Individual-based modelling is also a promising but as yet little utilised method that can explore possible linkages between the individual, species and food-web levels.

The so-called curse of the Latin binomial (Raffaelli, 2007) relates to the primacy of the taxonomic perspective in food-web and other kinds of ecological research,

with the exclusion of other perhaps equally valid and useful views (Yvon-Durocher *et al.*, 2011). Trait-based approaches are developing rapidly across ecology and could be developed more effectively in food-web research. Research based on body size and size spectra also has obvious applications in freshwater systems. Body size plus foraging behaviour are at the heart of the allometric diet breadth model (ADBM) (Petchey *et al.*, 2008), which predicts network structure in multiple habitats using species identity or size classes of individuals (irrespective of identity) as the relevant trophic entities (Woodward *et al.*, 2010b). The predictive power of the ADBM is almost twice as high in size-based webs (e.g. >80% accurate prediction of links) than in their species-based equivalents (Woodward *et al.*, 2010b). Increasingly, food-web studies are taking into account the role of functional traits (Costantini & Rossi, 2010) and as such are beginning to integrate species and even individual-level variability into large-scale ecological networks. It is increasingly recognised that food webs provide an ideal framework for integrating across topics and scales that span the biological disciplines. This is nicely illustrated by a recent study that individual variation in behaviour and physiology can cascade up to ecosystem processes via food-web processes (Hawlena & Schmitz, 2010). Food-web studies are now explicitly incorporating biological mechanisms from behaviour (Meerhoff *et al.*, 2007; Weidman *et al.*, 2011), functional traits (Costantini & Rossi, 2010) and ecosystem energy fluxes (Kawaguchi & Nakano, 2001).

Developing a more global perspective: looking beyond the temperate zone

If we are to make reliable generalisations about networks exposed to global drivers of change, we need to improve our understanding beyond the current reliance on data from species-poor temperate systems. The model systems we have relied on to date have served us well in terms of developing substantial new bodies of both theory and data in recent years, but more complex species-rich systems, especially those in the tropics, might not necessarily behave as if they were straightforward extrapolations from these simpler temperate webs. We have made some progress in this area. Our knowledge of freshwater food webs has been expanded in recent years by studies of streams from high latitudes (Parker & Hury, 2006) and from the tropics (Winemiller & Jepsen, 1998; Lau *et al.*, 2009). The Arctic stream research used a strong contrast in disturbance regimes to show how this may influence food-web structure and ecosystem functioning (Parker & Hury, 2006).

Studies of tropical stream food webs (e.g. Winemiller & Jepsen, 1998; Lau *et al.*, 2009) have shown some similarities to temperate streams with respect to major environmental drivers, despite differences in the taxonomic relationships of the dominant members of the fauna, although we are in need of more food webs from tropical fresh waters. Current studies suggest that warm water systems may have higher rates of omnivory than temperate systems (Lazzaro, 1997). A direct comparison of shallow lake systems from the tropics with those from temperate zones indicated that tropical lake food webs were more strongly structured by fish predation (Meerhoff *et al.*, 2007). Global coverage of detailed freshwater food-web studies now extends from grassland streams in New Zealand (Townsend *et al.*, 1998) to alpine lakes in North America (Weidman *et al.*, 2011), and encompasses Brazilian reservoirs (Okun *et al.*, 2008), Uruguayan lakes (Meerhoff *et al.*, 2007) and Japanese streams (Kawaguchi & Nakano, 2001). However, the majority of studies are still concentrated in the temperate lakes and streams of Europe and North America. A broader understanding of food-web structure at global scales, and the interacting roles of climate, biogeography and phylogenetic history, requires us to continue to extend geographic coverage.

Conclusions

Freshwater food webs have contributed considerably to the advancement of this branch of ecology, especially in the last decade, when several important leaps forward were made in both theoretical and empirical approaches (Fig. 1). Our understanding of freshwater food-web structure and dynamics is now vastly better than it was before this 'Renaissance' period, and the frontiers of network research are advancing on multiple fronts. Emerging directions in food-web research include the consideration of individual-level variation (Woodward *et al.*, 2010b; Stouffer *et al.*, 2011), long-term intergenerational change (Layer *et al.*, 2010b, 2011; Rawcliffe *et al.*, 2010) and evolutionary processes (Melian *et al.* 2011) (Fig. 1). In addition to detailed case studies of single systems and comparative work focussed on single webs from many habitats, more work needs to be done conducting analyses of replicate webs across environmental gradients (Layer *et al.*, 2010a,b) and in experimental systems (e.g. Brown *et al.*, 2011; Ledger *et al.*, 2011). Other new avenues will undoubtedly arise from these and other developments, and we speculate that these could include a more explicit network-based approach to biomonitoring, conservation and understanding of the provisioning of ecosystem goods and

services in fresh waters (Friberg *et al.*, 2011). The assimilation of food-web ecology into the applied sector seems increasingly inevitable, especially since it provides an obvious means of linking structure to functioning, and that more realistic predictions can now be made about likely responses to perturbations than was previously possible. This is especially true for climate change, where network approaches can be applied to provide some clear and testable predictions of higher-level responses based on first principles derived from ecological theory (Woodward *et al.*, 2010a,c).

Acknowledgments

This work was partially funded by Monash University via a Monash Research Accelerator grant to Ross Thompson. Ross Thompson was supported by an Australian Research Council Future Fellowship FT-11-0100957. Jennifer Dunne was supported by NSF DBI-0850373. Guy Woodward was supported by a U.K. Natural Environment Research Council grant (NE/I009280/1).

The following articles will appear in the accompanying virtual issue 'Advances in food-web research: a compendium of *Freshwater Biology* papers'. This can be located at [http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1365-2427/homepage/virtual_issue_advances_in_food-web_research.htm](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-2427/homepage/virtual_issue_advances_in_food-web_research.htm).

1. Thompson R. M., Dunne J. and Woodward G. (2012) Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology*, DOI: 10.1111/j.1365-2427.2012.02808.x.
2. Weidman R.P., Schindler D.W. & Vinebrooke R.D. (2011) Pelagic food web interactions among benthic invertebrates and trout in mountain lakes. *Freshwater Biology*, 56, 1081–1094.
3. Jones R.I. & Grey J. (2011) Biogenic methane in freshwater food webs. *Freshwater Biology*, 56, 213–229.
4. Costantini M.L. & Rossi L. (2010) Species diversity and decomposition in laboratory aquatic systems: the role of species interactions. *Freshwater Biology*, 55, 2281–2295.
5. Downing A.L. & Leibold M.A. (2010) Species richness facilitates ecosystem resilience in aquatic food webs. *Freshwater Biology*, 55, 2123–2137.
6. Rawcliffe R., Sayer C.D., Woodward G., Grey J., Davidson T.A. & Jones J.I. (2010) Back to the future: using palaeolimnology to infer long-term changes in shallow lake food webs. *Freshwater Biology*, 55, 600–613.

7. Lau D.C.P., Leung K.M.Y. & Dudgeon D. (2009) What does stable isotope analysis reveal about trophic relationships and the relative importance of allochthonous and autochthonous resources in tropical streams? A synthetic study from Hong Kong. *Freshwater Biology*, **54**, 127–141.
8. Okun N., Brasil J., Attayde J.L. & Costa I.A.S. (2008) Omnivory does not prevent trophic cascades in pelagic food webs. *Freshwater Biology*, **53**, 129–138.
9. Meerhoff M., Iglesias C., De Mello F.T., Clemente J.M., Jensen E., Lauridsen T.L. & Jeppesen E. (2007) Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology*, **52**, 1009–1021.
10. Parker S.M. & Huryn A.D. (2006) Food web structure and function in two arctic streams with contrasting disturbance regimes. *Freshwater Biology*, **51**, 1249–1263.
11. Rosi-Marshall E.J. & Wallace J.B. (2002) Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, **47**, 129–141.
12. Kawaguchi Y. & Nakano S. (2001) Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology*, **46**, 303–316.
13. 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**, 413–422.
14. Schmid-Araya J.M. & Schmid P.E. (2000) Trophic relationships: integrating meiofauna into a realistic benthic food web. *Freshwater Biology*, **44**, 149–163.
15. Lancaster J. & Robertson A.L. (1995) Microcrustacean prey and macroinvertebrate predators in a stream food-web. *Freshwater Biology*, **34**, 123–134.
16. Rounick J.S. & Hicks B.J. (1985) The stable carbon isotope ratios of fish and their invertebrate prey in 4 New Zealand rivers. *Freshwater Biology*, **15**, 207–214.

References

- Allesina S., Alonso D. & Pascual M. (2008) A general model for food web structure. *Science*, **320**, 658–661.
- Baiser B., Russell G.J. & Lockwood J.L. (2011) Connectance determines invasion success via trophic interactions in model food webs. *Oikos*, **119**, 1970–1976.
- Bascompte J., Melián C.J. & Sala E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences USA*, **102**, 5443–5447.
- Benke A.C. & Wallace J.B. (1997) Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology*, **78**, 1132–1145.
- Berlow E.L., Dunne J.A., Martinez N.D., Stark P.B., Williams R.J. & Brose U. (2009) Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 187–191.
- Berlow E.L., Neutel A.M., Cohen J.E., De Ruiter P.C., Ebenman B., Emmerson M. *et al.* (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, **73**, 585–598.
- Brett M.T. & Goldman C.R. (1996) A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 7723–7726.
- Brose U., Berlow E.L. & Martinez N.D. (2005) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters*, **8**, 1317–1325.
- Brose U., Jonsson T., Berlow E.L., Warren P., Banasek-Richter C., Bersier L.F. *et al.* (2006a) Consumer-resource body-size relationships in natural food webs. *Ecology*, **87**, 2411–2417.
- Brose U., Williams R.J. & Martinez N.D. (2006b) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, **9**, 1228–1236.
- Brown L.E., Edwards F.K., Milner A.M., Woodward G. & Ledger M.E. (2011) Food web complexity and allometric scaling relationships in stream mesocosms: implications for experimentation. *Journal of Animal Ecology*, **80**, 884–895.
- Camerano L. (1880) Dell'equilibrio dei viventi mercè la reciproca distruzione. *Atti della Reale Accademia della Scienze di Torino*, **15**, 393–414.
- Carpenter S.R. & Kitchell J.F. (1993) *The Trophic Cascade in Lakes*, p. 385. Cambridge University Press, Cambridge, UK.
- Cattin M.F., Bersier L.F., Banasek-Richter C., Baltensperger R. & Gabriel J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature*, **427**, 835–839.
- Closs G.P. & Lake P.S. (1994) Spatial and temporal variation in the structure of an intermittent-stream food-web. *Ecological Monographs*, **64**, 1–21.
- Cohen J.E. (1978) *Food Webs and Niche Space*. Princeton University Press, Princeton, NJ.
- Cohen J.E. (1989) *Ecologists' Co-operative Web Bank (ECOWeB), Version 1.0 (machine-readable database)*. Rockefeller University, New York.
- Cohen J.E., Beaver R.A., Cousins S.H., Deangelis D.L., Goldwasser L., Heong K.L. *et al.* (1993) Improving food webs. *Ecology*, **74**, 252–258.
- Cohen J.E., Jonsson T. & Carpenter S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 1781–1786.

- Cohen J.E. & Newman C.M. (1985) A stochastic theory of community food webs. I. Models and aggregated data. *Proceedings of the Royal Society B-Biological Sciences*, **224**, 421–448.
- Costantini M.L. & Rossi L. (2010) Species diversity and decomposition in laboratory aquatic systems: the role of species interactions. *Freshwater Biology*, **55**, 2281–2295.
- Darwin C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 1st edn. John Murray, London.
- Diaz S., Symstad A.J., Chapin F.S., Wardle D.A. & Huenneke L.F. (2003) Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution*, **18**, 140–146.
- Dossena M., Grey J., Montoya J.M., Perkins D.M., Trimmer M., Woodward G. *et al.* (2012) Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society of London*, DOI: 10.1098/rspb.2012.0394.
- Downing A.L. & Leibold M.A. (2010) Species richness facilitates ecosystem resilience in aquatic food webs. *Freshwater Biology*, **55**, 2123–2137.
- Dunne J.A. (2006) The network structure of food webs. *Ecological Networks: Linking Structure to Dynamics in Food Webs*, (Eds. M. Pascual & J.A. Dunne), pp. 27–86. Oxford University Press.
- Dunne J.A., Williams R.J. & Martinez N.D. (2002a) Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12917–12922.
- Dunne J.A., Williams R.J. & Martinez N.D. (2002b) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, **5**, 558–567.
- Dunne J.A., Williams R.J. & Martinez N.D. (2004) Network structure and robustness of marine food webs. *Marine Ecology-Progress Series*, **273**, 291–302.
- Forbes S.A. (1887) The lake as a microcosm. *Bulletin of the Peoria Scientific Association*, **7**, 7–87.
- Friberg N., Bonada N., Bradley D.C., Dunbar M.J., Edwards F.K., Grey J. *et al.* (2011) Biomonitoring of human impacts in freshwater ecosystems: the good, the bad and the ugly. *Advances in Ecological Research*, **44**, 1–68.
- Friberg N., Dybkjaer J.B., Olafsson J.S., Gislason G.M., Larsen S.E. & Lauridsen T.L. (2009) Relationships between structure and function in streams contrasting in temperature. *Freshwater Biology*, **54**, 2051–2068.
- Hagen M., Kissling W.D., Rasmussen C., de Aguiar M.A.M., Brown L.E., Carstensen D.W. *et al.* (2012) Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, **46**, in press.
- Hawlena D. & Schmitz O.J. (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, **176**, 537–556.
- Hernandez A.D. & Sukhdeo M.V.K. (2008) Parasites alter the topology of a stream food web across seasons. *Oecologia*, **156**, 613–624.
- Hildrew A.G., Townsend C.R. & Hasham A. (1985) The predatory Chironomidae of an iron-rich stream – feeding ecology and food web structure. *Ecological Entomology*, **10**, 403–413.
- Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hutchinson G.E. (1959) Homage to Santa-Rosalía or Why are there so many kinds of animals. *American Naturalist*, **93**, 145–159.
- Huxham M., Beaney S. & Raffaelli D. (1996) Do parasites reduce the chances of triangulation in a real food web? *Oikos*, **76**, 284–300.
- Ings T.C., Montoya J.M., Bascompte J., Bluthgen N., Brown L., Dormann C.F. *et al.* (2009) Ecological networks – beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.
- Ives A.R. & Godfray H.C.J. (2006) Phylogenetic analysis of trophic associations. *American Naturalist*, **168**, E1–E14.
- Jones R.I. & Grey J. (2011) Biogenic methane in freshwater food webs. *Freshwater Biology*, **56**, 213–229.
- Kawaguchi Y. & Nakano S. (2001) Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology*, **46**, 303–316.
- Kerfoot W.C. & Deangelis D.L. (1989) Scale-dependent dynamics – zooplankton and the stability of freshwater food webs. *Trends in Ecology & Evolution*, **4**, 167–171.
- Krause A.E., Frank K.A., Mason D.M., Ulanowicz R.E. & Taylor W.W. (2003) Compartments revealed in food-web structure. *Nature*, **426**, 282–285.
- Lafferty K.D., Allesina S., Arim M., Briggs C.J., De Leo G., Dobson A.P. *et al.* (2008) Parasites in food webs: the ultimate missing links. *Ecology Letters*, **11**, 533–546.
- Lafferty K.D., Dobson A.P. & Kuris A.M. (2006) Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 11211–11216.
- Laliberte E. & Legendre P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.
- Lancaster J. & Robertson A.L. (1995) Microcrustacean prey and macroinvertebrate predators in a stream food-web. *Freshwater Biology*, **34**, 123–134.
- Lau D.C.P., Leung K.M.Y. & Dudgeon D. (2009) What does stable isotope analysis reveal about trophic relationships and the relative importance of allochthonous and autochthonous resources in tropical streams? A synthetic study from Hong Kong *Freshwater Biology*, **54**, 127–141.
- Law R. & Blackford J.C. (1992) Self-assembling food webs: a global viewpoint of co-existence of species in Lotka-Volterra communities. *Ecology*, **73**, 567–578.
- Lawton J.H. (1989) Food webs. In: *Ecological Concepts* (Ed. J.M. Cherratt), pp. 43–78. Blackwell Scientific, Oxford.

- Lawton J.H. & Warren P.H. (1988) Static and dynamic explanations for patterns in food webs. *Trends in Ecology & Evolution*, **3**, 242–245.
- Layer K., Hildrew A., Monteith D. & Woodward G. (2010a) Long-term variation in the littoral food web of an acidified mountain lake. *Global Change Biology*, **16**, 3133–3143.
- Layer K., Hildrew A.G., Jenkins G.B., Riede J.O., Rossiter S.J., Townsend C.R. *et al.* (2011) Long-term dynamics of a well-characterised food web: four decades of acidification and recovery in the Broadstone Stream model system. *Advances in Ecological Research*, **44**, 69–117.
- Layer K., Riede J.O., Hildrew A.G. & Woodward G. (2010b) Food web structure and stability in 20 streams across a wide pH gradient. *Advances in Ecological Research: Ecological Networks*, **42**, 265–299.
- Lazzaro X. (1997) Do the trophic cascade hypothesis and classical biomanipulation approaches apply to tropical lakes and reservoirs? *International Association of Theoretical and Applied Limnology*, **26**, 719–730.
- Ledger M.E., Edwards F.K., Brown L.E., Milner A.M. & Woodward G. (2011) Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. *Global Change Biology*, **17**, 2288–2297.
- Lindeman R.L. (1942) The trophic-dynamic aspect of ecology. *Ecology*, **23**, 399–418.
- MacArthur R. (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology*, **36**, 533–536.
- Martinez N.D. (1991) Artifacts or attributes – effects of resolution on the Little-Rock Lake food web. *Ecological Monographs*, **61**, 367–392.
- Martinez N.D. (1993) Effects of resolution on food web structure. *Oikos*, **66**, 403–412.
- Martinez N.D. & Lawton J.H. (1995) Scale and food-web structure – from local to global. *Oikos*, **73**, 148–154.
- May R.M. (1972) Will a large complex system be stable? *Nature*, **238**, 413–414.
- McCann K. & Hastings A. (1997) Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London B*, **264**, 1249–1254.
- McCoy M.W., Bolker B.M., Warkentin K.M. & Vonesh J.R. (2011) Predicting predation through prey ontogeny using size-dependent functional response models. *American Naturalist*, **177**, 752–766.
- McHugh P.A., McIntosh A.R. & Jellyman P.G. (2010) Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters*, **13**, 881–890.
- McKee D., Atkinson D., Collings S.E., Eaton J.W., Gill A.B., Harvey I. *et al.* (2003) Response of freshwater microcosm communities to nutrients, fish, and elevated temperature during winter and summer. *Limnology and Oceanography*, **48**, 707–722.
- Meerhoff M., Iglesias C., De Mello F.T., Clemente J.M., Jensen E., Lauridsen T.L. *et al.* (2007) Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology*, **52**, 1009–1021.
- Melián C.J., Alonso D., Allesina S., Condit R.S. & Etienne R.S. (2012) Does sex speed up evolutionary rate and increase biodiversity? *PLoS Computational Biology*, **8**, e1002414.
- O'Connor M.I., Pehler M.F., Leech D.M., Anton A. & Bruno J.F. (2009) Warming and resource availability shift food web structure and metabolism. *Plos Biology*, **7**, e1000178.
- Okun N., Brasil J., Attayde J.L. & Costa I.A.S. (2008) Omnivory does not prevent trophic cascades in pelagic food webs. *Freshwater Biology*, **53**, 129–138.
- Olesen J.M., Dupont Y.L., O'gorman E.J., Ings T.C., Layer K., Melian C.J. *et al.* (2010) From Broadstone to Zackenber: space, time and hierarchies in ecological networks. *Advances in Ecological Research*, **42**, 1–69.
- Paine R.T. (1980) Food Webs – Linkage, interaction strength and community infrastructure – the 3rd Tansley Lecture. *Journal of Animal Ecology*, **49**, 667–685.
- Parker S.M. & Huryn A.D. (2006) Food web structure and function in two arctic streams with contrasting disturbance regimes. *Freshwater Biology*, **51**, 1249–1263.
- Petchey O. & Dunne J.A. (in press) Trophic relations and food webs. In: *Metabolic Ecology: A Scaling Approach* (Eds R.M. Sibley, J.H. Brown & A. Kodric-Brown). Wiley-Blackwell.
- 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 of the United States of America*, **105**, 4191–4196.
- Pimm S.L. (1982) *Food Webs*. Chapman and Hall, London.
- Pimm S.L. & Lawton J.H. (1978) On feeding on more than one trophic level. *Nature*, **275**, 542–544.
- Pimm S.L., Lawton J.H. & Cohen J.E. (1991) Food web patterns and their consequences. *Nature*, **350**, 669–674.
- Polis G.A. (1991) Complex trophic interactions in deserts – an empirical critique of food-web theory. *American Naturalist*, **138**, 123–155.
- Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.
- Polis G.A., Holt R.D., Menge B.A. & Winemiller K.O. (1996) Time, space and life history: influences on food webs. In: *Food Webs: Integration of Pattern and Dynamics* (Eds G.A. Polis & K.O. Winemiller), pp. 438–447. Chapman & Hall, New York.
- Polis G.A. & Strong D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Post D.M. (2002) The long and short of food-chain length. *Trends in Ecology and Evolution*, **17**, 269–277.
- Purdy K.J., Hurd P.J., Moya-Larano J., Trimmer M., Oakley B.B. & Woodward G. (2010) Systems biology for ecology: from molecules to ecosystems. *Advances in Ecological Research*, **43**, 87–149.
- Raffaelli D. (2007) Food webs, body size and the curse of the Latin binomial. in: *From Energetics to Ecosystems: the*

- Dynamics and Structure of Ecological Systems* (Eds N. Rooney, K.S. Mccann & D.L.G. Noakes), pp. 53–64. Springer, Dordrecht.
- Rawcliffe R., Sayer C.D., Woodward G., Grey J., Davidson T.A. & Jones J.I. (2010) Back to the future: using palaeolimnology to infer long-term changes in shallow lake food webs. *Freshwater Biology*, **55**, 600–613.
- Reiss J., Bridle J.R., Montoya J.M. & Woodward G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, **24**, 505–514.
- Rosi-Marshall E.J. & Wallace J.B. (2002) Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, **47**, 129–141.
- Rounick J.S. & Hicks B.J. (1985) The stable carbon isotope ratios of fish and their invertebrate prey in 4 New Zealand rivers. *Freshwater Biology*, **15**, 207–214.
- Schmid-Araya J.M., Hildrew A.G., Robertson A., Schmid P.E. & Winterbottom J. (2002) The importance of meiofauna in food webs: evidence from an acid stream. *Ecology*, **83**, 1271–1285.
- Schmid-Araya J.M. & Schmid P.E. (2000) Trophic relationships: integrating meiofauna into a realistic benthic food web. *Freshwater Biology*, **44**, 149–163.
- Shurin J.B., Borer E.T., Seabloom E.W., Anderson K., Blanchette C.A., Broitman B. *et al.* (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, **5**, 785–791.
- Sole R.V. & Montoya J.M. (2001) Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 2039–2045.
- Srinivasan U.T., Dunne J.A., Harte J. & Martinez N.D. (2007) Response of complex food webs to realistic extinction sequences. *Ecology*, **88**, 671–682.
- Stouffer D.B. & Bascompte J. (2011) Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 3648–3652.
- Stouffer D.B., Camacho J. & Amaral L.A.N. (2006) A robust measure of food web intervality. *Proceeding of the National Academy of Sciences*, **103**, 19015–19020.
- Stouffer D.B., Camacho J., Guimera R., Ng C.A. & Amaral L.A.N. (2005) Quantitative patterns in the structure of model and empirical food webs. *Ecology*, **86**, 1301–1311.
- Stouffer D.B., Camacho J., Jiang W. & Amaral L.A.N. (2007) Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 1931–1940.
- Stouffer D.S., Rezende E.L. & Amaral L.A.N. (2011) The role of body mass in diet contiguity and food-web structure. *Journal of Animal Ecology*, **49**, 879–898.
- Tavares-Cromar A.F. & Williams D.D. (1996) The importance of temporal resolution in food web analysis: evidence from a detritus-based stream. *Ecological Monographs*, **66**, 91–113.
- Thompson R.M., Hemberg M., Starzomski B.M. & Shurin J.B. (2007) Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, **88**, 612–617.
- Thompson R.M., Mouritsen K.N. & Poulin R. (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *Journal of Animal Ecology*, **74**, 77–85.
- Thompson R.M. & Townsend C.R. (1999) The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. *Oikos*, **87**, 75–88.
- 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**, 413–422.
- Thompson R.M. & Townsend C.R. (2004) Land-use influences on New Zealand stream communities: effects on species composition, functional organisation, and food-web structure. *New Zealand Journal of Marine and Freshwater Research*, **38**, 595–608.
- Thompson R.M. & Townsend C.R. (2005) Food-web topology varies with spatial scale in a patchy environment. *Ecology*, **86**, 1916–1925.
- Townsend C.R., Thompson R.M., Mcintosh A.R., Kilroy C., Edwards E. & Scarsbrook M.R. (1998) Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, **1**, 200–209.
- Valdovinos F.S., Ramos-Jiliberto R., Garay-Narvaez L., Urbani P. & Dunne J.A. (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters*, **13**, 1546–1559.
- Vander Zanden M.J. & Vadeboncoeur Y. (2002) Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, **83**, 2152–2161.
- Vermaat J.E., Dunne J.A. & Gilbert A.J. (2009) Major dimensions in food-web structure properties. *Ecology*, **90**, 278–282.
- Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, **277**, 102–104.
- Warren P.H. (1989) Spatial and temporal variation in the structure of a fresh-water food web. *Oikos*, **55**, 299–311.
- Weidman R.P., Schindler D.W. & Vinebrooke R.D. (2011) Pelagic food web interactions among benthic invertebrates and trout in mountain lakes. *Freshwater Biology*, **56**, 1081–1094.
- Williams R.J., Anandanadesan A. & Purves D. (2010) The probabilistic niche model reveals the niche structure and role of body size in a complex food web. *PLoS ONE*, **5**, e12092.
- Williams R.J. & Martinez N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180–183.
- Williams R.J. & Martinez N.D. (2004) Limits to trophic levels and omnivory in complex food webs: theory and data. *The American Naturalist*, **163**, 458–468.

- Winemiller K.O. & Jepsen D.B. (1998) Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, **53**, 267–296.
- Woodward G., Benstead J.P., Beveridge O.S., Blanchard J., Brey T., Brown L.E. *et al.* (2010a) Ecological Networks in a Changing Climate. In: *Advances in Ecological Research*, **42**, 71–138.
- Woodward G., Blanchard J., Lauridsen R.B., Edwards F.K., Jones J.I., Figueroa D. *et al.* (2010b) Individual-based food webs: species identity, body size and sampling effects. *Integrative Ecology: From Molecules to Ecosystems*, **43**, 211–266.
- Woodward G., Christensen J.B., Olafsson J.S., Gislason G.M., Hannesdottir E.R. & Friberg N. (2010c) Sentinel systems on the razor's edge: effects of warming on Arctic stream ecosystems. *Global Change Biology*, **16**, 1979–1991.
- Woodward G., Ebenman B., Emmerson M., Montoya J.M., Olesen J.M., Valido A. *et al.* (2005b) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402–409.
- Woodward G., Speirs D.C. & Hildrew A.G. (2005a) Quantification and temporal resolution of a complex size-structured food web. *Advances in Ecological Research*, **36**, 85–135.
- Wootton J.T. & Emmerson M. (2005) Measurement of interaction strength in nature. *Annual Review of Ecology Evolution and Systematics*, **36**, 419–444.
- Yodzis P. (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, **67**, 635–658.
- Yodzis P. & Innes S. (1992) Body size and consumer-resource dynamics. *American Naturalist*, **139**, 1151–1175.
- Yvon-Durocher G., Allen A.P., Montoya J.M., Trimmer M. & Woodward G. (2010) The temperature dependence of the carbon cycle in aquatic systems. *Advances in Ecological Research*, **43**, 267–313.
- Yvon-Durocher G., Reiss J., Blanchard J., Ebenman B., Perkins D.M., Reuman D.C. *et al.* (2011) Across ecosystem comparisons of size structure: methods, approaches, and prospects. *Oikos*, **120**, 550–563.

(Manuscript accepted 16 April 2012)