

REVIEW

Ecological networks – beyond food webs

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Summary

1. A fundamental goal of ecological network research is to understand how the complexity observed in nature can persist and how this affects ecosystem functioning. This is essential for us to be able to predict, and eventually mitigate, the consequences of increasing environmental perturbations such as habitat loss, climate change, and invasions of exotic species.
2. Ecological networks can be subdivided into three broad types: ‘traditional’ food webs, mutualistic networks and host–parasitoid networks. There is a recent trend towards cross-comparisons among network types and also to take a more mechanistic, as opposed to phenomenological, perspective. For example, analysis of network configurations, such as compartments, allows us to explore the role of co-evolution in structuring mutualistic networks and host–parasitoid networks, and of body size in food webs.
3. Research into ecological networks has recently undergone a renaissance, leading to the production of a new catalogue of evermore complete, taxonomically resolved, and quantitative data. Novel topological patterns have been unearthed and it is increasingly evident that it is the distribution of interaction strengths and the configuration of complexity, rather than just its magnitude, that governs network stability and structure.
4. Another significant advance is the growing recognition of the importance of individual traits and behaviour: interactions, after all, occur between individuals. The new generation of high-quality networks is now enabling us to move away from describing networks based on species-averaged data and to start exploring patterns based on individuals. Such refinements will enable us to address more general ecological questions relating to foraging theory and the recent metabolic theory of ecology.
5. We conclude by suggesting a number of ‘dead ends’ and ‘fruitful avenues’ for future research into ecological networks.

Key-words: mutualistic networks, host-parasitoid interactions, metabolic theory of ecology, ecological stoichiometry, foraging theory

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Introduction

A fundamental goal of ecological research is to understand the mechanisms that influence the stability of ostensibly fragile ecosystems. Ever since Darwin contemplated the interdependence of the denizens of his 'entangled bank' (Darwin 1859), ecologists have sought to understand how this seemingly bewildering complexity can persist in nature (Hutchinson 1957; McCann 2000; Montoya, Pimm & Solé 2006). The study of the nexus of interactions among organisms that comprise ecological networks has consequently played a central role in the development of ecology as a scientific discipline (Hardy 1924; Elton 1927; May 1972; McCann 2000).

Much of the research effort to date can be conveniently grouped into three types of network, defined by the types of organisms and interactions concerned: (i) 'traditional' food webs (FW), (ii) host-parasitoid webs (HPW), and, more recently, (iii) mutualistic webs (MW). In reality, of course, there are many other ways to classify networks and natural ecosystems will contain an amalgam of these divisions that currently represent relatively distinct research fields. In addition, parasitic and pathogenic interactions are also important in nature, but they have been rarely considered from an ecological network perspective although they are an area of growing interest (e.g. Huxham, Beaney & Raffaelli 1996; Vázquez *et al.* 2005; Lafferty, Dobson & Kuris 2006; Tylanakis, Tscharnkte & Lewis 2007; van Veen *et al.* 2008) and will no doubt feature prominently in future research. FWs and HPWs describe antagonistic interactions, whereas MWs include interactions that are beneficial to both partners (e.g. plant–pollinator and plant–frugivore networks).

In addition, a fundamental difference of approach exists among many studies, reflecting the historical schism of population and community ecology (e.g. after Elton 1927; MacArthur 1955) versus ecosystem (e.g. after Lindeman 1942; Odum 1953) approaches. In community studies, the nodes in the network are comprised of individuals that make up species populations, and the links connecting them indicate population effects. The ecosystem approach emphasizes pools and fluxes of energy, biomass or nutrients, rather than taxonomic units. Surprisingly, few studies have sought to unite these disparate strands (but see Brown *et al.* 2004; Ulanowicz 2004), perhaps reflecting our inability and/or reluctance to engage in truly interdisciplinary ecology (Woodward *et al.* 2005a) due to the so-called 'curse of the Latin binomial' (Raffaelli 2007), whereby a pre-occupation with using species as nodes may be hindering our ability to recognize the true entities of importance (e.g. individual body size). However, the interactions in all these types of network ultimately occur between individuals and they also involve fluxes of energy (and or gametes) – an important point that is often ignored, but one that we will give emphasis throughout this text.

Food web ecology has recently undergone something of a renaissance following a series of highly critical reviews in the late 1980s and early 1990s that questioned the validity of the field on both empirical and theoretical grounds (e.g. Paine

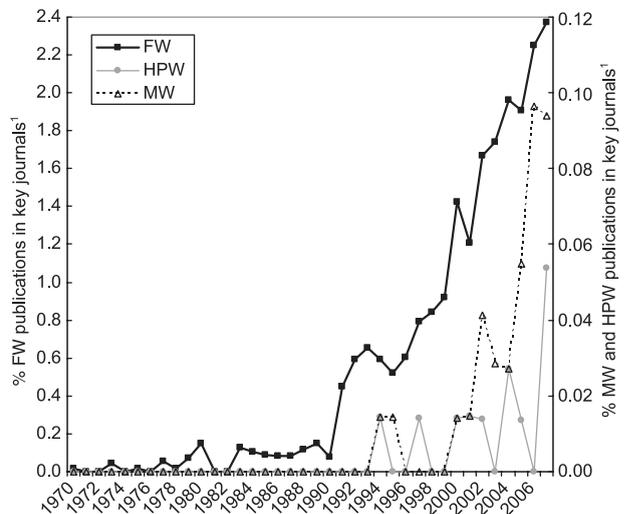


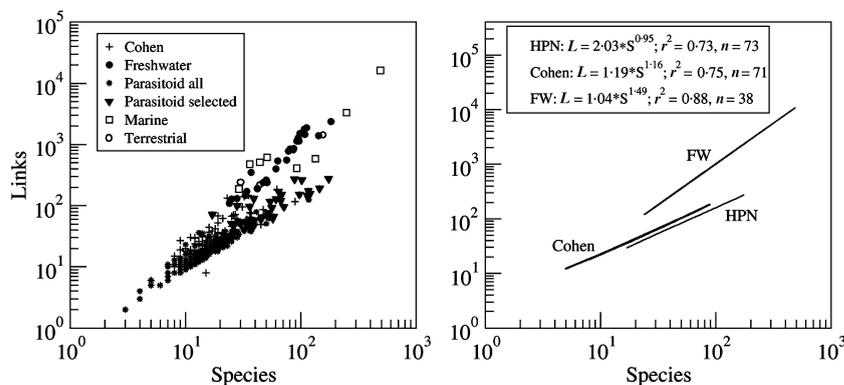
Fig. 1. Annual proportion of all papers published in key journals¹ between 1970 and 2007 that were related to ecological networks (primary axis, FWs; secondary axis, MWs and HPWs). Data were derived from searches carried out on the Web of Science data base (searched in March 2008). Search terms for the different network types were: FWs, Topic = ('food web*' or 'food-web*'); HPWs, Topic = [('host parasitoid' or 'host-parasitoid') and (web or network)] and MWs, Topic = [mutualist* and (web or network)].¹Set of publications used in searches (journals active for less than 20 years were excluded): *Nature*, *Science*, *Proceedings of the National Academy of Sciences*, *USA*, *Trends in Ecology & Evolution*, *Ecology*, *Proceedings of the Royal Society B: Biological Sciences*, *Oikos*, *Oecologia*, *Journal of Animal Ecology*, *Freshwater Biology*, *Marine Biology*.

1988; Polis 1991; Hall & Raffaelli 1993). A bibliographic analysis of articles published in key journals between 1970 and 2007, using the 'Web of Science' data base, revealed an exponential increase in the number of FW papers published each year (Fig. 1). Similar trends were also evident for MW and HPW studies, although they did not show any major increase until the 1990s and are still nearly two orders of magnitude below FWs. The time-lag for MWs highlights the fact that mutualistic interactions, although widely studied in behavioural ecology, have only recently been considered from a network perspective – the Jordano (1987) *American Naturalist* paper was one of the first in this field, although the seminal *Journal of Animal Ecology* paper of Paine (1980) made passing reference to mutualisms.

Of all the types of ecological networks, FWs are the most familiar and have arguably been the most influential during the early development of the field (Pimm 1982; Cohen *et al.* 1993; Hall & Raffaelli 1993; Woodward *et al.* 2005a). Although all three types of network contain trophic interactions, studies of FWs, in their most restrictive definition, typically focus on predator–prey interactions involving consumers that are usually bigger than their resources (Cohen *et al.* 1993; Brose, Berlow & Martinez 2005; Brose *et al.* 2006).

The advent of increasingly powerful computers and more sophisticated algorithms, many of which have been adopted from the study of other biological (e.g. genetic), technological (e.g. Internet) and social (e.g. friendship) networks

Fig. 2. Link (L)-species richness (S) relationships for different network types. Our set of highly resolved food webs (marine, freshwater, and terrestrial: see Table 1) have more links for the same number of species than a set of host-parasitoid networks and those reported in earlier studies (e.g. those based on the Ecowebs data base). Food webs were therefore more 'generalized' than host-parasitoid networks and none of the web compilations used here support the constant connectance hypothesis: $L = CS^2$.



(Borgatti & Everett 1997; Strogatz 2001; Barabasi *et al.* 2002; Dorogovtsev *et al.* 2003; Kossinets 2006; Montoya *et al.* 2006), have provided researchers not only with a more effective toolkit, but with a refreshing perspective to search for unifying network patterns and dynamics. In particular, there is increasing interest in more robust cross-comparisons among different network types (Solé & Montoya 2001; Dunne, Williams & Martinez 2002; Montoya *et al.* 2006). Such comparisons are starting to reveal interesting common ground, but also intriguing uniqueness, in FW, HPW and MW systems (Fig. 2). The main purpose of this paper is to review some of the exciting new developments in the study of ecological networks, to explore reasons for commonalities (and singularities), and to suggest how the field might move forward in the future. One of the primary sources of stimulation for this work was a thematic topic on ecological networks at the 2007 British Ecological Society Annual meeting in Glasgow. Therefore, we will concentrate on many of the issues raised during this meeting, while drawing upon other key studies to illustrate important contextual points. After introducing the three major classes of ecological network, we will discuss recent advances in the study of network topology, with a particular emphasis on novel and broad patterns across network types. We will then touch on issues relating to the quantification of links within networks, network assembly, appropriate levels of organization and the role that behaviour plays in the dynamics and structuring of networks. In the remaining sections, we will discuss new applications for ecological network studies within the wider research area of global change biology, and how we are overcoming previous limitations of ecological networks. Unfortunately, and despite the resurgence of interest in this field, almost all empirical studies of ecological networks and many of the models described to date are still phenomenological and lack a mechanistic basis, a shortcoming we discuss in *Future Directions*, where we highlight 'dead ends' and identify promising new vistas in research.

NETWORK TYPES

Traditional food webs (FW) stem from the population and community ecology school of thought and focus on trophic links among organisms, particularly predator-prey and

primary consumer-basal resource feeding relationships (Hall & Raffaelli 1993). Food webs are generally subdivided into community webs, which include all links among organisms in a defined community, or into smaller source or sink webs (Cohen 1978; Hall & Raffaelli 1993) that follow links upwards or downwards from a single focal species (or group of species), respectively. While there is a slight bias towards freshwater environments in the published FW catalogue, there are now good examples of marine (Bascompte, Melian & Sala 2005; Yvon-Durocher *et al.* 2008) and terrestrial (de Ruiter, Neutel & Moore 1995; Reagan & Waide 1996; Mulder *et al.* 2005, 2006; Rooney *et al.* 2006; Neutel *et al.* 2007) FWs. Typically, many FWs described since the mid-1980s are species rich, have blurred trophic levels, high levels of generalism and a prevalence of feeding loops (cannibalism and mutual predation) when compared with their earlier, simpler counterparts, for example, the catalogue of webs compiled in Cohen (1978). Generalism (species with many feeding links) and redundancy (species with equivalent trophic interactions) appear to be the norm in many FWs (Woodward & Hildrew 2002c; Shurin, Gruner & Hillebrand 2006). FWs, and especially predator-prey webs, tend to have well-defined body size relationships, with larger predatory consumers at the top and a more diverse group of smaller-sized 'resources' at the bottom (Memmott, Martinez & Cohen 2000; Mulder *et al.* 2005, 2006; Otto, Rall & Brose 2007). More recently, the incorporation of abundance data has revealed recurrent patterns in so-called trivariate webs (Müller *et al.* 1999), whereby mean individual mass ($\log M$) is plotted against numerical abundance ($\log N$) for each species population, with the feeding links between these nodes overlain on the resultant M vs. N scatterplot (Cohen, Jonsson & Carpenter 2003; Woodward, Speirs & Hildrew 2005b). These trivariate webs provide important insight into the structure of the network and energy fluxes can also be inferred (e.g. Reuman & Cohen 2005). One general pattern is that trophic links flow from many small individuals at the base of the web upwards into larger, rarer individuals at the top of the web, with a concentration of resources into a progressively smaller number of nodes (Cohen *et al.* 2003; Mulder *et al.* 2005, 2006; Woodward *et al.* 2005a). This approach links both community and ecosystem approaches, by combining measures of biomass

and numerical abundance in the study of ecological networks (e.g. Reuman & Cohen 2005; Yvon-Durocher *et al.* 2008).

Host–parasitoid webs also come from the population biology school of thought but they concentrate on the special type of ‘predator–prey’ feeding relationships between parasitoids and their hosts. In many instances, HPWs focus on distinct guilds of terrestrial insects (hosts) and trace the links from hosts to their parasitoids (mostly parasitic wasps). Much of the early work on HPWs is dispersed through the biological control literature, since parasitoids are natural enemies of many crop pests (Hawkins 1994; Vázquez *et al.* 2005). These systems are particularly well suited to the description of quantitative networks in which populations and interactions can be expressed in the same units (individuals m^{-2}) because the number of hosts killed and the number of parasitoid individuals produced from this can be observed directly (van Veen, Morris & Godfray 2006). Another advantage of these systems is that they are usually resolved to the level of biological species, avoiding potential problems with using ‘trophic species’, whereby species that share predators and prey are lumped together (Cohen 1978). A disadvantage is that they necessarily focus on a subset of the ecological community and are thus less suited to study energy fluxes. Recent advances in HPWs have focussed on the quantification of the potential for indirect population interactions (Müller *et al.* 1999; Lewis *et al.* 2002) and the effects these indirect interactions have on network structure (Morris *et al.* 2004; Bukovinszky *et al.* 2008). They have also been applied to measure the effects of biological invasions (Henneman & Memmott 2001) and habitat degradation (Tylianakis *et al.* 2007). Individual parasitoid body size scales with host body size by a power of three-fourths, but if species-averaged body sizes are used, which is typically the case in ecological networks, this relationship is not apparent (Cohen *et al.* 2005): this individual perspective represents an important new trend that we will return to later.

Mutualistic webs define the nexus of ecosystem services such as pollination and seed dispersal, rather than population dynamics or energy fluxes *per se*. Among the MWs studied so far, three systems have received particular attention: (i) *pollination networks*, which are maps of interactions between plants and their animal pollinators; (ii) *frugivore networks*, which examine interactions between plants and their animal seed dispersers; and (iii) *ant–plant networks*, which examine the interaction between plants that provide food and/or domatia for ants, which in turn provide protection for the plants. There are other forms of mutualism beyond these terrestrial above-ground domains that have not yet been considered from a network perspective, including: plant–mycorrhizal systems, coral–zooxanthellae associations, and the plethora of other interactions that involve microbial endosymbionts.

Specialism tends to be more common in some MWs (Fonseca & Ganade 1996; but see Waser *et al.* 1996) than in FWs, and this is probably even more marked in endosymbiotic systems. Important progress in understanding MWs can be obtained if these interactions are viewed as consumer–resource relation-

ships in a similar way to those in FWs, since many MWs such as (i) and (ii) involve consumption of plant-based nutritious resources. As in FWs, there may be clear morphological constraints related to body size, such as the correlations between corolla length and the length of the plant visitor’s tongue or proboscis (Jordano, Bascompte & Olesen 2003; Stang, Klinkhamer & van der Meijden 2006). Whereas flowers often constrain the consumer spectrum by morphological barriers, extrafloral nectaries are open and easily accessible resources to ants and other insects. This may be one of the reasons why networks involving ants and extrafloral nectaries are much less specialized than the more intimately associated pollinator webs (Blüthgen *et al.* 2007).

Clearly, it is important to choose an appropriate and relevant scale with which to classify the ‘size’ of both consumers and resources. For instance, granivorous rodents in the Coachella desert displayed a clear nested feeding hierarchy in relation to the seeds they consumed: this provided the best fit of the 15 networks examined by Petchey *et al.* (2008) to their size-based model, as this was the relevant unit of interaction, rather than the size of the parent plant. Similarly, the main resources in MWs are only parts of plants rather than entire individuals: pollen/nectar in pollinator webs and fruit pulp in frugivory networks. Individual food items such as pollen and berries are typically much smaller than (for instance) the bees and birds that consume them, yet the plants that produce these resources are often many times larger than the consumers. Because of this important difference, we suggest that focusing on the metabolic costs of producing the resources that are actually consumed, for example, nectar/pollen and fruit, might be a more meaningful way to compare the relationships among consumers and resources across networks.

RECENT ADVANCES IN NETWORK TOPOLOGY

The study of network topology is now far more sophisticated than the rather crude approach of measuring ‘connectance’ that defined the early forays into this field (Cohen 1978; Pimm 1982). Network theory is now a truly interdisciplinary topic and ecology has drawn heavily upon algorithms developed in other areas, such as social science and information theory (Solé & Montoya 2001; Dunne *et al.* 2002; Krause, Lehman & Wheeler 2003b; Almaas *et al.* 2004; Blüthgen, Menzel & Blüthgen 2006a).

One of the major structural properties of ecological networks to be studied extensively, beyond simple measures of connectance or link–species richness relations, is the distribution of links among species (connectivity distributions), which has often been linked to network stability. Seminal work by Robert May (1972, 1973) suggested the general mathematical condition for a complex ecological network to be stable: $i(SC)^{1/2} < 1$, where S is number of species, C is connectance and corresponds to the number of realized links L among those possible, so that $C = L/S^2$, and i is the mean interaction strength between connected species. This relationship triggered a heated debate as to how real systems can be stable, as

empirical data repeatedly demonstrated that complexity was the rule, not the exception, in nature (e.g. Polis 1991; Williams & Martinez 2000). One possible explanation might relate to May's assumption that connectivity distributions were random, which has since been discredited (Solé & Montoya 2001; Dunne *et al.* 2002; Montoya & Solé 2002; Jordano *et al.* 2003; Montoya *et al.* 2006). In MWs, for instance, most pollinators have a very restricted diet, whereas very few pollinate many plants (Jordano *et al.* 2003; Montoya *et al.* 2006). Within antagonistic interactions, we suggest two extremes: freshwater FWs tend to have many generalists (Woodward & Hildrew 2002c), and HPWs tend to have many specialized parasitoids (Blüthgen *et al.* 2008).

Given these patterns of relative specialization and generalization, how are feeding interactions organized? Ecological networks seem to be nested: a two-mode network such as the one between plants and their mutualistic animals is nested if specialists interact with species that form well-defined subsets of the species that generalists also interact with. A nested structure usually implies that there is a core of generalist species interacting among themselves, and a tail of specialists interacting with the most generalist species (Bascompte *et al.* 2003). While in essence this refers to the ordering of species in a network into hierarchies, there are a number of different measures of nestedness that are beyond the scope of detailed discussion here (Fig. 3). Some have suggested, by using null models, that nestedness simply reflects relative abundances such that rarely observed species typically interact with frequently observed partners (Lewinsohn *et al.* 2006). Whether nestedness is a consequence of abundance and/or geographical range is still unresolved, that is, is neutral association rather than specialization the underlying mechanism governing nestedness? Within FWs, especially in aquatic systems, nestedness appears to be related to body size because the diets of smaller predators tend to be nested subsets of those of larger predators (Woodward & Warren 2007; Yvon-Durocher *et al.* 2008), and phylogenetic constraints, whereby related taxa are nested based on their common evolutionary history, are also evident (Cattin *et al.* 2004).

Ecological networks, especially MWs, are generally very heterogeneous, consisting of areas with sparse links among species and distinct areas of tightly linked species. These regions of high link density are often referred to as cliques, hubs, compartments, cohesive sub-groups, or modules (Paine 1980; Pimm & Lawton 1980; Jordano 1987; Fonseca & Ganade 1996; Dicks, Corbet & Pywell 2002; Krause *et al.* 2003a; Olesen *et al.* 2007). Increasingly, topological research has focused on the concept of 'small world' networks which are composed of clustered nodes and short paths between pairs of nodes (Milgram 1967; Watts & Strogatz 1998; Strogatz 2001). Species within FWs are typically separated by fewer than three links (Dunne *et al.* 2002; Montoya & Solé 2002; Montoya *et al.* 2006): this has profound implications for the propagation of disturbances as the effect of one species on the density of another diminishes with the distance of the shortest path connecting them. The prevalence of such 'short circuits' suggests that disturbances may spread faster than

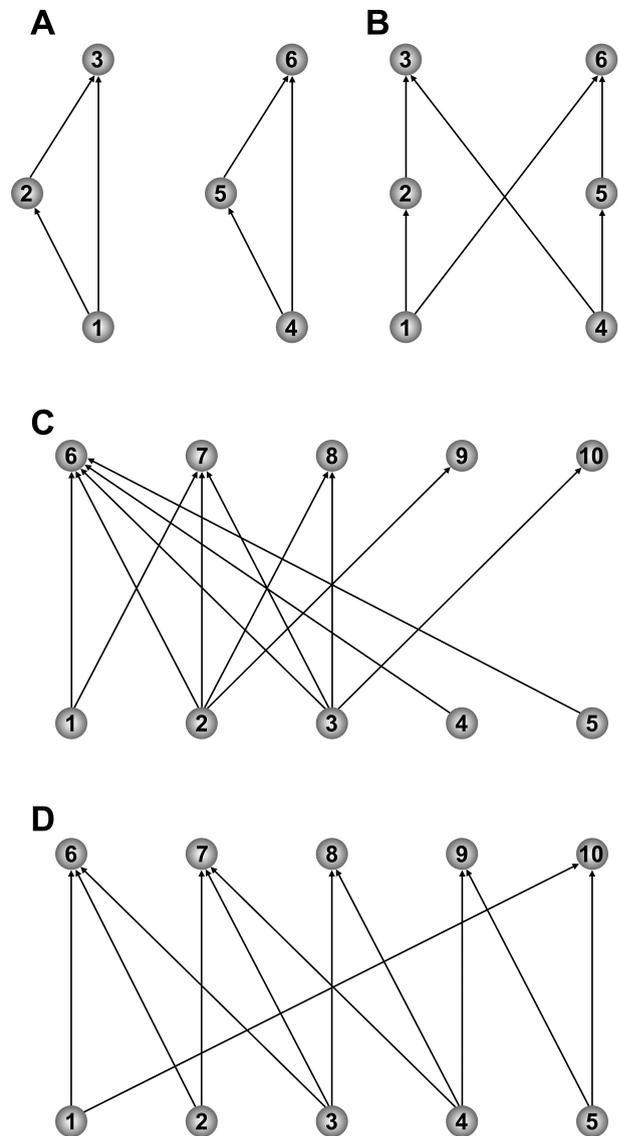


Fig. 3. Examples of clustering (a–b) and nestedness (c–d) in ecological networks. Arrows point from resource to consumer. Webs in a are clustered and have within-chain omnivory. Webs in b are not clustered with predators 3 and 6 feeding on different food chains. Within-chain omnivory is therefore a requisite for ecological networks to be clustered. Web in c is nested and d is not nested, given the same number of species and links. In c, the diet of consumer 8 is a subset of that of consumer 7, that, in turn, is a subset of consumer 6's diet, whereas in d, diet of consumers 6, 7, and 8, overlaps equally. Also, in c specialized consumers 9 and 10 use resources used also by generalist consumers such as 6, a pattern not observed in c.

previously expected, even in complex networks (Montoya *et al.* 2006; Woodward *et al.* 2008; Montoya *et al.* in press).

There has been some debate over the presence of species clusters in ecological networks, fostered by the analysis of small, poorly resolved, aggregated networks (Dunne *et al.* 2002; Montoya & Solé 2002). Highly resolved webs, however, where species are not aggregated into 'trophic' species show a higher degree of clustering than their random counterparts

(Montoya *et al.* 2006). Recently, Olesen *et al.* (2006) examined the structural properties of pollination networks by splitting them into their component plant and pollinator-centred one-mode networks, thus allowing them to compare the properties of MWs with those of FWs. Generally, there was much stronger clustering in the former than in the latter, which in combination with short path lengths, revealed that MWs had strong small world properties. Theoretically, compartments increase stability in ecological networks (Krause *et al.* 2003a) thereby providing a mechanism by which complexity can persist.

Network modules have stimulated much interest as foci for species interactions that may represent co-evolutionary units (Thompson 2005). Robust module-detecting algorithms are now available in other disciplines (e.g. metabolic networks: Guimerà & Amaral 2005) and Olesen *et al.* (2007) analysed qualitative pollination networks using this approach, and discovered that large (> 150 species) pollinator networks were modular and that modularity co-occurred together with nestedness. Furthermore, their study provided additional support for the importance of modules for network complexity and stability.

QUANTIFYING NETWORKS: WEIGHTING LINKS AND NODES

Virtually, all early FWs were binary networks that only depicted the presence or absence of feeding links (Hall & Raffaelli 1993). This method of depicting networks as nodes joined by lines remained largely unchanged for more than a century, since Camerano's first such graphical depiction of a FW in 1880 (Camerano 1880; Dunne 2005). This lack of quantitative data has long been recognized as a weakness in food web ecology, as not all species and interactions are equally important (Paine 1980; Benke & Wallace 1997).

The pioneering works of May (1972, 1973) mentioned, almost in passing, that weak interaction strengths tended to stabilize local community dynamics. This significant theoretical prediction was largely ignored in the ensuing complexity–stability debate. Several key studies in the 1990s however, such as Paine's (1992) experimental measurement of interaction strengths and McCann, Hastings & Huxel (1998) models, facilitated a rapprochement between the two camps, as they revealed the prevalence of weak interactions in nature (de Ruiter *et al.* 1995; McCann *et al.* 1998; Berlow 1999; McCann 2000; Kokkoris *et al.* 2002). The advent of increasingly quantified webs allowed these ideas on the importance of link strength to develop and the current consensus is that interaction (link) strength plays an important role in stability, with many weak and few strong links leading to stable, but potentially complex webs (Polis 1998; McCann 2000). However, this is only part of the story. More recently, the focus has shifted away from the *magnitude* of complexity and the strength of interactions *per se* towards the importance of the specific *configuration* of weak and strong links (Bascompte *et al.* 2005; Bascompte, Jordano & Olesen 2006; van Veen *et al.* 2006; Neutel *et al.* 2007). The recent work of Neutel *et al.*

(2007), for instance, has revealed the role of 'loop lengths' (where a loop is defined as the 'pathway of interactions from a certain species through the web back to the same species without visiting other species more than once': Neutel, Heesterbeek & de Ruiter 2002), embedded within complex networks, as important determinants of stability.

Across all network types, interactions are now increasingly being quantified (Bersier, Banasek-Richter & Cattin 2002; Woodward *et al.* 2005b; Blüthgen *et al.* 2007). This is clearly an important advance, but there is a huge array of measures and definitions of 'interaction strength' in current use that differ depending upon the questions asked and the system considered (Berlow *et al.* 2004). In addition, it is not yet clear whether these different measures describe similar phenomena: only a few studies have used more than one simultaneously, and while some have demonstrated consistent relations among different metrics (Woodward & Hildrew 2002d; Albrecht *et al.* 2007; Tylianakis *et al.* 2007), others have shown no pattern, or even negative correlations between metrics (e.g. Woodward *et al.* 2008). Clearly, we need to increase the sample size of quantified networks and to make multiple, simultaneous measures of interaction strength within and among systems in future research.

In summary, there is an emerging trend to abandon the 'random network' approach pioneered by May in the 1970s. Ecological networks are anything but randomly structured, as revealed by at least partially predictable trajectories of change in response to stressors (Raffaelli 2004), the ubiquity of nonrandom distribution of links and their strengths, and the observation of recurrent, recognizable modules and 'small-world properties'.

NETWORK ASSEMBLY AND EVOLUTIONARY CONSTRAINTS

Current patterns of network complexity reflect both evolutionary and ecological constraints (Olesen & Jordano. 2002; Cattin *et al.* 2004; Montoya *et al.* 2006; Petanidou & Potts 2006; Stang *et al.* 2006; Waser 2006; Bascompte & Jordano 2007; Blüthgen *et al.* 2007; Rezende *et al.* 2007). For instance, taxa that are closely related are also likely to occupy similar positions within a network (Cattin *et al.* 2004). Furthermore, many of the seemingly specialist interactions among organisms such as plants and their pollinators, and hosts and their parasitoids, have long been believed to be a consequence of co-evolution among partners (e.g. Pasteur 1982). However, this view may be biased by studying 'interesting' groups of species that fit preconceived ideas of co-evolution. It has been proposed that plant–pollinator interactions are more generalized than previously thought (Waser *et al.* 1996) and recent developments have challenged the view of strong pairwise co-evolution among plants and pollinators (Waser 2006). The application of network theory is now providing us with opportunities to move away from pairwise comparisons and to start searching for the existence of network-wide patterns of species dependences. Intriguingly, however, Olesen *et al.* (2007) showed that in at least some networks,

there was evidence of co-evolutionary modules represented by specific groups of plants associated with pollinating insect families.

These new patterns are challenging current network models to incorporate evolution, by changing mutation rates and altering the initial level of diversity of species genotypes. A new generation of models are appearing in which species composition and links can evolve over time (e.g. Bell 2007). Some broad topological patterns, for example, link-species richness relationships, and the predominance of weak interactions, have been reproduced using these novel techniques. Critically, from a network perspective, some of these models use the individual as the unit of evolution and selection. This individual-based approach is also starting to permeate much of the more recent research in ecological networks.

APPROPRIATE LEVELS OF ORGANIZATION: SPECIES AVERAGES OR INDIVIDUALS?

In almost all ecological network studies published to date, nodes and links represent average traits of species (or trophic species) and their interactions, respectively. In quantified networks, nodes are usually expressed in terms of population abundance (numerical or biomass) or, increasingly, body size (e.g. Brose *et al.* 2005, 2006). While this type of approach has been very productive in terms of developing theory and exploring macro-ecological patterns (Cohen *et al.* 1993; Hall & Raffaelli 1993), potentially important information is lost by the process of averaging species data, thereby increasing the risk of introducing artefacts (e.g. see Cohen *et al.* 2005).

Body size distribution patterns within food webs provide an excellent example of the potential pitfalls of species averaging. Many important species traits are allometrically scaled (often following quarter power laws), and consequently body size may be used as a convenient means of summarizing these into a single metric (Cohen *et al.* 1993; Mulder *et al.* 2005, 2006; Woodward *et al.* 2005a). When using species averaged data, body size distributions of many food webs do not conform exactly with the perfectly nested hierarchies predicted by traditional cascade models (e.g. Cohen & Newman 1985). 'Niche-based' models that relax these hierarchical constraints are often better representations (e.g. Williams & Martinez 2000). The philosophical problem with many of these latter models is that although they may capture the characteristics of the network, they are phenomenological, and require input parameters such as species richness or connectivity, rather than mechanistic, and we may ask, why should the hierarchy be relaxed to better fit the data?

One of the principal relaxations in these niche models is that species can feed to a limited degree on taxa above them in the hierarchy. If, for instance, we consider body size to be the determinant of trophic status, this would equate to predators eating species larger (on average) than themselves. This seems somewhat counterintuitive, but it is evident in many species-averaged webs (Diehl & Feissel 2000), and the prevalence of mutual predation (e.g. *a* eats *b* eats *a*) and cannibalism seems to undermine the cascade model and lend support to

relaxed-niche models. Much of this arises due to life-history omnivory and ontogenetic changes within nodes in the network. As an individual grows, it can shift from being a prey to being a predator of other species, and reversals in trophic status often arise when generations overlap, so that large individuals of 'small' species feed on small individuals of 'large' species (Woodward & Hildrew 2002a). Indeed, extreme life-history omnivory is one of the reasons why so few marine 'food webs' are available in the familiar form of node-and-link networks, as it is almost impossible to define a species as a discrete node. Consequently, trophic interactions are often inferred from the use of size spectra, whereby individuals are divided into log-bins based on their body size rather than species identity. This approach has revealed clear size structuring in marine fisheries, but a relatively weak effect of species *per se* (Jennings, De Oliveira & Warr 2007; Barnes *et al.* 2008).

If we take a step back at this point and consider nodes as distributions of individual data, rather than fixed singularities, then it seems plausible that the earlier cascade models may, after all, be more appropriate if we order the feeding matrix at the individual level: that is, the 'relaxation' of the hierarchy in the niche models might be simply capturing an artefact of species averaging. Woodward & Warren (2007) demonstrated this when they compared the distribution of body mass ratios in a food web with species-averaged feeding links and the same web with all individual feeding links. They found that the predator-prey body mass ratio increased by an order of magnitude by switching from a species-averaged web to one based on individual feeding events (i.e. the level of organization at which trophic interactions actually occur). This revised version of the web showed a clearer, more cascade-like hierarchy based on individual body mass (Fig. 4). Is it possible that other niche-based models are also describing mirages associated with artefacts derived from averaging data within nodes, rather than focussing on the individuals that are interacting within links? At present, very few data exist with which to test this more rigorously, and the Broadstone Stream food web is, to the best of our knowledge, currently the only system within which this has been carried out for a whole network. A new large, global data set from marine systems (Barnes *et al.* 2008) could help in this pursuit, although because it is based on ingested individuals it may be difficult to extrapolate to include data on those members of a population that are not interacting (i.e. the data include only realized links). As more individual-based food web data emerge, it would be insightful to re-examine some of the simpler cascade models. The effects of species averaging might also represent a problem for both MWs and HPWs, where some species show highly plastic behaviour that differs among individuals and over ontogeny.

THE ROLE OF BEHAVIOUR: FORAGING WITHIN ECOLOGICAL NETWORKS

Behaviour is beginning to be recognized as playing an important role within ecological networks (Beckerman, Uriarte & Schmitz 1997; Schmitz, Beckerman & O'Brien 1997; Luttbegg

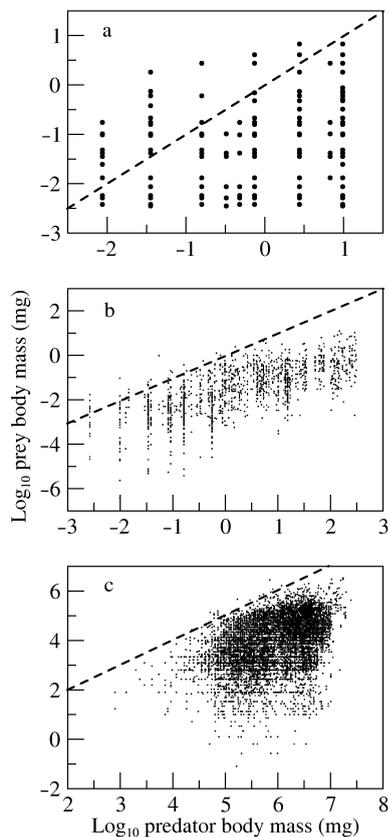


Fig. 4. Body-size determinants of predator–prey interactions in aquatic FWs. The three panels show the species-averaged feeding matrix for Broadstone Stream (a), the same data expressed for individual-based data (b) and individual-based data (c) extracted from a large marine data set (data from Barnes *et al.* 2008).

& Kerby 2005; Preisser, Bolnick & Benard 2005; Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008). For instance, prey species often show behavioural responses to the presence of predators, such as avoidance or reduced activity and feeding rates (Sih 1993; Werner & McPeck 1994; Sih, Englund & Wooster 1998; Suttle 2003; Heithaus *et al.* 2007; Wirsing, Heithaus & Dill 2007). In addition, predator behaviour, such as preferential targeting of prey species via microhabitat specialization and/or the development of searching images, will alter the strength of interactions within the network (Beckerman *et al.* 1997; Preisser, Orrock & Schmitz 2007; Schmitz 2008). The effects of behaviour are, of course, not restricted to predator–prey interactions in FWs. Within MWs, flower visitors can exhibit specialist behaviour when collecting pollen but generalist behaviour when collecting nectar (Waser *et al.* 1996). These inconsistencies could have consequences for measuring interaction strength, especially for plants. The ‘quality’ of an interaction between a flower and its visitor will depend on the behaviour of the latter, both before and after it visits the flower. Plant female success depends on conspecific pollen being deposited on the stigma (ideally from an unrelated flower), so a pollinator specializing on one flower species for pollen could represent a strong

interaction relative to one which is collecting nectar and less constant on any given flower species. In this respect, visitation webs may give an inaccurate impression of quantitative interactions.

Furthermore, many pollinators may be generalists at a colony or population level but specialists that show a high level of floral constancy at the individual level (Waser 1986; Cakmak & Wells 1994; White, Cribb & Heard 2001). This individual versus population niche breadth question undoubtedly applies to many network types but, again, data are still scarce. Also, individual sampling is often destructive, but developments in miniaturized electronic transponders (e.g. PIT tags) allow repeated tracking and sampling of individuals (via nondestructive gut flushing).

Incorporating individual behaviour into ecological network models gives us the opportunity to explore the mechanisms that control network structure and to move forward from solely phenomenological approaches. Beckerman *et al.* (2006) and Petchey *et al.* (2008) have paved the way by showing that individual diet breadth models from foraging theory can be used to predict the connectance of real food webs (used in niche models as an input parameter rather than an outcome), and its relationship to species richness. By extending these models, it should be possible to explore the effects of individual behaviour in a wide range of systems, and, perhaps, allow us to identify specific behavioural traits that might constrain the structure of different network types. Petchey *et al.* (2008) recently incorporated body size into the foraging approach of Beckerman *et al.* (2006) to produce a deterministic model that could predict up to 65% of the links present in real food webs. However, the model only worked well with size-structured FWs: further refinements, notably the inclusion of non-size-related traits, may be needed to better predict the structure of HPWs and MWs. It also seems likely that the truly individual-based food web data that are appearing on the horizon will improve the predictive power of these models still further, since both theory and data will be using the same level of organization.

NETWORKS IN THE REAL WORLD: GLOBAL CHANGE AND THE SIXTH MAJOR EXTINCTION

Ecological networks now provide an appropriate framework to explore the possible effects of global change and biodiversity loss on communities and ecosystems. Established and newly described networks are being used to examine the effects of perturbations arising from human-induced environmental change. For example, acidification of freshwaters has dramatic effects on network size and structure, yet these systems still manage to retain at least part of their ecosystem functioning, perhaps due to redundancy in the FW (Ledger & Hildrew 2005; Woodward 2008). Habitat loss in rainforests, for instance, often affects large predators first, triggering cascading indirect effects that alter the composition and biomass of the plant assemblage (Terborgh *et al.* 2001; Solé & Montoya 2006). Now, several exciting manipulative experiments are being carried out to quantify changes in network

metrics and configuration in relation to environmental perturbations (e.g. Fontaine *et al.* 2006). So far these studies seem to support inferences made from earlier observations from natural food webs, and experiments in laboratory cultures (e.g. Petchey *et al.* 1999). A recent long-term field experiment (Ledger *et al.* 2008; M.E. Ledger, F. Edwards, L. Brown & G. Woodward, unpublished data) on the effects of hydrological disturbance on replicated artificial stream FWs revealed significant species loss (mean n species decreased from 65 to 50), changes in the dynamics of basal taxa (Ledger *et al.* 2008) and shifts in network structure (e.g. n links decreased > 50%). Secondary production fell by almost half an order of magnitude as species were lost and resistant/resilient species remained at reduced abundance. Although no comparable manipulative experiments have been carried out on terrestrial systems, a comparison of HPWs across a habitat disturbance gradient (agricultural intensification) showed, in contrast to the freshwater FWs, little effect on species richness but strong effects on interaction strength and ecosystem functioning (Tylianakis *et al.* 2007). This suggests the patterning of interaction strength might lead to dynamical instabilities, eventually resulting in loss of biodiversity. At this stage, it is not possible to determine whether these differential responses relate to habitat, ecosystem, or network type. We need more manipulative studies on comparable systems to determine whether generalities or contingencies are the rule here.

An ecological network approach can also be invaluable for assessing the potential impacts of invasive species (e.g. Henneman & Memmott 2001). Individual species comparisons often reveal negative impacts of invasive plants on the reproductive success of native plants (Chittka & Schurkens 2001; Bjercknes *et al.* 2007), yet analysis of the whole pollination network for habitats invaded by the same plant species (*Impatiens glandulifera*) have shown increased visitation rates to native plants (Lopezaraiza-Mikel *et al.* 2007). Similarly, Bartomeus, Vilà, & Santamaría (2008) found that while invasive plants become super-generalists, this was only translated into competition for pollinators with native species in one of two cases. In the other case, the invader plant facilitated the visit of pollinators to native plants. However, alien pollen can dominate the network (Lopezaraiza-Mikel *et al.* 2007) and behaviour of individual pollinators carrying this pollen will be important, that is, do they transfer alien pollen to native flowers and clog their stigmas? Recently, more subtle, but potentially important, impacts of alien plants and pollinators on network structure have been detected (Aizen, Morales & Morales 2008). In invaded networks, overall network connectance remained unchanged, but connectivity among native species declined. Conversely, in a species-poor, yet reticulate stream FW, the invasion of a new top predator had little impact on the abundance of most prey species, even though connectance increased markedly (Woodward & Hildrew 2001).

An alternative way to investigate the effects of environmental change on communities is to apply ecological network techniques to long-term or palaeoecological data. For instance, it is possible to reconstruct ancient aquatic communities from fossil records contained in sediment cores, and to use these

data to infer past environmental conditions (Roopnarine 2006). Furthermore, by cross-referencing these communities with similar contemporary systems, it may be possible to infer 'palaeo-food webs' and, by extension, to track network responses to long-term environmental change (R. Rawcliffe, C. Sayer, J.I. Jones, J. Grey & G. Woodward, unpublished data). Such data could be vital to investigate the link between network structure and the stability of natural systems over temporal scales that reflect population level responses. This would provide a more mechanistic, and therefore predictable, explanation for the catastrophic shifts in structure modelled at an ecosystem level by Scheffer and co-workers (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; van Nes, Rip & Scheffer 2007). Given the potentially widespread occurrence of such dramatic shifts (Scheffer *et al.* 2001), this understanding is likely to be invaluable for predicting the impacts of future anthropogenic impacts. Using such an approach to extend the temporal scale of change in network structure in systems (other than lakes) with good preservation of biological remains (e.g. insects and pollen) or long-term data has the potential to provide important cross-system comparisons.

Ecological network theory could also stimulate a revision of many current conservation strategies by shifting the emphasis away from charismatic species towards a more holistic perspective, where both species and links matter (Tylianakis *et al.* 2007). Occasionally, conservation efforts have coincidentally (perhaps from expert knowledge of the systems) targeted 'keystone' species, whose loss can cause cascading effects (e.g. Pimm 1980; Solé & Montoya 2001; Dunne *et al.* 2002; Srinivasan *et al.* 2007). In fact, many rare species may not be fundamental for other species to persist: their impacts are most likely to be important when they are large and/or high in the FW. Topological keystones whose removal may promote a cascade of secondary extinctions, are well-connected species within the network, and probably relatively abundant at their trophic level are unlikely to be lost naturally, providing a high level of homeostasis (reviewed in Montoya *et al.* 2006). As well as conserving rare species, conservationists are increasingly advocating the re-introduction of extinct species (e.g. Wilson 2004), making an understanding of the recipient ecological networks, we believe, an essential prerequisite. For instance, over 20% of the Tuesday Lake species turned over following a manipulation of the higher predators, although the overall trivariate structure of the web was retained (Cohen *et al.* 2003). This suggests that body mass-abundance scaling relations, for instance, can be highly conserved in the face of dramatic species change (but see Mulder *et al.* 2005, 2006). In contrast, FWs in many marine fisheries have been perturbed so severely by selective harvesting of large individuals on an industrial scale that 'natural' body mass-abundance scaling has been disrupted (Jennings *et al.* 2007).

LIMITATIONS OF ECOLOGICAL NETWORKS: COMPLETENESS, RESOLUTION AND EFFORT

One of the major criticisms of early FWs was that they generally had poor and taxonomically biased resolution (Paine

Table 1. Comparative network statistics displaying the recent improvements in resolution and completeness in networks published in the last five years

System	Source	Type	S	L	N	M
Tuesday Lake	Cohen <i>et al.</i> 2003	FW	50–51	236–264	✓✓	✓
Broadstone Stream	Woodward <i>et al.</i> 2005b	FW	34	170	✓✓	✓
Bere Stream	Woodward <i>et al.</i> 2008	FW	142	1383	✓✓	✓
Selbrigg Pond	Rawcliffe <i>et al.</i> unpublished	FW	83	839	✓✓	✓
Felbrigg Hall Lake	Rawcliffe <i>et al.</i> unpublished	FW	64	424	✓✓	✓
Weddell Sea	Jacob <i>et al.</i> 2005	FW	489	16 200	✓	✓
Arctic Streams	Parker & Huryn 2006	FW	42–47	188–238	✓✓	✓
Mill Stream Channels	Ledger <i>et al.</i> 2008; unpublished	FW	84–88	422–574	✓✓	✓
Terrestrial FWs	van Veen <i>et al.</i> 2008	FW	13	61–83	✓	–
Plant – herbivore	Blüthgen <i>et al.</i> 2006c	FW	86	75	✓	–
Plant – herbivore	Blüthgen <i>et al.</i> 2006b	FW	52	55	✓	–
Pollinator networks	Blüthgen <i>et al.</i> 2007	MW	22–770	30–1206	✓	–
Seed disperser networks	Blüthgen <i>et al.</i> 2007	MW	25–252	46–659	✓	–
Ant/hemipteran network	Blüthgen <i>et al.</i> 2006c	MW	120	158	✓	–
Ant/hemipteran network	Blüthgen <i>et al.</i> 2004	MW	20	22	✓	–
H-P networks	van Veen <i>et al.</i> 2008	HPW	12–17	20–42	✓	–

S is the number of nodes in the network, L the number of links, N is a measure of abundance for each node and M denotes a measure of (usually mean) body mass for each node. For N, ✓ represent estimates of relative abundance (e.g. nos. of prey predator⁻¹, relative visitation rates in MWs etc.) and ✓✓ represents measures of absolute abundance (e.g. nos. m⁻² or nos. m⁻³).

1988; Cohen *et al.* 1993; Hall & Raffaelli 1993), with greater effort directed at the higher trophic levels than at the base of the web. However, in HPWs these asymmetries are not so evident because most nodes are resolved to species, although the limitation is that many focus on restricted host assemblages (e.g. sap feeders or leaf miners).

Clearly, inconsistent taxonomic resolution can impair cross-network comparisons, especially if we are looking for patterns in binary metrics, such as connectance and nestedness (Paine 1988). This potential problem remains largely unresolved and needs to be tested rigorously with empirical data (Montoya *et al.* 2006): this is now feasible due to the greater number of high-resolution networks available (Table 1). Several aquatic FWs, for instance, have resolved basal resources such as diatoms to species (Schmid-Araya *et al.* 2002; Figueroa 2007; Woodward *et al.* 2008), and studies on HPWs (van Veen *et al.* 2008) and MWs (Knight *et al.* 2005) are also starting to consider the wider community FW by including predators and pathogens.

Related to this taxonomic resolution issue is the practice of aggregating (often unrelated) taxa with similar feeding links into ‘trophic species’, especially in FWs (e.g. Martinez 1992; Williams & Martinez 2000). Although there are a number of arguments for using trophic species, such as reducing possible biases due to undersampling of poorly resolved links (e.g. Martinez 1992; Dunne *et al.* 2002), there is a danger that important interactions are overlooked and key patterns are disguised (Montoya *et al.* 2006). In networks where trophic species are delimited *post-hoc*, it seems wasteful to discard information already gathered, especially as species populations are discrete non-interbreeding entities with their own dynamics. Conversely, in situations where lumping is

performed a priori, there is a risk of introducing circularity in our descriptions of network structure.

It has often been argued that aggregating into ‘trophic species’ is useful when the objective is to explore fluxes of energy or nutrients in a mass-balance approach (e.g. after Lindeman 1942), whereas from the Eltonian (1927) perspective, where the network consists of reproductively isolated and distinct species populations, this approach is of questionable validity. For example, the taxa within a trophic species will interact differently with the constituent taxa subsumed within other trophic species. Consequently, there are strong reasons for treating trophic species cautiously, and we suggest that the best practice here should be to avoid lumping wherever possible, but where deemed insightful, published networks using trophic species should also include links to the fully resolved taxonomic data from which they were derived (e.g. in online appendices).

A recent advance in ecological network studies is the increasing sampling effort put into constructing more ‘complete’ webs (Table 1). This differs from taxonomic resolution *per se*, in that it relates to how well the whole community and its interactions have been characterized: that is, what proportion of a network’s total complement of nodes and links has been detected. Sampling effort can have especially strong effects on certain network metrics, such as web size and connectance (Goldwasser & Roughgarden 1997), whereas others, such as nestedness, appear to be more robust (Banasek-Richter, Cattin & Bersier 2004; Nielsen & Bascompte 2007). In an effort to account for some of the biases caused by sampling effort, Cohen *et al.* (1993) suggested that yield-effort curves (Fig. 5), showing the number of links as a function of cumulative sampling effort, should accompany all published FWs.

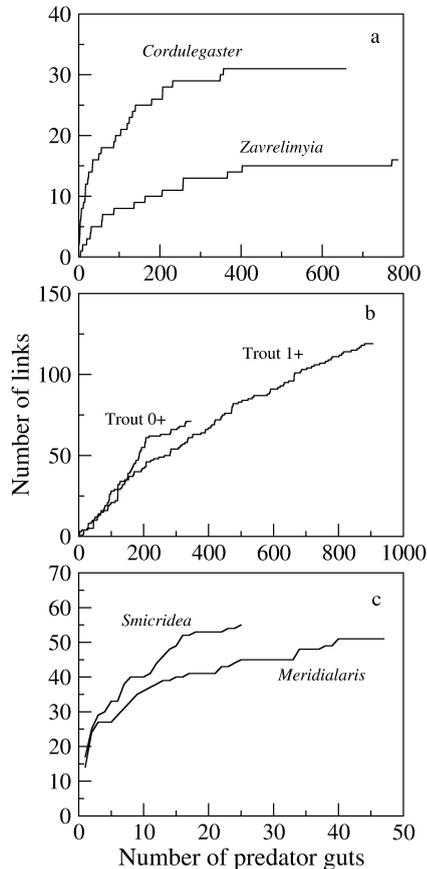


Fig. 5. Yield-effort curves for consumers in three different stream food webs, (a) Broadstone Stream, (b) Tadnoll Brook and (c) a Chilean stream. In (a) the top predator, *Cordulegaster boltonii*, and smallest macro-invertebrate predator, *Zavrelimyia barbatipes*, are shown; in (b) two cohorts of the top predator, brown trout (*Salmo trutta*) are shown; in (c) two macro-invertebrate species, a herbivore, *Meridalaris diguillina*, and an omnivore, *Smicridea chilensis* are shown (Figuroa 2007). These data reveal that the sampling effort required to fully characterize consumer diets varies among food webs and also among consumer species and size classes within webs.

While this advice has been followed by some authors (e.g. Woodward *et al.* 2005b), it is still very much the exception rather than the rule. Even when yield-effort curves are presented, they often show links pooled across the whole network (Martinez *et al.* 1999), even though different levels of sampling are necessary for different trophic levels, taxa and even life stages of certain taxa (Woodward *et al.* 2005b).

Network completeness also relates to the a priori definition of the network: for example, HPWs tend to ignore predatory 'FW' interactions. This narrowly focused approach is likely to miss important interactions, such as those mediated via apparent competition. Indeed, apparent competition has recently been revealed in more complete HPWs that have included predators and pathogens (van Veen *et al.* 2008). It would be insightful to compare the effects of sampling effort across (and within) different network types so that we can better identify robust metrics and standardization procedures for cross-system comparisons.

While we have good data on component networks (FWs, MWs and HPWs) within ecosystems, these are still viewed in isolation (but see van Veen *et al.* 2008). Clearly, such networks will overlap and interact with each other, and the same species can be a seed-disperser in the MW and a herbivore in the FW. Even within network types, certain species can act as bridges between seemingly disconnected ecosystems. Large, mobile predators with extensive home ranges can connect otherwise spatially segregated FWs (Woodward & Hildrew 2002c), and there is a strong theoretical basis for the stabilizing effect of such linkages (McCann 2000; Raffaelli 2004; Rooney *et al.* 2006). A very small number of pioneering studies (Nakano & Murakami 2001; Knight *et al.* 2005) have attempted to explore linkages between different network types and ecosystems, but we still have a long way to go and the logistics are challenging.

While considering network completeness, we cannot ignore the additional potentially confounding effects of seasonality and spatial sampling. Networks may be more completely described when abundances are highest, which in many webs will be in the summer months (e.g. Woodward *et al.* 2005b). For example, this is especially marked in plant-pollinator networks, as there is dramatic variation in plant and pollinator abundance and richness throughout the year. Pooling across seasons can overcome some of these sampling issues, but it introduces additional biases in network metrics. Basilio *et al.* (2006) showed that connectance in a plant-pollinator network can change dramatically through the seasons, with cumulative connectance (calculated as *all* interactions registered in the community divided by complete network size) greatly underestimating maximal seasonal connectance (by up to three times). Similar effects are likely in other network types (e.g. freshwater FWs: Closs & Lake 1994; Tavares-Cromar & Williams 1996; Woodward *et al.* 2005b) and need to be carefully considered when carrying out cross-network comparisons. Furthermore, both plant and pollinator distributions are spatially patchy (Waser *et al.* 1996), as are predators and prey within FWs (Woodward & Hildrew 2002b) and hosts and their parasitoids within HPWs (Hawkins 1994). Finally, pollination webs are plant-focussed, that is, they report the flower visitors on a given set of plants in the field. The alternative, complementary, and technically even more challenging approach of studying pollen in nests of different pollinators may give a rather different picture of the pollination web.

Rare species can also influence completeness and network metrics (Blüthgen *et al.* 2008) and although the use of trophic species may downweight their influence, this creates problems of its own (see above). Another obvious way of dealing with rare species is to omit them altogether (e.g. Woodward & Hildrew 2001), but the thresholds used are likely to differ within and across networks. Both these approaches also run the risk of masking true specialist interactions. A recent approach to overcome these issues is to include rare species but remove the potentially confounding effects of abundance by using the residuals from null models based on information theory (Blüthgen *et al.* 2006a, 2007), enabling the degree of

Table 2. Suggested 'dead ends' and alternative 'fruitful avenues' for future research in ecological networks

	'Dead ends'	'Fruitful avenues'
Aggregation		
a) Classification	'Trophic species' networks	Individual-based and trait-based networks
b) Interaction types	HPW/FW/MW single-layer networks	Integrated HPW + FW + MW multi-layer networks
Network metrics	Magnitude of complexity (e.g. connectance) Binary networks	Magnitude and configuration (e.g. link distributions; loop lengths) of complexity Quantitative networks
Perturbations	Isolated, unreplicated case studies	Networks along natural gradients (e.g. climate, nutrients, pH); manipulative experiments of whole networks
Scale		
a) Temporal	Intragenerational, short-term studies	Long-term studies (e.g. intergenerational studies; palaeo networks)
b) Spatial	Small-scale studies	Local-to-regional networks; cross-ecosystem networks
Models		
a)	Phenomenological models	Mechanistic models based on first principles (inc. neutral models)
b)	Pattern-fitting models	Predictive models
c)	Static models	Evolutionary and assembly models
d)	Modules within the network	Whole network models

specialism to be compared more reliably across network types. Of course, many of these issues related to completeness dissipate when nodes and links are quantified, as binary 'presence-absence' webs are particularly sensitive to the effects of sampling and taxonomic resolution, whereas quantification places greater emphasis on the main players (e.g. Benke & Wallace 1997; Woodward *et al.* 2005b).

FUTURE DIRECTIONS: 'FRUITFUL AVENUES' AND 'DEAD ENDS'

We have identified what, in our view, represent the principal areas in which research activity is likely to be particularly fruitful in the future, and areas in which significant progress is much less likely (Table 2). In essence, we are advocating moving away from phenomenological studies and moving towards those that are more mechanistic and, ultimately, predictive. Part of this shift in emphasis necessitates experimental manipulations of entire networks (e.g. Fontaine *et al.* 2006), rather than relying on inferential data, as we have carried out to date. We also stress the need to use more realistic yet simple models (e.g. networks with large numbers of species) and to collect more quantitative network data, rather than pursuing the simplistic presence-absence approach that has dominated the field for decades.

The study of ecological networks currently lacks a strong, unifying theoretical framework, and the need for a more mechanistic understanding is pressing, as many current models, especially those describing network topology (e.g. Cohen & Newham 1985; Williams & Martinez 2000), have no predictive power. A notable exception is the recent model of Petchey *et al.* (2008), which uses foraging theory (FT) to predict web structure based on body size. The metabolic theory of ecology (MTE) proposed by Brown *et al.* (2004) also offers

a potentially new framework that can be applied across multiple levels of biological organization. MTE is based on first principles of kinetics and stoichiometry and focuses on the effects of body size and temperature on basal metabolic rate, that is the power required to sustain an individual organism. A critical feature of MTE is that it incorporates mechanistic models that predict how the metabolism of individuals affects the dynamics and structure of populations, communities and ecosystems. The seminal, but still controversial, paper of Brown *et al.* (2004) outlined how the consequences of allometric scaling laws for individuals, such as the three-fourth power law relationship between body mass and metabolic rate, ramify to more complex systems, including food webs. This power law relationship arises, its proponents argue, because of the fractal branching properties of biological supply networks which ultimately end in termini of similar diameter (e.g. capillaries for animals). Recently, these ideas have been extended and explored more explicitly within the context of ecological networks, in particular to estimate interaction strengths between consumers and their resources (e.g. Emmerson, Montoya & Woodward 2005; Woodward *et al.* 2005a; Otto *et al.* 2007; Yvon-Durocher *et al.* 2008). Importantly, the use of MTE may reduce the number of variables of future realistic models of ecological networks, because many might be correlates of the same constraints imposed by metabolism, body mass and temperature.

The MTE was also used by Brown *et al.* (2004) to derive an equation for the exponent of the abundance-body size power law relationship. This approach implicitly assumed equilibrium populations existed but without considering the population dynamics driving them. Lewis, Law & McKane (2008) have since shown that a similar relationship is derived in simple FWs if population dynamics are explicitly considered and parameterized using simple body size assumptions and

metabolic scaling rules. Intriguingly, there is a suggestion that the more generalist networks, especially aquatic and soil FWs, are largely driven by body size and metabolic constraints (de Ruiter *et al.* 1995; Emmerson & Raffaelli 2004; Mulder *et al.* 2005; Woodward *et al.* 2005a), and many of these webs also have an important detritivore component. Co-evolution, and perhaps behaviour, may well play a far stronger role in autotrophic-based, above-ground terrestrial herbivore–plant webs, MWs and HPWs (Olesen *et al.* 2007).

We suggest that a new, individual-based perspective, which will enable us to incorporate ideas from the MTE and foraging theory (e.g. Petchey *et al.* 2008), offers a potentially fruitful way to develop a more mechanistic, and hence predictive, understanding of ecological networks. If this is combined with experimental manipulations of whole networks, responses to perturbations can be used to test theoretical predictions explicitly, rather than relying on the weaker inferential evidence that currently dominates the field. Furthermore, if we can strengthen our mechanistic understanding of networks, we will be better placed to identify instances where they manifest seemingly ‘emergent’ properties that arise spontaneously, as in other complex networks. For example, trophic pyramids in food webs may emerge from simple constraints on the growth rates of individuals of different body mass.

Extending this line of reasoning, it seems reasonable to suggest that novel individual-based approaches using FT and MTE could be used to predict network-level responses to environmental stressors. Undoubtedly, one of the most pressing concerns on a global scale is that of climate change, but most research in this field has focussed on the lower levels of organization (e.g. range shifts in species populations). The MTE is potentially useful here because it is based on individual metabolism, which is itself correlated with body size and, importantly, temperature (Peters 1983; Brown *et al.* 2004). Specifically, MTE predicts metabolic rates scale with individual body mass and is corrected for environmental temperature, T , via $e^{-E/kT}$, where E is the activation energy of metabolism and k is the Boltzmann factor (e.g. Brown *et al.* 2004). As such, MTE offers a promising framework to assess the effects of environmental warming. Similarly, much of FT (Beckerman *et al.* 2006; Petchey *et al.* 2008) is based on size-related interactions between individuals (e.g. size-dependent handling times). Therefore, both MTE and FT require a new individual, size-based network approach – unfortunately very few food webs have yet been constructed in this way (but see Woodward & Warren 2007; Barnes *et al.* 2008), highlighting the need to do so in future studies. We suggest that such a novel approach is ideally suited to developing a mechanistic basis for predicting the consequences of climate change, which could be tested experimentally (e.g. using artificially warmed mesocosms). A further advantage of characterizing networks from an individual perspective is that we can then test the relative importance of species versus size and the robustness of network patterns defined by each. This could then provide a means by which we might escape from the ‘curse of the Latin binomial’ (Raffaelli 2007) and consider

new size-based methods for describing networks: that is, is it possible to finally abandon the pervasive species-centric view?

CONCLUDING REMARKS AND UNANSWERED QUESTIONS

The study of ecological networks has moved on substantially in the last few years. There has been a shift away from exploring the magnitude of complexity (e.g. numbers of species and their interactions) towards understanding the configuration of complexity (e.g. clustering and loop lengths), and from a phenomenological towards a more mechanistic approach. We now have a more sophisticated and effective toolkit for studying ecological networks than ever before and there are a number of important issues that need to be resolved in the coming years.

Some caution still needs to be exercised when considering general patterns in ecological network structure and dynamics. Much of the theoretical and empirical work on network properties, especially in FWs, still relies upon a relatively small number of well-defined networks, although this situation is improving rapidly. While the small sample size might be a problem in itself, a larger concern is that, perhaps out of necessity, the best-defined networks are usually from less-productive, species-poor habitats, thus potentially confounding network and system characteristics. We need to know if the recurrent patterns we see are general or contingent for such systems, which represent a tiny subset of the universe of ecological possibilities. Do the same relationships hold in more productive, species-rich networks? We need to broaden the current catalogue by including such systems and it appears that this gap in our knowledge is now starting to be addressed (Table 1).

Similarly, when comparing across network and habitat types, we need to consider whether any observed differences are habitat driven (e.g. freshwater vs. terrestrial) rather than system specific (e.g. predator–prey vs. herbivore–plant). It has been remarked for instance that headwater stream FWs bear some striking similarities to soil food webs, yet both differ profoundly from many HPWs (Woodward *et al.* 2005b). Many aquatic plants also require animal pollination (Haynes 1988; Harder & Barrett 1992; Patt *et al.* 1995; Lippok & Renner 1997), so are aquatic and terrestrial MWs comparable – and indeed interconnected?

There is a new impetus towards integrating the different approaches used to study ecological networks. Across all network types, we are now beginning to recognize the importance of the specific configuration of complexity and interaction strengths, such as the presence of modules and loops, and the distribution of weak and strong links. The new generation of well-resolved, quantified networks is also enabling us to move beyond describing species-averaged data and to start exploring the role of individuals. In so doing, we are becoming better placed to test general ecological questions, including those relating to FT and the MTE. The common currencies used in the latter (body size, metabolism, temperature and stoichiometry) may provide a unifying framework within which we can begin to address some of the more

specific questions raised above. Furthermore, integrating MTE with new models incorporating foraging behaviour and comparing them with neutral assumptions will provide us with exciting opportunities to explore the mechanisms behind the patterns that we see in ecological networks.

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