Review

Network analysis shining light on parasite ecology and diversity

Robert Poulin

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

The vast number of species making up natural communities, and the myriad interactions among them, pose great difficulties for the study of community structure, dynamics and stability. Borrowed from other fields, network analysis is making great inroads in community ecology and is only now being applied to host–parasite interactions. It allows a complex system to be examined in its entirety, as opposed to one or a few components at a time. This review explores what network analysis is and how it can be used to investigate parasite ecology. It also summarizes the first findings to emerge from network analyses of host–parasite interactions and identifies promising future directions made possible by this approach.

Parasites in a complex world

Referring to natural communities as complex systems has become almost a cliché. Their complexity results both from the large number of different species that exist within a community and from the diverse nature and unequal strengths of the interactions among them. Parasites are an integral and important component of natural communities, not only because they represent a substantial portion of the species diversity and biomass [1,2], but also because they can directly or indirectly alter the structure of the community by impacting the number of free-living species or their relative abundance [3,4]. The traditional approaches to study the impact of parasites on communities rely either on experiments or on mathematical modelling; the former is logistically challenging in the field, the latter rests on several simplifying assumptions, and both can only address interactions among a few species at a time. These are serious shortcomings that limit our understanding of how parasites influence the assembly, functioning and stability of communities and ecosystems. Determining why some ecosystems incur few secondary species losses following an extinction (robustness), or return quickly to their pre-extinction properties (resilience), is a key priority in biodiversity research [5] that can only be addressed with a whole-system approach.

Recently, network analysis has been used with increasing frequency for the study of parasitism in natural systems. Network theory has been applied successfully to explain and predict the spread of parasitic diseases through host populations via social or sexual contacts [6–9]. Here, it is its application to interactions among species, not individuals, which is reviewed. By considering all species within a system as a network of interconnected entities, network analysis is a more effective and holistic form of analysis than its predecessors [10–12]. It can be used to identify the structural attributes of particular host species (such as their connectedness to the rest of the food web) and determine their likely dynamic importance. Network analysis can also serve to identify recurrent coevolutionary units within a larger system, just as it can be used to predict how a community will respond to perturbations such as the addition of species via migration or invasion, or their removal following local extinction. This review synthesises recent findings from network analyses of host–parasite interactions and of entire food webs, and highlights the advantages and disadvantages of this approach for ecological parasitology.

Network analysis as a tool

Networks can be used to represent any type of relations between discrete objects [13,14]. The relations can be symmetric in that any object can act as both recipient and donor of whatever passes between objects, or asymmetric, when one-way relations exist between one subset of objects and another. Although originally a branch of applied mathematics derived from graph theory, network analysis is now used in diverse disciplines as a means to analyse phenomena consisting of relational data and to construct predictive models of these phenomena. Social scientists were quick to adopt network analysis as a research tool, using it for anything from cross-cultural comparisons of patterns of acquaintances and relationships among people (which gave us the phrase ‘six degrees of separation’), to studies of the growth of the World Wide Web [15,16]. In addition to investigations of ecological interactions [11,12], recent biological applications of network analysis include studies of the structure of metabolic pathways and gene regulatory networks [17].

Treating interactions between species as a network provides not only a visual representation of complex ecological systems (Box 1), but also a formal mechanism to measure attributes of particular species and whole-system properties, and how they change in space or time. Host and parasite species meet the basic requirements to be considered as interacting objects, or nodes, within a network: they are discrete, definable, and of scientific relevance [18]. Flows of energy characterizing trophic relationships among species, such as parasites and predators feeding on hosts and prey, respectively, are measurable interactions, or links, between network nodes. Together, nodes and links form a network topology that captures the passage of

---

Corresponding author: Poulin, R. (robert.poulin@stonebow.otago.ac.nz)

1471-4922/$ – see front matter © 2010 Elsevier Ltd. All rights reserved. doi:10.1016/j.pt.2010.05.008

Box 1. Networks for ecological parasitology

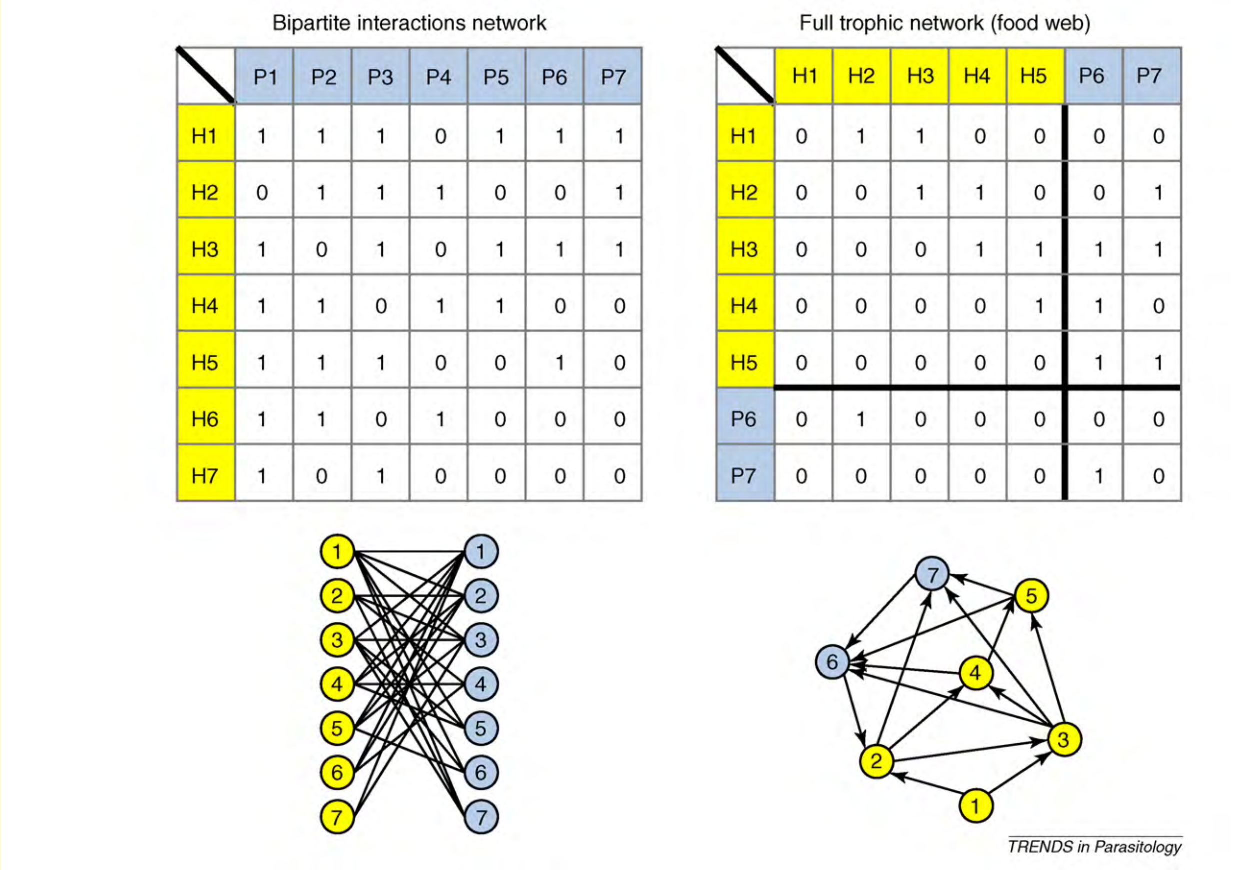
Networks are powerful tools to represent interactions among species and highlight their interdependence. In an ecological network, species are nodes, and the trophic connections between resources and consumers are shown as directional links between nodes. The network can be built from a species-by-species matrix of interactions, with consumers as columns and resources as rows. Binary entries (i.e. 1 or 0) in each cell of the matrix indicate whether or not a trophic link exists between two species. The most basic network property is its connectance, or the proportion of links realised out of all possible ones (in the matrix, the proportion of cells with a 1). Two types of networks are relevant for ecological parasitology:

Bipartite interaction networks

Particular sets of hosts and parasites can be identified within a community, corresponding to either taxonomic groups or ecological guilds, such as all helminth species parasitic in all fish species within a lake. A network can be used to illustrate host–parasite interactions between species belonging to the two different sets (Figure I), and to analyse the distribution of links among species of either set (host specificity in parasites, parasite species richness in hosts). Links between members of the same set, i.e. links between two host species or between two parasite species, are not permissible in a bipartite network. Bipartite networks then consist of P parasite species (columns) and H host species (rows), and their connectance is equal to L/PH, where L is the number of realised links.

Full trophic networks, or food webs

Food webs are depictions of existing trophic interactions among consumers, producers and non-living material. The topology of a food web indicates which species feed on which other species; it identifies all trophic links, including parasitism, and thus captures the paths along which energy and matter flow from one component of the community to another. The network considers all possible trophic interactions, and thus all species are included as both rows and columns; a link (i.e. a 1 in a matrix cell) indicates that the species in the column feeds on the species in the row (Figure I). The number of rows and the number of columns are therefore both equal to S, the number of species in the community. Free-living species include basal species that feed on no other species in the network (e.g. autotrophs such as algae) all the way to top predators. As proposed by Lafferty *et al.* [67], the full food web can be divided into four subwebs (Figure I). The first includes predator–prey interactions, the second includes host–parasite interactions, the third indicates which parasites act as prey for free-living species when, for example, the infective stages of trematodes are consumed by filter-feeders [76] or ectoparasites are eaten by cleaner organisms [77], and the fourth includes cases of parasites feeding on other parasites, as when the larval stages of certain trematodes consume those of other trematodes within the same snail intermediate host [78]. The connectance of the whole food web is equal to L/S^2, although it can also be computed for each subweb separately and should be calculated after exclusion of links that cannot conceivably occur.



Bipartite interactions network

	P1	P2	P3	P4	P5	P6	P7
H1	1	1	1	0	1	1	1
H2	0	1	1	1	0	0	1
H3	1	0	1	0	1	1	1
H4	1	1	0	1	1	0	0
H5	1	1	1	0	0	1	0
H6	1	1	0	1	0	0	0
H7	1	0	1	0	0	0	0

Full trophic network (food web)

	H1	H2	H3	H4	H5	P6	P7
H1	0	1	1	0	0	0	0
H2	0	0	1	1	0	0	1
H3	0	0	0	1	1	1	1
H4	0	0	0	0	1	1	0
H5	0	0	0	0	0	1	1
P6	0	1	0	0	0	0	0
P7	0	0	0	0	0	1	0

TRENDS in Parasitology

Figure I. Two types of interaction networks involving parasites shown in both matrix format (above) and as visual images (below). Parasite species are indicated by the letter P and shown in blue, and free-living species by the letter H and shown in yellow; an existing link is indicated by a 1 in the corresponding matrix cell, and by a connecting line in the image. In bipartite networks, the network displays associations between parasites (columns) and hosts (rows). In trophic networks capturing the whole food web, all species, whether free-living or parasitic, appear in both columns (consumers) and rows (resources), with realised links indicating which species are fed upon by each consumer; basal species, which feed on no other species in the community, are primary producers. The whole food web can be divided (thick lines in the matrix) into four categories of interactions: predator–prey interactions (top left), host–parasite interactions (top right), parasites serving as prey (bottom left), and parasites feeding on parasites (bottom right).

energy through the system. However, network analysis also requires that the set of nodes include all distinct entities that are capable of interacting [18]; in other words, an ecological network should include all species comprising the community under study. This can be achieved for communities with clear physical bounds, such as lake communities, but is problematic for 'open' communities in terrestrial or oceanic ecosystems. Inadequate sampling can also result in the possible exclusion of rare parasite species from many community data sets that would otherwise be well-suited for network analysis [19,20]. Another requirement of traditional network analysis has been that interactions be treated as a binary variable: there either is an interaction between two species, or there is not. This dichotomy is stretched in nature, where often interactions are seasonal (A feeds on B in summer, but not in winter) [21], and existing interactions vary in strength (A feeds on both B and C, but it feeds on B much more than on C). More sophisticated network analysis approaches can now take into account weighted links. Importantly, the temporal dynamics of networks and the proper time scale on which to study them must be taken into account to avoid misleading results. Too often, ecological networks are based on data collected over a relatively short time period, possibly misrepresenting what is really a dynamic network structure. With these caveats in mind, we can now examine what network analysis can tell us about the structure of host–parasite interactions and the general impact of parasitism on food webs.

Host–parasite interaction networks

Depending on the type of interaction, one can construct food webs, competitive or mutualistic networks, or even a mixture of these [22]. To maintain the focus on parasitic interactions, hosts and parasites in a community can be viewed as a bipartite network where interactions exist between species belonging to the two different sets, but not between species of the same set (Box 1). This approach has been extensively applied to mutually beneficial interactions such as those between plants and their pollinators or seed dispersers [23]. A look at any mutualistic network assembled from field observations is sufficient to dispel the misconception that coevolution leads toward specialized one-on-one interactions. Recurrent, almost universal, patterns emerge from studies of mutualistic networks. First, the vast majority of species in a network are specialists interacting with few other species, and a few species are generalists involved in many more interactions than expected from chance alone [23]. Second, mutualistic networks are nested, such that specialists interact with a proper subset of the group of species with which generalists interact [24–27]. Third, mutualist networks are often organized around a few modules, i.e. groups of species centred around a highly-connected 'hub' species and having many interactions among themselves but few with species in other modules [28,29]. Despite these common structural properties seen across various mutualistic networks, there remains much variation in their detailed architecture, explained in part by differences in patterns of relative species abundances among networks [30]. Nevertheless, network analysis has demonstrated that plant–animal mutualistic interactions are not randomly organized, and provides a tractable way of untangling their structural properties and what influences them.

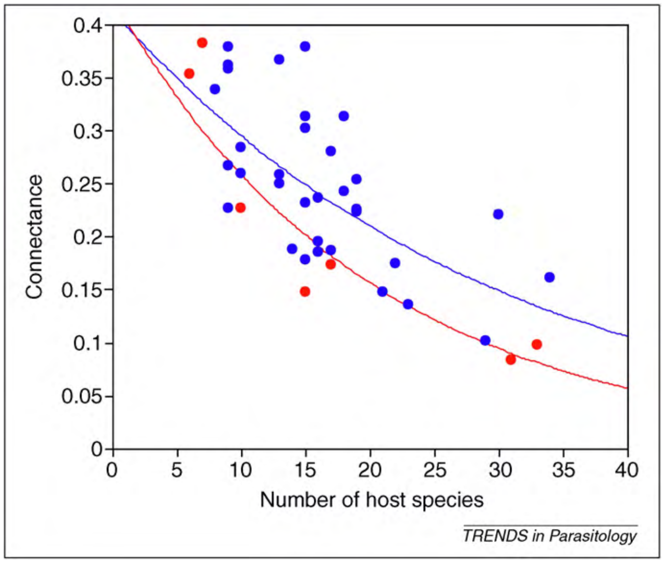


Figure 1. Exponential decrease in connectance, i.e. the proportion of realized links within a network, as a function of increasing host species richness. Each point represents a distinct local network of bipartite interactions between hosts and parasites. Data are from networks involving helminths that are fish parasites in seven Canadian bodies of freshwater (red, data from Ref. [31]), and networks involving fleas ectoparasitic on small mammals in 33 distinct regions of the Palaearctic and Nearctic (blue, data from Ref. [32]).

Network analysis is only beginning to be applied to host–parasite interactions. Already general relationships between network metrics are hinting at the way host–parasite communities are assembled. For instance, network connectance, which is the proportion of realized links within a network, decreases rapidly as a function of increasing network size, or the number of species in the network (Figure 1). This applies to networks comprising vastly different taxonomic groups of hosts or parasites [31,32]. Because all parasites show some degree of host specificity, not all possible links are realized, and this is more pronounced for species-rich networks. This might suggest that large networks can only accommodate new species if they are either host-specific parasites or hosts that are suitable to very few parasites. There is currently much effort put into understanding how network properties might determine the number of coexisting species [33], and network analysis can thus shed new light on how the diversity of parasites and diseases is regulated in natural ecosystems.

At a deeper structural level, other patterns emerge. Not surprisingly, given that the properties of most types of networks seem to transcend the nature of their components [13], host–parasite networks have architectures similar to mutualistic networks. Indeed, the uneven distribution of links among nodes and the nested structure seen in mutualistic networks are also evident in host–parasite networks [34,35]. Nested patterns of host use by the parasite species within a community have been well documented earlier by applying biogeographical methods to host–parasite associations [36,37]. However, not only can network analysis complemented by null models avoid the pitfalls associated with earlier metrics of nestedness

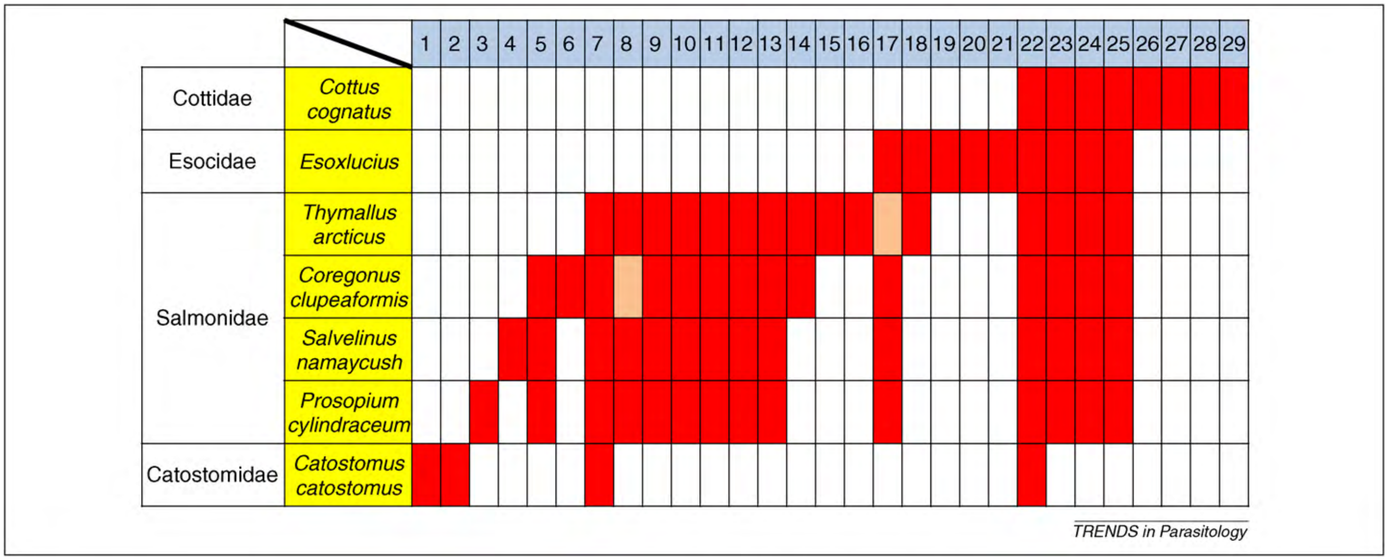
[38], it also provides a reciprocal view of asymmetric specialization from both the host and parasite perspective. If prevalence data are available, the strength of each link in the network, that is, of each host–parasite interaction, can be estimated assuming it is proportional to the frequency of interactions between host A and parasite B relative to all other interactions they have with other species [39]. As a rule, abundance (total number of individual of a species in the system) of interacting species correlates well with asymmetry of interaction strength in host–parasite networks; abundant species have many interaction partners, and they have strong effects on them, whereas rare species have few interaction partners and weak effects [35]. The relationship between species abundance and the number of interactions fits well with earlier comparative studies of the influence of host density on parasite species richness [1,40]. Abundance-driven asymmetries in ecological effects may also have evolutionary implications. The strength of reciprocal selection pressures between hosts and parasites is probably reflected by the strength of links in the network.

The signature of evolution should also be discernible in the structure of host–parasite networks. In particular, one would expect phylogenetic constraints to limit the number of potential interaction partners of any host or parasite to the subset with whom it shares a coevolutionary history. For instance, certain families of trematodes are only associated with certain families of fish [41]. In any host–parasite interaction matrix (Box 1), the order of either parasites (columns) or hosts (rows) can be rearranged without altering most network properties. By an iterative process, one can find the permutation of host species that minimizes the number of gaps in host ranges, i.e. the one that produces the most contiguous arrangements of host species used by each parasite (Figure 2). The minimum number of gaps corresponds to the intervality of a network, a property known to be important for the structure of food webs [42,43]. Among 40 interaction networks between metazoan parasites and freshwater fish, or fleas and small mammals, the observed minimum number of gaps did not differ from that predicted by a null model in which realized host–parasite links were constrained by allowing parasites to infect only host species from the same family [44]. This finding hints at a certain degree of determinism in the structure of host–parasite networks; host and parasite species come together in one locality in ecological time, but ultimately their past coevolutionary history might dictate which realized interactions are possible and which are not [45]. The studies reviewed above indicate that thinking of hosts and parasites in terms of interaction networks can allow predictions of not only the number, but also the identity of novel species that can successfully establish in a community.

Parasites in food web networks

Bipartite interaction networks include only a small subset of all species coexisting in a community, consisting of a guild of parasites and their guild of hosts (e.g. fleas on mammals). In contrast, food web networks are depictions of existing trophic interactions among all consumers and producers that capture the paths along which energy and matter flow from one component of the community to another (Box 1). Network analysis of food webs has indicated the existence of general patterns in their topological structure [46], and provides a framework for theoretical work on community structure and stability and on ecosystem functions [11,47].

Strong arguments for combining parasite and food web data are relatively recent [48–51]. One obvious practical benefit from the inclusion of parasitological data in food web studies is the improved resolution of predator–prey relationships. Trophically-acquired parasites survive in their host's gut for months or years, whereas the remains of prey items can only be identified from gut contents for a few hours or days following ingestion. Parasites thus provide a long-term signature of predator–prey relationships



		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Cottidae	*Cottus cognatus*																						🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
Esocidae	*Esoxlucius*																	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥				
Salmonidae	*Thymallus arcticus*							🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟧	🟥				🟥	🟥	🟥	🟥				
	Coregonus clupeaformis					🟥	🟥	🟥	🟧	🟥	🟥	🟥	🟥	🟥	🟥			🟥					🟥	🟥	🟥	🟥				
	Salvelinus namaycush				🟥	🟥		🟥	🟥	🟥	🟥	🟥	🟥	🟥				🟥					🟥	🟥	🟥	🟥				
	Prosopium cylindraceum			🟥		🟥		🟥	🟥	🟥	🟥	🟥	🟥	🟥				🟥					🟥	🟥	🟥	🟥				
Catostomidae	*Catostomus catostomus*	🟥	🟥					🟥															🟥							

TRENDS in Parasitology

Figure 2. Bipartite network of interactions between metazoan parasites and their fish hosts. The 29 parasite species (blue) and six fish host species (yellow) are from Aishihik Lake, Yukon Territory, Canada. Red cells indicate observed host–parasite interactions. The order of host species has been selected to minimize the number of irreducible gaps (pink cells) in host ranges, i.e. to generate the most contiguous arrangements of host species used by each parasite species. In the ideal arrangement shown here, host species end up sorted into their respective families. Adapted from Ref. [44].

that would otherwise be missed by researchers [48,52]. From the parasite's perspective, food webs represent templates for transmission routes. Most helminths have complex life cycles involving two or more host species. As a rule, transmission from the last intermediate host to the vertebrate definitive host occurs via predation of the former by the latter. This transmission event corresponds to a trophic link in the food web. The parallel routes followed by energy and parasites within a system allow us to superimpose parasite life cycles over a food web diagram. By treating parasites as outside the web but piggybacking on its internal dynamics to ensure their own transmission, one can identify other potential transmission routes, i.e. other energy flows that parasites could ride toward their definitive host [45,50]. Natural selection might have favoured parasites that exploit the strongest links, such that routes along which the greatest amounts of matter and energy flow through the web might also be the ones used by most parasite species as transmission pathways. Indeed, in a study of three intertidal food web networks, the few free-living species used by many parasite species tended to have a broad diet and occupy a central position in the web close to many prey species [53]. Thus, species best placed to accumulate resources and energy from lower trophic levels have many parasite species, too. Also, species used as intermediate hosts by parasites with complex life cycles tended to have more predators than those not used as intermediate hosts [53]. The search for the determinants of variation in parasite species richness among host species has a long history in ecological parasitology [1,54,55], and considering host species within a food web network could open up new ways of thinking about this aspect of parasite diversity.

The real challenge, and the greatest potential source of new insights about the structure and function of natural systems, comes from integrating parasites as actual nodes within a food web network (Box 1). This is not as straightforward as it may sound [56]. For instance, should parasites of top predators be viewed as the highest trophic level in the web? Isotope ratios, such as those between the nitrogen isotopes ^{14}N and ^{15}N, can serve as indicators of an organism's trophic position. Predators are almost always ^{15}N-enriched compared to their prey. In contrast, available data show that parasites are either ^{15}N-enriched or ^{15}N-depleted compared to their hosts, or they have the same isotope ratio [57–59]. Of course, some parasites feed on intestinal contents rather than host tissue, making their trophic position uncertain. In addition, the inclusion of parasites in food webs does not always sit well with existing theoretical frameworks. Two models, the cascade model and the niche model [60,61], have been repeatedly used to explain food web structure, even if they cannot fully reproduce observed food web patterns [62]. Both models rely on a feeding hierarchy underpinned by a body size gradient from top predators to basal prey species. Because their body sizes are typically orders of magnitude smaller than those of their hosts, parasites are at odds with the expectations of these food web models when placed in the uppermost trophic level [48]. Another problem comes from the different hosts used by parasites with complex life cycles. For instance, the first developmental stages of trematodes invariably exploit a mollusc. The next stage (metacercariae) parasitizes a second intermediate host that can be anything from an arthropod to a fish, and the adult stage lives inside a vertebrate. Should each stage of such a species be treated as a separate morphospecies, such as a separate node in the web, or should the species be treated as a single node characterized by a generalist diet of disparate hosts? There is no easy answer, and certainly no consensus regarding the best approach [56,63].

Regardless of these issues, integrating parasite species as distinct nodes within food web networks has consequences for network structure. Comparisons between food webs with parasites included and those same webs with parasites excluded indicate that some network properties are affected. For instance, connectance, average food chain length (the average number of links across all paths from basal species to the highest trophic level) or the proportion of species that feed on more than one trophic levels below theirs, can all be altered when parasites are considered [64–69]. In general, however, inclusion of parasites does not cause food web structure to shift radically from its parasite-free state. For instance, when parasites are added, values for basic network properties such as connectance remain within the range seen for parasite-free food webs [67]. Nevertheless, recent analyses make it very clear also that the topology and complexity of food webs is hugely determined by parasites since they dominate the links within the networks. A single predator–prey link can be used by several trophically-transmitted parasites, and thus for each predator—prey link there can be numerous host–parasite links. The many cases of

Box 2. Future questions for network analyses

For bipartite host–parasite interaction networks:

- How general is the apparent relationship between the abundance of a species and how many interaction partners it can have?
- Are modules of highly-connected species of hosts and parasites from different networks, such as lakes from different geographical areas, made up of taxonomically related species?
- Are the network properties of given species, such as the number of interaction partners (i.e. number of links) they have or the relative strengths of these interactions, consistent across their geographical range?
- Similarly, are there biogeographical patterns, such as latitudinal gradients, in the structure of networks, mirroring those in biodiversity or niche breadth?

For food web networks with parasites:

- Are there more trophically-transmitted parasite species transmitted along the strong (in terms of energy flow) trophic links within a food web than the weaker ones, and are there more parasites utilising nodes (hosts) characterized by either many/strong incoming links?
- Is the accumulation of certain types of parasites, such as those with complex life cycles and trophic transmission, in a community influenced by the topology and stability of its food web?
- How do the number of parasite species in a food web, as well as the number and relative strength of links in which they are involved, influence a community's resistance to invasive species?
- How does including parasites change the distribution of interaction strengths, that is, the distribution of energy flow values between nodes, within food webs, and how does that impact on the webs' resilience to extinction or to variation in abundance of key species?

free-living animals feeding on parasite infective stages, or of parasites feeding on each other within a host, add up to an impressive number of links within any food web. For example, about 78% of the 2313 trophic links in a California salt marsh food web involved parasites [67]. In a Norwegian subarctic lake food web, parasites accounted for 54% of the 432 observed trophic links [69]. These numbers provide strong arguments for the inclusion of parasites into food web networks whatever their consequences for network structure [56,63].

Network analysis of food webs can also reveal the role of parasites in food web stability, i.e. how the food web maintains its basic structure in the face of disturbances such as extinctions. Parasites themselves are prone to rapid secondary extinction following the local extinction of key hosts in their life cycle [70], and thus the loss of host-specific parasites ensuing the removal of free-living species from a food web can have profound consequences for network properties [71]. However, parasites might also be a critical element in preventing competitive exclusion in food webs. The dynamic role of parasites in population regulation is likely to increase with density, providing a mechanism whereby superior competitors might have their population size curtailed, allowing the persistence of inferior competitors in communities. In addition, generalist parasites might be the glue that holds together the free-living part of the food web. Indeed, theoretical network models have indicated that a high proportion of weak interactions and a high variance in interaction strength among links in a web contribute to its stability [72–74]. From an energetic perspective, trophic links between parasites and their hosts probably correspond to weak interactions, compared to predator–prey links. The cumulative effect of both weak and strong links on whole-system stability can only be appreciated with an analysis of the entire network. This approach might be our best way to elucidate how parasites affect community diversity, and determine whether parasitism is one of the reasons why natural systems are so stable.

Networks and parasites: the road ahead

Network analysis provides a set of well-developed tools for studies of complex dynamical systems with several interacting components. It provides a useful framework for the detection and interpretation of patterns, and for prediction of changes, within natural communities consisting of interacting species such as parasites and their hosts. Indeed, ecologists are now realising that understanding network structure and its underlying mechanisms will be crucial for assessing community and ecosystem responses to global change [75]. The few network analyses to date of either host–parasite bipartite networks or whole food webs including parasites have revealed recurrent structural properties across different networks, suggestive of fundamental and general processes. Still, challenges remain if we are to make full use of this approach and apply it to answer important questions (Box 2). For instance, most studies to date consider networks as static, providing only a snapshot of the topology of a network based on field data collected over a limited time scale. The dynamic nature of interactions within natural networks must now be considered using either simulation studies in which changes are imposed on the original networks, or field studies tracking temporal changes in specific network properties. Also, the focus of existing studies has been on the topology of the network, i.e. the patterns of links between nodes, rather than on the relative strength of these links. Interaction strength can be approximated in bipartite networks using data on prevalence and specificity [35,39], but for food webs this will require data on energy flow among nodes, a logistically more challenging proposition given the variety of taxa and trophic modes involved [51]. Nevertheless, network analysis allows an entire community to be analysed at once as opposed to the one host–one parasite approach of many earlier studies, and its benefits far outweigh its disadvantages.

Acknowledgements

I thank Mike Sukhdeo, Ross Thompson, and four anonymous reviewers for comments on an earlier version of the manuscript, and Juan Timi for his hospitality during my stay in Mar del Plata, Argentina, where this synthesis was written.

References

1 Poulin, R. and Morand, S. (2004) *Parasite Biodiversity*, Smithsonian Institution Press
2 Kuris, A.M. *et al.* (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515–518
3 Mouritsen, K.N. and Poulin, R. (2005) Parasites boost biodiversity and change animal community structure by trait-mediated indirect effects. *Oikos* 108, 344–350
4 Wood, C.L. *et al.* (2007) Parasites alter community structure. *Proc. Natl. Acad. Sci. U. S. A.* 104, 9335–9339
5 Groom, M.J. *et al.* (2006) *Principles of Conservation Biology* (3rd edn), Sinauer Associates Inc.
6 Eames, K.T.D. and Keeling, M.J. (2002) Modeling dynamic and network heterogeneities in the spread of sexually transmitted diseases. *Proc. Natl. Acad. Sci. U. S. A.* 99, 13330–13335
7 Eubank, S. *et al.* (2004) Modelling disease outbreaks in realistic urban social networks. *Nature* 429, 180–184
8 Perkins, S.E. *et al.* (2009) Comparison of social networks derived from ecological data: implications for inferring infectious disease dynamics. *J. Anim. Ecol.* 78, 1015–1022
9 Drewe, J.A. (2010) Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *Proc. R. Soc. Lond. B Biol. Sci.* 277, 633–642
10 Proulx, S.R. *et al.* (2005) Network thinking in ecology and evolution. *Trends Ecol. Evol.* 20, 345–353
11 Pascual, M. and Dunne, J.A. (2006) *Ecological Networks: Linking Structure to Dynamics in Food Webs*, Oxford University Press
12 Bascompte, J. (2009) Disentangling the web of life. *Science* 325, 416–419
13 Newman, M. *et al.* (2006) *The Structure and Dynamics of Networks*, Princeton University Press
14 Borgatti, S.P. *et al.* (2009) Network analysis in the social sciences. *Science* 323, 892–895
15 Freeman, L.C. (2004) *The Development of Social Network Analysis*, Empirical Press
16 Watts, D.J. (2003) *Small Worlds: The Dynamics of Networks between Order and Randomness*, Princeton University Press
17 Bower, J.M. and Bolouri, H. (2001) *Computational Modeling of Genetic and Biochemical Networks*, MIT Press
18 Butts, C.T. (2009) Revisiting the foundations of network analysis. *Science* 325, 414–416
19 Poulin, R. (1998) Comparison of three estimators of species richness in parasite component communities. *J. Parasitol.* 84, 485–490
20 Ricklefs, R.E. *et al.* (2005) Community relationships of avian malaria parasites in southern Missouri. *Ecol. Monogr.* 75, 543–559
21 Baird, D. and Ulanowicz, R.E. (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59, 329–364
22 Melian, C.J. *et al.* (2009) Diversity in a complex ecological network with two interaction types. *Oikos* 118, 122–130

23 Bascompte, J. and Jordano, P. (2007) Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38, 567–593
24 Bascompte, J. *et al.* (2003) The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. U. S. A.* 100, 9383–9387
25 Jordano, P. *et al.* (2003) Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* 6, 69–81
26 Guimaraes, P.R. *et al.* (2006) Asymmetries in specialization in ant-plant mutualistic networks. *Proc. R. Soc. Lond. B Biol. Sci.* 273, 2041–2047
27 Joppa, L.N. *et al.* (2009) Reciprocal specialization in ecological networks. *Ecol. Lett.* 12, 961–969
28 Olesen, J.M. *et al.* (2007) The modularity of pollination networks. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19891–19896
29 Dupont, Y.L. and Olesen, J.M. (2009) Ecological modules and roles of species in heathland plant-insect flower visitor networks. *J. Anim. Ecol.* 78, 346–353
30 Vázquez, D.P. *et al.* (2009) Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology* 90, 2039–2046
31 Poulin, R. (2007) Are there general laws in parasite ecology? *Parasitology* 134, 763–776
32 Mouillot, D. *et al.* (2008) Connectance and parasite diet breadth in flea–mammal webs. *Ecography* 31, 16–20
33 Bastolla, U. *et al.* (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1021
34 Vázquez, D.P. *et al.* (2005) Species abundance and the distribution of specialization in host-parasite interaction networks. *J. Anim. Ecol.* 74, 946–955
35 Vázquez, D.P. *et al.* (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116, 1120–1127
36 Valtonen, E.T. *et al.* (2001) The structure of parasite component communities in brackish water fishes of the northeastern Baltic Sea. *Parasitology* 122, 471–481
37 Krasnov, B.R. *et al.* (2005) Nested pattern in flea assemblages across the host's geographic range. *Ecography* 28, 475–484
38 Ulrich, W. and Gotelli, N.J. (2007) Null model analysis of species nestedness patterns. *Ecology* 88, 1824–1831
39 Vázquez, D.P. *et al.* (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8, 1088–1094
40 Morand, S. and Poulin, R. (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evol. Ecol.* 12, 717–727
41 Cribb, T.H. *et al.* (2002) The trematodes of groupers (Serranidae: Epinephelinae): knowledge, nature and evolution. *Parasitology* 124, S23–S42
42 Huxham, M. *et al.* (1996) Do parasites reduce the chances of triangulation in a real food web? *Oikos* 76, 284–300
43 Stouffer, D.B. *et al.* (2006) A robust measure of food web intervality. *Proc. Natl. Acad. Sci. U. S. A.* 103, 19015–19020
44 Mouillot, D. *et al.* (2008) High intervality explained by phylogenetic constraints in host-parasite webs. *Ecology* 89, 2043–2051
45 Marcogliese, D.J. (2003) Food webs and biodiversity: are parasites the missing link? *J. Parasitol.* 89 (Suppl.), S106–S113
46 Dunne, J.A. *et al.* (2004) Network structure and robustness in marine food webs. *Mar. Ecol. Prog. Ser.* 273, 291–302
47 Polis, G.A. and Winemiller, K.O. (1996) *Food Webs: Integration of Patterns and Dynamics*, Chapman and Hall
48 Marcogliese, D.J. and Cone, D.K. (1997) Food webs: a plea for parasites. *Trends Ecol. Evol.* 12, 320–325
49 Morand, S. and Arias-Gonzalez, E. (1997) Is parasitism a missing ingredient in model ecosystems? *Ecol. Model.* 95, 61–74
50 Sukhdeo, M.V.K. and Hernandez, A.D. (2005) Food web patterns and the parasite's perspective. In *Parasitism and Ecosystems* (Thomas, F. *et al.*, eds), pp. 54–67, Oxford University Press
51 Sukhdeo, M.V.K. Food webs for parasitologists: a review. *J. Parasitol.* 96, 273–284
52 Valtonen, E.T. *et al.* (2010) Vertebrate diets derived from trophically transmitted fish parasites in the Bothnian Bay. *Oecologia* 162, 139–152
53 Chen, H-W. *et al.* (2008) Network position of hosts in food webs and their parasite diversity. *Oikos* 117, 1847–1855
54 Poulin, R. (1997) Species richness of parasite assemblages: evolution and patterns. *Annu. Rev. Ecol. Syst.* 28, 341–358
55 Luque, J.L. and Poulin, R. (2008) Linking ecology with parasite diversity in Neotropical fishes. *J. Fish Biol.* 72, 189–204
56 Lafferty, K.D. *et al.* (2008) Parasites in food webs: the ultimate missing links. *Ecol. Lett.* 11, 533–546
57 Pinnegar, J.K. *et al.* (2001) Unusual stable-isotope fractionation patterns observed for fish host-parasite trophic relationships. *J. Fish Biol.* 59, 494–503
58 Deudero, S. *et al.* (2002) Insights into fish host-parasite trophic relationships revealed by stable isotope analysis. *Dis. Aquat. Org.* 52, 77–86
59 Persson, M.E. *et al.* (2007) Fractionation of δ15N and δ13C for Atlantic salmon and its intestinal cestode *Eubothrium crassum*. *J. Fish Biol.* 71, 441–452
60 Cohen, J.E. *et al.* (1993) Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* 62, 67–78
61 Williams, R.J. and Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature* 404, 180–183
62 Allesina, S. *et al.* (2008) A general model for food web structure. *Science* 320, 658–661
63 Byers, J.E. (2009) Including parasites in food webs. *Trends Parasitol.* 25, 55–57
64 Huxham, M. *et al.* (1995) Parasites and food web patterns. *J. Anim. Ecol.* 64, 168–176
65 Thompson, R.M. *et al.* (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J. Anim. Ecol.* 74, 77–85
66 Morand, S. and Arias-Gonzalez, J.E. (2006) Trophic functioning with parasites: a new insight for ecosystem analysis. *Mar. Ecol. Prog. Ser.* 320, 43–53
67 Lafferty, K.D. *et al.* (2006) Parasites dominate food web links. *Proc. Natl. Acad. Sci. U. S. A.* 103, 11211–11216
68 Hernandez, A.D. and Sukhdeo, M.V.K. (2008) Parasites alter the topology of a stream food web across seasons. *Oecologia* 156, 613–624
69 Amundsen, P-A. *et al.* (2009) Food web topology and parasites in the pelagic zone of a subarctic lake. *J. Anim. Ecol.* 78, 563–572
70 Dunn, R.R. *et al.* (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. Lond. B Biol. Sci.* 276, 3037–3045
71 Lafferty, K.D. and Kuris, A.M. (2009) Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 1659–1663
72 McCann, K. *et al.* (1998) Weak trophic interactions and the balance of nature. *Nature* 395, 794–798
73 Neutel, A-M. *et al.* (2002) Stability in real food webs: weak links in long loops. *Science* 296, 1120–1123
74 Gross, T. *et al.* (2009) Generalized models reveal stabilizing factors in food webs. *Science* 325, 747–750
75 Tylianakis, J.M. *et al.* (2008) Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363
76 Thieltges, D.W. *et al.* (2008) The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology* 135, 407–426
77 Grutter, A.S. (2008) Interactions between gnathiid isopods, cleaner fish and other fishes on Lizard Island, Great Barrier Reef. *J. Fish Biol.* 73, 2094–2109
78 Sousa, W.P. (1993) Interspecific antagonism and species coexistence in a diverse guild of larval trematode parasites. *Ecol. Monogr.* 63, 103–128