

Review

Network Analysis: Ten Years Shining Light on Host–Parasite Interactions

Rogini Runghen,¹ Robert Poulin,² Clara Monlleó-Borrull,³ and Cristina Llopis-Belenguer^{3,*}

Biological interactions are key drivers of ecological and evolutionary processes. The complexity of such interactions hinders our understanding of ecological systems and our ability to make effective predictions in changing environments. However, network analysis allows us to better tackle the complexity of ecosystems because it extracts the properties of an ecological system according to the number and distribution of links among interacting entities. The number of studies using network analysis to solve ecological and evolutionary questions in parasitology has increased over the past decade. Here, we synthesise the contribution of network analysis toward disentangling host–parasite processes. Furthermore, we identify current trends in mainstream ecology and novel applications of network analysis that present opportunities for research on host–parasite interactions.

Hosts, Parasites, and Their Interactions

Organisms in ecological communities interact with others in many ways that determine their fitness. This basic fact promotes a wide range of interactions among organisms from the same or different guild within a community, such as feeding, pollination, phoresis, or protection [1]. At the same time, interactions between organisms ensure the natural functioning of ecosystems [2]. For instance, networks of trophic interactions, or food webs, determine the flux of energy within a community [3]. Consequently, the disruption of biotic interactions might have disastrous outcomes for ecological and evolutionary processes. For example, climate change can accelerate the loss of species from a community due to secondary extinctions, that is, the extinction of a species may well cause the disappearance of its cointeractors [4].

Due to the vast number of interactions that must be considered to better understand ecosystem processes, studying ecological communities can be challenging. As such, network analysis represents a solid and versatile tool by accounting for all interactors (e.g., hosts or parasites) within a community. By doing so, network analysis overcomes limitations of traditional approaches, such as experiments or mathematical models that rest on oversimplified assumptions [5,6]. Specifically, network analysis extracts and predicts the properties of ecological communities according to the distribution of edges (or links) between interacting pairs of organisms (or any other entity, e.g., taxon or guild) [5]. In the context of parasite ecology, Poulin's review [5] was a pivotal study as it synthesised the use of network analysis within a parasite community framework. In addition, the author [5] posed several research questions for future studies to address and, thus, improve our understanding of host–parasite interactions as drivers of ecosystem processes. Since then, the study of host–parasite communities using a network analysis perspective has expanded, although it still lags behind compared with other ecological communities (e.g., plant–pollinators networks, see Figure S1 in the supplemental information online). For example, network analysis found support for enemy release (i.e., loss of parasites and other enemies) in an invasive host species, which would give an ecological advantage to invasive over native hosts [7]; and it served to disentangle the evolutionary immune response of hosts to parasitic infections [8]. As a result, network analysis has allowed parasitologists to move from traditional descriptive studies to

Highlights

Parasitologists are extending and integrating the use of network analysis to study host–parasite communities. With the increasing availability of data, parasitology is rapidly moving from mere description of interactions to understanding and predicting how these interactions happen. As a result, parasitology is turning into a computationally demanding science.

Parasite traits might be more relevant than their taxonomic affiliation to determine their performance within a community. Host phylogeny and phenotypic attributes affect their interactions within a parasite community.

Parasite species composition and parasite interaction patterns within a community might not display congruent variation under changing scenarios. Consequently, both of these components of diversity should be considered in community ecology studies to improve our understanding of ecosystem processes.

¹Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag 4800, 8140 Christchurch, New Zealand

²Department of Zoology, University of Otago, 340 Great King Street, 9054 Dunedin, New Zealand

³Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, PO Box 22085, ES-46071, Valencia, Spain

*Correspondence: cristina.llopis.belenguer@gmail.com (C. Llopis-Belenguer).



quantitatively assess and predict the contribution of parasites to ecological and evolutionary processes [9].

The aim of this review is threefold. Using Poulin's synthesis [5] as our main reference point, and due to the increasing number of studies in recent years (Figure S1), we focus on studies analysing **bipartite networks** (see Glossary) (Figure 1A, Key Figure) composed of metazoan parasites and their animal hosts. First, we present a synthesis of the main research areas in which network analysis has been useful to disentangle host–parasite processes and dynamics over the past decade. Second, we identify which questions out of those asked in [5] have already been answered (Box 1). Finally, we identify knowledge gaps in host–parasite evolutionary ecology that could be addressed with network analysis. In addition, we highlight current trends in mainstream research on ecological networks. These might help parasite ecologists to complete their picture of the contribution of parasites to ecosystem processes.

What Is Happening in Real Host–Parasite Communities?

Roles of Parasites in Their Interaction Networks

The way a particular individual interacts with other members in a community is key in determining their **role** in the community. Amongst the determining factors, the number of individuals with which they interact and the strength with which they interact with one another are fundamental [10]. Moreover, this role is related to the interactor's **functional traits** [11].

Parasites are considered as playing peripheral roles (i.e., low number of interactions) within their communities (e.g., [12,13]). Such a role reflects a trade-off between the benefit of having alternative hosts (i.e., establishing new edges with several host species) and the cost of developing adaptations to these host species. This trade-off has resulted in many parasite species evolving to become highly host specific [14]. Therefore, host specificity of parasites favours network structures with high **modularity** (i.e., partitioning of interactions within a network; but see [15]) and low **nestedness** (i.e., hierarchy in the edge distribution within a network; but see [16]). In particular, these patterns seem to be more pronounced for ectoparasite than for endoparasite communities [17], and also among obligate rather than facultative parasite communities [18]. Moreover, in the case of nestedness, the degree of nestedness in any antagonistic (i.e., host–parasite) network can result from coevolution leading to weak (i.e., high nestedness) or strong (i.e., low nestedness) trade-offs in parasite transmission [19].

However, the observed roles of parasites can change if parasite species are disaggregated into life stages for network analysis. In other words, parasites of the same species but at different developmental stages may be considered as different interactors [20]. Indeed, helminths not only undergo drastic morphological changes as they pass from one life stage to the next, but they also interact with completely different subsets of host taxa within the community. For example, some parasite species at the larval stage (e.g., *Contracaecum* sp. or *Anisakis* sp.) can play an important role in network **connectance** because they follow a generalist life strategy [14]. These results suggest that the parasite's ecology, and therefore its trait-mediated performance, might be more relevant than its taxonomic affiliation to predict its role within the community [14,17,18,21] (Box 1). However, contrary to these results, Poulin *et al.* [22] found that the role of a parasite species as a connector within its network is constrained by its phylogeny, at least for trophically transmitted helminths with complex life cycles. In addition, these authors found that food webs were still modular after removing parasites from the analyses, indicating that parasites do not generate a modular topology by themselves. However, when considered, parasites were important for the cohesion and integrity of the web, since parasites appeared in all modules identified and almost half of them were classified as connectors. In this regard, Cirtwill and Stouffer

Glossary

Bipartite networks: systems of interactions between nodes (e.g., species or individuals) of two distinct sets, such as host and parasites. In bipartite networks, edges connect nodes of different sets according to their interactions (i.e., infections) in a community. Nodes of the same set are not allowed to interact in bipartite network analysis.

Concomitant predation: when parasites are ingested alongside a prey host by a predator that is not a definitive host, hence parasites provide a nutritional supplement to the predator [85].

Connectance: the proportion of realised pairwise host–parasite interactions among all the potential ones.

Functional trait: a feature measurable at the host or parasite individual level, without reference to the environment or any other level of organisation, and which impacts the fitness of individuals and reflects their performance in ecosystems.

Infracommunity: the assemblage of all individuals of all parasite species in a single host individual.

Modularity: a measure of the compartmentalisation of a host–parasite network. Modular networks are composed of subsets (i.e., modules) of hosts and parasites that tend to interact more frequently among themselves than with other members of the community.

Nestedness: a description of the extent to which a group of specialist parasites use a subset of the hosts used by generalist parasites. In other words, specialist parasites interact with hosts with high parasite diversity, while generalist parasites exploit hosts with both rich and poor parasite communities.

Phylogenetic signal: the tendency for related species to be more similar (with respect to their role or position within a network, or to any other trait) to each other than to other species.

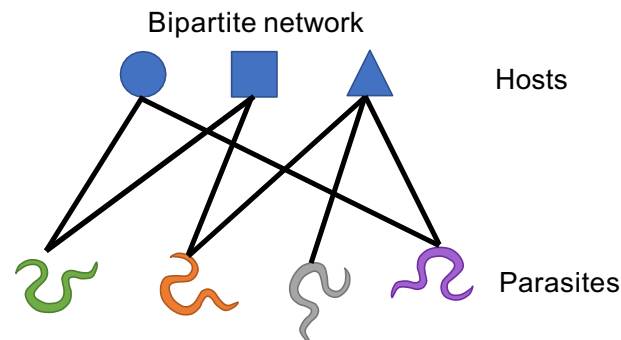
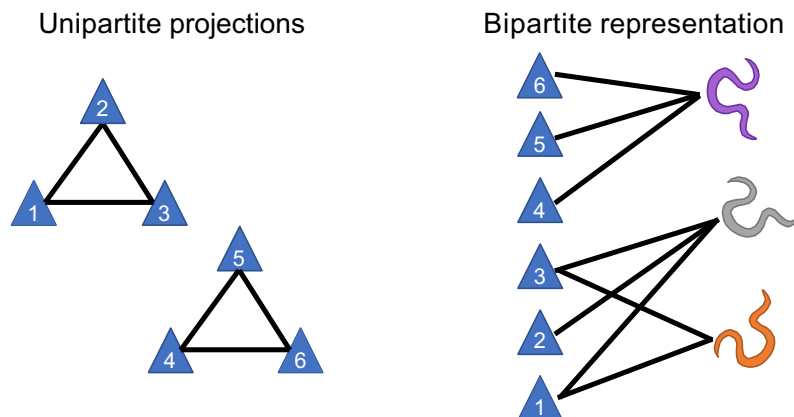
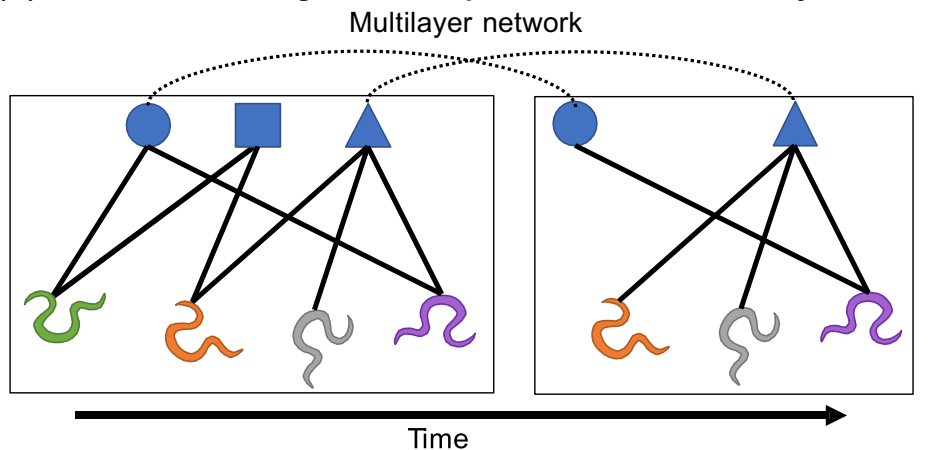
Rewiring: a change in the linking pattern among cointeractors.

Role: the contribution of an organism (or any other entity, e.g., taxon or guild) to the network topology (e.g., modular, nested). It is defined by the number and strength of edges the organism has with others in the community.

Social networks: these are a specific case of unipartite networks. Contrary to bipartite networks, unipartite networks depict interactions between nodes of the same set. Social networks usually assess contacts between organisms

Key Figure**Using Network Approaches to Understand Interactions in Host–Parasite Networks**

that, for example, represent pathways for parasite spreading. These are usually analysed as intraspecific networks; hence, analysis is performed at the host individual level. Note that most of what is discussed in this article involves interactions between different species (i.e., interspecific and species-level).

(A) Interactions among hosts and parasites in a community**(B) Interactions between and within host individuals****(C) Interactions among hosts and parasites in a community over time**

Trends in Parasitology

(See figure legend at the bottom of the next page.)

Box 1. Questions for Bipartite Host–Parasite Networks

Poulin's review [5] identified four research questions for bipartite host–parasite networks that should be addressed to improve our understanding of host–parasite diversity from a network analysis perspective. Here we discuss whether those questions have now been answered.

Question 1. How general is the apparent relationship between the abundance of a species and the number of interaction partners it can have?

In the case of the number of interacting partners, host species with dense populations – or that are more widespread – tend to share a greater number of parasites with a greater number of other host species, and hence, to occupy more central positions in parasite-sharing networks [27]. Regarding interaction strength, neutral theory of interactions predicts that the interaction strength between a host and a parasite species is proportional to their relative abundances. Conversely, niche theory acknowledges that biological traits constrain the interaction strength and define niche dimensions. Hence, interaction strength should be independent of abundance [86]. Canard *et al.* [86] found that both neutral events (abundance-based) and niche constraints (trait-based) drive the interaction strength in host–parasite networks. Neutrality was a good predictor of interaction strength at a large scale. However, it was not such a robust predictor when analyses were downscaled. In this case, abundances and trait information should be combined to accurately predict host–parasite interactions.

Question 2. 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?

The process of infection seems to be context-dependent, indicating that different networks may be affected by different processes even when having a similar taxonomic composition. Therefore, a host species which may be central for parasite transmission in one network may be less important in a different community, depending on the local ecological context [25]. However, network structure and properties seem to be preserved across equivalent communities, regardless of the taxonomic affiliation of interactors [37,44,45]. This fact suggests that different taxonomic entities of hosts and/or parasites assume redundant roles across ecological networks [45].

Question 3. 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?

In a biological invasion context, hosts and parasites cointroduced from a native area to an invaded area were found to display patterns of interactions that did not differ significantly across their geographical range. This result was explained by evolution being a strong determinant of host–parasite interactions [7]. However, the spatial stability of any given host or parasite species' network properties remains to be examined outside a biological invasion context, for instance within species with a naturally broad geographical range.

Question 4. Similarly, are there biogeographical patterns, such as latitudinal gradients, in the structure of networks, mirroring those in biodiversity or niche breadth?

Biogeographical patterns in the distributions of free-living and parasite species have been extensively reported (e.g., [81,87]). However, studies assessing biogeographical patterns in the structure of host–parasite networks are scarce (e.g., [88]) and only few compare the structure of the interactions with other structural patterns [44,45]. In one study, although the number of host–parasite associations did not significantly vary with latitude, host diversity decreased [44]. Furthermore, host–parasite network structure seems to be preserved across geographic distance, contrary to species compositional turnover [45]. Studies comparing the structure of host–parasite networks with other structural patterns, such as species composition or niche breadth, at a global scale are needed to elucidate macroecological patterns of host–parasite diversity [89].

[23] pointed toward **concomitant predation** on parasites by non-host predators as the key process allowing parasites to connect several hosts and/or predators in their communities. These findings [22,23] support the earlier proposal of Lafferty *et al.* [24] that parasites might play a role in promoting network stability since they connect several trophic levels.

Figure 1. (A) Bipartite network showing interactions (edges) between host species and parasite species – respectively represented by a set of nodes – in a community. (B) A unipartite projection showing interactions between host individuals within a community (left); the same network can also be represented as a bipartite network to show interactions between parasite species and the different host individuals (right). (C) A multilayer representation showing how a host–parasite bipartite network may vary over time. Unbroken lines represent intralayer edges. Broken lines represent interlayer edges.

Parasitism exerts selective pressure on hosts, and it can eventually drive host evolution [8,25]. Network analysis is a convenient tool for exploring the evolutionary outcomes of pressures from multiple parasites on the genetic diversity of multiple host species. For instance, host–parasite interaction matrices (ecological network) and the host-MHC allele supertype network (immunogenetic network) have been shown to correlate positively [8]. This result provided strong evidence for the interplay between host–parasite network structure and the diversity of MHC supertypes in different hosts. Moreover, associations between parasites and MHC supertypes were tight and significantly different from randomness within-modules. This indicated that the modular structure of indirect associations (i.e., parasite supertype) reflects actual coevolutionary interactions between hosts and parasites [8].

Host Characteristics Affect Host–Parasite Interactions

Studies have also shown that host characteristics affect host use by parasites, thereby impacting the topology of host–parasite networks (e.g., [25–27]). In this context, studies considering host characteristics at species level, such as host phylogeny [28], have helped to unveil network organisation (Figure 1A). However, some revealing studies have considered host characteristics at intraspecies level [i.e., at the level of individual hosts, each node in the network representing an individual host rather than a host species (Figure 1B)], for example, host behaviour [29]. Nonetheless, other attributes might be meaningful for parasites at both scales, for example, host body size [30]. In this section, we synthesise the contribution of three host characteristics to host–parasite network structure, namely: host phylogeny, host body size, and host behaviour; and we also discuss the possible impact of parasite manipulation of host behaviour.

Host phylogeny can dictate the topology of host–parasite networks and the role a host plays in parasite transmission [12,25,27,28,31–34]. For instance, host **phylogenetic signal**, but not parasite phylogenetic signal, was found in the module composition of a mammal–flea network [28]. These results suggest that nonphylogenetically related parasites converge in their traits to exploit phylogenetically close hosts, and these hosts and parasites form subsets of interactors within a community [28]. This finding, if broadly applicable to other communities, could have several implications. For instance, current global change is causing a greatly uneven loss of species across host lineages (e.g., [35]). Therefore, the loss of a host lineage that may be species-poor but is key to the network structure can result in a rapid decline in parasite diversity and a profound disruption of network structure [33]. Furthermore, the phylogenetic position of an introduced animal species might allow one to predict where it will fit within the invaded host–parasite network if module affiliation is determined by phylogeny.

Besides phylogeny, host phenotypic attributes can affect the overall structure of the host–parasite network. Host body size in particular might affect network dynamics [36]. For example, individual host body size explained heterogeneity in interaction strength among conspecific hosts in host individual–parasite species networks across habitats [37]. In addition, host body size is usually correlated with other host attributes. Therefore, characterising the host body size distribution within a network can capture much of the biologically meaningful variation in a relatively straightforward manner [30]. For example, the contribution of host ontogenetic dietary shifts to network topology should be easier to assess by measuring host body size rather than host age.

The idiosyncratic nature of animal behaviour generates heterogeneities among host individuals in their exposure to parasites and, hence, in their role for parasite transmission. Many parasites rely on either direct or indirect contact between hosts to transmit. Hence, when studying host behaviour, it can be particularly informative to perform network analysis as **social networks** of interacting hosts. Social networks connect host individuals in an epidemiological context which

allows us to account for heterogeneity within key host individual characteristics for parasite transmission [25,38] (Figure 1B). Different scenarios arise in this regard. One can think that a host individual having a high parasite load is more likely to have a central role in parasite transmission. That said, one can imagine another scenario where a host individual having a low parasite load but a close contact with other host individuals could equally play an important role in parasite transmission [39]. Furthermore, both parasite load and contact parameters in combination could determine the host's role in parasite transmission. For example, MacIntosh *et al.* [29] found that macaque hosts with a dominant position (i.e., high number of grooming partners) in their social networks are more likely to have higher levels of parasite infection than low-ranked hosts, indicating that social position is important for an individual's role in parasite transmission [29]. In addition, behavioural differences between males and females might make individuals of a sex more prone to parasite acquisition than individuals of the other sex. For example, male tuatara hosts have a more central position in their social network and have higher parasite loads than females. This finding suggests that behavioural differences between sexes generate heterogeneities in parasite loads and transmission [40].

Moreover, parasites can manipulate host behaviour [41]. Consequently, parasites can modify the role their host plays into a more convenient position within the social network (i.e., more or less connected to other hosts or centrally positioned) in order to enhance their transmission. In addition, the modified position of infected hosts can reorganise the interaction structure of other members (e.g., interaction strength) and/or of the whole community (e.g., increasing modularity) [42].

Environmental Influences on Host–Parasite Interactions

Ecological communities vary spatially in their species richness, composition, and abundance because species are replaced by others along environmental gradients (e.g., [43]). However, despite the compositional turnover in natural host–parasite communities, network structure and properties tend to be preserved across equivalent communities (e.g., [37,44,45]). This fact suggests that different taxonomic entities of hosts and/or parasites assume the same roles across ecological networks. In addition, it supports the idea that host and/or parasite traits could be redundant across communities and that few traits may be pivotal to determine host–parasite communities [45].

Host–parasite communities experience great temporal variability, not only in species diversity but also in interaction patterns [46]. Therefore, although persistent host–parasite interactions tend to be at the core of community dynamics, temporal **rewiring** can change the position a species occupies in a community. Rewiring is particularly relevant in antagonistic networks because it might dictate disease outbreaks [46,47].

Host–parasite networks might be affected if ecological conditions vary. For example, following an environmental perturbation, although host–parasite communities might suffer little variation in their species richness, the analysis of host–parasite interactions can reveal changes in the structure of these communities [48]. These results highlight that conventional species-composition descriptors can fail to discriminate adequately among habitats, and that, when the interactive structure of communities is overlooked, important effects of habitat modifications by humans can remain hidden. For instance, networks can become less connected and more modular even if their species richness is unchanged, which might complicate parasite sharing among host species as habitat disturbance increases [48].

The current rate of species introductions is accelerating the number of both non-native host and parasite introductions, which might disrupt the functioning of the recipient ecosystems [49].

Invasive hosts and parasites can alter the structure of the community they are introduced into because of the establishment of new interactions and the loss of those that existed previously [50,51]. However, although it seems appropriate to fully integrate network analysis into invasion ecology to accentuate the potential roles of new host–parasite interactions in an invaded network, only few studies have used network analysis to measure the actual extent of the impact of host and/or parasite invasions [7,31,50,52]. Specifically, trophically transmitted invasive parasites with complex life cycles might cause the most substantial shifts in network structure [53,54]. For example, the establishment of both arctic charr and three-spined stickleback in a subarctic lake enabled several additional parasite and predator species to enter the pelagic network. This invasion not only caused large changes in the species richness of the community but also resulted in a large increase in the number of interactions, and dramatically altered the overall topology of the original network. Consequently, the transmission rate and abundance of trophically transmitted parasites increased because of the key positions of the invasive hosts within the interaction network [52]. These newly created interactions open scenarios that can disrupt native host–parasite dynamics [7,52,55].

Contribution of Host–Parasite Studies to Mainstream Ecology and Network Analysis

In order to get an accurate understanding of the mechanisms governing and shaping interactions within host–parasite networks, information such as interaction strengths at the level of **infracommunities** and host density, as well as the abundance of parasites within different hosts, must be collected [56]. The use of such information to build host–parasite networks could provide an opportunity to answer fundamental questions in community ecology. For instance, since most parasites and pathogens infect multiple hosts [57,58], such data can improve our understanding of community assembly rules (i.e., elucidating the underlying mechanisms of species coexistence), species turnover [34,59], or even disease transmission [39,60], which could also help us to uncover the determinants of biological invasion [61]. Therefore, consideration of host–parasite systems by mainstream ecologists could replace the use of oversimplified biological models or the need for substantial field data collection to resolve the mechanisms governing biotic interactions [62,63].

One way in which host–parasite studies have contributed to ecological research is by developing an approach to account for missing links (i.e., unseen interactions) in bipartite networks. Distinguishing between whether a given pairwise interaction (or edge) is actually absent or whether falsely identified as absent is crucial when predicting interactions in networks [64]. Various sources of error, such as sampling bias, detection error either due to cryptic species and therefore to identifiability issues, or observer bias have been identified [65,66]. Not accounting for such bias can often lead to erroneous predictions and hence erroneous generalisation of patterns of interactions in a given network. Dallas *et al.* [26] developed a modelling framework specifically designed to predict the likelihood of interactions in an incomplete bipartite network using traits of both hosts and parasites. By doing so, they showed that they could predict the likelihood of interactions accurately. In most cases in ecology, sampling of a complete network is almost impossible and such missing data can be a limitation. Though link prediction is a known problem in network science, this method, initially developed for host–parasite systems, showcases how one could go about predicting interactions with missing data specifically for any type of ecological network.

Current Trends in Mainstream Ecology and Novel Applications

In the following section we discuss various aspects of research into ecological networks that have been considered outside of parasitology, and which present both challenges and opportunities for research on host–parasite interactions.

Consider Individual Variation

Most previous studies of host–parasite interactions have been carried out at species level (Figure 1A). However, interactions occur among individuals, and resolving interactions below the host species level can be relevant to understanding population dynamics [67]. As host individuals of the same species can have limited niche overlap, they can play very different roles for their parasite communities (Figure 1B). For example, host individuals of the same species can play very different roles simply because they vary in their diet preferences. Hence, such intraspecies heterogeneity, which is essential for parasite persistence and spread, might be overlooked if host individuals of the same species are pooled together in a species-level network analysis (i.e., species–species network analysis) [7,25] (Figure 1B).

Combine Network and Diversity Metrics

Over the past decade, the use of network analysis to improve our understanding of ecological interactions has moved from being descriptive (i.e., characterising networks based on their topology) to aiming at predicting patterns of biotic interactions in large-scale networks [68]. Despite such advances, most studies still focus on using network metrics that describe only the topology of networks as opposed to the underlying mechanisms governing the interactions within the network (however, refer to [69] for an extensive review on the meaning of different network metrics). In addition, commonly, research on variation among communities (β diversity, i.e., differences in diversity between sampling units, e.g., differences in parasite community composition between host species) has mostly focused on the turnover of taxonomic composition (i.e., identity and abundance of species in a community). Research of this kind usually neglects other facets of diversity, such as the phylogenetic (i.e., richness and abundance of genetically different entities in a community) and functional (i.e., richness and abundance of functional traits in a community) compositions [70]. Comparisons across different networks also generally ignore the variation in the way interactors associate with each other, despite accumulating empirical evidence that this is a major source of diversity [59]. Thus, although parasite communities can experience large spatiotemporal variations in their taxonomic composition, attention should be paid to the turnover in edge occurrences between taxonomic, functional, or phylogenetic entities to achieve a deeper mechanistic understanding of the relationship between diversity and ecosystem functioning [71]. For example, if the turnover in interactions among networks is not so significant in terms of functional and/or phylogenetic associations, this may indicate that communities tend to maintain an invariable structure by harbouring redundant entities (e.g., [45]).

Combine Network and Molecular Approaches

The integration of ecological network and molecular approaches provides opportunities to examine ecological interactions in new ways and with greater resolution [72]. From a technical point of view, DNA sequences can be used to confirm taxon identification or identify cryptic species, and then, their actual interactions. For example, metabarcoding can be used to quickly and precisely disentangle host–parasite associations via host faeces analysis [73]. From an applied perspective, molecular phylogenies can be useful to, for instance, disentangle the coevolutionary history of interacting pairs of lineages (e.g., [74]) or to provide valuable information about parasite transmission dynamics in host social networks (e.g., [72]). For instance, just as in microbial science, parasite genetic markers could be used to build host social networks because parasite transmission networks (i.e., based on hosts sharing parasites with the same genetic markers) are more likely to become established between host individuals that are strongly linked in social networks [75].

Consider Several Networks: The Multilayer Network Approach

Host–parasite networks have been studied as disconnected from other networks (i.e., as monolayer networks), characterised at a single point in space and time, and/or aggregated over multiple spatial locations and times. However, ecological processes affecting interactions in a target

community (e.g., hosts–parasites) can also affect other sets of interactors within the community (e.g., hosts–mutualists) or have consequences over communities at different points in space and time. Therefore, a particular network can be dependent on, and connected to, other networks of interactors. Such complex systems can be analysed as networks of networks, that is, multilayer networks [63,76] (Figure 1C). In this framework, interlayer edges connect counterpart interactors from different networks, hence interactors that appear in both layers have two instances corresponding to different state nodes, which can have different properties within the multilayer network. In other words, for example, state nodes can belong to different modules, but this will depend on the relative weights of interlayer and intralayer edges. Following this example, in ecological terms, module composition can be explained by the extent to which processes in one layer affect those in other layers [76]. Hence, the multilayer framework represents an increasingly realistic approach to study host–parasite interactions, although the amounts of data required can be challenging [63].

Control Disease Transmission in Human-Disrupted Habitats

Human-mediated disruptions to natural host–parasite networks may result from the encroachment of suburbs, agriculture, and aquaculture on natural environments (e.g., [77,78]). The unnaturally high densities of cultured species (e.g., grazing livestock, salmon in sea cages) may predispose them to become interactors within local wild host–parasite networks and/or vector borne-parasite networks. Determining the impact of habitat alteration on network structure could serve to better assess changes to disease dynamics, including zoonoses, and thus the risks for conservation and public health [79]. For instance, Samsing *et al.* [80] analysed salmon farms as nodes that were connected by biophysical parameters and, thus, they built a unipartite salmon-farm network for lice dispersal along the Norwegian coastline. According to their connectivity results, these authors presented a management plan consisting of a topological arrangement of salmon farms aimed at 'disconnecting' lice populations and reducing lice spread. More studies like this one can be useful to develop effective disease contingency plans, and improve the sustainability of the aquaculture or cattle industry, as well as our understanding of global anthropogenic change.

Furthermore, the increased close contact between human and wildlife because of environmental degradation has increased the probability of parasite spillover into humans [81]. Identifying host species that are key for the emergence of zoonotic diseases, as well as the development of computational tools to forecast infectious disease outbreaks, will help to address fundamental challenges in public health [82,83]. Network analysis can be a useful tool to map areas of high risk of zoonotic diseases for humans based on host geographic distribution, phylogenetic affinity, and/or social behavioural data [39,81]. For example, resolving the topology of bipartite and unipartite networks has proven useful to quantify and predict the importance of rodent host species in the transmission of pathogens to humans [82].

Concluding Remarks

Parasite ecologists and evolutionary ecologists are extending and integrating the use of network analysis to study host–parasite communities. This implementation has made it possible to reveal ecological and evolutionary processes that would otherwise have been neglected. Therefore, network analysis opens up the path to move parasitology from a descriptive to a predictive science and allows it to uncover the mechanisms that underlie interactions. In addition, network analysis has shown that, although parasites tend to play a peripheral role within a community, they are key to maintaining the structure of the network of interactions, and hence ecological and evolutionary processes of communities. Moving forward, it would be vital to establish a public online database of host–parasite network datasets similar to that of Sah *et al.* [84] for social networks to ensure reproducibility of the studies. This common database, encompassing both

Outstanding Questions

Can network analysis help to predict coevolutionary dynamics of hosts and parasites?

What characteristics make host individuals of different species play the same roles for parasite communities?

How does a host–parasite network relate to other sets of interactors (i.e., layers) within the same community? How does the disruption of a natural host–parasite network affect the natural functioning of the entire community?

How does global change and the extinctions predicted to ensue affect the loss of host–parasite interactions? What are their consequences for ecosystem functioning?

Can network analysis help practitioners to minimise transmission of undesired pathogens from cultured species to wildlife communities?

Can network analysis reveal the threshold of infection of biological systems which causes the collapse of an ecosystem or the extinction of a species?

field and experimental data collected on host–parasite networks, would simultaneously ensure availability of data to the wider scientific community. In addition, more studies taking advantage of the latest methodologies developed in mainstream ecological research on interaction networks (see Box S1 in the supplemental information online for a list of available tools) are needed to gain a deeper understanding and to improve our predicting ability to prevent the emergence of pathogens. These studies will allow us, for example, to account for more complex and multilayered interactions, delve deeper into the processes underpinning biological invasions, the repercussions of habitat perturbations, and minimise the transmission of undesired pathogens (see Outstanding Questions).

Acknowledgments

We thank two anonymous reviewers and the chief editor, Dr Kong, for their comments and suggestions to improve our former version of the manuscript.

Declaration of Interests

The authors declare no competing interests.

Supplemental Information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.pt.2021.01.005>.

References

- Fontaine, C. *et al.* (2011) The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14, 1170–1181
- Poisot, T. *et al.* (2013) Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecol. Lett.* 16, 853–861
- Thompson, R.M. *et al.* (2012) Food webs: Reconciling the structure and function of biodiversity. *Trends Ecol. Evol.* 27, 689–697
- Bascompte, J. *et al.* (2019) Mutualistic interactions reshuffle the effects of climate change on plants across the tree of life. *Sci. Adv.* 5, eaav2539
- Poulin, R. (2010) Network analysis shining light on parasite ecology and diversity. *Trends Parasitol.* 26, 492–498
- Dormann, C.F. *et al.* (2017) Identifying causes of patterns in ecological networks: opportunities and limitations. *Annu. Rev. Ecol. Syst.* 48, 559–584
- Llopis-Belenguer, C. *et al.* (2020) Native and invasive hosts play different roles in host–parasite networks. *Ecography* 43, 559–568
- Pilosof, S. *et al.* (2014) Host–parasite network structure is associated with community-level immunogenetic diversity. *Nat. Commun.* 5 art. no 5172
- Pedersen, A.B. and Fenton, A. (2007) Emphasizing the ecology in parasite community ecology. *Trends Ecol. Evol.* 22, 133–139
- Olesen, J.M. *et al.* (2007) The modularity of pollination networks. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19891–19896
- Coux, C. *et al.* (2016) Linking species functional roles to their network roles. *Ecol. Lett.* 19, 762–770
- Bellay, S. *et al.* (2011) A host–endoparasite network of Neotropical marine fish: are there organizational patterns? *Parasitology* 138, 1945–1952
- Poisot, T. *et al.* (2011) A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.* 14, 841–851
- Bellay, S. *et al.* (2013) Developmental stage of parasites influences the structure of fish–parasite networks. *PLoS One* 8, e75710
- Campião, K.M. *et al.* (2015) Diversity and patterns of interaction of an anuran–parasite network in a neotropical wetland. *Parasitology* 142, 1751–1757
- Graham, S.P. *et al.* (2009) Nestedness of ectoparasite–vertebrate host networks. *PLoS One* 4, e7873
- Bellay, S. *et al.* (2015) Ectoparasites and endoparasites of fish form networks with different structures. *Parasitology* 142, 901–909
- Poisot, T. *et al.* (2013) Facultative and obligate parasite communities exhibit different network properties. *Parasitology* 140, 1340–1345
- McQuaid, C.F. and Britton, N.F. (2013) Host–parasite nestedness: A result of co-evolving trait-values. *Ecol. Complex.* 13, 53–59
- Preston, D.L. *et al.* (2014) Complex life cycles in a pond food web: Effects of life stage structure and parasites on network properties, trophic positions and the fit of a probabilistic niche model. *Oecologia* 174, 953–965
- Bellay, S. *et al.* (2015) The patterns of organisation and structure of interactions in a fish–parasite network of a neotropical river. *Int. J. Parasitol.* 45, 549–557
- Poulin, R. *et al.* (2013) Phylogeny determines the role of helminth parasites in intertidal food webs. *J. Anim. Ecol.* 82, 1265–1275
- Cirtwill, A.R. and Stouffer, D.B. (2015) Concomitant predation on parasites is highly variable but constrains the ways in which parasites contribute to food web structure. *J. Anim. Ecol.* 84, 734–744
- Lafferty, K.D. *et al.* (2006) Parasites dominate food web links. *Proc. Natl. Acad. Sci. U. S. A.* 103, 11211–11216
- Pilosof, S. *et al.* (2015) Potential parasite transmission in multi-host networks based on parasite sharing. *PLoS One* 10, e0117909
- Dallas, T. *et al.* (2017) Predicting cryptic links in host–parasite networks. *PLoS Comput. Biol.* 13, e1005557
- Dallas, T.A. *et al.* (2019) Host traits associated with species roles in parasite sharing networks. *Oikos* 128, 23–32
- Krasnov, B.R. *et al.* (2012) Phylogenetic signal in module composition and species connectivity in compartmentalized host–parasite networks. *Am. Nat.* 179, 501–511
- MacIntosh, A.J.J. *et al.* (2012) Monkeys in the middle: parasite transmission through the social network of a wild primate. *PLoS One* 7, e51144
- Woodward, G. *et al.* (2005) Body size in ecological networks. *Trends Ecol. Evol.* 20, 402–409
- Lima Jr., D.P. *et al.* (2012) Patterns of interactions of a large fish–parasite network in a tropical floodplain. *J. Anim. Ecol.* 81, 905–913
- Braga, M.P. *et al.* (2014) Patterns of interaction between Neotropical freshwater fishes and their gill Monogeneoidea (Platyhelminthes). *Parasitol. Res.* 113, 481–490
- Dallas, T. and Cornelius, E. (2015) Co-extinction in a host–parasite network: identifying key hosts for network stability. *Sci. Rep.* 5, 13185

34. Dallas, T.A. *et al.* (2019) Detecting parasite associations within multi-species host and parasite communities. *Proc. R. Soc. B Biol. Sci.* 286, 20191109
35. Verde Arregoitia, L.D. *et al.* (2013) Phylogenetic correlates of extinction risk in mammals: species in older lineages are not at greater risk. *Proc. R. Soc. B Biol. Sci.* 280, 20131092
36. Dáttilo, W. *et al.* (2020) Species-level drivers of mammalian ectoparasite faunas. *J. Anim. Ecol.* 89, 1754–1765
37. Campião, K.M. and Dáttilo, W. (2020) Biological drivers of individual-based anuran-parasite networks under contrasting environmental conditions. *J. Helminthol.* 94, e167
38. Godfrey, S.S. (2013) Networks and the ecology of parasite transmission: A framework for wildlife parasitology. *Int. J. Parasitol. Parasites Wildl.* 2, 235–245
39. Albery, G.F. *et al.* (2021) Unifying spatial and social network analysis in disease ecology. *J. Anim. Ecol.* 90, 45–61
40. Godfrey, S.S. *et al.* (2010) Social network structure and parasite infection patterns in a territorial reptile, the tuatara (*Sphenodon punctatus*). *Int. J. Parasitol.* 40, 1575–1585
41. Sato, T. *et al.* (2012) Nematomorph parasites indirectly alter the food web and ecosystem function of streams through behavioural manipulation of their cricket hosts. *Ecol. Lett.* 15, 786–793
42. Poulin, R. (2018) Modification of host social networks by manipulative parasites. *Behaviour* 155, 671–688
43. Poulin, R. (2007) The structure of parasite communities in fish hosts: Ecology meets geography and climate. *Parassitologia* 49, 169–172
44. Guilhaumon, F. *et al.* (2012) Latitudinal mismatches between the components of mammal–flea interaction networks. *Glob. Ecol. Biogeogr.* 21, 725–731
45. Dallas, T. and Poisot, T. (2018) Compositional turnover in host and parasite communities does not change network structure. *Ecography* 41, 1534–1542
46. Plosos, S. *et al.* (2013) Temporal dynamics of direct reciprocal and indirect effects in a host–parasite network. *J. Anim. Ecol.* 82, 987–996
47. Bellekom, B. *et al.* (2021) A network perspective on the vectoring of human disease. *Trends Parasitol.* 37, 391–400
48. Bordes, F. *et al.* (2015) Habitat fragmentation alters the properties of a host–parasite network: rodents and their helminths in South-East Asia. *J. Anim. Ecol.* 84, 1253–1263
49. Britton, J.R. (2013) Introduced parasites in food webs: New species, shifting structures? *Trends Ecol. Evol.* 28, 93–99
50. 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
51. Anderson, T.K. and Sukhdeo, M.V.K. (2011) Host centrality in food web networks determines parasite diversity. *PLoS One* 6, e26798
52. Amundsen, P.-A. *et al.* (2013) New parasites and predators follow the introduction of two fish species to a subarctic lake: implications for food-web structure and functioning. *Oecologia* 171, 993–1002
53. Hernandez, A.D. and Sukhdeo, M.V.K. (2008) Parasites alter the topology of a stream food web across seasons. *Oecologia* 156, 613–624
54. Poulin, R. and Leung, T.L.F. (2011) Body size, trophic level, and the use of fish as transmission routes by parasites. *Oecologia* 166, 731–738
55. Roy, H.E. and Lawson Handley, L.-J. (2012) Networking: a community approach to invaders and their parasites. *Funct. Ecol.* 26, 1238–1248
56. Benesh, D.P. and Kalbe, M. (2016) Experimental parasite community ecology: intraspecific variation in a large tapeworm affects community assembly. *J. Anim. Ecol.* 85, 1004–1013
57. Cleaveland, S. *et al.* (2001) Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. *Philos. Trans. R. Soc. B Biol. Sci.* 356, 991–999
58. Woolhouse, M.E.J. *et al.* (2001) Population biology of multihost pathogens. *Science* 292, 1109–1112
59. Gravel, D. *et al.* (2019) Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. *Ecography* 42, 401–415
60. Walker, J.G. *et al.* (2017) Uncertain links in host–parasite networks: lessons for parasite transmission in a multi-host system. *Philos. Trans. R. Soc. B Biol. Sci.* 372, 20160095
61. Godoy, O. (2019) Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. *Funct. Ecol.* 33, 1190–1201
62. Bolker, J. (2012) Model organisms: There's more to life than rats and flies. *Nature* 491, 31–33
63. Hutchinson, M.C. *et al.* (2019) Seeing the forest for the trees: Putting multilayer networks to work for community ecology. *Funct. Ecol.* 33, 206–217
64. Guimera, R. and Sales-Pardo, M. (2009) Missing and spurious interactions and the reconstruction of complex networks. *Proc. Natl. Acad. Sci. U. S. A.* 106, 22073–22078
65. Blüthgen, N. *et al.* (2006) Measuring specialization in species interaction networks. *BMC Ecol.* 6, 9
66. Boulinier, T. *et al.* (1998) Estimating species richness: The importance of heterogeneity in species detectability. *Ecology* 79, 1018–1028
67. Rudolf, V.H.W. and Lafferty, K.D. (2011) Stage structure alters how complexity affects stability of ecological networks. *Ecol. Lett.* 14, 75–79
68. Poisot, T. *et al.* (2016) Describe, understand and predict: why do we need networks in ecology? *Funct. Ecol.* 30, 1878–1882
69. Delmas, E. *et al.* (2019) Analysing ecological networks of species interactions. *Biol. Rev.* 94, 16–36
70. Pavoine, S. and Bonsall, M.B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.* 86, 792–812
71. Dehling, D.M. and Stouffer, D.B. (2018) Bringing the Eltonian niche into functional diversity. *Oikos* 127, 1711–1723
72. Gilbertson, M.L.J. *et al.* (2018) Incorporating genomic methods into contact networks to reveal new insights into animal behaviour and infectious disease dynamics. *Behaviour* 155, 759–791
73. Clare, E.L. *et al.* (2019) Approaches to integrating genetic data into ecological networks. *Mol. Ecol.* 28, 503–519
74. Hutchinson, M.C. *et al.* (2017) paco: implementing Procrustean Approach to Cophylogeny in R. *Methods Ecol. Evol.* 8, 932–940
75. VanderWaal, K.L. *et al.* (2014) Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *J. Anim. Ecol.* 83, 406–414
76. Plosos, S. *et al.* (2017) The multilayer nature of ecological networks. *Nat. Ecol. Evol.* 1, 0101
77. Start, D. *et al.* (2020) Urbanization reshapes a food web. *J. Anim. Ecol.* 89, 808–816
78. Krkošek, M. *et al.* (2005) Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proc. R. Soc. B Biol. Sci.* 272, 689–696
79. Espinaze, M.P.A. *et al.* (2018) Domestic mammals facilitate tick-borne pathogen transmission networks in South African wildlife. *Biol. Conserv.* 221, 228–236
80. Samsing, F. *et al.* (2017) Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. *Landsc. Ecol.* 32, 1953–1967
81. Stephens, P.R. *et al.* (2016) The macroecology of infectious diseases: a new perspective on global-scale drivers of pathogen distributions and impacts. *Ecol. Lett.* 19, 1159–1171
82. Bordes, F. *et al.* (2017) Forecasting potential emergence of zoonotic diseases in South-East Asia: network analysis identifies key rodent hosts. *J. Appl. Ecol.* 54, 691–700
83. Han, B.A. *et al.* (2015) Rodent reservoirs of future zoonotic diseases. *Proc. Natl. Acad. Sci. U. S. A.* 112, 7039–7044
84. Sah, P. *et al.* (2019) A multi-species repository of social networks. *Sci. Data* 6, 44
85. Johnson, P.T.J. *et al.* (2010) When parasites become prey: Ecological and epidemiological significance of eating parasites. *Trends Ecol. Evol.* 25, 362–371
86. Canard, E.F. *et al.* (2014) Empirical evaluation of neutral interactions in host–parasite networks. *Am. Nat.* 183, 468–479
87. Dallas, T.A. *et al.* (2018) Gauging support for macroecological patterns in helminth parasites. *Glob. Ecol. Biogeogr.* 27, 1437–1447
88. Bellay, S. *et al.* (2018) Host–parasite networks: an integrative overview with tropical examples. In *Ecological Networks in the Tropics* (Wesley, D. and Rico-Gray, V., eds), pp. 127–140, Springer International Publishing
89. Morris, R.J. *et al.* (2014) Antagonistic interaction networks are structured independently of latitude and host guild. *Ecol. Lett.* 17, 340–349