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CONCEPT

Expanding network ecology in freshwater ecosystems

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Abstract

1. Research in freshwater ecosystems has always had a strong focus on ecological interactions. The vast majority of studies, however, have investigated trophic interactions and food webs, overlooking a wider suite of non-trophic interactions (e.g. facilitation, competition, symbiosis and parasitism) and the ecological networks they form.
2. Without a complete understanding of all potential interactions, ranging from mutualistic through to antagonistic, we may be missing important ecological processes with consequences for ecosystem assembly, structure and function. Ecological networks can be constructed at different scales, from genes to ecosystems, but also local to global, and as such there is significant opportunity to put them to work in freshwater research.
3. To expand beyond food webs, we need to leverage technological and methodological advances and look to recent research in marine and terrestrial systems—which are far more advanced in terms of detecting, measuring and contextualising ecological interactions.
4. Future studies should look to emerging technologies to aid in merging the wide range of ecological interactions in freshwater ecosystems into networks to advance our understanding and ultimately increase the efficacy of conservation, management, restoration and other applications.

KEYWORDS
ecological interactions, ecological networks, multilayer networks, spatial networks

> When one starts to trace out the dependence of one animal upon another, one soon realises that it is necessary to study the whole community living in one habitat, since the interrelations of animals ramify so far.
>
> Elton (1927)

1 | INTRODUCTION

Ecological interactions and freshwater ecosystems have a long partnership, with early studies by ecologists such as Kathleen Carpenter (1925), Charles Elton (1927, 1929) and G. Evelyn Hutchinson (1941), highlighting the importance of predation and competition, amongst other interactions. A diverse array of interactions has been investigated in freshwaters (predation, parasitism, herbivory, facilitation and symbioses; Holomuzki et al., 2010); however, the vast majority of research has focused on trophic interactions and the food webs they generate (Silknetter et al., 2020). Although this bias is common to all ecosystems (Ings et al., 2009), there is a substantial body of research in marine and terrestrial environments investigating a range of different types of interactions (Hutchinson et al., 2019; Kéfi et al., 2015). Investigating the full spectrum of mutualistic and antagonistic interactions has the potential to make great advances through combining different types of interactions together using a network and complexity science framework (Harvey et al., 2017), something which is less common in freshwaters.

The lack of information on non-trophic interactions, and the restricted development of network ecology, in freshwaters is problematic for a number of reasons. First, non-trophic interactions have been shown to play a crucial role in the structure and function of ecosystems (Fricke et al., 2019; Rogers et al., 2021), as well as the vital ecosystem services they support (The QUINTESSENCE Consortium, 2016). Second, freshwater ecosystems have distinctive eco-evolutionary conditions (e.g. the colonisation and adaptive radiation of a small number of taxonomic groups; Wootton, 1988), unique environmental conditions and high biodiversity (Dudgeon et al., 2006) and are experiencing significant rates of poorly explained biodiversity decline (WWF, 2020), all of which make them a priority ecosystem that we need to understand. Third, without a comprehensive understanding of ecological interactions, predictive ecology is not possible, and across other ecosystems ecological networks have been shown to provide valuable and accurate insights for conservation, restoration and management (Windsor et al., 2022, 2023). Finally, it is important to understand the differences between different ecological networks (i.e. terrestrial vs. freshwater; Chase, 2000), including those composed of non-trophic interactions, for the purposes of both fundamental and applied ecology.

Expanding our current focus from food webs to complete ecological networks, encapsulating the wide array of different ecological interactions, is the next step in this field. Below I outline some of the major outstanding gaps in our knowledge, how we might go about collecting data to assemble complete ecological networks, as well as the benefits and challenges of this avenue of research. It is my aim that this manuscript stimulates research in this area of freshwater ecology—one that I contend is of critical importance to understanding how and why these ecosystems are rapidly degrading.

2 | ECOLOGICAL INTERACTIONS IN FRESHWATERS

When most people think about ecological networks, they have interspecific interactions in mind (Figure 1). As such, in this section, I focus on this subset of ecological networks for simplicity and clarity. In a latter section, however, I provide more comprehensive discussion surrounding where network thinking could be applied from cellular to global scales (see Section 5).

Ecological interactions in freshwater ecosystems range from mutualistic through to antagonistic, as is the case in other ecosystems. Of the interactions visualised in Figure 1, there is evidence for the vast majority, yet they are often investigated as isolated components of the ecosystem, either focusing on individual taxa or on types of interaction. Very rarely are network analyses used to understand the wider structure, function or context of these ecological interactions. It is not the purpose of this section to provide an exhaustive list or comprehensive explanation of the different types of interactions that might be present in freshwaters, especially considering others have done so previously (e.g. positive ecological interactions; Silknetter et al., 2020). Here, however, I provide a brief summary of the interactions identified to date as an introduction to set the scene for the latter topic of generating more complete ecological networks in freshwater ecosystems (Section 4).

At the mutualistic end of the spectrum, symbioses are one of the obvious interactions that result in mutual benefits, with ample examples in freshwater environments, including crayfish–annelids (Brown et al., 2002), sponges–algae (Wilkinson, 1980) and plants–fish (Anderson et al., 2009). Facilitation, which can be mutualistic or commensalistic, is also commonly observed in freshwaters (Silknetter et al., 2020), and its importance has been shown experimentally and across a range of taxa (Albertson et al., 2021). This process can generate benefits across different functional groups, for example shredders can process coarse particulate organic matter into fine particulate organic matter, allowing other organisms to interact and ingest the smaller materials (Heard & Richardson, 1995; Iwai et al., 2009; Navel et al., 2011). There are a range of other commensalistic interactions in freshwaters, where one organism benefits whilst the other is neither positively or negatively affected, for example phoresis (attachment for the purpose of dispersal; Silknetter et al., 2020) and case-building with vegetative materials (Mendes et al., 2019). Yet, this class of interactions has been less well documented in comparison to others.

Antagonistic interactions, forming the majority of research to date (Albertson et al., 2021; Holomuzki et al., 2010; Silknetter et al., 2020), can be summarised into three distinct groups: amensalisms, predation (including herbivory and parasitism) and competition. Amensalisms are interactions where one organism negatively affects another with no beneficial or detrimental return effects, and they are sometimes referred to as asymmetrical competition (Lawton & Hassell, 1981). Examples of such processes in freshwaters are uncommon, yet processes such as nest-building or benthic foraging by fish may have immediate negative effects on invertebrates through physical damage and forced energy expenditure. Predation in all its forms is a primary focus of network ecology in freshwater ecosystems (Silknetter et al., 2020). There are many different forms that predator–prey or resource–consumer interactions can take—for example, plant–herbivore and host–parasite. However, these interactions all share the commonality that one organism is negatively affected and the other benefits. This research is often presented in the guise of food webs, and is a substantial subfield of freshwater ecology (Thompson et al., 2012) with a significant theoretical basis (e.g. size–structure; Hildrew et al., 2007). Competition forms the final group of antagonistic interactions where both organisms are negatively affected to one degree or another. There are several different types of competition; intraspecific and interspecific, as well as direct and indirect, and interference and exploitative (Birch, 1957). In freshwaters, there are ample examples of all types of competition (Schoener, 1983),

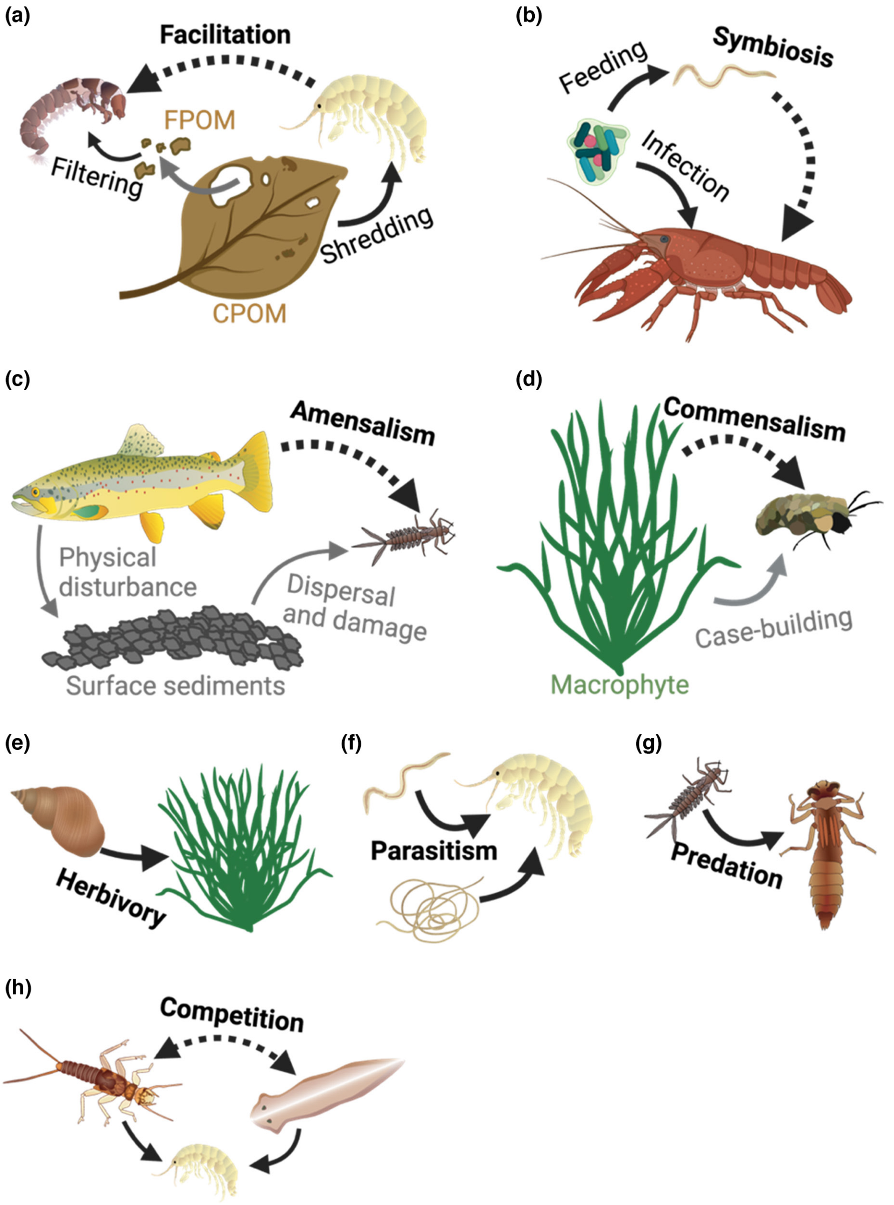

FIGURE 1 Examples of direct and indirect ecological interactions in freshwater ecosystems. (a) Facilitation between two detritivores which feed on different sizes of organic matter (fine and coarse). (b) Symbiosis between annelids and crayfish, with worms feeding on ectoparasites and biofilms that have adverse effects on crayfish. (c) Amensalistic interaction between fish and other invertebrates through intermediate influence on physical processes, such as disturbance of sediments. (d) Commensalistic interaction between an aquatic macrophytes and a case-building caddisfly using plant material as case material. (e) Herbivorous interaction with a snail feeding on a plant. (f) Parasitic interactions between endoparasites and freshwater shrimp. (g) Predator–prey interaction between a dragonfly and a mayfly. (h) Competition between two predators over a shared prey.

and secondary to predation, competition is one of the most commonly investigated ecological interactions (Silknetter et al., 2020).

Although there is literature supporting a breadth of interspecific interactions in freshwater ecosystems, it is not common to assess these interactions in a network context and our understanding of their relative importance is limited. Across other ecosystems, for example terrestrial and marine, there is a more complete understanding of the role of mutualistic and antagonistic interactions in determining the assembly, structure and function of ecosystems, whilst also appreciating that the strength of these interactions varies in space and time (Fontaine et al., 2011). This research in terrestrial and marine ecosystems has led to significant developments in knowledge, conservation, restoration and affiliated policy and management decisions (Hutchinson et al., 2019; Windsor et al., 2021). Further developing our understanding of these processes in different freshwater habitats and ecosystems is therefore a priority.

3 | FILLING THE GAPS IN FRESHWATER ECOLOGICAL NETWORKS

Food web research has dominated network ecology in freshwater ecosystems primarily due to technological and methodological constraints surrounding the identification of other ecological interactions. Direct observations, using a variety of different methods, have been the mainstay for detecting interactions in freshwaters (e.g. bankside observation and underwater snorkelling; Jackson et al., 2017; Power et al., 1988). Yet, there are a range of methods that could be leveraged to detect and quantify ecological interactions in freshwater ecosystems (Table 1), and therefore construct complex ecological networks (see Section 4). Technological and methodological developments in this sphere are recent and this is an emerging field of research (Besson et al., 2022). Below I summarise some of the current options for detecting and quantifying ecological interactions and constructing ecological networks in freshwater

TABLE 1 Potential methods for constructing ecological networks in freshwater ecosystems.

Method	Example techniques	Ecological interactions	Benefits	Drawbacks
Direct observation	Gut content analysis Underwater surveys	Predation Competition Facilitation Symbiosis Parasitism Commensalism Amensalism	Well established and understood Low consumable costs Quantitative data	Time-consuming Requires high levels of expertise Slow to produce data Spatially and temporally restricted
Video capture and processing	Camera traps Continuous video recording Artificial intelligence and machine learning (e.g. deep learning, convolutional neural networks)	Predation Competition Facilitation Symbiosis Parasitism Commensalism Amensalism	Continuous Real time Spatially distributed Automated	High computational requirements Requires interpretation and expertise
Stable Isotopes	δ^{15}N, δ^{13}C and δ^{34}S Ratios Mixing models	Predation Competition	Quantitative data Long-term detection (i.e. days to weeks)	Low resolution (pooled samples) Difficulties distinguishing sources Infers interactions based on isotope signatures (not direct detection)
Molecular methods	Barcoding Metabarcoding Metagenomics	Predation Symbiosis[a] Parasitism[a]	Detects cryptic interactions Additional information: • Evolutionary (e.g. phylogenies) • Functional (for metagenomics)	Qualitative interactions (binary networks) High expertise Reliant on reference database coverage
Statistical inference	Maximum entropy Co-occurrence analysis Latent variable analysis Hierarchical models	Predation Competition Facilitation Symbiosis Parasitism Commensalism Amensalism	Reduced data collection requirements Potential for greater spatial and temporal coverage (presence–absence and abundance)	Unknown type I and type II errors Difficult to distinguish between direct and indirect interactions

[a] Passive detection (i.e. incidental detection of a symbiote and/or parasite from a whole-body sample of the host).

ecosystems. These methods can be used in isolation or conjunction, as long as data integration is appropriately considered (see Cuff et al., 2022).

3.1 | Video capture and processing

A promising avenue of technological development surrounds the capture and analysis of both images and videos. This suite of methods offers an opportunity to gain information on a variety of ecological interactions, from mutualistic through to antagonistic. Furthermore, these data can be collected at different scales—for example individual through to interspecific ecological networks. These methods have already been used to understand herbivory in fish (Ditria et al., 2021), movement behaviour (Lopez-Marcano et al., 2021) and terrestrial species interactions (e.g. plant–pollinator interactions; Ratnayake et al., 2021).

The essence of these methods is to collate a series of images or videos and process them using machine learning or artificial intelligence algorithms, including techniques such as deep learning (Borowiec et al., 2022; Christin et al., 2019). Although this area of research is not well developed, there are examples where video recording and post-processing are used to identify sections of video to manually identify interactions (Droissart et al., 2021). Building on the current algorithms for species identification and movement tracking may be possible to create a series of rules to detect different types of ecological interaction: (i) predation, when two individuals come into close proximity and the signal from one individual is lost; (ii) parasitism or symbiosis, when a signal from one organism is detected consistently on another (combined with natural history information to determine the degree to which the interaction is antagonistic or mutualistic); (iii) resource competition, when three individuals interact and the signal from one is lost and signal from another moves away from the remaining signal (N.B. this would be limited to direct interactions, and would not account for competition between organisms interacting with resources asynchronously, for example, nocturnal and day-time feeding by different organisms).

Methods of this nature are non-invasive, and compared to other options for constructing ecological networks (i.e. dietary analyses), they do not require destructive sampling. This is a substantial benefit, and means that there is an opportunity to look at how interactions change over time with the same individuals. This opens the door for understanding the evolution and adaptation of ecological interactions over time in response to biotic or abiotic changes (e.g. biological invasions, temperature change or nutrient additions). Further to this, and as mentioned above, this method allows for the simultaneously collection of information on multiple ecological interactions. Again, this is highly beneficial and allows for the construction of the networks (see Section 4) with a reduced likelihood of issues surrounding aggregating different types of data from multiple methods.

There are also limitations to be aware of. Detecting interactions using video footage is computationally expensive, and also requires substantial data storage capacity as file sizes for video of suitable resolution and frame rate are large (Droissart et al., 2021). As such, the capacity to record and detect a suitable number of interactions and thus achieve an acceptable sampling completeness for networks may be out of reach of many researchers who do not have access to high-performance computing suites or cloud computing platforms. There are methods of reducing the computational demand of these methods, for example recording a 1-min video every 15 min rather than capturing continuous video footage, as is the case for audio recordings (e.g. Silent Cities Project; Challéat et al., 2020). Alternatively, using motion sensor cameras which record only when movement is detected may be feasible. It is, however, worth noting that adapting sampling regimes in such a way compromises the ability to continuously detect ecological interactions and provide real-time monitoring.

3.2 | Stable isotopes

Classically, stable isotopes of carbon, nitrogen and sulphur (^{13}C, ^{15}N and ^{34}S) have been used to understand trophic interactions in freshwaters (Layman et al., 2012). Individual interactions can be monitored, but also entire ecological networks—for example, mixing models, and other techniques, have been used to construct freshwater food webs (Parnell et al., 2013). There are, however, opportunities for investigating other ecological interactions using stable isotopes. Specifically, current methods can be adjusted to investigate resource competition by determining the overlap in isotope space for two consumers (Newsome et al., 2007), where high overlap would indicate a high level of resource competition. In this instance, the overlap could also be used as a relative measure of interaction strength (i.e. 0%–100%). Further to this, host–parasite interactions can be investigated using stable isotopes, including both the identity and strength of interactions, but also the effects of parasites on host interactions (Sabadel et al., 2019). With an ever-increasing accuracy and precision of stable isotope analysis, the ability to detect and understand ecological interactions at greater resolutions is growing. For example, ultra-low element abundance analysers allow for the quantification of stable isotopes in individual invertebrates due to low detection limits (≤10 nmol), something which has not been possible prior to this point. This offers the opportunity to construct individual networks, as well as better resolve the intraspecific variation in interaction strengths.

A major benefit of using stable isotopes is that methods such as mixing models make it possible to quantify ecological interactions and understand longer-term patterns of interactions (e.g. stable isotopes can represent diet over weeks to years; Davis & Pineda-Munoz, 2016). For example, through calculating the intake of different resources from the environment based on the enrichment of the different stable isotopes, or calculating overlap in resource, it is possible to gain quantitative estimates of predation and resource competition, respectively. Thus, unlike many other methods, stable isotopes provide an opportunity to derive quantitative estimates of interaction strengths over long periods of time.

Despite the benefits of stable isotopes, there are some limitations. In particular, the biological/ecological resolution of stable isotope-based methods is lower in comparison to other methods. This mainly results from the fact that stable isotopes do not directly observe the ecological interactions. Instead, the stable isotope concentrations measured in organisms across an ecosystem are used to infer the consumption of different resources based on a shared isotopic signature present in both the resource and the consumer. Thus, in some cases, it is not possible to discriminate between the use of different resources if they have the same isotopic signature (Boecklen et al., 2011). Therefore, the quantitative ability of stable isotopic analyses is somewhat offset by the lack of resolution.

3.3 | Molecular methods

Using molecular tools to understand ecological interactions is an established but rapidly evolving area of research (Cuff et al., 2022; Derocles et al., 2018; Dubart et al., 2021). The methods have primarily been described for terrestrial ecosystems (Evans et al., 2016), yet they have been applied in aquatic systems (Compson et al., 2019) and new techniques (e.g. RNA barcoding to discriminate between scavenging and predation; Neidel et al., 2022) could be translated with relative ease. Currently, molecular tools have been paired with existing methods of sampling individual organisms (e.g. pond nets, Surber samplers and Eckman grab samplers), but also used with novel collection methods for communities, for example filtering water samples (Peixoto et al., 2021) or using passive samplers (Verdier et al., 2022) to analyse environmental DNA. The entire spectrum of ecological interactions, from mutualistic through to antagonistic, could be assessed using molecular methods. As such, the applications of these techniques for ecological network construction are relatively unbounded, and new methods are continually being developed that either improve the accuracy or coverage of the resulting ecological networks. For a detailed appraisal of the applications, benefits and challenges of molecular techniques for detecting ecological interactions, see Derocles et al. (2018) and Evans et al. (2016). Below, however, I highlight some of the most relevant benefits and challenges of these methods for applications for advancing the field of network ecology in freshwater ecosystems.

Molecular methods for ecological interaction detection, such as DNA metabarcoding, have typically been destructive, yet there are a range of methods for non-invasive sampling (e.g. faecal samples and mandible/mouthpart swabs; Evans & Kitson, 2020). Furthermore, they surpass many methods of collecting network data as many methods are limited in their ability to detect cryptic species or those which are difficult to identify (Derocles et al., 2015; Evans et al., 2016; Wirta et al., 2014). As well as offering a complementary method for detecting interactions which can fill gaps in other network construction methods, molecular methods offer an opportunity to gain extra information on networks. For example, it is possible to construct phylogenetic trees for species where full genome sequences exist, or where samples are sufficient for sequencing the full genome (which is far less expensive: ~$1000 USD per species, depending on genome length; Lewin et al., 2018). This provides an opportunity to understand how evolutionary processes influence interactions (see Segar et al., 2020).

A limitation of molecular techniques is that generating quantitative data, although technically possible (Thomas et al., 2016), is fraught with biases and caveats (Elbrecht et al., 2017; Elbrecht & Leese, 2015). This means that networks constructed using these methods are limited to binary interactions, unless you have replicated sampling (i.e. multiple individuals per species) in which case you can generate information on the frequency of occurrence of interactions and produce semi-quantitative networks (Cuff et al., 2022). Molecular methods are also strongly dependent on the quality and coverage of reference databases (Keck & Altermatt, 2022). Although large-scale projects have drastically improved the coverage of barcode databases (e.g. GenBank and BOLD; Benson et al., 2013; Ratnasingham & Hebert, 2007), there are still gaps for certain groups of organisms—including aquatic species (Weigand et al., 2019). Therefore, although you might be able to detect a wider range of ecological interactions using molecular methods, it may be the case that most of those interactions are not quantified, or limited to identifying interactions between organisms which cannot be taxonomically identified to a meaningful resolution. Furthermore, in the absence of adequate barcode databases, and thus species identities, vital data on biological traits (e.g. body size, feeding habits, habitat use) are lost from assessments.

3.4 | Statistical inference

It is possible to construct ecological interactions, and estimate their strengths, without using methods that directly observe interactions. This suite of methods can be summarised as 'interaction inference', where alternative data types, for example presence–absence or abundance data for different groups of organisms, are used to infer either positive or negative interactions between organisms. A range of methods exist, from maximum entropy (e.g. Banville et al., 2022), through to more data intensive methods that combine a series of environmental, evolutionary and functional data to account for all other forms of variation in community structure, and ascribe the resulting unexplained variance (through latent variables) to that of biotic/ecological interactions (Ovaskainen et al., 2017).

A substantial benefit of this suite of methods is that it is not necessary to directly monitor ecological interactions, which as described above, is expensive and time-consuming. Instead, a range of more easily attainable data, such as species presence/absence and abundances, can be used. These data are also often collected at higher spatial and temporal resolutions that ecological interaction data can be automated (e.g. Besson et al., 2022) and exist in a range of long-term as well as spatially expansive, data repositories (e.g. GBIF; www.gbif.org). Thus, these methods offer the potential to generate data on ecological interactions at high spatial and temporal resolutions.

Aside from fundamental ecological concerns surrounding the use of inference methods (see Blanchet et al., 2020), it is also a limitation that there is a priori knowledge required to identify the types of interaction driving patterns in species abundances. Furthermore, differentiating between direct and indirect interactions is difficult, if not impossible, and interactive effects add extra complication.

4 | MERGING ECOLOGICAL INTERACTIONS INTO NETWORKS

Ecological interactions do not operate in isolation, they form complex interdependent networks (Melián et al., 2009). Certainly, the nature and strength of different types of interactions can be influenced by others (Kéfi et al., 2016). For example, non-trophic interactions have been shown to influence trophic interactions and enhance the persistence of food webs (Hammill et al., 2015). Assessing multiple interaction types allows for a more accurate representation of ecosystems (Fontaine et al., 2011), but also an improved understanding of the reliance of different organisms on one another (Mougi & Kondoh, 2012). This means that collecting data on one type of interaction may not tell the full story, and certainly would not provide the mechanistic and causal basis for the observed patterns. It is therefore important to collect, analyse and interpret ecological interactions, and ultimately create an information system at a useful scale for representing complex ecological systems, as well as effective decision-making surrounding their management.

Growing attention is being afforded to these merged networks, and studies have been working towards frameworks for integrating different data types in a sensible and robust manner (e.g. Cuff et al., 2022). Theoretically, it is possible to merge interactions into one network as long as the nodes represent the same units (i.e. individuals or species). There are several different methodological options for combining these data in one analytical framework. Interactions that are measured using similar units, for example resource–consumer interactions (e.g. plant–herbivore and predator–prey) are typically measured in units of mass or energy consumed, can be merged into one network without much further consideration. However, for truly widening the breadth of interactions included within freshwater ecological networks, other more complicated frameworks are needed. One set of methods that has particular promise is that of multilayer network analyses (Pilosof et al., 2017). The 'layers' in multilayer networks can be used to represent different types of interactions, communities of species, or points in time or space (Kivelä et al., 2014). There are several components of these networks: (i) physical nodes, which represent the ecological entities (e.g. species); (ii) layers, which can be single or multiple types (e.g. temporal or both spatial and temporal); (iii) state nodes, the manifestation of the physical nodes on a specific layer; and (iv) weighted or unweighted edges, which connect nodes within and between layers (intra and inter-layer edges, respectively, Pilosof et al., 2017). These features enable significant flexibility, but also align with current methods of network analysis, making multilayer networks a powerful tool for future research.

Using multilayer networks, a series of standard and novel analyses can be completed to understand important features of freshwater ecosystems (see Box 1 for an example). The benefit of including spatial and temporal elements in a network framework is that ecological dynamics can be included (Hutchinson et al., 2019), and thus previously intangible or poorly defined measures, such as stability or resilience (Van Meerbeek et al., 2021), can be investigated. For example, spatially and temporally resolved networks (i.e. ecological interactions across habitats structured around dendritic river networks) combined with adaptive network models (Maia et al., 2021; Raimundo et al., 2018) would enable an understanding of ecosystem resilience to perturbations across different scales (Moreno-Mateos et al., 2020).

Combining ecological interactions into complex networks will allow for comparisons of interactions and their relative importance for the structure and function of freshwaters. With this enhanced knowledge, it would be possible to move towards predictive ecology and better protection and conservation of freshwater ecosystems.

5 | WIDENING NETWORK ECOLOGY IN FRESHWATERS

Beyond expanding ecological networks to include a greater diversity of ecological interactions (e.g. intraspecific and interspecific interactions), there is a wider field of applied network science that can be used to investigate the interactions found in freshwaters in a broader sense. Networks can be constructed at any scale (Guimarães, 2020), from sub-cellular through to global (i.e. cell signalling through to long-distance migration), and as such freshwater ecosystems can too be viewed through a network lens at multiple scales (Figure 2). As similar premises have been explored in other papers (e.g. Lowe et al., 2006), I will not provide an exhaustive coverage of this topic here; however, I provide examples of network thinking to demonstrate the wider applicability of network science to freshwater ecology.

5.1 | Operating across scales

At small scales (e.g. cells), networks can be used to describe interactions within and between cells, tissues and organs within organisms (Kitano, 2002; Olff et al., 2009). At the sub-organismal scale, networks have been used to understand brain activity in response to different stimuli (Petri et al., 2014), cell-signalling interactions in *Caenorhabditis elegans* (Armingol et al., 2022). Understanding changes in the interactions between different organs, however, is also possible—for example, endocrine disruption and subsequent

BOX 1 A hands-on example of multilayer network construction and analysis in a freshwater context

This example is specific to streams. However, parallels can be drawn with other types of freshwater ecosystem and also other ecological questions.

Multilayer networks could be used to interrogate the biotic drivers (e.g. competition and niche partitioning) of a classic concept in stream ecology, patch dynamics (Townsend, 1989). Below is a simple example demonstrating a workflow that could be adopted to tackle such a study and the potential advances generated.

Sampling

Macroinvertebrates could be sampled using a variety of methods; however, fixed-area samplers such as Surber or Hess samplers would be best used to sample specific habitats across the stream reach as well as providing density estimates for taxa. A mesohabitat sampling regime (i.e. proportionally sampling the different habitats present across a stream reach) would sample replicates of the different habitats in the reach (e.g. riffles, pools, glides, macrophytes and fine sediments), which could also be mapped spatially (Figure B1a) to inform later multilayer network construction.

Constructing the multilayer network

Intralayer edges (i.e. the biological interactions occurring within each habitat patch; Figure B1b) could be identified and quantified using a combination of gut dissections and either visual analysis or molecular methods, for some resource–consumer interactions, and stable isotopes to characterise resource use and overlap in dietary niches to estimate interspecific competition between consumers. Interlayer edges would link the same species across different patches, but their weights are more difficult to define.

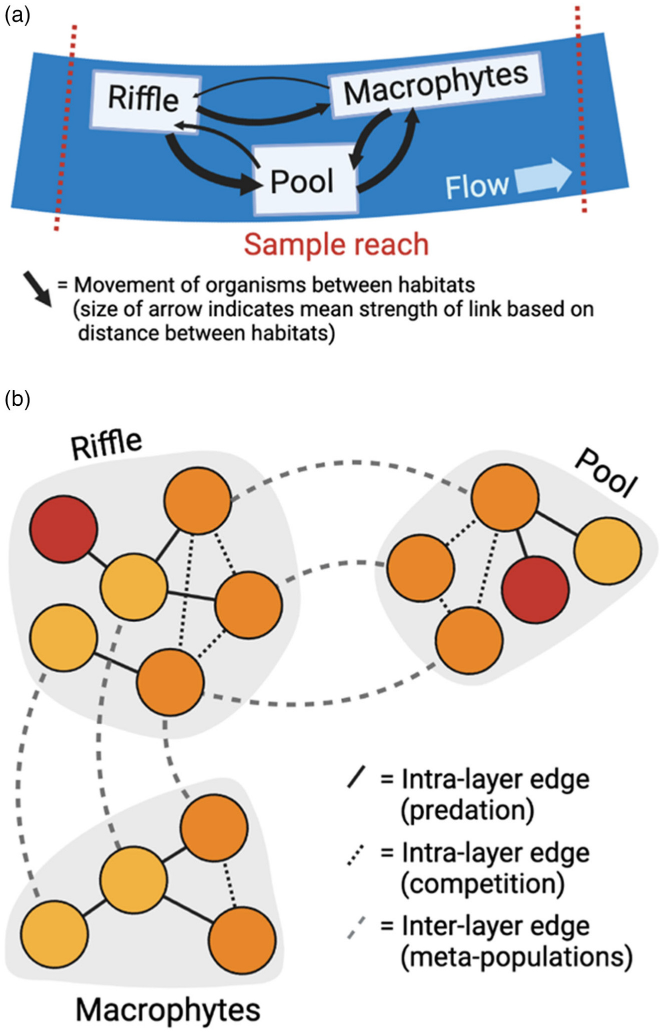

FIGURE B1 Conceptual diagrams of sampling and multilayer networks in a stream reach. (a) An example of stream reach with sample locations and links (arrows) between the locations indicating potential for movement between habitats (contingent upon flow direction and distance between patches). (b) A simplified multilayer network with links (predation and competition between different taxa (node colours indicate approximate trophic level (yellow = resource, orange = consumer, red = predator) and links between the same taxa across habitats.

Box 1 (Continued)

Nevertheless, the edges could be the Euclidean distance between patches, or distances weighted by flow direction (to account for having to move against the current to move upstream; see Figure B1a). The weights of the interlayer edges could also be adjusted for individual species based on their dispersal ability (e.g. swimming strength) or another measure of probability of movement between patches (e.g. differences in abundances of species between habitats). The weights of intra and inter-layer edges measured in different units or using different methods will likely need to be standardised (e.g. scaled to between 0 and 1), to prevent certain types of interactions biasing the subsequent network analyses.

Data analysis

The multilayer network could be analysed using standard network (e.g. connectance, nestedness or modularity) or node (e.g. betweenness or centrality) metrics to understand how species differentially use patches within a stream reach. These metrics could be calculated for individual interaction types and compared to one another to better understand how different interactions vary across habitat patches. Furthermore, the diversity of different interactions and their patch dependence (e.g. whether there are interactions that occur in only one or a handful of habitat patches) can be investigated using these techniques, amongst others commonly used to interrogate ecological networks (see Delmas et al., 2019). Careful thought is required when calculating metrics for merged networks, and further work is needed to refine methods for calculating properties such as network robustness based on networks comprised of both antagonistic and mutualistic interactions.

Meta-community models, such as that recently proposed by Terui et al. (2021), could be parameterised based on theoretical understanding of patch dynamics (e.g. competition drives individuals to find different patches—a process governed by density dependence or distance is the dominant factor driving patch occupancy in meta-communities). Subsequent comparisons between model outputs and empirical data could provide new insights.

Potential advances

Previously, patch dynamics have been investigated from either a predation or competition perspective, with limited consideration of their potential interaction, as well as other positive interactions, such as mutualisms (Liao et al., 2016). The methods above would allow for this combined analysis and understanding of the dominant driving processes under different circumstances and across environmental gradients. Furthermore, by collecting data on interactions across scales and combining these data with model outputs, there is an enhanced opportunity for deriving mechanistic and causal understanding from field data (see Poisot et al. (2016) for a more detailed discussion).

changes in hormone release and distribution could be analysed using network techniques for freshwater organisms (see review in Windsor et al., 2018). Moving up to the intraspecific interaction scale, an example provided in Figure 2a, is that of a social network between individual fish, which can be used to answer questions surrounding the dynamics of interactions over time or in response to a given stressor (e.g. neuroactive chemicals or water temperature). For interactions between different species, the classical resolution at which ecological networks are constructed, it is possible to monitor the entire range of interactions and how they may change in response to different environmental or biological factors (e.g. temperature or body size). Examples of such analyses are widespread in freshwater food web ecology (e.g. warming was shown to affects the top-down and bottom-up controls on pond food webs; Shurin et al., 2012). Finally, networks can be constructed in space, connecting habitats, ecosystems, regions or continents (Windsor et al., 2023). These spatial networks can describe a variety of different ecological interactions, for example the dispersal of individuals (Baguette et al., 2013) or the flow of genetic information between populations (Savary et al., 2021). In freshwaters, interactions could represent the unidirectional and bidirectional movement of nutrients, organisms or other components of ecosystems. For rivers, this is particularly intuitive—for example mapping ecological networks onto dendritic river networks (Peterson et al., 2013).

Network ecology provides an opportunity to integrate different scales of interactions within the same framework. Thus, you can include, for example, neurological signalling networks for individuals together with networks of social interactions between organisms to understand how decision-making alters social network structure. Through incorporating different scales, both spatial and temporal, within a unified framework, it is possible to move towards a more predictive form of ecology in freshwater ecosystems.

5.2 | Social–ecological networks

In network ecology, more generally, there has been a push towards the combination of social and ecological networks to understand

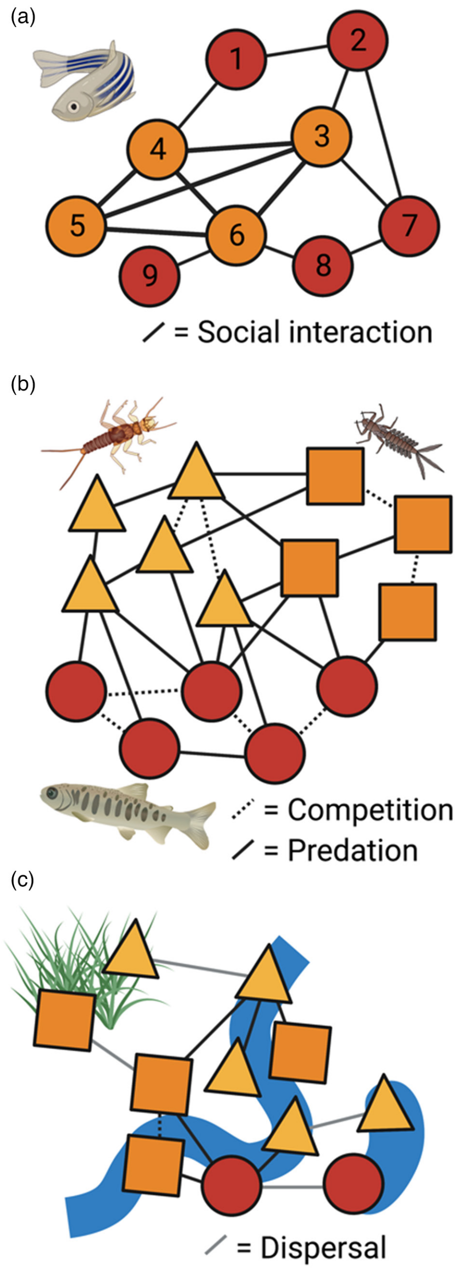

FIGURE 2 Ecological networks at different scales in freshwater environments. (a) An individual–individual network for a fish species (*Danio rerio*) where the numbers identify individual fish and colours represent core and periphery structures in the network (i.e. a densely connected subnetwork and a loosely connected series of nodes around the edges). (b) An interspecific interaction network between consumers (orange squares) and both invertebrate (yellow triangles) and vertebrate predators (red circles), including both predator–prey interactions (solid lines) and competition (dashed lines). (c) A dispersal network of organisms across ecosystems within a river catchment (shapes represent the same taxa as in b) where solid lines indicate movement between habitats.

their interactions (Felipe-Lucia et al., 2022). Doing so allows for an understanding of feedbacks between these two systems (Bodin et al., 2019), which is, in turn, useful for decision-making and management (Dee et al., 2017). To achieve this, however, not only must interactions within social networks (i.e. communication and/or knowledge sharing) and ecological networks (i.e. interspecific interactions) be measured, but also the interactions between these two networks. This is challenging, and many suggestions have been provided with regards to approaches for consolidating these two types of networks (Felipe-Lucia et al., 2022), yet there remains room for innovation and development.

Merging social and ecological networks is possible for freshwaters and would allow for an inclusion of ecosystem service provision into network analyses in these ecosystems, allowing for a direct understanding of how humans link into freshwater ecosystems in terms of the benefits they derive (Chung et al., 2021). This framework would also allow for the effects of humans on ecosystems to be incorporated (see threats-ecosystems-services framework; Dee et al., 2017; Windsor et al., 2022) and provide an enhanced and interconnected evidence base for management decisions across a range of freshwater ecosystems.

6 | CONCLUSIONS

Expanding network ecology in freshwaters is a vital step in understanding and conserving these imperilled ecosystems. There are many challenges, however, with advances in methods and technologies, there is now an opportunity to collect data on a range of interactions, and thus construct complex merged networks, to understand better how these systems are structured and function.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

No new data were created during this study. [Correction added on 10th June, after first online publication: Data Availability Statement has been added].

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