

Positive biotic interactions in freshwaters: A review and research directive

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Abstract

1. Positive interspecific interactions such as mutualism, commensalism, and facilitation are globally ubiquitous. Although research on positive interactions in terrestrial and marine systems has progressed over the past few decades, comparatively little is known about them in freshwater ecosystems. However, recent advances have brought the study of positive interactions in freshwater systems to a point where synthesis is warranted.
2. In this review, we catalogue the variety of direct positive interactions described to date in freshwater ecosystems, discuss factors that could influence prevalence and impact of these interactions, and provide a framework for future research.
3. In positive interactions, organisms exchange key resources such as nutrients, protection, transportation, or habitat to a net benefit for at least one participant. A few mutualistic relationships have received research attention to date, namely seed-dispersing fishes, crayfishes and their ectosymbiotic cleaners, and communal-spawning stream fishes. Similarly, only a handful of commensalisms have been studied, primarily phoretic relationships. Facilitation via ecosystem engineering has received more attention, for example habitat modification by beavers and bio-turbation by salmon.
4. It is well known that interaction outcomes vary with abiotic and biotic context. However, only a few of studies have examined context dependency in positive interactions in freshwater systems. Likewise, positive interactions incur costs as well as benefits; conceptualising interactions in terms of net cost/benefit to participants will help to clarify complex interactions.
5. It is likely that there are many positive interactions that have yet to be discovered in freshwater systems. To identify these interactions, we encourage inductive natural history studies combined with hypotheses deduced from general ecological models. Research on positive interactions must move beyond small-scale experiments and observational studies and adopt a cross-scale approach. Likewise, we must progress from reducing systems to oversimplified pairwise interactions, toward studying positive interactions in broader community contexts. Positive interactions have been greatly overlooked in applied freshwater ecology, but have great potential for conservation, restoration, and aquaculture.

KEYWORDS

commensalism, community, conservation, context dependence, ecosystem, facilitation, management, mutualism

1 | INTRODUCTION

Positive interspecific interactions are ubiquitous in nature, and are important drivers of abundance and community structure (Boucher, James, & Keeler, 1982; Bronstein, 1994a, 1994b). Despite their ubiquity and importance, direct positive interactions such as mutualism and commensalism remain understudied relative to negative interactions such as competition, predation, and parasitism. Potential mutualisms were noted by Greek scientists over 2000 years ago, but were not examined in an empirical scientific framework until the mid-1900s (Boucher et al., 1982). Moreover, it is well recognised that positively interacting foundation species play a key role in establishing patterns of succession. Because of their visibility and tractability as study systems, most early experimental work focused on pollination and seed dispersal mutualisms involving terrestrial plants, as well as mutualisms involving microbes and small invertebrates (Bronstein, 1994a). Similarly, there has been extensive research in marine systems, including coral–zooxanthellae relationships (Muscattine & Porter, 1977), coral–crustacean protection mutualisms (Glynn, 1976), and cleaning symbioses (Bshary & Cote, 2008; Grutter, 1999; Limbaugh, 1961). Accordingly, much of our current understanding of positive interactions and their effects on communities and ecosystems is based on research from terrestrial and marine ecosystems. In contrast, there has been relatively little research on positive interactions in freshwater systems, although some mutualistic interactions have been known for over a century (Cope, 1867; Reighard, 1920). Considering that freshwater organisms are among the most imperilled in the world, and freshwater systems are under increasing pressure from anthropogenic influences (Jelks et al., 2008), understanding the full spectrum of biotic interactions in freshwaters will provide much better information for protecting these systems.

Direct positive interactions are particularly understudied in freshwater—a point made by a recent review of biotic interactions in freshwater systems (Holomuzki, Feminella, & Power, 2010). However, over the last 20 years, more freshwater ecologists have begun studying direct positive interactions and there is now sufficient literature for review and synthesis. Accordingly, we begin this review with a brief synthesis of current knowledge of positive interactions in freshwater systems. We then establish a directive to guide future research and highlight the importance of understanding positive interactions for conservation and management of freshwater biota and systems. Our scope comprises direct positive interactions among macro-organisms in freshwater systems including streams, rivers, lakes, and wetlands. We include interactions ranging from obligate endosymbiotic relationships to

facultative and context-dependent relationships. As noted below, we are not including discussion of indirect positive interactions (e.g. keystone species effects, trophic cascades, ecosystem engineering effects) as these have been well-studied in freshwater systems and have been the subject of other reviews (Hay et al., 2004; Holomuzki et al., 2010; Mermillod-Blondin & Rosenberg, 2006; Moore, 2006; Ripple et al., 2016; Soluk & Collins, 1988; Sommer, 2008).

2 | DEFINITIONS

The terminology of positive interactions has not been satisfactorily resolved and can be confusing. For example, mutualism is often considered synonymous with symbiosis, and the definition of facilitation likewise has been problematic (Hoeksema & Bruna, 2015). Since debate over this terminology is likely to persist for some time, definitions of the terms used by researchers will aid in discussions of these interactions and their effects. Accordingly, we use definitions presented by Hoeksema and Bruna (2015), and provide further clarification where necessary (Table 1). With respect to the term *positive interactions*, these are defined by (Stachowicz, 2001) as “encounters between organisms that benefit at least one of the participants and cause harm to neither.” This definition clearly includes intimate associations between taxa such as cleaning symbioses and transportation commensalisms, as well as direct facilitation. For the purposes of this review, we make two important distinctions as it relates to the Stachowicz (2001) definition: first, that benefits are determined in terms of net fitness consequences; and second, that only direct benefits (exchange of resources, provision of services, amelioration of stressors) are considered. This perspective expands the scope of positive interactions to include not only symbiotic mutualisms, but also facultative or incidental positive interactions and facilitative interactions that may result in beneficial outcomes for at least one of the participants (Table 1). Further, we define the term *resources* as any item or activity that may improve the fitness of an organism (Creed 1994; Creed, 2000; Noë & Hammerstein, 1994).

We consider positive interactions that require an intermediary species, e.g. trophic cascades, keystone species effects, as indirect. There is a rich history of research focused on interactions that generate indirect positive effects in freshwater systems—e.g. keystone species effects (Creed, 1994, 2000); trophic cascades (Carpenter, Kitchell, & Hodgson, 1985; Power, Matthews, & Stewart, 1985); ecosystem engineering effects (Creed & Reed, 2004; Flecker, 1996); and facilitation cascades (Thomsen et al.,

TABLE 1 Definitions of critical terms used in this review

Term	Definition	Notes and examples
Mutualism	Interaction in which both species involved receive a measurable net benefit	
Commensalism	Interaction in which one species benefits while the other has no net cost or benefit	
Facilitation	Interaction in which the presence of one species alters the environment or reduces interaction with enemies to enhance fitness for a neighbouring individual (Callaway 2007; Bronstein, 2009)	Often discussed in relation to ecosystem engineering or habitat amelioration, but can apply to other fitness benefits
Symbiosis	Intimate (and not exclusively positive) interspecific relationship with prolonged physical contact	Terms are largely synonymous, with the only distinction here as the presence or absence of prolonged contact
Partnership	Interspecific association with beneficial fitness consequences for at least one organism, but which is not biologically obligatory or lacks prolonged physical contact	
Phoresis	Commensal interaction in which an animal (phoront) superficially attaches itself onto a host animal for the purpose of dispersal (White et al., 2017)	Considered commensalism, but context may affect outcomes
Host	The interacting species that provides the physical space or resource initiating the interaction. The host always provides a measurable benefit to its partner.	Not all positive interactions require a host; particularly for interactions within a single trophic level (Milbrink, 1993)
Symbiont Partner Beneficiary Phoront Epibiont	Interacting species that benefit from the physical space or resource provided by the host (or other interacting species when no host exists).	Terms are synonymous, but apply to one of three different interaction types (as defined above); beneficiary can be used to generally apply to all three

2018) and they have been the subject of a number of reviews (Hay et al., 2004; Holomuzki et al., 2010; Mermillod-Blondin & Rosenberg, 2006; Moore, 2006; Ripple et al., 2016; Soluk & Collins, 1988; Sommer, 2008). Many of the common types of indirect positive interactions in freshwaters are summarised in Table 2, but are excluded from discussion in this review.

Some interaction-specific terminology is used in the literature (i.e. cleaners and clients in cleaning interactions, hosts and associates in reproductive interactions), and all case studies discussed herein will include any specific terminology if necessary.

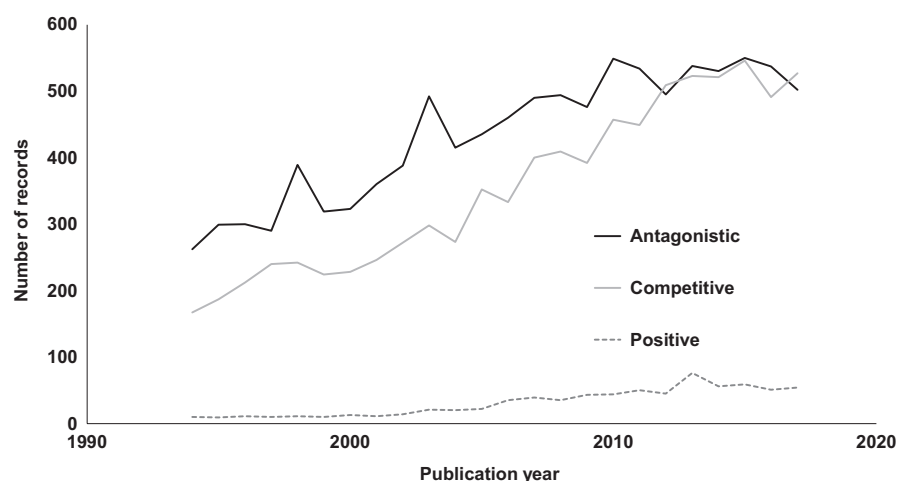
3 | DATABASE SEARCH

We conducted a thorough review to present the state-of-the-knowledge of positive interactions in freshwaters. We searched the

Web of Science online database, and all keywords and combinations for searches are included in Table S1. Studies were peer-reviewed original research and review articles published from 1 January 1994 to 31 December 2017, reflecting the most current research available upon initiation of this literature review in March 2018. The search yielded >800 studies; all titles and abstracts were reviewed for relevance. Our review of the literature was then greatly expanded by examining: (1) references in the papers queried in the database search; and (2) the studies that cited those articles. This process was expanded outward until studies were exhausted. Our search for analogous interactions in other ecosystem types, conceptual models, general ecological principles, etc. were not exhaustive, but came from: (1) primary sources included in this review; (2) recommended articles based on a subset of key references (*related searches* tool in Google Scholar); and (3) the combined expertise of the authors.

TABLE 2 Common examples of indirect positive effects in freshwater ecosystems. These effects can occur among any organism in any freshwater habitat globally

Interaction type/mechanism	Description	Key references	Examples
Allogenic ecosystem engineering: bioturbation	Organisms indirectly facilitate consumers by disturbing the benthos, thereby releasing sediment and nutrients and directly increasing production of lower trophic levels	Flecker (1996), Creed and Reed (2004), Mermillod-Blondin and Rosenberg (2006), Moore (2006)	Fish, crayfish, and other organisms remove sediment from substrate which benefits herbivorous insects
Allogenic ecosystem engineering: bioclarification	Organisms facilitate consumers indirectly by reducing turbidity, thereby increasing primary production and associated increases in primary and secondary consumers	Zhu, Fitzgerald, Mayer, Rudstam, and Mills (2006)	Plants reduce current velocity, demobilising suspended sediment and increasing water clarity for other primary producers
Foundation species or autogenic ecosystem engineering: prey concentration	Organisms facilitate consumers indirectly by allowing colonisation of their bodies by epibionts, thereby concentrating prey for consumers	Diehl and Kornijów (1998)	Aggregations of freshwater bivalves provide hard substrate where it would otherwise be unavailable, concentrating benthic invertebrates for predators
Trophic cascades: (indirectly benefitting species in non-adjacent trophic levels)	Strong consumption at one trophic level has indirect positive effects on non-adjacent trophic levels by reducing production of the next-lowest trophic level	Predation: Carpenter et al. (1985), Power (1990), Herbivory: Matthews et al. (1987), Planktivory: DeVanna et al. (2011)	Predatory fish consume zooplanktivorous fish which benefits zooplankton; fish consume predatory insects, which benefits herbivorous insects
Keystone consumers: indirectly benefit species in next trophic level beneath them	Predators and herbivores can indirectly benefit species in trophic level beneath them by removing the competitive dominant in that same trophic level	Creed (1994), Creed (2000)	Crayfish consume large, filamentous alga, which benefits smaller algae; weevils consume dominant macrophyte, which increases macrophyte diversity
Trait-mediated indirect effects (responses to non-consumptive effects of consumers)	Top predators can alter behaviour and distribution of their prey (e.g. consumers in trophic level beneath top carnivore), which can benefit the prey of these consumers	Power et al. (1985), Turner and Mittelbach (1990)	Presence of predatory causes planktivorous fish (bluegills) to avoid open water, which indirectly benefits zooplankton; presence of predatory forces algivorous minnows into shallow habitats, benefitting algae in open water

**FIGURE 1** The number of Web of Science core collection publications per year (dating from 1994 to 2017) related to species interactions in freshwater habitats. Freshwater habitats include wetlands, streams, rivers, lakes, and synonymous terms. Antagonistic interactions include predation, parasitism, and herbivory; positive interactions include mutualism, commensalism, and facilitation

As can be seen in Figure 1, the number of studies focused on positive interactions in freshwater systems is a fraction of those focused on antagonistic interactions and competition. Note also that

the number of positive interaction studies has been increasing, although not at the same rate as studies of the other categories of interaction.

TABLE 3 Examples of well-known direct positive interactions in freshwater ecosystems. Table organised alphabetically by key resource exchanged

Key resource		Organisms	Habitat, region	Description	Key reference
Species A	Species B				
Facilitation: habitat amelioration		Benthic invertebrates	Rivers, global	Nets of web-spinning caddisflies reduce sheer stress, creating hydrological refugia for other benthic invertebrates	Nakano et al., (2005)
Facilitation: habitat amelioration		Macrophytes	Rivers, global	Macrophytes slow current velocity, trapping and stabilising fine sediments and concentrating nutrients for various organisms	Sand-Jensen (1998)
Facilitation: protection from consumption		Fishes	Freshwaters, global	Mixed-species shoals of fish create potential for interspecific competition, but reduce predation risk	Matthews (1998)
Nutrition	Nutrition	Oligochaete worms	Mesotrophic lakes, Europe	<i>Potamothenis</i> and <i>Tubifex</i> worms produce faecal pellets with bacterial assemblage better suited for consumption by the other species, resulting in increased growth for both species when they co-occur	Milbrink (1993)
Nutrition	Protection	Sponges and zoochlorellae	Freshwaters, global	Freshwater sponges host zoochlorellae algal symbionts that provide photosynthate in exchange for nutrients	Wilkinson, (1980)
Protection	Nutrition	Crayfish and branchiobdellid worms	Streams, North America	Host crayfish provide nutrition to symbiotic worms in the form of biofilms and ectoparasites. Worms provide protection (<i>sensu stricto</i>) by consuming ectoparasites; classic <i>cleaning mutualism</i>	Brown et al. (2002)
Protection	Protection	Fishes	Freshwater, global	Nest building fishes protect eggs of <i>associate</i> species. In greatly outnumbering host eggs, associate eggs provide reduced odds of predation on host eggs (protection)	Johnston (1994a), Johnston (1994b)
Protection	–	Various sessile hosts and epibionts	Freshwater, global	Macrophytes and bivalves colonise soft substrates, creating hard structure and allowing epibionts to colonise their bodies	Taniguchi et al. (2003)
Transport	–	Midge larvae and benthic invertebrates	Streams, global	Chironomid midge larvae engage in phoresy as a commensal, attaching to a more mobile invertebrate while providing the host no apparent benefit	Tokeshi (1993)
Transport	Nutrition	Riparian trees and fishes	Rivers, western hemisphere	Fishes receive nutrition by eating fleshy fruits of trees. Trees receive seed dispersal as seeds pass through fish digestive tract	Horn et al., (2011)

4 | TYPES OF POSITIVE INTERACTIONS IN FRESHWATERS

Most mutualisms involve the provision or exchange of at least one of three key resources or services: nutrition, transportation, and protection (Table 3; Hoeksema & Bruna, 2015), although not all resources or services exchanged neatly fit these categories—e.g. gas exchange (Tumilson & Trauth, 2006); or substrate (Beekey, McCabe, & Marsden, 2004). We recognise this perspective is not comprehensive and does not account for multi-species interactions, multiple resources exchanged, novel resources, etc. However, this approach is a useful starting point to discuss the types of positive interactions that occur in freshwater ecosystems. In addition to protection from enemies, facilitative interactions can have positive effects by providing ameliorated habitat. Any combination of the first key resources

can be exchanged in mutualism and commensalism, but habitat amelioration is unique to facilitation (Bronstein, 2009). Moreover, facilitation can be either commensalistic or mutualistic, depending on whether the facilitating species receives a positive feedback from beneficiaries.

Boucher et al., (1982) were the first to classify mutualisms, and successive studies have re-evaluated those groupings to include species complexities and other nuances (e.g. Feldman, Morris, & Wilson, 2004). Others group mutualisms based on *rewards* and *services* (Hoeksema & Bruna, 2015) or by mechanisms by which resources are exchanged (Connor, 1995). In this section we use the *biological markets* (*sensu* Noë & Hammerstein, 1994) framework provided by Bronstein (2009) to classify mutualism and commensalism. We follow Bertness and Callaway (1994) in discussing the two general types of facilitation, protection and habitat modification (Table 1).

4.1 | Common positive resource exchanges

Nutrition is one of the most commonly traded resources in mutualisms (Boucher et al., 1982). While nutritional interactions are well represented in ecological literature, most examples come from microbes (e.g. mycorrhizae or gut bacteria) and plants (e.g. nectar from angiosperm flowers); few have been documented in freshwaters. One example involves freshwater sponges that host and provide nutrition to endosymbiotic green algae in exchange for glucose excreted by the algae (Frost & Williamson, 1980; Skelton & Strand, 2013). Another example of reciprocal nutritional exchange occurs between two species of oligochaete worms throughout European mesotrophic lakes. Each species excretes faecal pellets with unique bacterial communities that are well suited for the diet of the other species, causing both species to grow larger when co-occurring than when occurring separately. This nutritional mutualism is credited with the expansion of the *Potamothrix* genus throughout much of Europe (Milbrink, 1993). Perhaps the most widespread nutritional exchange occurs in periphyton, the matrix of algae, diatoms, cyanobacteria, and heterotrophic microbes that cover hard substrates in most freshwater ecosystems around the world (Larned, 2010). Periphyton includes taxa supporting one another through nutrient exchanges and structural support, though parsing out pairwise costs and benefits to interacting species is difficult (Biggs, Goring, & Nikora, 1998). This last example involves multiple interacting taxa and can be considered a mutualism network *sensu* Bascompte (2009).

Transport is a commonly traded resource in positive interactions, especially for organisms with limited dispersal capability. Transport mutualisms probably are best represented in freshwater systems by fish-borne seed dispersal, also known as *ichthyochory*. In *ichthyochory*, plants exchange nutrition (fruit) for seed transport (reviewed by Horn et al., 2011; Parolin, Wittmann, & Ferreira, 2013). Consumed seeds usually pass through fish digestive systems unharmed, and often have better germination rates than non-consumed seeds (although findings are variable; Correa, Winemiller, Lopez-Fernandez, & Galetti, 2007). In large rivers, highly mobile *ichthyochorous* fishes can transport seeds long distances upstream and across floodplains during floods (Anderson, Nuttle, Saldaña Rojas, Pendergast, & Flecker, 2011; Horn, 1997), and are key to maintaining floodplain plant diversity (Anderson, Rojas, & Flecker, 2009). Given that multiple species of fish may transport seeds of multiple tree species this may also be a mutualistic network. Another transport interaction is *phoresy* (Table 1), in which a phoront attaches itself to a mobile host for the purpose of transport (Steffan, 1967). Many chironomid larvae engage in phoretic associations with various aquatic insects and fish (Freihofer & Neil, 1967; Pennuto, 1997). Living on these hosts may provide better feeding opportunities, increased mobility, protection from disturbance, and reduced predation risk for the phoront (Tokeshi, 1993). These associations appear to be commensalisms since no effects on the hosts have been reported.

Protection is traded when organisms reduce contact of beneficiaries with enemies (Hopkins, Wojdak, & Belden, 2017). One of

the most widespread provisions of protection occurs when the organisms themselves provide habitat for epibionts—a form of autogenic ecosystem engineering (Jones, Lawton, & Shachak, 1994). For example, rooted macrophytes provide three-dimensional structure to an otherwise two-dimensional benthos. These structures increase habitat availability and complexity, and support a diversity of epibionts and their predators (Taniguchi, Nakano, & Tokeshi, 2003). In return, removal of epiphytic algae by epibionts provides a mutualistic benefit to the macrophytes (Brönmark, 1989). By constructing calciferous shells, freshwater bivalves may host unique invertebrate assemblages (Hopper, DuBose, Gido, & Vaughn, 2019). In colonising habitats with fine substrates, bivalve aggregations provide coarse substrate to freshwater organisms where it would have otherwise not been available (Beekey et al., 2004). Moreover, bivalve shells persist in the benthos long after death, providing benthic structure for long periods (Gutiérrez, Fernández, Seymour, & Jordano, 2005).

Other common protection mutualisms are cleaning interactions in which cleaners remove ectoparasites and other epibionts from host species or clients. Cleaning interactions are well studied in marine systems, where specific locations become *cleaning stations* to which large organisms travel to have parasites removed. Although once thought to be an entirely marine phenomenon (Côté, 2000; Limbaugh, 1961), cleaning stations have recently been documented in freshwaters, and may be more common than previously known (Severo-Neto & Froehlich, 2016). Perhaps the best-studied freshwater cleaning symbiosis occurs between crayfish and a group of epibiotic worms called branchiobdellidans. The worms consume epibiotic parasites and biofilms that colonise crayfish gills (Brown, Creed, & Dobson, 2002; Brown, Creed, Skelton, Rollins, & Farrell, 2012; Brown et al., 2012), which increases crayfish survival and growth probably through increased ammonia excretion across the gills of the crayfish. The primary benefit for the worms is that they only reproduce on a live crayfish host (Creed et al., 2015) although they are also likely to benefit from reduced predation risk. A similar cleaning mutualism occurs between a widespread oligochaete and pulmonate snails. The oligochaete attaches to the snail's mantle or pulmonary cavity and consumes passing microorganisms (Stoll, Früh, Westerwald, Hormel, & Haase, 2013), but can also protect the snail host from trematode infections (Ibrahim, 2007).

Organisms also exchange protection from predators and herbivores for increased access to resources. When injured by herbivores, water caltrop release chemicals that attract predacious water striders. Striders benefit by being made aware of the prey resource, while providing protection for the caltrop (Harada, Yamashita, & Miyashita, 2008). Another protection interaction is *nest association*, a form of alloparental care in fishes where *nest associates*, or partners, spawn in nests constructed by hosts and abandon their eggs (Johnston & Page, 1992). In the association between chubs (*Nocomis* sp.) and shiners (*Notropis* sp.), the primary benefit to the shiner partners comes from the brood guarding activities of the chub host (Johnston, 1994a), as well as the physical structure of the constructed nest (Peoples & Frimpong, 2013). In exchange, the

nest-building hosts receive decreased probability of brood predation (Johnston, 1994b)—a *dilution effect* from having high percentages of partner eggs in the nest (up to 97% in one estimate; Wallin, 1992).

There are also some freshwater taxa (e.g. fish, insects, crustaceans) that provide protection for a range of ectosymbionts. Holarctic crayfish host branchiobdellidan worms that may not always benefit the host (Hobbs, Holt, & Walton, 1967; Skelton, Creed, Landler, Geyer, & Brown, 2016a), and southern hemisphere crayfish host temnocephalan flatworm commensals (Jones & Lester, 1996). These other branchiobdellidan species and the temnocephalans get necessary breeding habitats and protection but provide no obvious benefits to their hosts. Crayfish, isopods, and planktonic crustaceans may also host protozoans, ostracods, rotifers, and bacteria (Cook & Chubb, 1998), many of which do not appear to benefit their hosts, but receive substrate, mobility, and protection from the relationship. All these associations appear to be commensalisms. Undoubtedly, more positive ectosymbiotic relationships remain to be discovered in freshwater systems. Further, experimental assessment of these interactions may demonstrate that interaction outcomes are dynamic, as symbionts may reduce parasite load, predation susceptibility, or fouling of the host (e.g. Svensson, 1980) under certain contexts.

4.2 | Facilitation

Facilitation is generally a unidirectional interaction in which the activities of one species improve fitness of beneficiary species through either (1) habitat amelioration or (2) protection from enemies. Habitat amelioration is generally better studied in freshwaters than mutualism or commensalism (e.g. Moore, 2006). One of the most ubiquitous examples of facilitative habitat amelioration is provided by sessile organisms such as macrophytes and mussels. In addition to providing direct habitat to epibiotic periphyton and invertebrates, these organisms function to stabilise substrates, ameliorating habitat for benthic organisms (Gregg & Rose, 1985; Vaughn & Spooner, 2006). Macrophytes reduce current speed, which traps nutrients, stabilises sediment (Schulz, Kozerski, Pluntke, & Rinke, 2003; Wharton et al., 2006), and provides velocity refugia in habitats with high flows (Atkinson, Vaughn, Forshay, & Cooper, 2013). Likewise, the filtering activities of mussels serves to contrate nutrients in the benthos, supporting higher biomass of benthic invertebrates (Vaughn, Nichols, & Spooner, 2008). At certain densities and complexity, macrophytes also provide reduced predation pressure to a variety of organisms (Padial, Thomaz, & Agostinho, 2009; Stansfield, Perrow, Tench, Jowitt, & Taylor, 1997).

Mobile organisms are also important facilitators in aquatic ecosystems. In constructing dams and modifying flow, beavers (*Castor* sp.) directly provide habitat for numerous aquatic organisms (Wright, Gurney, & Jones, 2004; Wright & Jones, 2006), although their effects are not always positive for every species (Jones, Lawton, & Shachak, 1997). Bioturbation, the process by which organisms disturb and

release benthic sediments and nutrients, is another well-studied example of facilitation via habitat amelioration (Creed & Reed, 2004; Flecker, 1996; Statzner, Fievet, Champagne, Morel, & Herouin, 2000), especially in nutrient-limited streams (Adámek & Maršálek, 2013). A well-studied example of bioturbation occurs when migrating salmon, or other anadromous fishes that make spawning migrations *en masse*, construct redds for spawning in headwater rivers. This sudden, intense activity disturbs and releases large amounts of sediment, which facilitates algal growth and abundance of some invertebrate taxa (Janetski, Chaloner, Tiegs, & Lamberti, 2009; Moore, 2006).

There are other less-known but equally ubiquitous habitat ameliorating facilitations in freshwater ecosystems. For example, net-spinning caddisfly larvae construct retreats in high-flow regions of streams to filter food from the water column. These retreats significantly reduce flows in the areas immediately downstream, creating low-flow microhabitats that increase sediment stability (Albertson et al., 2014; Albertson, Sklar, Cooper, & Cardinale, 2019) and facilitate colonisation by other benthic invertebrates (Nakano, Yamamoto, & Okino, 2005; Tumolo, Albertson, Cross, Daniels, & Sklar, 2019). Removal of case-building caddisflies can also result in shifts in community composition (Nakano, Kuhara, & Nakamura, 2007). Nest associative minnows engage in another example of this type of facilitation in streams of eastern North America. Adult male chubs (*Nocomis* spp.) construct large gravel nests for spawning. These nests often occur in large aggregations (Peoples, McManamay, Orth, & Frimpong, 2014) and usually differ starkly from the surrounding substrate (Bolton, Peoples, & Frimpong, 2015; Maurakis, Woolcott, & Sabaj, 1992); chub nests are often the only sources of concentrated, un-silted gravel in heavily embedded or sediment-starved reaches during spawning season (McManamay, Orth, Dolloff, & Cantrell, 2010; Peoples, Tainer, & Frimpong, 2011). Nest building thus provides critical microhabitat for lithophilic-spawning fishes, allowing *Nocomis* and associates to reproduce and persist in reaches of poor substrate quality (Hitt & Roberts, 2012; Peoples, Blanc, & Frimpong, 2015). Nests also facilitate a large number of benthic macroinvertebrates that begin colonising nests immediately upon construction (Swartwout, Keating, & Frimpong, 2016).

In their seminal paper on positive interactions in communities, (Bertness & Callaway, 1994) noted that the study of protection facilitations has “not been given the empirical and theoretical attention they deserve, and are not widely appreciated”. In the quarter-century since then, examples of protection facilitations remain largely undescribed in freshwaters. One area of research that has received some attention, however, are positive neighbourhood effects from mixed-species schooling. Fish in hetero-specific shoals experience reduced predation through a confusion effect and early predator warning (Krause & Ruxton, 2002). Mixed-species shoaling has been shown to facilitate invasion success in the freshwater guppy (Camacho-Cervantes, Garcia, Ojanguren, & Magurran, 2014), and is hypothesised to be a common, yet underappreciated positive interaction among freshwater fishes (Matthews, 1998).

5 | CONTEXT DEPENDENCY IN POSITIVE INTERACTIONS

Like other biotic interactions, the strength and outcomes of positive interactions are dynamic, changing predictably with abiotic and biotic context (Bronstein, 1994a). Species interactions occur along a continuum ranging from antagonistic to mutually beneficial (Figure 2; Bronstein, 1994a; Ewald, 1987), and recent work has shown that in *mutualist* systems, outcomes along biotic and abiotic gradients can be highly variable (Brown et al., 2012; Chamberlain, Bronstein, & Rudgers, 2014). If this is the case then changes in the abiotic environment, the density of one or both partners involved in a positive interaction may change the outcome of that interaction. As ecologists grapple with anthropogenic impacts and a changing climate, it becomes even more vital to understand how the sign and strength of positive interactions are dependent on environmental and biotic context. Context-dependent outcomes have become a major theme of current mutualism research, but there has been limited evaluation of these effects in freshwater systems.

In freshwaters, costs of positive interactions can be broken down into at least three main categories. The first are costs associated with a behaviour or action by hosts or facilitators that reduce their own performance, such as energy expended during habitat modification or effort spent regulating symbionts. The second type of cost is incurred when one interacting species, most often the beneficiary, causes a cost to the other interacting species. Examples from the latter are common in cleaning interactions, where cases of cleaners feeding on host tissues are well documented (Brown et al., 2012; Severo-Neto & Froehlich, 2016; Stoll, Hormel, Früh, & Tonkin, 2017). The third way by which mutualism may incur costs is through the exploitative action of species external to the mutually beneficial

relationship; these include (1) mimics or *cheaters* of the true partners that contribute no benefits to the partners (Ferriere et al., 2002) and (2) the numerical response of predators to prominent and vulnerable aggregations of the partners. Understanding the context-dependent nature of these interactions will be necessary to identify the role of positive interactions in shaping communities.

Environmental variables can affect the interplay between costs and benefits. For example, (Peoples & Frimpong, 2016b) found that in the presence of egg-eating suckers (Catostomidae) decreasing substrate quality caused the association between two nest associative fishes to switch from mutualism to commensalism. In the crayfish-worm cleaning symbiosis, experimental manipulations of environmental fouling resulted in different interaction outcomes. Under low fouling conditions, the association between crayfish and the worms was commensalistic, as only the worms benefitted (Lee, Kim, & Choe, 2009). In high-fouling environments, the worms cleaned the gills and benefitted the crayfish; the association was now a mutualism (Lee et al., 2009). Worm reproduction is also higher under high fouling conditions when resources on the exoskeleton of their crayfish host were more abundant (Thomas, Creed, & Brown, 2013).

Positive interactions are also contextualised by biotic factors such as condition, abundance, and ontogeny of one or both partners. For example, larger individuals of ichthyochorous *Pacu* spp. confer increased survival to the seeds they ingest: large *Pacu* pass seeds through their digestive tract intact, whereas smaller fish damage the seeds and significantly decrease germination rates (Galetti, Donatti, Pizo, & Giacomini, 2008). The crayfish-worm interaction can switch from mutualism to parasitism when worm densities are high and worms are apparently resource-limited, which causes the worms to feed on crayfish gills (Brown et al., 2012; Creed & Brown,

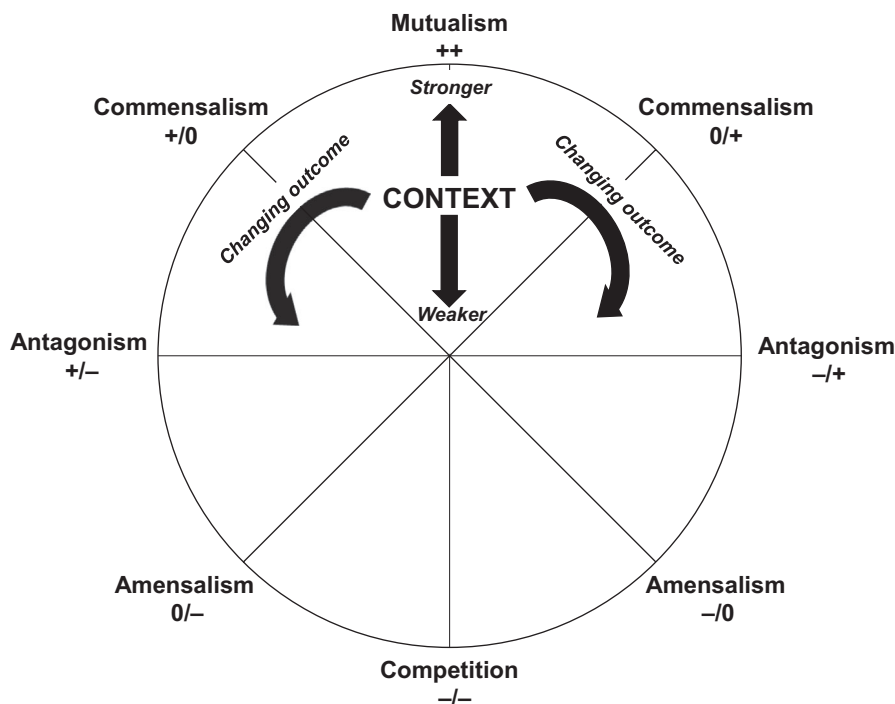


FIGURE 2 All possible pairwise species interactions can be depicted using an interaction wheel modified from the *coaction compass* (Haskell, 1949; Hoeksema & Bruna, 2015). By adding context to the compass (black arrows), we can better understand how sign (changing outcomes: movement around the wheel) or strength (change in net cost/benefit: movement along the spokes) of an interaction may vary over space and time. Interaction strength increases toward the edge of the circle. Outcomes of strong interactions are further in distance to other interaction outcomes than weak ones, and are thus less likely to be affected by context

2018). However, some crayfish species actively groom themselves, removing worms and keeping worm densities at levels that confer benefits (Farrell, Creed, & Brown, 2014). This grooming behaviour is also affected by host ontogeny, with host age and size influencing worm removal (Skelton, Creed, & Brown, 2014, 2015). Because young crayfish frequently moult, which relieves their gills of fouled cuticles, they do not benefit from hosting worms and thus remove them (Thomas, Creed, Skelton, & Brown, 2016). Older crayfish moult less, and allow worms to colonise and engage in a mutualism (Skelton et al., 2014; Skelton, Doak, Leonard, Creed, & Brown, 2016b).

Abundance of participants is another key source of biotic context (Morales, 2000; Palmer & Brody, 2013). An over-abundance of partners can cause an imbalanced exchange of resources or services and can switch mutualism to parasitism, as discussed in the crayfish–worm interaction (Brown et al., 2012). In other interactions, a *critical mass* of participants is needed for an interaction to benefit all species. For example, Silknetter et al. (2019) found that increased partner density caused nest association to switch from parasitism to mutualism: low densities of partners made nests more conspicuous (attracting predators) without providing a beneficial dilution effect, and chubs were better off spawning without partners than with them at low densities. To manage these conflicting interests, some hosts punish over-exploitation by partners (Creed & Brown, 2018; Farrell et al., 2014; Frost & Elias, 1990), whereas others appear to have no defences for over-exploitation (Stoll et al., 2017) or over-exploitation is not predicted to occur (Peoples & Frimpong, 2016a).

Effects of symbiont/partner abundance on outcomes for hosts can be conceptualised by two relationships (Figure 3). The fitness outcomes observed along a continuum of partner abundance are likely to differ between studies. Silknetter et al. (2019) identified parasitism at low partner abundances and mutualism at high abundances and this result is likely to be the result of novel resource

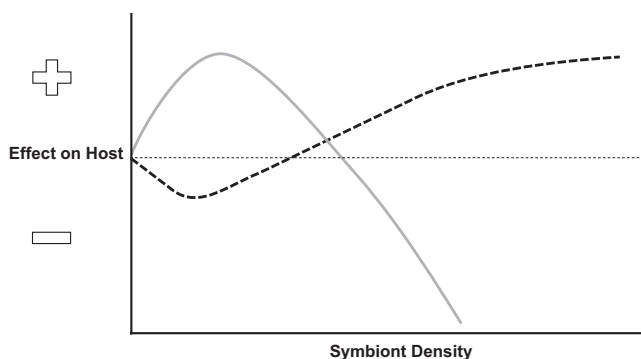


FIGURE 3 Two possible effects of symbiont density on host fitness. The solid grey line indicates interactions in which low to moderate symbiont density results in benefits to the host, but becomes increasingly costly at higher densities. Some hosts have the ability to modify symbiont density to maintain beneficial outcomes (e.g. Brown et al., 2012), while other hosts are unable to mitigate these costs (e.g. Stoll et al., 2017). The dashed black line indicates a relationship in which low symbiont densities are actually detrimental to the host, and do not benefit host fitness until a *critical mass* has been reached (sensu Silknetter et al., 2019)

trade; spawning substrate/parental care provided by the host in exchange for brood dilution. In contrast, Brown et al., (2012) observed a mutualistic outcome at moderate partner densities but parasitism at high partner densities. Although symbiont/partner abundance can provide meaningful biotic context, how it may predict fitness outcomes will require detailed system-specific information.

6 | POSITIVE INTERACTIONS IN A COMMUNITY CONTEXT

Most models and empirical studies reduce complex systems to simple pairwise interactions that are rarely ecologically realistic (Bascompte, 2009; Thrall, Hochberg, Burdon, & Bever, 2007). This approach is understandable, as ecological communities can be challenging to manipulate. However, species interactions occur in a community context that can result in variable outcomes influenced by community composition and the specific traits of community members. Although pairwise frameworks have heuristic value, moving from a pairwise to a community-based framework of understanding positive interactions in freshwater systems will enable scientists to provide more realistic predictions of whole community response to environmental change in the context of positive interactions.

Community ecologists have long recognised that the relative importance of biotic interactions in structuring communities is influenced by abiotic factors such as disturbance (e.g. Bertness & Callaway, 1994; Creed, 2006; Menge & Sutherland, 1976, 1987; Peckarsky, 1982; Poff & Ward, 1989). The stress-gradient hypothesis (SGH) proposed by Bertness and Callaway (1994) is the only framework that has specifically evaluated the relative importance of positive biotic interactions along an environmental gradient. The SGH predicts that competitive interactions will be more frequent in habitats that are physically benign or have low herbivore or predator pressure, and facilitation will become more frequent as habitats become more physically harsh and/or experience more consumer pressure (Figure 4). This model provides a testable

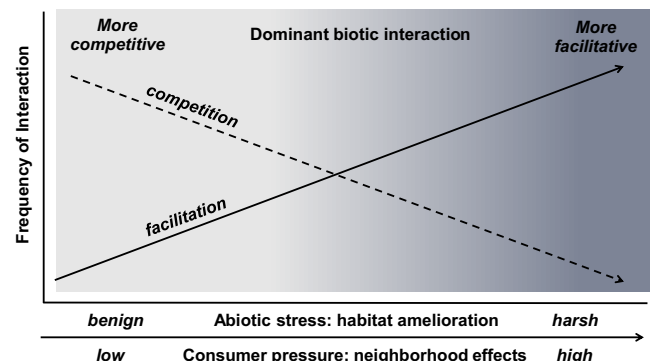


FIGURE 4 As currently formulated, the stress-gradient hypothesis (re-conceptualised from Bertness & Callaway, 1994) depicts increasing frequency of positive interactions with stress–habitat amelioration for abiotic gradients, and neighbourhood effects for consumer pressure

framework for examining the trade-off between negative and positive interactions along abiotic and biotic gradients in freshwater systems.

The SGH has been rigorously tested in a variety of terrestrial and marine settings (Bertness, Leonard, Levine, Schmidt, & Ingraham, 1999; Bruno, 2000; Callaway et al., 2002), and has undergone robust revisions over the past 2 decades (He & Bertness, 2014; Maestre, Callaway, Valladares, & Lortie, 2009). However, only a handful of studies have applied it to freshwater systems. Fugère et al., (2012) found that in an assemblage of headwater stream detritivores, a decrease in resource quality, and thus increased abiotic stress, shifted interactions from competitive to more neutral outcomes. Peoples et al., (2015) found that proportions of positively-interacting nest associative stream fishes increased along a stress gradient of anthropogenic land cover and stream size. In highly stressful environments, facilitation by one or more species may allow other species to persist thus increasing biodiversity (McIntire & Fajardo, 2014) or expanding the ranges of species that benefit from the facilitation effect (He & Bertness, 2014). More studies are needed to see how facilitation may influence freshwater communities along various gradients of environmental stress.

7 | POSITIVE INTERACTIONS ACROSS SPATIAL SCALES

Understanding the mechanisms that contribute to species coexistence is a fundamental goal of ecology. However, testing hypotheses about species interactions can be greatly affected by the spatial scale at which they are examined (Levin, 1992). Freshwater habitats are hierarchical, and scales range from hyper-local microhabitats to entire continents (Domisch, Jähnig, Simaika, Kuemmerlen, & Stoll, 2015; Frissell, Liss, Warren, & Hurley, 1986). At small scales, predation studies often find patterns of avoidance, as prey species distributions are shaped largely by predator avoidance (Power, 1984). At the same scale, competition studies exhibit *checkerboard* distributions as species confine themselves to habitats devoid of their competitor (Pearson & Dawson, 2003). At larger scales in the river network, predation studies often find positive or null patterns as a result of similar habitat requirements. Predator distributions can also be determined by their ability to colonise and persist in particular habitats (Creed, 2006; Wellborn, Skelly, & Werner, 1996). Antagonistic interactions typically give way to environmental conditions in shaping freshwater communities at large scales (Creed, 2006; Peres-Neto, 2004; Poff & Ward, 1989; Wellborn et al., 1996), but there have been too few examinations of positive interaction patterns at different scales to make similar inferences.

Another key goal in ecology lies in identifying the spatial scale(s) at which biotic interactions are meaningful or can be inferred (Kissling et al., 2012). Biotic interactions affect spatial patterns of species distributions at local scales, but beyond this fine-grained approach they have typically been dismissed as unimportant (Pearson & Dawson, 2003; but see Creed, 2006; Wellborn et al., 1996). While most studies addressing this question have focused on negative interactions (Shurin & Allen, 2001), emerging research is focusing on positive interactions.

For example, Hopkins et al., (2017) provide examples of studies that have investigated the role of spatial scale in influencing interactions. However, their review of defensive symbionts' roles at multiple scales included only a few examples from freshwaters (Rodgers, Sandland, Joyce, & Minchella, 2005; Skelton & Strand 2013), and relationships between scale and significance of positive interactions were not explicit.

Studies examining species distributions at multiple temporal and spatial scales can be used to infer the importance of positive interactions to maintaining broad-scale and long-term patterns of species diversity. For instance, by comparing historical accounts of symbiont species distributions to contemporary multi-scale survey data, Skelton, Creed, et al. (2016a) found that variation in host affinities maintain broad-scale geographic patterns in symbiont species composition over decadal time scales, despite massive seasonal changes in local abundances of symbiont species. Patterns of symbiont species diversity are maintained because host species composition tracks geographic habitat variation, and symbiont composition tracks host species composition (Skelton, Creed, et al., 2016a). We encourage future researchers to take a cross-scale approach to investigating positive interactions in freshwater ecosystems.

8 | A RESEARCH DIRECTIVE FOR STUDYING POSITIVE INTERACTIONS IN FRESHWATER SYSTEMS

The preceding sections have reviewed our current understanding of positive interactions in freshwater ecosystems. We now look toward the future of research on positive interactions as well as their application. Accordingly, we propose a four-step research directive for advancing the study of positive interactions in freshwater ecosystems (Figure 5).

8.1 | Identifying new positive interactions and causal mechanisms

To date, most of our knowledge about positive interactions in freshwater systems has come from an inductive approach—exploring basic biology and ecology upon which to construct generalised inference. As we progress through this age of global connectivity and big data, large-scale macroecological studies have become increasingly prevalent; this expansion is an important step. However, while we advocate a cross-scale approach, we caution strongly against the wholesale replacement of small-scale natural history studies (Frimpong, 2018; Ricklefs, 2012). The call for the *resurrection* of natural history studies (Able, 2016) coincides with a realisation that modelling, species inference, and big data are only as good as the foundational ecology behind them (Matthews, 2015). Many of the examples of positive interactions discussed here have stemmed from the observations of earlier naturalists seeking to simply describe and understand the phenomena they witnessed; this type of science is irreplaceable.

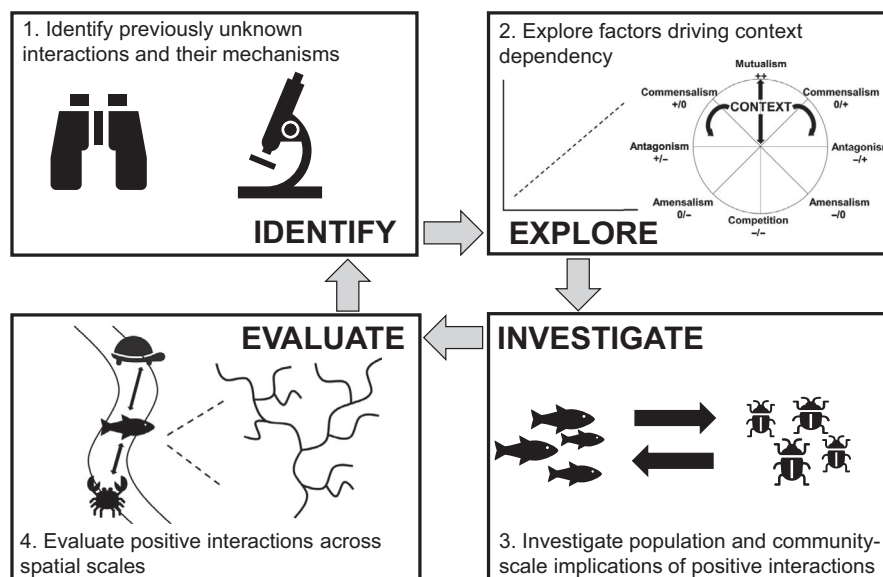


FIGURE 5 An informational graphic for the research directive. The process of understanding positive interactions in freshwaters begins with the identification of new interactions and mechanisms (Panel 1). Ecologists should then explore the role of context dependency in those systems to determine the range of possible interaction outcomes (Panel 2). An investigation of population- and community-level effects can help to explain the drivers and significance of complex interactions (Panel 3). Lastly, we must evaluate our findings and scale them to understand the broad impacts of positive interaction (Panel 4). Evaluation will allow new knowledge to inform future cycles of identification, exploration, and investigation of positive interactions in freshwaters

In moving forward, however, we encourage a more deductive approach—using general ecological models developed largely outside freshwater systems, to make predictions on where to look for positive interactions, which organisms will engage in them, and how their presence and impact may change across abiotic and biotic gradients. For example, the biological markets model (BMM) predicts mutually beneficial interspecific resource exchanges will occur when three conditions are met: when interacting species (1) produce an excess of a key resource, (2) benefit from acquiring more of a resource, and (3) have differences in resource production and acquisition sufficient to allow for efficient trade (Table 4; Noë & Hammerstein, 1994). The BMM is useful to evaluate when and why partners choose to engage in a mutually beneficial interaction, and for understanding potential

evolutionary benefits of engaging in positive interactions (Palmer et al., 2010).

Using the BMM to find new positive interactions (mutualism and commensalism in this case), we should identify species that may be producing excess of a key resource (i.e., the producer). We understand this is a vague guidance, and this scenario could be everywhere for a given species or resource. From a consumer's perspective, we should focus on (1) species with traits that limit resource acquisition in (2) potentially resource-limited environments. For example, we would expect to find exchanges of other resources for transport among sessile organisms with no natural means of dispersal, particularly in lotic systems with unidirectional unassisted dispersal (downstream in streams and rivers; horizontal in floodplains). Likewise, we

TABLE 4 Examples of potential conditions that will give rise to positive interspecific interactions, as deduced from the biological markets model (BMM) and stress-gradient hypothesis (SGH)

Limiting resource	Traits of symbiont/beneficiary	Environmental scenario	Deductive basis
Transport/dispersal, usually of juveniles	Sessile, little ability for dispersal	Dispersal-limiting habitats such as flowing water	BMM
Nutrition	Limited ability to acquire key nutrients, or reliance/preference of better nutrients provided by host/partner	Microhabitats with limited nutrients or with numerous nutrients of differing quality	BMM
Protection	Species at risk of herbivory or predation that benefit from protection additional to self-defence (e.g. mixed-species shoaling)	High density of consumers	BMM, SGH
Siltation	Silt-intolerant	Fine sediments ameliorated by facilitator species	SGH
High temperature	Thermally intolerant	Facilitator species (e.g. riparian plants or macrophytes) ameliorate high temperatures	SGH

should expect to find exchanges for nutrition among species with limited acquisitive abilities in potentially nutrient-limited microhabitats for that species. Finally, exchanges for protection should occur for species under threat of herbivory or predation at a certain life stage, perhaps in contexts of higher predator density (Table 4).

The SGH will also be helpful for deductively searching for facilitation in freshwaters. Based on the SGH, we should expect to see increasing importance of facilitative interactions in more stressful contexts. For habitat amelioration, facilitation takes the form of modifying the state of a key stressor to the benefit of other species. For example, siltation is a common stressor in lotic systems and is modified to the benefit of other species by bioturbating taxa such as macrophytes (Sand-Jensen, 2003), crayfishes (Creed & Reed, 2004), predatory invertebrates (Zanetell & Peckarsky, 1996), and nest-building minnows (Peoples et al., 2015). Many freshwater habitats are naturally stressful along various abiotic gradients (Creed, 2006; Poff & Ward, 1989; Wellborn et al., 1996), and the SGH may be helpful in understanding community structure in stressful habitats like headwater streams, vernal pools and temporary wetlands, streambanks and shorelines, but also anthropogenically stressed habitats related to dams, reservoirs, or sites with impaired water quality. Likewise, for consumer pressure, we should expect to find facilitation via neighbourhood effects (e.g. mixed-species groups) for species at high risk of predation or herbivory in habitats with high densities of enemies.

Applying the SGH in freshwaters may yield novel inferences for inductively improving the model itself. A shortcoming of the SGH in its current form is that it can predict the frequency of interactions in a community, but not community composition. This issue stems from the assumption that all beneficiary species can and must be facilitated as environmental conditions worsen (He, Bertness, & Altieri, 2013). This prediction appears to be due to the fact that the SGH has been applied to systems dominated by sessile organisms. However, we know that there is variation in (1) species-specific responses to stressors (Maestre et al., 2009), and (2) species' ability to participate in facilitative associations (Butterfield & Callaway, 2013). These differences arise from variability in functional traits. For each trait associated with a response to a stressor, species respond along a continuum ranging from highly sensitive to highly tolerant. Likewise, species' propensity to participate in facilitative symbioses is a continuous trait. Some species are obligate beneficiaries, others may only participate opportunistically in certain contexts, and others still cannot participate at all. Integrating species identity via functional traits provides a means for using the SGH to predict community composition and its drivers along gradients of environmental change.

Here, we suggest an extension to the SGH that accounts for trait-induced differences in population-level response to abiotic or biotic stress (Figure 6). Consider the following scenarios: for a particular source of stress, numerical abundance of facilitator species should be invariant of stress because their activities ameliorate it. Likewise, stress-tolerant non-facilitator species should also show little to no numerical relationship with particular stress gradients. In all

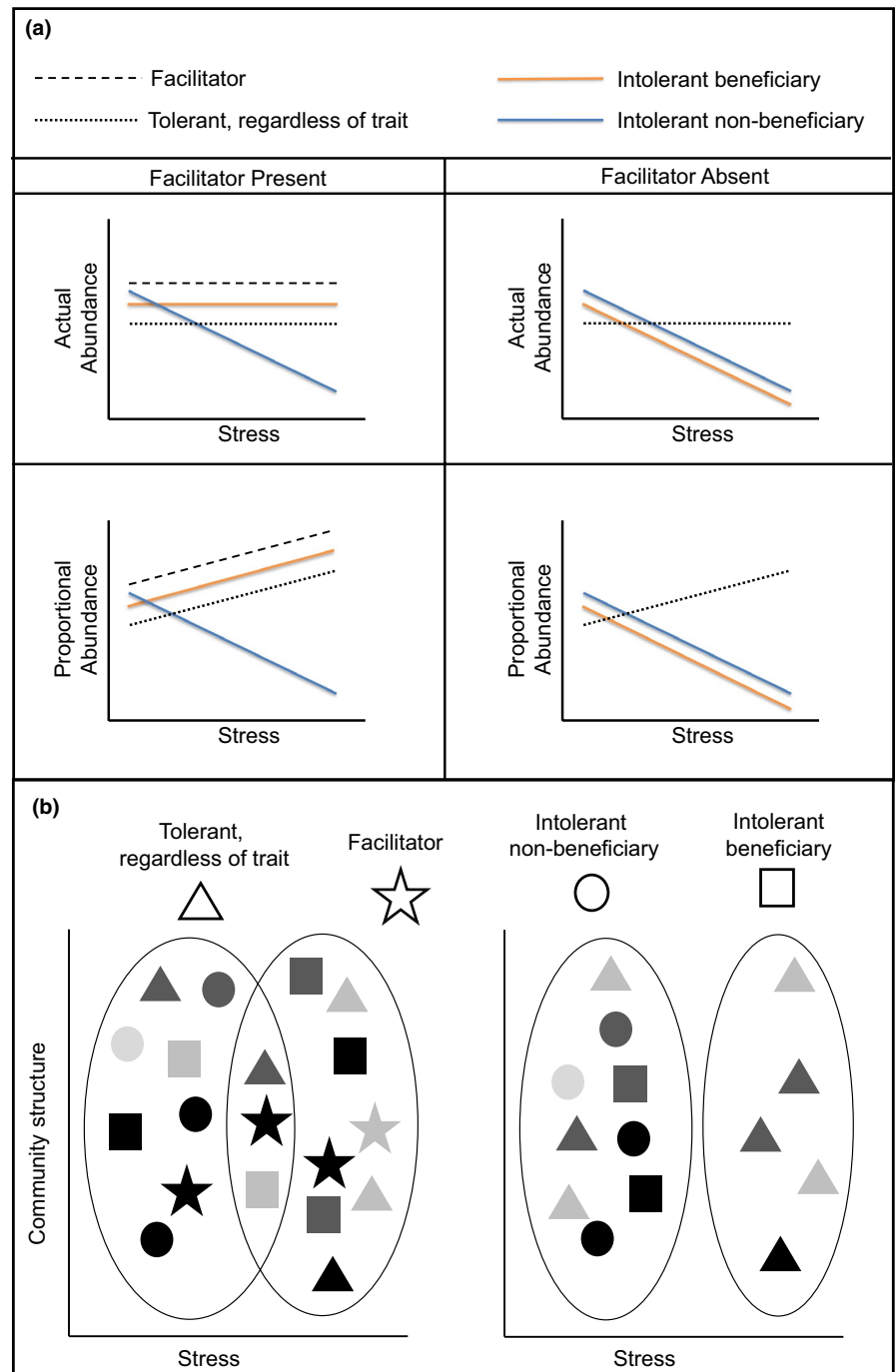
situations, species that are (1) less tolerant of stress, and (2) cannot benefit from facilitation will decrease as stress increases. However, for stress-intolerant species that can take advantage of facilitation, we should expect to observe little numerical relationship with increased stress (Figure 6a, left panels). In the absence of a facilitator species, numerical abundance of all intolerant beneficiaries should decrease with stress (Figure 6a, right panels). Decreasing numerical abundances of less tolerant species can cause increased proportional representation of tolerant ones, and intolerant beneficiaries in the presence of a facilitator (Figure 6a). These trait-based differences in response to stress will ultimately cause shifts in community structure along the stress gradient (Figure 6b). When facilitators are present, communities at low stress should be comprised of a mix of species with various tolerances to stress and abilities to take advantage of facilitation. However, as stress increases, communities will be dominated by stress-tolerant species, facilitators, and beneficiaries (Figure 6b, left panel). In the absence of facilitators, low-stress communities should similarly be comprised of species representing all traits, but will be reduced to only tolerant species, regardless of ability to take advantage of facilitation (Figure 6b, right panel). This model provides a straightforward framework for generating hypotheses about community composition based on two traits that are testable among species with experiments involving exclusion or removal of facilitator species.

We can also use existing knowledge of positive interactions in other systems to predict where and when others may occur in freshwater ecosystems (Table 4). Convergent evolution has resulted in similar interactions between highly diverse taxonomic groups in different systems. Cleaning symbioses, for example, had only been documented in marine systems for decades (Trivers, 1971). However, in the last 20 years cleaning symbioses have been identified that involve freshwater taxa (Brown et al., 2002, 2012; fishes: Severo-Neto & Froehlich, 2016). Likewise, it is well demonstrated that marine seaweeds and mollusc epibionts engage in protection-cleaning mutualisms (Peterson & Heck 2001; Stachowicz & Whitlatch 2005). Given the widespread relationships between macrophytes and epibionts in freshwater, similar widespread mutualisms may currently exist. Similarly, algal *farming* is well documented among marine reef species (Hata & Kato, 2006), but may also be employed by common algivorous minnows throughout North America (Gelwick & Matthews, 1992). It is also unsurprising that some freshwater sponges, which diverged from a common marine ancestor, use mutualist zoochlorellae for carbon fixation (Frost & Williamson, 1980), similar to many marine sponges. Aside from future studies of natural history, following clues from evolutionary biology is a clear way to find new examples of positive interactions and their implications for coevolution.

8.2 | Explore and quantify factors contributing to context dependency

In addition to identifying conditions in which facultative mutualisms will occur, the BMM also predicts that differential resource need,

FIGURE 6 (a) By considering species traits—particularly the ability to participate in facilitation often exhibited by mobile organisms, the stress-gradient hypothesis can be extended to predict community structure, as represented by a species' actual and proportional abundance in a local community. In the presence of a facilitator species ameliorating a particular source of physical stress or consumer pressure, relative abundance of facilitators and intolerant beneficiary species should increase with physical stress, while those that cannot participate in facilitation (intolerant non-beneficiary species) are extirpated. In the absence of facilitators, proportional representation of all intolerant taxa should be low or decrease with increasing stress. (b) Communities will be comprised of a diversity of traits at low levels of stress. Facilitators should support a community of tolerant species and beneficiaries as stress increases, but communities will be dominated by tolerant species at high levels of stress



provision, and availability among interacting species will lead to context dependent or facultative associations (Hoeksema & Schwartz, 2003). The BMM is useful to evaluate when and why partners choose to engage in positive resource exchanges, instead of obtaining resources alone or even competing. This can help guide investigations into existing negative or neutral interactions that have the potential to become positive in some contexts. Likewise, the SGH can help guide predictions on context-dependency at the community level. For example, it is possible that species that compete in benign habitats may engage in facilitation in habitats with increased abiotic stress.

8.3 | Investigate the effects of complex interactions on populations and communities

Models of population dynamics and community structure generally do not include the effects of positive interactions (Bronstein, 1994a; Stachowicz, 2001, but see Jones et al., 1994 and Bertness & Callaway 1994), and thus their inclusion may alter predictions of those models (Agrawal et al., 2007; Bruno, Stachowicz, & Bertness, 2003). Models of freshwater populations and communities also need to include potential impacts of positive interactions. This could improve our understanding of population dynamics and factors influencing community structure.

Population dynamics are affected by biotic context in the form of density dependence, and it is well understood that increased density is a limiting factor to population growth. Increased population sizes in a fixed space results in increased competition and predation between and among species, and diseases and parasites often become more effective at infecting hosts. One well-understood caveat to density-dependent relationships is the Allee effect, which results in increased abundance due to intraspecific cooperation at low densities (Courchamp, Clutton-Brock, & Grenfell, 1999). However, some work has shown that interspecific mutualism and facilitation, analogous to intraspecific cooperation, can result in beneficial outcomes even at high density (Bertness et al., 1999). In freshwater systems where ontogenetic shifts may change the nature of an association (Skelton et al., 2014) or seasonal symbioses occur (Gottsberger, 1978), we may expect to find temporally discrete instances where density-dependence increases some measure of fitness.

Positive interactions can be observed and tested at the individual level, but understanding their collective importance within a population or a community can be difficult. Many positive interactions occur in complex, multi-species aggregations in which sets of pairwise interactions may be contextualised by other interactions happening simultaneously, such as cheating. One way to address this difficulty is to conduct multi-factor experiments comparing within and among factors of interest to address some biotic or abiotic gradients. Using standardised effect sizes (Agrawal et al., 2007) allows researchers to determine how the sign and strength of interactions are context dependent along those gradients, and whether they are consistent across broad spatial or temporal ranges. However, we caution readers about the difficulty of conducting in situ experiments in freshwater ecosystems, especially streams. While large-scale, multi-factor experiments have provided powerful insight into freshwater ecosystem dynamics, they are notoriously difficult to conduct. Difficulties with construction and maintenance of enclosures can lead to low sample sizes and highly variable results.

Lastly, there is a need to incorporate positive interactions into our understanding of ecosystem function. A major finding in several recent reviews is that biodiversity plays a significant role in shaping a suite of ecosystem services (marine systems: Stachowicz, Bruno, & Duffy, 2007; terrestrial plants: Hooper et al., 2012). Positive interactions can affect biodiversity in variable but important ways, exemplified by Engelhardt and Ritchie (2001) who quantified the benefits of diverse macrophyte assemblages on wetland ecosystem functioning. Greater richness of submerged wetland plants decreased competition due to a sampling effect, resulting in increased algal and total plant biomass (Engelhardt & Ritchie, 2001). Positive interactions may have strong indirect benefits on diversity because of the sampling effect or complementarity (Batstone, Carscadden, Afkhami, & Frederickson, 2018; Cardinale, Palmer, & Collins, 2002; Stachowicz et al., 2007). Furthermore, foundation species (*sensu* Dayton 1972) or habitat modifiers may have direct effects; symbiont or indirect benefactor diversity may increase, while non-associative species or weak, facultative symbionts may exhibit diversity declines (Bulleri, Bruno, Silliman, & Stachowicz, 2016; Hacker & Gaines, 1997). Even

though freshwater lakes, reservoirs, and rivers make up <1% of all available waters globally (Carpenter, Stanley, & Vander Zanden, 2011), the biodiversity and ecosystem services they provide are vastly disproportionate to their volume. Quantifying the direct and indirect effects of positive interactions on ecosystem function will better guide future predictions and allow for more effective management and conservation of biodiversity (Halpern, Silliman, Olden, Bruno, & Bertness, 2007).

8.4 | Evaluate positive interactions across spatial scales

With the advent of high-speed analysis software, geospatial tools, and large datasets, our ability to quantify biotic interactions at larger spatial scales (say >10 m²) has greatly improved. Species distribution modelling is a suite of methods for predicting how species occur across landscapes at different spatial scales (Elith & Leathwick, 2009). Biotic interactions are being increasingly incorporated into species distribution models (Joseph, Stutz, & Johnson, 2016; Wisz et al., 2013), but only recently have positive interactions been considered (Afkhami, McIntyre, & Strauss, 2014; Duffy & Johnson, 2017; Filazzola et al., 2017). These models provide a framework to directly test for positive spatial correlations between species, even when those associations and their outcomes are context dependent (Tikhonov, Abrego, Dunson, & Ovaskainen, 2017). Peoples and Frimpong (2016a) examined species co-occurrence resulting from positive interactions, but there have been few similar studies examining larger scale patterns of positive co-occurrence in freshwaters (Arnhold, Penha, Peoples, & Mateus, 2019). Referring back to the goal of *identifying new positive interactions*, there are now models that infer species associations from large datasets (Cordero & Jackson, 2019; McGarvey & Veech, 2018; Morueta-Holme et al., 2016). Species involved in positive interactions often co-occur at small spatial scales, and many mutually beneficial symbioses are obligate for at least one of the participants. It is therefore plausible that feedbacks between local observations and large-scale patterns will provide a means for identifying previously unseen positive interactions. Understanding how positive interactions change across spatial scales should be a top priority.

Freshwater ecologists are currently engaged in determining the factors that generate large scale patterns of biodiversity. As our appreciation for the ubiquity and importance of positive interactions grows, so does a need to incorporate these interactions into our understanding of patterns of biodiversity in freshwaters. Metacommunity ecology has become an important approach for elucidating the drivers that shape biodiversity patterns. A metacommunity is a set of local communities of interacting species that are linked by dispersal (Leibold et al., 2004). Host-symbiont systems are inherently metacommunities (Mihaljevic, 2012). However, where the traditional local community occurs in a habitat patch, the patches of local symbiont metacommunities are hosts, each containing one or more species of symbiont, and those symbionts are connected

to other hosts by dispersal. While this perspective may be different from the traditional conception of metacommunities, the frameworks, predictions, and tools developed by metacommunity ecology are equally applicable to the study of symbiont metacommunities. However, metacommunity theory cannot be simply lifted from other applications and immediately applied to host-symbiont systems. There are a number of considerations and potential modifications necessary to apply metacommunity theory to these host-symbiont systems. First, an interesting facet of host-symbiont systems is that they are actually two nested metacommunities, with the symbiont metacommunity nested in a more traditional host metacommunity in which multiple species of hosts occur in landscape patches connected by dispersal, and this nested structure will need to be accounted for in studies at larger spatial scales. Second, there are a number of properties of *host patches* that differ from traditional landscape patches. Hosts are born, die, behave, and can change ontogenetically. These challenges in applying metacommunity theory to host-symbiont systems are not insurmountable but, to date, no standard framework exists for examining host-symbiont systems in a metacommunity context. There has been wide recognition that symbiosis ecology needs to embrace metacommunity ecology, although most of this recognition has come from research on disease and microbiomes (Christian, Whitaker, & Clay, 2015; Johnson, Ostfeld & Keasing, 2015; Mihaljevic, 2012; Miller, Svanbäck, & Bohannan, 2018), and no symbiosis-wide framework for the integration of metacommunity ecology into symbiont systems has yet emerged.

9 | POSITIVE INTERACTIONS IN FRESHWATER MANAGEMENT AND CONSERVATION

Understanding the impacts of positive interactions on freshwater systems can have major implications for conservation and management. One emerging theme focuses on conserving species interactions, as well as habitats (Halpern et al., 2007). For example, ichthyochory interactions are threatened by overharvesting of frugivorous fishes and hydrologic alteration (Correa et al., 2015). If fish are harvested before they can reach maturity, or if natural flood pulses are removed, fish will either lose access to the fruits or prevent them from germinating which could dramatically affect tree community structure. Examples such as ichthyochory show how the conservation of a few key taxa may provide an efficient means of benefitting multiple species. Efforts focused on conserving key host or facilitator taxa are also likely to provide quantifiable benefits to multiple partners (Byers et al., 2006). The hosts are often generalists or locally abundant, yet support diverse taxa that may be particularly threatened by anthropogenic impacts. Mutualisms are ubiquitous in marine and terrestrial systems (Mills, Soulé, & Doak, 1993), and may support more biodiversity in freshwater than we currently realise. Identifying and protecting these interactions should be imperative moving forward.

Habitat restoration is another potential research area in which application of positive interaction research could be beneficial (Byers et al., 2006; Halpern et al., 2007; Pollock et al., 2014). Facilitator species are often necessary for colonisation of harsh habitats (Diamond, 1986; Nakano et al., 2005), which is particularly important for high-gradient streams characterised by dynamic flows. It is often necessary to introduce foundation species in areas that are regularly exposed to stressful conditions. As shown in an arid terrestrial system by Filazzola et al., (2017), the management of dominant foundation species can have multiple community benefits through interaction networks. Managing foundation taxa in addition to making habitat improvements typical of restoration plans represents a novel way to leverage positive interactions for ecological benefit.

Recent work has also examined the ability of positive interactions to cause alternative stable-states within certain ecosystems (Kéfi, Holmgren, & Scheffer, 2016; Matsuzaki, Usio, Takamura, & Washitani, 2009). Positive feedback loops are a necessary condition for alternative states to occur, and facilitation or other positive interactions appear to play an integral role. For example, environmental degradation (decreased resource availability, increased abiotic stress, etc.) may result in a shift from a highly productive stable state to one with decreased productivity. In this case, it may take the restoration of facilitator or other positive-interacting species to restore the site to its previous state (Kéfi et al., 2016).

Positive interactions can also be key features of species invasions. Non-native species benefiting from positive interactions in their native range may be able to exploit similar interactions with related native species in their new ecosystem. For example, nest-building chubs have been found to facilitate expansion of non-native symbionts in numerous river systems of the south-eastern U.S.A. (Buckwalter, Frimpong, Angermeier, & Barney, 2018; Walser, Falterman, & Bart, 2000). Moreover, novel mutualisms by two non-native species have the potential to create an *invasion meltdown* in which non-native species may rapidly proliferate and cause changes to native community composition (Simberloff & Holle, 1999). For example, invasive carp (*Cyprinus carpio*) feed on and disperse seeds of both native and non-native vegetation in the Illinois River, U.S.A., and may be a vector for dispersal of range-limited invasive plants (VonBank, DeBoer, Casper, & Hagy, 2018).

Invasive ecosystem engineers can have immense effects on the invaded ecosystem, facilitating some species to the detriment of others. For example, the prolific filtering capacity of invasive zebra and quagga mussels (*Dreissena* spp.) has dramatically affected the water clarity of the Laurentian Great lakes (Higgins & Zanden 2010). In doing so, non-native dreissenids have formed mutualistic and facilitative relationships with a diversity of native and non-native species (DeVanna et al., 2011; Ricciardi, 2001). As another example, invasive carp and crayfish, have also been identified as causing catastrophic regime shifts in shallow lakes, changing the system from clear water lakes dominated by macrophytes to turbid and phytoplankton-dominated systems (Matsuzaki et al., 2009). While some evidence for such catastrophic *invasion meltdowns* does exist, such fears have been largely tempered after follow-up examination of this

phenomena (Simberloff, 2006). Regardless, conservationists should be aware of potential positive interactions that may aid establishment or spread of potentially harmful non-native species.

10 | CONCLUSIONS

Much more research is required before we can fully appreciate and understand the occurrence and impacts of positive interactions in freshwater ecosystems, but perhaps one benefit to our late start is that we do not need to make the same mistakes or rehash arguments that have been resolved in other disciplines. The studies discussed here shed light on the diversity of taxa engaged in positive interactions in freshwaters as well as their effects on their communities. The interaction between freshwater cleaner fishes and their clients, for example, illustrates two important concepts that were evident throughout much of this review: (1) freshwater positive interactions, even when analogous with interactions in other systems, are generally less studied; and (2) positive interactions need not be symbiotic, pairwise, long-term, or require significant investment to play a meaningful role in shaping ecological communities. That freshwater cleaning stations have only been identified within the last several years emphasises the point that the study of positive interactions in freshwaters is in an early stage (Severo-Neto & Froehlich, 2016). Examinations of basic life history will be necessary to identify examples and causal mechanisms driving positive interactions, but can be guided by deducing general ecological models. Positive interactions may be evolutionarily stable (Frederickson, 2017), but the changing context of climate and species invasions are certain to affect outcomes of pairwise and multi-species interactions (Six, 2009). Symbiont density is an important element of biotic context that needs to be considered as we identify and explore new positive interactions (Brown et al., 2012). Identifying novel mechanisms and processes in freshwaters can help to inform general ecological principles, and in turn, we can use the predictions and theory from broader ecology to understand the interactions we see in freshwater systems around the globe.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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