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SYSTEMATIC REVIEW

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Multispecies assemblages and multiple stressors: Synthesizing the state of experimental research in freshwaters

Fengzhi He[1,2,3] | Roshni Arora[4] | India Mansour[5]

[1]Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
[2]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany
[3]Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) and Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark
[4]India Program, The Nature Conservancy, New Delhi, India
[5]Institut für Biologie, Freie Universität Berlin, Berlin, Germany

Correspondence
Fengzhi He, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany.
Email: fengzhi.he@igb-berlin.de

India Mansour, Institut für Biologie, Freie Universität Berlin, Berlin, Germany.
Email: india.mansour@gmail.com

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Abstract

Recent decades have witnessed a sharp biodiversity decline in freshwaters due to multiple stressors. The presence of multiple stressors is expected to affect community structure and interactions in freshwater ecosystems, with subsequent functional consequences. We synthesized the state of experimental, manipulative multiple-stressor studies that focused on multispecies assemblages in freshwaters. Compared to rivers and lakes, wetland and groundwater ecosystems have received much less attention in identified multiple-stressor research. Most of the identified studies investigated combinations of abiotic stressors (e.g., nutrients, pesticides, heavy metals, warming, altered flow and sedimentation) on microbes and invertebrates while biotic stressors and vertebrates have been largely overlooked. The responses of community structure (e.g., alpha diversity, biomass, and abundance), some community/ecosystem functions (e.g., photosynthesis and autotrophic activity, leaf litter degradation), and morphological traits like body size and growth forms were frequently investigated. We observed a clear gap in biotic interactions under multiple-stressor conditions, which, although difficult to study, could impede a deeper mechanistic understanding of how multiple stressors affect freshwater assemblages and associated ecological processes. Although information on ecosystem recovery pathways following restoration is critical for freshwater management, few studies were designed to provide such information, signifying the disconnections between multiple-stressor research and environmental practice. To bridge these gaps, researchers and environmental practitioners need to work together to identify key stressors and interactions at different spatial and temporal scales and prioritize stressor management. Such collaborations will enhance the translation of multiple-stressor research into efficient management strategies to protect and restore freshwater ecosystems.

This article is categorized under:

Water and Life > Stresses and Pressures on Ecosystems
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KEYWORDS
biodiversity, freshwater, management, multiple stressors, systematic literature review

1 | INTRODUCTION

Freshwaters including rivers, lakes, wetlands, and groundwater are among the most diverse ecosystems (Balian et al., 2008; Reid et al., 2019). At the same time, freshwater ecosystems have higher percentages of extinct and threatened species and a sharper decline of vertebrate populations than marine or terrestrial realms (Costello, 2015; McRae et al., 2017). For example, monitored populations of freshwater vertebrates have declined by 84% from 1970 to 2016 (WWF, 2020). One of the key reasons behind such a drastic biodiversity decline, is the presence and cumulative impacts of multiple stressors, such as overexploitation, flow modification, habitat destruction, pollution, biological invasions, and salinization, in freshwater ecosystems (Dudgeon et al., 2006; Reid et al., 2019). Considering their inherent connectivity and topographic positions (e.g., rivers and lakes often occupy low points in landscapes), freshwater ecosystems usually are exposed to integrated effects of local catchment stressors and regional atmospheric processes, thereby bearing the greatest impacts of multiple stressors (Jackson et al., 2016). These impacts when viewed together with future threats, such as increasing water and energy demand and climate change, portray a very alarming picture for freshwater biodiversity and ecosystems (Albert et al., 2021).

Given the unprecedented pressure on freshwater ecosystems and rapid loss of freshwater biodiversity (He et al., 2019; Reid et al., 2019), scientists have called for scaling up and a focus on efficient management and conservation of these ecosystems to slow, halt or reverse these trends (Albert et al., 2021; Maasri et al., 2021; Tickner et al., 2020). The urgent need to restore damaged ecosystems has been recognized by the United Nations (UN), with 2020–2030 as the UN Decade on Ecosystem Restoration. For effective conservation and restoration of freshwater ecosystems, successful management of multiple stressors is imperative, which in turn requires holistic and forward-looking management practices, policies, and governance (Sabater et al., 2019). It is only recently that policies have begun to acknowledge that multiple stressors act simultaneously in freshwater ecosystems, though consideration and representation of multiple-stressor interactions and impacts are still very limited (Spears et al., 2021). This is largely due to gaps in our scientific knowledge of multiple-stressor interactions at different spatial and temporal scales, underlying mechanisms, and ecological responses across both degradation and recovery pathways. Furthermore, for many stressors (particularly emerging ones) we do not have a mechanistic understanding of individual stressors, let alone the complexity of multiple stressors (Côté et al., 2016; Gutiérrez-Cánovas et al., 2022; Jackson et al., 2021; Sabater et al., 2019; Segurado et al., 2021; Spears et al., 2021). These knowledge gaps hinder concrete management actions, as environmental practitioners and policy-makers have limited information to determine the probability of multiple stressor effects on their system and whether or how this can be addressed through management (Côté et al., 2016).

Efforts to identify multiple-stressor impacts on individual organisms or populations have been ongoing for almost a century (Orr et al., 2020). Multiple-stressor research in freshwater ecosystems has gained increasing focus in the past decade (Nõges et al., 2016; Jackson et al., 2016; Villar-Argaiz et al., 2016; Birk et al., 2020; Isaza et al., 2020; Goussen et al., 2020; Orr et al., 2020; Simmons et al., 2021). Despite considerable research thus far, informative evidence that could help develop generalisable practices for effectively managing multiple-stressor impacts on freshwater ecosystems is still limited (Reid et al., 2019; Spears et al., 2021). Conclusions from existing reviews show that there is considerable variation and uncertainty among outcomes (Jackson et al., 2016; Nõges et al., 2016; Orr et al., 2020).

To date, freshwater multiple-stressor research, though considering a wide variety of stressors, has largely focused on a single taxa or trophic group (Jackson et al., 2016). Thus, translating theory into targeted on-ground conservation interventions is very challenging as a result of our limited knowledge. Addressing these challenges requires the focus of research to move beyond being species or population centric and toward larger ecological scales, such as communities, food webs, and ecosystem functions, in order to assess impacts at a scale relevant for environmental practitioners. Given the rapid pace of freshwater habitat and biodiversity loss and the ubiquity of multiple-stressor impacts (Dudgeon, 2019), there is a pressing need to reassess the focus and goals of multiple-stressor research in freshwater ecosystems and realign to assist in accomplishing freshwater conservation goals regionally and globally. In this paper, we first review the state and focus of global multiple-stressor research, specifically those that have experimentally manipulated multiple stressors simultaneously and measured responses of multispecies assemblages (i.e., biotic interactions, community- and ecosystem-level responses) in freshwaters. Through this review, we synthesize the diversity of stressors, organisms, ecosystems, types of ecological responses, and the geographic focus in identified multiple-stressor research. We follow with a call for more research focusing on trophic interactions and ecosystem functions. We then present a forward-looking perspective on translating multiple-stressor research into conservation and restoration actions to safeguard freshwater biodiversity.

2 | LITERATURE REVIEW AND DATA CLASSIFICATION

The literature search included studies published before 2021 (i.e., papers in a journal issue published in 2020 or earlier). We conducted literature searches on the Web of Science twice. The first search was performed on January 27, 2020 to include papers published before 2020 while the second search was conducted on April 8, 2021 to include all the papers published in 2020. We generated a list of search terms including different terms for freshwater ecosystems and types of biotic interactions, as well as several synonyms for multiple stressors. We did not include the terms "driver" or "factor," which are more frequently applied in terrestrial multiple stressor studies (Orr et al., 2020), or the term "disturbance"—this may have biased our collections toward research from the freshwater scientific community. We also may have missed some studies that were conducted before the use of the term "multiple stressors" became more widespread. The following search string was used:

> *Topic = ((freshwater OR river OR stream OR lake OR pond OR groundwater OR wetland OR riparian OR aquifer OR estuar* OR floodplain OR headwater OR basin OR catchment OR intermittent OR spring OR creek OR pool OR brook) AND (multiple stressor* OR multistressor* OR multi-stressor* OR stressors) AND (communit* OR food web OR trophic OR predat* OR prey OR top down OR top-down OR bottom up OR bottom-up OR competit* OR parasit* OR symbios* OR trait OR guild OR *diversity))*

In the first round of screening, duplicates (i.e., 28 articles) in yielded results from the Web of Science were removed with the package *revtools* (Westgate, 2019) in R (R Core Team, 2021). For the screening, the articles were divided equally between three assessors, with 20% of articles assigned to more than one person (to ensure that screening parameters were being applied similarly). In the second round of screening, the 240 included articles that passed the abstract screening during the first round were checked by all three assessors to identify studies that fulfilled the inclusion criteria. The primary aim of focusing on peer-reviewed papers was to target published studies with factorial/manipulative experimental designs altering multiple stressors relevant to freshwater ecosystems. We included experimental, manipulative studies conducted in the laboratories or in the field. Most of the studies followed a full factorial design while the experimental design of a few studies was partially factorial. This systematic review (Figure 1) adhered to the Preferred Reporting Items for Systematic reviews and Meta-Analyses guidelines (O'Dea et al., 2021).

The relevant studies were identified based on the following inclusion criteria: (1) investigated a freshwater or brackish (i.e., estuaries) environment; (2) applied a manipulative, experimental design; (3) investigated a multispecies assemblage; (4) measured at least one community- or ecosystem-level response variable or interactions between different species. In total, 167 studies fulfilled all criteria and were selected for review (details on literature screening are described in the Supporting information). Metadata was then extracted from each article, including study location, ecosystem type, organisms, stressors, and ecological responses (Appendix S2). [Correction added on 6 March 2023, after first online publication: The appendix number has been updated.] Stressor interaction types (e.g., additive, synergistic, antagonistic) were outside of the scope of our work and were not extracted from our article collection; however, recent studies applying quantitative approaches report stressor interactions for large datasets from freshwater systems (Birk et al., 2020; Jackson et al., 2016).

After extracting the stressor types, we classified them into 12 fine categories (Table S1) and then further into four broad categories: water pollution and chemistry, hydromorphological stressors, climatic stressors, and biological stressors. Study organisms were classified into 12 fine categories (Table S2) based on their taxonomy, body size, and life history (e.g., habitat and trophic position). They were then grouped into five broad categories, namely microbes, parasites, invertebrates, vertebrates, and plants. Ecological responses were grouped into 31 fine (Table S3) and four broad categories, namely, species interactions, fitness, traits and life history, community structure, and community/ecosystem function. Only those response variables that measured a response of an organism, multispecies assemblage or ecosystem function were extracted from studies (i.e., physicochemical response variables such as nutrient concentrations were not included). Derived or calculated response variables (e.g., alpha diversity, ecosystem metabolism) that were relevant for understanding effects at the community or ecosystem levels were also included.

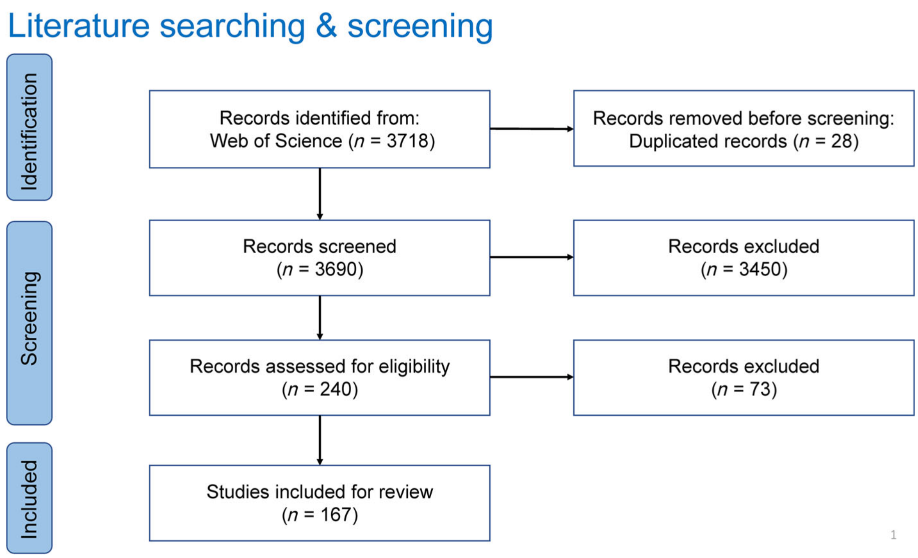

FIGURE 1 Flow diagram of the literature search and screening protocol implemented in this study.

3 | SPATIAL AND TEMPORAL DISTRIBUTION OF IDENTIFIED STUDIES

Among the 167 identified studies, most of them were conducted in Europe (85), North America (44), and Oceania (23), with the United States (31), Spain (29), New Zealand (21), and Canada (13) contributing to over 50% of all studies (Figure 2a). Prior to 2005, all the identified studies were conducted in the US and Canada (Figure S1a). Nine studies were conducted in South America including Argentina (7), Brazil (1), and Chile (1), while China (6), and South Africa (1) represented the only countries with identified studies in Asia and Africa, respectively. Although tropical regions harbor a high level of freshwater biodiversity (Collen et al., 2014), only 1 out of 167 studies was conducted in the tropics (i.e., Gomes et al., 2018). The geographic pattern in the identified multiple-stressor research aligns with that of overall biodiversity research efforts (Williams-Subiza & Epele, 2021), reflecting the major geographic gap in research on biodiversity and stressors in the Global South. In these regions, freshwater biodiversity is subject to rapidly growing pressure caused by human activities, with hundreds of freshwater species considered threatened on the IUCN Red List (Carrizo et al., 2017). Threats to freshwater ecosystems, including hydropower development, land use change, and invasive species, have increased rapidly during the last few decades in these regions (Barlow et al., 2018; Pyšek et al., 2020; Song et al., 2018; Winemiller et al., 2016). The lack of experimental studies that consider local environmental situations (e.g., the type, combination, and intensity of stressors, and biotic communities that occur in freshwaters in these regions) impedes a contextualized mechanistic understanding of multiple-stressor impacts on freshwater ecosystems and could hinder the development of effective conservation and restoration strategies in these regions.

Across ecosystem types, estuaries (12 studies) and wetlands (5) have received much less research attention than rivers (98) and lakes (52). Although the majority of the identified studies investigated river ecosystems, nearly all studies that were published before 2008 focused on lake, wetland, and estuary systems; post which river studies have become dominant. Compared to lake studies, which were often conducted using flasks or tanks, it is more technically challenging to simulate flowing environments in rivers. Innovation and technological advancements in recent times have enabled experimental simulation of such environments (e.g., artificial channels, ExStream System) which likely explains the observed sharp increase in studies focusing on multiple stressors in river ecosystems.

An increasing trend of publications was observed over time (annual growth rate = 10.7%; Figure 2b). Among the 10 countries with most published articles, there was a variable international collaboration (based on corresponding authors' institutional addresses at the time of publication; Figure 2c). Scientists from Germany and Sweden were highly collaborative (75% and 70% international teams, respectively), while those from France and the United States had proportionally fewer international collaborations (10% and 12%, respectively). Increasing focus on multiple stressors and freshwater ecosystems in the Global South may likely lead to changes in observed international collaboration trends. For example, there are increasing numbers of multiple-stressor studies conducted in China during the last 5 years (Pu, Zeng, Mo, Liao, & Chen, 2019; Pu, Zeng, Mo, He, et al., 2019; Liu et al., 2020; Juvigny-Khenafou et al., 2020; Juvigny-Khenafou,

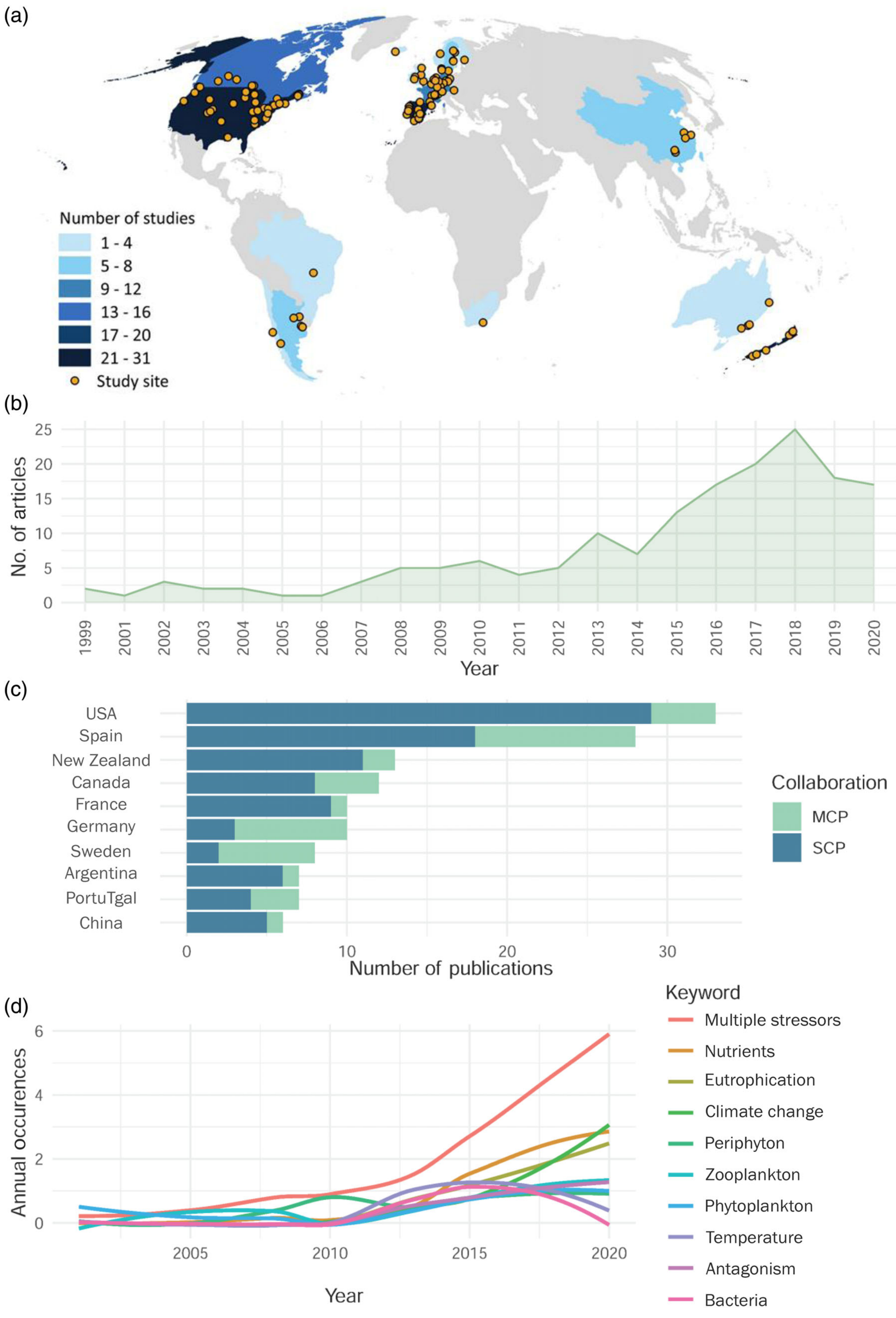

FIGURE 2 Results of bibliometric analyses of identified articles, including (a) geographic locations; (b) the number of articles published per year; (c) the number of articles published by each of the 10 countries with the most articles from our collection, MCP, multiple country publication; SCP; single country publication; (d) keyword occurrences over time.

Piggott, Atkinson, Zhang, Wu, & Matthaei, 2021; Juvigny-Khenafou, Piggott, Atkinson, Zhang, Macaulay, et al., 2021; Zhang et al., 2022) and many of them included international collaborations. Unsurprisingly, "multiple stressors" was the most frequently occurring keyword in our collection of articles (Figure 2d). The keywords "climate change" and "eutrophication" have been trending upwards over the past 5 years, while "temperature" and "bacteria" are trending downwards, possibly indicative of a shift in the research focus of groups investigating the influence of multiple-stressor impacts on multispecies assemblages. However, these changes could also simply reflect the changes in the popularity of terms used to describe multiple-stressor research (e.g., studies that used 'climate change' as a keyword often investigated temperature).

4 | TRENDS AND GAPS IN STUDIED STRESSORS, ORGANISMS, AND ECOLOGICAL RESPONSES

4.1 | Stressors

Among the fine stressor categories, impacts of nutrient pollution were the most studied (53% of the studies; Figure 3a), followed by sedimentation and substrate disturbance (25%), temperature (23%), flow regime (23%), and pesticide pollution (22%). The most-studied stressors in the identified studies are also commonly reported stressors in freshwaters (Nõges et al., 2016; Orr et al., 2020) and are regarded as critical threats to freshwater biodiversity (Dudgeon, 2019; Reid et al., 2019). Among the broad categories, abiotic stressors were well-represented: stressors relating to water pollution and chemistry were included in 96% of the identified studies, followed by hydromorphological stressors (37%) and climatic stressors (23%). Biological stressors such as invasive species, infectious diseases, and weakened biological interactions due to biodiversity loss have been less frequently investigated and were included in only 19% of the identified studies. In addition, stressors such as overexploitation and habitat fragmentation, which directly increase species mortality and impede species migration (Dudgeon et al., 2006), did not appear in identified studies. Several factors may explain the predominance of abiotic stressors. First, in the regions where most studies were conducted (e.g., Europe, North America, and New Zealand), pollution, flow modification, altered sedimentation, and warming are regarded as the prominent stressors on freshwater ecosystems (Birk et al., 2020; Matthaei & Piggott, 2019; Sullivan et al., 2019). Second, stressors such as pollution, flow modification, and sedimentation are relatively easy to manipulate under experimental conditions, whereas it is challenging to comprehensively include complex biotic interactions in experiments (Morales-Castilla et al., 2015). Third, most of the investigated freshwater organisms are microbes and invertebrates (see Section 4.2). Stressors such as pollution, flow modification, altered sedimentation, and climate change, are regarded as highly relevant stressors for these taxa (Stendera et al., 2012).

While nutrient pollution received the most research attention across all ecosystem types, there was variation in other frequently investigated stressors. Sedimentation and substrate disturbance and modified flow regime were often included in river studies; unsurprisingly, as freshwater organisms in lotic environments are more likely to be affected by these stressors than those in lentic ecosystems (Elosegi et al., 2019; Stendera et al., 2012). Only four studies considered low dissolved oxygen as one of the stressors in their experiments (Calapez et al., 2017, 2018; Gomes et al., 2018; Lowell & Culp, 1999). Surprisingly, none of these studies focused on lake ecosystems, given the fact that deoxygenation has been widely observed in lakes worldwide and is associated with other stressors such as climate change and eutrophication (Jane et al., 2021). The decline of dissolved oxygen in lakes could lead to altered biogeochemical cycling (North et al., 2014), increased algal blooms (Michalak et al., 2013), and fish kills (Godinho et al., 2019). Such evidence warrants the need for more studies focusing on the impacts of interactions between deoxygenation and other stressors in lake ecosystems (e.g., warming and nutrients).

Estuaries and wetlands were underrepresented ecosystem types in the identified studies. In estuaries, nutrient and metal pollution were the most investigated stressors. In the five studies that focused on wetland ecosystems, various stressor types were considered in experiments, including nutrients, pesticides, increased salinity, invasive species, altered sedimentation, and warming. The diverse stressors in the identified wetland studies indicate that these ecosystems are subject to various anthropogenic stressors (Fluet-Chouinard et al., 2020; Reis et al., 2017). We also observed a glaring lack of experimental studies investigating multiple-stressor impacts in groundwater ecosystems. Although multiple-stressor issues in groundwater ecosystems have been highlighted (Nõges et al., 2016), none of the identified experimental studies focused on these ecosystems, likely because of the technical challenge of simulating groundwater ecosystems and monitoring their responses to multiple stressors in laboratories. Groundwater ecosystems are subject to intensifying stressors,

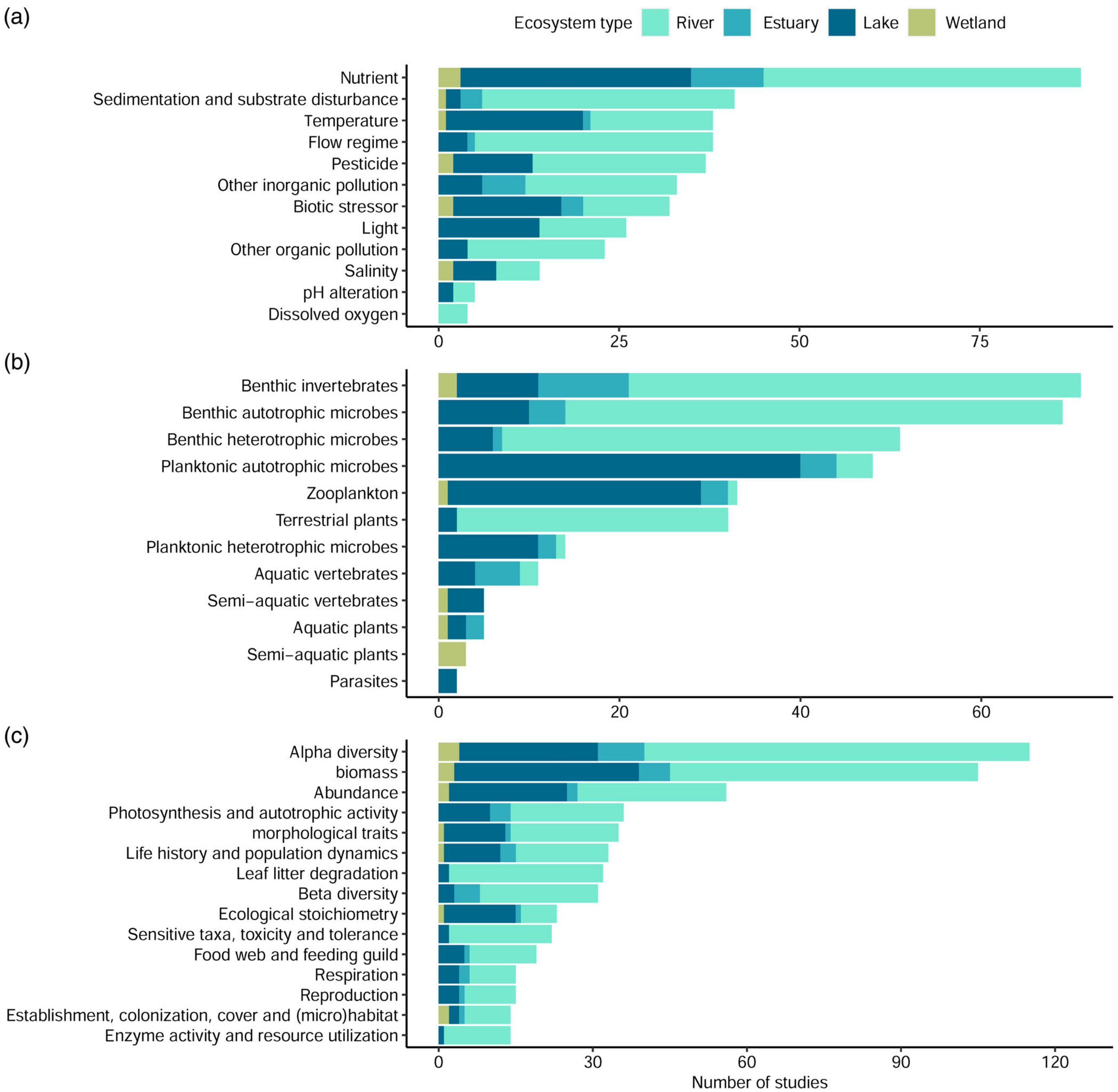

FIGURE 3 Number of investigated fine categories of (a) stressor, (b) organism type, and (c) ecological response in each ecosystem. Only fine categories of response variables that were investigated in more than 10 studies are shown here.

including contamination, depletion, and climate change (Lall et al., 2020); however, our knowledge of biodiversity and ecological processes in these ecosystems remains limited (Gibert & Culver, 2009; Griebler et al., 2014). Although wetland and groundwater ecosystems are subject to multiple stressors, they have received less research attention compared to rivers and lakes. Hence, more studies quantifying multiple-stressor impacts on wetland and groundwater ecosystems are needed to better predict their responses to environmental change, ultimately contributing to holistic and effective conservation and restoration plans (Griebler & Avramov, 2015; Xu et al., 2020; Zedler & Kercher, 2005).

Temporally, most identified studies focused on the impacts of nutrients and heavy metals prior to 2005 (Figure S1b), along with a few studies that included dissolved oxygen (Lowell & Culp, 1999), UV radiation (Xenopoulos et al., 2002), dissolved organic carbon (Klug & Cottingham, 2001), and sedimentation (Mahaney et al., 2005). Prior to 2009, all studies that included nutrients as one of the multiple stressors focused on lakes, wetlands, and estuaries. From 2009 to 2020, the number of identified studies related to rivers (i.e., 44 studies) outnumbered the sum of other ecosystems (33).

In the last decade, the impacts of altered sedimentation and flow regime on rivers have received rapidly increasing attention while was frequently included as one of the stressors in both river and lake studies. Indeed, the impact of hydromorphological and climatic stressors on freshwater ecosystems and their interactions with other stressors have been widely reported in the last decade and hence, received greater research attention (Elosegi et al., 2019; Johnson & Penaluna, 2019). In addition, a growing number of studies focusing on these stressors, as well as on pesticides, pharmaceuticals, and salinization reflects the increased recognition of emerging threats to freshwater ecosystems (Reid et al., 2019).

We observed distinct patterns of stressor combinations between ecosystems (Figure 4a). The investigated combinations of stressors in rivers were more diverse than those in lakes, which often involved water pollution and chemistry. The most frequently studied combination of fine stressor categories was nutrients together with sedimentation and substrate disturbance, particularly in rivers (Figure 4b). Indeed, increased nutrient pollution and fine sediment from agricultural activities has been a major threat to river ecosystems globally (Blann et al., 2009; Elosegi et al., 2019; Evans et al., 2019). With current projections of future agricultural expansion and intensification, river ecosystems will receive considerably higher loads of nutrients, sediment, and other organic and inorganic pollutants (Xie & Ringler, 2017; Borrelli et al., 2020). Altered flow regime is another persistent threat to river ecosystems (Dudgeon, 2019). Hydropower dams, water abstraction, climate change, as well as land-cover change can all contribute to the modification of natural flow regimes in rivers (Poff et al., 1997; Schneider et al., 2013). In our identified studies, altered flow regime has been frequently paired with other stressors such as sedimentation and substrate disturbance, nutrients, other organic pollution, pesticides, and warming. Given the increasing human population, energy and food demands, and climate change, it is very likely that a greater extent of river ecosystems will be subjected to these stressor combinations in the future (Johnson & Penaluna, 2019; Reid et al., 2019). In lakes, stressors within the pollution and water chemistry category were often paired with each other. It was unexpected that the light-nutrient combination predominantly involved lake ecosystems, as both light and nutrient

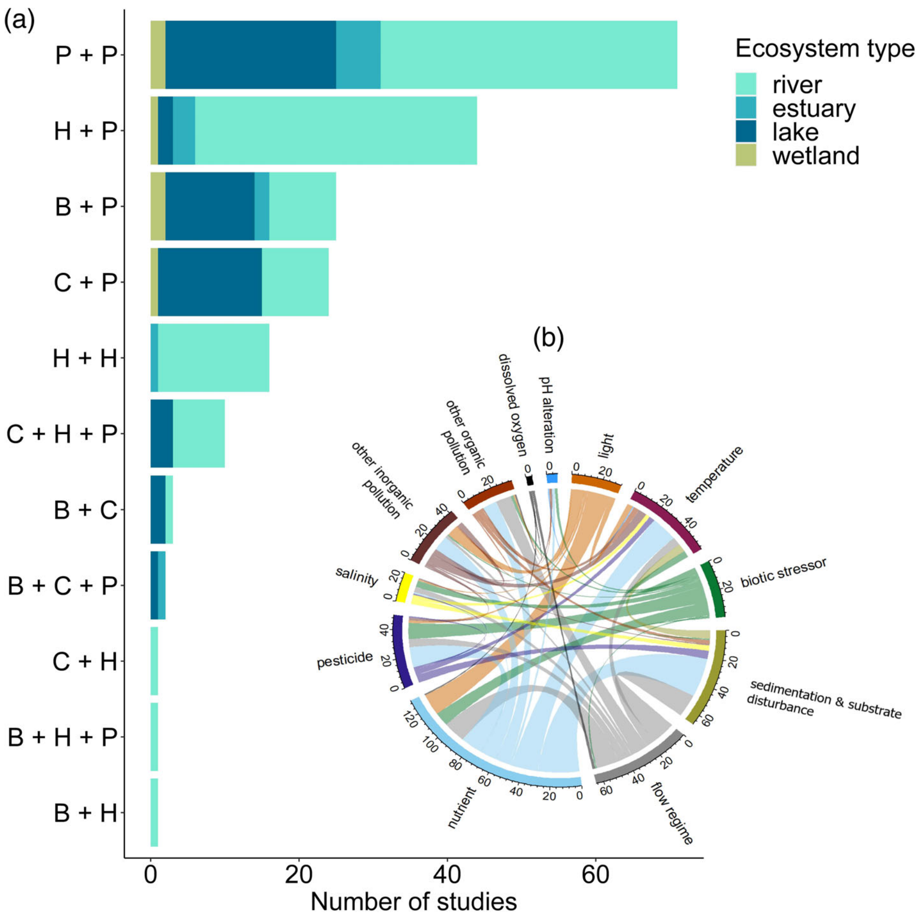

FIGURE 4 Number of investigated combinations of (a) broad stressor categories in each ecosystem and b) fine stressor categories. Abbreviations for broad stressor categories: B, biological stressor; C, climatic stressor; H, hydromorphological stressor; P, water pollution and chemistry.

pollution are widely reported in rivers (Strokal et al., 2019; Jechow & Hölker, 2019). In both wetlands and estuaries, most stressor combinations were unique, with only the interactions between nutrients and pesticides being investigated in more than one study (Baker et al., 2014; Slocum & Mendelssohn, 2008).

4.2 | Organisms

Organisms living in the benthic zone were the most-studied group in the identified studies (Figure 3b; Figure S2). Most studies on benthic organisms were conducted in rivers, with only about 12% focusing on lakes and 1% on wetlands. On the contrary, plankton were mainly studied in lakes (75%). Compared to invertebrates and microbes, freshwater vertebrates and plants have received much less attention. Studies that included vertebrates focused more on rivers and estuaries while none of the five studies that included semi-aquatic vertebrates was conducted in lotic environments. Four out of these five studies focused on juvenile stages of anurans (i.e., tadpole or metamorph) in lentic environments (Distel & Boone, 2010; Van Meter et al., 2012; Jones et al., 2017; Buss & Hua, 2018). Interestingly, terrestrial plants have been mostly included in experiments focusing on river ecosystems.

Temporally, organism types included in the identified studies were not randomly distributed (Figure S3a). All studies focusing on terrestrial plants were conducted after 2008. This was likely a consequence of a rapidly increased number of experiments focusing on river ecosystems after 2008, particularly those measuring leaf litter decomposition. Similarly, an upsurge in studies investigating riverine benthic organisms has also occurred since 2008. In general, there is a trend toward studying a broader diversity of taxa in both lakes and rivers, which indicates the increasing awareness of multiple-stressor impacts on these ecosystems (Birk, 2019; Heino et al., 2021).

A clear gap exists in the studied organisms, with vertebrates being underrepresented. Four main factors might have contributed to the underrepresentation of vertebrates in identified studies. First, the size of the infrastructure is often small due to technical and financial limitations. The river channels used in the identified studies ranged from 0.76 m (Kashian et al., 2007) to 12 m (Baattrup-Pedersen et al., 2020) in length and were often less than 1 m wide. Circular stream mesocosms were also used to simulate river environments and often had an approximate volume of less than 5 L (e.g., ExStream System; Piggott, Townsend, & Matthaei, 2015; Piggott, Salis, et al., 2015; Elbrecht et al., 2016). For the experiments focused on lentic ecosystems, the volume of the simulated lakes ranged from less than 1 L (e.g., Interlandi, 2002) to 4000 L (Angeler & Moreno, 2007). The size of these artificial streams and lakes is not likely sufficient to support vertebrate communities or large taxa. Hence, the vertebrates included in the identified studies were either small species (Breitburg et al., 1999; Geyer et al., 2016) or juveniles of large vertebrates (Bruder et al., 2017; Lopez et al., 2018). Second, small organisms such as invertebrates and microbes typically have shorter life cycles and can establish in new environments (i.e., simulated freshwater ecosystems in mesocosms) faster than vertebrates. In addition, invertebrates and microbes often show rapid responses to environmental stressors while it might take years or decades to observe the impacts of stressors on vertebrate communities due to their long generation time (Resh, 2008). Therefore, invertebrates and microbes have clear advantages over vertebrates as model organisms in short-term experiments. Indeed, over 80% of the identified studies were based on experiments with a duration of less than 2 months. Third, vertebrates often occupy upper trophic positions and have more complex requirements of habitats and co-occurring biotic communities. It might be technically challenging to these requirements for functioning vertebrate communities over a long period. The unfit environment itself might result in reduced fitness or even increased mortality which would make it difficult to disentangle such an effect from the influence of manipulated stressors. Lastly, issues related to animal welfare and permit might arise when vertebrates are included in the experiment (Sloman et al., 2019), particularly for animals that are protected by legal regulations. Hence, they might be excluded from experiments to avoid these potential issues and efforts in applying for permits.

4.3 | Ecological responses

Alpha diversity metrics and biomass were by far the most-studied response variables (Figure 3c). Metrics of community structure and community/ecosystem function were more frequently studied than interactions between organisms (e.g., predation and parasitism). There were few clear patterns of response variables across ecosystem types. The three most-studied response variables (alpha-diversity, biomass, and abundance) were investigated in all four ecosystem types (Figure S4). The fourth most-studied response variable, photosynthesis and autotrophic activity, has mostly been investigated in rivers and lakes since 2010 (Figure S3b). Before this, one group of studies reported results from a long-term outdoor mesocosm study in estuaries (Breitburg et al., 1999; Laursen et al., 2002; Riedel et al., 2003). Leaf litter degradation and sensitive taxa/toxicity were also most studied in river ecosystems, likely because of the historical development of these fields (e.g., the study of allochthonous material in the context of the River Continuum Concept, Vannote et al., 1980). Resistance/resilience and heterotrophic production were more frequently studied in lakes than in other ecosystem types.

Studies were categorized based on whether they investigated species interactions within or across trophic levels, or both. The majority (60%) of studies investigated species interactions within a single trophic level, and about one quarter of studies reported data regarding species interactions both within a single trophic level and across trophic levels. There did not appear to be a bias for a particular type of response variable within these different classes of studies: measured response variables were generally distributed proportionally to the overall distribution. Comparing the most frequently reported response variables, alpha diversity was slightly more likely to be reported in studies focusing on a single trophic level, while studies reporting biomass were slightly more likely to include multiple trophic levels. Leaf litter degradation and food web/feeding guild studies generally included multiple trophic levels.

Studies investigating species interactions were sparse in the identified literature, with 3 or fewer studies investigating predation, parasitism, and commensalism—competition was studied slightly more frequently. We did not find any examples of studies investigating the influence of multiple stressors on symbiotic relationships in freshwaters; although our search terms may have limited our ability to identify studies investigating other types of positive species interactions such as facilitation. Both parasitism studies focused on lake ecosystems and investigated Daphnia (Manzi et al., 2020) and tadpole (Buss & Hua, 2018) as host organisms. A wide range of stressors was studied in this small group of studies, and all but one of the studies are fairly recent (since 2015), which may indicate increasing interest in how species interactions are influenced by multiple stressors. Shifts in species interactions in a multiple-stressor context can sometimes explain shifts in community structure under multiple stressors (Orr et al., 2020; Schuwirth et al., 2016). Such studies could provide a deeper mechanistic understanding of how multiple stressors affect freshwater communities.

While many studies reported information about changes in species abundances and/or alpha diversity metrics in multiple stressor contexts, only a small fraction of these studies ($n = 31$) calculated species turnover. Particularly for those studies that were conducted in situ, information about changes in beta diversity would be informative: because colonization processes are faster than extinction, changes in richness alone are not likely to indicate multiple-stressor impacts, and in fact could even rise as the result of the immigration of new species (Hillebrand et al., 2018). This could provide the opportunity for an informative data synthesis: many identified studies report species abundance data that could be used to calculate species turnover.

A variety of ecosystem-level response variables were reported in the identified studies, including food-web/trophic complexity, nutrient cycling and utilization, and ecosystem metabolism and stability. There were marked biases in the ecosystem types in which these response variables were measured: litter decomposition and enzyme activity/resource utilization were almost entirely reported from studies in riverine systems while ecosystem metabolism, ecological stoichiometry, heterotrophic production, and resistance/resilience were largely studied in lakes. Photosynthesis, respiration, and food webs/trophic dynamics were reported from multiple ecosystem types. Our investigation of the literature focused on manipulative/factorial studies, that is, those which are well-suited to hypothesis testing and determining causality. However, few studies analyzed community or food web networks (e.g., Pu, Zeng, Mo, Liao, & Chen, 2019), which, although computationally intensive, is important for scaling up multiple stressor impacts. Additionally, ecosystem-level responses were studied less frequently than population- and community-level response variables. This is troubling because information about the mechanisms underlying ecosystem (dys)functioning is required to support the development of targeted restoration and conservation practices.

5 | LINKAGES BETWEEN STRESSORS, ORGANISMS AND ECOLOGICAL RESPONSES

The combinations of different stressor categories were not evenly distributed between organism groups. Under all the combinations of stressor categories, microbes and invertebrates were always the two most-studied groups (Figure 5a). Among all stressor combinations, only water pollution and chemistry stressors and biological stressors have been jointly investigated for all five major groups of organisms. Although most of the studies that focused on vertebrates fell into this category, vertebrates were often included as a stressor (e.g., predation and grazing) rather than organisms responding to stressors. Over half of all identified studies combined at least two different stressors under the same broad stressor category. For example, the combined effects of different pollutants and chemical stressors were widely investigated on all organism groups, particularly on microbes and invertebrates. In addition, the joint effects of different hydromorphological stressors (e.g., flow and sedimentation) were also frequently investigated for microbes and invertebrates. Although plants were also often included in these studies, they only functioned as litters for measuring degradation rate (Matthaei et al., 2010; Bruder et al., 2016; Mustonen et al., 2016; Röhl et al., 2017; Juvigny-Khenafou et al., 2020).

Compared to frequently investigated pollutants such as nutrients, pesticides, and heavy metals, pollutants such as pharmaceuticals, antimicrobial compounds, and microplastics and their interactive effects with other stressors received relatively little attention (Corcoll et al., 2015; Winkworth et al., 2015; Serra-Compte et al., 2018; Subirats et al., 2018). There have been growing concerns about the impacts of these emerging pollutants in freshwater environments (Kümmerer, 2009; Reid et al., 2019). In addition, these emerging pollutants can interact with each other. For example, microplastics may adsorb other pollutants and increase their bioaccumulation and toxicity in freshwaters (Atugoda et al., 2021; Wang et al., 2021). None of the identified studies investigated the combined effects of microplastics and other stressors on freshwater assemblages or species interactions, which stands in contrast to the fact that microplastics widely occur in freshwater environments and exert negative impacts on freshwater organisms (Eerkes-Medrano et al., 2015; Blettler et al., 2018; Li et al., 2018). The lack of research focusing on these emerging stressors is likely because they have only recently attracted major attention among scientists. The amount and types of evidence regarding stressor types and response variables also depend on the historical and current popularity as a research focus.

Although a handful of studies identified in our review investigated the interactive effects of invasive species and other stressors, this number lagged far behind compared to physicochemical stressors. Nonnative species have been introduced to freshwaters worldwide which have altered biotic interactions and ecosystem functions in the introduced ecosystems (Moorhouse & Macdonald, 2015). Expanding human activities and ongoing environmental change could further assist the spread and establishment of invasive species. For example, thousands of dams have been constructed or planned to meet the growing demand for energy and water (Zarfl et al., 2015). The reservoirs associated with these dams could assist the establishment of invasive species in new freshwater environments (Havel et al., 2015). In addition, invasive species may also interact with other emerging stressors such as climate change and infectious diseases and pose negative impacts on freshwater ecosystems (Conn, 2014; Havel et al., 2015).

Research attention differed across different stressors and response variable combinations (Figure 5b). Most of the studies (92%) combined stressors in less than three broad categories. Among these studies, over 90% of the studies investigated

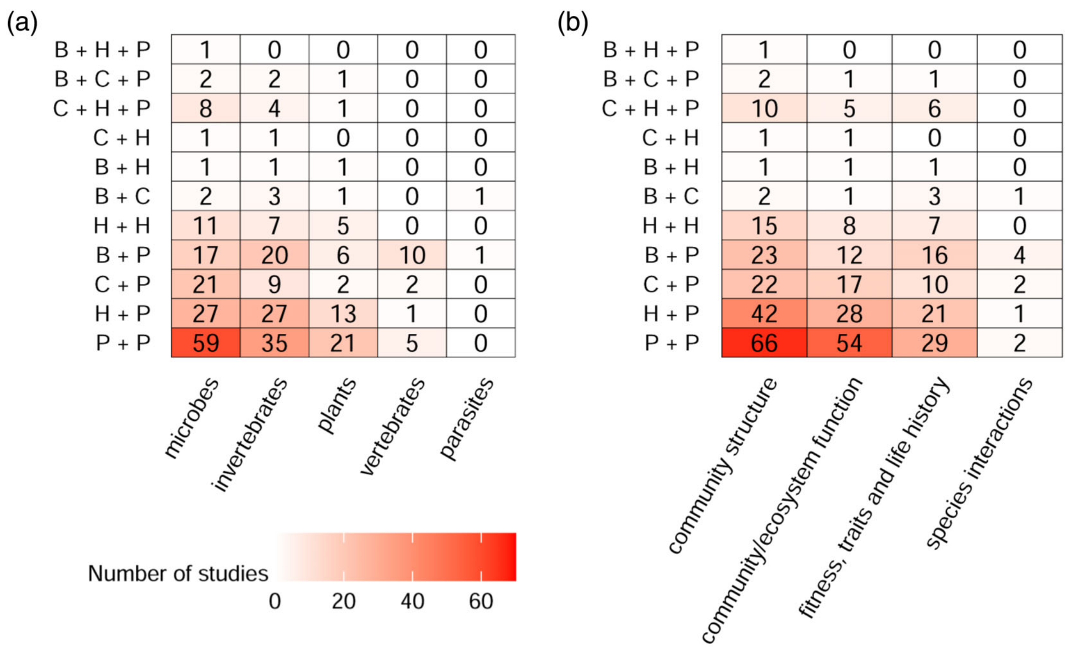

FIGURE 5 Heatmap of identified combinations of stressor categories and broad categories of (a) organism and (b) ecological response. Abbreviations for broad stressor categories: B, biological stressor; C, climatic stressor; H, hydromorphological stressor; P, water pollution and chemistry.

the impacts of multiple stressors on community structure, with biomass, abundance, and alpha diversity metrics being most frequently studied. Although ecosystem functions have been investigated in over half of the identified studies, microbe- and invertebrate-related responses (e.g., leaf litter decomposition, photosynthesis and autotrophic activity) were most frequently investigated. Species interactions were only investigated in a few studies, including competition (McKie et al., 2009; Bray et al., 2019), predation (Alexander et al., 2016), and commensalism (Cabrerizo et al., 2019).

The responses of communities and ecosystems to multiple stressors depend on the configuration of ecological networks and biotic interactions (Bruder et al., 2019; Beauchesne et al., 2021). The strength, length and structure of ecological networks influence the propagation of stressors and the stability of whole systems. Multiple stressors have the potential to reconfigure entire food webs, thereby, impacting ecosystem functioning and resilience (Beauchesne et al., 2021). Much of the focus of multiple-stressor research that we identified is on species that occupy lower trophic levels such as microbes and invertebrates, despite that freshwater vertebrates are subject to multiple and growing stressors (He et al., 2017, 2018) and are prone to stressor interactions (Lange et al., 2018). Biotic interactions which govern how species are connected within communities and ultimately govern ecosystem functioning, resilience and vulnerability (Bruder et al., 2019; Seibold et al., 2018) have largely been overlooked in the identified studies, which is likely because biotic interactions are often difficult to measure. However, information on the responses of biotic interactions to multiple stressors is crucial to advance our knowledge of multiple-stressor effects on ecological processes. More studies assessing the impacts of multiple stressors on biotic interactions and how biotic interactions mediate the effects of multiple stressors across ecological networks are needed.

6 | CONCLUSION

Our review shows that certain persistent stressors such as nutrients, pesticides, heavy metals, warming, flow modification, and altered sedimentation in freshwaters have been consistently the major focus of multiple-stressor research (Figure 6). While these stressors remain prominent and relevant to freshwater ecosystems, the societal development and climate change trajectories in recent times have led to the emergence of new stressors such as invasive species, pharmaceuticals, antimicrobial compounds, and microplastics (Reid et al., 2019). Thus, their interactions with other stressors and the subsequent effects on freshwater ecosystems need to be considered in future multiple-stressor studies. In terms of investigated organisms, the identified multiple-stressor studies mainly focus on those at low trophic levels (i.e., microbes and invertebrates) and interactions between them. The responses of vertebrates and associated biotic interactions to multiple stressors were largely overlooked. Given the profound influence of vertebrates on trophic dynamics and ecosystem functions, this could impede our understanding of multiple-stressor impacts at larger ecological scales (e.g., ecosystem level). Indeed, most of the identified studies investigated the impacts of multiple stressors on community structure, with much less attention being paid to species interactions and ecosystem functions. We call for future studies to focus more on ecosystem-level responses, including trophic complexity, nutrient cycling and utilization, and ecosystem metabolism and resilience to multiple stressors in freshwaters (Gutiérrez-Cánovas et al., 2022). It will provide holistic information on multiple-stressor impacts at an ecosystem level and on associated ecosystem services, which can help environment managers and conservation practitioners understand the relevance of such impacts and develop timely and efficient management strategies (Craig et al., 2017).

Science-based and holistic strategies and approaches that are informative to sustainable management are urgently needed to deal with growing challenges in freshwater ecosystems (Arthington, 2021). Targeting and translating multiple-stressor research to inform conservation and management is critical for facilitating freshwater biodiversity recovery. Although an increasing number of studies have shed light on the nature of multiple stressor interactions on freshwater species, these efforts are limited in scale (e.g., space and time) and context (e.g., communities, ecosystems, geographies, and number of stressors considered at a time), as also observed here. These limitations may impede the transfer of research results to conservation practice. This poses a major challenge for freshwater ecosystem conservation and management, which still often focuses on tackling one stressor at a time (Spears et al., 2021). To effectively choose and implement conservation actions, conservation practitioners and environment managers require information that can help them prioritize the stressors to manage and foresee how these actions can lead to effective and observable conservation outcomes in the short- and long-term. Hence, it is essential for the freshwater scientific community to involve environmental practitioners to better focus on the most pressing issues and needs for freshwater conservation and restoration at local and regional levels. In addition, most identified studies have focused on degradation pathways resulting from multiple stressors. While this information is important, conservation practitioners and environment managers also

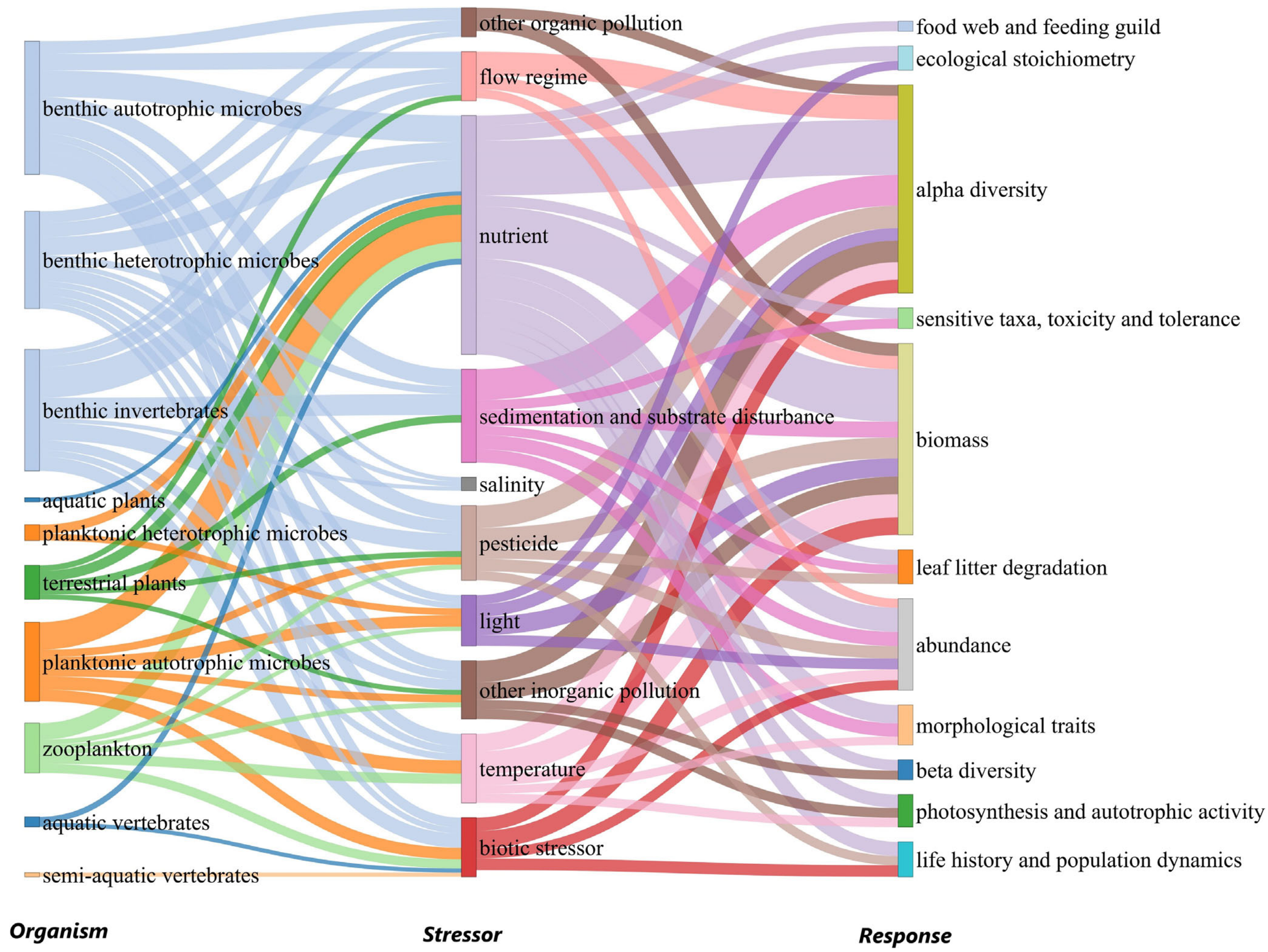

FIGURE 6 The frequency of combinations between organisms, stressors, and ecological responses (all fine categories) used in identified multiple-stressor experimental studies. The stressor-response linkage nodes with ≥10 counts and organism-stressor linkage nodes with ≥5 counts were included in this diagram for purposes of clarity.

need to assess how a particular ecosystem recovers (i.e., recovery pathways) after conservation actions are implemented (Spears et al., 2021). For example, research focusing on the responses of multispecies assemblages and ecosystem functioning to the removal of multiple stressors (e.g., Dabney et al., 2018), or following their reduction or mitigation will provide critical information for planning restoration actions and predicting conservation outcomes. Our window to galvanize conservation and restoration actions to bend the biodiversity curve in freshwaters to recovery is small (Tickner et al., 2020). Hence, collaborative research and action between scientists and practitioners is the need of the hour. Such collaborations will enhance the potential of multiple-stressor research for protecting and restoring freshwater environments, biodiversity, and associated ecosystem services.

AUTHOR CONTRIBUTIONS

Fengzhi He: Conceptualization (equal); data curation (equal); formal analysis (equal); writing – original draft (equal); writing – review and editing (equal). **Roshni Arora:** Conceptualization (equal); data curation (equal); formal analysis (equal); writing – original draft (equal); writing – review and editing (equal). **India Mansour:** Conceptualization (equal); data curation (equal); formal analysis (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors have declared no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created. All the identified studies are listed in Appendix S2. [Correction added on 6 March 2023, after first online publication: The appendix number has been updated.]

ORCID

Fengzhi He https://orcid.org/0000-0002-7594-8205
Roshni Arora https://orcid.org/0000-0003-4699-7603
India Mansour https://orcid.org/0000-0002-7403-7733

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SUPPORTING INFORMATION

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