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REVIEW PAPER

Exploring the nature, origins and ecological significance of dissolved organic matter in freshwaters: state of the science and new directions

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The challenge

Over 83% of freshwater habitats in the EU were classed as being in unfavourable condition in 2015, higher than any other habitat type (European Environment Agency 2015). Similarly, freshwaters in North America are reported to be losing species at a rate of 4% per annum, five times faster than in terrestrial ecosystems (Vaughn 2010). Meanwhile, more than 50% of freshwater flora and fauna have declined in the past 40 years in the UK with 13% threatened with extinction and many more are already functionally extinct, while 25% of species in ponds with statutory protection have been lost since the 1990s alone (Hayhow et al. 2016). Over 25% of all freshwater species are currently threatened with extinction globally (Tickner et al. 2020) and freshwater fauna declined globally by 83% from 1970 to 2014, compared to 60% for all habitat types (WWF 2018; Reid et al. 2019). In no other planetary domain is biodiversity declining so rapidly, despite the raft of domestic and international legislation requiring action to halt this decline. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) has called for transformative change in our approaches to management of freshwaters to meet this challenge and restore and protect nature (IPBES 2019), and the research community has proposed an emergency recovery plan to ‘bend the curve’ of freshwater biodiversity loss (Tickner et al. 2020).

Freshwater ecosystem decline is caused by a multitude of different stressors, including nutrients and other contaminants flushed from the land and atmosphere to adjacent waters, habitat loss through physical modification, climate change and invasive species. This presents the freshwater biota with a myriad of changes in stressors at rates which frequently preclude evolutionary adaptation (Tickner et al. 2020). Impacts include changes to species distributions, phenology, population dynamics, food webs, local extinction, and modification of ecosystem function through alterations to metabolism from organism to community level (Reid et al. 2019; IPBES 2019). Of these stressors, increasing flux of inorganic and organic nutrient compounds containing carbon (C), nitrogen (N) and phosphorus (P) is a ubiquitous

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problem, occurring in all farmed landscapes, all catchments where people live and discharge their wastes to waters via sewerage systems, and from every landscape receiving increased atmospheric N deposition that itself originates from fossil fuel combustion and food production systems (Carpenter et al. 2011; Moss 2012; Steffen et al. 2015; Wymore et al. 2021). Their combined impacts include the promotion of harmful algal blooms generating hepato- and neurotoxins as well as taste and odour problems in water supplies, and filamentous algal or excessive macrophyte growth. Rapid microbial decomposition of this excess biomass can generate oxygen depletion, enhancing resupply of nutrients from the sediment into the water, and in extreme cases this may lead to anoxia and fish kills, with knock-on consequences for ecosystem and human health.

Research to date

The impacts of nutrient enrichment on freshwater biota have been widely researched to date, but progress in defining and controlling its impacts on freshwater biodiversity has been limited by the physical challenge of experimentation and observation in a rapidly changing environment, particularly in streams and rivers where conditions vary over timescales of seconds to minutes.

Much of the research conducted so far has been based on narrowly focussed, outdated paradigms including concepts of 'single nutrient limitation' of biological processes that assume that a single stressor is controlling the response of the whole ecosystem. This fails to account for the control of multiple stressors on the structure and function of freshwaters. Furthermore, of the myriad of nutrient compounds present in freshwaters, often only the inorganic nutrient fractions (typically nitrate NO_3^-, ammonium NH_4^+, orthophosphate PO_4^{3-}) are considered to be 'bioavailable' to autotrophs in freshwaters (Fig. 1). This fails to recognise that several nutrients can co-limit freshwater productivity (Elser et al. 2007; Harpole et al. 2011), and that multiple nutrient forms including dissolved organic matter (DOM) have been shown to be bioavailable to a diverse range of freshwater species (Jorgensen 1987; Nedoma et al. 1994; Bronk et al. 2007; 2010; Liu et al. 2012; Qin et al. 2015; Thompson and Cotner 2018; Brailsford et al. 2019a; Mackay et al. 2020). The concentration of DOM is increasing in many freshwaters globally, but the impact of this increase on ecosystem functioning remains largely unknown (Regnier et al. 2013; Creed et al. 2018; McDonough et al. 2020; Rodríguez-Cardona et al. 2022).

Current theories framing nutrient cycling and transport in running freshwaters are thus incomplete, and current policy and management are rooted in this outdated thinking. As current theory has sought to isolate the key nutrient driving ecosystem decline in freshwaters, typically assumed to be P (predominantly orthophosphate, PO_4^{3-}) despite evidence of N limitation, co-limitation and no nutrient limitation reported in a multitude of recent papers (Harpole et al. 2011; Mackay et al. 2020; Brailsford et al. 2019a), this has entrenched a view in policy and management that, if we can identify 'the' single stressor driving eutrophication and target mitigation to control it, we can reduce impacts on whole ecosystems without having to deal with the other stressors. This includes other nutrient stressors such as DOM that continue, largely unregulated, to drive ecosystem damage in freshwaters, undermining mitigation efforts and conceptual progress in the field.

The absence of a holistic understanding of how freshwater biota access essential nutrients currently limits our ability to interpret trends in observational research from individual sites and draw out generic and transferable principles. It is vitally important that future research on nutrient enrichment does not ignore key biotic groups actively involved in nutrient cycling and metabolic responses to enrichment, such as the consumers (Small et al. 2009; Sutherland et al. 2013; Stewart et al. 2018; Hammerschlag et al. 2019). Current theory urgently needs revision to incorporate the growing evidence, including our own, that the organic nutrients are often the dominant (> 80%) fraction in natural freshwaters (Durand et al. 2011; Yates et al. 2019; Johnes et al. 2020; Wymore et al. 2021), and highly bioavailable to single-celled organisms, higher plants and consumers, which exhibit taxon-specific preferences for different DOM compounds and can thus simultaneously access different parts of the nutrient pool to support production (Brailsford et al. 2019a; Mackay et al. 2020; Tada and Grossart 2014; Canelhas et al. 2016; Rofner et al. 2016; Pisani et al. 2017).

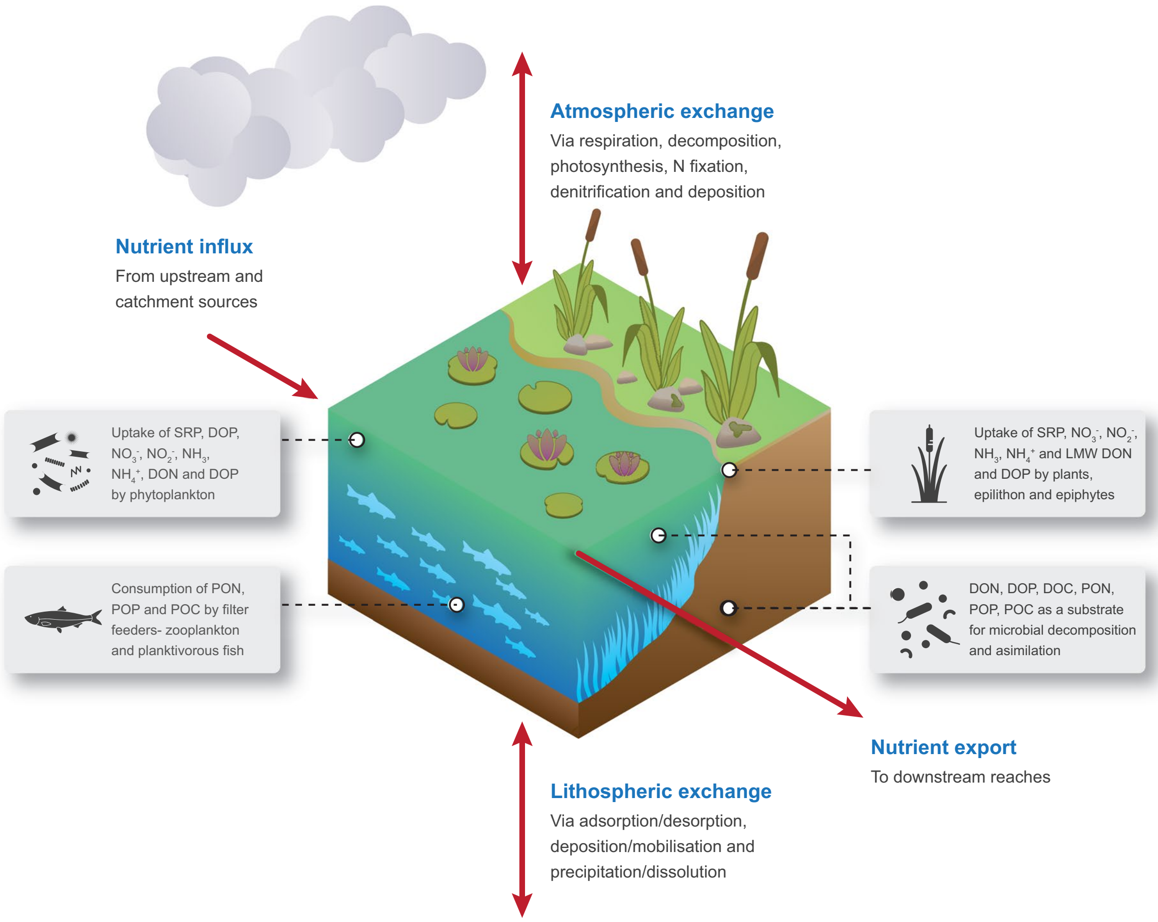

Fig. 1 The multiple nutrient stressors driving ecological impacts in freshwater ecosystems. Where: NO_3^- Nitrate, NO_2^- Nitrite, NH_3 Ammonia, NH_4^+ Ammonium, *DON* Dissolved Organic N, *PON* Particulate Organic N, *SRP* Soluble Reactive P (measured as PO_4^{3-}), *DOP* Dissolved Organic P, *POP* Particulate Organic P, *DOC* Dissolved Organic C, *POC* Particulate Organic C, and *LMW* Low molecular weight

The DOM pool contains many thousands of compounds of anthropogenic and biological origin including pharmaceuticals, personal care products, cleaning agents, peptides, free amino acids, amino sugars, nucleic acids, lipids, organophosphates, excretion products such as urea and methylamines, and substances deriving from the breakdown of biopolymers, such as chitin and plant biopolymers, i.e. lignin and suberin (Pemberton et al. 2019; Lloyd et al. 2022a). Whole ecosystems have access to this portfolio of compounds, alongside inorganic nutrient fractions, and different biotic components of the ecosystem are able to access multiple nutrient compounds, driving changes in cell metabolism, physiological and behavioural adaptation, habitat modification and species shifts that contribute to freshwater ecosystem decline. Attention to the role of DOM as a bioavailable nutrient resource in freshwaters is thus required to change fundamentally the ways in which freshwaters are conceptualised, studied and managed (McDowell 2022).

The state of the science

More recently, there has been a shift to research linking macroecological responses to inorganic or total nutrient loading, particularly in lakes, which has taken a multiple stressor perspective, investigating relationships between ecosystem status, nutrient loading and other environmental stressors including a suite of climate change proxies (Smeti et al. 2019; Birk et al. 2020; Leavitt et al. 2020). However, there are still substantial gaps in our knowledge of the role of DOM as a nutrient resource in freshwater ecosystems. In particular:

- There is currently insufficient evidence available to determine the ecosystem functional role of discrete DOM compounds in freshwater ecosystems, or the impact of the changing mix of DOM compounds on different biotic groups as a system undergoes enrichment or nutrient reduction through mitigation.
- The functional mechanisms by which the biota access this material are not fully known, and how these mechanisms vary according to the specific DOM chemistry is not established.
- The range of genes undergoing changes in expression to allow the biota to access the different nutrient forms as nutrient pool composition varies in space and time are not understood.
- The identity and role of different natural DOM compounds as a source of essential nutrients in cell metabolism is not known, nor are the potentially disrupting effects of anthropogenically produced DOM compounds on biota understood.
- While the role of DOM as an energy resource driving microbial activity in freshwaters is well established (e.g. Battin et al. 2008) current fundamental theories for running freshwater ecosystems, including the Nutrient Spiralling Concept (Newbold et al. 1983; Ensign and Doyle 2006) and the River Continuum Concept (Vannote et al. 1980), do not account for DOM as a nutrient resource driving ecosystem function. As a result current predictive models reflecting this thinking, and mitigation efforts based on their simulations are misguided and ineffective.

There is a clear need to address these knowledge gaps and properly situate DOM in freshwater biogeochemical cycling theory. As Fig. 2 illustrates for N, as an example, DOM is flushed into freshwaters from the surrounding catchment, taken up by the primary producers and non-photosynthetic microbes, cycled through the food web, synthesised instream by the biota including by both producers and consumers, and flushed downstream. It is a key component of stream elemental nutrient cycles. Yet, while C processing in freshwaters has received wider attention, including the role of DOM as a microbial energy resource (Battin et al. 2008; Brailsford et al. 2019a, b; Berggren and del Giorgio 2015; Creed et al. 2015), its role as a nutrient resource relative to the well-researched inorganic forms of N and for P is poorly established and not embedded in current theory or practice for the management of nutrient-enriched freshwaters.

Exploring new dimensions in the diagnosis of ecosystem responses to nutrient enrichment

Recently developed and applied environmental omics (Ficetola et al. 2008; Russo et al. 2016; Bista et al. 2017; Smith et al. 2018; Cristescu 2019; Broman et al. 2020; Launay et al. 2020; Mikan et al. 2020), optical approaches including spectral absorbance and fluorescence of DOM (Weishaar et al. 2003; Hernes et al. 2008, 2013; Fellman et al. 2010; Inamdar et al. 2012; Minor et al. 2014; Pereira et al. 2014; Eckard et al. 2017), high resolution mass spectrometry (Dittmar et al. 2008; Zark and Dittmar 2018; Pemberton et al. 2019; Minor and Oyler 2020; Lloyd et al. 2022a, b), stable isotope probing (Knowles et al. 2010; Kellerman et al. 2013; Charteris et al. 2016; Gooddy et al. 2016; 2018; Marina Tcaci et al. 2019; Reay et al. 2019; Mena-Rivera et al. 2022), and field experimentation methods (McKee et al. 2003; Payn et al. 2005; O'Brien et al. 2012; Richardson et al. 2018; Roth et al. 2019; Hensley and Cohn 2020; Maberly et al. 2020) provide new opportunities to shed light on the multiple stressors driving freshwater ecosystem decline, taxonomic information on the biota present, active and responding to these stressors, and the specific metabolic, physiological and behavioural adaptations and impacts generated at the single organism to whole ecosystem level.

The potential of these techniques is explored in a series of papers in this volume. We start with an overview of the development of research on DOM in the environmental sciences with a paper by McDowell (2022), which contemplates the origins of our interest in DOM and the development of our capacity to determine its nature and origins in complex environmental systems. His paper then reaches forward to envision future directions for researchers, including the need to focus not only on understanding the functional significance of DOM in freshwaters but also

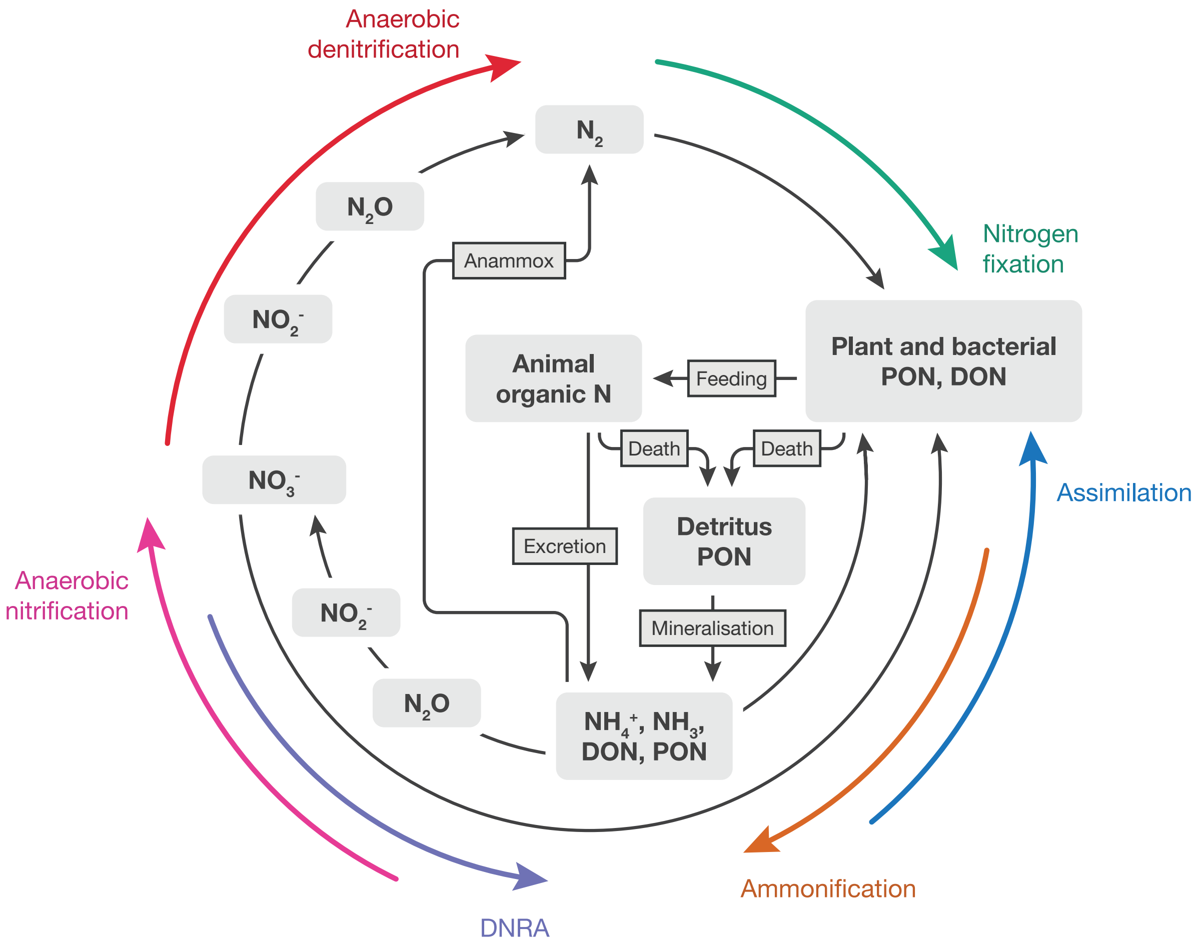

Fig. 2 Situating DOM in the freshwater nitrogen cycle. *DNRA* Dissimilatory nitrate reduction to ammonium

its wider evolutionary role in multiple environmental compartments.

Our first group of papers then explore the myriad of analytical and optical techniques which now exist to help us understand the nature, composition and complexity of the DOM pool, from Arctic soils and vegetation (Allain et al. 2022) and temperate headwater forests (Ryan et al. 2022), to riverine systems (Lloyd et al. 2022a) and large lakes (Minor and Oyler 2020). Allain et al. (2022) reveal how changes in the vegetation of the Arctic and Subarctic regions influences the composition of the DOM pool flushed to streams. Meanwhile Ryan et al. (2022) use optical techniques to demonstrate how tree-derived DOM was evident in throughfall and stemflow collected in temperate forests, enriching DOC by 4–70 times over background concentrations in rainfall. Moving on to river systems, Lloyd et al. (2022a) use a suite of novel, high resolution chromatographic and mass spectrometric techniques to show how DOM character and molecular composition varies markedly in rivers of differing environmental character, from acid peatland headwaters to intensively farmed and/or populated circumneutral clay streams. Minor and Oyler (2020) then contemplate how different techniques used to determine DOC concentrations, chromophoric DOM, and the molecular scale character of DOM, can provide a suite of complementary insights into C cycling in large lakes globally, focusing on data from Lakes Baikal, Superior, Michigan, Tanganyika and Malawi. Each paper demonstrates the nature and complexity of the DOM pool arriving in, and produced within, freshwaters, and how these techniques can reveal its biogeochemical processing in freshwaters under contrasting environmental conditions.

We then move on to a suite of papers in which the authors apply these techniques at scale, often over multiple catchments with varying environmental character, to reveal the origins of DOM in freshwaters as this varies in space in time. The multi-catchment research of Williamson et al. (2021) demonstrates landscape-scale controls on DOC flux to rivers across Great Britain, and the importance of landscape character as well as land use and management in controlling this flux. Meanwhile the work of Yates et al. (2022) uses a combination of nutrient quantification and optical approaches to determine how DOC, DON and DOP flux (as a component of total C, N and P flux) and composition vary according to land use and management in another pan-UK research programme. This shows how DOM composition varies consistently in relation to soil C:N ratios in particular. The work of Vaughn et al. (2021) tackles a major river basin, the Mississippi, USA, using optical and molecular-scale approaches to reveal the impacts of anthropogenic land cover on DOC flux and the molecular composition of the stream DOM pool, with many parallels to be drawn between this study and the DOC findings reported by Yates et al. (2022) and Williamson et al. (2021). Voss et al. (2022) then use a suite of molecular and isotope chemistry approaches to infer the likely sources of DOC and the role of organic matter respiration on stream DOM pool composition in another large river basin: the Fraser River, in SW Canada. In this work they demonstrate the close coupling between DOC and DIC, with around a third of DIC deriving from DOC respiration, confirming the active biogeochemical processing of C in the river, and the importance of the DOM pool in this cycle. Meanwhile, Holt et al. (2021) explore the evolution of stream DOM composition following glacial retreat in SE Alaska using a suite of isotopic and molecular scale techniques. They report increasing abundance of soil and vegetation-derived DOM compounds with a more modern radiocarbon age in streams furthest from glaciers, and anticipate shifting DOM pool composition towards a terrigenous signature, altering stream DOM composition and bioavailability under a changing climate.

In our final group of papers, the authors explore the ecological role and significance of DOM in freshwaters, drawing on the recently published work of many prior authors, such as those referred to above (e.g. papers by Brailsford et al. 2019a, b; Mackay et al. 2020, as well as earlier work by Tada and Grossart 2014; Canelhas et al. 2016; Rofner et al. 2016; Pisani et al. 2017). Glibert et al. (2021) focus on a major estuary, Chesapeake Bay, USA, examining observational records of water quality and environmental conditions from 2009 to 2019. Their work suggests that organic nutrient loading to the estuary increases during periods of intense rainfall and during hurricanes, creating favourable conditions for picocyanobacterial bloom formation, from which they infer a likely causal link between DON loading in particular and the ability of the picocyanobacteria to access this material as a nutrient resource. Paerl et al. (2020) examine how increasing rainfall and flooding from tropical cyclones in North Carolina generate marked increases in C, N and P flux to the Neuse River Estuary, USA, with terrestrial sources dominating riverine C pools under baseflow conditions, but with marked increases in wetland-derived C during storm events, changing the composition of the estuarine DOM pool. Their work also reveals both qualitative and quantitative impacts of the changing rates and composition of this nutrient flux on primary producers and associated microheterotrophs in the estuary. The work of Mena-Rivera et al. (2022) and Behnke et al. (2022) takes a more focused look at the bioavailability and processing of organic matter in headwater streams, using high resolution mass spectrometry and in the case of Mena-Rivera et al. (2022) compound-specific stable isotope probing, to track biological responses to OM availability and character in streams. Behnke et al. (2022) detect differences in the DOM pool composition in forests, fens and wetlands of SE Alaska (Behnke et al. 2022), while Mena-Rivera et al. (2022) report experimental outcomes demonstrating the bioavailability of the particulate organic matter (POM) pool in an intensively farmed clay catchment in the UK, which also receives sewage effluent discharges. Behnke et al. (2022) demonstrate the high bioavailability of both tree-derived and soil- and wetland- derived DOM to the soil biota, and how climate change is likely not only to increase the rate of tree leaching and soil DOM flushing to freshwaters, but also to drive changes in the stream DOM pool composition, influencing its ecological role and significance in freshwaters. Mena-Rivera et al. (2022)

demonstrate that this high degree of bioavailability of OM to stream biota is also evident in the POM pool, encouraging us to consider not only how DOM may act as a nutrient resource in freshwaters, but to also consider POM as an integral component of the stream OM pool that is bioavailable, and likely to change in both quantity and composition in the future.

The papers in this volume thus report not only the novel approaches than may be adopted to explore the central role that OM plays in freshwater nutrient cycling, but also how research can be designed from soil column to pan-continental scale to reveal how environmental character and function and the biota can both shape the composition of the OM pool, and are impacted by its changing size and composition. It is an exciting time to be working in this field with huge potential to push the frontiers of current knowledge away from the current low risk focus on individual stressors, to the holistic work needed on multiple stressors that operate in synergistic, additive or antagonistic ways to impact on and interact with the freshwater biota. The papers in this volume demonstrate the potential for future ground-breaking science that will inform more effective policy and practice for these most damaged of habitat types, globally.

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Data availability There are no data associated with this paper.

Declarations

Competing interests The authors declare there are no competing interests.

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