Addressing grand ecological challenges in aquatic ecosystems: how can mesocosms be used to advance solutions?

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Editor's Choice OIKOS

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Rapid and drastic anthropogenic impacts are affecting global biogeochemical processes and driving biodiversity loss across Earth's ecosystems. In aquatic ecosystems, species distributions are shifting, abundances of many species have declined dramatically, and many are threatened with extinction. In addition to loss of diversity, the ecosystem functions, processes and services on which humans depend are also being heavily impacted. Addressing these challenges not only requires direct action to mitigate environmental impacts but also innovative approaches to identify, quantify and treat their effects in the environment. Mesocosms are valuable tools for achieving these goals as they provide controlled environments for evaluating effects of stressors and testing novel mitigation measures at multiple levels of biological organisation. Here, we summarise discussions from a survey of marine and freshwater researchers who use mesocosm systems to synthesise their opportunities and limitations for advancing solutions to grand ecological challenges in aquatic ecosystems. While most research utilising mesocosm systems in aquatic ecology has focused on quantifying the effects of environmental threats, there is a largely unexplored potential for using them to test solutions. To overcome spatio-temporal constraints, there are opportunities to scale up the size and timescales of mesocosm studies, or alternatively, test the outcomes of habitat-scale restoration at a smaller scale. Enhancing connectivity in future studies can help to overcome the limitation of isolation and test an important aspect of ecological recovery. Conducting 'metacosm' studies: coordinated, distributed mesocosm experiments spanning wide climatic and environmental gradients and utilising more regression-based experimental designs can help to tackle the challenge of context dependent results. Finally, collaboration of theoretical, experimental and applied ecologists and biogeochemists with environmental engineers and technological developers will be necessary to develop and test the tools required to advance solutions to the impacts of human activities on Earth's vulnerable aquatic ecosystems.

Keywords: connectivity, distributed experiments, ecology, freshwater, global change, gradient designs, marine, metacosm studies, restoration

Introduction

Addressing the grand ecological challenges of the Anthropocene

The 'Anthropocene' (Crutzen and Stoermer 2000) is characterised by unparalleled environmental changes caused by human activities (Crutzen 2002, Lewis and Maslin 2015). The extent of these anthropogenic impacts such as alterations in land use, pollution, climate change, biotic homogenisation and overexploitation are so great that many of Earth's major system processes are now considered to have exceeded safe operating spaces for humanity (Rockström et al. 2009, Richardson et al. 2023). Global biogeochemical processes and the functioning of ecosystems are being affected, and numerous species are threatened with extinction (Steffen et al. 2015, Turvey and Crees 2019, IUCN 2022). Aquatic ecosystems are highly vulnerable and have had significant losses of biodiversity and functionality in recent decades (Nagelkerken and Connell 2015, Dudgeon 2019, Tickner et al. 2020, IUCN 2022). Without intervention, many threatened species are likely to become locally or globally extinct in the coming decades (Dudgeon 2019) and, preceding extinction, changes in species abundances, community structure and shifts in distribution will occur in response to global changes (Pereira et al. 2010). Indeed, poleward shifts of marine organisms are occurring five times faster than on land, resulting in reduced species diversity at the equator (Chaudhary et al. 2021). Given the pace and extent of their effects, understanding the key drivers, threats and stressors contributing to the decline of aquatic ecosystems and finding solutions to mitigating them is therefore a crucial challenge of the 21st century.

Numerous reviews have identified the key threats to biodiversity and functioning in freshwater (Brönmark and Hansson 2002, Dudgeon et al. 2006, Strayer and Dudgeon 2010, Vörösmarty et al. 2010, Reid et al. 2019, Williams-Subiza and Epele 2021) and marine (Halpern et al. 2007, Crain et al. 2008, Nagelkerken and Connell 2015, Borja et al. 2020, Herbert-Read et al. 2022) ecosystems. A compilation of grand ecological challenges in aquatic ecosystems reveals interrelated direct anthropogenic drivers of environmental change (cf. direct natural or indirect drivers; IPBES 2019) related to climate change, biodiversity, land/sea use and pollution (Fig. 1; Triple Planetary Crisis (TPC), plus 'land/sea use' which is covered under 'biodiversity and nature loss' in the TPC; UNEP 2024). In this conceptualisation, biodiversity loss is included as a biodiversity-related challenge in consideration of its action as a cause of environmental change (Hooper et al. 2012), though clearly it is a major

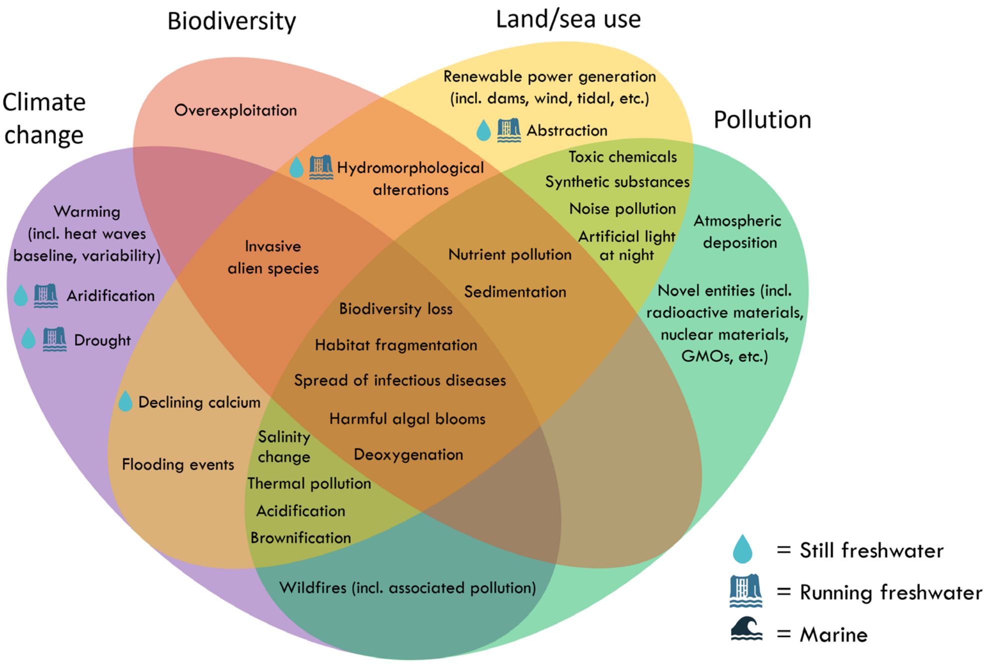

Figure 1. Conceptual diagram of grand ecological challenges in aquatic ecosystems, illustrating the interrelatedness of drivers of ecological change associated with climate change, biodiversity, land/sea use and pollution. When specific to lentic (still) freshwater, lotic (running) freshwater or marine systems, this is indicated by the presence of the respective symbol in the key. The absence of any symbol indicates that all aquatic ecosystems are affected by this in some way. Note, overexploitation (overfishing) and invasive alien species, considered as key drivers of environmental change (Dudgeon 2019, Diaz et al. 2019) are both included as biodiversity-related challenges.

consequence of the threats shown, just as many challenges are also consequences of each other with complex relationships and feedback cycles. While not universally applicable to every aquatic realm, these ecological challenges collectively impact water physiochemistry and biodiversity in all aquatic ecosystems (IPBES 2019), water quantity in freshwaters, brackish and saline inland systems (UNEP 2019), and ultimately pose threats to the stability and resilience of Earth system as a whole (Steffen et al. 2020, Richardson et al. 2023).

Effectively addressing these challenges requires a comprehensive strategy that leverages a diverse array of scientific approaches to identify and quantify environmental impacts and provide a robust scientific basis for preventative and mitigative interventions. Field observations play a vital role in providing essential evidence of environmental changes, such as shifts in carbon dioxide concentrations, temperature fluctuations, or nutrient alterations within waterbodies. Long-term monitoring data, in particular, yield valuable insights into changes over time, and palaeontological data – such as sediment and ice cores – allow comparisons with historical conditions. While field surveys enable correlations between environmental parameters and biological variables, establishing causal relationships often requires more than observation alone (De Boeck et al. 2015). Advances in time-series analyses and spatio-temporal co-occurrence models have improved the causal inference that can be drawn from purely observational data, but experimental approaches are generally necessary to identify the causal mechanisms driving observed environmental changes (Underwood 1996).

Laboratory-based experiments, despite offering a high degree of mechanistic insight, inherently simplify complex systems which limits the extrapolation of findings to natural ecosystems. Mesocosms serve as an intermediary, bridging the gap between highly controlled laboratory experiments and field observations (Fig. 2; Fraser and Keddy 1997, Petersen et al. 2009). By reproducing natural communities or ecosystems under controlled conditions, mesocosms have become invaluable tools for investigating solutions to ecological challenges. They provide controlled, replicable environments conducive to evaluating effects of stressors and testing novel mitigation measures across multiple levels of biological organisation. Combining these methods into an integrative approach that also includes theoretical and modelling perspectives establishes a robust research framework, effectively balancing the strengths and weaknesses inherent in any single approach (Petersen et al. 2009, Stewart et al. 2013).

This paper aims to synthesise the applications of mesocosm systems in addressing grand ecological challenges in aquatic ecosystems and to propose future research directions that can advance solutions to these challenges. To aid this synthesis, we compiled survey data provided by researchers who have utilised aquatic mesocosm systems in their research. The survey aimed to identify the environmental threats investigated using mesocosms, assess whether researchers have also used their systems to explore solutions, and evaluate the potential utility of mesocosm systems in both threat assessment and solution development. We fostered cross-system collaboration by inviting experts in both freshwater and marine ecology

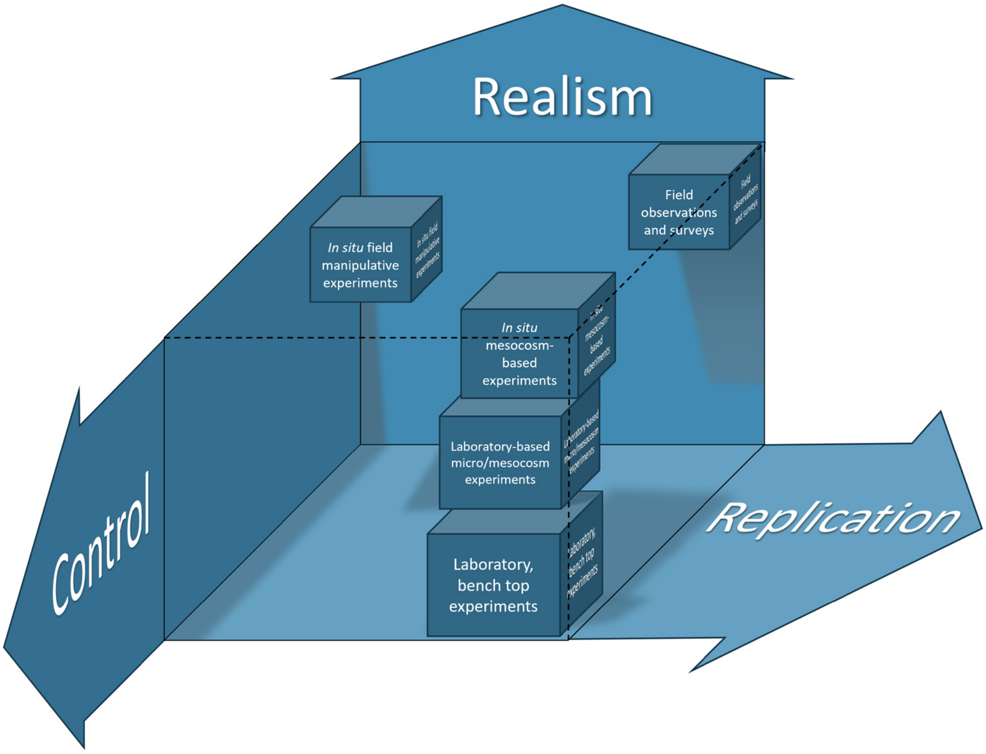

Figure 2. Conceptual diagram representing an empirical domain space for ecological research constrained by scales of realism, replication and control. The relative placement of different approaches to empirical research represented by the cubes within the three-dimensional space illustrates the advantages and disadvantages of each approach, with the advantages of micro/mesocosm-based approaches in balancing and extending these three dimensions (scales) illustrated by the positioning of these cubes towards the upper corner nearest the viewpoint. Clearly, specific study designs and experimental systems using the approaches pictured will vary considerably and influence the positioning of any one study within this space. The approach taken and experimental design used to address a particular research question will be informed by the ecological and biological variables of interest, factors manipulated, responses measured and desired application of the findings (e.g. Fig. 1 in Gerhard et al. 2022 and Fig. 7 in Orr et al. 2024). The positioning of the cubes here is intended to illustrate the general tradeoffs within these key three scales relative to other approaches.

to participate, encouraging a more integrated approach to addressing ecological challenges. Survey results were subsequently discussed at an international workshop, which revealed a predominant focus on quantifying effects of environmental threats in aquatic ecology and under-explored potential for using mesocosms to develop solutions. This article thus provides an overview of the utility of mesocosms for addressing grand ecological challenges and synthesises key constraints, limitations and opportunities of mesocosm systems in advancing solution-oriented research within aquatic ecology.

Defining mesocosms and their utility for addressing grand ecological challenges

Mesocosms can be defined as experimental systems that replicate a representative natural community or ecosystem under controlled but realistic environmental conditions. This definition encompasses three key aspects of mesocosms that provide advantages for ecological research: replication, control and realism (Fraser and Keddy 1997, Stewart et al. 2013, Fig. 2). Replication allows testing the effects of factors across multiple independent units, providing statistical power to the experiments (or observations, in the case of survey data). Control enables the manipulation of specific variables to test causal relationships between factors, which is often difficult in field studies. Realism is a more subjective aspect and involves a tradeoff between simulating natural conditions and controlling confounding variables. We refrain from trying to put fixed boundaries on how realistic a mesocosm system must be. While outdoor mesocosms are more realistic in terms of representing natural environmental conditions, indoor systems often offer advantages of increased control and monitoring of experimental conditions. It should also be noted that this definition may include systems that have previously been termed ‘microcosms’ rather than ‘mesocosms’, as well as enclosures or limnocorrals (Beyers and Odum 1993, Fraser and Keddy 1997, Benton et al. 2007, Petersen et al. 2009), however, we consider the defining aspect of a mesocosm to be the replication of a representative natural community or ecosystem, which enables measurements at multiple levels of biological organization.

The choice of mesocosm design depends on the specific research question and the tradeoffs between scales of replication, realism and control that best suit the question (OECD 2006b, Stewart et al. 2013; Fig. 2). How to optimise a specific experimental system within these constraining scales for any given research question will depend on several aspects including the study organisms or processes of interest, the factors or variables to be manipulated (and controlled) and the desired application of the results. For example, experiments investigating community ecological theory or concepts in a controlled environmental might optimise control and replicability over realism. For such research, laboratory-based, bench top experiment with only a few trophic levels and limited species composition might suffice. Whereas experiments designed with the purpose of testing a proposed management intervention or simulating a natural phenomenon will likely prioritise aspects of realism over achieving optimal control (and edge further towards the positioning of in situ field manipulative experiments, i.e. lacking enclosure, in Fig. 2). Moreover, the choice of experimental design adds another important aspect to consider, with the degree of replication often being the key constraint in this context. We discuss aspects of experimental design and the advantages of mesocosm systems with high numbers of experimental units to be leveraged in gradient designs in a later section addressing the challenge of context dependency (Tackling context dependency with 'metacosm' studies and gradient designs).

How have mesocosms been used in applied aquatic ecological research?

A survey of aquatic ecologists was conducted to gather insights on the utility of aquatic mesocosm systems in addressing grand ecological challenges and to understand perspectives on their potential for future solution-oriented research (see the Supporting information for survey methods, questions and participant demographic information). While the survey was open and advertised to ecologists across different fields of aquatic ecology – encompassing both freshwater and marine systems to foster cross-system perspectives – regardless of prior use of mesocosms, the majority of respondents were those with experience using mesocosm systems in their research. It is therefore acknowledged that survey respondents may have had an intrinsic bias towards the use of mesocosms, particularly if they are active users of these methods. Future research could complement this more qualitative approach by employing alternative sampling strategies, such as literature-based meta-analyses, to obtain quantitative evidence and reduce subjective influence. However, advantages of the survey approach were that it enabled gathering information not yet available in the published literature. This includes insights from recent or ongoing research, for example, where time lags from data collection to publication are common (especially in ecological studies requiring lengthy sample processing) or from new and emerging areas of research that may not yet be represented in the literature. Moreover, a balanced approach to discussing both the limitations and opportunities of mesocosm systems has intentionally been taken throughout.

Overall, our results revealed a predominant focus on quantifying stressor impacts in aquatic ecology (Fig. 3a), with limited attention to investigating solutions to them (Fig. 4a). In addressing environmental threats, our survey indicated that most aquatic mesocosm research has focused on the effects of climate change, nutrient pollution/eutrophication and interactions of multiple stressors (including the cumulative effects of human impacts; Fig. 3a). Several environmental threats have only been addressed to a limited extent in mesocosm experiments, especially declining calcium concentrations (relevant in lentic ecosystems; Reid et al. 2019), spread of infectious diseases, and atmospheric deposition. In marine mesocosm research, survey respondents indicated that the direct threat of urban development is lacking research attention, however, many related threats and stressors associated with urbanisation have received some attention, such as pollution of toxic chemicals, novel entities including emerging contaminants, light, noise, and expanding renewable power generation (Fig. 1). By contrast, according to our survey, there has been more mesocosm-based research addressing acidification and atmospheric deposition in marine environments than in the other aquatic environments. Whereas most experiments addressing urban development and aridification have been done in lotic freshwaters, likely reflecting the direct impacts of hydromorphological alterations (i.e. channelisation, dams for renewable power generation, etc.), and drought on stream flow. Survey respondents generally saw strong potential for continuing to address environmental threats in aquatic mesocosm-based research (Fig. 3b), with potential only really limited in addressing the impacts of expanding renewable power generation. This is likely due to the practical constraints of mesocosms (spatial and temporal, discussed in 'Spatio-temporal constraints'), as very large systems and long-term studies would be required to replicate and assess their ongoing impacts. However, different forms of renewable energy generation would have different degrees of potential. For example, while the utility of mesocosms for investigating the impacts of offshore wind, wave and tidal energy generation might be limited by practical constraints, investigating the effects of cropland conversion for biofuel generation or shade caused by solar-panel installations are more feasible, though the stressors associated with these forms of renewable energy are also relevant to other land-use changes. It is also necessary to differentiate between the shorter-term impacts during construction versus the ongoing effects during operation and potential impacts after the operational period.

Studying stressor impacts provides important evidence for management, particularly regarding novel substances such as emerging contaminants (e.g. nanomaterials and microplastics; Bucci et al. 2020, Surette et al. 2021, Wang et al. 2022) and the interactions of multiple stressors (Folt et al. 1999, Crain et al. 2008, Ormerod et al. 2010, Jackson et al. 2016, Nõges et al. 2016, Orr et al. 2024). Yet most of these studies are still conducted at lower levels of biological organisation, investigating effects on physiology, individuals and populations (Crain et al. 2008, Boyd et al. 2018, Orr et al. 2024). Although such research can provide valuable insight into

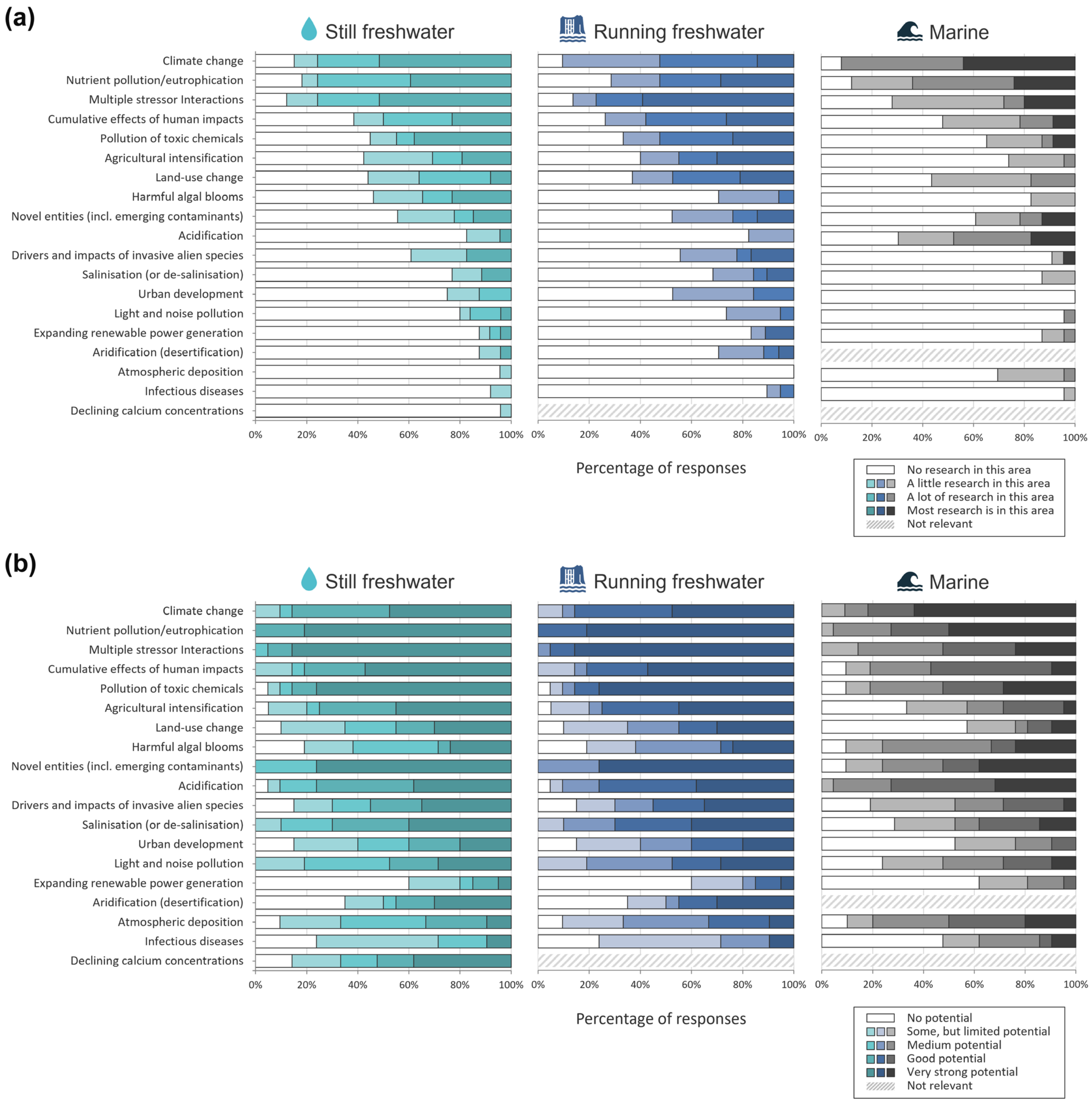

Figure 3. Researcher responses to questions from our online survey (Supporting information) of aquatic ecologists working in still freshwater (n = 35), running freshwater (n = 23) and marine (n = 26) ecosystems asking (a) how much research has been done using their mesocosm system to address the listed environmental threats (respondents could select a weighting from 1 to 4, indicating 1 'no research in this area', 2 'a little research in this area', 3 'a lot of research in this area' and 4 'most research is in this area'); and (b) the perspective of the same researchers on the potential to use their mesocosm systems to address these threats in aquatic ecology research (respondents could select a weighting from 1 to 5, indicating 1 'no potential', 2 'some, but limited potential', 3 'medium potential', 4 'good potential' and 5 'very strong potential'). Bars show percentages of responses for each qualitative category, with the darker shading indicating more research or potential research in each area. Bars have dashed diagonal shading where environmental threats were not considered relevant for those systems.

mechanisms and modes of action (or modes of interaction; Boyd and Brown 2015), understanding individual and combined stressor effects at community- and ecosystem-levels is crucial for effective environmental management (De Laender 2018, Thompson et al. 2018, Vos et al. 2023). Mesocosms serve as a useful tool for generating these data (Petersen et al. 2009), providing opportunities to explore how biological interactions may modify stressor interactions (Bray et al.

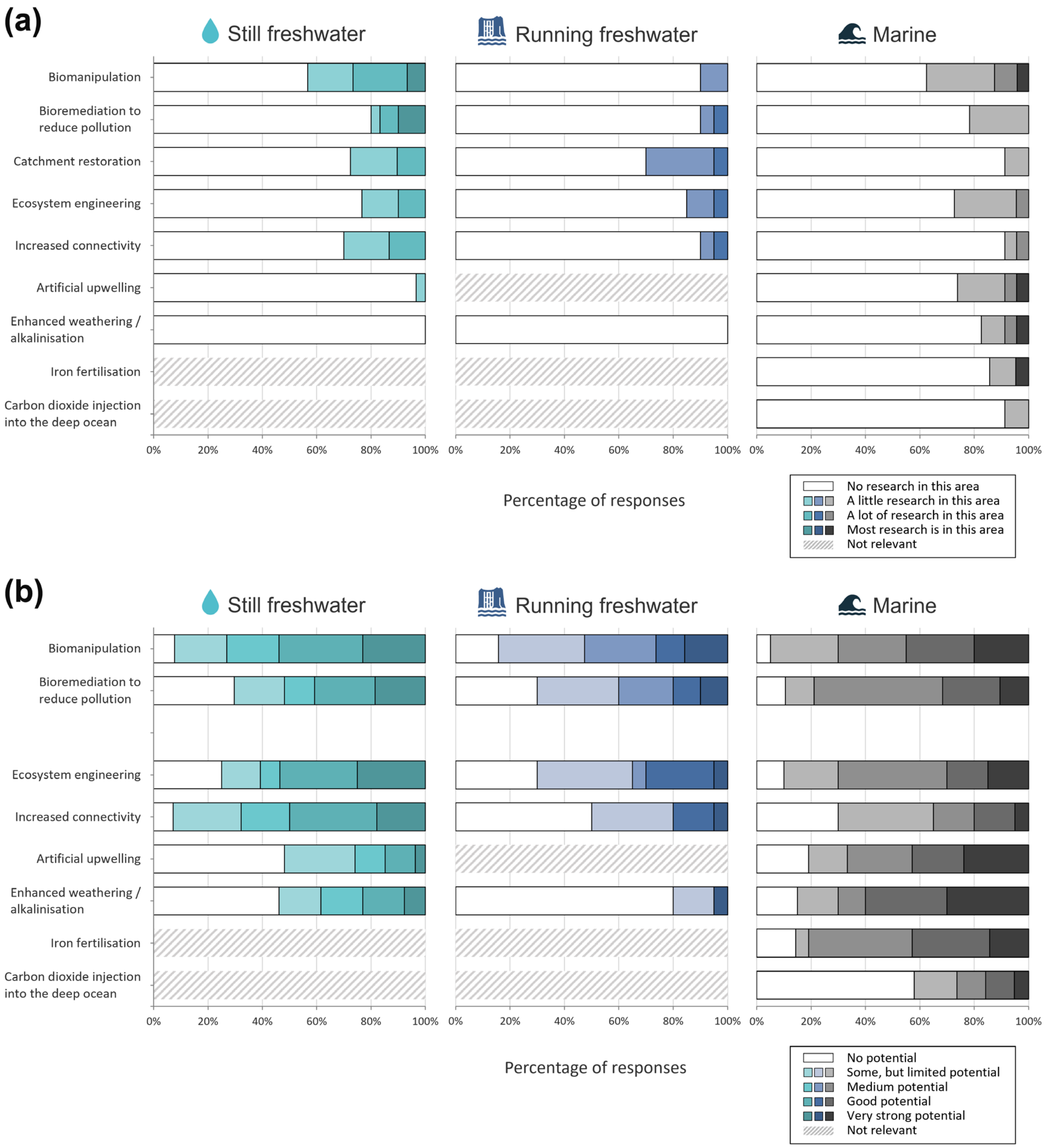

Figure 4. Researcher responses to questions from our online survey (Supporting information) of aquatic ecologists working in still freshwater (n = 35), running freshwater (n = 23) and marine (n = 26) ecosystems asking (a) how much research has been done using their mesocosm system to address the listed solution-focused research topics (respondents could select a weighting from 1 to 4, indicating 1 'no research in this area', 2 'a little research in this area', 3 'a lot of research in this area' and 4 'most research is in this area'); and (b) perspectives of the same researchers on the potential to use their mesocosm systems to investigate these solutions in aquatic ecology research (respondents could select a weighting from 1 to 5, indicating 1 'no potential', 2 'some, but limited potential', 3 'medium potential', 4 'good potential' and 5 'very strong potential'). Bars show percentages of responses for each qualitative category, with the darker shading indicating more research or potential research in each area. Bars have dashed diagonal shading for categories that were not considered relevant for that system. Note, catchment restoration is missing from (b) due to an error in the survey.

2018, Bruder et al. 2019) and whether interactions at lower levels of biological organisation scale up (Simmons et al. 2021). However, caution is warranted in the selection and use of null models to test interactions at higher levels to avoid misinterpretations of interactive effects at these levels (discussions and proposals for addressing this issue from Boyd

Box 1. Case study: marine mesocosms for ocean-based carbon dioxide removal.

Even with very ambitious emissions reductions policy supported and implemented by all states, humankind is still expected to emit at least ten to 20% of current carbon dioxide emissions in three decades' time, further advancing climate change (Smith et al. 2024). To limit global warming and its impacts as laid down in the Paris Agreement, however, greenhouse gas emissions have to reach 'net zero'. Net zero means achieving a balance between human-induced greenhouse gas emissions and greenhouse gases removed from the atmosphere and stored long-term. This requires active CDR from the atmosphere, which compensates unavoidable residual emissions. The urge of implementing CDR approaches on a global scale already within the next decade demands for rapid progress in the research of feasibility and safety of suggested technologies, to provide recommendations to regulators and policy makers as well as to inform the general public. This urgency is underpinned by the fact that some companies have already begun implementing CDR strategies, such as ocean alkalinisation.

The extent to which the ocean can support CDR and what ecological risks and co-benefits might be associated with this has recently come into the focus of marine research. Various approaches are presently considered for active CO_2 removal in the ocean, including ocean alkalinity enhancement, iron fertilization, artificial upwelling or downwelling and blue carbon approaches such as macroalgal farming, which together are grouped under the term marine CDR approaches (mCDR). Testing these approaches on an adequate scale in field trials poses some difficulties for most of them. For instance, given the hydrographic complexity of most marine systems, with lateral advection (currents, tides), vertical flow (convection, up- and downwelling) and wave-driven mixing, it is extremely challenging to monitor the intended effect as well as potential unintended environmental impacts of the applied mCDR manipulation in open waters, let alone perform a dose-response type (gradient) analysis. Take iron fertilisation research, for example: even after 13 open ocean iron fertilization field experiments, each in itself a major investment of financial and human resources, the key question about its potential for CO_2 removal and long-term storage is still not resolved (de Baar et al. 2005, Yoon et al. 2018). In this context, mesocosm experiments provide a more affordable and accessible tool to investigate the suitability of mCDR approaches for natural communities under semi-controlled conditions and thus assess their impacts on key ecosystem services such as biodiversity, trophic transfer and carbon sequestration (Fig. 5).

Most mCDR-related mesocosm research to date has explored the approaches of artificial upwelling and ocean alkalinity enhancement (Baumann et al. 2021, Baños et al. 2022, Ferderer et al. 2022, Gómez-Letona et al. 2022, Goldenberg et al. 2022, Ortiz et al. 2022a, b, Baumann et al. 2023, Riebesell et al. 2023, Spilling et al. 2023). While in principle iron fertilisation can be tested in mesocosms (Guieu et al. 2010), the extra effort required to ensure trace metal clean conditions during mesocosm operation and the relative ease in performing iron fertilisation field experiments have precluded the wider use of mesocosms in this field of research. In the context of mCDR research, mesocosm experimentation allows for testing diverse applications, e.g. different minerals considered for ocean alkalinity enhancement or different deep-water nutrient stoichiometries for artificial upwelling. Employing a gradient design, for example with the level of

Figure 5. Mesocosm study on the effect of ocean alkalinity enhancement using the Kiel Off-Shore Mesocosms for Ocean Simulations (KOSMOS) conducted in the Raunefjord, Norway, in 2022. Photo by Uli Kunz.

alkalinisation or the intensity of simulated artificial upwelling as a continuous factor, can enable the identification of non-linearities, thresholds and tipping points in the ecosystem responses. By measuring all relevant components in the water (dissolved organic and inorganic, suspended and sedimented particulate inorganic and organic) and determining air-sea gas exchange, mass balances for biogeochemically relevant elements can be calculated (Boxhammer et al. 2018). Testing mCDR applications in mesocosm enclosures has the additional benefit of minimizing public concern and regulatory requirements when compared to field trials. The urge for rapid advances in this area of research and the diverse merits of mesocosm studies will make this experimental tool an integral part of the emerging mCDR research.

and Brown 2015, De Laender 2018, Schäfer and Piggott 2018, Thompson et al. 2018, Duncan and Kefford 2021, Spake et al. 2023).

How are mesocosms best used to investigate solutions?

An improved understanding of (multiple) stressor impacts (and their interactions) will always be beneficial for environmental managers and policymakers to guide stressor prioritisation in risk assessment and management (Vos et al. 2023). Beyond identification and quantification of risk and impacts, however, our survey indicated that mesocosms offer largely untapped potential for investigating solutions for mitigation. Although existing research in solution-focused topics is relatively limited across all aquatic ecosystems, survey results indicate that lotic freshwaters have had less than lentic freshwaters and marine ecosystems overall (Fig. 3a; mainly investigating catchment restoration). At least some research has been done in marine mesocosms to address each listed solution, with some groups having a lot addressing artificial upwelling, enhanced weathering/ocean alkalinisation and iron fertilisation (marine-specific) as approaches to carbon dioxide removal (CDR) from the atmosphere (Box 1). The potential for using mesocosms in solution-focused research far outweighs the amount of existing research (Fig. 4b). This includes for enhanced weathering/alkalinisation, indicating the relevance of and requirement for research into this CDR approach across all aquatic ecosystems. In marine systems, carbon dioxide injection into the deep ocean has the lowest degree of indicated potential, likely due to the logistical challenges of replicating deep ocean conditions in mesocosm systems, especially in situ. However, applying some systems to this research area will still be possible, with over 40% of survey respondents indicating at least some potential to address this topic with their systems.

One reason why solution solution-oriented research might be more limited in aquatic ecological research utilising mesocosms is because many established strategies for addressing environmental issues are preventative solutions that can now be implemented in the real world without necessarily requiring testing in an isolated environment. For example, reducing reliance on fossil fuels and cutting greenhouse gas emissions is the essential solution to mitigate climate change (IPCC 2023). Similarly, actions like fencing off waterways from livestock and re-planting riparian zones can reduce nutrient runoff, sedimentation and increase shading (Allan 2004, O'Sullivan et al. 2024). The specific measures for a given location can now be implemented or tested in real-world field trials without first requiring evaluation in an enclosed environment (i.e. mesocosm). This is not to say that experimental approaches have not been used to better understand these mitigation strategies, or that mesocosm-based or other controlled experiments will not be useful for further evaluation of their efficacy in the future. Just that an enclosed environment is not necessarily required now to understand their effects, rather, real-world trials and actioning, together with ongoing monitoring to assess effectiveness, can now be implemented (e.g. meta-analysis of ecological restoration studies by Benayas et al. 2009).

A medical analogy might be useful here. These solutions are comparable to implementing preventative measures to improve health such as adopting dietary changes, exercising or improving sleep patterns. These measures can generally be tested in clinical trials with human participants (i.e. in the 'field'). In contrast, treating a disease or its symptoms with new medication requires careful testing in a controlled setting (e.g. in vitro and/or in vivo trials) before implementation in human clinical trials. Mesocosms offer a way to test new forms of treatment for environmental challenges, such as novel technologies or methodological developments, in controlled yet environmentally realistic scenarios before full implementation in the field (Fig. 6), like how new drugs or medical treatments are tested in vitro or in vivo trials before human trials (Elosegi et al. 2017). A good example is the established use of mesocosms to test the environmental side effects of new biocides, alternatives to biocides or less harmful compounds (Caquet 2002). Such ecotoxicological tests provide data useful for making realistic predictions of the fate and effects of these compounds in natural ecosystems, including bioaccumulation through the food chain (Landner et al. 1989). Indeed, mesocosm facilities are used around the world (though not universally) for higher-tier testing of new chemicals before they are brought to market or to inform environmental risk assessments/re-assessments of chemicals already on the market (EFSA 2013). Mesocosms are also employed to assess the efficacy of bioremediation techniques, such as removal of biotoxins (Sylvers and Gobler 2021), chemical remediation with activated carbon (Kupryianchyk et al. 2013), the addition of iron to suppress harmful algal blooms (Orihel et al. 2016), and potential side effects of nitrification inhibitors used to mitigate nitrogen leaching (Bruder et al. 2017, Salis et al. 2019). Utilising marine mesocosms in studying CDR methods to address climate change and related

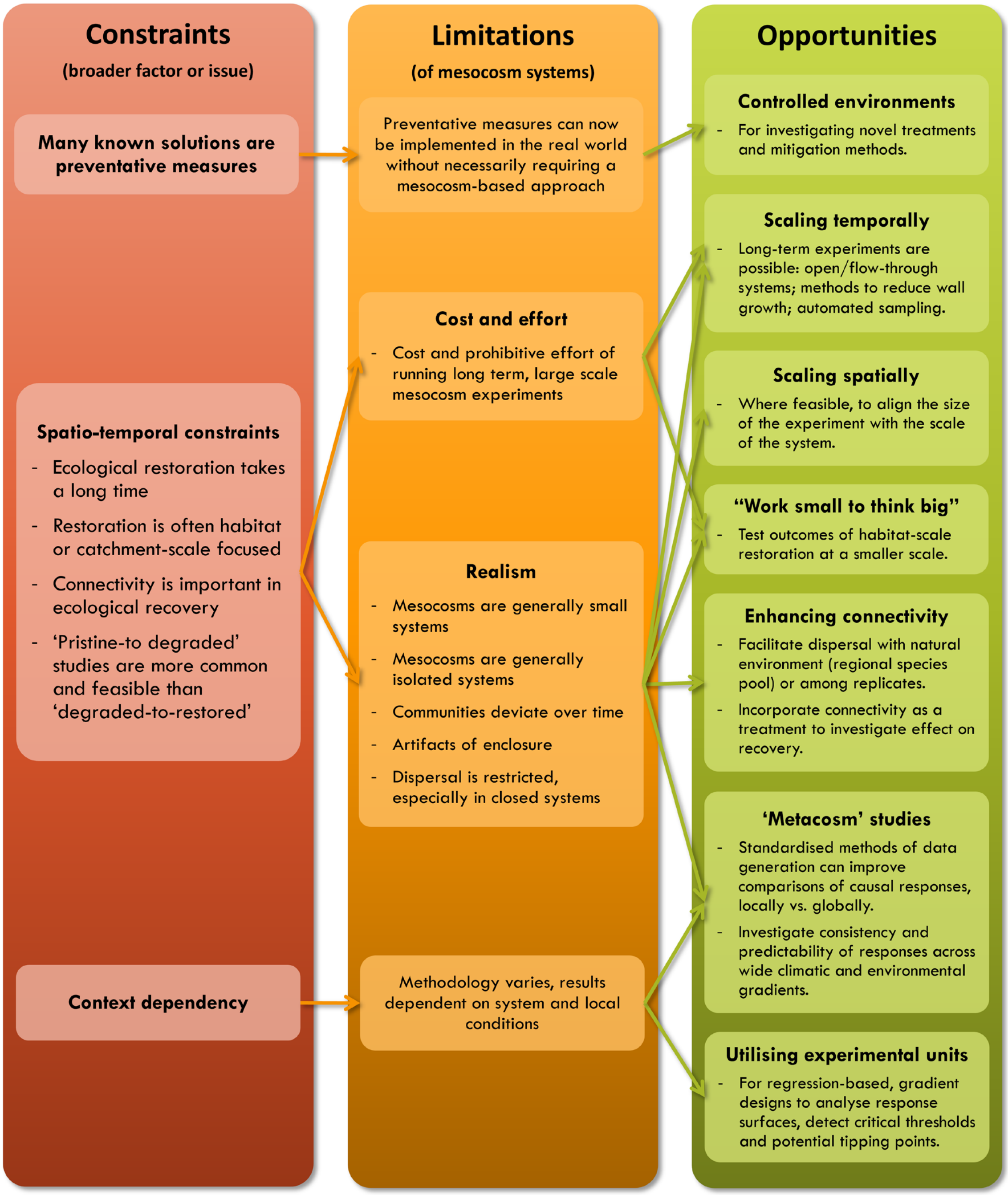

Figure 6. A traffic light framework of constraints, limitations and opportunities in aquatic mesocosm research for advancing solutions to environmental threats. Constraints represent broader factors or ecological issues that might limit solution-focused research relative to research quantifying anthropogenic impacts (as indicated by our survey results). Associated with these are more specific limitations of mesocosm systems that might halt or hinder solution-oriented research with mesocosms. Thirdly are the opportunities for overcoming these, which highlight several directions for moving forward in future solution-oriented research utilising mesocosms.

threats such as ocean acidification is another notable example of the opportunity offered by a controlled yet realistic environment for testing these novel approaches (Riebesell et al. 2023, Box 1).

There are several constraints in research addressing solutions that likely also contribute to there being relatively less mesocosm-based research in this area, compared to research quantifying the effects of threats. These include temporal constraints, spatial constraints and the challenge of context dependency (Fig. 6). Despite inherent limitations of mesocosm experiments associated with these constraints, opportunities arise in 1) scaling up the size and timescales of mesocosm studies or, alternatively, 2) taking a 'work small to think big' approach by testing habitat-scale restoration at smaller scales. Further, 3) enhancing connectivity, 4) conducting 'metacosm' studies – coordinated, distributed mesocosm experiments spanning wide environmental gradients, and 5) employing regression-based experimental designs offer opportunities for moving forward in future solution-oriented research using mesocosms (Fig. 6).

Constraints, limitations and opportunities for using mesocosms in solution-oriented research

Spatio-temporal constraints

Ecological recovery and restoration are prolonged processes (Sas 1989, Dobson et al. 1997, Benayas et al. 2009). Investigating the short-term impacts of stress on a community or ecosystem is, therefore, generally more feasible than assessing long-term recovery from it. While aquatic ecosystems can have 'shorter' recovery times than terrestrial ecosystems (Jones and Schmitz 2009), this still often spans years to decades (Søndergaard et al. 2003, Anderson et al. 2005, Jeppesen et al. 2005). Though, notably, some aquatic communities, such as pelagic zooplankton, phytoplankton and fish, may recover on a scale of months in lakes and marine systems (Borja et al. 2010, Verdonschot et al. 2012, Gergs et al. 2016, McCrackin et al. 2016). However, functional recovery (i.e. biomass, abundance and univariate diversity measures) is generally more likely than compositional recovery (multivariate community composition), which may imply longer-lasting consequences for biodiversity and associated emergent functions (Hillebrand and Kunze 2020). A limitation of mesocosms linked to this constraint is the prohibitive effort required for long-term mesocosm experiments which often demand large research teams. Additionally, reliable, renewable funding for multi-year studies is scarce, though this constraint is not unique to research using mesocosms.

In addition to constraints on temporal scales, mesocosms are often constrained in spatial scales (Englund and Cooper 2003, Petersen et al. 2009, Stewart et al. 2013). This is particularly relevant in solution-oriented research due to 1) restoration efforts often targeting habitat- or catchment-scale processes, and 2) the importance of connectivity in ecological recovery (Tickner et al. 2020). However, 1) mesocosms are generally small systems that reproduce a representative community or ecosystem on a smaller scale, and 2) they are generally enclosed or isolated systems (Petersen et al. 2009). Therefore, testing the effects of habitat-scale restoration in temporally and spatially constrained systems has limitations in terms of realism. For instance, well-known and important restoration processes of aquatic ecosystems such as replanting the surrounding catchment of rivers, lakes, wetlands, estuaries and other coastal environments (Benayas et al. 2009), are difficult to replicate in mesocosm studies, highlighting the importance of catchment-scale field research in addressing such questions (Feld et al. 2011, Verdonschot et al. 2012, Palt et al. 2023).

A limitation of many mesocosm systems in addressing solution-focused research associated with spatio-temporal constraints is that mesocosm communities diverge from natural communities over time. This deviation often results from practical limitations associated with artifacts of enclosure such as wall growth and restricted dispersal (Petersen et al. 2003, 2009). Although limited connectivity to natural ecosystems or other experimental units may be desired (and be part of the experimental manipulation), it can limit recovery potential and realism in experiments with longer durations. As mesocosm experiments run longer, stochastic divergence occurs within both the system itself and among replicates due to selection for different species in an artificial environment compared to what would occur in nature (Petersen et al. 2003, Schmidt et al. 2018). Species sorting may occur faster in a mesocosm as smaller, more homogenous environments provide fewer refuges for less competitive taxa (Cardinale 2011). Thus, mesocosm communities may show an expected response to a given manipulation in terms of initial species sorting but, if lacking connection to a regional species pool, potential recovery or subsequent responses to changing seasonal conditions may be hampered if the experiment is extended (Vad et al. 2023). Consequently, long-term enclosure experiments may result in responses that deviate from realistic or representative outcomes in natural communities or ecosystems. Notably, in experiments focusing on pelagic communities, benthic algal growth on walls can lead to undesired feedbacks between benthic and pelagic organisms, such as nutrient loss from the pelagic environment to the benthic community (Petersen et al. 2009).

A fourth aspect to consider concerning spatio-temporal constraints is that applied ecologists have typically been interested in quantifying how a relatively clean or undisturbed reference ecosystem is impacted by some form of stress, mirroring the effects of humanity on Earth's pristine ecosystems over centuries. However, it is just as important, and indeed even more urgent, to focus on improving already degraded ecosystems. Advancing solutions to humanity's environmental impacts therefore requires a reversal of the common order or 'paradigm' of experimental applied ecological research from 'pristine-to-degraded' to 'degraded-to-restored'. Shifting this order of experimentation confronts a pervasive academic pressure that affects researchers in every field. Positive publication bias pressures researchers toward testing things that are likely to cause an effect (Joober et al. 2012). Therefore, research can be biased towards testing the effects of stressors where a known effect or outcome is likely or expected, rather than investigating solutions to degraded ecosystems when observing a positive outcome might be less likely or expected (Kimmel et al. 2023), at least within the timeframe of a typical experiment. Moreover, due to inherent variation among replicates, there is a tendency to use strong treatments to ensure differences from controls (Birk et al. 2020), leading to more extreme experimental setups with limited realism (Korell et al. 2020). For many mesocosm experiments that typically run on scales of weeks to months, compared to the long timescales of ecological recovery, significant restorative effects may not be observable within the timeframe of an experiment investigating an aspect of restoration (e.g. field restoration studies reviewed by Benayas et al. (2009) ranged from < 5 to 300 years). Again, this highlights the importance of long-term field restoration studies with ongoing monitoring (which are not limited by the same spatio-temporal constraints), to observe such effects. However, the advantage of replicability is generally traded-off with improved realism in such studies (Fig. 2), and investigating novel restoration or mitigation methods might require a closed, controlled environment, therefore it is important to consider how mesocosms can best be implemented to overcome these constraints.

Opportunities in solution-focused mesocosm-based research to overcome spatio-temporal limitations

There are strategies that can be implemented which facilitate scaling study timeframes, spatial realism and investigating the effects of habitat-scale restoration in mesocosm studies. This possibility has perhaps been most clearly demonstrated in the long-term warming-by-nutrients shallow lakes experiment at Aarhus University, which has run continuously for over two decades. Comprising 24 flow-through mesocosms fed by groundwater, these mesocosms realistically mimic the residence time of a shallow lake (approximately three months; Liboriussen et al. 2005, Jeppesen et al. 2021, Saar et al. 2022) which reduces the temporal divergence from natural systems that occurs more rapidly in closed systems. In coastal marine systems, flow-through mesocosms have also been utilised for long-term eutrophication studies lasting several years, including investigations of recovery over two years (Kraufvelin et al. 2006, 2010). Concerning issues of benthic algal wall growth, for mesocosms simulating ponds, shallow lakes or benthic marine systems (described above), benthic organisms are a natural part of the system. In contrast, to overcome time-related problems of wall growth in pelagic systems, mitigating measures have been developed (Jechow et al. 2021, Ptacnik et al. 2021), or increasing the surface-to-volume ratio can reduce the issue. The general challenge of the cost and prohibitive effort of running long term mesocosm experiments may partly be alleviated with technological advancements, such as autonomous in situ sensor systems and machine learning imaging techniques, which offer promising avenues for reducing sampling efforts and time-consuming tasks like classification of organisms (Orenstein et al. 2022).

The scale-dependence of mesocosm experiments involving multiple trophic levels has been identified as a critical issue limiting extrapolation of results to larger scales (reviewed by Englund and Cooper 2003 and Petersen et al. 2009). Practical limitations such as periphyton wall growth, phytoplankton diversity and the ability to include food web interactions driven by larger organisms scale with system size (Berg et al. 1999, Petersen et al. 2003, Smith et al. 2005). Therefore, where feasible, aligning the size of experimental units with the scale of the system of interest is advisable (Petersen et al. 2009). Clearly, achieving this alignment is more practical for smaller aquatic systems like small streams and ponds. For example, experimental units ranging from 100–1000 litres can adequately represent a pond ecosystem, whereas replicating larger systems such as lakes and marine environments poses greater challenges. Nevertheless, with sufficient funding, scaling to replicate lake habitat-level environments is possible, exemplified by the LakeLab at the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin. Comprising 24 large-scale mesocosms (with volumes of ca 1300 m^3), lake parameters such as stratification and thermocline depth can be manipulated at a 1:1 vertical scale of the lake it is situated within, enabling realistic experimental simulations of future climate change scenarios that are difficult to investigate in a whole lake system (Jechow et al. 2021, Lyche Solheim et al. 2024). Simulating other habitats at natural scales, such agricultural ditches, for example, can be more easily achieved by creating separated, in-field channels fed by natural water sources (Barmentlo et al. 2019, 2021). However, generally, scaling the size of mesocosms poses cost challenges and often reduces the degree of replication that is affordable. Some issues such as the wall effect on altered wind patterns, for example, are also inherent limitations of using an enclosed system. Although the effects of such artifacts of enclosure might become less significant in larger experimental systems, such effects will always remain in some capacity. Therefore, scaling the system size must be weighed against the relative cost of upscaling and will depend on the question being addressed.

Some habitat-scale processes might not be initially testable at scale. Mesocosms offer significant opportunities to examine the outcomes of habitat-scale restoration at a smaller level prior to applying at larger scales, which might be thought of as a 'work small to think big' approach (Fig. 6). For instance, marine mesocosms have tested large-scale processes in the open ocean such as artificial upwelling and weathering to induce ocean alkalinisation (Riebesell et al. 2023, Box 1). Similarly, data from field surveys on catchment restoration effects can inform mesocosm experiments examining these effects with control over confounding variables or other environmental parameters, the results from which can subsequently be fed back into ecosystem-scale models. Examples of using this approach in examining the effects of nutrient loading variation are widespread in both freshwater (Stephen et al. 2004, Liboriussen et al. 2005, Jeppesen et al. 2021, Cabrerizo et al. 2020) and coastal marine (Berg et al. 1999, Kemp et al. 2005, Petersen et al. 2009) mesocosm experiments. Coastal mesocosms have been instrumental in investigating several nature-based solutions to eutrophication, such as the extensive work in the Chesapeake Bay by the Multiscale Experimental Ecosystem Research Centre, including biofiltration by oyster and clam populations (Porter et al. 2004, 2013) and restoration of submerged aquatic vegetation and tidal marsh plant communities (Sturgis and Murray 1997, Moore and Wetzel 2000, Stevenson 2009). In lotic freshwater ecosystems, the effects of increased shading simulating riparian vegetation restoration have been studied using outdoor flumes and circular stream mesocosms (Calvo et al. 2022, Winkworth et al. 2015). In many of these examples, data from mesocosm experiments were used together with field observations and ecosystem-level models (Cerco and Moore 2001, Kemp et al. 2004) to inform management decisions concerning reduced nutrient loading and ecosystem restoration measures (Kemp et al. 2005).

To enhance spatio-temporal realism there are several possibilities for incorporating connectivity into future mesocosm studies which can help to overcome the limitation of isolation and test an important aspect of ecological recovery. Clearly, outdoor systems are more realistic than indoor, and open systems, particularly those with flow-through designs providing opportunities for natural colonisation (Lange et al. 2011, Macaulay et al. 2021), are more realistic than closed systems that have limited potential for dispersal from the natural environment (Schmidt et al. 2018). In closed systems, manual manipulation of connectivity – such as dispersing communities among mesocosms (Thompson et al. 2014) or introducing them from a regional species pool (Symons and Arnott 2013) – offers exploration of the buffering effect of dispersal against environmental stressors and the role of dispersal in enhancing ecological recovery (Howeth and Leibold 2010). Different levels of connectivity can be implemented as a treatment to test theory such as the spatial insurance hypothesis (Loreau et al. 2003), which has been done in combination with other stressors including heatwaves, warming, nutrients and salinisation in ponds (Thompson and Shurin 2012, Symons and Arnott 2013, Vad et al. 2023). Another option is to design continuously connected systems that allow for 'natural' dispersal, for example, Juvigny-Khenafou et al. (2024) used spatially connected experimental stream channels to experimentally assess the effects of upstream stress on downstream communities and ecosystem processes. A final aspect to consider in overcoming limitations of isolation is to employ realistic inoculation and colonisation procedures in the preparation phase of mesocosm experiments. For example, given many organisms have resting stages in sediment, using sediment collected from natural systems will ensure measures of biodiversity loss are not severely affected, a factor which is especially relevant for systems that lack connectivity to a regional species pool to enable natural emigration

Lastly, it has also been proposed to scale up field experiments at the spatial scale of the whole experiment rather than the individual plot/experimental unit. Combining global change experiments and gradient studies by conducting the same experimental manipulations along climatic gradients, as recommended by Dunne et al. (2004) and De Boeck et al. (2015), can enhance the validity of extrapolation to broader spatial scales. We agree that a promising research direction to improve the generalisability of findings drawn from mesocosm experiments involves coordinating experiments distributed across wide geographical areas, and discuss this topic in more detail next. Although logistically challenging, and likely dependent on cross-collaboration between multiple research groups and funding agencies, such projects have significant potential to address some of the limitations associated with both spatial and temporal constraints, tackle the challenge of context dependency, and to generate valuable information for advancing solutions to the environmental challenges of the 21st century.

Tackling context dependency with 'metacosm' studies and gradient designs

A significant constraint in advancing solutions to environmental threats is the context dependency of responses, particularly concerning interactions (i.e. when responses are contingent on specific contexts; Orr et al. 2020, Spake et al. 2023). This complexity complicates the quest to discover generalised patterns in ecology and hinders our ability to develop predictive frameworks. To confront this challenge within mesocosm research, a promising approach involves conducting coordinated distributed mesocosm experiments in a space-for-time substitution (SFT) approach (Pickett 1989). This has become a popular approach in ecological and climate change research, such as in spatial regression modelling, where ecological or environmental variables with spatial variation are regressed on each other to test hypotheses about ecological processes (Damgaard 2019). The SFT method accommodates key differences among similar ecosystems due to their position along broad latitudinal and altitudinal gradients, facilitating an assessment of how factors influencing ecosystem structure and function vary across these gradients of climate and ecosystem types. It's strengths lie in the fact that biological communities have had time to evolve to the environment in which they exist. However, with the rate of environmental change in the Anthropocene, statistical relationships observed in SFT spatial regression models may be a result of recent environmental changes or events, rather than supporting a hypothesised causal mechanism (Damgaard 2019). Moreover, purely observational studies have the potential weakness of biogeographical factors confounding correlations, limiting the ability to determine causal relationships (Meerhoff et al. 2012) so manipulative experiments become important for identifying causal mechanisms underlying ecological responses (Underwood 1996). And yet, the ability to extrapolate the results from single experiments yielding site-specific information is inherently constrained by context dependent factors such as the scales of these studies (Fraser et al. 2013) and different approaches and methodologies (Borer et al. 2014).

To capitalise on the strengths of both observational and experimental approaches, coordinated distributed experiments, also called the 'comparative experimental approach' (Menge et al. 2002), have been used to integrate experimental manipulations into a correlative framework (see reviews of marine studies by Hewitt et al. 2007 and terrestrial experiments by Fraser et al. 2013). By extension, to utilise the increased control and replicability afforded by mesocosm experiments compared to large-scale in situ field manipulations, coordinated distributed mesocosm experiments – what we might term 'metacosm' studies – provide a further way forward in this field. Such experiments, involving networks of replicated mesocosm systems across regions with observed spatial variation, have the advantage of simultaneously addressing global environmental problems and exploring general ecological theory through the evaluation of interactions between local and regional processes, while offering

Table 1. Metacosm studies – coordinated, distributed mesocosm experiments – conducted in aquatic ecosystems.

Study/Network name	Study system	Countries included	Key study question	Notable finding from study	References
SWALE International Mesocosm Experiment	Shallow lakes	Finland, Sweden, England, the Netherlands, Spain	How do top–down (fish predation) and bottom–up (nutrient loading) influences on plankton vary across latitudes?–	Variability in the relative importance of top–down and bottom–up influences across years and location increased with latitude due to greater weather variability.	Moss et al. 2004, Stephen et al. 2004
REFRESH	Shallow lakes	Sweden, Estonia, Germany, Czech Republic, Turkey, Greece	How does climate change affect community structure, functioning and metabolism in shallow lakes?	Primary productivity (Chl a) and macrophyte abundance increased with increasing temperature (decreasing latitude), while net primary production (DO) peaked at intermediate temperatures.	Landkildehus et al. 2014
Iberian Pond Network (IPN)	Ponds	Spain, Portugal	How does colonisation of different microplastic surfaces by microalgae vary across environmental gradients?	Local species pool and nutrient concentration, rather than plastic polymeric composition, was the key determining factor of colonising microalgal community.	Pereira et al. 2021, Nava et al. 2022
SITES AquaNet	Lakes	Sweden	How does top–down pulse disturbance interact with bottom–up press disturbance to affect lake plankton community composition and functioning across space and season?	Community composition responses to disturbances were highly divergent between lakes and seasons: temporal accumulated community turnover of the same trophic level either increased (destabilization) or decreased (stabilization) in response to disturbance.	Urrutia-Cordero et al. 2021a, b

the inherent precision of controlled experiments to obtain information on underlying causal mechanisms (Fraser et al. 2013, Benedetti-Cecchi et al. 2018, Urrutia-Cordero et al. 2021b). In addressing global issues, metacosm studies would, ideally, be global in scale (Yahdjian et al. 2021). A significant constraint to conducting global metacosm studies, however, is obtaining international support from funding agencies. Unless multiple projects can simultaneously be funded from different funding bodies, globally distributed metacosm studies would require greater flexibility from agencies to support researchers from different jurisdictions. To achieve the former, global networks such as mesocosm.org can help in gathering facilities from around the world to simultaneously apply for local funds and communicate the breadth of the targeted study to different funders. Moreover, the aforementioned issue of recent changes or historical legacies confounding observed differences in ecological responses at different locations (Damgaard 2019) remains in metacosm studies; therefore, this approach may be most applicable to studying ecological responses that occur rapidly compared with changes in the environment. To tackle large-scale and long-term responses, a hybrid approach integrating large observational time-series datasets with causal data obtained from distributed experiments into emerging time series analyses and species distribution modelling techniques could provide important advancements (proposals suggested by Benedetti-Cecchi et al. 2018).

Several cross-latitudinal lake and pond 'metacosm' experiments have already been conducted (Table 1; notably, limited to Europe, where transnational funding is accessible). The first involved a series of 11 parallel mesocosm experiments conducted as part of the SWALE Pan-European project (Moss et al. 2004, Stephen et al. 2004). In the European REFRESH project, a highly standardised metacosm experiment was conducted along a temperature gradient from Sweden to Greece (Landkildehus et al. 2014). The Iberian Pond Network (IPN), established in 2014, consists of 192 pond mesocosms distributed across six sites located from alpine to semi-arid climate regions (Pereira et al. 2021, 2023). The SITES AquaNet mesocosm infrastructure is another network of mesocosms located in five Swedish lakes, covering a 760 km latitudinal gradient (Urrutia-Cordero et al. 2021b). A cross-continental lake salinisation experiment incorporated three of the SITES AquaNet facilities, together with fifteen other existing mesocosm systems across Europe and North America, to study global patterns of salinisation on zooplankton communities (Hébert et al. 2022). While it was less standardised in terms of the system (many different mesocosm systems were used, ranging from 20–32 experimental units and 80–2500 l volumes), it was still highly standardised in terms of salinity treatment (an unreplicated regression design), study time frame, and sampling protocol. This distributed experiment was able to quantify overall effects of elevated chloride on zooplankton abundance, taxon richness and functional diversity. Despite significant among-site variation in community structural responses, the study demonstrated that key community metrics can be affected by chloride levels relevant to current anthropogenic salinisation (Hébert et al. 2022), with the important message for management that existing guidelines in North America and Europe are not sufficiently protective of lake ecosystems (Hintz et al. 2022).

While not a complete solution to the problem of context dependency, 'metacosm' experiments can at least standardise methods of data generation, providing a common framework within which to compare causal responses and interaction types across geographical and environmental gradients, as well as among specific sites. As demonstrated by the existing studies to have carried out such research (Table 1), this enables comparison of the relative importance of factors manipulated in the experiments with variation attributable to site location, i.e. global versus local effects. Consistent trends and relationships across sites enhance the validity of extrapolation and generalisability of responses, whereas differing responses among sites would indicate increased importance of local conditions and context dependency. When manipulating multiple stressors in community and ecosystem-level studies, there is the controversial view that overcoming the challenge of context dependency requires, at least initially, focusing less specifically on the form and direction of interactions and rather on the presence and distribution of higher-order interactions (Simmons et al. 2021, Kefford et al. 2023). This approach would help to evaluate the consistency and predictability of effects across multiple ecological scales (Simmons et al. 2021). Combining these approaches has the potential to yield powerful insights into the generalisability of multiple stressor effects across broad geographical scales. For example, a metacosm experiment involving two or more manipulated factors with sites spanning temperate to tropical climates could first identify whether interactions occur consistently across the latitudinal gradient and explore any patterns in the occurrence of higher-order interactions at the different levels of biological organisation measured (i.e. species population responses, community metrics and ecosystem-level responses). Initially, without exploring the type of interactions, this provides valuable insight into how predictable the effects of multiple factors (whether stressors, or 'solutions' to stress, i.e. mitigation measures) are across climate and/or environment types. Subsequently, where specific interactions are consistently occurring (at a particular response level, for example), the shape of these interactions can then be compared to explore, more specifically, how the manipulated factors interact and whether the nature of these interactions is consistent or changes across a climatic or environmental gradient (e.g. as done by Kefford et al. (2023) for observational macroinvertebrate community patterns).

A further opportunity for metacosm studies is to coordinate the testing of novel solutions to environmental threats across regions, especially those providing promise for global and real-world application, and for which a controlled setting is required to investigate their ecological effects (Fig. 6). This would provide crucial insights into their generalisability and success across geographical regions. The specific solutions to be tested might not yet exist, but a good example are the several novel negative emissions technologies in mCDR research (Box 1), the success and potential ecological effects of which will need to be tested in different marine environments, likely in a controlled settings prior to larger scale field manipulations, in order for mCDR methods to be implemented globally. With the rate of technological advancement in the 21st century and advancement of ecological theory, it is not difficult to imagine the development of other novel strategies to mitigate the problems generated by human-induced environmental change. However, collaboration across often separated research disciplines will be key (Orr et al. 2020). Ecologists will need to establish synergic relationships with a wide array of disciplines, not least engineers who have the knowledge and technological skills to develop novel techniques that could advance solutions to many environmental threats. For metacosm projects to be successful, collaboration between research groups and funding agencies will be crucial to achieve consistent, coordinated data collections across large-scale, distributed network experiments (e.g. considerations suggested by Borer et al. 2014). From this multidisciplinary and collaborative approach, important research advancing solutions to environmental threats in aquatic ecology can arise.

Utilising high numbers of experimental units in gradient designs

Mesocosm systems comprising many experimental units are well-suited for regression-based experimental designs that best predict the response surface of continuous, variable and potentially interacting environmental drivers (Kreyling et al. 2018, Gerhard et al. 2022, Thomas and Ranjan 2024). Employing regression-based designs can help tackle the challenge of context dependency by covering broader gradients of predictor variables, reducing prediction error, and enhancing comparability between studies that might otherwise use different treatment levels. Using five or more levels of an environmental variable allows for the prediction and comparison of ecological responses at levels not measured in the experiment (Thomas and Ranjan 2024). Additionally, these designs can contribute further to solution-oriented research by identifying non-linearities such as such as non-linear interactions (Duncan and Kefford 2021), potential thresholds, tipping points and biphasic biological responses to stressors and environmental drivers such as temperature, CO_2, pH, salinity and nutrients (Scheffer and Carpenter 2003, Orr et al. 2024), particularly in their potential application for management (but see further discussions on the issue of identifying thresholds by Hillebrand et al. 2020).

The use of wide gradients of chemical concentrations is common in ecotoxicology, where identifying threshold concentrations at which a certain magnitude of response is elicited in individuals, populations or communities is a core aim (Cairns Jr 1992). Testing responses to only two or three levels is generally insufficient due to sensitivity variations among species and the non-linear nature of toxicity responses (OECD 2006a). Similarly, other continuous stressors or environmental drivers often exhibit non-linear response patterns (e.g. temperature and nutrients) necessitating wider stressor gradients (at least 5 or 6 levels) for more accurate predictions of their response surfaces (Boyd et al. 2018, Thomas and Ranjan 2024).

However, the inherent tradeoff between realism and control in mesocosm-based research poses a limitation to using unreplicated regression designs. Large within-treatment variation (noise) due to environmental variability and the presence of natural ecological communities in mesocosm experiments (Gerhard et al. 2022) may necessitate some treatment replication (Cottingham et al. 2005, but cf. discussion from Kreyling et al. 2018, Gerhard et al. 2022, Thomas and Ranjan 2024). Systems comprising a high number of experimental units can employ replicated gradient designs, including with multiple stressors, allowing for the detection of non-linear responses and interactions while still enabling true replication of each treatment level to reduce the influence of noise. For example, systems with 128 experimental units can be used for 8 × 8 full-factorial response surface experiments with two replicates (Wagenhoff et al. 2012, 2013). But even a system comprising 50 experimental units could still employ a 5 × 5 full factorial response surface design with two replicates of each treatment level. Thomas and Ranjan (2024) discuss the opportunities for employing alternative regression-style designs in multiple stressor/driver experiments given a limited number of experimental units, such as space-filling designs for which mesocosm may be well-suited if treatment conditions can be manipulated precisely. Providing this, and consistency of ecological communities within, moving towards regression-style designs over replicated designs with only 2–3 treatment levels will generate more informative data for evaluating theory or models. This will improve prediction of non-linear ecological responses, reduce the context dependency of results involving only two treatment levels of a continuous predictor (e.g. in present-versus-future designs or 2 × 2 factorial designs) and deliver critical information for management and mitigation (Kreyling et al. 2014, 2018, Gerhard et al. 2022, Orr et al. 2024). For example, the aforementioned study by Hébert et al. (2022), involving a series of coordinated mesocosm experiments, investigated the effects of a wide chloride concentration gradient across multiple continents, and led to the important policy recommendation to establish more protective salinity guidelines (Hintz et al. 2022).

Investigating non-linearities also requires attention to the frequency of monitoring responses due to their temporal dynamics. The detection of tipping points, for example, might require higher sampling frequency to identify their occurrence in time and detect early warning signals preceding critical transitions (Urrutia-Cordero et al. 2021b, Gsell et al. 2023). Combining increasingly available high-frequency monitoring methods (discussion by Marcé et al. 2016) with gradient designs can generate valuable experimental output for informing process-based models (Kong et al. 2019) and, potentially, even digital twins of ecological systems (de Koning et al. 2023).

Conclusions

Addressing the grand ecological challenges of the Anthropocene demands immediate and concerted efforts from the global scientific community. Established preventative measures should be actioned to reduce greenhouse gas emissions, pollution of toxic chemicals and novel entities, overexploitation of species, spread and impacts of invasive species and loss of natural habitats. In addition to these important actions, there are opportunities to apply both existing and novel solutions to mitigate threats and restore ecosystems. As indicated by our survey results, mesocosm studies that replicate natural ecosystems in a controlled and realistic manner present valuable tools for testing and refining these solutions. Some recommendations for future studies to harness the potential of aquatic mesocosm systems in solution-oriented research are:

- Where feasible and appropriate to the scale of the research question, scale up the timeframe and spatial scale of experiments. The former can be achieved by using open or flow-through systems to reduce the temporal divergence that occurs in static systems, implementing methods to mitigate artifacts of enclosure including wall growth, and utilising automated sensors and sampling techniques. In addressing the latter, it is advisable to align the size of the mesocosm with the scale of the system. Depending on the study and system, effort in scaling up spatially might be best directed toward the geographical scale of the experiment rather than the size of the mesocosm specifically, for example, by distributing experiments across broader spatial gradients to improve generalisability and extrapolation of results (fourth recommendation, below).
- Alternatively, adopting a 'work small to think big' approach in testing the outcomes of habitat-scale restoration at a smaller scale can be particularly useful when restoration or mitigation measures cannot initially be tested at scale or require a controlled environment for investigating their potential environmental effects before implementation in the real world.
- Enhancing connectivity in future studies by facilitating dispersal from a regional species pool, for example, with open systems allowing natural colonisation or by manually manipulating dispersal can help to overcome the limitation of isolation. Incorporating different degrees of connectivity as a treatment, together with other manipulated factors, can deepen understanding of how this important feature of ecological recovery operates under varying degrees of human impact.
- Conduct 'metacosm' studies: coordinated, distributed mesocosm experiments spanning diverse climatic and environmental gradients. Such experiments hold promise in addressing global environmental challenges and exploring general ecological theory by providing a common

framework for comparing causal responses and interactions across local and global scales.
- Leverage the high number of experimental units available in many mesocosm systems to employ regression-based designs. Implementing gradient designs that analyse response surfaces can reduce the context dependency of results, generate more informative data for evaluating theory or models and improve solution-oriented research by helping to detect thresholds and potential tipping points of biological responses to continuous and variable environmental factors, guiding prioritised interventions for mitigating environmental stress.

Future studies could incorporate multiple aspects of these recommendations into their design. The path forward involves a collaborative, multidisciplinary approach that embraces technological, theoretical and data analytical advancements. Ideally, data generated from empirical studies would be integrated with increasingly available large-scale observational datasets by utilising advancements in modelling techniques such as time-series analyses, species distribution models and process-based models. Such integrated approaches that leverage the advantages of controlled manipulative experiments, field monitoring and modelling represent comprehensive strategies for discovering the required management solutions to ameliorate the impacts of human activities on Earth's vulnerable aquatic ecosystems.

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Data availability statement

The data that support the findings of this study (survey results presented in Fig. 3 and Fig. 4) are openly available in Dryad at https://doi.org/10.5061/dryad.jm63xsjn0 (Macaulay et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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