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Title: The case for research integration, from genomics to remote sensing, to understand biodiversity change and functional dynamics in the world's lakes

Running title: Research integration and lake ecosystems

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Abstract

Freshwater ecosystems are heavily impacted by multiple stressors, and a freshwater biodiversity crisis is underway. This realisation has prompted calls to integrate global freshwater ecosystem data, including traditional taxonomic and newer types of data (e.g. eDNA, remote sensing), to more comprehensively assess change among systems, regions, and organism groups. We argue that data integration should be done, not only with the important purpose of filling gaps in spatial, temporal and organismal representation, but also with a more ambitious goal: to study fundamental cross-scale biological phenomena. Such knowledge is critical for discerning and projecting ecosystem functional dynamics, a realm of study where generalisations may be more tractable than those relying on taxonomic specificity. Integration could take us beyond cataloging biodiversity losses, and toward predicting ecosystem change more broadly. Fundamental biology questions should be central to integrative, interdisciplinary research on causal ecological mechanisms, combining traditional measures and more novel methods at the leading edge of the biological sciences. We propose a conceptual framework supporting this vision, identifying key questions and uncertainties associated with realising this research potential. Our framework includes 5 interdisciplinary “complementarities”. First, research approaches may provide *comparative complementarity* when they offer separate realisations of the same focal phenomenon. Second, for *translational complementarity*, data from one research approach is used to translate that from another, facilitating new inferences. Thirdly, *causal complementarity* arises when combining approaches allows us to “fill in” cause-effect relationships. Fourth, *contextual complementarity* is realised when together research methodologies establish the wider ecological and spatio-temporal context within which focal biological responses occur. Finally, integration may allow us to cross inferential scales through *scaling complementarity*. Explicitly identifying the modes and purposes of integrating research approaches, and reaching across disciplines to establish appropriate collaboration will allow researchers to address major biological questions that are more than the sum of the parts.

Keywords: limnology, harmful algal blooms, interdisciplinarity, monitoring, palaeolimnology, spatial scale, temporal scale

1. Introduction

Freshwaters face significant, and multiple, pressures which are already having a discernible impact upon biodiversity, ecosystem processes and states, and ecosystem services (Jackson, Loewen, Vinebrooke, & Chimimba, 2016; Ormerod, Dobson, Hildrew, & Townsend, 2010). Indeed, some existing data sources suggest that freshwater systems are especially imperiled at a global scale, compared to their marine and terrestrial counterparts (e.g. 83% decline in freshwater vertebrates over the last 50 years; Darwall et al., 2018; WWF, 2016). If we are to manage, conserve, and adapt to such profound and widespread change in freshwaters, we require robust scientific evidence of patterns of ecological change, and underlying causal factors. Crucially, we need to use this knowledge to enhance our ability to predict future change, so that we can effectively plan and prioritise management and conservation interventions. Currently this essential evidence is produced by investigations adopting a variety of approaches, and that are distributed unevenly across temporal and spatial scales, driven largely-independently by a wide variety of questions. As a result, a comprehensive integrative understanding of biological response to global change can be envisioned but still is rarely realized.

At the broadest extent, it is well known that freshwater studies are biased in their global and taxonomic coverage (Alahuhta et al., 2018; Dudgeon et al., 2006; Jackson, Weyl, et al., 2016), as is the case for biodiversity monitoring more generally (Navarro et al., 2017; Schmeller et al., 2017). A recent analysis of biodiversity literature (Tydecks, Jeschke, Wolf, Singer, & Tockner, 2018) noted that the majority of study sites are in Asia (24.9%), Europe (19.6%), and North America (13%); furthermore, 83.3% of these publications focus on terrestrial systems, specifically plants (55%). Mindful of the gaps in ecological understanding that this situation creates, there have been calls to integrate existing research approaches more effectively, including the adoption of relatively new investigative technologies such as remote sensing and environmental DNA (eDNA), in order to fill gaps in the global evidence base (Jackson, Weyl, et al., 2016; Navarro et al., 2017; Proença et al., 2017).

Whilst biodiversity monitoring and assessment is crucial to our understanding of ecosystem responses to stress, an essential goal is to move beyond “filling gaps” in biodiversity data *per se* and toward understanding how such changes impact upon ecosystem functional dynamics (Box 1; Levin et al., 2013; Turak et al., 2017). Such a move could potentially utilize evidence from a wide range of environmental research approaches. For example, remote sensing creates opportunities for large-scale monitoring of habitat structural features, cyanobacterial growth and possibly submerged macrophyte extent in inaccessible or unsafe regions; metagenomic and other ‘omic approaches facilitate understanding of biodiversity at high taxonomic resolution, with promise for understanding functional diversity; use of DNA metabarcoding, image and acoustic analysis, and citizen science may allow more rapid and widespread data collection for specific taxonomic groups. Use of these approaches adds substantially to the knowledge base that largely has developed based on *in situ* sampling and labor-intensive identification of taxa within visibility constraints of standard light microscopy.

Yet even as we wholeheartedly encourage the adoption of these approaches that broaden our understanding of freshwater biology, we recognize that by using and developing each approach alone we potentially widen the gaps among the researchers and the knowledge that they produce. In tandem with the adoption of new techniques, we argue that problem-focused integration of multiple approaches is key to addressing major, basic biological knowledge gaps that currently hinder our ability to predict biological responses to global change.

Box 1: A focus on function

A considerable challenge in making robust inferences and projections about the responses of lakes to environmental stressors will be to move from the exploration of single-lake responses ("every lake is a snowflake") to an understanding of generic, widely-relevant functions. Integration of research methodologies around ecosystem functions is more likely to facilitate cross-system comparison and inform on landscape-scale processes (e.g. cycling and processing of carbon, Figure 1) since the precise taxa that are present, dominate, and contribute to ecosystem function vary among lakes, according to processes such as dispersal and habitat filtering. As such, the construction of globally-relevant generalisations about ecological responses, based upon the autecology of specific taxa within single-sites is complex. Another advantage of a more functional focus is that associated ecological modelling approaches could incorporate important intraspecific (and intra-population) variation which, at times, produces greater ecological variation than interspecific differences (Des Roches et al., 2018; Raffard, Santoul, Cucherousset, & Blanchet, 2019). Further, focus on function can facilitate identification of common questions across evolution and ecology, from micro- to macro-scales (McGill et al., 2019).

Functional traits assigned to species may differ by the questions at hand. Common groupings have included those associated with trophic relationships, stress tolerance, body size and dimensions (reviewed in Salmaso, Naselli-Flores, & Padisák, 2015). Some researchers have shown the possibilities that arise when deriving functional information from taxonomic data (e.g. inferring nutritional value and potentially trophic transfer for primary producers (Galloway & Winder, 2015), or trophic level differences in phenological responses to climate change (Thackeray et al., 2016)). More recently functional traits have been defined using metabolomics, in which all molecules present in an organism create a "metabolic fingerprint", considered to be the final expression of genotype; either this full suite of molecules or a subset of metabolites associated with specific metabolic processes can be examined (Sardans, Peñuelas, & Rivas-Ubach, 2011). An advantage of these molecular approaches to characterizing function is the ability to examine 'cryptic adaptive traits,' such as cellular change that facilitates adaptation to stress, both within and among populations (Salmaso, Naselli-Flores, & Padisák, 2015). The field of functional, trait-based, ecology in freshwaters is rapidly developing, with recognition of the complexities that come with understanding relationships between environmental stress, traits, and functional properties (Alahuhta et al., 2018; Hamilton et al., 2019). As such, resolution of the form of relationship between global change stressors and functional properties, in different ecological contexts, is a high priority. While the importance of methodological continuity within long-term research programmes cannot be overstated, we must also ask what the leading edge of functional biology can offer to augment the core measurements collected within these schemes, providing novel insights into ecosystem responses.

2. The challenge of research integration

There is clearly the potential for great complementarity among approaches, because research methodologies vary in their spatial and temporal scales (spatial extent, length of time) and resolutions (frequency of observations in time and space), and ecological focus (Hampton, 2013; Proença et al., 2017). As a result each approach will be well suited to the detection of a different subset of ecological phenomena. Therefore there is an opportunity to apply the current heterogeneous mix of evidence of the freshwater impacts of global change drivers, to detect ecological responses at multiple scales and resolutions. To fully realise the potential of this global research “landscape”, we must embrace the challenge of combining individual research approaches into a cohesive whole; an emergent property of this complex monitoring and observation system, which is greater than the sum of its parts. Importantly, integration should be ambitious in answering new questions of ecosystem function rather than solely focused on filling temporal or spatial gaps in understanding. Such interdisciplinary working represents a major scientific and cultural challenge (Palmer, Kutser, & Hunter, 2015), in which we would need to address not only among-approach differences in data scales and resolutions, but also in data precision and accuracy (Blair et al., 2019).

A major goal is to combine new technologies with more traditional approaches to do analyses that are more forward-looking and less forensic in nature, using monitoring not only to understand the trends but to develop a predictive understanding of fundamental processes currently emerging in the leading edge of biological research. Without an intentional and ambitious effort toward integration of research approaches that push fundamental scientific frontiers, we run the risk of increasing the disparity among studies that independently leverage new technologies within the technological boundaries that have been set by other use cases (e.g. remote sensing products optimized for terrestrial or marine environments). Using the example of lake ecosystem responses to climate change here, we illustrate our central tenet that the most critical gaps in our basic biological knowledge must be addressed through an integration of research approaches around well-defined questions regarding ecosystem functional dynamics, and that this integration should be based upon vigorous interdisciplinary dialog.

3. A convergence of biological subdisciplines

The spatio-temporal scales and focal ecological phenomena of any specific research approach will influence which hypotheses can be generated and tested. Frequently research approaches are tied very closely to specific fields of inquiry - from population genetics to ecosystem metabolism - such that researchers reach for familiar techniques without substantial deliberation about the extent to which the technique itself begins to define the questions, rather than the questions defining the approaches.

As largely independent studies proceed using multiple research approaches, the research community continues to generate multi-scale and multi-resolution data for freshwater systems in which the ecological processes that we wish to observe are themselves scale-dependent. Where the temporal and spatial scales of an ecological process roughly match the scale at which a specific research approach produces data, we would expect ecological phenomena to be discernible, while processes operating over much finer and coarser scales would be harder to detect and attribute. For example, compensatory dynamics may allow functionally if not taxonomically similar taxa to maintain overall biomass at the scale of months or seasons, even while the taxonomic composition shifts at weekly scales (e.g. Fischer, Frost, & Ives, 2001). If the key variable of interest is standing algal biomass, remote sensing may be used (for relatively large lakes), but if the interest is in taxonomic biodiversity or in predicting harmful algal blooms, *in situ* sampling and genomic approaches may be the tools of choice. Without combining these approaches, a deeper understanding of the biological processes that contribute to the stability of primary production, biodiversity, microbial dynamics, and toxin production will not be achieved. Furthermore, due to practical difficulties and limitations in financial resources, any single approach will necessarily omit certain ecological variables, and thus risk failure to detect important changes, or misattribution of changes that are observed.

Over time, as research techniques mature and accrue data, within-approach scientific advances will be made, generating valuable system knowledge. However, the processes that can be studied using data generated by any single research technique, whether it be *in situ* monitoring, sensor-based measurement, remote sensing or molecular investigation, will remain constrained by the “design features” of that technique (e.g. spatial, temporal and taxonomic resolution, range of ecological parameters that can be directly observed). Most of the “design features” for emerging tools have not been optimized for aquatic systems or indeed for ecological questions. For example, at one end of the proverbial spectrum, freshwater scientists are currently in a state of “hacking” information that can be derived from remote sensing tools that were largely derived for terrestrial, and more recently marine, research (Geller et al., 2017; Palmer et al., 2015). The selection and optimisation of algorithms for the quantification of primary producers in freshwater systems is a non-trivial task and, although strong vertical heterogeneity exists within lake ecosystems, remotely-sensed data do not directly reveal ecosystem states and processes at-depth. Therefore, if we focus only on remote sensing tools, we will neglect exciting emerging fields of freshwater biology, such as the implications of connectivity between pelagic and benthic habitats (Vadeboncoeur, Vander Zanden, & Lodge, 2002), the role of microbial biomass in supporting higher trophic levels (e.g. Cotner & Biddanda, 2002), or the complexities of mixotrophy that contribute to gene expression in some harmful algal blooms (Liu et al., 2015). At the other end of the spectrum, the cost of molecular tools has dropped precipitously due to medical applications, bringing metagenomics tools within reach for aquatic scientists; however, ecological inference is still constrained by the size and completeness of relevant DNA reference libraries and a functional understanding of genes beyond those of immediate interest to human welfare such as antibiotic resistance (Salmaso, Anneville, Straile, & Viaroli, 2018). As such, there exist hypotheses that will remain out of reach given data gathered from any single approach, unless a) technological innovations widen the phenomena that can be investigated within a subdiscipline, or b) we can meaningfully integrate diverse subdisciplines so that the limitations of each approach are overcome by the possibilities of others. Thus the convergence of biological subdisciplines is useful to consider, spanning the full range of biological organisation from molecular biosciences to ecosystem ecology.

4. A conceptual framework for research integration

We argue that any attempt to integrate across research subdisciplines, to tackle the “big questions” around how freshwaters respond to global change drivers, must be underpinned by a conceptual (causal) model i.e. a series of hypotheses and assumptions regarding the perceived “true” mechanisms and states of the ecosystem phenomena of interest. This begins with the recognition that 1) lake ecosystems, our focus, are networks of exogenous and endogenous drivers affecting interconnected physical, chemical and biological properties, 2) each lake ecosystem rests in a wider context, set within a landscape, biogeographic province or climatic zone and 3) that different research approaches may deliver understanding of different components of this overall system, or different realisations of the same underlying process (Fig. 2).

We must then consider how currently available research methodologies map onto these ecological contexts and processes, in terms of spatio-temporal scaling and resolution, apparent overlaps and complementarities with respect to the data delivered by different approaches, and also in terms of the directness with which focal ecological processes and states can currently be measured. Broadly, we can envisage three ways in which data from different research methods can be integrated around hypothesised, true, ecological processes: 1) *post hoc* combination of consistent but separate analyses of each relevant data set (effectively meta-analysis), 2) inclusion of different data sets in the same statistical model with the aim of arriving at more precise estimates of underlying ecosystem behaviour, and 3) constructing separate models of data generated by different research methodologies and then linking these in a model network.

Despite the complexity of lake ecosystem dynamics (e.g. Bruder, Frainer, Rota, & Primicerio, 2019) we propose that there are distinct, idealised types of research method integration, which we term complementarities. Each of these cases assumes the presence of an underlying causal "truth", and together these cases frame a diversity of opportunities for interdisciplinarity in lake ecology. Crucially, each of these types of research integration makes key assumptions, that give rise to important uncertainties worthy of further investigation. We term these cases: comparative, translational, causal, contextual, and scaling complementarities.

Comparative complementarity (Fig. 2a): In some cases, data gathered through different monitoring approaches are not combined within a single modelling approach, but are instead used in parallel as separate realisations of the same focal phenomenon. For example, a recent study by Taranu et al (2015) used a combination of paleao- and neo-limnological data to powerfully demonstrate accelerating nutrient-driven increases in cyanobacterial dominance in lakes throughout the north temperate and subarctic zone. While *in situ* water column monitoring data showed that the magnitude of cyanobacterial biomass trends varied with the eutrophication status of water bodies at the decadal scale, phytoplankton pigments preserved in sediment cores showed consistent trajectories in cyanobacterial dominance at the centennial scale. In such cases, the parallel use of data gathered using two different investigative approaches increases confidence in observations of the focal phenomenon, here a rising community dominance of cyanobacterial populations. Key assumptions here are that 1) the data from the different research methods represent alternative realisations of the same underlying state or process, and 2) the same (shared) underlying causal factors have a discernible effect in the different data sets. Though the data within the Taranu et al. (2015) study are effectively used in parallel, and not integrated within the same statistical model of an underlying process, there are techniques that would allow the latter approach and, in doing so, would potentially increase the precision with which the "true" state of the system could be estimated.

Translational complementarity (Fig. 2b): There are situations in which data gathered, and models constructed, from one research approach have the potential to enhance the capabilities of another. For instance, Earth observation provides great promise for widespread and frequent monitoring of freshwaters globally (Dörnhöfer & Oppelt, 2016; Palmer et al., 2015; Tyler et al., 2016) but, on its own, is restricted to the inference of a core set of ecological parameters, including surface water temperature, chlorophyll *a* and phycocyanin concentrations, water colour, transparency and suspended solids. Some ecologically and socio-economically important parameters cannot be directly estimated from reflectance, but can be inferred by driving empirical models constructed using detailed *in situ* data with remotely sensed information. As an example, Shi et al (2015) use satellite-derived chlorophyll *a* data, in conjunction with an empirical model of the relationship between *in situ* measured cyanotoxin and chlorophyll concentrations, to infer spatial variability in cyanobacterial toxins at scales observed by the satellites.

However, the robustness of such inferences is likely to vary greatly as a function of ecological parameters that determine when and where toxins are likely to be produced. For example, toxin production varies among cyanobacterial species and genotypes (Sivonen & Jones, 1999), such that ecological processes that are relevant to selection will also impact upon the likelihood of toxin production. The evolutionary ecology of cyanotoxin production is in itself a leading edge for freshwater biology, currently limited by an understanding of genes and environmental cues involved, as well as the broader ecosystem effects of the toxins (Huisman et al., 2018; Murray, Mihali, & Neilan, 2011; Rantala et al., 2004). As knowledge develops in the basic biology of cyanotoxins, updated parameterization of empirical models can provide increasingly refined predictions of cyanotoxin concentration based on *in situ* or remote sensing products, demonstrating the synergy between basic and applied biology and the application of diverse approaches. The development of metagenomics is similarly dependent on other approaches to translate its findings (Salmaso et al., 2018), since traditional microscopy and taxonomy are used to build DNA libraries that translate genomic information into taxonomic identification, and laboratory experiments that examine functions such as nitrogen fixation can allow inference of functional genes.

Another recent example of translational complementary, demonstrated by Saros et al. (2019) involved the modelling of satellite-derived ice-out dates as a function of weather station air temperature data, so that the resulting model could be used to reconstruct longer time series of ice-out. Along with a diversity of other evidence, these modelled data allowed resolution of non-linear climate impacts in Greenland.

In these cases, data and models delivered by one research approach are used to extend the inferences that can be made using data produced by other approaches, providing opportunities to push the boundaries of basic research in freshwater biology. Effectively, translational complementarity allows us to observe what would be unobservable within a single discipline study. A key assumption here, however, is that there exists a strong relationship between the properties that can be observed from one research approach (e.g. reflectance measured by Earth observation) and properties these observations can be used to infer (e.g. cyanobacterial toxins via a model constructed from *in situ* data). If this relationship is statistically weak (i.e. high residual variance), or is obscured by covariation in other environmental factors, we can expect the translation of one type of data into another to come with considerable uncertainty. This issue is well-recognised in the field of palaeolimnology, where the efficacy of historical reconstructions can be undermined by ill-defined causality between sediment-based proxies and water column conditions, and confounding factors (Juggins, 2013). As a result, to facilitate translational complementarity we must have a clearly-defined causal reasoning for data integration.

Causal complementarity (Fig. 2c): There are frequently multiple direct and indirect causal mechanisms that could potentially “explain” observed correlations between environmental stressors and ecosystem responses (Downes, 2010). However, a single research approach may omit observations of important causal linkages between driver and response; a problem that has been recognised in proxy-based palaeolimnological reconstructions of historical environmental change (Davidson, Sayer, Perrow, Bramm, & Jeppesen, 2010; Juggins, 2013). In such a situation we might envisage that interdisciplinary working could fill these gaps in the causal chain. As an example, the influence of changing water chemistry on phytoplankton growth may be mediated by bacterial-algal mutualisms or parasitism (Cirri & Pohnert, 2019; Kojadinovic-Sirinelli et al., 2018). In the absence of recent developments in molecular and ‘omics approaches, we would have very limited understanding of these influential dynamics that are beginning to change the way we view freshwater food webs (Cooper & Smith, 2015). In this case, a combination of multi-parameter *in situ* ecosystem monitoring and ‘omics based investigation could complete the causal chain in a field setting. Similarly, combined traditional *in situ* monitoring and metagenomic sampling shows promise for understanding the environmental drivers of viral communities, and their potential impacts upon ecosystem functioning (Palermo, Fulthorpe, Saati, & Short, 2019). Another example of causal complementarity comes from the Earth observation field; here spatial and temporal variations in algorithm performance for retrieval of phytoplankton biomass data (i.e. the strength of the relationship between water-leaving radiance and water column chlorophyll *a* concentrations) can be marked (Boucher, Weathers, Norouzi, & Steele, 2018), and may be a result of species turnover within the observed plankton community (Ligi et al., 2017). Clearly there remains a role for *in situ* taxonomic monitoring to quantify community structure and change, and allow the development of causal understanding of the ecological mediators of the relationship between satellite-derived reflectance and integrative ecosystem properties.

While, here, research integration ideally allows us to gather empirical evidence that would “fill gaps” in our causal understanding, we would be making the implicit assumption that the combination of research approaches being used is one that can shed light on the most influential causal mechanisms. We would therefore need to ground such research integration in clear hypotheses regarding which causal linkages between states/processes A and B exist, which are observable via different research approaches, and which are likely to be most “important” in any given ecological context.

Contextual complementarity (Fig. 2d): By bringing together research methodologies we can establish the ecological and spatio-temporal context within which focal biological responses should be interpreted. The context of a study can be viewed in many ways. Taking an example from the ecological stability literature, it has been shown that multi-trophic level diversity, and not just the diversity of a specific organismal group, is an important determinant of the temporal stability of aggregate ecosystem properties (Jiang & Pu, 2009), ecosystem functioning and service provision (Soliveres et al., 2016). Research integration would open up opportunities to greatly enhance understanding of the functional importance of diversity in lakes. While detailed *in situ* observation would deliver robust data on the temporal stability of a suite of aggregate ecosystem properties (e.g. total abundance and biomass) and services, molecular techniques would provide a more holistic, multi-trophic, assessment of the diversity context in which ecosystem stability is being observed (Banerji et al., 2018; Cahoon, Huffman, Krager, & Crowell, 2018). Such a synergy would allow one to discern gradients of whole system diversity, and provide opportunities for large-scale modelling of the responses of ecosystem state and stability in the face of multi-trophic biodiversity loss (Duffy et al., 2007; Ives & Carpenter, 2007). Another example of integration to provide context is that spatially-extensive methods can be used to assess land cover, land use and waterbody connectivity within the wider catchments of lake ecosystems, as well as large-scale gradients in factors that may mediate relationships between environmental pressures and ecosystem responses at a local scale. For example, Huang et al (2014) use Landsat data to demonstrate increasing catchment urbanisation during a period in which phytoplankton blooms have been increasing, inferring that land use change was impacting lake ecology.

Research integration also allows us to place findings within the context of ancient or recent history, and thus address the predictions of the growing field of temporal ecology (Ryo, Aguilar-Trigueros, Pinek, Muller, & Rillig, 2019). By combining *in situ* monitoring with palaeolimnological study, we can assess whether current ecological states and shorter-term trends depart from longer-term trajectories, and whether they represent unprecedented conditions or recovery to a notional historical baseline. Such an approach has recently been demonstrated for lake organic carbon concentrations responding to land-use change (Meyer-Jacob, Tolu, Bigler, Yang, & Bindler, 2015) and cladoceran assemblages responding to declining calcium concentrations (Redmond, Jeziorski, Paterson, Rusak, & Smol, 2016). Over shorter temporal scales, combined high-resolution sensor and traditional *in situ* monitoring allows us to resolve lagged ecosystem-scale responses to short-lived antecedent weather extremes (de Eyto et al., 2016). With respect to contextual complementarity, one would be making assumptions regarding the ability of available approaches to deliver data at appropriate spatial and temporal scales (i.e. those relevant to focal ecosystem responses), and also that these data capture the key contextual factors that moderate the ecological behaviours being investigated.

Scaling complementarity (Fig. 2e): Although research approaches each have their own time and space scales and resolutions, there is the potential for research integration to allow for the flow of knowledge among these scales. Recently, Bogard et al. (2019) challenged the prevailing viewpoint that high-latitude lakes are important sites of terrestrial carbon mobilization, an idea that has received a great deal of attention as permafrost thaws and ancient carbon is exposed. Pairing *in situ* lake metabolism and isotope measurements across a gradient of high-latitude lakes with remote sensing products that enable extrapolation to circumpolar extent, the researchers found that circumpolar permafrost systems commonly have C cycles dominated by the recycling of internally derived organic carbon. The findings of Bogard et al. (2019) have great importance for anticipating large-scale greenhouse gas contributions from melting permafrost. Similarly, Kraemer, Mehner, & Adrian (2017) combined theory and localised *in situ* observations with remotely-sensed data, to test whether global-scale relationships between surface water warming and phytoplankton biomass match with expectations based upon the metabolic theory of ecology. Crucially, in both of these cases, the integration of *in situ* and remotely sensed observations permitted large scale inferences based upon detailed, but localised, mechanistic study. In the pursuit of such inferential scaling, we must be aware that we are implicitly assuming that processes that dominate at one observational scale remain dominant at the scales at which we wish to make our inferences; an assumption that may in fact be built into ecological models that have been parameterised using data from specific experiments and locations. However, this is not necessarily the case. For example, with increases in observational scale we may see a lengthening of ecological gradients, particularly with respect to confounding factors that might mask effects that appear to be highly influential at local scales. Therefore, efforts to up-scale or down-scale ecological responses must also consider other causal factors that come into play as the extent of the domain of inference changes.

Summary: While there are many types of interdisciplinary complementarity that can arise through research method integration, to the benefit of fundamental understanding of freshwater ecosystem function, it is clear that all must be carefully designed with a conceptual model in mind. By constructing our underpinning concept of the causal mechanisms by which freshwater ecosystems respond to environmental change, and assessing the ability of available research methods to map onto these causal linkages, we can make suitably careful and informative steps towards a more integrated understanding of freshwater dynamics. Critically we argue that the biological questions should lead the refinement and integration of research approaches, rather than constraining the biological questions by the technologies at hand. We demonstrate such an approach taking the example of potentially-harmful cyanobacterial blooms (Box 2).

Box 2: Research integration and the problem of cyanobacterial blooms

There is clearly great potential for co-ordinated, interdisciplinary, leading edge research to transform our understanding of biodiversity and ecosystem response to global change. Nowhere is this more apparent than in the case of potentially-harmful cyanobacterial blooms. If we are to fully understand the drivers of these extreme ecological events, we need to investigate processes at multiple spatio-temporal and biological scales; including (but not limited to) sources and cycling of nutrients at catchment-scale, delivery of those nutrients to waterbodies over different temporal scales, impacts of regional climate and local weather on physical lake conditions, in-lake biological interactions including "microbiome dynamics", evolutionary ecology of toxin-production, and functional genomic processes. Ecosystem-level prediction of such complex biological responses will be further complicated by any process that affects the development of phenotype from genotype within or across generations, including epigenetic phenomena (Bossdorf, Richards, & Pigliucci, 2008; Latzel et al., 2013) or conditions that promote horizontal gene transfer (Aminov, 2011), necessitating largely unprecedented scales of integration.

Focusing on the issue of cyanobacterial blooms, one can construct a simplified causal diagram illustrating potential drivers of bloom events, and map onto this the available research methodologies (Fig. 3). Such an exercise allows us to explicitly consider how different approaches complement each other, and identify areas of our basic causal model where we may lack crucial evidence. Here, we envisage that satellite observation and citizen science could deliver essential data on the extent of human land use pressure in the catchments of focal lake systems (contextual complementarity). Within this spatial context, traditional *in situ* approaches can deliver knowledge of long-term trajectories in nutrient loading, water column physico-chemical conditions and species-level cyanobacterial responses. Alongside centennial-scale sediment pigment analyses, these long-term neo-limnological data provide ecological baselines against which specific present-day ecological events can be compared (contextual complementarity). Sensor technologies, in particular, would play an important role in resolving the time scales of these events e.g. pulses of nutrient delivery and reductions in lake residence time with high rainfall, short-term weather variability that affects growing conditions, and rapid (total) cyanobacterial responses. By integrating such approaches with rapidly-advancing eDNA and metabolomics techniques we would enable a more mechanistic understanding of drivers of change through, for example, epigenetic effects, rapid evolution, or more complex microbiome and food web interactions (causal complementarity). If we can meet the challenge of developing effective predictive models of bloom dynamics, and drive these with spatially-extensive reflectance-based proxies from satellites and citizen science data (translational complementarity), we may be able to make new inferences over large spatial scales (scaling

5. Conclusions: Challenges for research integration

Herein, we have argued that the integration of research approaches could allow us to greatly advance our knowledge of the impacts of global change drivers on the state and functioning of freshwaters. However, this integration must be grounded in ecological theory and we have suggested some idealised, conceptual ways in which data from different approaches may complement each other and permit us to make new, or more robust, inferences. We believe that, to realise this potential, the international freshwater research community needs to work towards answering some key questions:

- What is the most parsimonious causal model that could potentially explain any given global change impact on freshwater ecosystems?
- Which research methodologies would deliver information on the causal linkages, states and processes identified within this model?
- Do existing international research efforts allow us to link together research approaches in space and time so that we can evaluate our conceptual models, or are new targeted research campaigns necessary to fill data gaps?
- What are the key uncertainties that apply to each research approach, and how do we propagate these through our causal models to articulate a degree of confidence in our inferences?

Answering these questions will require open and effective knowledge exchange among specialists from multiple, widely disparate research domains. Inherently, an exploration of using tools at the leading edge demands an undoubtedly tremendous effort to understand the meaning and utility of the tools independently and in combination. Relevant expertise spans academic departments, professional societies, journals, and thus cultures and incentive systems, ranging across physical, natural, and computational sciences. Most individual researchers are unlikely to master the technologies, modeling, and scholarship that span from micro- to macroscales. Rather, through more intentional and systemic interaction with colleagues working across scales, researchers can become better prepared for the collaboration most likely to produce transformative discoveries in forecasting biological change.

In principle, such integration will allow investigation of ecological responses over short-to-long timescales and local-global spatial scales, increasing our chances of observing climate impacts over the same (or similar) scales to ecosystem responses. We envision an integrated approach to research in which we more commonly investigate not only population- and community-level patterns but also the evolutionary and biochemical processes that underlie ecosystem-level phenomena, enabling a scaling of ecology and environmental sciences not previously feasible.

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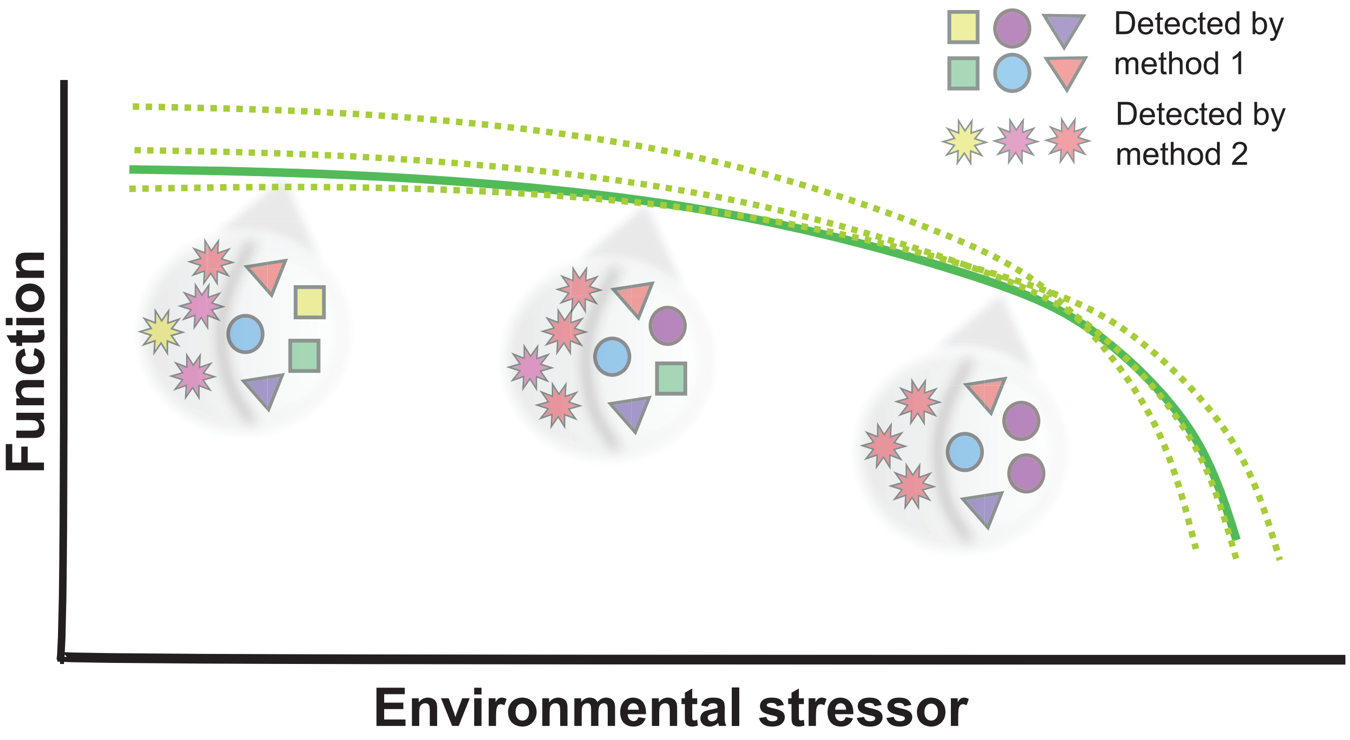
Figure legends

Figure 1. Data integration, diversity and ecosystem function. Data integration could produce useful insights on each side of the relationship between diversity and ecosystem function. Different research methodologies could yield alternative realisations (dashed green lines) of an assumed "true" ecosystem functional state (thick green line), which responds to environmental stress. At the same time alternative research methods may each yield insights into a component of total ecosystem diversity (symbols within circles represent different species) and, together, allow a more comprehensive assessment of the diversity underpinning function.

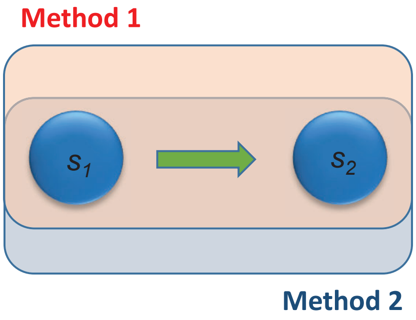
Figure 2. Schematic representation of the different ways in which research approaches can complement each other. For simplicity we use the case of a simple association between two variables; a global change driver (e.g. water temperature, s1) and an ecological response (s2). In the special case of causal complementarity we also indicate an intermediate variable (s3) that causally links s1 and s2. Rectangles indicate the domain of each research method i.e. which variables are observed by which approach. Research integration may allow us to a) observe the same phenomenon using more than one approach, increasing confidence in observed ecological change, b) use data from one approach to extend the capabilities of another, c) combine approaches to fill

empirical evidence gaps in our causal understanding, d) use one method to understand the spatio-temporal context within which observations from another method are made and e) apply empirical models from one location, based upon one method, to make predictions as other locations.

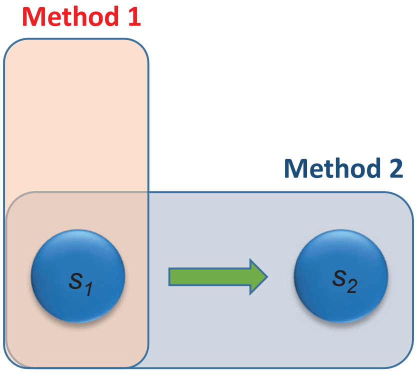
Figure 3. Example of a simplified conceptual model for phytoplankton blooms, overlaid by available research methodologies (red text).


Detected by method 1
Detected by method 2
Function
Environmental stressor

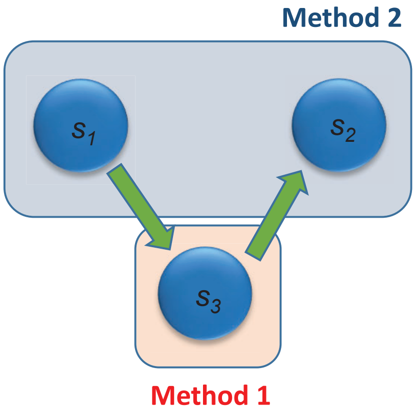
(a) Comparative complementarity



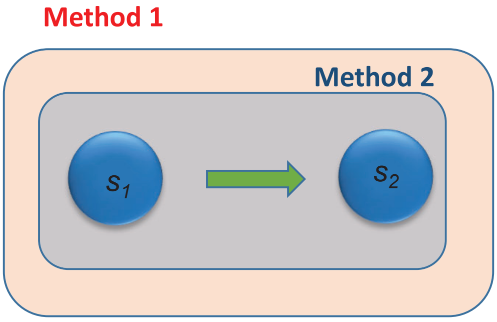
(b) Translational complementarity



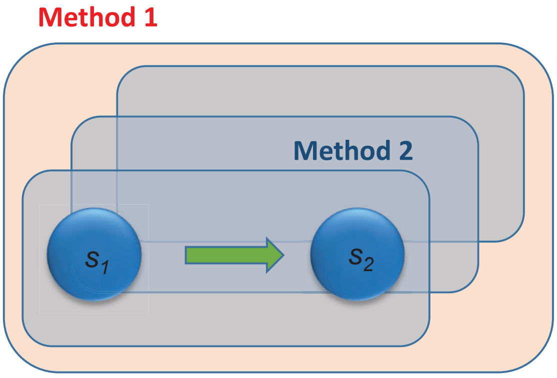
(c) Causal complementarity

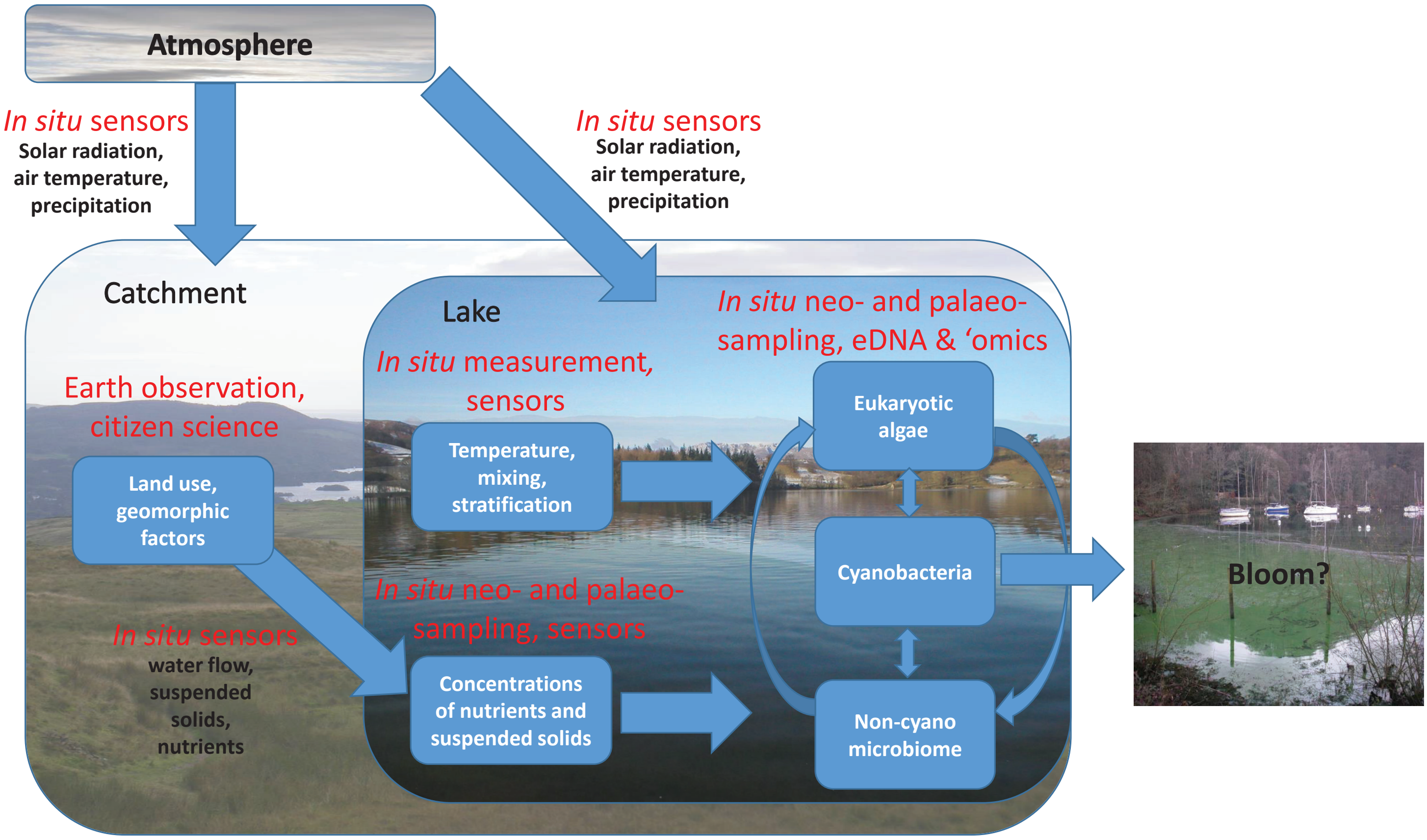


(d) Contextual complementarity



(e) Scaling complementarity




Atmosphere
In situ sensors
Solar radiation,
air temperature,
precipitation
In situ sensors
Solar radiation,
air temperature,
precipitation
Catchment
Earth observation,
citizen science
Land use,
geomorphic
factors
In situ sensors
water flow,
suspended
solids,
nutrients
Lake
In situ measurement,
sensors
Temperature,
mixing,
stratification
In situ neo- and palaeo-
sampling, sensors
Concentrations
of nutrients and
suspended solids
In situ neo- and palaeo-
sampling, eDNA & 'omics
Eukaryotic
algae
Cyanobacteria
Non-cyano
microbiome
Bloom?