

Realizing the potential of trait-based aquatic ecology: New tools and collaborative approaches

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Abstract

Trait-based ecology, which focuses on using the traits of species and individuals to understand ecology (from populations to ecosystems), is becoming an increasingly productive and widely employed paradigm. To date, trait-based approaches have been used to study taxa from microbes to megafauna in every major area of aquatic ecology yielding exciting results. However, this promising field faces a number of significant obstacles, including: (1) identifying and measuring ecologically relevant traits, (2) integrating inter- and intra-specific trait variation, (3) detecting and quantifying trait correlations and trade-offs, and (4) accounting for the context dependency of traits. These issues are often particularly acute for specific taxa or systems. This paper highlights these looming challenges, as well as ways to address them. Proposed solutions center around using new technologies to collect trait data, coordinating research efforts, and curating and sharing data. Throughout, we take an interdisciplinary approach, sharing examples spanning a wide range of aquatic taxa and systems. It is our hope that this paper will stimulate frank discussions and help the growing field of trait-based aquatic ecology maximize its potential.

The trait-based approach to ecology focuses on deriving a quantitative, mechanistic understanding of ecological processes that is built on the measurable properties (or traits) of organisms. It unites classical ideas and approaches in ecology behind the intuitive idea that characterizing the important features of a species allows us to predict its interactions with other species and its environment. Trait-based ecology is a growing area of research within the aquatic sciences, applied across a wide range of taxa (from microbes, including Archaea, Bacteria, and phytoplankton, to zooplankton and fish) and environments (including freshwater and marine ecosystems). The trait-based perspective is advancing ecology and enhancing our ability to predict ecological dynamics in a rapidly changing, human-influenced world. While the potential of trait-based ecology is clear, there are a number of critical challenges researchers must confront as this field

matures. These range from the difficulty of determining which traits to measure, to accumulating enough trait data to adequately capture trait variation within and between species. In the current paper, we provide a summary of trait-based ecology (for more detailed reviews, see for example McGill et al. 2006; Gibert et al. 2015). Next, we outline four critical challenges confronting trait-based ecology. Finally, we describe potential solutions to these challenges, emphasizing collaboration and new technologies. Future advances in aquatic ecology through trait-based approaches depend on combining these new tools with conceptual advances.

What are traits? There are many detailed and competing definitions (see Violle et al. 2007). For our purposes, we will define traits as measurable or quantifiable properties of individuals (following McGill et al. 2006). Examples of traits range from gene sequences, to the production of specific molecules (e.g., proteins, toxins), to organismal morphology, physiology, and behavior, as well as ecological properties (e.g., diet, mixotrophy). Traits have been reviewed for many

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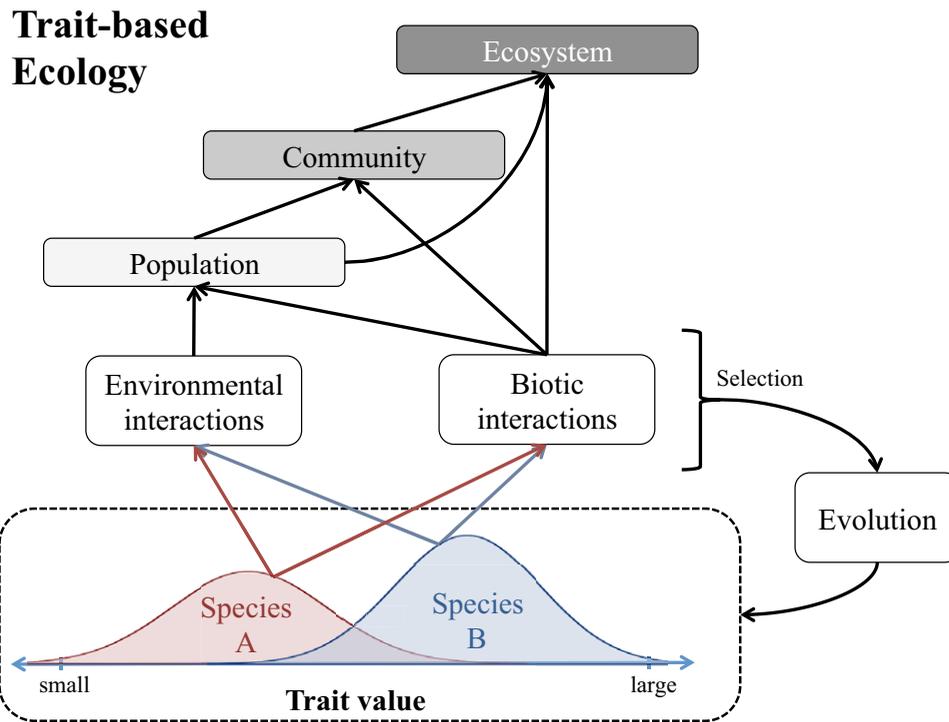


Fig. 1. A conceptual overview of trait-based ecology. Trait-based ecology is built around the idea that differences in the functional and physiological traits of species can be used to explain and understand how species interact with each other and their environment. Trait variation can occur intra-specifically (e.g., Species A includes individuals with a range of trait values), as well as inter-specifically (e.g., Species A and B have different mean trait values, although their trait distributions overlap). This trait variation structures species’ interactions, determining the patterns that arise at population, community, and ecosystem scales. Finally, trait values can change through evolutionary processes, as a species’ ecological context determines the selective environment it faces. [Color figure can be viewed at wileyonlinelibrary.com.]

aquatic taxa, including: microbes (Brown et al. 2014; Krause et al. 2014; Martiny et al. 2015), benthic invertebrates (Bremner et al. 2003), phytoplankton (Reynolds 2006; Litchman and Klausmeier 2008), zooplankton (Barnett et al. 2007; Litchman et al. 2013), fish (Erős et al. 2009; Frimpong and Angermeier 2010), and mammals (Flynn et al. 2009).

While a vast number of traits can be measured for any organism, not all are equally useful. Generally, traits determining the environmental effects or fitness of an organism, as well as variation in these properties across environments, are particularly valuable to ecologists. These “functional traits” (McGill et al. 2006) include properties such as rates, size, shape, behavior, life history, and resource utilization (e.g., Fig. 1 of Litchman and Klausmeier 2008). Species can be organized into functional groups based on functional trait similarities, rather than phylogenetic relationships (e.g., Reynolds et al. 2002; Reynolds 2006; Kruk et al. 2010). This can reveal ecological generalities: patterns of occurrence across seasons and physical lake environments may be highly idiosyncratic at the species level, yet consistent at the level of functional groups (Reynolds 2006). Trait-based theory, which benefits from the quantitative nature of traits, represents a substantial and growing body of work. This includes

many newer efforts referring explicitly to trait-based ecology (e.g., Norberg 2004; Bruggeman & Kooijman 2007; Merico et al. 2009; Webb et al. 2010; Kremer and Klausmeier 2013), as well as classic theories (e.g., Lotka-Volterra models, MacArthur and Levins 1967; CSR theory, Grime 1977; resource competition, Tilman 1982), whose parameters can be considered traits (e.g., growth rate, carrying capacity, competition coefficients, R^*). Ultimately, trait-based approaches excel when we can identify relevant traits, and when these traits are moderate in number and straightforward to measure. Trait-based approaches have been productively applied to questions spanning levels of ecological organization from populations to ecosystems, as well as evolution (Fig. 1).

Populations

Population ecology seeks to understand changes in the abundance and structure of populations. Critical traits for population ecology include birth rates, death rates, development times, survival rates, and the sensitivity of such traits to the environment. Demographic models based on these traits can predict the abundance and dynamics of populations over time (McGraw and Caswell 1996). Such

quantitative predictions can benefit efforts to manage essential resources (e.g., fisheries) and conserve threatened populations and endangered species (Crouse et al. 1987; Fujiwara and Caswell 2001).

Communities

Community ecology explores how species interactions, moderated by the environment, determine the diversity and composition of communities, including the presence and abundance of particular species. Traditionally, this field focuses on studying species' niches, seeking to understand when and where species can occur and coexist (Hutchinson 1959; Chase and Leibold 2003). Traits allow us to characterize the set of environments in which a single species can live alone, dictating its fundamental niche (Chase and Leibold 2003). These include traits such as thermal tolerance and minimum resource requirements, among others. Traits can also inform our understanding of the ecological interactions (e.g., predation, competition, facilitation) that may restrict or expand a species' niche, determining its realized niche (Chase and Leibold 2003). Such traits include dispersal rate, predator defense, disease resistance, and competitive ability. Some traits, such as maximum growth rate, influence both the fundamental and realized niches of species. Collectively, information on the traits of multiple species allow us understand ecological communities. For example, traits including affinity and competitive ability for nitrogen, phosphorus, and light predicted changes in the abundance of different phytoplankton species through time in the English Channel (Edwards et al. 2012a) and across lakes in the United States (Edwards et al. 2013b).

Ecosystems

Ecosystem ecology investigates flows of energy and matter among species and between species and their environment, processes that depend on species' traits. Some traits can directly affect ecosystem processes. For example, rates of nitrogen fixation and the conditions under which certain bacteria are able to fix nitrogen control the flow of nitrogen from the atmosphere to the biosphere. Traits also affect ecosystem processes indirectly: the diversity and composition of communities influence ecosystem function and stability (Tilman 1996; Ives et al. 1999, 2000). Trait-based studies of aquatic ecosystems often focus on microbes, given their critical role in nutrient cycling (Krause et al. 2014). Other recent studies use traits to explore how climate change will affect ecosystem function and biogeochemical cycles (Wallenstein and Hall 2012; Litchman et al. 2015).

Evolution

While our primary focus is ecological, trait-based approaches also integrate well with evolutionary questions, given a shared focus on traits determining fitness. Evolution by natural selection occurs when fitness differences among individuals arise from variation in heritable phenotypes (or traits), causing the traits of a population to change through

time. In some cases, this can happen on ecologically relevant time scales (Yoshida et al. 2003; Carroll et al. 2007; Post and Palkovacs 2009), often through co-evolutionary interactions, such as predator-prey or host-pathogen systems, or in organisms with short generation times (like microbes). Rapidly changing traits can in turn alter ecological processes, potentially creating eco-evolutionary feedbacks (Post and Palkovacs 2009; Schreiber et al. 2011). Having a framework that can readily incorporate both ecological and evolutionary processes may prove vital to efforts to understand the ecological consequences of global change (Litchman et al. 2012).

As trait-based approaches continue to develop and become more regularly applied to aquatic ecology, it is important to recognize and anticipate the challenges this body of research faces. In the following section, we outline the biggest of these challenges, as well as how we might address them, taking advantage of new technologies as well as experimental and collaborative tools.

Challenges of the trait-based framework

Ecological systems are extremely complex, often consisting of hundreds to thousands of diverse, interacting species. For paradigms such as trait-based ecology to help us advance our understanding of these complex systems, empirical and theoretical research must be tightly coupled. Currently, there is a growing disconnect within trait-based ecology between the type and amount of trait data available and the capacity of theoretical and mathematical approaches to interpret and apply this data. In particular, existing theory is limited by the availability of trait estimates (used to parameterize models) and observations (used to test theoretical predictions). Reducing gaps between theoretical and empirical work requires both increased efforts to collect the kinds of data that contemporary theories demand, and the development of new theoretical approaches that require less data, and/or more easily obtained data. While progress in both directions is necessary, in the current paper we focus on the substantial data-related challenges implied by current ideas in trait-based ecology. In the following sections, we identify and discuss four major hurdles faced by trait-based approaches: (1) Identifying and measuring ecologically relevant traits, (2) Integrating inter- and intra-specific trait variation, (3) Detecting and quantifying trait correlations and trade-offs, and (4) Accounting for the context dependency of traits. The severity of these challenges varies among systems and taxa, but none are fundamentally insurmountable.

Identifying and measuring ecologically relevant traits

When applying a trait-based approach to an ecological system, the first challenge is often identifying which traits are relevant. This task can be guided by the system's natural history and the physiology of species of interest. Traits that can be linked to fitness or performance are often the most

valuable (McGill et al. 2006). For trait differences to be useful, there must also be sufficient trait variation at a scale appropriate to the study (e.g., between individuals, populations, or species). Ultimately, experiments may be required to demonstrate when and if trait differences between otherwise similar or closely related species (or populations, or individuals) can explain differences in their fitness or coexistence (Narwani et al. 2013) or the productivity of communities (Stockenreiter et al. 2013).

Even if we can identify the most predictive organismal traits, they may be difficult to measure. Trait assays can require finicky or expensive measurements, laboratory experiments, and substantial amounts of time. Traits that are easy to measure in some organisms can be difficult to obtain in others: for example, it is much easier to measure the exponential growth rate of a phytoplankton culture than it is to obtain a similar estimate for organisms with long or complex life cycles, such as whales, parasites, jellyfish, or anadromous fish. Traits that can only be measured in laboratory settings become impossible to determine for species that cannot be brought into the lab, whether for microbes that evade culture (Rappé and Giovannoni 2003) or large or endangered animals. There can also be a significant disconnect between the traits that are easy to measure, and the traits that are informative. For example, it is cheaper and easier than ever to obtain large amounts of genetic data. In some cases, this data can reveal important differences in individual or community physiological potential (e.g., toxin production, Savichtcheva et al. 2011; size and function of gas-vesicles, Becker et al. 2005; see also the review of Raes et al. 2011). However, in many cases links between genotypes and phenotypes (or traits) are complex and difficult to establish (Zhang et al. 2014; Martiny et al. 2015; Rocca et al. 2015) and most remain unclear. Looking forward, we need to either improve methods for measuring relevant traits, or develop ways to relate more easily measured traits to other derived traits that ultimately determine an organism's fitness and performance. This will require an expanded understanding of mechanisms, and advances in theory. Compromises between collecting large amounts of slightly useful data, and small amounts of highly useful data, will also be important.

Inter- and intra-specific trait variation

Addressing questions at the community level (or above) requires measuring the traits of many different species to quantify inter-specific trait variation. However, collecting comprehensive and accurate trait data across a whole community (or even its dominant species) is challenging. Currently, trait data for most aquatic species is sparse or non-existent. In some cases, the measurement and analysis of organismal traits has a long history, leading to a rich primary literature consisting of hundreds of individual studies (e.g., Eppley and Sloan 1966; Smayda 1969; Eppley 1972; Verity and Smayda 1989; among many others). This body of work has made it

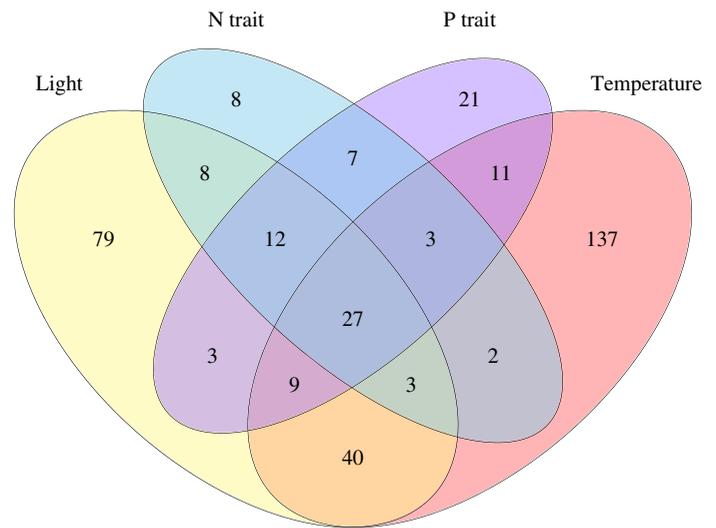


Fig. 2. This figure illustrates the overlapping coverage of recent efforts to assemble phytoplankton trait data from the primary literature (Schwaderer et al. 2011; Edwards et al. 2012b; Thomas et al. 2012, 2016; Kremer et al. 2014). Out of the ~370 marine and freshwater species included, very few (27 or ~7%) can be completely characterized by their responses to light, nitrogen, phosphorus, and temperature at this time. [Color figure can be viewed at wileyonlinelibrary.com.]

possible to compile trait databases providing valuable insights into patterns of inter-specific variation (for example, in phytoplankton: Schwaderer et al. 2011; Edwards et al. 2012b; Thomas et al. 2012, 2016; Kremer et al. 2014; in zooplankton: Hirst and Kiorboe 2002; in fish: Frimpong and Angermeier 2009). However, these hard-won data sets have important limitations. They typically contain only a few dozen species, lack information on more than a few traits per species, and suffer from the use of inconsistent methods between studies. For example, recent efforts to assemble comprehensive trait data sets for phytoplankton encompass ~370 species (Schwaderer et al. 2011; Edwards et al. 2012b; Thomas et al. 2012; Kremer et al. 2014; Thomas et al. 2016). Of these, only ~7% (27 species) appear in databases of light, nitrogen, phosphorus, and temperature responses; most species are represented in only one or two databases (Fig. 2). In contrast, there are roughly 3–4000 species of marine phytoplankton (Sournia et al. 1991; de Vargas et al. 2015), and perhaps as many as 25,000 (morphologically defined) phytoplankton total (Falkowski et al. 2004). Additionally, studies that simultaneously manipulate multiple factors (e.g., nutrients and temperature) are especially scarce, yet essential for detecting interactions among traits. Further advances in trait-based ecology, especially at the community level, require expanding these resources to encompass additional species, particularly dominant or keystone species, and additional traits.

Intra-specific trait variation can also be critical to the study of populations and communities (Bolnick et al. 2003,

2011; Careau and Garland 2012; Violle et al. 2012). For example, intra-specific variation in freshwater macroinvertebrate body size was found to have greater effects on community structure and ecosystem function than variation between species (Woodward and Hildrew 2002; Rudolf and Rasmussen 2013). Collecting data at the individual level is challenging, especially for small organisms such as bacteria or plankton that are difficult to examine individually. When individuals are pooled and measured collectively, the resulting population-level trait estimates obscure variation among individuals. Intra-specific variation may persist even among individuals receiving identical treatments in controlled settings (e.g., among copepods exposed to paralytic shellfish toxins; Finiguerra et al. 2015). Significant variation can also occur across populations of the same species through local adaptation, which we discuss later. The existence of inter- and intra-specific variability makes it risky to base conclusions on the traits of only a few individuals or species. To avoid mistakes, it is critical to determine the levels where relevant amounts of trait variation occur, and then collect the necessary data. Trait variation can have additional structure as well, including relationships between traits, or between traits and the ecological or environmental context in which they are expressed. Understanding the forces structuring trait variation creates additional challenges and opportunities, discussed in the next two sections.

Uncovering trait correlations and trade-offs

In many cases, trait values within or across species are related. Some correlations are obvious (e.g., surface area to volume relationships generally scale with size), while others can be difficult to uncover and characterize. Trade-offs are an important subset of trait relationships, encompassing situations where the ability to perform one beneficial function comes at the cost of a reduced capacity for performing other functions. Trade-offs imply that no single individual or species can exhibit every advantageous trait or perform maximally in every context. These relationships are central to trait-based ecological theory and affect both ecology and evolution (McGill et al. 2006; Litchman and Klausmeier 2008). Trait correlations may reveal the limits of plasticity, and either impede or enhance trait evolution (Conner 2012). Across species, trade-offs are essential to coexistence theories, which explain why species with different traits can persist, forming diverse communities (Tilman 1990; Kneitel and Chase 2004; Edwards et al. 2013a; but see Hubbell 2001).

Trait correlations and trade-offs vary in their origin. They can arise from underlying genetic correlations (linkage or pleiotropy), potentially reflecting selection over many generations (evolution). Physical constraints also drive correlations; for example, well-documented relationships exist between growth rate, body size, and temperature in phytoplankton (Bissinger et al. 2008), zooplankton (Huntley and Lopez 1992), and fish (Savage et al. 2004). Finally, trade-offs often emerge when

organisms are forced to allocate their resources or energy to different functions (Tilman 1990). For example, phytoplankton have finite resources to allocate to mutually exclusive cellular processes which maintain: structural components (cell walls, membranes), photosynthetic apparatus (chloroplasts, pigments), or biosynthesis (production of carbohydrates, lipids, proteins) (Schuter 1979; Clark et al. 2013). As structural components do not scale uniformly with cell size, allocation choices generate trade-offs between size, growth rate, and nutrient and light affinity (Clark et al. 2013). Other examples include trade-offs between predator defense and growth, or generalist and specialist foraging strategies.

Establishing trait relationships requires data on multiple traits across individuals or species. While trade-offs between two traits are the easiest to conceptualize and detect, organisms may actually be subject to multi-dimensional trade-offs that are not detected in bivariate analyses (van Noordwijk and de Jong 1986). For example, Edwards et al. (2011) discovered a three-way tradeoff between cell size and nitrogen and phosphorus competitive abilities. This study, synthesizing data from many sources, had to overcome the effects of patchy data: many species were missing one or more traits. Incomplete datasets are a common impediment to searches for trade-offs. Statistical techniques such as multiple imputation can be helpful in such cases (Edwards et al. 2011), but are not panaceas. Making matters worse, theoretical work reveals that subtle differences in the shape or strength of trade-offs can have large ecological consequences, for example, influencing host-parasite or predator-prey interactions (e.g., Jessup and Bohannan 2008), and the traits and diversity of coexisting species (e.g., Kremer and Klausmeier 2013). Quantifying these subtleties requires high quality data on several traits, for multiple individuals or species.

On a positive note, when strong trait relationships are detected, they can alleviate data shortages. Essentially, if one trait of an individual or species is measured, the value of other, unmeasured trait(s) can be inferred. For example, the typical cell size of a phytoplankton species (easily measured) can be used to estimate its growth rate and nutrient traits (harder to measure) (Bruggeman 2011). Relying on allometric relationships, this approach can be integrated with phylogenetic techniques (which take advantage of the possibility that closely related species may have similar trait values) (Bruggeman et al. 2009; Bruggeman 2011; Schrodte et al. 2015). Phylogenetic relationships can predict, for example, the sensitivity of different diatom taxa to herbicides (Larras et al. 2014). This rapidly growing set of techniques offers significant hope for expanding the body of trait data supporting trait-based studies.

Accounting for the context dependency of traits

Trait variation is often structured in space and time, emerging from community assembly and the plastic and evolutionary responses of individuals and populations to

their ecological and environmental contexts. The resulting context dependence of traits (also described as trait-environment relationships) can help us better understand ecology. For example, particularly strong associations help identify which traits are important to measure, and stimulate research into the mechanisms essential for living in particular environments. However, context dependency also creates problems: it implies that the traits a species expresses in one context may tell us little about its traits in another location or community. In the following paragraphs, we discuss the value of distinguishing between mechanisms that generate context dependencies. We also review how context dependent issues make it essential to collect and associate trait and environmental data across a realistic range of conditions, carefully design and interpret lab-based trait assays, and account for the influence of species interactions on trait expression.

Context dependencies arise from mechanisms ranging from phenotypic plasticity to local adaptation. Phenotypic plasticity allows genetically identical individuals to express different traits if exposed to or reared under different environmental conditions (e.g., *Daphnia* sp. develop spines when exposed to predators; Tollrian and Harvell 1999). Plasticity can arise from physiological, behavioral, or developmental processes (Miner et al. 2005; Dingemans and Wolf 2013). When linked to development, plasticity in some traits may only be detected in certain life stages of organisms. Plastic responses mean that instead of measuring one trait value per organism or species, it may be necessary to quantify reaction norms, functions relating trait values to environmental conditions, such as temperature, nutrient availability, salinity, or acidity. Quantifying the form, rate, and limits of phenotypic plasticity is critical to understanding how organisms respond to heterogeneous environments.

Evolutionary processes also drive context dependency in traits: selection promotes local adaptation to biotic and abiotic conditions, while genetic drift and gene flow alter patterns of variation. Local adaptation among populations can generate environmentally structured intra-specific variation. As genetically distinct ecotypes emerge, the niche, function, and ecological role of a species differs across locations. For example, copy numbers of phosphorus acquisition genes are enriched in bacterial populations of *Prochlorococcus* and *Pelagibacter* (SAR11) in the Atlantic Ocean, which has exceptionally low phosphate concentrations relative to the Pacific Ocean (Coleman and Chisholm 2010). Populations of the copepod *Acartia hudsonica* along the northeastern US are better adapted to toxic algae than southern populations (Colin and Dam 2004). Patterns of local adaptation can also be detected across species, in the form of trait-environment relationships. As an example, the thermal traits of phytoplankton species are related to broad environmental gradients in temperature in both marine and freshwater ecosystems (Thomas et al. 2012, 2016). When we can detect local adaptation across environmental contexts, we can begin to understand

how species adapt, including the evolutionary constraints they face, and how they may respond to global change.

Quantifying trait variation across contexts requires sampling quite broadly, paying attention to the source and diversity of measured individuals and populations. The challenges of this task often constrain what data are available. For example, trait data from marine phytoplankton are strongly biased toward near-shore, northern hemisphere locations, often due to logistic constraints and resource availability. Random sampling across a species' range could provide better information on the typical distribution of traits it expresses, while stratified sampling across environments will inform the extremes of the range of traits it exhibits. While gathering trait data across locations helps characterize trait variation, it is difficult to detect mechanisms behind context dependency unless we also collect associated environmental data. For example, Thomas et al. (2012) were able to understand the relationship between phytoplankton thermal traits and ocean temperatures using geo-referenced thermal trait data. A lot of additional thermal trait data relevant to this study exists in the literature, but was discarded because isolation locations were not reported. It can be logistically and economically challenging for individual scientists or research groups to collect trait and environmental data from many locations, making it hard to gather the information required to understand the context dependency of traits.

Trait measurements are regularly made in controlled laboratory settings and on single species. This process removes species from both their abiotic and biotic contexts, which can lead to trait estimates that are biased or irrelevant. When traits are plastic, lab measurements will not reflect in situ values, unless experimental conditions closely mimic the real environment or a wide range of conditions is explored. Working with single species in isolation also prevents key species interactions, removing competitors, mutualists and predators. This can have large effects on the traits species express. For example, the removal of a vitamin B₁₂-producing bacteria decreases the thermal tolerance of the phytoplankton *Chlamydomonas reinhardtii* (Xie et al. 2013). Plasticity can lead to similar biases: the presence of grazers increases the toxicity of the phytoplankton *Alexandrium* spp. (Senft-Batoh et al. 2015), and host-associated bacteria affect toxin production in the phytoplankton *Pseudo-nitzschia* (Sison-Mangus et al. 2014). The absence of grazers and bacteria, commonly excluded in laboratory assays, might lead to underestimates of these species' toxicity. This points toward larger issues regarding the pros and cons of traits measured in laboratory conditions (where significant control is possible) vs. in situ estimates (realistic, but uncontrolled). "Bottle effects" are commonly observed in microbial systems: natural communities perform differently or exhibit different activity in vitro than the same microbes under field conditions (e.g., Calvo-Díaz et al. 2011). These issues are important for larger organisms held in captivity, as well: while

certain behavioral traits measured in captivity correspond well with those observed in the field (e.g., Herborn et al. 2010), this is not always the case. Lab conditions may also elicit evolutionary changes in smaller organisms, which may be held in culture for decades before trait measurements are eventually made. For example, copepod size decreases in culture while the chance of genetic drift increases (Breteler and Gonzalez 1982). The ability to produce certain compounds can also be affected by culture conditions. Helliwell et al. (2015) observed that a *Chlamydomonas reinhardtii* strain able to produce vitamin B₁₂ was rapidly displaced by an evolved, vitamin B₁₂-dependent clone when grown in the presence of vitamin B₁₂. In *Escherichia coli*, cultures maintained over > 40,000 generations and > 20 yr in a seemingly simple lab environment have shown extensive levels of genomic adaptation and diversification (Lenski et al. 1991; Barrick et al. 2009). While some traits may be more susceptible to selection under culture conditions than others, care must clearly be taken in asserting that the traits of cultured microbes (especially those long in culture) reflect the traits of microbes in the field.

As with the earlier challenges, context dependencies represent both conceptual and empirical obstacles to trait-based aquatic ecology, as well as important opportunities. In particular, we have highlighted how these challenges create an intensive demand for data that: measures relevant traits, quantifies variation at the inter- and intra-specific level, and characterizes the correlations and context dependencies of traits. Meeting these demands requires accounting for the biology, adaptability, and ecology of organisms. Trait-based ecology must confront these challenges to realize its potential and advance our understanding of ecology. In the next section, we explore a variety of technological and collaborative solutions that offer ways to address these challenges and turn them into opportunities.

Potential solutions and future directions

The solutions we propose are twofold: (1) We can selectively develop and apply new tools to gather increasingly large amounts of relevant trait data, more quickly, cheaply, and easily. (2) We can make better use of the data that we already have, as well as new data that we collect, by coordinating our research efforts and sharing data as a common resource. Below, we provide specific examples of exciting new tools and their applications to aquatic ecology, we describe the general features that distinguish these and other useful tools, and we outline collaborative, data sharing efforts and associated platforms.

Developing and applying new tools to collect more and better trait data

As we have discussed, many of the existing challenges in trait-based ecology can be addressed by generating larger datasets that capture more traits, trait variation, and relationships between traits. Recent technological advances have greatly improved the capacity for rapid data collection and

analysis, resulting in several tools that can be applied to trait-based research (e.g., Dell et al. 2014; Krause et al. 2014). To provide concrete examples, without being exhaustive (given the wide range of organisms and systems encompassed by aquatic ecology), we feature three vignettes. Each demonstrates how trait-based ecology, with the help of technology, can address fundamental ecological questions relevant to a variety of aquatic organisms. Featured problems include estimating phytoplankton niches (Box 1), linking microbial communities with ecosystem function (including Bacteria and Archaea) (Box 2), and evaluating the existence and strength of consumer/resource interactions within megafaunal food webs (Box 3). While these boxes describe many contemporary tools and their application, methods are continually changing and advancing. Therefore, rather than just recommending specific techniques, which may quickly become obsolete, we next consider the essential features driving the development of these technologies, to help readers identify valuable new tools that arise in the future.

The tools described in Boxes 1–3 largely fall within three broad categories involving: high-throughput data collection, image analysis, and field functionality. In general, high-throughput techniques are revolutionizing science; applied to trait-based ecology, high-throughput tools may make it possible to obtain comprehensive data sets on trait variation. With rapid data collection becoming financially and physically feasible, fine-scale variability in traits, including inter- and intra-specific variation, can potentially be resolved (Zimmerman et al. 2015). Technologically, it has been possible to collect large numbers of digital images for quite a while. Increases in the availability and quality of image analysis tools have made it easier to extract useful trait data from these images (Dell et al. 2014). The expanding capabilities of imaging hardware and its successful deployment in situ have also made it possible to capture previously unknown behavioral traits (Dell et al. 2014). These techniques are powerful, but limited to organisms that can be imaged and traits that can be quantified from images, either directly (e.g., size, shape, color), or through the use of probes that produce visual signals (e.g., fluorescent tags). Finally, tools that can be easily deployed into the field, especially if they can operate autonomously and/or are affordable enough to be deployed in large numbers, offer unparalleled opportunities to unravel the context dependency of traits. Tools in these three categories are clearly powerful, but not without limitations. By integrating multiple approaches within individual studies, these potential limitations can often be addressed, as illustrated by the following examples, which target very different taxa and ecological questions.

First, combining complementary imaging and high-throughput tools can overcome the challenge of quantifying intra- and inter-specific variability. For example, Zimmerman et al. (2015) quantified metabolic traits (carbon and nitrogen fixation rates) of individual microorganisms at very low

natural abundance using nanometer-scale secondary ion mass spectrometry (Nano-SIMS). This imaging tool holds great promise for future trait-based microbial ecology by resolving and measuring the biological uptake of isotopically labeled compounds in individual cells. However, within a 24 h period, only 5–10 images capturing ~100 cells each can be processed with Nano-SIMS alone, increasing the chance that any rare (but functionally significant) microorganism would be missed. In this study, the authors first labeled cells of their target species using a fluorescent probe, a process termed catalyzed-reporter deposition fluorescence in situ hybridization, (CARD-FISH), then separated and concentrated target (fluorescent) cells using high-throughput flow-assisted cell sorting (FACS). Isolated cells were subsequently imaged using Nano-SIMS, allowing the detection of correlations between metabolic traits, as well as phenotypic heterogeneity among individual cells within this population (Zimmerman et al. 2015).

Second, carefully designed studies can disentangle the direct and indirect effects of environmental factors on species' traits, as well as how these traits in turn can have multiple ecological effects. For example, Majdi et al. (2014) examined both direct and indirect effects of predators, in order to evaluate how the alteration of prey traits in response to predation risk can affect trophic interactions. Predators were found to directly control food webs by classic lethal consumption pathways and also by non-consumptive, trait-mediated indirect effects. These effects included both the improvement and deterioration of invertebrate habitat through either increased sedimentation along mucus-covered foraging tracks or by stimulating bacterial degradation, respectively (Majdi et al. 2014). By evaluating both trophic and non-trophic pathways simultaneously, the authors were able to better constrain the context dependency and trade-offs among prey traits in this aquatic ecosystem. Looking forward, studies like these that employ integrated approaches and high-throughput, field-ready tools will be vital to the success of trait-based approaches.

Maximizing the value of trait data

Current and developing technologies may place more extensive, high-resolution data within our reach. However, our ability to apply this data toward understanding ecology through the lens of traits depends on how we handle new data collectively. The way that science is funded and conducted often promotes fragmented research efforts addressing specific questions. This results in mismatches in how data are collected, what data and metadata are retained, and how they are shared. Recently, high profile journals and funding sources, including the National Science Foundation, have started to "strongly encourage" or require contributors to make their data publicly available. Data sharing is valuable, and stimulates additional research including synthetic studies and meta-analyses. For example, the ~2700 datasets deposited in PubMed in 2007 were used in 1150 new studies

within 3 yr (Piwowar et al. 2011). Although this mainly reflects the quantity of papers produced and not the quality of new understanding gained, it illustrates the value of data collected by single individuals and labs to the broader scientific community. We propose three main avenues for maximizing the value of trait data: (1) coordination of trait measurements across researchers and fields, (2) data sharing, and (3) interdisciplinary and collaborative work.

First, coordinating trait measurements can increase the efficiency and usefulness of our data, ultimately extending the impact of grant dollars used to obtain trait data. As a field, we can develop standard sampling schemes and methods, and by identifying which metadata to collect, yield data that can be incorporated into larger studies and support modeling efforts. Standards for ecological metadata are becoming both more formal and more commonly implemented (Michener 2006), and there are excellent examples of fields coming together to discuss and agree on standard protocols for research (e.g., Riebesell et al. 2010). In recent work, a multi-lab collaboration generated high quality data on the thermal tolerance curves of diverse phytoplankton strains, obtained through shared protocols, supporting a comparative analysis of traits and intra-specific variation (Boyd et al. 2013). With the proper metadata and a little additional effort, traits that were explicitly measured for one species or group could be used for other purposes, such as meta-analyses. For example, individual sequences of the functional gene of ammonia-oxidizing Archaea were compiled from a public database, classified according to sample metadata, and analyzed together to show that distinct clades of Archaea partitioned available habitats (Biller et al. 2012). Additionally, issues of comparability across datasets could be reduced if methods and the collection of metadata were standardized. There are important differences between systems, disciplines, and organisms that should inform best practices and which metadata are collected; these standards should be developed through clear discussion and communication.

Second, as we accumulate more trait data, aided by new technology, we can become more efficient and productive as a community through data sharing. Compilations of trait data can be powerful: in phytoplankton, aggregations of nutrient, light, size, growth rate, and temperature traits have advanced our understanding of physiological trade-offs, patterns of local adaptation, and differences between functional groups (Edwards et al. 2011, 2012b, 2015; Schwaderer et al. 2011; Thomas et al. 2012, 2016). Currently, there are two major ways to share data (benefiting the community) that provide mechanisms for citing contributors (recognizing individuals). Data sets can be published individually along with the papers they support and directly as data papers (e.g., Whitlock 2010; Chavan and Penev 2011; Reichman et al. 2011). As a recent example, Kremer et al. (2014) assembled and published >100,000 phytoplankton biovolumes as

Box 1. Determining the niches and distributions of phytoplankton species

The problem. The niche concept is a foundational idea in ecology, concerned with determining the range of biotic and abiotic factors that govern when and where a species can grow (Chase and Leibold 2003; Mesz ena et al. 2006). Niche ideas have been used to understand and predict the abundance of species through seasons and across environments (Edwards 2012a, 2013b), and to study how climate change may drive range shifts (e.g., Thomas et al. 2012). However, in practice it can be difficult to quantify species niches. Common approaches are based on correlations that associate presence/absence data to environmental variables (Pearson and Dawson 2003). Trait-based approaches provide a powerful alternative, mechanistically defining species' niches. While both approaches can, in principle, incorporate the effects of biotic interactions on species' realized niches, trait-based approaches lend themselves easily to capturing the effects of competition, predation, and other interactions. What tools can we use to advance our understanding of phytoplankton niches using traits, in the face of the obstacles of trait-based approaches?

Identifying relevant traits. Which traits determine a species' niche? For phytoplankton, some choices are obvious: maximum uptake rates, half-saturation constants, and storage capacities determine their ability to compete for essential resources including light, nitrogen, and phosphorus. These traits can be determined in the lab and collated in trait databases (Edwards et al. 2012b, 2015). Other important traits are more difficult to identify and measure, including micronutrient requirements or interactions with bacteria, viruses, and predators. Remote sensing techniques can provide in situ estimates of key traits, such as size distributions, as well as estimating the distributions of phytoplankton functional types (Nair et al. 2008; Brewin et al. 2011). These methods rely on differences in the absorption and scattering of light, and invoke several different algorithmic approaches (Nair et al. 2008; Brewin et al. 2011). Methods such as metatranscriptomics can reveal fine-scale nutrient partitioning in the field. For example, temporal variation in the metatranscriptomes of two dominant diatoms in Narragansett Bay, RI revealed differential expression of nitrogen and phosphorous metabolic processes, suggesting fine-scale resource partitioning between competitors (Alexander et al. 2015).

Intra- and inter-specific variation. Quantifying trait variation in phytoplankton is chiefly limited by our ability to count and measure properties of individual cells. Information about clonal (intra-specific) trait variation is especially scarce. Technological advances in flow cytometry offer exciting new ways to collect high-throughput data on individual cells and strains including but not limited to, size, photopigment content, and activity (Czechowska et al. 2008; Lomas et al. 2011; Malkasian et al. 2011), without having to isolate and culture them individually, a time-consuming and difficult endeavor. For example, scanning flow cytometry devices capable of measuring community samples in the field are in development (e.g., CytoBuoy, Pomati et al. 2011, 2013; Imaging FlowCytobot, Campbell et al. 2013). Current limitations include automating species identification and working with community samples containing individuals of a wide range of sizes and shapes.

Trait correlations. Some progress has been made in detecting relationships between phytoplankton traits across groups (e.g., Edwards et al. 2011, 2012b). Some easily measured traits (e.g., cell size) can serve as proxies for estimating other correlated traits that are harder to measure (e.g., growth rate) (Bruggeman 2011). These efforts could be substantially improved if: multiple traits are collected for the same species, consistent methodologies are used across labs, and researchers coordinate efforts to fill in gaps in existing data (Boyd et al. 2013). Tools that allow multiple traits to be estimated for individuals or populations, including the flow cytometry approaches described above, will be valuable in this endeavor.

Context dependency. Assessments of the context dependency of phytoplankton traits hinge on obtaining and improving in situ trait estimates and gathering isolates of more phytoplankton species and strains across populations and environmental gradients. Tools such as the transcriptomics can be deployed in the field (e.g., Alexander et al. 2015), avoiding the difficulties associated with isolating and studying species in the lab. Other in situ estimates of traits (including cell size distribution, chlorophyll content, pigmentation) can be obtained through increasingly sophisticated remote sensing/satellite observations (Nair et al. 2008; Brewin et al. 2011). Remote sensing offers broad spatial coverage, but has limited taxonomic resolution, although recent developments are allowing rough partitioning of functional groups. Finally, for isolate- or laboratory-based trait measurements, recording the source location of isolates and their corresponding environmental conditions is essential.

a data paper through Ecological Archives (Ecological Society of America, <http://www.esapubs.org/archive/default.htm>, accessed 6/06/2016). These practices are increasingly common and sometimes even required by publishers, and benefit the community by making it easier to replicate individual studies and perform meta-analyses. However, it can be

difficult and time consuming to identify and combine relevant data across dozens or hundreds of disparate studies. As an alternative, data can be contributed to repositories or trait databases. Databases attempt to compile data from many different sources, standardizing metadata and providing a central, searchable resource. Within terrestrial plant ecology,

Box 2. Linking microbial traits to ecosystem function

The problem. To better understand how communities of microbes drive biogeochemical cycles and regulate ecosystem processes it is essential to investigate how microbes function, including which compounds they assimilate, transform, and excrete. Microbial communities are highly responsive to environmental variability, as the abundance, activity, and function of species can change rapidly. This dynamism hampers efforts to understand relationships between microbes and ecosystems. Yet this knowledge is pivotal to forecasting the behavior of future ecosystems, as microbial communities respond to increased temperature, decreased pH, and other effects of climate change (Williamson et al. 2008). While trait-based approaches can shed light on compositional and functional shifts of microbial communities (Martiny et al. 2015), they also face the challenges we have identified previously. How can we apply trait-based approaches, aided by available and emergent technologies, to investigate relationships between the structure and function of microbial communities?

Identifying/measuring relevant traits. Microbial traits range from simple traits, involving few genes with a direct connection between genotype and phenotype (e.g., organic phosphate uptake), to complex traits that involve many portions of the genome (e.g., salinity preference) (Martiny et al. 2015). Some microbial traits directly contribute to biogeochemical cycling (e.g., rates of nitrification, methanogenesis, and respiration) while other traits act indirectly, altering the relative fitness of populations or strains. Genetic information, including which genes are in an organism's genome and under what conditions specific genes are transcribed, offers significant insights into the traits of uncultured environmental microorganisms. What is sorely needed are ways to connect this genetic information to other traits, such as through matching genetic data with physiological measurements (nucleic acid content; Vila-Costa et al. 2012) or by observing how gene expression responds to changing conditions. Traits related to enzyme kinetics and physiological properties can be used to predict microbial community structure and activity, as Bouskill et al. (2012) have demonstrated using nitrifier diversity, ammonia oxidation rates, and nitrous oxide production.

Intra/inter-specific variation. The first obstacle in distinguishing intra- and inter-specific variation in microbes is assigning organisms to species. For our purposes, intraspecific variation includes traits differentiating organisms that are phylogenetically assigned to the same species-like group (i.e., microdiversity or strain-level variation, Jaspers and Overmann 2004). Community function emerges from the trait diversity within a community, as resident species contributing to specific functions over time. High-throughput sequencing of microbial community DNA and RNA (i.e., metagenomics and metatranscriptomics), combined with advanced computational algorithms that assemble genomes from fragments of genetic material (e.g., PhyloCNV, Nayfach and Pollard 2015; ConStrains, Luo et al. 2015), can provide unprecedented insight into genomic differences between species and even strains. Using high-powered microscopy and spectroscopy, it is now possible to determine the identity of individual cells that have taken up a specific substrate in a mixed community (e.g., through MAR-FISH using microautoradiography; or SIP-RAMAN-FISH combining stable isotope probing and Raman spectroscopy). This can even provide estimates of the growth rates of individual cells, simultaneously characterizing intra- and inter-specific variability (G.T. Taylor, E.S. Suter, Z.Q. Li, S. Chow, D. Stinton, and S.R. Beauré, unpubl.).

Context dependency. The environmental context of microbial samples is especially important given the rapidity of many microbial responses (minutes to hours). Patterns of gene expression change over daily cycles; for example, the timing of nitrogen fixation activity differs across groups of diazotrophs (Church et al. 2005). On longer time scales, patterns such as seasonal microbial "blooms" further complicate efforts to draw conclusions from few observations; e.g., nitrification rates in Thaumarchaeota are 10- to 100-fold higher in summer than during non-bloom periods (Hollibaugh et al. 2014). To sample at frequencies appropriate to particular questions, investigators can use in situ autonomous collection and preservation methods to capture the DNA and RNA of microbial communities (Ottesen et al. 2014; Robidart et al. 2014). Although it is difficult (or impossible) to consistently correlate rates to gene or transcript abundance (Santoro et al. 2010; Tolar et al. 2016), there is a chance that trait-based analyses may give insight into which populations within a community are contributing the most to the observed rates, enhancing links between genetic data and function.

coordinated efforts have produced extensive trait databases (e.g., the TRY database, Kattge et al. 2011), but similar attempts have lagged in aquatic ecology. Some good examples do exist, generally targeting specific ecosystems, regions, or taxa (Table 1).

However, even the best aquatic trait databases right now are sparsely populated, seldom updated, difficult to find, and may lack necessary metadata (see Barton et al. 2013). Efforts

to assemble trait databases face several challenges. First, if databases are not visible enough, they can be difficult to find, sometimes leading to duplicated efforts. Such issues can be prevented by using centralized data initiatives (e.g., DataONE, <https://www.dataone.org/> accessed 6/06/16); this makes databases easier to access, and the data contributed by individual scientists easier to find (Michener and Jones 2012). Second, long-term investments are required to

Box 3. Trait-based approaches to studying aquatic food webs

The problem. Consumer-resource interactions are a key force structuring aquatic communities (Zaret 1980; Heithaus et al. 2008). Food webs are networks of consumer-resource interactions, which depict species as nodes linked by pathways of energy flow. Due to their high complexity, food webs are frequently simplified by lumping species together (typically based on size or trophic level). When distinct species are resolved, they are usually characterized by traits, such as diet, representing averages across individuals. These simplifications, which require suppressing intra- and/or inter-specific variation, can be problematic. Grouping species based on body size may ignore critical inter-specific variation in key traits such as foraging strategy (Schmitz 2008) or habitat preference (Rudolf et al. 2014). Intra-specific variation in body size can also enhance predictions of the topology and dynamics of food webs (Brose et al. 2006; Otto et al. 2007; Petchey et al. 2008). How can we use trait-based approaches and technologies to improve food web studies?

Identifying relevant traits. Body size is by far the most important trait governing consumer-resource interactions, because many traits, such as attack rate and handling time, scale predictably with consumer-resource body size ratios. These allometric constraints allow a more mechanistic understanding of food webs than species identities alone provide (Brose 2010; Kalinkat et al. 2013; Toscano and Griffen 2013). However, because body size represents only one axis of trait variation, size-based food webs discount the important effects of other functional traits including behavior, habitat preferences, vulnerability to predation, morphology and nutritional requirements. Identifying which of these traits have the greatest consequences is an open question (Rohr et al. 2010; Klecka and Boukal 2013; Boukal 2014). However, these traits are harder to measure than body size and often more sensitive to variation in measurement techniques and contexts.

Intra- and inter-specific variation. Several approaches offer new opportunities to collect both body size and other trait data within and among species. Stable isotope techniques are an established, but under-utilized, method for quantifying the existence and importance of intraspecific trait variation in food webs (e.g., Layman et al. 2012). They provide a long-term integration of food resource use and are thus advantageous over stomach content analyses that yield only a snapshot of an organism’s feeding history. Isotopic signatures can be used to examine differences in resource use among conspecific consumers that vary in their functional traits, such as distinguishing between sticklebacks that forage in benthic vs. littoral regions (Matthews et al. 2010). Other aspects of consumer-resource interactions, such as habitat use and individual size, can be captured using digital devices. For example, WHOI/NOAA have developed HabCam a device which can be deployed from a ship to record multiple high-resolution images per second of the benthos, including ground fish, scallops, and an invasive tunicate (<http://habcam.whoi.edu/index.html>, last accessed 5/24/2016; York 2009). The large task of extracting data from these images was reduced by enlisting citizen scientists to identify, enumerate, and estimate the size of species captured in images (Seafloor Explorer; <https://www.seafloorexplorer.org/#!/science>, last accessed 5/24/2016).

Context dependency. Context dependency is another major issue for using functional traits to better understand aquatic consumer-resource interactions. Even body size, often considered a relatively fixed trait, can depend on environmental conditions. For example, size is sensitive to resource limitation and may decrease with climatic warming (Gardner et al. 2011). Size is also a major target of selection: predators often select prey based on size (Zaret 1980; DeLong et al. 2014). Size-based selection can drive trait evolution on ecological time scales, affecting consumer-resource interactions (e.g., Yoshida et al. 2003) and demographic traits such as birth rates and size at maturation (de Roos and Persson 2013). Accounting for context dependency starts with using techniques such as those described above (from stable isotopes to citizen science) to measure relevant traits more frequently in space and time, while recording the location and environmental conditions corresponding to these trait measurements.

develop, maintain, and adequately preserve data in archives. Funding to support these demands can be limited, and short-term; when databases are not updated and maintained, their usefulness declines, and they may be lost from sight. This problem is particularly acute for big data, such as genomic data, which requires vast amounts of storage space. Overall, perhaps the most challenging aspect is motivating individuals to archive their data and contribute to a common resource (Jones et al. 2006). However, we believe that these issues are not fundamental flaws, but represent temporary problems that we can and should overcome to advance trait-based ecology.

Stressing the importance of coordinating trait measurements and sharing trait data leads us to arguing for an increased focus on interdisciplinary and collaborative work. It is evident that we must improve communication between and within fields. This goes far beyond standardizing methods. In order to make advances in trait-based ecology, or ecology in general, we need to consider the interplay between experimentation, field-work, modeling, and theory (Carpenter et al. 2009). If we collect data without considering ways to maximize its utility and potential for multiple applications, we have missed our mark. Data collection should be motivated by theory, and new theory should try

Table 1. Examples of aquatic trait databases.

Name	Habitat	Organisms	Citation
Biological Traits Information Catalogue (BIOTIC)	Marine, benthic	invertebrates, macrophytes	MarLIN 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. < www.marlin.ac.uk/biotic > Accessed 6/01/2016.
Freshwater Biological Traits Database	Rivers and streams; N. America	macroinvertebrates	(US EPA 2012). Data set finalized in 2012; does not appear to be updated. < http://www2.epa.gov/risk/freshwater-biological-traits-database-traits > Accessed 6/01/2016.
Freshwater Ecology	Freshwater; Europe	phytoplankton, macrophytes, macroinvertebrates, fish	(Schmidt-Kloiber and Hering 2015). Actively maintained and curated; covers a broad range of taxa.
TraitBank	Marine and freshwater	Various	Encyclopedia of Life. < http://eol.org/traitbank > Accessed 6/01/2016. Aggregates published trait values from primary literature and reviews, as well as new data contributions. This new and actively growing resource encompasses a heterogeneous range of traits, organisms, and ecosystems (including terrestrial taxa). A new and actively growing resource.

to incorporate existing data. This highlights the need for more collaborative approaches in order to synthesize information gained from different fields to improve ecological understanding. Trait-based ecology is a prime example of a field where adopting a collaborative approach could be an essential catalyst (Carpenter et al. 2009; Cheruvilil et al. 2014). As we have illustrated above, the wealth of new technologies and interdisciplinary techniques that are available make it the perfect time to get started.

In concluding our discussion of potential solutions, we wish to emphasize that financial resources are a critical component of efforts to collect more trait data (using either new or well-established techniques). Resources are also needed for the continued existence and improvement of data sharing and collaborative platforms. Individual proposals to collect trait data may risk being considered “important but boring” and consequently fail to attract support, facing challenges similar to natural history research (Tewksbury et al. 2014). Coupling data collection initiatives with new ideas or technologies can help, but even basic measurements using well-established techniques are sorely needed. A centralized effort to collect trait data and supply

it to the research community might allow us to avoid this tragedy of the commons. We hope that continued discussion of the utility of trait-based ecology, including ways of overcoming its challenges, can help us identify and articulate research and funding priorities, stimulating scientific advances across our discipline.

Conclusions

Trait-based approaches to aquatic ecology have gained increased attention in the literature, and with good reason: they offer numerous ways to advance our mechanistic understanding of ecology, from populations to ecosystems. While we share in this enthusiasm, there are several challenges this field must confront as it evolves, if it is to make effective and lasting contributions to aquatic ecology. In particular, we need to think critically about the demands implicit in current trait-based theories, which require large amounts of data. Can we develop more sophisticated theories that reduce this demand? For which systems, questions and organisms is this demand unavoidable? In some cases, perhaps for studying large-scale processes and patterns

ranging from global ecosystem dynamics to macroecology, detailed knowledge of species traits may be irrelevant. When must we account for intra-specific variation, trait correlations, and context dependency? If faced with the need to obtain significant amounts of data, what sorts of technologies, tools, and resources can we effectively bring to bear on the challenge? High throughput techniques, or combinations of techniques may succeed where a single method is insufficient. Despite new technologies, however, it will not always be possible to collect all the data we need through individual research efforts. In such situations, collaboration and targeted funding can extend our ability to make progress, through coordinated data collection and data sharing. In extreme cases, for some questions or organisms, it may simply not be possible to gather sufficient data to effectively apply trait-based approaches. Rather than being a fatal flaw for trait-based ecology, this is expected: as with technology, no single tool or conceptual approach is appropriate for all problems. Overall, however, we believe that the future of the trait-based approach to aquatic ecology is bright, especially if we acknowledge its limitations and address them carefully, harnessing new technologies and working together.

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Conflict of Interest

None declared.

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