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Functional trait-based approaches as a common framework for aquatic ecologists

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Abstract

Aquatic ecologists face challenges in identifying the general rules of the functioning of ecosystems. A common framework, including freshwater, marine, benthic, and pelagic ecologists, is needed to bridge communication gaps and foster knowledge sharing. This framework should transcend local specificities and taxonomy in order to provide a common ground and shareable tools to address common scientific challenges. Here, we advocate the use of functional trait-based approaches (FTBAs) for aquatic ecologists and propose concrete paths to go forward. Firstly, we propose to unify existing definitions in FTBAs to adopt a common language. Secondly, we list the numerous databases referencing functional traits for aquatic organisms. Thirdly, we present a synthesis on traditional as well as recent promising methods for the study of aquatic functional traits, including imaging and genomics. Finally, we conclude with a highlight on scientific challenges and promising venues for which FTBAs should foster opportunities for future research. By offering practical tools, our framework provides a clear path forward to the adoption of trait-based approaches in aquatic ecology.

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The aquatic realm encompasses very diverse environments from freshwater ponds, lakes, and rivers to estuaries, salt marshes, mangroves, coasts, continental shelves, deep-seas, marginal seas, and open ocean areas. It plays a major role in the Earth's climate system and supplies important ecosystem services for human populations (Grizzetti et al. 2016). Yet, different aquatic ecosystems are still studied by distinct scientific communities that have limited interactions with each other, as illustrated by the tendency to train graduate students independently, to publish in different journals and to attend distinct conferences (with a few exceptions, such as the Association for the Sciences of Limnology and Oceanography and its conferences and journals, including Limnology and Oceanography). Freshwater and marine ecosystems even belong to different Sustainable Development Goals for the United Nations, with one dedicated to the marine environment (#14: Life below water), and another to terrestrial systems including freshwater (#15: Life on land) (United Nations 2015).

Ecology seeks to understand interactions between organisms and the environment, as well as to identify general rules that elucidate the functioning of ecosystems, to ultimately improve our ability to predict ecosystem changes (Loreau 2010). In both freshwater and marine environments, and for both pelagic and benthic habitats, the crucial questions remain the same (Heino et al. 2015): (1) What are the processes that control the structure and functioning of aquatic ecosystems? (2) What ecological patterns emerge at various spatio-temporal scales, and what are their key drivers? (3) How will aquatic organisms respond to increasing anthropogenic pressures? Some efforts have been made to integrate aquatic ecology for planktonic (Margalef 1978; Hecky and Kilham 1988; Leibold and Norberg 2004; Litchman and Klausmeier 2008) and benthic (Mermillod-Blondin and Rosenberg 2006) studies. Despite recent efforts to bring the communities together (e.g., the AQUASHIFT and DynaTrait projects priority programs of the German Research Foundation, or such as the biannual Trait workshop https://www.traitspace.com/ including limnologists, benthic ecologists, terrestrial ecologists), a unified framework for addressing ecological questions in pelagic and benthic habitats of both environments has been slow to develop. A recent review highlights the potential of trait-based ecology for studying aquatic ecosystems and the need for collaborative approaches among aquatic ecologists was emphasized (Kremer et al. 2017). In addition to bridging the gap between freshwater and marine studies, there is a crucial need to integrate planktonic and benthic studies, especially because of the strong coupling between these two habitats (Griffiths et al. 2017). The present synthesis proposes a practical framework to address these needs.

Indeed, trait-based approaches, defined in ecological research as any method that focuses on individual properties of organisms (so-called traits) rather than species, could provide this common framework (McGill et al. 2006; Kremer et al. 2017). These approaches emerged from terrestrial ecology when attributes at the individual level, initially used to describe ecosystem function based on elements common to multiple species, were considered to gather individuals into functional groups (i.e., "plant functional types") based on their physical, phylogenetic, and phenological characteristics, rather than on their taxonomy (e.g., species). Trait-based models of aquatic ecosystems can be traced back to the pioneering work of Riley in the 1940s (Riley 1946), who modeled the phytoplankton bloom dynamics in the North Atlantic focusing on the main physiological and biological characteristics of phytoplankton as a group. Since earlier attempts to classify phytoplankton by "life-forms" (Sournia 1982; Reynolds 1988), a similar approach was applied to identify functional groups for freshwater benthic macrofauna (Usseglio-Polatera et al. 2000*a*, *b*, 2001), marine benthos (Rigolet et al. 2014), benthic algae (Tapolczai et al. 2016), submerged plants (Willby et al. 2000; Lukács et al. 2019), or marine zooplankton (Benedetti et al. 2016). The underlying assumption is that functional grouping would make it easier to link community ecology to biogeochemical processes and biodiversity to ecosystem functioning (Naeem and Wright 2003). Through the study of functional diversity and functional traits, these approaches allow for the quantitative assessment of community or ecosystem resistance or resilience to changes through functional redundancy (Lavorel and Garnier 2002; McGill et al. 2006) which could potentially enhance generality and predictability in future projections of ecosystem function and service provision than the species-centered or taxonomic approaches (Levine 2016).

In aquatic ecology alone, more than 2476 articles were published between 1991 and 2018 using the terms "functional trait" or "trait-based" (see Supplementary Information). The percentage of those publications relative to the total ones published in freshwater and marine ecology (using those terms as keywords in Web of Science) has increased over time. This emergent and still increasing area of research in aquatic ecology has been the topic of several recent reviews, which summarize the state of the knowledge with regard to specific taxonomic or trophic groups, or traits (Litchman and Klausmeier 2008; Litchman et al. 2013; Nock et al. 2016; Beauchard et al. 2017; Hébert et al. 2017; Kremer et al. 2017; Meunier et al. 2017; Degen et al. 2018; Kiørboe et al. 2018). Previous studies focused either on one species (Pardo and Johnson 2005), on one taxonomic group of organisms (e.g., crustaceans in Hébert et al. 2016, 2017), on one compartment of the ecosystem (e.g., pelagic primary producers in Litchman and Klausmeier (2008); benthic primary producers in Tapolczai et al. (2016); zooplankton in Litchman et al. (2013) and Hébert et al. (2017); stream fish in Frimpong and Angermeier (2010)), on a particular ecosystem (e.g., oceans in Barton et al. (2013) and Kiørboe et al. (2018) marine benthos in Degen et al. (2018); running water benthos in Statzner and Bêche (2010)) or even on a single type of trait (e.g., size in Andersen et al. (2016) or stoichiometric traits in Meunier et al. (2017)). A network analysis of key words associated with the aquatic trait-based literature highlights differences between studies, both in the terminology used to

characterize traits and in the application of trait-based approaches in studies of freshwater and marine systems (Fig. S1).

The goal of this review is to facilitate exchanges of functional trait-based approaches (FTBAs) and their products across different aquatic fields. To do so, we propose (1) a table compiling the main definitions of traits that are commonly used in trait-based studies, in addition to recommendations for using a common and unambiguous vocabulary; (2) a unified typology of 40 aquatic functional traits that could be used in multicompartment studies (including several biological compartments, or different habitats, for example, sediment and water); (3) a summary of existing databases that contain information on functional traits; (4) a review of traditional and emerging methods for estimating and using traits of aquatic organisms; and (5) The main challenges that aquatic ecologists can now address using FTBAs and that should inspire future studies.

Trait definition and aquatic trait description

The term "trait" depicts specific attributes of an individual that are both inherent and characteristic to its nature. However, as highlighted by our literature survey (Figs. S1, S2, see also Supplementary Information), this term is used in multiple contexts to describe a diverse set of attributes such as "physiological traits," "functional traits," "life history traits," "biological traits," "ecological traits," "response traits," "effect traits," "behavioral traits," and so on (see Table 1). To avoid misunderstandings, clear definitions of these concepts are needed (Violle et al. 2007).

Adopting common definitions for aquatic FTBAs

Trait definitions vary between scientific communities, from the individual organism (e.g., life-history traits) to the population (e.g., demographic traits), community (e.g., response traits), and the ecosystem scale (e.g., effect traits; Hébert et al. 2017). Traits can also be directly measured in situ (e.g., realized traits) or inferred from the literature (e.g., potential traits). Realized traits are ultimately one of the sources for potential traits found in databases (see section "Imaging and acoustic techniques"). To establish a unified framework and avoid subjectivity in these definitions, we recommend the use of the definitions that focus on the individual level only. These are the ones proposed by Violle et al. (2007), by Litchman and Klausmeier (2008), and by Reu et al. (2011) are summarized in Table 1.

Since it is the diversity of organismal functions that structures communities and eventually ecosystems, trait-based approaches should rather refer to "functional traits" (sensu

Table 1. Main definitions related to traits in aquatic trait-based studies. Examples are given in gray. For clarity and consistency in trait-based aquatic ecology, this table presents only recommended definitions, while a full table including all the definitions currently used is available as Table S1.

Term	Recommended definitions	References	Examples
Trait	Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization.	Violle et al. (2007)	
Functional trait	Any trait that impacts fitness indirectly via its effects on growth, reproduction and survival.	Violle et al. (2007)	
Realized trait	Trait actually measured in situ or in the laboratory	Reu et al. (2011)	
Potential trait	Trait described from the literature, usually at the species level, and ideally covering a large variety of environmental conditions.	Reu et al. (2011)	
Life history traits	Traits referring to life history	Litchman and Klausmeier (2008)	Type of reproduction (sexual vs. asexual) or the ability to form resting stages.
Morphological trait	Traits related to the morphology of organisms	Litchman and Klausmeier (2008)	Cell size, cell shape.
Physiological trait	Traits related to the physiology of organisms	Litchman and Klausmeier (2008)	Nutrient acquisition, response to light.
Behavioral trait	Traits related to the behavior of organisms	Litchman and Klausmeier (2008)	Motility.

Violle et al. 2007: any trait that impacts fitness indirectly via its effects on growth, reproduction, and survival) than to "traits" and should in fact be called FTBAs. Functional traits have been further divided into four types: life history traits, morphological traits, physiological traits, and behavioral/mobility traits (Litchman and Klausmeier 2008; Litchman et al. 2013, 2015; Desrosiers et al. 2019). The term "ecological traits" has also been used in the context of "functional traits" to describe the environmental preference of the organisms, especially for benthic ones (e.g., Desrosiers et al. 2019). Where "ecological traits" refer to ecological or environmental preferences of organisms, they should rather be called physiological traits (e.g., salinity preference/tolerance) or behavioral traits (e.g., relationship with the substrate). In contrast, ecological traits referring to taxonomic information, sampling location or habitat features (e.g., depth, substratum type) should neither be considered as functional traits nor as traits.

Functional traits as a common framework beyond taxonomy to transcend ecosystems

Functional traits provide a "common currency across biological organizational levels and taxonomic groups" (Violle et al. 2014), beyond taxonomic variation and geographic or ecosystemic peculiarities. Firstly, functional trait-based ecology describes emergent properties related to ecosystem functioning, without necessarily having to explicitly identify the organisms at a given taxonomic level. Secondly, FTBAs in aquatic ecology can account for a continuous degree of plasticity in the trait expressed (Chevenet et al. 1994), thus allowing for a better quantification of intra-specific variability (see also section "Documenting the variability of key traits"). Moreover, phenotypic plasticity can result in substantial intra-specific variation (Des Roches et al. 2018), with clonal differences in plasticity. For instance, many aquatic species can exhibit a high degree of morphological plasticity in response to different environmental cues. Zooplankters such as *Daphnia* can form elongated carapaces (e.g., longer tailspines or helmets) in response to strong predation (O'Brien et al. 1979; Lüning 1992; Swaffar and O'Brien 1996) while the freshwater phytoplankters *Desmodesmus* can increase the size of their colonies to avoid mortality from numerous grazers (Lürling 2003). These are examples of abilities for phenotypic plasticity that can be seen as functional trait of the organisms that possess such flexibility (Barnett et al. 2007; Weithoff and Beisner 2019). Intra-specific variability can be substantial in aquatic organisms (e.g., Sanford and Kelly 2011), and can impact community and ecosystem dynamics similarly to inter-specific trait variability (Des Roches et al. 2018; Raffard et al. 2019). Within the climate context, understanding the drivers and link between intra- and inter-specific trait variability is another argument for the use of FTBAs instead of species-centered approaches (Violle et al. 2012).

To go further toward a unified framework, we propose a common typology of functional traits for aquatic organisms (Fig. 1). It not only follows what was previously proposed for phytoplankton (Litchman and Klausmeier 2008) and zooplankton (Litchman et al. 2013; Brun et al. 2016*a*,*b*) but now incorporates new elements proposed for marine benthic ecosystems (Degen et al. 2018). Moreover, in the typologies proposed by Litchman and colleagues, functional traits are classified in one of four types (morphological, physiological, behavioral, and life history) and associated to three main ecological functions (resource acquisition, reproduction, and predator avoidance for phytoplankton; feeding, growth/reproduction, and survival for zooplankton). Here we propose to separate growth and reproduction into two distinct columns (Fig. 1). Compared to earlier typologies, ours identifies key functional traits that can be used for multicompartmental studies because they transcend the taxonomic specificities of the different aquatic ecosystems (Salguero-Gómez et al. 2018). For instance, it includes some traits that have been disregarded so far in studies focusing on only one compartment. These traits are water content, color, breeding type, life cycle, life span, diapause, reproduction strategy, salinity preference/tolerance, chemical compounds for mating or detecting congeners, diet/food preference, allochemical compounds, dissemination potential, substrate relation (plankton/benthos, including substrate specific relation for benthos), ecosystem engineering, including bioturbation/irrigation for benthos, and finally perception/production of sounds. Most of the 40 functional traits presented in this typology can be estimated quantitatively (Costello et al. 2015), making them good candidates for comparative studies. In addition, a dynamic representation of this typology is proposed as an online mental map (http://doi.org/10.5281/zenodo.3635898), which links to associated research articles. This mental map is not only a different way to represent the functional traits proposed in Fig. 1, but it also provides a dynamic visual representation. It can serve as a pedagogical tool for teaching purposes and as a basis to identify trade-offs between related traits. Further work could initiate a globally shared ontology for aquatic traits, for instance as part of Open Biological and Biomedical Ontology Foundry (http://obofoundry.org/).

Estimating functional diversity from functional traits

Traits are useful tools to quantify not only the functional biogeography of a system or organism, but also the diversity of a system, its functional redundancy, and/or its likely resilience to perturbations. Those traits that have been measured at the individual level, or estimated for each species of a given community, can be used to estimate trait-based Shannon diversity (Usseglio-Polatera et al. 2000*a*,*b*) or Rao's quadratic entropy indices (Rao 1982). Functional diversity (FD) and its various dimensions, such as functional richness, functional divergence, or functional evenness (Mason et al. 2005; Ricotta 2005) can further be quantified, either using dendrogram-based metrics (e.g., Petchey and Gaston 2007; Mouchet et al. 2008), or from the definition of a functional space (e.g., Villéger et al.

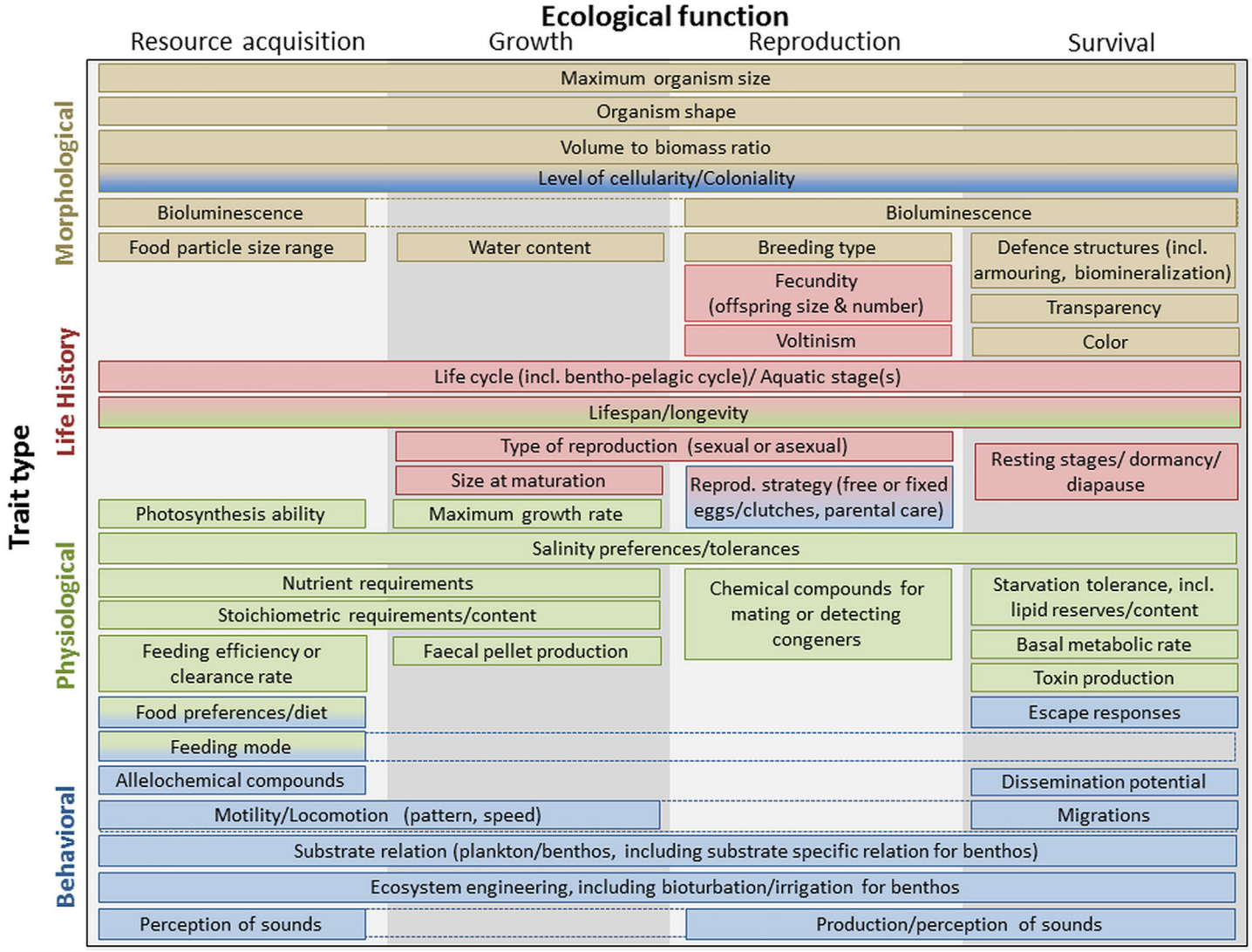


Fig. 1. Unified typology of aquatic functional traits that could be used in multicompartmental studies. This typology focuses on the key functional traits that transcend taxonomic peculiarities of the different aquatic ecosystems. Traits are classified by type and ecological function (as in Litchman and Klausmeier 2008) and most of them are quantitative. The dashed lines are a representation for similar traits crossing multiple ecological functions that are not close. A mental map providing a network visualization of this figure is available online, with each trait node linking towards associated research articles (http://doi.org/10.5281/zenodo.3635898).

2008; Laliberté and Legendre 2010). Several indices taking explicitly into account intraspecific trait variability were also proposed (e.g., de Bello et al. 2011; Carmona et al. 2016). Functional beta diversity can be estimated too, including through the more classical biological trait analysis (e.g., Bremner et al. 2006; Beauchard et al. 2017). To aid ecologists in finding their way among the many functional diversity metrics, several guides were published about their definition and use (Schleuter et al. 2010; Mason et al. 2013; Mouillot et al. 2013; Carmona et al. 2016; Schmera et al. 2017; Legras et al. 2018). Many of these indices are sensitive to the number and the type of traits that are considered (e.g., Legras et al. 2019), as well as to the species richness of the communities, meaning that the comparison of sites with different richness levels would require using comparable indices that are unbiased by species richness and trait selection.

Estimating and using traits: Tools and limits for studying functional traits

Several observational methods, both used in situ as well as in vitro, allow for the quantification or identification of functional traits; but they are predominantly used in either oceanographical or limnological applications, not both. Currently available methods to measure or estimate traits include classical trait measurements (laboratory and field), imaging and

acoustic techniques, as well as molecular sequencing (-omics). These methods will be described in the following sections and opportunities for sharing between scientific communities will be outlined.

Empirical studies of traits as a source for trait databases

The investigation of functional traits has been largely based on empirical studies. Such studies rely on three complementary approaches that can be described by (1) measurements of traits in situ, (2) measurements of traits under controlled laboratory conditions, and (3) metadata analyses of databases and literature (Fig. 2A). The metadata approach has been undoubtedly the most developed across aquatic ecosystems (Degen et al. 2018; Kiørboe et al. 2018) and the literature has been the basis of a number of reviews describing functional traits. For example, in freshwater ecology, Kolkwitz and Marsson (1909) pioneered a compilation of types of organisms in relation to the presence of various pollution levels. In marine ecosystems, metadata compilations allowed mapping of key traits of marine copepods at a global scale and evaluation of their relationships with environmental conditions (Brun et al. 2016*b*; Benedetti et al. 2018). One effective way to merge functional traits with taxa, based on a variety of sources and literature, is the fuzzy coding procedure (e.g., Chevenet et al. 1994). In FTBAs, the fuzzy coding uses positive scores to describe the affinity of a species for the different categories of a given trait, for example, using "0," "1," "2," and "3" for species exhibiting, respectively, "no," "weak," "moderate," and "strong" link with a given trait category (Chevenet et al. 1994; Usseglio-Polatera et al. 2000*a*, *b*). When a trait applies to a subset of the different stages of the species life cycle (egg, larva, pupa, and adult), the relative duration of each stage is considered in assigning appropriate scores to the different categories of this trait. To standardize the description of species attributes, trait category scores are converted into a relative abundance distribution so that the sum of the trait category scores for an individual trait and a given taxon equals one. This technique of coding is robust enough to compensate for different types and levels of information available for different taxa.

In recent years, numerous open-access databases recording functional traits have been developed to document traits included in existing databases (Table 2). This diversity of databases gathers trait information not only for widely studied traits (e.g., body size or feeding strategy), but also for less common traits or for those that are more difficult to measure (e.g., age at first reproduction, migration mode, or nutrient affinities). Some large trait databases were published online and open access (e.g., Herring 1987; Barnett et al. 2007; Benedetti 2015; Hébert et al. 2016; Degen and Faulwetter 2019), thus allowing for follow-up studies that compare and merge trait data across taxa, species, and environments. In some instances (e.g., freshwater invertebrates), published databases rapidly became foundational for environmental assessment procedures (e.g., Mondy et al. 2012; Mondy and Usseglio-Polatera 2013; Larras et al. 2017). The main caveat of these FTBAs is that only a limited number of species and/or traits have been reported so far, thus not yet allowing for a generalization of findings across taxa, the definition of fitness landscapes, and/or the characterization of ecological niches or responses to environmental change. Indeed, these databases often focus on the dominant and most easily sampled or cultivable species. Moreover, metadata associated with trait measurement methods are usually lacking. Until now, shortfalls in the knowledge of many aquatic taxa (Troudet et al. 2017) restrict the application of trait databases at the community scale and remain a limiting factor for the integration of FTBAs into macroecology (Tyler et al. 2012; Borgy et al. 2017). However, the main limit so far to provide and share trait data remains the lack of an ecological standard for data (Schneider et al. 2018). Attempts to increase unification are currently emerging on various fronts such as the terminology of traits (e.g., Schmera et al. 2015 for stream ecology), the cross-taxa compatibility of functional traits (e.g., Weiss and Ray 2019 for plants and animals) or the actual measurements of such traits (e.g., Moretti et al. 2017 for terrestrial invertebrates). Large efforts are still needed to combine and integrate all these various trait databases (Degen et al. 2018), but applying Open Science principles should accelerate trait-based science (see, e.g., the Open Traits Network initiative, Gallagher et al. 2019). Such databases are already numerous, large-sized, and of increasing complexity. Therefore, their manipulation requires strong computational abilities (Durden et al. 2017). As a result, aquatic research is evolving into a more biostatistical- and bioinformatical-based field, enabling the extraction of large-scale information on traits and putting to full use taxonomic surveys recorded over time. Despite this, naturalist taxonomic knowledge per se remains critical and future challenges in ecology will undoubtedly benefit from a combination of modern FTBAs and a modern integrative taxonomic knowledge.

The traits documented by these databases originate from direct measurements of realized traits in the laboratory or in situ (Fig. 2A). Laboratory experiments allow for the quantification of functional traits of model species within a large range of controlled environmental conditions. They provide a well-constrained system, both in physical variables and species content, to measure functional traits at the individual level. However, they are often limited to a few cultured species that do not necessarily reflect the actual functional diversity and complexity of whole ecosystems, as should FTBAs do. One of the few examples of lab-measured traits tested the existence of trade-offs across many phytoplankton species between maximum growth rate, competitive ability for phosphorus acquisition, and ability to store phosphorus (Edwards et al. 2013*a*).

In recent years, innovative instruments and tools have become available to measure in situ new functional traits. They include imaging and genomics tools that have the potential to provide a comprehensive picture of aquatic ecosystem composition, structure, and function. Their implementation should

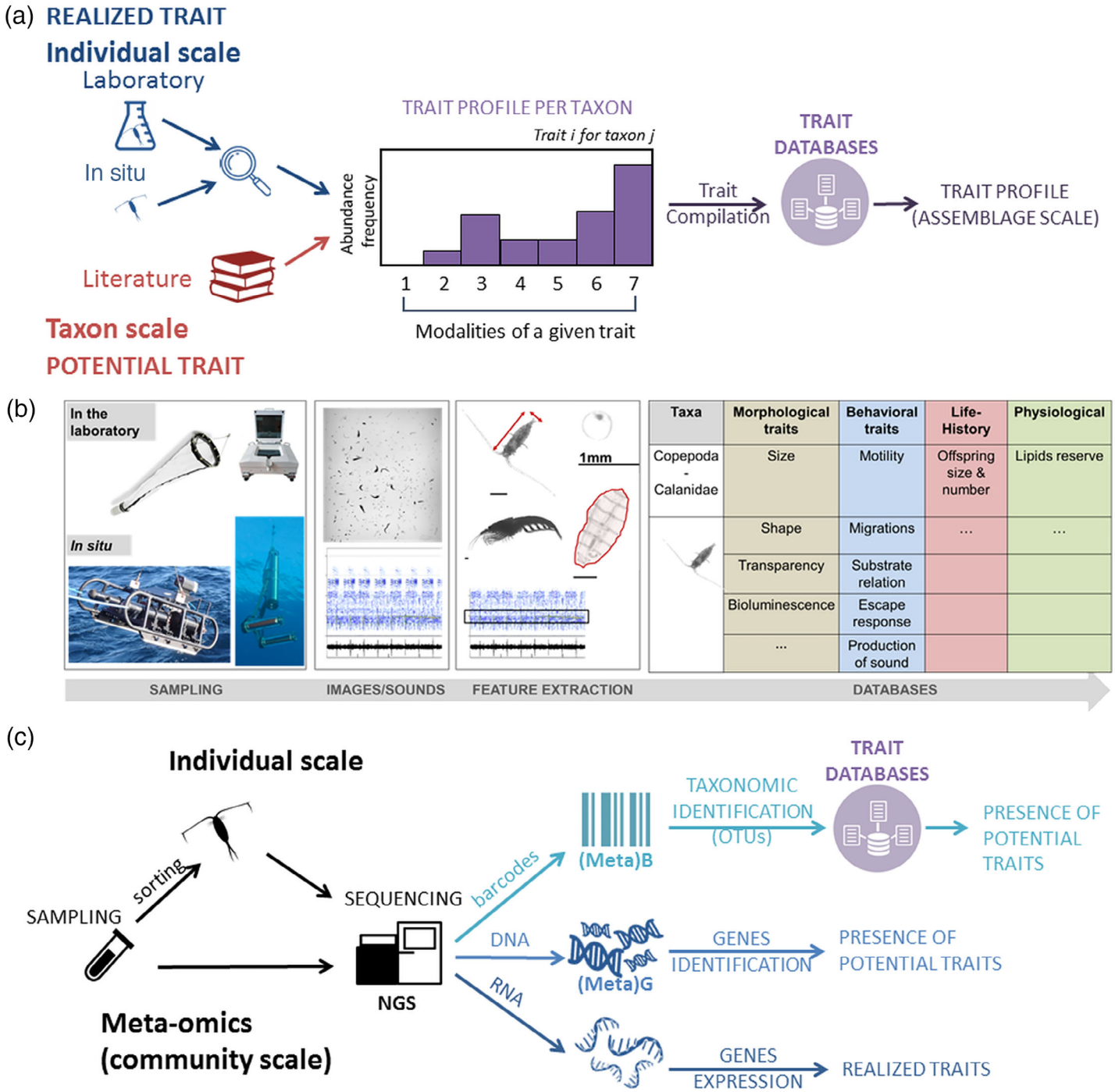


Fig. 2. Main methods to study traits. (**A**) Use of empirical studies to measure realized traits (in laboratory or in situ) or to estimate potential traits from the literature. The abundance frequency the modalities a given trait can be used to code trait profile by taxon using fuzzy coding and thereby inform trait databases. (**B**) Use of imaging and acoustic techniques to identify or measure functional traits of aquatic organisms from sampling, images/sound recording, features extraction to databases (ZooVis picture has been kindly provided by H. Bi). (**C**) Use of sequencing techniques to identify or measure functional traits. Sequencing can be done at the community scale (meta-omics) or at the individual scale after manual or automatic sorting. (Meta)B, (Meta) Barcoding; (Meta)G, (Meta)Genomics; (Meta)T, (Meta)Transcriptomic.

Table 2. Online databases documenting functional traits of aquatic organisms. Databases without a primary focus on traits, but that also provide trait information, are included. A regularly updated version of this list is available at https://github.com/severine13/FonctionalTrait_databases.

Name of the database	Taxonomic groups of interest and habitats	Reference	Brief description	Web link
Traitbank—encyclopedia of life	All taxa across the tree of life, including marine and freshwater organisms	Parr et al. (2014)	Provides traits, measurements, interactions and other facts. Actively growing resource covering all ecosystems (not restricted to aquatic ecosystems).	http://eol.org/info/516
Bromeliad invertebrate traits	Aquatic invertebrates in bromeliads from South America	Céréghino et al. (2018)	12 functional traits of 852 taxa	https://knb.ecoinformatics.org/#view/doi:10.5063/F1VD6WMF
South-east Australian freshwater macroinvertebrate traits	Freshwater macroinvertebrates from South-East Australia	Schäfer et al. (2011)	9 traits, described at the family level for 172 taxa	Supplementary information to the article
EPA freshwater biological traits database	Freshwater macroinvertebrates from North America rivers and streams	U.S. EPA (2012)	Includes functional traits (e.g., life history, mobility, morphology traits) but also ecological and habitat information for 3857 North American taxa.	https://www.epa.gov/risk/freshwater-biological-traits-database-traits
Biological Traits Information Catalogue (BIOTIC)	Benthic marine macrofauna and macroalgae	MARLIN (2006)	Includes 40 biological trait categories.	http://www.marlin.ac.uk/biotic
EMODnet Biology database	European seaweeds	Robuchon et al. (2015)	Functional traits (morphology, life history, ecophysiology) and ecological information (incl. Biogeography) for the 1800 seaweed species listed in Europe.	Ongoing work
Functional traits of marine macrophytes	European marine macrophytes, including seaweeds	Jänes et al. (2017)	Functional traits (morphology, ecophysiology) and ecological information for 68 species.	https://www.datadryad.org/resource/doi:10.5061/dryad.964pf/1
Polytraits	Marine polychaetes	Faulwetter et al. (2014)	47 traits describing morphological, behavioral, physiological, life-history characteristics, as well as the environmental preferences, for a total of 27,198 trait records for 952 species.	http://polytraits.lifewatchgreece.eu/
The Arctic Traits Database	Marine organisms from the Arctic	Degen and Faulwetter (2019)	Traits for 478 species-level taxa.	https://www.univie.ac.at/arctictraits/team
WoRMS Marine Species Traits portal	Marine species	WoRMS Editorial Board (2019)	Provides 10 traits that have been prioritized within EMODnet Biology, as part of the World Register of Marine Species (WoRMS).	http://www.marinespecies.org/traits/index.php

(Continues)

Table 2. Continued

Name of the database	Taxonomic groups of interest and habitats	Reference	Brief description	Web link
Functional traits of marine protists	Marine protists, including fungi.	Ramond et al. (2018)	Provides 30 functional traits for 2007 taxonomic references associated to V4 18S rDNA sequences.	https://doi.org/10.17882/51662
COPEPEDIA/COPEPOD	Marine plankton	O'Brien (2014)	Database of plankton taxa distribution maps, photographs, biometric traits, and genetic markers.	https://www.st.nmfs.noaa.gov/copepod/documentation/contact-us.html
Trait database for marine copepods	Marine pelagic copepods	Brun et al. (2017)	Trait databases providing 9306 records for 14 functional traits of about 2600 species.	https://doi.pangaea.de/10.1594/PANGAEA.862968
Mediterranean copepods' functional traits	Marine copepods present in the Mediterranean Sea	Benedetti (2015, 2016)	Seven functional traits for 191 species.	https://doi.org/10.1594/PANGAEA.854331
Freshwater ecology	European freshwater organisms belonging to fishes, macro-invertebrates, macrophytes, diatoms and phytoplankton	Schmidt-Kloiber and Hering (2015)	Covers environmental preferences, distribution patterns, and functional traits for 20,000 taxa.	https://www.freshwaterecology.info/
Freshwater benthic diatoms	European rivers	Rimet and Bouchez (2012)	Life-forms, cell-sizes and ecological guilds for c.a. 1200 taxa	https://data.inra.fr/dataset.xhtml?persistentId=doi:10.15454/XLQ40G
	Fresh and weakly brackish waters in the Netherlands	Van Dam et al. (1994)	First comprehensive checklist of ecological traits (pH, saprobity…) for 948 diatom taxa	https://doi.org/10.1007/BF02334251
Phytoplankton of temperate lakes	Phytoplankton of temperate lakes	Rimet and Druart (2018)	Database of morphological and physiological traits of more than 1200 taxa.	https://zenodo.org/record/1164834#.XRNrPXvgrOR
Freshwater benthic micro-meiofauna	River benthic micro-meiofauna	Neury-Ormanni et al. (2019)	First integrative database of 23 morphological traits linked to resource acquisition for 35 taxa	https://doi.org/10.1007/s10750-019-04120-0
FishBase	Fishes	Froese and Pauly (2019), Beukhof et al. (2019)	Provides information on 34,100 species, including traits related to trophic ecology and life history.	www.fishbase.org https://doi.org/10.1594/PANGAEA.900866.
The Coral Trait Database	Coral species from the global oceans	Madin et al. (2016))	Includes 68,494 coral observations with 106,462 trait entries of 158 traits for 1548 coral species.	https://coraltraits.org/
FishTraits	Freshwater fishes of the United States	Frimpong and Angermeier (2010)	More than 100 traits are informed for 809 fish species of the United States, including 731 native and 78 exotic species.	http://www.fishtraits.info/

(Continues)

Table 2. Continued

Name of the database	Taxonomic groups of interest and habitats	Reference	Brief description	Web link
ECOTAXA	Marine planktonic eukaryotes and prokaryotes (viruses in prep.)	Picheral et al. (2017)	50 morphological features including size, shape or opacity.	http://ecotaxa.obs-vlfr.fr/ http://ecotaxa.sb-roscoff.fr
Protist Ribosomal Reference database (PR2)	Protists	Guillou et al. (2013)	Sequence database for which the inclusion of functional traits is under development.	https://github.com/pr2database/pr2database
Eukaryotic reference database (EukRef)	A wide range of eukaryotic organisms across the tree of life	del Campo et al. (2018)	Collaborative annotation initiative for referencing 18S rRNA sequences, for which the inclusion of functional traits is under development.	https://eukref.org
The Kyoto Encyclopedia of Genes and Genomes (KEGG)	A wide range of organisms across the tree of life	Kanehisa and Goto (2000)	Collection of databases on genomes and biological pathways that provides molecular-level information on gene functions, which could inform on potential functional traits.	https://www.genome.jp/kegg/
sFDvent: A global trait database for deep-sea hydrothermal vent fauna	Deep-sea hydrothermal-vent fauna with species-level identification present or in progress	Chapman et al. (2019)	646 vent species names, associated location information, and scores for 13 traits	https://doi.org/10.5061/dryad.cn2rv96

greatly help advance the use of functional traits in aquatic studies.

Imaging and acoustic techniques

Imaging systems are best suited not only for the quantification of morphological traits, such as size, transparency, bioluminescence, or shape (Forest et al. 2012; Barton et al. 2013; Fontana et al. 2014; Andersen et al. 2016), but also for the estimation of some behavioral (e.g., motility or substrate relationships), life-history, or physiological traits (Fig. 2B; Table 1; Schmid et al. 2018; Ohman 2019). Imagery has been used as a tool in marine science since the 1950s and a variety of imaging systems have been successfully developed to record individual characteristics (see imaging and acoustic instruments listed in Table 3; e.g., Lombard et al. 2019). Over the last 15 yr, novel imaging techniques have allowed for rapid and less-intrusive visual observation of organisms' traits from picoscale to macroscale (e.g., (Culverhouse et al. 2006; Stemmann et al. 2008; Sieracki et al. 2010; Biard et al. 2016). To date, imaging tools have mostly been used by marine ecologists (Table 3), in both benthic and pelagic ecosystems, with only a few implementations in freshwater environments (e.g., (Althaus et al. 2015; González-Rivero et al. 2016). This is mainly due to the large amount of particles, the higher turbidity and the relatively smaller size of the crustacean zooplankton in freshwater ecosystems. Benthic imaging tools include baited, unbaited, towed, autonomous- and diver-operated systems (Matabos et al. 2014; de Juan et al. 2015; Mérillet et al. 2018), while pelagic ones are mainly in situ or bench-top systems. Since the turbidity and obstacles in benthic, coastal or river ecosystems strongly modify optical characteristics, systems with external light are more commonly used to efficiently capture morphological traits of aquatic organisms.

A major advantage of imaging systems is their variable degree of invasiveness during observation. Imaging systems can analyze discrete measurement of water samples (living or fixed samples), but they can also acquire in situ continuous records on living organisms. For instance, imaging techniques applied to marine plankton revealed that the abundance of the most fragile organisms (such as gelatinous zooplankton, Rhizaria, etc.) has been underestimated for a long time using traditional observation techniques (e.g., Biard et al. 2016), as they tend to break when collected using plankton nets

Table 3. Examples of instruments for imaging and acoustic assessment, used for trait description and quantification in aquatic ecosystems.

Taxonomic groups	Instrument	References	Applications
Protists	FlowCam	Sieracki et al. (1998)	Marine microplankton, abundance, size
	Imaging FlowCytobot (IFCB)	Olson and Sosik (2007)	Marine coastal, nanoplankton and microplankton, quantification, particle profile (morphology)
	Cytobuoy	Dubelaar et al. (1999), Dubelaar and Gerritzen (2000)	Freshwater and marine coastal, phytoplankton biomass, particle profile (morphology)
Large protists and mesoplancton	Zooscan	Gorsky et al. (2010)	Marine, shelf, coastal, pelagic plankton, morphological features
	Zooglider	Ohman et al. (2019)	Imaging and acoustics, marine, shelf, coastal, pelagic plankton, morphological features
Macro-organisms and fish	Laser optical plankton counter (LOPC)	Finlay et al. (2007)	Freshwater and marine, zooplankton size, biomass, abundance
	ZOOplankton visualization and imaging system (ZOOVIS)	Bi et al. (2012)	Marine pelagic, zooplankton, size
	Underwater video profiler (UVP)	Picheral et al. (2010)	Marine, shelf, coastal, pelagic plankton, morphological features
	Lightframe on-sight Keyspecies investigation (LOKI)	Schulz et al. (2010), Schmid et al. (2016)	Marine zooplankton, species, stages, morphological features
	In situ Ichthyoplankton imaging system (ISIIS)	Cowen and Guigand (2008)	Marine, ichtyoplankton, mesozooplankton, abundances, species
	Hydrophone	Coquereau et al. (2016), Desjonquères (2016))	Marine, freshwater, benthic

(Stemmann et al. 2008). The use of in situ imaging systems also provides information on poorly studied traits, such as transparency and water content of gelatinous organisms. For benthic systems, imaging techniques provide nonintrusive and nondestructive methods that can be valuable to assess endangered habitats and/or marine protected areas and to collect information on the distribution of large over-dispersed epifaunal species inadequately sampled by traditional gears like grabs (e.g., Althaus et al. 2015).

In addition to classical imaging, acoustic methods (passive and active) are also tools of increasing importance to quantify particular functional traits. Acoustic Doppler current profilers have been successfully used in lakes to capture diel migration behavior in larger planktonic species such as the insect larval predators of zooplankton (e.g., *Chaoborus*; Lorke et al. 2004). Hydrophone recordings can be used to record sound emissions by the organisms themselves. The sounds produced by freshwater organisms represent a highly overlooked trait and such trait recordings might provide relevant noninvasive tools to monitor the complexity and changes in aquatic communities. In a literature survey, Desjonquères (2016) showed that at least 271 freshwater species among French aquatic fauna (89% insects, but also fish and crustaceans) produce sounds. Using continuous underwater recordings with hydrophones, it was shown that the acoustic diversity of ponds and floodplain water bodies reflects the taxonomic diversity of aquatic communities (Desjonquères et al. 2018). Similarly, sound production by benthic invertebrates in the bay of Brest (France) was used to describe the soundscape and assess the ecological status of maerl beds (Coquereau et al. 2016).

One of the main caveats of imaging methods for FTBAs is that imaging tools have a low resolution below a certain size (most of these tools are of limited accuracy below a size limit of 200 μm for zooplankton, and 30–40 μm for phytoplankton, see Table 3), and may not allow for a reliable analysis of smaller size fractions, often associated with detrital matter or particles with a lack of discernible morphological differences. This limit is especially true for organisms without hard structures such as naked dinoflagellates or aloricate ciliates. However, imaging and acoustic methods generate high-frequency and automated data sets at large spatial scales, with some of them recorded by intercalibrated instruments, which allow for their comparison and combination in space and time (e.g., Underwater Video Profiler [UVP] for marine plankton;

Table 3). These data are also suitable for the validation of trait-based marine ecosystem models (Kiørboe et al. 2018) and new ecological questions have been addressed by combining both recent imaging techniques and FTBAs (Schmid et al. 2018). New opportunities using imaging and acoustics include the evaluation of feeding behaviors and network associations (Choy et al. 2017), filtration rates and carbon fluxes (Katija et al. 2017), and migration patterns of zooplankton (Benoit-Bird and Lawson 2016).

Because the number of images stored on acoustic and imaging systems is limited, and even short deployment times lead to considerable data volumes, the development of artificial intelligence techniques such as machine learning, deep learning recognition, and classification has been a crucial tipping point in the extraction of traits from these large data sets (Villon et al. 2016; Maps et al. 2019). Bigger storage capacity, standardized learning sets for machine learning combined with the automatized preprocessing of data directly in autonomous sampling instruments are already under development and will be an asset for the future of functional traits quantification by imaging.

Omics techniques for FTBAs

Another opportunity for automatic measurements of functional traits has emerged from the recent rise of high-throughput sequencing techniques (also called next-generation sequencing, or "-omics" in the broader sense). These techniques provide fast and relatively cheap nucleic acid sequencing and have opened new perspectives for investigating the structure and functioning of aquatic communities, both in marine (Raes et al. 2011; Sunagawa et al. 2015; Mock et al. 2016) and freshwater systems (Chonova et al. 2019). Methods based on DNA or RNA sequencing can be used for large-scale studies of environmental samples, investigating water samples in which any nucleic acid that is present can theoretically be retrieved.

For FTBAs, the identification of targeted DNA sequences (or metabarcoding; Bucklin et al. 2011; Valentini et al. 2016) can be used as a first step for fast and automatic taxon recognition, prior to the attribution of traits to the respective taxa using trait databases (Fig. 2C; Table 2). This was recently done to describe the biogeography of mixotrophic traits of marine protists at global scale (Faure et al. 2019), or to estimate the functional diversity of coastal protist communities (Ramond et al. 2019). In freshwater systems, metabarcoding of benthic diatoms was used to assess the water quality status of rivers (Vasselon et al. 2017) and metabarcoding was combined with text-mining or phylogenetic inference of ecological profiles and traits for biomonitoring (Compson et al. 2018; Keck et al. 2018). Yet, metabarcoding is inherently biased in multiple ways, such as its lack of quantitative link between the number of copies of barcodes (targeted DNA sequences) and the biomass or abundance distribution of organisms, the risk of gene amplification from dead material (not currently influencing ecosystem function), or the use of universal barcodes that may not be adapted to distinguish taxa for all lineages (e.g., Deiner et al. 2017). However, the main obstacle to using metabarcoding data for FTBAs is the low number of taxa for which barcodes have been documented (in addition to the low number of taxa for which trait information is available). This limitation precludes a full assessment of ecosystem structure from metabarcoding (e.g., de Vargas et al. 2015; Le Bescot et al. 2016). Thus, a strong effort remains to be made to supplement existing genomic databases with more taxonomically referenced sequences and trait information to allow the metabarcoding-based monitoring of aquatic functional traits (e.g., Ramond et al. 2018; PR2: Guillou et al. 2013; EukRef: del Campo et al. 2018; Diat.barcode: Rimet et al. 2019).

Beyond metabarcoding, -omics approaches are of particular interest to identify or measure functional traits linked to metabolic pathways (e.g., photosynthesis, nitrification, diazotrophy, calcification, etc.), using either (meta-)genomic or (meta-)transcriptomic approaches (Fig. 2C). When combined with databases like Kyoto Encyclopedia of Genes and Genomes or KEGG (Kanehisa and Goto 2000), which includes the genes (for genomics/transcriptomics), proteins (for proteomics), and metabolites (for metabolomics) implied in a specific pathway, -omics approaches open up the possibility of monitoring functional traits (defined at the individual level) across different levels of biological organization (from organisms to communities). For example, approaches that report the expression level of genes, proteins, and metabolites are increasingly used in ecotoxicology to assess functional traits (e.g., photosynthesis, chemical degradation) in response to stressor(s) via targeted approaches (e.g., q-PCR on preidentified candidate genes, Pesce et al. 2013; Moisset et al. 2015). Although it is still very challenging to relate -omics data to functional traits (Stec et al. 2017), the identification of certain genes coding for particular metabolic or physiological traits (e.g., iron uptake, nitrogen fixation) may help to directly link ecosystem structure to ecosystem functions (Mock et al. 2016), while taking into account the majority of organisms that in fact cannot be classified based on their morphological characteristics (e.g., picophytoplankton), and/or cannot be captured by imaging methods due to their small size or behavior. For instance, using metagenomic data, Farrell et al. (2018) created a machine-learning algorithm that can predict values of 65 phenotypic traits with more than 90% accuracy, thus allowing the investigation of the functional profiles of 660 uncultured marine prokaryotes based only on their Metagenomically Assembled Genomes or MAGs (i.e., genomes putatively reconstructed from metagenomics data). This very promising method cannot yet be applied to eukaryotes, as relating genes to potential traits in eukaryotes remains much more challenging than for prokaryotes (Sunagawa et al. 2015; Salazar et al. 2019). However, transcriptomics techniques were successfully used to estimate putative traits for marine protists using sequence similarity network-based approaches (i.e., toxicity and symbiosis for dinoflagellates; Meng et al. 2018). For pluricellular organisms, many challenges remain for the application of such methods in FTBAs, especially because of the large size of their genomes and because reference genomes are lacking (hence, the function of their DNA or RNA remains

unknown). Yet, the use of transcriptomics approaches seems promising for these organisms (e.g., Lenz et al. 2014; Blanco-Bercial and Maas 2018).

Substantial progress remains to be made before aquatic ecologists can fully exploit -omics information using a FTBA. This includes the design of new methods to estimate the quantitative aspects of -omics information, but also to decipher the large quantity of sequences that cannot be assigned to any taxon in an environmental sample, and to circumvent the low proportion of genomic functional annotation (especially for eukaryotes). However, ongoing and future -omics studies may allow skipping taxonomic assignation and even the identification of gene functions as an intermediary between ecosystem composition and function. Such studies would fully contribute to FTBAs of aquatic ecosystems by targeting the -omics signature of relevant functional traits (Mock et al. 2016; Stec et al. 2017).

Another application would be the use of -omics data to develop a new generation of trait-based models (Mock et al. 2016; Coles et al. 2017; Stec et al. 2017). Metatranscriptomic data could be used to identify physiological traits of phytoplankton, combined with a mechanistic model of the phytoplankton cell, and used to construct a trait-based global marine ecosystem model (Mock et al. 2016). Emergent communities of marine microbes (from bacteria to phytoplankton) have already been predicted by directly simulating their metagenomes and metatranscriptomes (Coles et al. 2017). In summary, the idea of improving ecosystem models using -omics is not new (Hood et al. 2006), but FTBAs could constitute the common framework needed for next-generation ecosystem modelers, observers, molecular biologists, and ecologists working in limnology and oceanography. This would advance our ecological understanding of aquatic ecosystems and the links between ecosystem structure, function and ecosystem services or bioindicators relevant for ecosystem monitoring and management.

Using either empirical studies, imaging/acoustics, or -omics, both quantitative and qualitative traits can be estimated. One advantage of qualitative traits is that they do not have to be measured using the same instruments and can be more easily described across compartments and realms. For quantitative traits, metrics, and indices, one challenge is to be able to compare trait-based functional diversity among studies. In the next section, we will focus on such traits that can be shared between ecological compartments and we will describe new opportunities in aquatic ecology to highlight spatiotemporal patterns, study anthropogenic impacts and better describe trophic interactions between plankton species (Fig. 3).

Future opportunities for aquatic FTBAs

Going further toward a trait-based aquatic ecology by identifying key traits

Documenting key traits in multicompartment studies

Given that the main power of FTBAs is to transcend both taxonomy and realms, trait-based ecological studies could result in a common set of ecological rules and theoretical principles that could be applied to multiple systems (e.g., benthos and pelagos, including plankton and fish). Following our framework, aquatic functional traits could be described at various spatiotemporal scales for both benthic and planktonic organisms, for instance taking benthic-pelagic coupling into account. To do so, we recommend a closer collaboration among aquatic ecologists, including process-oriented projects and comparative studies of freshwater and marine systems, focusing on the aquatic functional traits that we have identified and on their links to ecosystem functions (Fig. 1). In addition to morphological traits that are relatively easy to identify and to measure (such as size, shape, cellularity, defenses, and color), priority traits to be investigated should also include (1) life history traits such as voltinism (number of generation or breeding per year), life cycle, life span, type of reproduction, and reproduction strategy; (2) physiological traits such as photosynthesis ability, diet, feeding mode, salinity preference, and trophic regime; and (3) behavioral traits like motility, dispersal potential, and substrate relation. Indeed, among all the traits identified in Fig. 1, these traits are the most easily identified for any aquatic organisms, including both unicellular and pluricellular organisms, and cover all ecological functions and all types of traits (Fig. 3(1)).

One recent example, that could lead future novelty in trait-based studies, is the use of morphological traits estimated from multiple images. Statistically defined multidimensional morphological space can be synthesized from many individual images to generate a suite of interpretable continuous traits. Looking at the spatial distribution across the Arctic ecosystem of key traits, including body size, opacity, or appendage visibility, revealed meaningful information of copepods distribution and ecology in relation to ice-coverage (Vilgrain et al. 2021). Such statistical approaches using these continuous traits can easily be applied to multicompartment studies (e.g., using transparency to describe gelatinous ecological patterns).

Documenting the trade-offs between key traits

Multicompartmental studies that aggregate effects across species and trophic levels, hence taking into account the network structure of a community or the food-web structure of an ecosystem, would also enable a better understanding and quantification of the trade-offs occurring between two or multiple traits. Trade-offs, which result from the inherent metabolic, energetic or behavioral costs associated with each expressed trait, provide the fundamental basis to understand species coexistence and the trait composition of communities (Ehrlich et al. 2017). In particular, the competition-colonization trade-off is a major mechanism for biodiversity maintenance (Tilman 1994; Ehrlich et al. 2020; Muthukrishnan et al. 2020). Strong competitors able to exclude other species in any given habitat are often slow dispersers. In contrast, poor competitors are often strong colonizers, able to easily disperse, and find unoccupied niches.

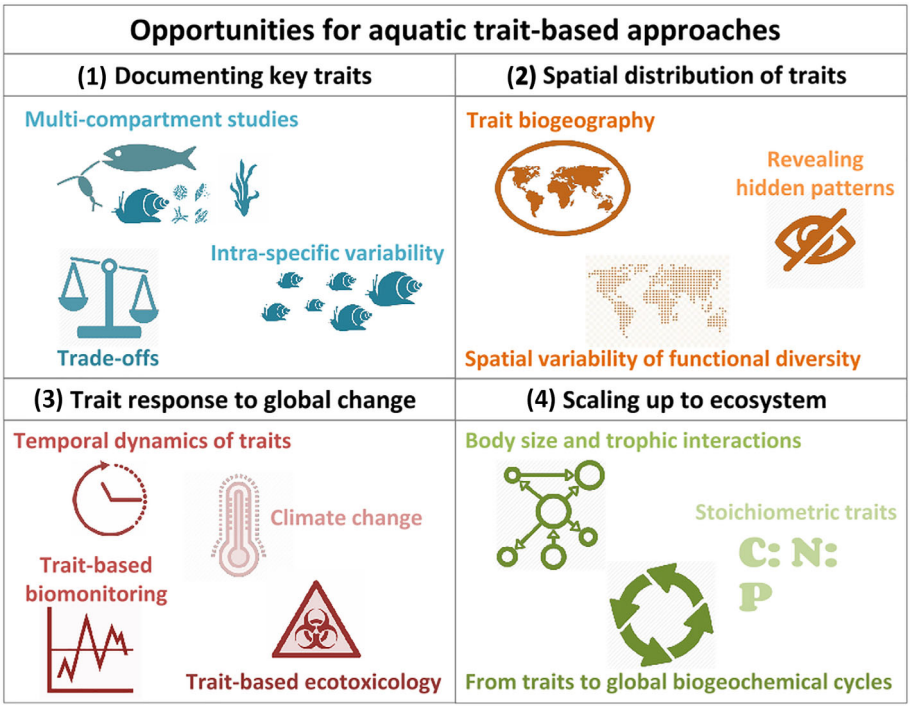


Fig. 3. Main opportunities for trait-based approaches in aquatic ecology. These four opportunities are described in section "Future opportunities for aquatic FTBAs."

A trade-off between resource acquisition and survival (or predation vulnerability) was reported for zooplankton: organisms that feed using feeding currents, increase their risk of being detected by predators that are sensitive to flow disturbances (Kiørboe and Hirst 2014). Unexpected trade-offs can often explain the relative mismatch between expected and observed individual traits in aquatic communities along gradients of anthropogenic pressure, complexifying the trait-based diagnostic of water bodies (Resh et al. 1994; Mondy and Usseglio-Polatera 2014; Desrosiers et al. 2019). Indeed, the success of a species in adverse conditions might be due to a particularly effective adaptation without the need for further adaptive traits. Moreover, investing in a given adaptation can leave fewer resources available for the investment in another adaptation. Species of various lineages (e.g., different phyla in invertebrate assemblages) may also solve the same ecological constraint with different adaptations.

Trade-offs have been globally recognized as a central component of trait-based approaches in aquatic ecology (Resh et al. 1994; Kremer et al. 2017) especially in plankton ecology (Litchman et al. 2007, 2013, 2015; Litchman and Klausmeier 2008; Hébert et al. 2017; Kiørboe et al. 2018; Ehrlich et al. 2020). In benthic studies, there has been a clear lack of work that considers simultaneously several traits relative to what has been done in studies on marine plankton (e.g., Litchman et al. 2013) and in freshwater ecology (Verberk et al. 2008). As a case in point, the term trade-off is not mentioned in the recent review on benthic traits by Degen et al. (2018). More studies are needed to explore trade-offs among traits across compartments and realms in order to identify the rules governing the links between traits, trade-offs, community structure, and function. To accomplish this, researchers will have to put effort on measuring multiple traits, focusing on those related to resource acquisition, growth, storage, and predation avoidance (i.e., directly related to fitness) on a variety of taxa within the same habitat. Comparison of how such relationships that trade-off (i.e., negatively related) change under different abiotic or biotic conditions will allow determination of how flexible such trade-offs are as ecological conditions change. Recently, the shape of the trade-off curve, representing the boundary of the set of feasible trait combinations, has been described as explaining traits of co-existing species and changes in trait values along environmental gradients (Ehrlich et al. 2017, 2020). Convex trade-offs would facilitate the coexistence of specialized species with extreme trait values while concave trade-offs would promote species with intermediate trait values.

To further explore trait relationships, aquatic ecologists may be inspired by what has been done in terrestrial plant ecology: the identification of so-called trait syndromes. Trait syndromes are relationships between traits that are defined by fundamental trade-offs among taxa that determine their ecological roles in ecosystems. The classic example in plant ecology is the "leaf economics spectrum" that characterizes

taxa according to the speed at which they are able to take up nutrients and invest in leaf biomass (Wright et al. 2004). In this vein, some work was done with aquatic organisms by considering trade-offs among lotic insects (e.g., Poff et al. 2006), fishes (e.g., Winemiller et al. 2015), and phytoplankton (e.g., Edwards et al. 2013a). By considering trait syndromes, FTBAs are likely to better predict competitive outcomes as well as distributions of traits across environmental gradients. We thus encourage the aquatic ecology community to engage with the vast array of accessible trait databases provided in Table 2 and to take the next steps to characterize trait syndromes across the different groups of aquatic organisms.

Documenting the variability of key traits

Finally, more attention should be given to document the variability of all key traits at all organizational levels, that is, at the community scale, between individuals in a given population (i.e., intra-specific variability; Raffard et al. 2019), but also for one individual throughout its lifespan (i.e., ontogenic variability; e.g., Zhao et al. 2014). Indeed, with the exception of a few studies (e.g., Maps et al. 2014; Banas and Campbell 2016), intra-specific variability of traits is rarely taken into account, mainly because of a lack of empirical information on this variability. For example, the ability to engage fully in autotrophy or to add in heterotrophic feeding is a characteristic of mixotrophic phytoplankton taxa. By characterizing the conditions under which one or the other condition is utilized by a taxon, we can begin to characterize intra-specific variability. Therefore, the question of the scale of variation of functional traits, both at community and population scales, and its impact on ecosystem structure and functioning should be further explored, especially with the use of new methodological development to measure traits (see section "Estimating and using traits: Tools and limits for studying functional traits"). Trait-based models could also be used (see review on trait-based modeling in Kiørboe et al. 2018) to quantify the impact of environmental changes on the intra- and inter-specific variability of functional traits (e.g., lipid content and size of copepods, Renaud et al. 2018), and to assess the variation of peculiar traits along environmental gradients (Edwards et al. 2012).

Identifying key traits common in limnology and oceanography and their trade-offs, syndromes, and variability will allow aquatic ecologists to better address central ecological questions, including understanding: (1) the spatial patterns of functional diversity and its drivers, (2) the effects of environmental and anthropogenic pressures on ecosystem structure and functioning, and (3) the interactions among organisms and associated food web organization and dynamics. For each of these main opportunities, we will briefly describe what has been done to date and then identify potential ways to advance the field of aquatic ecology using FTBAs.

New opportunities emerging from the study of the spatial distribution of aquatic traits

The description of aquatic trait biogeography

To date, trait biogeography has been studied for a few compartments in marine ecosystems, such as marine plankton (Barton et al. 2013) including bacterioplankton (Brown et al. 2014), zooplankton (Prowe et al. 2019), copepods (Brun et al. 2016*b*; Record et al. 2018), pelagic diatoms (Fragoso et al. 2018), estuarine fish (Henriques et al. 2017), and reef fish (e.g., Stuart-Smith et al. 2013). Large-scale studies of the trait biogeography of freshwater organisms are more rare (e.g., for amphibians see Trakimas et al. 2016). Aquatic trait biogeography studies covering multicompartments, including plankton, fish, and benthos, remain scarce and usually focus on one realm (e.g., marine organisms in Pecuchet et al. 2018). Similarly, aquatic trait biogeography studies covering different environments (marine and freshwater) are few and usually target only one compartment (e.g., phytoplankton in Thomas et al. 2016).

Based on the biogeography of some key traits (e.g., size, feeding strategy), aquatic ecologists can now relate functional traits to environmental conditions and identify general rules governing trait diversity distribution. For instance, the description of key traits of marine copepods (body size, offspring size, and myelination) has highlighted latitudinal global patterns in trait biogeography. These patterns are in agreement with the temperature-size rule and have unveiled relationships between these traits and environmental conditions, such as water column transparency, but also biotic conditions, such as chlorophyll seasonality or phytoplankton size (Brun et al. 2016*a*). More recently, the study of taxonomic and functional diversity of fish communities between two different regions (Caribbean and Great Barrier Reef) and among three habitats (coral reef, seagrass, and mangrove) revealed that traits and functional groups varied among habitats, whereas taxonomic composition varied between regions (Hemingson and Bellwood 2018). Similar relationships should now be tested across ecosystems, geographical regions and trophic levels to verify whether these findings can be generalized to other aquatic organisms/ecosystems (Fig. 3(2)). The trait databases now available for many groups of aquatic organisms (see Table 2) should provide relevant information to explore this direction.

Using traits for revealing hidden community assembly rules at various spatial scales

Based on the spatial description of functional traits, hypotheses underlying community assembly rules can also be tested and community composition can be predicted (Cadotte et al. 2015). For example, the description of physiological and behavioral traits of dragonfly larvae in various lakes recently suggested that traits can drive species distribution and community assembly, through the direct impact of physiological and behavioral traits (activity rate and burst swimming speed)

on foraging and predator avoidance behavior (Start et al. 2018). The traits considered in this study were driven by two biomolecules, the expression of which could predict more than 80% of the variation in dragonfly community structure across lakes, and which were involved in the interactions between the dragonfly larvae and their fish predators. Measurements made by new observational methods such as metabolomics, transcriptomics (see section "-Omics techniques for FTBAs") or in situ imaging (see section "Imaging and acoustic techniques") would nicely complement presence–absence data by providing indication of the physiological state (e.g., healthy or stressed) of the individuals and hence help teasing apart the ideal and realized niche of organisms.

From trait biogeography to spatial variation in functional diversity

Traits that are shared among compartments could also be used to describe the spatial variability of functional diversity (Petchey and Gaston 2006). Among the metrics that were proposed to measure functional diversity and its different dimensions (see section "Estimating functional diversity from functional traits"), aquatic ecologists have to adopt common metrics for comparative studies. Based on these common metrics, the spatial variation of the functional diversity of aquatic communities could be estimated across environments and in multicompartment studies. For example, the functional diversity of macrophytes was described along a water depth gradient in a freshwater lake (Fu et al. 2014): future studies could cover similar environmental gradients in both freshwater and marine environments (e.g., rivers, estuaries, coasts, islands, etc.) and also include other organisms and higher trophic levels, both benthic and pelagic, to test whether the resulting spatial patterns of functional diversity can be generalized. The spatial distribution of traits and functional diversity could also be used to identify functional diversity hotspots and propose protected areas for a trait-based conservation. The diversity of functional traits is indeed correlated to both taxonomic diversity (e.g., Petchey and Gaston 2006) and the provision of ecosystem services. Conservation programs usually aim to protect both. Trait-based conservation could then rely on the rarity of species traits (or functional rarity) to identify conservation priorities (e.g., for coral reef fish in Grenié et al. 2018).

In addition to studying spatial patterns, traits can be used to study the temporal variation of functional diversity and how aquatic organisms respond to increasing global changes from anthropogenic pressures in the context of biomonitoring.

Trait response to global changes

Temporal dynamics of traits and their response to climate change

FTBAs can be used to estimate the temporal response of aquatic organisms and ecosystems to environmental forcing (Fig. 3(3)). For example, functional traits have been shown to explain community structure and seasonal dynamics of marine phytoplankton (Edwards et al. 2013*b*). It is also possible to combine classical data sets, and especially time series of species abundance, with trait databases described at the species level (see section "Empirical studies of traits as a source for trait databases") to apply a FTBA to in situ observations and/or monitoring data sets previously collected. In such reanalyses, key traits could be targeted (see section "Going further towards a trait-based aquatic ecology by identifying key traits") to compare their temporal changes, identify tipping points, and reveal trade-offs among traits. Hence, FTBAs offer novel perspectives for a posteriori (re)analysis of historical or long term monitoring data for the study of climate change and its impact on communities and ecosystem functioning (Pomerleau et al. 2015; Abonyi et al. 2018; Floury et al. 2018).

Marine ecologists have long since used FTBAs to study the impact of climate change on aquatic ecosystems (c.f. purple cluster in Fig. S1). For example, numerous marine studies explored the response of individual size to climate change (e.g., Schmidt et al. 2006; Finkel et al. 2010; Genner et al. 2010), showing that ocean warming is likely to cause a shift toward a larger contribution of smaller organisms to total biomass. Freshwater ecology could benefit from this experience, but currently, two main challenges can be pointed out for both freshwater and marine systems: the identification of links between functional traits and climate-change related variables (e.g., acidification and temperature increase in oceans, rivers and lakes; increase of freshwater shortage/scarcity in small streams) but also the deconvolution of the effects of multiple stressors on marine ecosystems (Mouillot et al. 2013). The joint pressure of multiple simultaneous stressors makes the identification of relationships between stressors and functional traits even more complicated, since interactions (e.g., synergism, antagonism, additivity, or inhibition) need to be taken into account. Under such conditions, monitoring functional traits of various types (Fig. 1) may prove useful to disentangle these complex interactions.

Impact of climate change on functional diversity

The study of functional diversity may also reveal functional redundancies at the community scale, which may have implications for ecosystem responses to climate change. As a consequence, because functional groups gather together individuals belonging to different species, the loss of a given species with a particular function does not necessarily mean that such function will be lost at higher ecological scale. Indeed, some ecosystems were shown to be insensitive to species loss because multiple species share similar functional roles (mixotrophy, nutrient uptake, or requirements), or some species only make a small contribution to the ecosystem processes (Hooper et al. 2005). Recently, it was suggested that climate change may have minor impacts on marine zooplankton functional diversity, due to strong functional redundancy (Benedetti et al. 2019). Conversely, climate change may have contrasting impacts on stream fishes (Buisson and Grenouillet 2009) or decrease their

functional diversity (Buisson et al. 2013). By combining climate change scenario modeling with species distribution modeling and functional trait databases, the impact of climate change on the functional diversity of aquatic ecosystems can be assessed at broader scales and across biological compartments and ecosystem boundaries. For aquatic insects, such a combined modeling-FTBA study revealed the spatial patterns of vulnerability to climate change, which also opens opportunities for biomonitoring (Conti et al. 2014). However, limitations remain in the use of trait-based approaches for the assessment of the effects of multiple stressors in the context of climate change, as emphasized recently by (Hamilton et al. 2019) for freshwater invertebrates. These authors pointed out the need to better account for trait redundancy, to better define the appropriate spatial scales for trait applicability and to progress towards the quantification of categorical traits.

Trait-based biomonitoring

Traditionally, the ecological health or "good environmental status" of aquatic ecosystems has been assessed in terms of species composition or relative abundance/biomass of specific indicators, initially within the context of the European Water Framework Directive (WFD-2000/60/CE). However, trait-based approaches offer new opportunities for the monitoring of aquatic ecosystems (Culp et al. 2011), since they can provide new tools that transcend taxonomical denomination, directly related to ecological functions, and exploit the traits available in open databases (Usseglio-Polatera et al. 2000*a*,*b*; Baird et al. 2011, see also Table 2). To date, trait-based biomonitoring has been mainly applied to freshwater ecosystems (cf. the corresponding cluster in Fig. S1). Indeed, the links between traits of organisms and natural environmental variables (e.g., pH, flow velocity) or even anthropogenic pressures (e.g., nutrient or organic matter contamination) have been explored for decades by freshwater ecologists. More specifically, biomonitoring studies put a strong emphasis on the definition and the attribution of traits to taxa such as freshwater benthic macroinvertebrates (Usseglio-Polatera et al. 2000; Menezes et al. 2010), benthic diatoms (Van Dam et al. 1994; Passy 2007) and phytoplankton (Reynolds et al. 2002). As a consequence, the last versions of several biological indices for stream monitoring are mainly based on functional traits (e.g., I_2M_2 in Mondy et al. 2012, BDI in Coste et al. 2009). Within the context of lake monitoring, FTBAs mainly investigated the abundance and the seasonal variability of phytoplanktonic functional groups, as they are known to respond to nutrient concentrations (St-Gelais et al. 2017; Huang et al. 2018). Furthermore, the traits of macroinvertebrates (e.g., reproduction mode, size) and diatoms (e.g., auto-ecological guilds, life form) are now used in ecotoxicological and ecological models to identify the probability that chemical and/or land use related pressures impair natural communities (Mondy and Usseglio-Polatera 2013; Larras et al. 2017) even in multiple stressor scenarios. Combined with statistical modeling, traits also allow deriving stressor-specific models to assess environmental quality (e.g., focusing on invertebrates inhabiting large rivers; Desrosiers et al. 2019).

In comparison to routine monitoring activities in freshwater systems, the use of trait-based monitoring of marine ecosystem is still in its infancy, yet under active development for coastal environments, especially through the implementation of the European Marine Strategy Framework Directive (MSFD-2008/56/EC). FTBAs were proposed to monitor the effects of human activities on benthic communities (e.g., Xu et al. 2018), such as bottom trawling and dredging (Tillin et al. 2006), aggregate dredging (Bolam et al. 2016) or pollution (Oug et al. 2012). These approaches can also be used to estimate the success of management strategies, and to predict the effects of future disturbances (including climate change) for marine benthos, by defining critical limits beyond which ecosystem functioning is altered (Bremner 2008). However, functional traits are not yet included in biological indicators and institutional monitoring programs of marine ecosystems, in contrast to what is included in freshwater monitoring efforts. Assessments of functional diversity could inform different MSFD indicators (such as "biological diversity," "habitat condition," and "ecosystem structure"). To our knowledge, trait-based monitoring on marine pelagic ecosystems does not exist. Similar efforts should be extended to open ocean monitoring, for example by incorporating trait data in the reanalysis of long term observations such as the Continuous Plankton Recorder time-series in the North Atlantic existing since the 1930s (Richardson et al. 2006).

Both the European Water Framework Directive and the European Marine Strategy Framework Directive require the estimation of the biological status of aquatic ecosystems from the evaluation of each compartment (benthic diatoms, macrophytes and macroalgae, benthic macroinvertebrates, phytoplankton, zooplankton, and fish) independently (e.g., Birk et al. 2012). Universal and standardized trait-based indices for biomonitoring should now cover all compartments (Borja et al. 2010). To this end, freshwater ecologists, who have a greater experience in multi-compartment monitoring (Lainé et al. 2014), could inspire marine ecologists, who are more used to focus on one compartment only (e.g., benthos, plankton, or fish).

Trait-based ecotoxicology

Besides the policy frameworks, FTBAs can also be used in ecotoxicology to highlight the impact of various stressors (e.g., organic synthetics products) on aquatic ecosystems (Baird and Van den Brink 2007). In fact, trait-based ecological risk assessments have been proposed as the new frontier in ecotoxicology (Baird et al. 2008; Rubach et al. 2011). In freshwater systems, diatom traits such as life form (e.g., colonial, solitary) or affinities to water quality have already been linked to pesticides contamination (Roubeix et al. 2011). The deformation of their silicified exoskeleton (teratology) has also been

considered as a morphological trait that can inform on organisms exposure to heavy metals or pesticides (Lavoie et al. 2017). Similar studies have reported the response of freshwater benthic macroinvertebrate traits to environmental stressors (e.g., Statzner and Bêche 2010). For example, Peter et al. (2018) demonstrated that functional traits such as the feeding mode of zooplankton can be used as indicators for the level of metal pollution in freshwater invertebrates at the community level. For marine ecosystems, trait-based ecological risk assessments remain scarce (e.g., Neuparth et al. 2002 for marine amphipods). More recently, -omics techniques offer new ways for estimating physiological traits related to pollutant catabolism, for example, by detecting the activity of particular genes (e.g., mercury methylating genes in the ocean, Villar et al. 2019). The recent development of appropriate statistical tools will help to integrate omics data within the framework for ecological risk assessment (Larras et al. 2018). Similarly, imaging could allow to automatically identify changes in morphological traits as a response to environmental stressors (e.g., Maps et al. 2019). Altogether, the high-throughput acquisition of -omics data and images could allow the detection of new environmental stressors (e.g., Bowler et al. 2009; Reid and Whitehead 2016). Such state-of-the-art tools can contribute to the development of universal multicompartment indices, that could provide estimates automatically and in almost real time. Ultimately, this could expand biomonitoring approaches beyond traditional taxonomically based assessments.

Scaling up from functional traits to community structure and ecosystem functions

Finally, FTBAs could be used to explore trophic interactions and food webs (Reiss et al. 2009). Indeed, several traits directly reflect trophic interactions (e.g., diet, size, stoichiometric traits) and can be used to better understand food web structure and dynamics (Fig. 3(4)). However, scaling-up from individual traits to populations, communities, and ecosystems requires taking trait variation at multiple intermediate organization scales into account (e.g., population, meta-population, and community scales; Gibert et al. 2015). Rather than considering a collection of traits independently, one approach is to analyze how these traits influence or reveal the biotic interactions and trophic structure of aquatic communities. To do so, the numerous traits that are directly related to the way consumers interact with their prey (e.g., diet, feeding modes, motility, and perception of sounds) or the way prey interact with their predators (e.g., toxin production, bioluminescence, migration) are emphasized in the following subparts.

Body size as a major functional trait driving trophic interactions

The functional trait of body/cell size plays a particularly important role and is often referred to as "a master trait." Size influences most of the ecological, physiological, and behavioral functions of organisms due to metabolic laws, underpinning trophic position and interactions that are especially influenced by relative prey and predator sizes (Weitz and Levin 2006; Conley et al. 2018). Size or morphological characteristics can potentially be measured directly using imaging methods (see section "Imaging and acoustic techniques"), and could be used to infer trophic relationships. Predator traits (i.e., body/cell size and motility type) may also be responsible for the body-size architecture of natural food webs in freshwater, marine, and terrestrial ecosystems (Brose et al. 2019). At large spatial scales, body size, and prey selection were shown to be modified by climate change and therefore to strongly impact food webs and ecosystem functions in return (Hoegh-Guldberg and Bruno 2010; Sheridan and Bickford 2011). For example, ocean warming was associated with a reduction in copepod body size, which may impact upper trophic levels and ultimately fisheries (Beaugrand et al. 2010, but see also Renaud et al. 2018). More general laws between size, trophic interactions and environmental variables could be tested in future trait-based studies, especially by taking advantage of automatic morphological measurements (including but not restricted to size) through imaging. More specifically, direct observations of predator–prey interactions and associated traits could be performed by combining imaging (Choy et al. 2017; Ohman 2019) with gut content and/or feces analysis based on taxonomic and/or -omics description, such tools being complementary and sometimes even more informative than the stable isotope methods that have been traditionally used so far (e.g., Majdi et al. 2018).

Including stoichiometric traits to study trophic interactions

In addition to body size, stoichiometric traits are highly promising for integrating FTBAs into food web models and to bridge the gap between community structure and ecosystem functioning (Meunier et al. 2017). Because all organisms are composed of the same major elements (e.g., C, N, and P), their balance not only reflects nutrient cycling in the ecosystem but also food web topologies. Quantifying stoichiometric traits across taxonomic and trophic groups allows the depiction of trophic interactions. In food web approaches, trophic position is associated with significant changes in C : N : P ratios, as well as altered isotope ratios due to selective uptake. As an example, heterotrophs are generally relatively less rich in carbon than autotrophs (Hessen et al. 2004; Persson et al. 2010). However, while stoichiometric composition and variation have been quantified for some species in different taxonomic groups (e.g., some plants, marine bacteria or plankton), there is still a lack of knowledge of the C : N : P ratios and their variations for numerous taxa, including higher-level consumers (e.g., Frost et al. 2002, 2006). Stoichiometric gradients may also inform on some specific traits such as growth rate, food preferences, nutrient acquisition, and on some life history traits type such as fecundity, or even genome and cell size (see review in Carnicer et al. 2015). Indeed, stoichiometric ratios have the advantage of being directly related to organismal growth rates, which are central life history traits. The "growth

rate hypothesis" demonstrates that rapidly growing organisms commonly have low biomass C : P and N : P ratios. This observation is explained by a high demand for P-rich ribosomal RNA, but also by the shorter lifespan of faster growing organisms, which prevents large investments into reserve structures (Elser et al. 1996, 2003). Consumers stoichiometry, in addition to metabolic characteristics, also gives important information on consumers driven nutrient recycling (Allen and Gillooly 2009). Better documenting the stoichiometric ratios of aquatic organisms in existing trait databases would help to identify their drivers and thus improve our understanding of the impact of stoichiometric traits on food web dynamics and ecosystem functioning.

From aquatic functional traits to global biogeochemical cycles

Finally, studying aquatic food webs following a FTBA should improve predictions of nutrient and carbon fluxes at the ecosystem scale (Vanni and McIntyre 2016). For example, trait-based models of food webs could be constructed to infer trophic interactions influencing ecosystem stocks and fluxes (Woodward et al. 2005). In addition to size and stoichiometry, several other functional traits could be taken into account in these models, such as predator foraging and prey vulnerability traits (Boukal 2014). To do so, one promising pathway is to increase the exploitation of trait databases. For example, global datasets of marine plankton abundances and biomass were recently coupled with a trait-based model used to predict dominant feeding strategies in pelagic ambush predators and to estimate the effects of these feeding traits on energy and biomass transfer efficiency (Prowe et al. 2019). For fish, diets and trophic strategies can be predicted from their functional traits (Albouy et al. 2011). This approach could be extended to other aquatic organisms. Scaling-up from individual traits to food web dynamics should ultimately contribute to better understand the response of aquatic ecosystems to environmental changes in terms of biogeochemical cycling, ultimately improving long-term prediction of ecosystem dynamics and feedback mechanisms to climate.

Conclusions

The main goal of FTBAs is to improve our understanding of the links between community structure, ecosystem function and ecosystem service provision. The main advantages of such approaches come from the definition of traits at the individual level. Indeed, this allows for the direct measurement of the functional traits of any organism without an additional step of taxonomic assignment that may be time-consuming. This can also provide access to universal ecological rules (transcending trophic levels and ecosystems). On the contrary, FTBAs would neither be adapted to study population dynamics that require taxonomic description at the species level, nor to directly estimate bulk properties of the communities (which would require summing of individual-level information). For these reasons, the description and quantification of functional traits provide a common basis across diverse ecological fields, from ecophysiology to community and ecosystem ecology, via population and evolutionary biology. Yet, distinct questions and methods are often specific to each identified habitat (i.e., benthic and pelagic) or even to each biological compartment (i.e., invertebrates and diatoms for the freshwater benthic habitat). Here, we proposed functional trait-based pathways across multiple ecological components. As a first step, we (1) homogenized the terminology used in FTBAs and provided a common typology for aquatic functional traits that can be used across various aquatic systems and for multi-compartment studies, (2) listed the currently available databases dedicated to (aquatic) functional traits, (3) described classical and emerging methods for estimating traits of marine and freshwater organisms, and (4) highlighted some key traits that could be used for multicompartment and trans-ecosystem studies. Establishing such a common ground among aquatic ecologists is required to further encourage and stimulate collaborative research across disciplines. The next step would be to create a common ontology dedicated to FTBAs, such as the Open Traits Network initiative (Gallagher et al. 2019), in order to improve the sharing of trait information in databases.

The recent methodologies we described offer new opportunities to study traits at various scales, from -omic sequences to whole-ecosystem approaches and biogeochemical cycles. Imaging, -omics and modeling tools are among the most promising emerging approaches to work with traits across the tree of life. We propose extending discussions within aquatic ecologists, including freshwater, marine, benthic, and pelagic fields, to better share expertise in these tools, thereby improving our knowledge on potential and realized functional traits. With these methodologies, FTBAs provide promising foundations for the development of integrated frameworks that combine ecological theories with empirical knowledge across scales.

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Supporting Information

Code and resource for the bibliographic network (Fig. S1) is available at: https://github.com/severine13/Biblio-Functional-traits. The mental map presenting the functional trait typology is available online at http://doi.org/10.5281/zenodo.3635898.

Conflict of interest

None declared.

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