


Use of trait concepts and terminology in freshwater ecology: Historic, current, and future perspectives

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Abstract

1. Trait-based approaches have received increasing interest among freshwater scientists given their capacity to predict community structure and biodiversity effects on ecosystem functioning. However, the inconsistent development and use of trait concepts and terms across freshwater scientific disciplines may have limited realisation of the potential of traits.
2. Here, we reviewed trait definitions and terms use to provide recommendations for their consistent application in freshwater science. To do so, we first reviewed literature to identify established trait definitions, historical and current use of trait terms and challenges restricting the application of trait-based approaches in freshwater science. Next, we surveyed 414 freshwater researchers from 54 countries to assess variability in the current use of trait terminology in relation to respondent characteristics (i.e., professional experience, geographical region, research discipline, and focal freshwater ecosystem, biotic group, and ecosystem function).
3. Our literature review identified two well-established trait definitions, which emphasise individual phenotypic characteristics that influence either eco-evolutionary aspects (i.e., organism performance and fitness) or ecosystem dynamics and processes (i.e., responses to the environment and/or effects on ecosystem functioning). Publications used a range of trait-related terms and their frequency of use varied among scientific fields. The term *functional trait* dominated fields such as biodiversity conservation, environmental sciences and ecology, plant sciences and microbiology. In contrast, the terms *biological trait*, *functional trait*, and *species trait* were used with similar frequencies in fields such as entomology, fisheries, marine and freshwater biology, and zoology. We also found that well-established trait definitions are difficult to apply to freshwater unicellular organisms, colonial multicellular organisms, genomic information, and cultural traits.
4. Our survey revealed highly inconsistent use of trait terms among freshwater researchers. Terms including *biological trait*, *functional trait*, *structural measure*, and

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ecosystem function were commonly used to describe the same traits or functions. Variability in the use of terms was generally explained by research discipline, geographical region, and focal biotic group and ecosystem functions.

5. We propose making the trait concept flexible enough to be applicable to all freshwater biota and their characteristics, while keeping and integrating links to eco-evolutionary and ecosystem aspects. Specifically, our new definition expands the established functional trait definition by considering also supra-individual scales of trait measurement (colonial- or community-mean traits), genotypic traits (e.g., functional gene markers of enzymes) and cultural traits (e.g., feeding behaviours, communication skills). To reduce terminological ambiguity, we also recommend that researchers define trait terms, prioritising the use of *functional trait* as an overarching term over alternative terms (e.g., *biological trait*), and restricting specific terms (e.g., *morphological trait*) to situations in which such precision is desirable. The findings of our integrative study could help to improve terminological consistency across freshwater disciplines and to better recognise the potential of traits to elucidate the mechanisms behind ecological patterns.

KEYWORDS

biological trait, ecosystem functioning, functional trait, species trait, trait-based ecology

1 | INTRODUCTION

Trait-based approaches have received growing interest from freshwater researchers in recent decades (Litchman & Klausmeier, 2008; Martini et al., 2021; Townsend & Hildrew, 1994). This increasing attention reflects the potential of traits to generate a mechanistic understanding of multiple aspects of freshwater ecosystems (Verberk et al., 2013), including biodiversity effects on ecosystem functioning (Hébert et al., 2016), trophic interactions (Gutiérrez-Cánovas et al., 2021), responses to natural and anthropogenic stressors (Belmar et al., 2019; Dolédec & Statzner, 2008), and the effectiveness of restoration measures (Dolédec et al., 2015; van Kleef et al., 2006). A key advantage of trait-based approaches over traditional taxonomic information is their capacity to identify general rules and mechanisms governing community structure and ecosystem functioning (Lavorel & Garnier, 2002; McGill et al., 2006). The rationale is that organism traits capture aspects of individual performance (McGill et al., 2006; Violle et al., 2007), ecological niches (Devictor et al., 2010; Poff et al., 2006), biotic interactions (Kraft et al., 2015), and functional roles (Díaz & Cabido, 2001) more effectively than taxonomic identities. Traits thus represent a continuum of ecological strategies that evidence evolutionary and biophysical trade-offs (Díaz et al., 2015), in turn influencing susceptibility to extinction (Cooke et al., 2019). Traits may also enhance spatiotemporal comparability of communities relative to taxonomic methods (Chakraborty et al., 2020; Dolédec et al., 1999; Kearney & Porter, 2009), because they are broadly shared across ecosystems, regions, and the tree of life (Carmona et al., 2021). For example,

traits, such as the body size (i.e., individual biomass) or elemental content (i.e., stoichiometric traits) of different organisms, can be compared across ecosystems and over latitudinal gradients (Beck et al., 2022; Moleón et al., 2020; Woodward et al., 2005). However, inconsistent use of trait concepts and terminology across research disciplines, ecosystems, and biotic groups can limit the benefits provided by trait-based approaches (Dawson et al., 2021; Kunz et al., 2022; Martini et al., 2021).

The use of diverse trait definitions and perspectives within scientific fields may have contributed to varying interpretations and implementations of these concepts in freshwater science. Well-established trait definitions focus on the phenotypic features of organisms, which are measured at the individual level and which influence performance (Violle et al., 2007), responses to the environment (Mori et al., 2013) and/or ecosystem functioning (Lavorel & Garnier, 2002). However, these complementary definitions have been differently adopted and developed across scientific disciplines, potentially limiting the progress that could be made by the trait-based approach and the potential for interdisciplinary collaboration. For example, studies in freshwater ecosystems have usually focused on trait-based responses over environmental gradients (Hamilton et al., 2020; Passy, 2007; Townsend et al., 1997), with a limited investigation of which traits explain the functioning, trophic dynamics and biogeochemistry of freshwater ecosystems (Lecerf et al., 2006; Vinebrooke et al., 2004; but see Litchman et al., 2015 and Hébert et al., 2016). In addition, because of the original focus on individual-scale features and inheritable phenotypes, new challenges emerge when extending trait concepts to microorganisms,

colonial organisms, genomic features and non-inheritable traits (Dawson et al., 2021; Kremer et al., 2017; Lajoie & Kembel, 2019). This restricted conceptual and research focus limits current applications of trait-based approaches in freshwaters, highlighting the need to clarify and adapt trait concepts to encompass all freshwater biota and their characteristics.

The use of multiple trait terms, with contrasting links to well-established trait concepts, has also limited terminological comparability and consistency in and beyond freshwater research. Some trait terms used in freshwater research, such as *functional trait*, were borrowed from plant ecologists (Poff et al., 2006), reflecting well-established concepts. Other terms originated in freshwater research, such as the *biological and ecological trait* framework (Tachet et al., 2002; Usseglio-Polatera et al., 2000), and simpler (e.g., *species traits, traits*; Townsend et al., 1997) or nuanced forms were also adopted (e.g., *life-history traits*; Verberk et al., 2008). Thus, the availability of a diverse pool of terms now poses difficulties in deciding when and how they should be used and if they represent comparable concepts and attributes. In addition, this terminological variability may be linked to the independent generation of trait databases across geographical regions, research disciplines and biotic groups (Maasri, 2019; Martini et al., 2021; Weiss & Ray, 2019). For example, exhaustive trait databases have been developed for macroinvertebrates and fish in different regions, but using different traits and trait coding approaches (Cano-Barbacid et al., 2020; Kunz et al., 2022; Schmidt-Kloiber & Hering, 2015). Also, whereas trait-based approaches have mainly been applied to macroinvertebrates in riverine ecosystems (Dolédec & Statzner, 2010; Statzner et al., 2001), lake ecologists have concentrated on phytoplankton (Padišák et al., 2009; Reynolds et al., 2002). In parallel, diatom (Lange et al., 2016; Litchman & Klausmeier, 2008; Passy, 2007) and zooplankton ecologists (Hébert et al., 2016) have developed trait databases that encompass all aquatic environments. In contrast, aquatic plants are largely under-represented in existing functional trait repositories (Dalla Vecchia et al., 2020). Therefore, understanding how researcher characteristics affect their use of trait concepts and terms could identify biases and inform recommendations for harmonised use.

Here, we review trait definitions and term use to provide recommendations for their consistent application in freshwater science and to address conceptual limitations that constrain the application of trait-based approaches. Specifically, we first review and evaluate well-established trait definitions and the historical use of trait terminology in freshwater literature. We also identify limitations in the application of well-established trait concepts in freshwater science. We then characterise patterns of current trait term use in freshwater science through a survey of international freshwater researchers, in which we also determine how respondent characteristics (e.g., geographical region, discipline) influence variability in current trait term use. Finally, we develop an integrative definition of the functional trait concept and make recommendations to support consistent use of trait concepts and terminology.

2 | TRAIT DEFINITIONS, TERMS, AND LIMITATIONS: A REVIEW

2.1 | Well-established trait definitions

Early use of the trait concept dates back to Greek times (300BCE), where Theophrastus provided the first conceptualisation of functional diversity and classified plants according to their height and stem density (for details of the historical development of trait concepts see Laureto et al., 2015). More recently, Darwin used functional traits to explain niche partitioning and differentiated ecological functions in Galapagos finches based on their beak size (Darwin, 1859). Plant ecologists then came to lead the use and development of trait concepts, classifications, and theories (Díaz & Cabido, 2001; Grime, 1977; Raunkjær, 1934), resulting in the use of widely accepted trait concepts and terms within plant ecology (Lavelle & Garnier, 2002; McGill et al., 2006; Violle et al., 2007). Violle et al. (2007; pp. 884) provide perhaps the most widely used definition of a trait, as “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 [biological] organization”. From this core, two well-established functional trait definitions emerged with either an eco-evolutionary or ecosystem focus. The eco-evolutionary view considers functional traits as well-defined characteristics measured at the individual level that influence organism performance (McGill et al., 2006; Violle et al., 2007) and, ultimately, fitness (Arnold, 1983; Laughlin et al., 2020). Thus, eco-evolutionary definitions are based on a hierarchical interdependence among traits, performance and fitness, reflecting how fitness is maximised by the phenotypic attributes (traits) best adapted to an environment (i.e., environmental selection; Arnold, 1983; Violle et al., 2007). In contrast, ecosystem-focused definitions consider functional traits as characteristics of an organism that influence its response to environmental change and/or its effects on ecosystem functioning (Díaz & Cabido, 2001; Lavelle & Garnier, 2002; Suding et al., 2008), i.e., on the processes that regulate ecosystem-level fluxes of energy or matter, such as biomass production, organic matter decomposition, or nutrient cycling (Hooper et al., 2005; Jax, 2005). However, comparable functional trait profiles can differentially affect performance (Pilière et al., 2016) and/or ecosystem functions (van der Plas et al., 2020) in different organisms and environmental contexts. Such context-dependency might constrain the realisation of the advantages provided by trait-based approaches (Kremer et al., 2017; Poff et al., 2003; Vaughn, 2010).

Within the context of the ecosystem-centred definition, functional traits can be further classified according to their influence on community responses or ecosystem aspects, using the *response-effect trait* classification (Lavelle & Garnier, 2002; Mori et al., 2013; Suding et al., 2008). Traits are also classified according to the nature of their measurement, using the *hard-soft trait* classification (Hodgson et al., 1999). As such, *soft traits* are easy to measure features that provide a rough representation of performance (e.g., body

size), whereas *hard traits* better capture variations in performance, but are more difficult and expensive to measure (e.g., metabolic rate). However, trait plasticity may not relate to fitness (Acasuso-Rivero et al., 2019), which may prevent accurate classification of organism features into *hard* and *soft traits*.

Despite their different emphases, the eco-evolutionary and ecosystem-centred definitions are complementary. Both definitions generally describe traits as individual attributes, but they differ in the scale at which trait effects are evaluated. Whereas the eco-evolutionary definition assesses effects on individual performance and consequences for population dynamics, the ecosystem-centred definition focuses on community- and ecosystem-level effects. Nonetheless, these ecological scales are interrelated because community-level responses to environmental change depend on the aggregated response of individual performances (Lavorel & Garnier, 2002; McGill et al., 2006; Violle et al., 2007). As such, most conceptual studies adopting the eco-evolutionary definition make explicit links with ecosystem functioning (Table 1). In addition, ecosystem functioning is also affected by changes in organism performance, influencing per capita effects on ecosystem processes and properties (Geber & Griffen, 2003; Suding et al., 2008; Violle et al., 2007). For example, the trait *growth rate* influences measures of individual survival (an aspect of performance), which can help to predict secondary production and community biomass.

2.2 | Historical and current use of trait definitions and terms across disciplines

Both eco-evolutionary and ecosystem-centred trait definitions have been adopted, with perspectives and use of terms varying among disciplines (Table 1). Most studies adopting the eco-evolutionary trait definition also acknowledge that functional traits are drivers of a community's environmental responses and ecosystem functioning (e.g., Litchman & Klausmeier, 2008; Mouillot et al., 2013; Violle et al., 2007). In some cases, authors explicitly adopted and combined both definitions to highlight their strong interrelationship (Dawson et al., 2021; Fontana et al., 2021; Luck et al., 2012). Traits are generally described as individual attributes (Table 1), but some conceptual studies do not specify the scale of trait measurement (e.g., Hooper et al., 2005) or suggest integrative scales spanning genes and proteins (Kremer et al., 2017) to supra-individual aggregations, such as populations (Luck et al., 2012), colonies (Dawson et al., 2021; Fontana et al., 2021), or biofilms (Escalas et al., 2019; Krause et al., 2014). Individual-based definitions assume that species-level traits are calculated as a mean or fuzzy-coding profile of a given feature across individuals of the same species, but this approach might be challenging to adopt for microorganisms, for which the individual boundary is unclear. In some cases, mean trait values for a given taxon can be obtained from cultured colonies or artificial assemblages (Graça et al., 2022; Krause et al., 2014; Lennon et al., 2012). However, the most common approach is to use community-mean traits and associated variance (Escalas et al., 2019;

Fierer et al., 2014), which contrasts with established functional trait definitions.

To review patterns of trait term use in the published literature, we conducted a search in Web of Science of three typical broad trait terms ("biological trait*", "functional trait*", "species trait*") on 31 May 2021. We retained records from scientific fields encompassing ecological and related scientific fields, which we used to illustrate historical and current patterns of trait use. For more details about our literature review methodology see Methods S1. This search identified 82,325 articles and reviews containing one of three typical broad trait terms, where the *functional trait* term was used more (60%) than the *biological trait* (18%) and *species trait* (22%) terms (see full results in Table S1). In particular, *functional trait* dominated in plant sciences (75%; 6,114 of 8,124 records), microbiology (73%; 765 of 1,042), biodiversity conservation (64%; 5,683 of 8,920) and environmental sciences—ecology (62%; 8,977 of 14,479; Figure 1). In contrast, in the fields of entomology, fisheries, marine and freshwater biology and zoology, use of these three terms was more variable, with no term having a frequency of occurrence >50% (Figure 1). Although not dominant, the term *biological trait* was used more frequently in fisheries (45%; 183 of 409), entomology (38%; 329 of 868), marine and freshwater biology (28%; 1,003 of 3,596) and zoology (25%; 1,741 of 6,849 records) than in biodiversity conservation (11%; 987 of 8,920) and plant sciences (8%; 640 of 8,124; Figure 1).

2.3 | Historical use of trait terms in freshwater research

Freshwater disciplines developed trait-based approaches based on different theoretical frameworks, adopting a range of definitions (Table 2). For example, trait-based approaches for fishes (Olden et al., 2006), macroinvertebrates (Olden et al., 2006; Schmera et al., 2017; Townsend & Hildrew, 1994), and phytoplankton (Litchman & Klausmeier, 2008; Reynolds et al., 2002) have adopted eco-evolutionary definitions, with a greater focus on predicting responses to environmental change. In contrast, zooplankton (Hébert et al., 2016, 2017), phytoplankton (Litchman et al., 2015; Litchman & Klausmeier, 2008), and macrophyte ecologists (Dalla Vecchia et al., 2020; Fu et al., 2018) tended to adopt ecosystem-centred definitions, considering both environmental responses and effects on ecosystem functioning. In other cases, fish ecologists have adopted eco-evolutionary definitions and concepts (Cano-Barbacid et al., 2020), but explicitly acknowledge trait influences on ecosystem functioning (Villéger et al., 2017). Associated with this conceptual variability, trait-based studies conducted across freshwater ecology and related disciplines have introduced a range of broad and specific terms (Table 2). Broad trait terms usually meet well-established trait definitions, and most can be considered as synonyms as they are generally used to refer to the same organism features. Examples include *biological trait* (Usseglio-Polatera et al., 2000), *functional trait* (Martini et al., 2021), *species trait* (Statzner et al., 1994; Townsend & Hildrew, 1994), or simply

TABLE 1 Variation in trait definitions and trait scale of measurement across organisms and environments for a list of influential and/or recent conceptual frameworks.

| Term | Reference | Type of definition | Measurement scale | Focal organism | Citations |
|-----------------------|--------------------------------|-------------------------------|-------------------|----------------|-----------|
| Trait | McGill et al. (2006) | Eco-evolutionary | Individual | Broad | 4397 |
| | Violle et al. (2007) | Eco-evolutionary ^a | Individual | Plants | 4227 |
| | Sobral (2021) | Eco-evolutionary ^a | Individual | Plants | 9 |
| | Dawson et al. (2021) | Both ^b | Flexible | Broad | 8 |
| Functional trait | Díaz and Cabido (2001) | Ecosystem-centred | Individual | Plants | 3482 |
| | Lavorel and Garnier (2002) | Ecosystem-centred | Individual | Plants | 3357 |
| | Naeem and Wright (2003) | Ecosystem-centred | ns | Broad | 808 |
| | Hooper et al. (2005) | Ecosystem-centred | ns | Broad | 8462 |
| | McGill et al. (2006) | Eco-evolutionary | Individual | Broad | 4397 |
| | Petchey and Gaston (2006) | Ecosystem-centred | ns | Broad | 2422 |
| | Violle et al. (2007) | Eco-evolutionary ^a | Individual | Plants | 4227 |
| | Litchman and Klausmeier (2008) | Eco-evolutionary ^a | ns | Phytoplankton | 1104 |
| | Suding et al. (2008) | Ecosystem-centred | Individual | Plants | 1265 |
| | Reiss et al. (2009) | Ecosystem-centred | Individual | Broad | 660 |
| | Laliberté et al. (2010) | Ecosystem-centred | ns | Plants | 589 |
| | Luck et al. (2012) | Both ^b | Individual | Vertebrates | 253 |
| | Mori et al. (2013) | Ecosystem-centred | ns | Broad | 558 |
| | Mouillot et al. (2013) | Eco-evolutionary ^a | Individual | Broad | 1460 |
| | Krause et al. (2014) | Both | Individual | Microorganisms | 337 |
| | Kremer et al. (2017) | Eco-evolutionary ^a | Individual | Broad | 38 |
| | Moretti et al. (2017) | Both ^b | Individual | Invertebrates | 299 |
| | Dawson et al. (2019) | Eco-evolutionary ^a | Individual | Fungi | 46 |
| | Escalas et al. (2019) | Both ^b | Flexible | Microorganisms | 89 |
| | Lajoie and Kembel (2019) | Eco-evolutionary ^a | ns | Microorganisms | 34 |
| Weiss and Ray (2019) | Ecosystem-centred | Individual | Broad | 59 | |
| Zanne et al. (2020) | Eco-evolutionary ^a | ns | Fungi | 132 | |
| Fontana et al. (2021) | Both | Flexible | Broad | 7 | |

^aTraits are defined according to the eco-evolutionary definition, but authors explicitly link traits to ecosystem functioning; ns: scale of measurement non-specified.

^bTraits are not directly defined by authors, but they made explicit links between traits, performance, environmental responses and ecosystem functioning. Citations were retrieved from Google Scholar on 10/11/2022.

trait (Schmera et al., 2015). A notable exception is the term *ecological trait*, which makes explicit reference to environmental preferences and thus does not meet well-established trait definitions (e.g., Violle et al., 2007). Ecological traits are typically part of the *biological-ecological trait* framework (Cano-Barbacid et al., 2020; Tachet et al., 2002; Usseglio-Polatera et al., 2000), representing organism-specific environmental preferences inferred from their spatial distribution and from individual measurements (Moretti et al., 2017). Ecological traits represent elements of the realised (Grinnellian) niche, but not the organism features responsible for these environmental preferences (e.g., growth rate, morphology) (Devictor et al., 2010; Mondy & Usseglio-Polatera, 2014).

Besides, freshwater scientists use a wider range of specific trait terms that refer to particular organism characteristics. Examples of

such terms include *behavioural trait* (Harris et al., 2011), *cultural trait* (Cantor et al., 2015), *ecological guild* (Passy, 2007), *functional feeding group* (Cummins & Klug, 1979; Wallace & Webster, 1996), *functional response* (Stefani et al., 2020), *functional genes* (Burke et al., 2011), *geographic trait* (Dawson et al., 2021), *life-history trait* (Blanck & Lamouroux, 2007), *morphological trait* (Sarremejane et al., 2020), *phenological trait* (Haraldstad et al., 2017), *thermal trait* (Duffy et al., 2021), *trophic group* (Cummins, 1973), *stoichiometric trait* (Beck et al., 2022), and *structural characteristic* (Petrie, 2005). However, some of these terms conflict with well-established trait definitions. For example, *geographic trait* (e.g., range size) neither meets well-established *functional trait* definitions, nor is typically considered as a *functional trait* by researchers (Dawson et al., 2021). In other cases, the same term (e.g., thermal preference, salinity tolerance) can be

used to describe *functional traits*—because they are directly measured on organisms without any reference to the environment—or environmental preferences—because they are inferred from spatial distributions—which may lead to terminological confusion. Trait terms describing tolerances to abiotic factors can be considered as

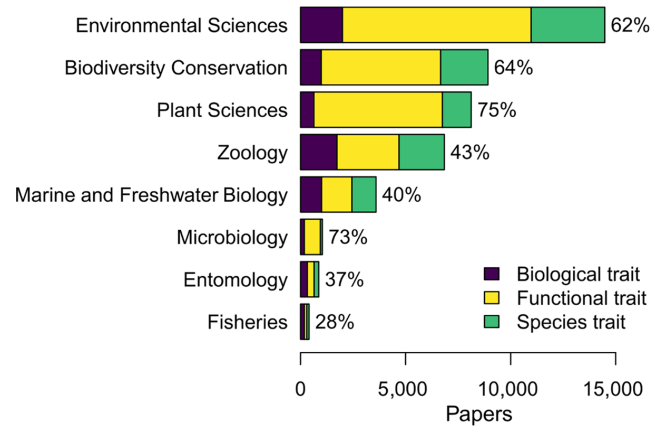


FIGURE 1 The number of papers including the terms *biological trait*, *functional trait*, or *species trait* and the percentage of studies using *functional trait* in different research disciplines, as identified by our literature review.

functional traits only when they are measured experimentally on organisms (e.g., critical lower and upper thermal limits), so they reflect aspects of the fundamental niche (Devictor et al., 2010). Both *geographic traits* and *ecological traits* represent aspects of the realised niche that result from complex interplay among multiple *functional traits* and biotic interactions, and should be considered as outside of the *functional trait* concept. Terms such as *structural characteristic* or *structural trait* (Verbeeck et al., 2019) may be also interpreted inconsistently, because 'structure' and 'structural' have various meanings and are used at multiple levels of biological organisation, ranging from community features (e.g., taxonomic richness) to ecosystem properties (e.g., standing stocks).

2.4 | Limitations of well-established trait definitions in freshwater research

Despite the inclusive nature of well-established trait definitions, their focus on multicellular organisms and genetically inheritable phenotypic features have limited the application of trait-based approaches in freshwater ecology and other disciplines. These limitations highlight that trait definitions require adaptation to recognise all types of individual and aggregated organisms and their characteristics

TABLE 2 Variation in trait term use and conceptual relationships across a list of influential and/or recent conceptual studies for freshwater organisms.

| Terms | References | Focal organisms | Type of definition |
|-------------------------------------------------|---------------------------------|-----------------------------|-------------------------------|
| Biological trait/Functional trait/Species trait | Poff et al. (2006) | Invertebrates | Eco-evolutionary |
| | Schmera et al. (2017) | Macroinvertebrates | Eco-evolutionary ^a |
| Biological trait/Species trait | Statzner et al. (2001) | Invertebrates | Eco-evolutionary |
| | Lamouroux et al. (2002) | Fishes | Eco-evolutionary |
| Biological-ecological traits | Usseglio-Polatera et al. (2000) | Invertebrates | Eco-evolutionary |
| | Tachet et al. (2002) | Invertebrates | Eco-evolutionary |
| | Cano-Barbacid et al. (2020) | Fishes | Eco-evolutionary |
| Ecological guilds | Passy (2007) | Diatoms | Eco-evolutionary |
| | Rimet and Bouchez (2012) | Diatoms | Eco-evolutionary |
| Functional group | Vannote et al. (1980) | Macroinvertebrates | Both |
| | Reynolds et al. (2002) | Phytoplankton | Eco-evolutionary |
| Functional trait | Litchman and Klausmeier (2008) | Phytoplankton | Eco-evolutionary |
| | Fu et al. (2018) | Macrophytes | Both |
| | Hébert et al. (2016) | Zooplankton | Ecosystem-centred |
| | Villéger et al. (2017) | Fishes | Eco-evolutionary ^a |
| | Dalla Vecchia et al. (2020) | Macrophytes | Eco-evolutionary ^a |
| | Martini et al. (2021) | Broad | Eco-evolutionary |
| | Hose et al. (2022) | Invertebrates | Ecosystem-centred |
| Trophic categories and relationships | Cummins (1973) | Macroinvertebrates | Both |
| | Species trait | Townsend and Hildrew (1994) | Broad |
| Schmera et al. (2015) | | Lotic organisms | Eco-evolutionary |

^aTraits are used following the eco-evolutionary definition, but authors also linked traits to ecosystem functioning.

through better integration of ecological scales and non-inheritable traits.

The trait concept was developed for multicellular individual organisms, limiting its application to unicellular life forms and conspecific organisms living in close association (colonies), for which trait definitions remain elusive (Escalas et al., 2019; Lajoie & Kembel, 2019). For example, in animals or plants, environmental filtering generally operates at the individual level (McGill et al., 2006; Violle et al., 2007). As a result, inheritable, individual-level traits of multicellular organisms that maximise performance or fitness in a given environment can be identified and their vertical heritability tracked from a single individual to its descendants. However, the application of the trait concept to the microbial world is limited (Lajoie & Kembel, 2019). First, because unicellular organisms can aggregate into colonies or biofilms, which functionally operate as a whole (Battin et al., 2016; Escalas et al., 2019; Krause et al., 2014), making their environmental responses and the effects of individual cells on ecosystem functioning difficult or impossible to isolate. A similar limitation applies to multicellular colonial organisms, such as eusocial insects, corals, or bryozoans, where colony traits influence individual performance, responses to the environment and/or ecosystem functions (Brittain & Potts, 2011; Linksvayer & Janssen, 2009; McWilliam et al., 2018). Second, some microorganisms can acquire genes from other species, for example, by horizontal gene transfer (Abby et al., 2012; Polz et al., 2013), limiting the capacity to relate inherited cell traits to fitness. Third, whereas some functional traits can be measured at the cellular level (e.g., cell size, shape, and cell wall structure; Litchman & Klausmeier, 2008), others are difficult to measure or cannot be attributed to a single cell (e.g., exo-enzymatic activity and photosynthetic pigment composition; Gionchetta et al., 2020; Colls et al., 2021).

The strong emphasis of well-established definitions on phenotypic traits also challenges the recognition of genomic and transcriptomic characteristics as traits, even though these features underlie the phenotype (Fontana et al., 2021) and are widely used as traits in microbial ecology. For example, ecologists have traditionally focused on easy-to-measure traits such as body size or leaf area, which result from a complex network of molecular mechanisms and interactions (e.g., gene expression and metabolic pathways). Recent conceptual advances call for the integration of a continuum of traits across biological scales (from genes to phenotypes) to better reflect the range of mechanisms and other factors influencing performance, environmental responses and effects on ecosystem functioning (Fontana et al., 2021; Kremer et al., 2017). Thus, genotypes, metabolic pathways and phenotypes would represent an increasing gradient of trait integration, in which phenotypes result from the interaction of multiple traits at lower scales (Goberna & Verdú, 2016). This may represent a promising avenue that enables extension of trait-based approaches to microorganisms (Fierer et al., 2014; Wallenstein & Hall, 2012; Wang et al., 2022), for which available trait data based on genes (genomics), RNA (transcriptomics), proteins (proteomics), and metabolites (metabolomics) are rapidly growing.

Finally, limitations of the well-established trait concepts also affect some macroorganism characteristics, which are not genetically inherited. For example, despite the strong influence of learned behaviours on performance and fitness, the corresponding term *cultural trait* does not meet well-established eco-evolutionary definitions given that these traits are not inherited genetically, but passed by knowledge transfer between generations (Cantor et al., 2015; Dawson et al., 2021; Sheppard et al., 2018).

3 | SURVEY OF FRESHWATER SCIENTISTS TO ASSESS USE OF TRAIT TERMS

3.1 | Survey design and data analysis

To assess variability in the use of trait-related terminology and potential biases attributed to respondent characteristics (e.g., expertise or geographical region), we created an anonymous online survey using Google forms (<https://www.google.es/intl/en/forms/about/>). We distributed this survey through mailing lists of scientific societies and networks (European Federation of Freshwater Sciences, Global Lake Ecological Observatory Network, Iberian Association of Limnology, Macrolatinos network, and the Science and Management of Intermittent Rivers and Ephemeral Streams COST Action), our own contacts and social networks (i.e., Twitter). The survey was active from April to September 2020. We obtained responses from 414 freshwater scientists based in 54 countries, covering all inhabited continents. Respondents participated on a voluntary basis and were informed about the purpose of the survey prior to participation. Respondents did not provide any personal information that could be used to identify them, which guaranteed that answers remained anonymous.

Our survey included six questions summarising respondent characteristics: (1) their professional research experience; (2) the country in which they were based; and their (3) focal freshwater ecosystem type(s); (4) research area; (5) focal biotic group(s); and (6) focal ecosystem function(s) (Table S2). Responses included fixed answers and a free-text field. To summarise responses and enhance the statistical power of our data analysis, original survey responses for Q1–4 were grouped into existent or new categories. The resultant categories for each respondent characteristic are in shown in Table S3.

The survey also included seven questions designed to determine how freshwater scientists use trait terminology (Q7–Q13; Table S4). Question 7 assessed terminological consistency in relation to the ecosystem-centred definition of a trait, asking respondents to select *biological trait*, *ecosystem function*, *functional trait* or *none* as the term they used to refer to any well-defined, measurable characteristic of an organism. Questions 8–12 assessed consistency in the use of trait terms by asking respondents to use one of five terms (*biological trait*, *ecosystem function*, *functional trait*, *structural measure*, *I don't know*) to classify six measures commonly used in freshwater science: a measure of (Q8) body size; (Q9) community-level enzymatic activity; (Q10) chlorophyll-*a* content at the individual level; (Q11) plant growth

form/life form; (Q12) nutrient uptake at the individual level; and (Q13) organic matter decomposition. These measures represent potential challenges for trait measurement in a wide range of organisms, including macroorganism and microbial characteristics at individual and ecosystem levels. Finally, a multiple-choice question (Q14) assessed respondents' familiarity with trait classifications, by choosing how many they know (*none*, *biological-ecological traits*, *response-effect traits*, *hard-soft traits*). The survey data are available in Data S1.

To measure the consistency of responses to Q7–Q13, we estimated Pielou's evenness (J) across the relative frequency of answers to each question, where 0 indicates that all respondents selected the same answer and 1 indicates equal distribution across all answers. We explored if respondent characteristics influenced the use of trait terminology using a multinomial regression (R package *nnet*; Venables & Ripley, 2016) and multi-model inference (Grueber et al., 2011; R package *MuMIn*; Bartoń, 2016). We built seven multinomial regression models predicting the percentage of use of each trait term in Q7–Q13. Six models included one of the six respondent characteristics as a predictor, plus a null model, which did not include any respondent characteristics but a constant random term. Null models determined if respondent characteristics had a higher predictive capacity than expected by chance. For each question, the seven models were ranked using Akaike information criteria and model weights (w) were calculated accordingly. Model weights were used as proxies of predictor importance, as they indicate the likelihood of being the best model (range 0–1). For each question, we retained models with a cumulative likelihood of $\geq 95\%$ of including the best model (cumulative $w \geq 0.95$).

3.2 | Survey results

Respondents had different levels of research experience, including a relatively even contribution of professors (30.9%), early-career postdoctoral (24.4%), mid-career postdoctoral (24.2%) and predoctoral researchers (20.5%; Figure S1). Surveyed scientists mainly worked in Europe (53.9%) and the Americas (34.5% overall; Central and South America: 18.3%; North America: 16.2%), followed by Oceania (7.5%), Africa (2.4%), and Asia (1.7%). Respondents worked primarily on rivers (60.4%), followed by lakes and reservoirs (23.2%), ponds (6.3%), wetlands (6.0%), and other aquatic systems (4.1%). Community ecology was the most frequent discipline (52.4%), followed by biogeochemistry (20.0%), functional ecology (12.6%), ecohydrology (7.5%), and other disciplines (7.5%). Most surveyed scientists worked with invertebrates (40.1%), followed by those studying multiple organisms (20.8%), microorganisms (15.7%), vertebrates (6.0%), riparian vegetation (3.9%), and macrophytes (2.7%); 10.9% did not study any type of organism. Of the respondents, 35.0% worked with multiple ecosystem functions, followed by trophic interactions (13.3%), organic matter decomposition (8.0%), nutrient cycling (7.5%), and ecosystem metabolism (3.4%); 32.9% did not study any type of ecosystem function.

No answer to the trait definition question (Q7) dominated ($J=0.93$; Figure 2), with responses spread mainly across three

options (Figure 2a): *functional trait* (36.2%); *biological trait* (30.0%); and *name of the measured characteristic* (24.9%). *Ecosystem function* was selected less frequently (8.9%). Variability in these responses was explained by researchers' focal biotic group ($w=0.81$) and discipline ($w=0.18$). *Functional trait* was chosen mainly by those studying riparian vegetation (68.8%), multiple organisms (41.9%), or vertebrates (40.0%). Among disciplines, functional ecologists (50.0%) and community ecologists (38.7%) chose *functional trait* more frequently. Invertebrate ecologists used *biological trait* (38.6%) and *functional trait* (35.5%) with a similar frequency, whereas respondents with no focal biotic group commonly used the *name of the measured characteristic* (53.3%). Microbial ecologists used *functional trait* (32.3%), the *name of the measured characteristic* (30.8%), and *biological trait* (24.6%) at comparable frequencies, with none of them dominating.

Responses to Q8–Q12 were evenly distributed ($J=0.86$ – 0.95), whereas responses to Q13 primarily defined organic matter decomposition as an ecosystem function (72%; $J=0.56$; Figures 2b and 3). Each researcher used a median of three trait terms to answer Q8–Q13. The *I don't know* answer was selected by (mean \pm SD) $11 \pm 5\%$ of respondents per question (range: 6%–20%; Figure 3). Variability in responses to Q8–Q12 was generally explained by researcher discipline and, to a lesser extent, by researcher region and focal ecosystem function (Figure S2).

Body size (Q8) was most frequently described as a *biological trait* (51.2%), followed by *structural measure* (22.0%) and *functional trait* (18.6%). Researcher discipline was the only important predictor of answer variability ($w=1.00$). Community ecologists selected *biological trait* (58.5%) more frequently than other disciplines (38.5%–47.0%). *Structural measure* and *functional trait* were more commonly selected by ecohydrologists (38.7%) and functional ecologists (25.0%), respectively.

Enzymatic activity (Q9) was most frequently described as an *ecosystem function* (34.3%) or *functional trait* (33.3%), with 19.8% selecting *I don't know*. The null model was the most explanatory ($w=0.61$), but geographical region ($w=0.20$) and focal ecosystem function ($w=0.17$) showed some predictive capacity. Researchers from Europe (37.7%) and Oceania (58.1%), and those focusing on organic matter decomposition (51.5%) classified enzymatic activity as an *ecosystem function* more frequently than those based in other geographical areas (0.0%–26.6%) or focusing on other ecosystem functions (12.9%–35.7%).

Chlorophyll-*a* content (Q10) was mostly classified as a *biological trait* (31.6%), followed by *functional trait* (26.3%) and *structural measure* (17.4%). Researcher discipline was the most important predictor of answer variability ($w=0.56$), followed by the null model ($w=0.44$). Ecohydrologists (45.2%) classified *chlorophyll-a* as a *biological trait* more frequently than researchers from other disciplines (9.7%–36.1%). A substantial proportion of community ecologists (28.1%), functional ecologists (26.9%), and biogeochemists (25.3%) described this measure as a *functional trait*.

Plant growth form (Q11) was most frequently classified as a *biological trait* (40.6%), followed by *functional trait* (30.0%) and *structural*

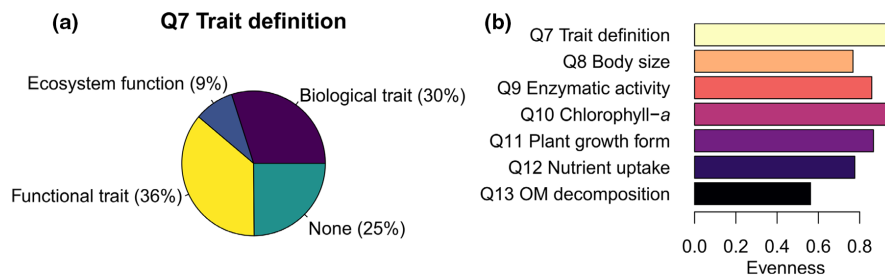
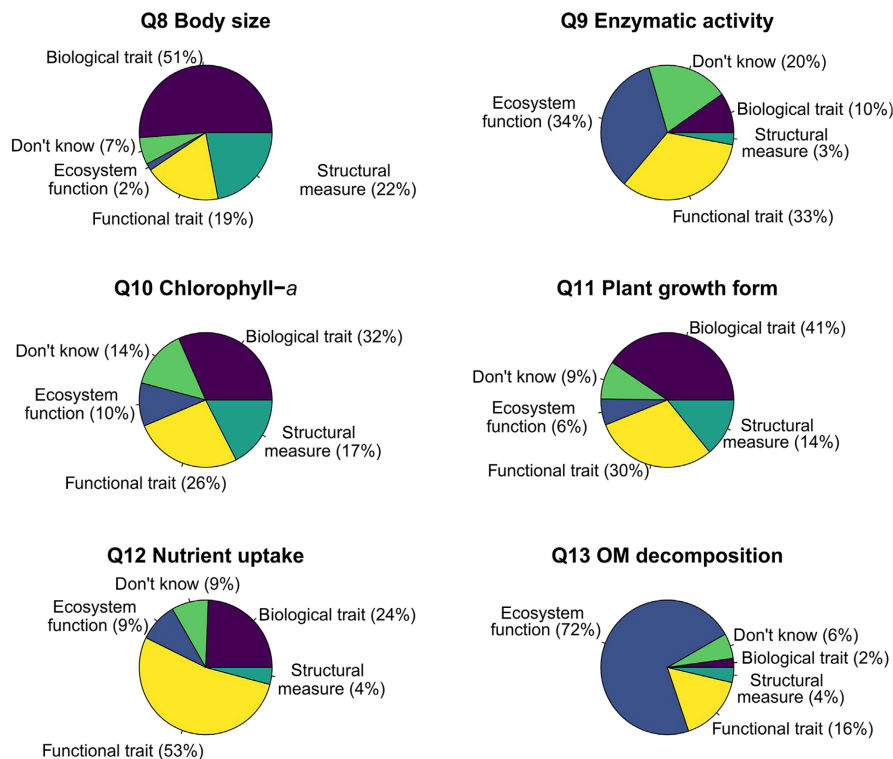


FIGURE 2 Survey results showing: (a) the percentage of respondents using each broad term to refer to any well-defined, measurable characteristic of an organism that influences its effects on ecosystem functioning and/or its responses to environmental factors (Q7); and (b) variability in responses (Pielou's evenness) to Q7 and to questions about terms that best represent measures of (Q8) body size, (Q9) enzymatic activity, (Q10) chlorophyll-*a*, (Q11) plant growth form, (Q12) nutrient uptake, and (Q13) organic matter (OM) decomposition, where 0 indicates that all respondents selected the same answer and 1 indicates equal distribution across all answers. Potential answers to Q8–Q13 were: *biological trait*, *ecosystem function*, *functional trait*, *structural measure*, and *I don't know*.

FIGURE 3 Survey results showing the percentage of respondents selecting each term to best represent measures of (Q8) body size, (Q9) enzymatic activity, (Q10) chlorophyll-*a*, (Q11) plant growth form, (Q12) nutrient uptake, and (Q13) organic matter (OM) decomposition.



measure (14.0%). Variability in these responses was mainly explained by geographical region ($w=0.89$). Most researchers based in Oceania (54.8%) classified this measure as a *biological trait*, whereas those based in Europe described it as either a *biological trait* (43.9%) or a *functional trait* (35.0%). Responses of researchers based in North and South America, and Asia and were evenly distributed across *biological trait* (42.9% and 34.3%, respectively), *functional trait* (28.6% and 26.6%, respectively) and *structural measure* answers (28.6% and 22.4%, respectively). Researchers based in Africa classified this measure more frequently as an *ecosystem function* (30.0%) than as a *functional trait* (20.0%) or *biological trait* (10.0%).

Nutrient uptake (Q12) was most frequently described as a *functional trait* (53.1%), followed by *biological trait* (24.4%) and *ecosystem function* (9.4%). Organic matter decomposition (Q13) was most commonly described as an *ecosystem function* (72.0%), followed by *functional trait*

(16.2%), with 6.0% selecting *I don't know*. For both questions, variability in responses was poorly explained by respondent characteristics (null model weights $w=0.94$ and $w=0.75$, respectively).

Most respondents to Q14 were familiar with the *biological-ecological trait* classification (77.7%), but fewer with the *response-effect* (30.7%) or *hard-soft* (7.7%) trait classifications. Only 16.4% of respondents were unfamiliar with all three trait classifications.

4 | PATTERNS AND DRIVERS OF TRAIT TERM USE IN FRESHWATER ECOLOGY

Our literature review and survey revealed considerable variability in the use of trait terms across disciplines and respondent characteristics. Variable use of trait terms was more frequently observed

in published studies in animal and aquatic fields (entomology, fisheries, marine and freshwater biology, and zoology), whereas use of the term *functional trait* was particularly consistent in plant sciences and microbiology. However, we found a strong mismatch between our literature review and survey results for the use of trait terms in microbiology. In addition, our survey of freshwater scientists identified that variability in the use of trait terms was mainly explained by researcher discipline and, to a lesser extent, by their geographical region and focal ecosystem function. Specifically, in six questions describing characteristics that can be classified as *traits* (Q8–Q12) according to well-established definitions, respondents selected three terms—*biological trait*, *functional trait* and *structural measure*—at comparable frequencies, with none of them dominating.

The results of our literature review and survey showed that plant ecologists used the term *functional trait* more frequently than those studying other biotic groups or in other disciplines, probably because they have greater affinity for well-established trait terms and definitions (Dawson et al., 2021). Similarly, functional ecologists (whose expertise is in trait ecology) and those working with multiple biotic groups were more likely to use the term *functional trait*. This could indicate that researchers experienced in linking traits to ecosystem functions are more aware of the functional potential of traits or more familiar with well-established trait concepts and definitions. In addition, integrative views spanning various taxonomic groups could favour the use of *functional trait*, due to its more frequent use in cross-taxon disciplines such as environmental sciences and biodiversity conservation.

Our study demonstrates that freshwater scientists use trait classifications developed by terrestrial plant ecologists (the *response-effect* and *soft-hard* trait classifications) much less frequently than those specifically coined for aquatic organisms (*biological-ecological trait* classification). In particular, the strong implementation of the *response-effect* trait framework in terrestrial ecology (Coutinho et al., 2018; Laliberté et al., 2010; Mori et al., 2013) could suggest opportunities for freshwater scientists to better integrate ideas from terrestrial ecology into their disciplinary or cross-disciplinary practice. Limited knowledge of the *response-effect* framework by respondents could also have been influenced by the stronger focus of freshwater trait-based studies on exploring how organisms respond to environmental change rather than investigating how they influence ecosystem processes (Schmera et al., 2017; van der Plas, 2019).

Notably, researchers chose the term *functional trait* more frequently in questions regarding traits closely related to ecosystem functions (e.g., enzymatic activity, nutrient uptake), probably due to the clearer functional potential of such traits. The greatest use of the term *biological trait* was by researchers working with invertebrates and in the disciplines of community ecology in our survey, and entomology, fisheries, marine and freshwater biology, and zoology in the literature review. Furthermore, in our survey, *biological trait* was preferred to classify morpho-anatomical features (i.e., body size, plant growth form), probably because these are visible biological features

that have an indirect relationship with performance, responses to environmental change and ecosystem functioning (Belluau & Shipley, 2018; Hodgson et al., 1999).

The fact that research discipline, geographical region, and focal ecosystem function drove terminological variability highlights the need to make trait concepts inclusive enough to represent the characteristics of all freshwater biota. Strong terminological inconsistencies and biases also indicate the need to provide recommendations for consistent trait term use (Martini et al., 2021; Schmera et al., 2015), and the adoption of an overarching term that enables the full potential of trait-based approaches to be realised in freshwater ecosystems.

5 | RECOMMENDATIONS FOR THE USE OF TRAIT TERMINOLOGY IN FRESHWATER SCIENCE

We propose expanding the application of the functional trait concept to encompass all freshwater biota and their characteristics, while keeping links to performance, responses to environmental change and ecosystem functioning. Specifically, we propose expanding the scope of current definitions to encompass a flexible scale of trait measurements from genes to whole organisms (Fontana et al., 2021; Kremer et al., 2017), including supra-individual aggregations of organisms (e.g., colonies and biofilms) that have coherent eco-evolutionary origins and ecosystem functions (Dawson et al., 2021; Escalas et al., 2019; Krause et al., 2014). This flexible scale of trait measurement enables trait-based approaches to represent a greater number of freshwater organisms and traits. Thus, under this expanded definition, information from novel molecular techniques (e.g., high-throughput omic tools) allows the application of trait-based approaches to unicellular organisms (Lajoie & Kembel, 2019) and a new opportunity to widen trait data for multicellular organisms. The large number of traits that can be characterised by molecular tools, in combination with traditional trait measures (Martini et al., 2021; Sagova-Mareckova et al., 2021; Wang et al., 2022), will help to identify patterns and mechanisms of trait interactions across organisational scales, and thus to explain eco-evolutionary and ecosystem dynamics (Fontana et al., 2021). Our proposal aligns with recent, integrative views that expand well-established trait concepts by considering the interactions of traits across organisational levels (Dawson et al., 2021; Fontana et al., 2021) and highlight the need to adapt the scale of trait measurement for microorganisms (Escalas et al., 2019; Krause et al., 2014; Lajoie & Kembel, 2019) and colonial multicellular organisms (Linksvayer & Janssen, 2009; McWilliam et al., 2018). Considering the complementarity and partial overlap of eco-evolutionary and ecosystem-centred definitions, we also advocate their integration into a single definition to better describe how traits can influence organism- and ecosystem-level functions in freshwater ecosystems. Therefore, building on Dawson et al.'s (2021) definition of a trait, we define a functional trait as:

A genotypic or phenotypic characteristic measurable at levels of biological organisation that include the molecule, cell, individual and the supra-individual assemblage, which influences organism performance, environmental responses and/or ecosystem functioning.

This integrative definition expands the application of functional trait concepts and approaches to molecular and supra-individual characteristics, and non-inherited phenotypic characteristics (cultural traits), thus covering a wider range of organisms and features than established definitions (Table 3). These benefits go beyond the freshwater realm and respond to recent calls to make the functional trait concept more inclusive (Dawson et al., 2021; Escalas et al., 2019; Fontana et al., 2021). By restricting the trait definition to individual-level features, established definitions have been overlooking supra-individual features that give rise to emergent properties influencing eco-evolutionary and ecosystem aspects (Boon et al., 2014). For example, despite not being measured at the individual scale, features such as colony size, form and growth, and social organisation in multicellular organisms could be considered as functional traits because they can influence their individual performance, environmental responses and/or ecosystem functioning (Hartikainen et al., 2014; McWilliam et al., 2018; Whitehorn et al., 2012). In addition, aggregated microorganisms in colonies and biofilms provide functions in a similar way as aggregations of body cells (e.g., organs) within individual multicellular organisms, suggesting that the choice of an individual scale of trait measurement can be subjective and not sufficiently inclusive. As such, measures of colony or community-level traits encompassing microorganism aggregations represent an alternative way to understand environmental responses and effects on ecosystem functioning (Colls et al., 2021; Gionchetta et al., 2020; Graça et al., 2022).

Other authors have also suggested the use of standardised areas or specific parts of the organisms (Dawson et al., 2021), whenever possible (Dawson et al., 2019; Mallen-Cooper & Eldridge, 2016). Nonetheless, in these cases, it is not possible to relate traits with individual performance and fitness as the scope of trait influence transcends the individual level. For example, a microbial taxon niche cannot be estimated from community-mean traits. Clear definition and critical evaluation of approaches adopting supra-individual scales of trait measurement will help to clarify the scope of application and advantages in freshwater science. Besides phenotypes, the use of molecular features across the continuum from genes to proteins could foster the application of a trait-based approach to microorganismal studies (Nagler et al., 2021; Powell et al., 2015; Trivedi et al., 2016) and increase the capabilities of the trait-based approaches in macroorganisms (Martini et al., 2021). Genotypic characteristics such as functional gene markers of enzymes (Nagler et al., 2021; Trivedi et al., 2016) and genome characteristics (Barberán et al., 2012) have proved useful descriptors of organism performance, functional roles and environmental responses. Non-inherited cultural traits are also

recognised by our definition, allowing their integration into the functional trait approach and extending its advantages to the study of organisms with complex hierarchies and cultural systems, such as freshwater cetaceans, water birds, or elephants (Cantor et al., 2015; Hill et al., 2008). Cultural traits meeting this definition include acoustic communication signals (Cantor et al., 2015) and foraging specialisation and behaviour (Kopps & Sherwin, 2012; Mann et al., 2012; Sheppard et al., 2018).

To reduce terminological variability, we recommend the overarching term *functional trait* for general use and suggest keeping specific terms (e.g., *morphological trait*, *response traits*, and *effect traits*) for contexts requiring greater precision. The term *functional trait* is preferable to more specific terms in general and introductory contexts, because it improves terminological comparability across organisms and disciplines and enhances recognition of the traits that influence both eco-evolutionary and ecosystem aspects. Prioritising use of the term *functional trait* could promote consistency among disciplines as well as collaborative interdisciplinary research (e.g., Carmona et al., 2021). Although the *response-effect* trait framework represents an informative approach, its implementation in freshwater organisms could be challenging due to the limited knowledge of traits explaining the role of most freshwater taxa in ecosystem processes and the potential overlap between response and effect traits (Portela et al., 2022). Nonetheless, the use of the overarching term *functional trait* accommodates progressive adoption of *response* and *effect trait* terms in freshwater science for a range of organisms (Bruno et al., 2016; Engelhardt, 2006; Hose et al., 2022), which could enable a fuller realisation of the potential of trait-based approaches.

Functional traits represent different features and concepts than *ecological traits* (i.e. habitat preferences), which relate to elements of the realised niche and contrast with the focus on drivers of the fundamental niche in both established and our proposed trait definition. Although some authors have discouraged the use of *ecological traits* and other elements of the realised niche to predict community and ecosystem functioning dynamics (Schmera et al., 2017; Violle et al., 2007), such concepts can be useful when information on the underlying functional traits is scarce and/or difficult to measure (Luck et al., 2012). A clear definition of the term ecological trait and an evaluation of its limitations could enable a more precise use of this concept in freshwater ecology. Whenever possible, we advocate replacing the term *biological trait* with *functional trait*. Using *biological trait* as an additional broad term increases term variability without providing a clear advantage because of its conceptual similarity to *functional trait* and its restricted use to certain disciplines (e.g., fisheries, entomology, marine and freshwater biology, and zoology). In addition, biological traits are generally considered response traits, which overlooks their potential to influence ecosystem functioning. However, recognising the contrast between this approach and much previous literature, we encourage researchers to accompany their use of this term with a clear, precise definition (e.g., Cano-Barbacil et al., 2020). The use of harmonised trait terminology and

TABLE 3 Examples of supra-individual (colony and community-mean traits), genotypic, and cultural traits and their influence on organism performance, ecosystem functioning, and responses to the environment.

| Type | Trait | Organism | Performance | Ecosystem function | Environmental response | Reference | |
|------------------|--------------------------------------------------------|-------------------------------------------------------------------|---------------------------------------------|-----------------------------------------|------------------------------------------------------|--------------------------------------------------------|----------------------------------------------------|
| Colony traits | Colony growth | Bees | Growth and survival | Secondary production | Sensitive to pesticides | Whitehorn et al. (2012) | |
| | Queen production | Bees | Reproduction | Secondary production | Sensitive to pesticides | Whitehorn et al. (2012) | |
| | Colony size | Corals | Growth and survival | Secondary production | | McWilliam et al. (2018) | |
| | Colony form | Bryozoa | Growth and survival | Secondary production | Adjusting form to optimise metabolism | Hartikainen et al. (2014) | |
| | Colony age structure | Ants | Growth and survival | Secondary production | | Maak et al. (2019) | |
| | Growth rate | Fungi | Growth and survival | Secondary production | Sensitive to warming, nutrient enrichment and drying | Graça et al. (2022) | |
| | Biofilm production | Bacteria | Growth and survival | | Protection against desiccation | Lennon et al. (2012; 2016), Lennon and Lehmkuhl (2016) | |
| | Biofilm production | Bacteria | Growth and survival | Soil water retention | | Lennon and Lehmkuhl (2016) | |
| | Community-mean traits | Extracellular enzyme activity (e.g., β -glucosidase enzyme) | Bacteria, Fungi | Growth and survival | Organic matter decomposition | Sensitive to drying intensity | Gionchetta et al. (2020) |
| | Genotypic traits | Photosynthetic pigments (e.g., chlorophyll, carotenoids) | Bacteria, diatoms | Growth and survival | Primary production | Mediate responses to drying | Colls et al. (2021) |
| Genotypic traits | Enzyme gene markers (e.g., Acetylglucosaminidase gene) | Bacteria, fungi | Growth and survival | Organic matter decomposition | Sensitive to carbon availability and pH | Trivedi et al. (2016) | |
| | Nitrate reductase gene marker (nirS genes) | Bacteria | Growth and survival | Nutrient cycling | | Powell et al. (2015) | |
| | GC content | Bacteria | Growth and survival | | Habitat preferences | Barberán et al. (2012) | |
| | Genome size | Bacteria | Growth and survival (nutrient conservation) | Secondary production | Sensitive to resource availability | Li et al. (2019) | |
| | 16S rRNA gene copy number | Bacteria | Growth and survival (nutrient conservation) | Secondary production | Sensitive to resource availability | Li et al. (2019) | |
| | <i>mcrA</i> -gene | Archaea | Growth and survival | Respiration (methane production) | | Oswald et al. (2015) | |
| | <i>pmoA</i> -gene | Bacteria | Growth and survival | Respiration (aerobic methane oxidation) | | Nagler et al. (2021) | |
| | Cultural traits | Foraging behaviour (specialised foraging niche) | Mongoose | Growth and survival | Secondary production | | Sheppard et al. (2018) |
| | | Foraging behaviour (sponging, using hunting tools) | Dolphins | Growth and survival | Secondary production | | Mann et al. (2012), May-Collado and Wartzok (2007) |
| | | Acoustic communication signals | Whales | Growth and survival | Secondary production | | Cantor et al. (2015) |

definitions will promote accessibility of some scientific disciplines (e.g., fisheries, entomology, marine and freshwater biology, and zoology) to a broader interdisciplinary community.

Our recommendations contrast with the suggestion that all traits are functional and, thus, that the functional adjective is redundant (Dawson et al., 2021; Sobral, 2021) or misleading (Streit & Bellwood, 2022). Specifically, Sobral (2021) argues that, from an evolutionary perspective, all traits are functional because any trait can influence organism fitness at least in one environmental context. Similarly, Dawson et al. (2021) suggest using the simplified term *trait* to reduce complexity and avoid context-dependency related to the different functional trait definitions. In addition, Streit and Bellwood (2022) propose to identify traits that can explain ecosystem functions of interest, rather than considering that all traits should be functional. Although these arguments are compelling, we support the use of the composite term *functional trait* over the simple term *trait* in general and introductory contexts for two reasons. First, both our review and survey of freshwater scientists highlight the need to prioritise terms that help readers to assess a trait's influence on performance and fitness, environmental responses and/or ecosystem functioning. As such, the simple term *trait* may be too broad and ambiguous to replace *functional trait* in general contexts, because some traits, including *geographic* and *ecological traits*, do not relate to characteristics influencing eco-evolutionary or ecosystem processes. Second, our survey results suggest that many freshwater researchers may not recognise the capacity of traits to predict ecosystem functioning. This might explain the strong bias in trait-based freshwater studies towards exploring responses to environmental change rather than how traits influence ecosystem functioning (Schmera et al., 2017; van der Plas, 2019). Although functional traits have contrasting capacities to enable prediction of organism-, population-, and ecosystem-scale dynamics (Frances et al., 2021; Pilière et al., 2016; van der Plas et al., 2020), they offer a powerful but underexploited capacity to explain changes in freshwater ecosystem functioning, as frequently demonstrated in plant ecology (Hooper et al., 2005; van der Plas, 2019). By clearly identifying and naming traits that have this capacity as functional traits, researchers will be better informed of their potential uses. The benefits of a composite labelling go beyond the core *trait* term and apply to a range of related terms used in ecology, including *functional composition*, *functional diversity*, *functional genes*, and *functional group*.

6 | CONCLUSIONS

Our study provides a basis from which to work towards harmonisation of trait terms and concepts in freshwater science. We suggest the use of the term *functional trait* in general contexts to reduce terminological inconsistency and resultant ambiguity. Our proposed *functional trait* definition enables the application of trait-based approaches to all freshwater biota and their characteristics, by identifying features influencing eco-evolutionary and ecosystem

aspects across a continuum from genes to multicellular organisms and encompassing multicellular aggregations. These benefits can be applied in and beyond freshwaters, being potentially useful for terrestrial and marine ecologists facing similar challenges (Dawson et al., 2021). In addition, our findings suggest that cross-taxonomic and cross-disciplinary discussions are fundamental to the identification of challenges and commonalities in trait-based ecology and thus progress towards a terminological consensus (Kremer et al., 2017). Furthermore, agreeing a set of common functional traits that can be measured across freshwater organisms and systems (e.g., organism biomass and growth rate; Martini et al., 2021) could promote progress towards the construction of global databases of functional traits for freshwater organisms and their comparison across biomes and environments (Litchman & Klausmeier, 2008; Mammola et al., 2021; Weiss & Ray, 2019). Such research could be supported by guidelines that standardise the measurement of traits across ecosystems and taxa, as done for plants (Pérez-Harguindeguy et al., 2013), terrestrial fungi (Dawson et al., 2019), invertebrates (Moretti et al., 2017) and vertebrates (Luck et al., 2012). Collectively, this progress is key to answer pressing questions regarding the biomonitoring, conservation and management of freshwater biodiversity in a context of global change (Maasri et al., 2022) and the role of freshwater ecosystems in global biogeochemical cycles (Gounand et al., 2018). We hope that our recommendations can inform the development of a coordinated research agenda that realises the full potential of trait-based approaches in freshwater ecosystems.

AUTHOR CONTRIBUTIONS

Conceptualisation: C.G.-C., D.B.. Developing methods: C.G.-C., R.S., D.v.S., R.B., M.C., D.B. Data analysis: C.G.-C. Preparation of figures and tables: C.G.-C. Conducting the research, data interpretation, C.G.-C. led the writing and R.S., D.v.S., R.B., M.C., R.M., T.D., D.B. revised and edited the text, providing critical comments.

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CONFLICT OF INTEREST STATEMENT

All authors agree with the submission of the manuscript, and declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available at GitHub (https://github.com/tanogc/freshwater_traits_review).

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