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Opinion

Towards a trait-based framework for protist ecology and evolution

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Protists comprise the vast majority of eukaryotic genetic and functional diversity. While they have traditionally been difficult to study due to their small size and varied phenotypes, environmental sequencing studies have revealed the stunning diversity and abundance of protists in all ecosystems. Protists are key primary and secondary producers across many biomes, with ecological specializations that range from mutualism to parasitism, complex predation behaviors, mixotrophy, detritivory, and saprotrophy. Current genomic and transcriptomic approaches provide valuable insights into protist diversity at the genetic level, but they fall short in capturing the morphological and behavioral traits critical for understanding the functional roles of protists in ecosystems. This knowledge gap hinders our ability to answer important questions about protist functional diversity, including how protist functional groups will respond to environmental change. In this opinion article, we advocate adopting a traits-based approach for studying protist diversity and developing a trait database for protists to support this goal. By integrating examples of recent work characterizing protist functional diversity using a range of approaches, we emphasize the opportunities that trait databases offer and propose strategies for moving towards a trait-based framework to guide future research in protist ecology and evolution.

Highlights

Knowledge of the functional diversity of protists is crucial for understanding their responses to, and influences on, the environment.

Functional characterizations of protist species are scattered in the literature, making it challenging to synthesize them into ecological and evolutionary insights.

Recently developed environment- and taxon-specific trait databases are a strong foundation for studies of protist functional diversity, but efforts remain fragmented and their broader utility is limited by a lack of standardization.

We argue that a unified trait database for protists is timely, achievable, and would catalyze transformative research on their biodiversity, ecology and evolution.

A growing need for a traits-based approach in protistology

Protists (see Glossary) are key components of the microbial world, holding major evolutionary and ecological significance. Through more than two billion years of evolutionary history, protists have populated the entirety of the eukaryotic tree of life, spanning seven to ten major evolutionary supergroups – with only two of them including all animals, plants, and fungi [1]. Protists are increasingly recognized for their functional roles in terrestrial and aquatic environments (including extreme habitats) [2–4], and as symbionts of healthy and diseased plants and animals [5]. Protists are key contributors to CO_2 fixation [6,7], mediate energy transfer between smaller and larger organisms, and participate in decomposition and nutrient recycling [8]. Thus, through the production, transformation, and export of organic matter, protists play a crucial role in sustaining life, regulating biogeochemical cycles, and influencing climate regulation in all biomes on Earth.

While our understanding of protist biodiversity has expanded considerably since the use of classical microscopy to modern DNA-based surveys, these advances have focused on the taxonomic richness and distribution of protist lineages [9,10]. We argue that to gain a deeper knowledge of protist ecology and evolution, we must also consider their functional diversity – particularly to better understand how protist activities influence ecosystems across space and time, and how their functional diversity may respond to the ongoing climate and environmental crises [11].

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The functional diversity of protists is shaped by their staggering variety of **traits** and **modalities** (Figure 1, Box 1; and see Table S1 in the supplemental information online). Organismal sizes span several orders of magnitude, and their shapes and motility are driven by various arrangements of flagella, cilia, or pseudopodia, with many taxa producing elaborate exoskeletons or shells [12]. Lifestyles encompass free-living, symbiotic, and parasitic forms [13], and trophic strategies range from phagotrophy to diverse types of mixotrophy to autotrophy [14]. Primary producers rely on diverse nutrient uptake systems, and some species produce toxic or otherwise ecosystem-disruptive blooms [15]. Consumers have feeding mechanisms ranging from passive filtration to the use of weapon-like structures [16,17]. These few examples of protist trait diversity highlight the need for linking their taxonomy with functional traits, as functional diversity shapes both responses to and influences on the environment [18–20].

While the need for bridging taxonomic and functional diversity is evident, we lack a unified trait-based diversity framework for all protists. By contrast, trait databases have been instrumental in yielding crucial insights into the ecology and evolution of animals and plants [21–23], or more recently, prokaryotes [24,25]. We argue that there is an urgent need to collect protistan trait information at the species level and to establish a common **ontology** of traits that could enable the

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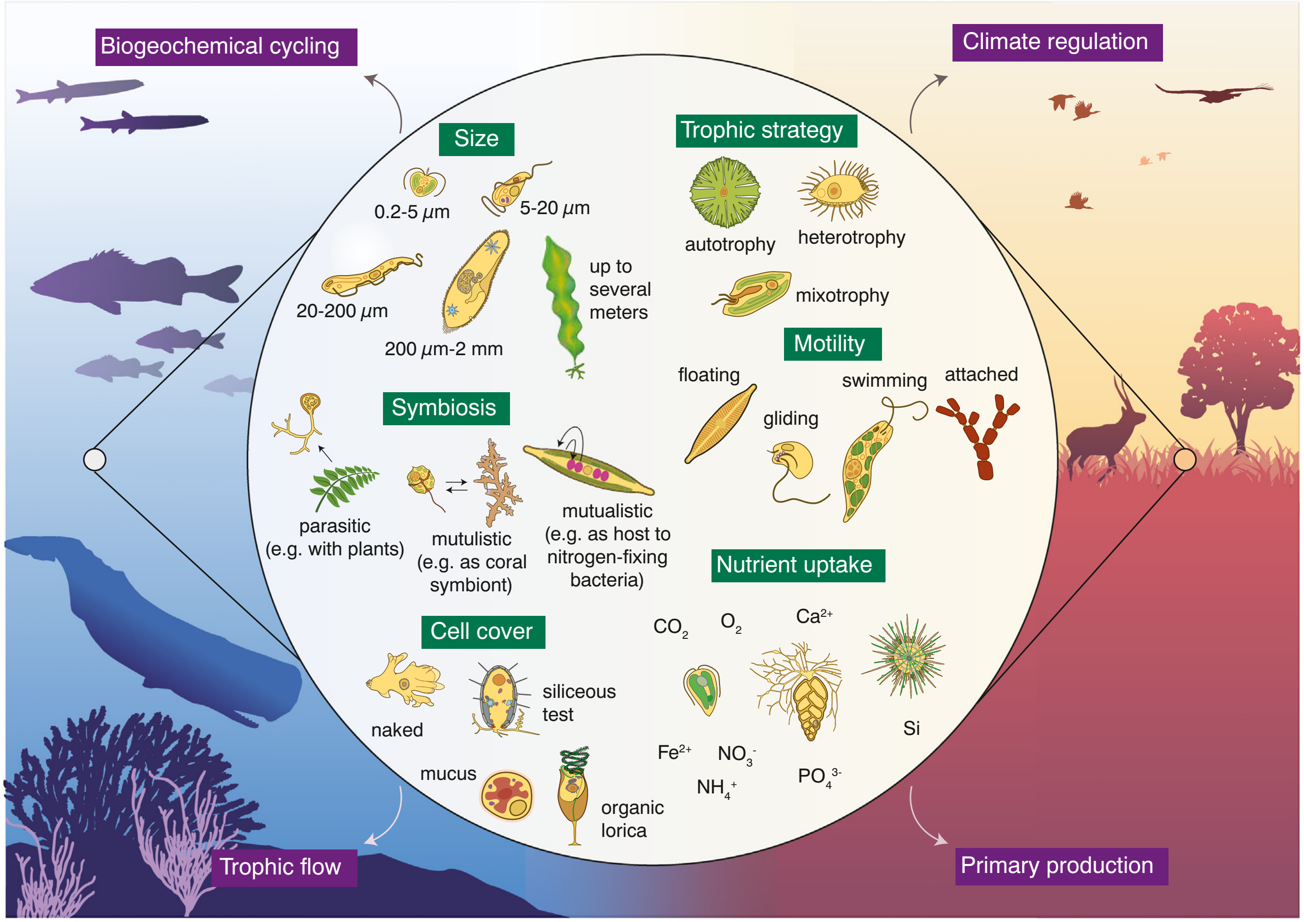

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Figure 1. Protist functional diversity. A schematic representation of selected functional traits in protists that contribute to ecosystem functioning. Protist drawings were adapted from [81].

Box 1. Some important traits to include in protist trait databases

We highlight traits and modalities that can commonly be extracted from the literature. These and other less frequently measured traits (e.g., growth, grazing and resource acquisition rates) are relevant for a species' ecological fitness and its contributions to ecosystem functioning. Many species exhibit phenotypic plasticity driven by environmental conditions or life-cycle polymorphy, manifested as a range of values in continuous traits or as different modalities in categorical traits. This list is not comprehensive and Table S1 provides additional traits, modalities, and references.

Size.

Usually measured as cell length and width. It may be expressed as area or biovolume when combined with cell shape. Size influences resource uptake and trophic interactions. In phototrophs, uptake rate per unit of cell surface area is higher in smaller cells. In phagotrophs, cell size tends to set prey size range, although there are many exceptions.

Cell cover.

A protective layer that may reduce palatability, limit predation, affect buoyancy, or prevent cellular desiccation. Cells may be naked, harbor scales, be encased in mucus or a shell, or possess a skeleton. Composition (e.g., organic, silica, calcite, or strontium sulfate) links protists to biogeochemical cycles.

Motility.

Cellular movement via structures like vacuoles, flagella, and pseudopodia. Motility enhances resource access, affects boundary-layer exchanges, predator avoidance, habitat preferences, and dispersal. Motility is often stage-specific in polymorphic life cycles. Modalities include: sessile, attaching, floating, gliding, dwelling, swimming.

Colony formation.

Some protists are solitary or can form colonies depending on life-cycle stage or environmental conditions. These can deter predators, improve buoyancy control, and enhance resource renewal around the cell. Colony forms include: contained in a self-produced matrix or mucus, attached (e.g., chains, networked), multicellular life-cycle stage.

Plastid presence and origin.

Plastids may be absent, acquired (kleptoplastidic, or via endosymbionts), or constitutive (innately produced).

Nutritional mode.

Protists may acquire resources via osmotrophy, saprotrophy, myzocytosis, phagotrophy, phototrophy or photophagotrophy. Phagotrophs use diverse mechanisms (e.g. filter feeding or raptorial feeding using peduncles, pallium veils, etc). Nutritional modes link to ecosystem roles (e.g., primary or secondary producer, decomposer) and resource specialization (e.g., live prey, detritus).

Symbiosis.

Stable biological associations with one or more species. Interactions influence community dynamics and biogeochemical fluxes. Depending on the outcomes for the host and the partner, interactions may include mutualism, commensalism, amensalism, or parasitism.

Resting stage.

Dormancy is present in different forms among some protists. It confers tolerance to stress, aids in dispersal, and prolongs survival.

Glossary

DNA metabarcoding: a method involving high-throughput DNA sequencing of a targeted, taxonomically useful marker (for protists, usually the V4 or V9 hypervariable region of the 18S rRNA gene) from environmental samples.

Metagenomics: high-throughput sequencing of total environmental DNA to characterize the taxonomic composition and functional diversity of microbial communities. Sequencing data can be assembled and binned into metagenome-assembled genomes (MAGs).

Metatranscriptomics: sequencing of total RNA from environmental samples to study gene expression profiles and active metabolic functions within microbial communities at the time of sampling.

Modality: a subcategory within a broader categorical trait. Each trait can encompass multiple modalities that describe distinct variations of the trait. For example, the trait motility may include modalities such as sessile, attached, gliding, and swimming.

Ontology: a structured framework for representing knowledge in which biological concepts are formally defined using a controlled vocabulary, and the relationships between terms are specified.

Protist: an informal name given to any eukaryote that is not a plant, animal, or fungus – usually a unicellular and microscopic species. Typical examples include diatoms, dinoflagellates, amoebozoans, and ciliates.

Trait: functional traits are measurable features that can affect the organism's capability to proliferate. Traits can be morphological, behavioral, physiological, or related to life-history. Examples include cell size, motility, and ingestion method.

development of a comprehensive, unified trait database for protists. Such a resource will be critical for adopting a trait-based approach for the study of protist ecology and evolution, including in predictive models, thus unlocking new research directions (see Outstanding questions).

Current approaches in protist functional diversity

The study of protist organismal biology and functional diversity has a rich history, from early microscope-based descriptions to modern integrative approaches. These efforts have characterized protist species individually, based on traits such as cell size and shape, intracellular content, motile structures, life-history, and feeding strategies [26,27]. Today, classical light microscopy can be integrated with advanced techniques, such as 3D imaging or expansion microscopy, to study intracellular space [28], fluorescence in situ hybridization to infer symbiotic interactions or predator–prey relationships [29,30], and cryo-electron microscopy for quantifying nutrient uptake and potential impacts on biogeochemical cycles [31,32]. Similarly, experimentation on physiology (e.g., growth rates) and species interactions that rely on cultivation [33] are being accelerated by new techniques that combine high-throughput cell isolation (e.g., using fluorescence-activated cell sorting or microfluidics) and co-cultivation [34]. These approaches have resulted in a substantial, and still growing, body of morphological, physiological, and behavioral data. However, translating scattered, species-specific knowledge into comprehensive insights at the community, ecosystem, or macroevolutionary scale remains a major challenge.

Many investigations at the community level are conducted using high-throughput molecular methods, notably **DNA metabarcoding**. This approach has unveiled numerous undescribed taxa and enabled the study of protist communities across space and time [9,10]. However, while metabarcoding provides deep insights into taxonomic diversity, linking genetic sequences to ecological roles remains difficult. To move beyond taxonomy, metabarcoding must be complemented with functional data.

To overcome the limitations of metabarcoding, genome-scale approaches such as genomics and **metagenomics** have been widely used to study the functional diversity of prokaryotes. However, applying these methods has proven more challenging for protists. Early expectations regarding methodological transferability to protist research were rapidly undermined by the challenges posed by the larger size and complexity of eukaryotic genomes. In turn, transcriptomic analyses of protist cultures, and more recently **metatranscriptomics** of communities, have yielded insights into gene expression and aided in the reconstruction of metagenomic-assembled genomes [35–37]. These findings unveiled molecular mechanisms underpinning key functions such as bacterivory [38], and differences in molecular strategies across taxonomic [39] and functional groups [40]. However, both metagenomics and metatranscriptomics face important limitations. Chief among these is the scarcity of reference genomes and functional annotations for microbial eukaryotes, resulting in large numbers of poorly characterized genes in environmental surveys and the difficulty of linking community-aggregated gene patterns to specific species. Moreover, gene expression is regulated by post-transcriptional and translational processes, as well as substrate availability, making it difficult to relate gene presence and expression directly to quantitative ecosystem processes [41]. Importantly, protist functional diversity is mainly exerted at the cellular level, with trophic roles and specialization being principally driven by cellular structures, behaviors, or interactions, which we have yet to decipher from gene expression [42,43].

In this context, trait databases represent a crucial bridge, linking studies of protist morphology, physiology, and behavior to broad patterns at the community and ecosystem scale. To this end, several context-specific databases have been developed, synthesizing relevant traits across freshwater [44,45], marine [46,47], and soil environments [48,49]. Other databases focus on specific traits such as nutrient utilization [50], trophic strategies [51], and ecological interactions [52,53], or particular taxonomic groups [54–56]. Such databases have provided many novel insights into protist biology, including evidence for functional redundancy in protist communities [46], the interplay between abundance, species size, nutrition, and trophic regime in marine coastal ecosystems [57], the functional succession of soil communities following glacier retreat [58], and improved characterization of potential prey–predator interactions [59]. Trait databases are also a required interface for population and ecosystem modeling, as models need observational data for both calibration and validation [14,60,61].

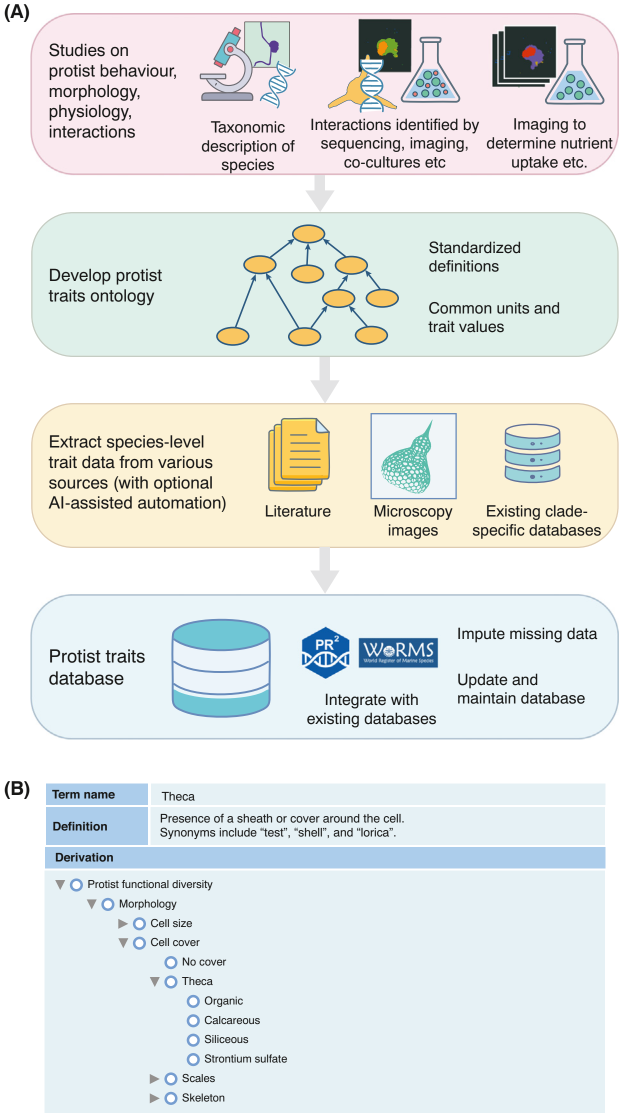
Most existing trait databases have been developed independently, and thus, new frameworks have frequently introduced their own sets of traits, modalities, and definitions. Such fragmentations have hindered the integration and widespread adoption of these resources. We argue that unifying efforts and compiling trait data of protist species is highly feasible and represents a great avenue to explore their functional diversity. We present a compilation of traits and modalities extracted from existing protist trait databases, alongside their definitions and potential relevance to protist ecology and functional roles across ecosystems and biomes (Box 1, Table S1 in the supplemental information online). Through this effort, we seek to catalyze a community-wide initiative to develop a shared ontology of protist traits – one that effectively represents their functional diversity across biomes. In the following section, we suggest key steps required to achieve this objective and discuss the broader perspectives it offers, both within protistology and in the wider fields of ecology and evolution.

Towards a trait-based framework: challenges and opportunities

The recent proliferation of environment- and taxon-specific trait databases reflects the growing interest in understanding protist ecology and evolution through the lens of functional diversity. To fully embrace a trait-based framework and enable protist-wide and cross-ecosystem analyses, we propose developing an ontology that standardizes key morphological and functional traits of protists into a shared, structured vocabulary (Figure 2). Such an ontology will enable researchers to speak the same language by harmonizing terminologies, descriptions, measurement units, and hierarchical relationships among trait attributes. Different databases currently employ inconsistent definitions and measurement approaches for the same terms. For instance, the commonly used trait 'size' can refer to linear measurements (e.g., length, width, and depth), volume (e.g., estimated spherical diameter), and/or categorical size classes depending on the dataset [46,51,55]. A shared ontology will help lay the foundation for the development of standardized databases of protist traits, promoting the interoperability of datasets and enhancing protist research across domains, and laying the foundation for a protist-wide trait database. The flexible, interconnected structure of this ontology would also accommodate adding trait terms over time as the need arises, similar to the strategy used for the Environment Ontology (ENVO) [62]. Establishing a shared trait ontology will certainly require cross-disciplinary collaborations – including specialists in various taxonomic groups (e.g., ciliates, dinoflagellates, amoebae) and environments (e.g., aquatic, terrestrial). Such a community-driven effort will lay the groundwork for a unified, and FAIR (findable, accessible, interoperable, reusable) protist traits database.

An important step in building a protist trait database is compiling informative functional traits (Box 1, Table S1 in the supplemental information online). Substantial progress has been made in this regard, with various works proposing key traits that best capture protist functional diversity across different biomes [14,48,63]. For a protist-wide trait database, we advocate for an inclusive approach that incorporates a wide range of traits. While not all traits and modalities are broadly applicable – for example, benthic versus planktonic habitat is relevant for aquatic protists, but not for soil protists – our approach provides a route to broader compatibility and reusability, maintaining the option of filtering traits based on taxonomic or ecological context. Equally important is the inclusion of both qualitative and quantitative traits, as these usually complement each other (e.g., type of prey and grazing rates). We recommend that quantitative traits are recorded as continuous measurements rather than categorical, as continuous data can always be binned post-hoc, whereas fixed categories may limit reuse.

Selecting traits that are both important and commonly measured for protist species requires balancing data availability with biological relevance. For example, physiological rates (such as



Term name	Theca
Definition	Presence of a sheath or cover around the cell. Synonyms include “test”, “shell”, and “lorica”.

Derivation

- ▼ ○ Protist functional diversity
  - ▼ ○ Morphology
    - ▶ ○ Cell size
    - ▼ ○ Cell cover
      - ○ No cover
      - ▼ ○ Theca
        - ○ Organic
        - ○ Calcareous
        - ○ Siliceous
        - ○ Strontium sulfate
      - ▶ ○ Scales
      - ▶ ○ Skeleton

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Figure 2. Roadmap towards a trait-based approach for protists. (A) A schematic outlining the key steps for developing a comprehensive traits database for protists across all ecosystems, which in turn will lead to more studies on protist morphology, physiology, and behavior. (B) An illustration of a potential structure for the protist traits ontology, using the trait 'Theca' as an example. Each term in the ontology has a standardized definition and relevant synonyms. In this example, 'Theca' is categorized under the parent terms 'Cell cover' and 'Morphology'. Theca includes the following modalities based on composition: 'Organic', 'Calcareous', 'Siliceous', and 'Strontium sulfate'. Additional traits under the parent term 'Morphology' could include 'Cell shape', 'Symmetry', 'Polarity', 'Presence of defense protrusions', etc. (see Table S1 in the supplemental information online).

rates of growth, resource uptake, photosynthesis or grazing) are highly informative about species' ecological fitness and their contribution to ecosystem processes [61]. However, these difficult-to-measure traits (often referred to as 'hard' traits in trait literature) require culturing and/or experimentation, and are therefore recorded for only a relatively small fraction of protist species. In contrast, 'soft' traits such as cell size, motility or presence of chloroplasts are more readily inferred from species descriptions and, while their ecological relevance is less direct, they can be annotated for a much broader range of taxa and often serve as useful proxies of function (e.g., cell size may correlate with prey size) [64]. Annotating both hard and soft traits is thus not only necessary, but also complementary, and will support a wide range of inquiries. Advancing the annotation of hard traits will help to refine our understanding of biological rules and trade-offs, and help mechanistically link protist species to ecosystem functioning. For example, compiling data on maximum growth rates can provide modelers with empirical values for different functional groups (such as diatoms and mixotrophs), enabling more accurate simulations of carbon flow, nutrient cycling, and ecosystem response to environmental change [65]. At the same time, expanding the annotation of soft traits will allow large-scale evolutionary and ecological studies across taxa and biomes. For example, compiling data on cell size can enable investigations of how size variation within taxonomic groups correlates with environmental gradients such as temperature and nutrient concentrations.

An extensive body of literature can be leveraged to populate a unified trait database at the species level – the most basic taxonomic unit. Although manually extracting and harmonizing data from scattered sources can be laborious and time-consuming, clade-specific databases show that such efforts are both valuable and feasible. Emerging machine learning techniques present an exciting opportunity to accelerate and scale up the process. Indeed, this approach has successfully been applied for collecting arthropod and plant trait data [66,67]. Machine learning techniques can also be used to extract species trait data from images (e.g., cell size, photosynthetic ability, presence of structures involved in nutrition), as recently demonstrated for marine plankton [68]. Extracted information should be reviewed by experts for quality control to ensure accuracy and reliability of the database. Additionally, newly available tools for building trait databases can be used to streamline the process of harmonizing trait data from heterogeneous sources based on an underlying ontology [69]. Another challenge will be to account for trait polymorphism within species (e.g., across life cycles). Previous approaches have focused either on the trophic phase of protist species or on their dominant life-cycle stage. Fuzzy-coding, which enables annotation of multiple modalities within one categorical trait, represents a promising path forward once a comprehensive trait ontology is developed [70]. The annotation can be done – either in a binary fashion (e.g., a species has both an attached and swimming phases) or quantitatively based on proportion of lifespan (e.g., 70% swimming, 30% attached) [70]. Finally, while a key challenge in any database is the presence of unavailable or incomplete records, missing values will eventually be filled in as more data becomes available or may be imputed depending on the degree of phylogenetic conservatism in the trait of interest [71,72].

All the steps outlined above – developing a protist-wide trait ontology, mining data to populate a trait database, and managing missing values – are realistically feasible in the near future with existing resources and coordination. Ongoing community-driven initiatives that have successfully developed and maintained a taxonomic framework and integrated sequence databases for protists can be leveraged to support a parallel trait database. Developing and maintaining this trait database could adopt the model used for the PR^2 (Protist Ribosomal Reference) database: researchers update their clades of expertise with the process being facilitated by workshops [73,74]. Furthermore, to ensure longevity and broad usability, we recommend incorporating trait databases into established taxonomic databases such as PR^2 and WoRMs, which are widely used by the protist community and regularly updated [74,75].

Concluding remarks and future perspectives

We have accumulated more than two centuries of biological knowledge on protist species from all biomes, and we are now poised to integrate this information in ways that can transform our understanding of their functional roles in ecosystems. To reach this goal, we must systematically organize, standardize, and synthesize existing trait data into an accessible and interoperable database. We outlined a roadmap that includes: (i) building a standardized ontology of protist traits and modalities, (ii) building a trait database following this ontology, and (iii) integrating this database into the larger framework of tools routinely used in protistology. While this represents a significant effort, its perspectives extend far into questions on protists' evolution, ecology, and the future of ecosystem functioning across Earth (see Outstanding questions).

Outstanding questions

How is protist functional diversity distributed across space and time?

How is functional diversity related to species diversity and phylogenetic diversity? And how much functional redundancy exists in protist communities across biomes?

What is the contribution of rare taxa to functional diversity?

Which functional traits show the strongest relationships to environmental gradients?

Can the relationship between protist functional traits, diversity, and redundancy explain ecosystem resistance and resilience – and how can this be applied to identify at-risk biomes and guide conservation and restoration efforts under environmental change?

How do ecological interactions shape the coevolution of functional traits?

What is the tempo and mode of evolution of key functional traits? Did the emergence of these traits, or combination of them, coincide with major geobiological transitions or shifts in ocean/atmosphere chemistry?

How do traits impacting dispersal ability, such as body size and ability to enter dormancy, impact diversification rates?

A unified trait database for protists would represent a transformative resource to study their functional diversity and to advance ecological insights. For example, by complementing environmental sequencing data with trait information, we will be able to test longstanding questions about the extent of functional trait redundancy in ecosystems, the roles of rare taxa, responses to environmental and climate changes, and how specific protist traits relate to ecosystem processes [76,77]. A protist trait database would also open up new avenues for macroevolutionary analyses across the eukaryotic tree of life. It would enable investigations into the evolutionary history of key traits, the degree of phylogenetic conservatism, the tempo and mode of trait evolution across diverse protist lineages, and their links to diversification rates [78,79]. These are examples of questions that remain largely unexplored for protists, and mapping functional traits to dense phylogenetic trees will allow addressing them. A trait database would also be invaluable for refining ecosystem and climate models that, at best, incorporate protists as broad functional groups. A trait database can thus help create more realistic predictive models by providing the experimental data needed for validating outputs and refining theoretical predictions [60,80]. By facilitating the integration of sequencing, experimentation, and modelling, a comprehensive protist trait database will lay the foundation for a new era of hypothesis-driven research on protist functional ecology and evolution. Finally, a unified protist trait database holds significant educational potential by enhancing cross-disciplinary communication and engaging stakeholders and the public with the remarkable diversity of microbial eukaryotes.

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Declaration of interests

No interests are declared.

Supplemental information

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