

Protists and protistology in the Anthropocene: challenges for a climate and ecological crisis

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Abstract

Eukaryotic microorganisms, or"protists," while often inconspicuous, play fundamental roles in the Earth ecosystem, ranging from primary production and nutrient cycling to interactions with human health and society. In the backdrop of accelerating climate dysregulation, alongside anthropogenic disruption of natural ecosystems, understanding changes to protist functional and ecological diversity is of critical importance. In this review, we outline why protists matter to our understanding of the global ecosystem and challenges of predicting protist species resilience and fragility to climate change. Finally, we refect on how protistology may adapt and evolve in a present and future characterized by rapid ecological change.

Keywords Climate breakdown, Algae, Thermal niche, Meta-genomics, Decarbonization of research, Decolonialization of science

Protists: hidden and fundamental contributors to global ecology

The vast majority of earth's biodiversity is microbial. Single-celled organisms (bacteria, archaea, viruses, and protists), while frst visualized by humans in 1677 predate us by billions of years [\[1](#page-9-0), [2\]](#page-9-1). Protists, or eukaryotic microorganisms, are found across all habitats [[3\]](#page-9-2), ranging from the deep sea to the stratosphere [\[4](#page-9-3), [5\]](#page-10-0), and from hypersaline geothermal springs to the polar ice-caps [\[6](#page-10-1), [7\]](#page-10-2). Protists are taxonomically far more diverse than multicellular eukaryotes, belonging to multiple supra-kingdom level groups that are distinct from animals, plants,

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and one another [[8,](#page-10-3) [9](#page-10-4)]. Protists are furthermore functionally heterogeneous, comprising phototrophs and heterotrophs, aerobes and anaerobes [\[10](#page-10-5), [11](#page-10-6)], single-celled and colonial forms [[12,](#page-10-7) [13\]](#page-10-8), and free-living species and obligate symbionts in mutualistic, commensal, and parasitic interactions $[14, 15]$ $[14, 15]$ $[14, 15]$ $[14, 15]$. These are underpinned by diverse genomes, with individual lineages separated from one another over one billion years of evolution with histories punctuated by gene gains, losses, and endosymbiotic and horizontal acquisitions [\[16–](#page-10-11)[18\]](#page-10-12). Many remain anonymous, with some groups only starting to enter laboratory study [\[19](#page-10-13)[–21\]](#page-10-14).

In all these habitats, protists perform essential ecosystem functions. Photosynthetic protists, or "algae," which possess chloroplasts, are responsible for nearly half of all planetary primary production $[2, 22]$ $[2, 22]$ $[2, 22]$ $[2, 22]$ and form the trophic basis of worldwide fish stocks $[23, 24]$ $[23, 24]$ $[23, 24]$ $[23, 24]$. These include essential symbionts of macrofauna, e.g., in coral reefs [\[25,](#page-10-18) [26](#page-10-19)]. Many algae are mixotrophs, i.e., can perform both phototrophy and heterotrophy, and have roles both in carbon fxation and predation [\[11](#page-10-6)]. Some

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phototrophs (diatoms, coccolithophores) are biomineralizers and contribute to the sedimentation and burial of dissolved silicon and calcium respectively [[27](#page-10-20), [28\]](#page-10-21). Others form symbiotic interactions with bacteria that perform nitrogen fixation or synthesize vitamin B_{12} from dissolved cobalt [[29,](#page-10-22) [30\]](#page-10-23), and their photosynthetic activity thus supports the incorporation of these nutrients into biological systems.

Heterotrophic protists play important roles in decomposing and recycling organic carbon and nitrogen. Terrestrial heterotrophs support global soil cycles [[3,](#page-9-2) [31](#page-10-24)], with some (e.g., plasmodiophorids) integral components of the plant rhizosphere [\[32](#page-10-25), [33](#page-10-26)]. By consuming and collating nutrients from primary producers, aquatic heterotrophs contribute to the biological carbon pump, removing organic matter from the surface and allowing burial in sediment $[11, 34]$ $[11, 34]$ $[11, 34]$ $[11, 34]$ $[11, 34]$. The respiratory activity of both photosynthetic and heterotrophic protists can change the availability of limiting nutrients in terrestrial and aquatic ecosystems, either by competitive uptake and occlusion or by recycling reserves stored in prey [\[35](#page-10-28), [36\]](#page-10-29). Protist metabolism can even directly impact on precipitation, e.g., the production of cloud-nucleating DMSP (dimethyl-sulfonopropionate) by some dinofagellates [[37,](#page-10-30) [38](#page-10-31)].

Protists have important and often under-realized potentials in industry and agriculture. Algae may serve as a chassis for biofuel, nutriceuticals, feedstock, fertilizer and food production, and even green carbon capture [[39–](#page-10-32)[41](#page-10-33)]. These applications are appealing given the lower demands of algal bioreactors than traditional biofuel and fodder crops for productive arable land [[42\]](#page-10-34). Other protists may act as biomarkers of ecosystem health, excluding pathogens [\[43](#page-10-35)–[45\]](#page-10-36).

Yet, other protists have harmful impacts on human society. Protist-borne diseases include malaria, caused by *Plasmodium* spp., and African sleeping sickness, caused by *Trypanosoma brucei* [[46,](#page-10-37) [47\]](#page-10-38). Some protist pathogens (e.g., *Naegleria fowleri*, *Balamuthia mandrillaris*) remain essentially untreatable with high mortality rates [\[48](#page-10-39), [49](#page-10-40)]. Protist pathogens of animals (*Babesia bovis*, Babesiosis), crops (*Phytophthora infestans*, late potato blight), and trees (*Phytophthora ramorum*, sudden oak death) can have equally grave impacts on food security and on forestries [\[50–](#page-10-41)[52\]](#page-11-0). Harmful bloom-forming algae (HABs) are severely detrimental to coastal aquaculture [[53](#page-11-1)[–56](#page-11-2)], although they may otherwise be important to marine carbon fxation [[11](#page-10-6), [34\]](#page-10-27).

Finally, even protists with limited industrial applications may provide important reserves of genetic information for understanding cell metabolism [\[56](#page-11-2), [57](#page-11-3)]. Careful study of protist diversity can change our view of the genetic composition, and synthetic potential, of life [[58\]](#page-11-4). Reflecting their multifaceted centrality to planetary ecology, protists are implicated in over half the UN Sustainable Development Goals [[59\]](#page-11-5) (Fig. [1](#page-2-0)).

The threats of the climate and ecological crisis to all living systems

As a result of human activity, the Earth biosphere is moving irreversibly to a new state, termed the Anthropocene [[61,](#page-11-6) [62\]](#page-11-7). The anthropogenic release of $CO₂$, enriched from pre-industrial atmospheric levels of<280 to>420 parts per million in 2024, and other greenhouse gasses (methane, nitrous oxide) has caused global heating [[63](#page-11-8), 64. This is accelerating rapidly and will escalate as feedback loops and tipping points are initiated [[65\]](#page-11-10).

Anthropogenic heating is projected to have multiple impacts on diferent ecosystems. In marine ecosystems, heating increases thermal stratifcation, which severely reduces the available nutrients in the surface layer [\[66](#page-11-11)], and can even change the marine light feld due to deepening of the euphotic zone [[67](#page-11-12)]. Changes to marine cycling, brought in part by melting of polar ice caps [\[68,](#page-11-13) [69\]](#page-11-14), can further alter the abundance and distribution of nutrients in the ocean. The enrichment in atmospheric $CO₂$ drives marine acidifcation, and negatively impacts on nutrient availability [\[70\]](#page-11-15).

In freshwater, warming may conversely drive eutrophication, e.g., by augmenting local precipitation, and increasing runoff of soil nutrients and mineralization of groundwater [[71](#page-11-16), [72\]](#page-11-17). Changing rainfall directly afects soil hydration and nutrient availability and indirectly impacts on terrestrial nutrient cycling via changes in vegetation [\[73,](#page-11-18) [74\]](#page-11-19). Pollution (e.g., nitrates, phosphates, particulates, plastics) has dramatically changed nutrient availability and toxicity, in particular in coastal, freshwater, and terrestrial ecosystems [[75](#page-11-20), [76\]](#page-11-21).

The climate crisis sits at the center of a wider biospheric crisis $[77]$ $[77]$. This relates to the erosion of wild habitats (vegetation, aquatic and soil ecosystems) that have fundamental roles in regulating the planetary ecosystem. Biodiversity collapse, as an irreversible process with unknown consequences, may itself pose a much greater danger to the long-term survival of humanity (e.g., enabling the emergence of novel infectious diseases) [\[78\]](#page-11-23) and have top-down impacts on the functions of individual ecosystems [\[79](#page-11-24)]. Habitat turnover, and the anthropogenic introduction of non-native species, has also changed the distribution of harmful algal blooms and pathogenic protists, both of which have consequent impacts on ecosystem composition and function [\[80](#page-11-25)–[83\]](#page-11-26).

As of 2023, six of the nine Stockholm Planetary Boundaries that constitute a safe operating space for humanity

Fig. 1 Importance of protists to the global earth ecosystem. The inner wheel of this fgure shows 8 UN Sustainable Development Goals (SDGs), adapted freely from [\[59](#page-11-5)]. The outer wheel shows drawings of representative protists, adapted freely from [[60](#page-11-37)], overlaid over SDGs to which they are particularly relevant. For clarity, each protist is only shown once even if it is relevant to multiple SDGs, and the visual organization of the drawings are independent of taxonomic affiliation, for which the reader is directed to [[60](#page-11-37)]

have been surpassed $[84, 85]$ $[84, 85]$ $[84, 85]$ $[84, 85]$ $[84, 85]$. The impacts are felt globally but unequally; no region will be immune to systemic risks as these continue to mount $[86]$ $[86]$. These changes and instabilities naturally implicate protists- and the biologists that study them.

Bench‑to‑feld approaches for understanding protist biology

Protists include many appealing models for eukaryotic cell biology (e.g., *Paramecium*, *Tetrahymena*, *Dictyostelium, Chlamydomonas, Phaeodactylum*) [87-[90\]](#page-11-31). These

species are characterized by easy cultivability and amenity to laboratory manipulation, via comparative physiological, transcriptomic, and metabolic profling [[91](#page-11-32)[–93](#page-11-33)]; analysis of adaptation through experimental evolution $[94]$ $[94]$; and reverse genetics in the growing number of protists amenable to transformation [[95](#page-11-35)]. To some extent, the ongoing isolation of cultivable strains [\[20](#page-10-42)] and deposition of these in culture collections [[7,](#page-10-2) [96](#page-11-36)] continue to close knowledge gaps in our understanding of protist evolutionary diversity. Even in the past decade, the description of new phylum- and

kingdom-level protist clades (e.g., Rapphephyceae, Provora, CRuMS) has substantially changed our view of the eukaryotic tree of life [\[97](#page-11-38)[–99\]](#page-12-0). Beyond classical taxonomy by morphological description, this has been enabled by the sequencing of an ever-greater range of protist genomes, with multigene phylogenies largely supplanting single-gene trees for reconstructing protist taxonomy [\[8,](#page-10-3) [22](#page-10-15), [100](#page-12-1)].

Nonetheless, bench studies provide limited insights into the biology of uncultured protists (e.g., MASTs, MALVs, and MOCHs), many of which are important to global ecology [\[20](#page-10-42), [101\]](#page-12-2). Bench studies likewise provide no information into protist responses to biotic and abiotic changes in the wild [\[55](#page-11-39)]. Here, the use of metagenomic approaches (direct sequencing of environmental samples) allows us to study protists within their natural habitats at a correlative level. This includes the enumeration of species abundances and distributions, using classical meta-barcoding (e.g., 18S, 16S rDNA), primer-free approaches such as *psbO* meta-transcriptomics [[19,](#page-10-13) [102](#page-12-3)], or high-throughput imaging $[15, 103]$ $[15, 103]$ $[15, 103]$ $[15, 103]$. The recent development of single-cell genomics and genome-quality assemblies from environmental data, i.e., metagenomeassembled genomes (MAGs), continues to illuminate protist orders not yet in culture [[21,](#page-10-14) [104](#page-12-5)]. Meta-genomic, meta-transcriptomic, and meta-metabolomic approaches allow us to understand protist physiology in the wild, and predict gene phenotypes that can be validated at a laboratory level [\[26](#page-10-19), [93](#page-11-33), [105\]](#page-12-6). In all of these approaches, measured physical and environmental conditions allow us to reconstruct protist ecological niches and functions, and to predict future species distributions [[104,](#page-12-5) [106\]](#page-12-7).

On longer time-scales, paleontological records (including fossils, isoprenoid biomarkers, and ancient DNA) [[107,](#page-12-8) [108](#page-12-9)] and monitoring programs may provide information into protist community changes across the Holocene or beyond $[109-111]$ $[109-111]$ $[109-111]$. These approaches can be used in conjunction with more speculative techniques, e.g., experimental evolution [\[94](#page-11-34), [112\]](#page-12-12), and biologically grounded or theoretical mathematical modeling [[109](#page-12-10), [113](#page-12-13)], to predict protist evolutionary trajectories in an uncertain future.

Known unknowns in protist adaptations to changing climates

Climate change is causing disruptions to ecosystem composition, including protists. Evaluating these impacts poses both conceptual and technical problems, refecting both the complexity of these changes and the rapidity with which they are occurring. Typically, the growth of microorganisms in culture typically follow an "Eppley envelope," i.e., with increasing exponential-phase growth rates with temperature up to a critical mortality threshold [[114,](#page-12-14) [115\]](#page-12-15). Beyond enhanced growth, however, the impacts of heating on microbial physiology are complex. For example, diatom algae show decreases in cell volume, moderate increases in photosynthesis and large increases in respiration [[116](#page-12-16)[–119](#page-12-17)], amidst remodeling of lipid and nitrogen metabolism [[120](#page-12-18), [121\]](#page-12-19) at elevated, sublethal temperatures. Mixotrophic algae (e.g., chrysophytes) increasingly rely on heterotrophy [[91,](#page-11-32) [122](#page-12-20)], and mineralizing ones (e.g., haptophytes) demonstrate changes in elemental stoichiometry [\[123](#page-12-21), [124](#page-12-22)], under heating conditions. $CO₂$ enrichment (including acidification) have similarly complex impacts on protist physiology and are likely to have neutral or detrimental impacts on primary production [\[79,](#page-11-24) [112](#page-12-12)].

Both long-term monitoring and ecosystem modeling of protists suggest poleward migrations in the Anthropocene, with an expansion of tropical species to higher latitudes, and increased biodiversity in polar regions [[24](#page-10-17), [104](#page-12-5), [125,](#page-12-23) [126](#page-12-24)]. These changes are associated with redistributions of primary production and nutrient cycling [[127,](#page-12-25) [128\]](#page-12-26). Time-series observations have noted that the migratory speeds of protists are slower than the rate at which planetary isotherms are moving [\[107,](#page-12-8) [129](#page-12-27), [130](#page-12-28)], i.e., average temperatures are changing too fast for protists to avoid, with heating likely to incur species loss. Specifc ecosystems are changing beyond bounds associated with recent earth history, e.g., the tropics, impacted by more frequent extreme heatwaves and temperatures that go beyond previously known maxima [\[131](#page-12-29)], and the Arctic, impacted by the rapid loss of sea-ice, which may both curtail summer productivity and allow the incursion of novel algal blooms in the autumn [[132](#page-12-30)[–135](#page-12-31)]. Heating can also perturb the biotic structure of protist ecosystems, disrupting trophic interactions [\[106,](#page-12-7) [136](#page-12-32), [137](#page-12-33)]. Multicellular predators of protists may have more restricted distributions [[104,](#page-12-5) [130](#page-12-28)] and respond more slowly to environmental changes than their prey [[24](#page-10-17), [110](#page-12-34), [129](#page-12-27)]. Changes to these connections may cause catastrophic "top-down" ecological cascades on protist communities [[79,](#page-11-24) [138](#page-12-35)].

Nonetheless, the long-term consequences of global heating for protists remain poorly understood. Below, we outline work on algal temperature sensitivity from our groups, considering lab (growth rate) and feld (metagenomic distribution) evaluations. Figure [2](#page-4-0) focuses on taxonomically diverse algae indigenous to the Arctic Ocean [\[8](#page-10-3)], and Fig. [3](#page-5-0) focuses on geographically diverse strains of haptophyte algae [\[22](#page-10-15), [139\]](#page-12-36). We do not pretend that these data, which relate primarily to free-living marine phototrophs, provide an exhaustive overview of the future distributions of protists from other functional groups and habitats. Instead, we use them to illustrate the limitations of culture-based or ecosystem analyses in

Fig. 2 Temperature optima of phylogenetically distant Arctic algae from experimental and field data. The strains in this figure are derived from the NCMA and RCC culture collections [[96](#page-11-36), [140](#page-12-40)], alongside new ones (RCC7840-7856) isolated from seawater collected during the 2021 Amundsen Darkedge expedition. Top: heatmap of measured exponential growth rates, over seven temperatures (from 0 °C to 32 °C) under 35‰ salinity, and three additional salinities (from 14‰ to 3.5‰) at 4 °C. Species are shaded by taxonomic affiliation. Double-lined boxes show strains that show>99% 18S rRNA sequence identity to one another and can be considered as species. Bottom: plot of *Tara* Oceans 18S v4 ribotype relative abundances of the most abundant diatom (*Chaetoceros* sp. RCC7850) and fagellate (*Pyramimonas* sp. RCC7841) shown relative to station latitude and temperature. Complete data for all distributions are provided in Table S1

isolation and the need for complementary approaches to understand protist responses to climate change.

What can feldwork tell us that laboratory experiments cannot?

Laboratory experiments, despite allowing precise understanding of individual physiological responses, may not be able to recreate the nuances of natural ecosystems. Micro-organisms cultured at the bench often show growth temperature optima several degrees above those of their native habitats $[54, 141]$ $[54, 141]$ $[54, 141]$ $[54, 141]$. The Arctic algae in Fig. [2](#page-4-0) are restricted within environmental data to polar (Arctic and Southern Ocean) sites with temperatures below 5 °C, despite some diatoms demonstrating growth at 12 °C (e.g., *Attheya* sp. RCC7856) or even 19 °C (*Chaetoceros* sp. RCC7850) in laboratory culture. This discrepancy may relate to a thermal safety margin that bufers their sensitivity to heating in the wild [[142,](#page-12-38) [143](#page-12-39)]. Alternatively, the highly non-naturalistic light regimes, nutrients (i.e., eutrophication in standard growth media), and population bottlenecks (regular dilution of cultures) of the

Fig. 3 Temperature optima of and collection sites of phylogenetically close but geographically distant haptophytes. This figure shows (top) measured growth rates and (bottom) collection sites of 15 haptophyte strains from the genera *Pavlova* and *Imantonia/ Pseudohaptolina*, shown as per Fig. [2.](#page-4-0) *Tara* Oceans distributions for all strains are provided in Table S1

laboratory may change protist physiology, such that we overestimate their tolerance of temperature stress [[101](#page-12-2)].

Protist distributions in the wild are constrained by multiple factors, including temperature, nutrients, light, and rainfall [[23](#page-10-16), [73](#page-11-18)[–75,](#page-11-20) [144\]](#page-13-0). For example, heating of the Arctic changes not only seawater temperature but also salinity, via increased precipitation and sea-ice loss [[132](#page-12-30), [133](#page-12-41)]. Within Figs. [2](#page-4-0) and [3](#page-5-0), Arctic chrysophytes and chlorophytes (e.g., *Ochromonas* sp. RCC7855, *Pyramimonas* sp. RCC7841) are viable only at low temperatures \langle <4 °C) but are tolerant of salinities as low as 3-4‰. These species show overlapping feld distributions with more thermotolerant diatoms and may outcompete them in meltwater-impacted conditions despite being more sensitive to heating. Moreover, bench studies in axenic or single-strain cultures provide limited insights into protist biotic interactions [[106](#page-12-7)] with viruses [[134\]](#page-12-42), parasites, and

predators [\[75,](#page-11-20) [79](#page-11-24)]. By "scaling up" bench experiments to ecosystems, feld data allow us to consider the impacts of these biotic and abiotic changes collectively [[79](#page-11-24), [145\]](#page-13-1).

What can laboratory experiments tell us that feldwork cannot?

While meta-barcoding can provide insights into global species ranges, it provides less insight into population variation in thermal tolerance [[22,](#page-10-15) [139](#page-12-36)]. For example, the six *Imantonia* strains in Fig. [3](#page-5-0) have identical 18S rDNA meta-barcodes but show distinct temperature growth relationships over a range of 0 to 24 °C. Strainspecifc genetic diferences (horizontal gene transfers, gene duplications and loss, chromosome rearrangements, individual point mutations) that underpin such trait variations are detectable in *pan*-genomes of cultured protists [[8](#page-10-3), [100](#page-12-1), [146,](#page-13-2) [147\]](#page-13-3). While single-celled and meta-genome-assembled genomes may allow us to understand the population genomics of wild protists [[148,](#page-13-4) [149\]](#page-13-5), these are currently only achievable for abundant species.

Reconstructing species distributions from environmental data principally allows us to explore physical parameters currently observed in the feld. For example, the maximum temperature of the subtropical ocean is cur-rently around 29-32 °C [[150](#page-13-6), [151\]](#page-13-7), and it is still largely unknown what protists will survive in hotter conditions [[54,](#page-11-40) [104](#page-12-5), [152](#page-13-8)]. Some of the *Pavlova* strains in Fig. [3](#page-5-0) (e.g., RCC2550, RCC6257) show tolerance in culture up to 32 °C, and we may be able to explore their biology beyond environmental maxima at the bench. Simulating extreme heating in the feld is possible, e.g., in mesocosms, although to our knowledge, it has principally been applied to soil protists [\[25](#page-10-18), [74,](#page-11-19) [144,](#page-13-0) [153](#page-13-9)]. Similarly, understanding protist trophic fuxes in the feld, e.g., via stable isotope labeling [\[92](#page-11-41), [154](#page-13-10)] is possible but depends on physiological priors established within cultured species.

Which protists need the most future study?

While some protists and protist ecosystems are well represented in culture collections and meta-genomics datasets, others are not [\[155](#page-13-11), [156](#page-13-12)]. Knowledge gaps in our understanding of protist diversity limit our ability to conserve them; to our knowledge, no comprehensive "red list" of endangered protists yet exists [\[157,](#page-13-13) [158\]](#page-13-14). Protists may be understudied due to low cultivability (e.g., open ocean algae) [\[45](#page-10-36), [159](#page-13-15)], inaccessibility of the ecosystems they inhabit (e.g., polar and mountain glacier ice) [[160](#page-13-16), [161](#page-13-17)], or both (e.g., the aerosphere, deep-sea hydrothermal vents and the abyssal plain), limiting their study to meta-genomics $[5, 162, 163]$ $[5, 162, 163]$ $[5, 162, 163]$ $[5, 162, 163]$ $[5, 162, 163]$ $[5, 162, 163]$. The rare protist biosphere, encompassing new groups present at low levels in environmental data, may conversely be best studied in-lab via enrichment-based techniques $[20, 164]$ $[20, 164]$ $[20, 164]$. These rare species may be sensitive to ecosystem disruption or play increasingly important roles due to changes in dominant overlying taxa [\[165](#page-13-21), [166\]](#page-13-22).

In general, protists that live as commensals of other organisms remain globally understudied [\[79,](#page-11-24) [106](#page-12-7), [156](#page-13-12)]. These may form cryptic reserves of biodiversity, with conservative estimates of termite protist symbionts suggesting no more than a tenth are known to science [\[14](#page-10-9)]. Protists that live in other animal guts are even less well studied and may be particularly vulnerable to co-extinction alongside their hosts [[44,](#page-10-43) [167](#page-13-23)]. Some endosymbiotic protists are also pathogens of humans (e.g., *Plasmodium* as a mosquito endosymbiont) [\[168](#page-13-24), [169](#page-13-25)], and the destruction of wild habitats may cause more frequent contact between their vectors and humans [[170,](#page-13-26) [171](#page-13-27)], with disproportionate impacts on marginalized peoples [[172](#page-13-28), [173](#page-13-29)].

Alongside describing where protists are found in the wild, more information is generally needed on when protists are abundant in their habitats. Time-series and long-term observation studies, ranging from classical morphology [\[55](#page-11-39), [109](#page-12-10)] to meta-genomic and remote sensing [\[174](#page-13-30), [175](#page-13-31)], have described recent changes to the amplitude and timing of protist abundances over annual cycles. These changes relate not only to abiotic factors and predator and vector distributions [[176\]](#page-13-32) but also to protist life-cycles, e.g., resting stages induced by extreme heating [\[177](#page-13-33), [178](#page-13-34)] or implicated in the dispersal of invasive protist species into new habitats [\[179](#page-13-35), [180](#page-13-36)]. With suffcient input data, we may be able to train detailed global systems models that can integrate protist life-cycles and seasonality into future distributions [[24](#page-10-17), [55,](#page-11-39) [67](#page-11-12), [126](#page-12-24)].

More information is also needed concerning protist acclimation and adaptation to heating over longer time-scales [[181\]](#page-13-37). Here, protists may be valuable models for experimental evolution, for themselves and for macro-eukaryotes, given their small cell sizes, rapid generation times, and large populations at laboratory scales $[112, 182-184]$ $[112, 182-184]$ $[112, 182-184]$ $[112, 182-184]$. Nonetheless, it is difficult to generalize evolutionary trajectories anticipated from bench experiments to wild communities, with mutation rates varying between species and physiological conditions [[185\]](#page-13-40); genome content and physiology varying at population scales [\[186](#page-13-41), [187\]](#page-13-42); and adaptive responses to temperature dependent on the magnitude, direction, and fuctuation of stresses [\[188\]](#page-13-43). Long-term observation data [[189,](#page-13-44) [190\]](#page-14-0), alongside theoretical $[113, 191]$ $[113, 191]$ $[113, 191]$ $[113, 191]$ and phylodynamic modeling of speciation and extinction [\[19](#page-10-13), [107](#page-12-8)], may allow us to translate experimental evolution into real-world biology.

Finally, we note the importance of continued research into applied protist biology, including the development of green technologies from model photosynthetic species [\[39](#page-10-32), [40](#page-10-44)], and therapeutic strategies for parasitic protists emerging as a result of global heating and ecosystem breakdown $[48, 49]$ $[48, 49]$ $[48, 49]$ $[48, 49]$. These challenges nonetheless require a comprehensive understanding of protist biology and evolution. For example, new treatments of protist parasites may depend on cell organelles (e.g., the apicoplast of *Plasmodium* [[192\]](#page-14-2)) or organelle trafficking complexes [[193\]](#page-14-3) identifed in these organisms, but missing from humans.

"No research on a dead planet": protistology in the era of climate breakdown

Protistology research remains valuable in a rapidly changing world, providing insights into the diversity of life and opportunities to confront global challenges [[40](#page-10-44),

[57,](#page-11-3) [155\]](#page-13-11). At the same time, for our research to continue and its potential to be realized, we are dependent on the functioning of socio-ecological systems that are existentially threatened by the climate and ecological crisis. This is an uncomfortable truth and one that the scientific research community has been slow to confront [\[194](#page-14-4)]. Many of us are, consciously or unconsciously, navigating a paradox of pursuing a life science career in an escalating biospheric emergency that may not be compatible with organized human society $[195, 196]$ $[195, 196]$ $[195, 196]$ $[195, 196]$. The tensions inherent in performing research in the era of climate collapse, at the expense of recognizing and taking action to address these threats, may feel particularly acute for younger researchers [\[197](#page-14-7), [198](#page-14-8)].

Questions and considerations for sustainable protistology research

Having refected on *what* protistology questions are in most pressing need of further research, we invite you to consider *how* research science activities, cultures, and communities can—and must—evolve in the light of

the climate and ecological crisis (Fig. 4). These considerations are not unique to protistology but will shape how our research is performed in the future, refecting that life science research practices are often generally resource- and carbon-intensive [[199\]](#page-14-9). Some of their negative impacts can be—albeit only partially—mitigated through shifts such as reducing consumption of singleuse plastics or replacement with glassware [[200,](#page-14-10) [201](#page-14-11)]; minimizing energy-intensive bioinformatics via software upgrades and new programs with lower computational requirements [[202,](#page-14-12) [203\]](#page-14-13); and repairing, sharing, reusing, and recycling laboratory equipment [\[203](#page-14-13), [204\]](#page-14-14). There are multiple open-access tools and organizations that can support the evaluation of research carbon footprints and development of management plans (e.g., GES 1point5, PyJoules) [\[205,](#page-14-15) [206](#page-14-16)].

More systemic changes are required to avoid or minimize harm associated with research activities and to enable genuinely sustainable alternatives. Typically, the largest contributor to the researcher carbon footprint, usually outstripping that of heating and cooling

From Science... to Society

How can the role of protist research & researchers evolve to address the challenges of the Anthropocene?

What we research

Key focus areas might include:

Scoping & modeling ecosystem risks to better anticipate impacts on and of protist species in a warming world.

Conservation & ecosystem restoration: How can we protect diverse protist species, and can they help us restore and remediate environments?

Understanding emergence and spread of infectious diseases caused by parasitic protozoa, informing prevention and treatment.

Biotechnology: Can protist biology inspire or form part of genuinely sustainable alternatives e.g. in foods, fuels or CO2 removal?

How can protistology research skills also be applied beyond this field to contribute to positive system transformations?

How we research

Open, collaborative & intentional practices, sharing knowledge and data, valuing impacts beyond traditional metrics.

Target negative climate and biodiversity footprint of research activities e.g.

- Mitigate avoidable impacts of lab work through energy efficiency, phase out of single-use labware, equipment sharing etc.
- Conscious computing, paying attention to \bullet device maintenance, coding efficiency, data storage etc.
- Rationalise and decarbonize travel, using online participation to widen meetings access. Increase collaboration with local researchers and community members for fieldwork.

Take a critical approach to partnerships and funding relationships with bodies whose activities do not align with action on the climate & ecological emergency. See, for example, the fossil-free research movement.

Beyond research

Learn and connect with the crises affecting life, possible interventions, and our roles as scientists and citizens.

Communicate scientific insights via academic teaching roles, workshops, articles, public engagement etc.

Challenge and influence institutions and decision-makers such as universities, learned societies, politicians & industry leaders

Support campaigns & social movements as visible advocates and/ or participants, or 'behind the scenes' e.g. with research, advice & fact-checking

Cultivate supportive networks and spaces, acting with care for one another as we face difficult realities and create positive alternatives together.

Fig. 4 Roles and actions for the protistologists of the Anthropocene. Diferent actions that the protistology community might consider taking, within and beyond our research. These are divided into what we study, how this research is performed, and actions we can take beyond scientifc research to advocate for planetary ecology

laboratories, is air travel [[207,](#page-14-17) [208](#page-14-18)]. Alongside rationalizing how often, how far, and which researchers travel, we can facilitate and incentivize the use of less-polluting modes of transport and move to hybrid and online conference formats [[209](#page-14-19), [210\]](#page-14-20). Access to networking or learning opportunities that require international travel is inherently unequal with respect to intersecting demographic and personal factors including wealth, nationality, health, safety, and caring responsibilities, with the expectation that scientists from high-income economies can and should travel for research, and researchers from elsewhere must travel to train (i.e., "parachute science"), both socially and environmentally unsustainable [[211–](#page-14-21)[213](#page-14-22)]. Environmentally conscious feldwork necessitates greater involvement of, and exchange of knowledge with, Indigenous communities that are stakeholders in the ecosystems concerned [[214](#page-14-23)[–216\]](#page-14-24). Similarly, supporting ambitious protistology projects (e.g., pan-genomes [[217,](#page-14-25) [218\]](#page-14-26)) led by researchers in under-resourced settings complements and reinforces progress towards equitable and anti-colonial research science.

Ultimately, designing sustainable research involves careful evaluation of the balance between its ecological "footprint" and its contribution to our ability to understand, communicate, and educate for change [[219\]](#page-14-27). If our work considers protist evolutionary diversity or environmental trends, can it be useful in mitigating harm, conserving, or restoring ecosystems [\[157](#page-13-13), [159](#page-13-15)]? If our work deals in innovative bio-based "solutions," can we ensure their promise is not used to delay necessary actions (such as decarbonization) or support an unsustainable *status quo* [\[220](#page-14-28)]? Does our research engage democratically with the public and global research community [\[221](#page-14-29)[–223\]](#page-14-30) in a way that will be listened to and acted upon [[224\]](#page-14-31)? Whatever the focus of our research, are we content that the pursuit of that knowledge justifes the—often substantial [[225–](#page-14-32)[227](#page-14-33)]—environmental cost?

Advocating for protists beyond research

As protistologists, we advocate for often-overlooked organisms which are diverse, essential, and infuential [[9,](#page-10-4) [155\]](#page-13-11). Amidst growing calls for academic practice to engage with the biospheric emergency [[219,](#page-14-27) [228,](#page-14-34) [229](#page-14-35)], that role now requires co-creating conditions where the study of life will remain possible (Fig. 4). Through our teaching and mentoring roles [[221,](#page-14-29) [230](#page-14-36)], we have opportunity—and arguably responsibility—to discuss climate and ecosystem breakdown and challenge the prioritization of traditional metrics of "success" (publications, awards) over impactful, collaborative work [[219](#page-14-27), [231](#page-14-37)]. Moreover, the skills of researchers have broad transferability and actionability beyond science [[224\]](#page-14-31). Scientists can play valuable supportive and public roles in political and social movements, from providing advice to participating in non-violent civil disobedience [\[228](#page-14-34), [232,](#page-14-38) [233\]](#page-14-39).

We know that intersecting crises—caused by people are changing the global biosphere, with much greater disruption ahead. In parallel, scientists, like the life we study, must adapt, confronting uncomfortable realities, shifting mindsets, and showing leadership in realigning our actions. We hope that our communities will empower one another to respond to the demands of the Anthropocene, for people, planet, protists, and protistology.

Methods

Cultures

Haptophyte and Arctic strains shown in Figs. [2](#page-4-0) and [3](#page-5-0) were maintained in an enhanced seawater (ES) base with k/2 amendment (https://roscoff-culture-collection.org/ [medium-id/k2-i](https://roscoff-culture-collection.org/medium-id/k2-i)), under 50 μ E m⁻² s⁻¹ cool white LED light, following [[93](#page-11-33)].

Novel species included in this study (Arctic strains RCC7840-7856) were isolated from seawater harvested from the surface chlorophyll maximum (SCM) of the CCGS Amundsen during the October 2021 DarkEdge campaign in Baffin Bay $[234]$ $[234]$. Species were isolated by serial dilution until only individual strains could be identifed by light microscopy. New strains were barcoded using consensus eukaryotic primers (see below), and only strains producing clean sequences corresponding to one unique species were used for future study. All strains included in this study have been deposited in the Roscof Culture Collection [\[96](#page-11-36)].

Tara **Oceans distributions**

The 18S V4 rDNA relative abundances of each strain was mapped to complete meta-barcode data from the *Tara* Oceans and *Tara* Polar Circle expeditions using a previously defined phylogenetic technique $[8]$ $[8]$. Briefly, this involved extracting genomic DNA from each strain using a DNeasy Plant Pro Kit (Qiagen), amplifying the complete 18S sequences from extracted DNA of each strain using consensus eukaryotic primers (e.g., EAF3: TCGAC AATCT GGTTG ATCCT GCCAG and BR: TTGAT CCTTC TGCAG GTTCA CCTAC) using a previously defned protocol [\[235](#page-14-41)], purifcation with a Macherey– Nagel PCR cleanup kit, and Sanger sequencing of amplifed products (Eurofns Genomics).

The amplified sequences were compiled against previously generated sets of 18S nucleotide sequences from cultivated members of the same algal order [\[8](#page-10-3)]. Next, complete *Tara* Oceans V4 ribotypes that corresponded to the same order were searched against the cultured species reference dataset using BLASTn [[236](#page-15-0)]. Ribotypes

that retrieved a given strain within the best five hits were retained and aligned against the cultured strain reference data using maft v 7.2 under the –auto setting [\[237](#page-15-1)]. Cultured strains with>99% identity to one another and their corresponding ribotypes were pooled for this analysis. Finally, reference trees were built for each ribotypeenriched alignment using RAxML version 8.0, 350 bootstrap replicates and automated best-scoring tree fnding [\[238\]](#page-15-2). Ribotypes that resolved as monophyletic to given strains to the exclusion of all others (typically with>97% pairwise sequence identity) were assigned to that strain.

Species relative abundances were calculated as the total proportion of ribotypes at each *Tara* Oceans station that reconciled to each strain, with each depth and size fraction treated as separate data. Barcode sequences, alignments, phylogenetic trees, and complete ribotype relative abundances as well as averages obtained across all depths and size fractions for each station are provided in Table S1.

Growth measurements

Exponential phase growth rates (expressed as relative number of doublings per day) were measured for each strain across 7 diferent growth temperatures (0 °C, 4 °C, 12 °C, 19 °C, 24 °C, 28 °C, 32 °C). Growth measurements were performed at 0 °C and 4 °C under continuous illumination and at 19 °C, 24 °C, 28 °C, and 32 °C under 12 h light:12 h dark cycling. Growth measurements for strains at 12 °C were performed under both continuous illumination (Arctic species) or light–dark cycling (haptophytes), with little observed diference in growth kinetics for species (e.g., *Pavlova* sp. RCC1539, *Imantonia* sp. RCC4501) where both conditions were tested (Table S1).

Typically, growth curves were started with an initial density of 10,000 cells ml⁻¹, as diluted from optical density counts evaluated using a Malassez hemocytometer, and counted with a ParTec flow cytometer, following [[93](#page-11-33)]. At least two replicates were performed for each strain: condition combination with three in most cases. Cell growth rates were calculated by taking the rate of change in the $log₂$ cell concentrations from densities of 50,000 cells ml^{-1} with a minimum of three successive time measurements used for each rate calculation. The linear correlation of the $log₂$ concentration was calculated against time, with only time intervals producing correlation values *r*>0.9 used to calculate growth rates. Complete growth data including individual rate calculations for each experiment replicate are provided in Table S1.

Accession numbers

18S and 16S chloroplast rDNA sequences for new strains described in this study are provided in GenBank OR840005-OR840020.

Supplementary Information

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Additional fle: Table S1. Calculated growth rates and mapped environmental distributions of cultivated Arctic and haptophyte algae.

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Authors' contributions

AJP and RGD co-wrote the review. RGD provided Figs. [1](#page-2-0), [2,](#page-4-0) and [3,](#page-5-0) and AJP provided Fig. [4.](#page-7-0) Both co-authors read, critically modifed, and approved the fnal version of the manuscript prior to submission.

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Data availability

Growth curve data, 18S and 16S plastid rDNA sequences, and mapped 18S v4 ribotypes are provided in Table S1.

Declarations

Competing interests

The authors declare that they have no competing interests.

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