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A New Dawn for Protist Biogeography

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ABSTRACT

Aim: Biogeographers have believed for a long time that the geographical distributions of protists are only determined by environmental conditions, because dispersal is not limited. During the past two decades, the field has come a long way to show that historical and spatial factors also significantly contribute to shaping protist distributions, calling for a reappraisal of our understanding of protist biogeography.

Methods: We review the current state-of-the-art on the field of protist biogeography, highlighting several outstanding questions and opportunities. Our review brings together insights from different disciplines, ranging from morphology-based research to environmental, population and speciation genomics.

Results: Protist communities harbour cosmopolitan and geographically restricted species and are shaped by both local environmental conditions and historical processes, yet the relative contributions of these patterns and processes likely differs depending on the geographic scale, protist lineage and the habitat that is being investigated. The field is ready to move beyond the decades-long ubiquity versus (moderate) endemicity discourse and to instead ask why and where specific protist species and clades are more prone to widespread or restricted distributions. With the advent of next-generation sequencing technologies, from whole-genome sequencing to environmental and ancient DNA surveys, it is now possible to integrate insights from multiple lines of evidence and investigate protist communities, species and populations at an unprecedented scale and detail.

Outlook: To further advance the field, the protist community needs to focus on understudied habitats and protist lineages, study the impact of protist traits on biogeographical patterns, perform targeted field and experimental work to disentangle the processes that underlie protist biogeographies and expand and develop databases with sequence, trait, distributional and phylogenetic information of protists. Given that a good understanding of species boundaries is central to unravelling protist biogeography, it remains crucial to invest in polyphasic taxonomic research.

1 | Introduction

Protists represent the vast majority of lineages in the eukaryotic tree of life. Collectively, they harbour at least 30 divisions (Guillou et al. 2013) with widely different life strategies, trophic modes, clade ages and morphological and functional diversity. New protist lineages, even including novel 'kingdom-level' taxa, are regularly discovered (Burki et al. 2020). Protists play diverse and pivotal roles in ecosystem functioning such as primary production and biogeochemical cycling in marine, freshwater and terrestrial environments (Worden et al. 2015; Crowther et al. 2019). Understanding the drivers of (eco-)evolutionary dynamics and biogeographical distributions of protists is therefore paramount to predict their future performance on our rapidly changing planet (Cavicchioli et al. 2019).

Several publications reviewed major advances or outstanding questions in protist biogeography (Fontaneto 2011), often focusing on specific topics, such as the processes that shape microbial biogeography (Hanson et al. 2012; Soininen 2012), the relevance of macroecological rules for protist biogeography (Dickey et al. 2021), soil protists (Geisen et al. 2017) or taxonomic groups such as tintinnids (Dolan and Pierce 2012) or diatoms (Vanormelingen, Verleyen, and Vyverman 2008; Soininen and Teittinen 2019). Here, we complement these reviews by integrating recent insights from different disciplines, ranging from morphology-based approaches to experimental, population and speciation genomics, covering auto-, mixo- and heterotrophic protist lineages from marine, freshwater and terrestrial environments worldwide. As such, our review brings together decades of insights from microscopy studies on community composition, with recent important developments in the field since the introduction of DNA sequencing techniques. Especially the decreasing costs of whole-genome sequencing and environmental genomics, including metabarcoding of environmental DNA (eDNA), metagenomics, metatranscriptomics and sequencing of ancient DNA (aDNA), has allowed the field of protist biogeography to prosper. Our review first discusses how different lines of evidence helped researchers to chart protist distributions. The second part of our review focuses on major outstanding questions regarding the processes and organismal traits that shape protist biogeographies, as well as how they have been impacted by human activities. Our review highlights major opportunities for improving our understanding of the ecological and historical biogeography of protists in the years to come.

2 | Charting Biogeographical Patterns of Protist Species

2.1 | A Decades-Long Debate: Ubiquity Versus Moderate Endemicity as Revealed by Morphological Data

Documenting patterns in the geographical distributions of protists has long been based on morphological species concepts. Observations of highly similar morphotypes in suitable habitats worldwide gave rise to the idea that protist distributions are solely governed by local environmental conditions (Baas Becking 1934). The combination of astronomically large population sizes and small cell sizes of protist species would result in unlimited, neutral dispersal. This idea is now mostly referred to as the *ubiquity hypothesis* (Finlay 2002). Evidence for the ubiquity hypothesis came from, among others, ciliates and flagellates for which morphological observations suggested low global species richness and broad species distributions (Finlay and Clarke 1999; Finlay, Esteban et al. 1999; Finlay 2002). Opponents of this view argued that protists do have biogeographies and that their distributions are also governed by historical factors, that is, the persistent imprints of past geological, climatological or other historical events on the geographic distributions of protists due constraints on dispersal and/or colonisation (Foissner, Chao, and Katz 2008). Evidence for this moderate endemicity hypothesis came from a number of protist flagship species (i.e., hard-to-underreport species with highly distinct and unique morphologies, Foissner 1998; Foissner, Chao, and Katz 2008) with restricted distributions, attributed to dispersal limitation (Foissner 1998; Foissner, Chao, and Katz 2008). What followed was a heated debate between the proponents of these hypotheses, often focused on (dis)proving the endemic distributions of specific protist taxa (Mitchell and Meisterfeld 2005). New (flagship) species with restricted distributions were reported in phyla with diverse and often easily recognisable morphologies, such as desmids, dinoflagellates, testate amoebae, myxomycetes and diatoms (Tyler 1996; Vyverman et al. 1998; Stephenson, Schnittler, and Novozhilov 2008; Vanormelingen, Verleyen, and Vyverman 2008; Duckert et al. 2021), but also ciliates (Foissner, Chao, and Katz 2008). Whereas several of these flagships have since been disproved (Hines, McCarthy, and Esteban 2016, 2020; Bourland 2017; Bourland, Rotterová, and Čepička 2017), many others have stood the test of time, with additional evidence only strengthening their endemic status (Pinseel et al. 2021).

A second line of evidence to evaluate protist biogeographies focuses on community-level analyses enabled by careful taxonomic curation and standardisation of morphology-based global or regional datasets. Only a limited number of studies used this approach and most focused on ciliates, flagellates or diatoms. For instance, a global-scale analyses of ciliate communities found many ciliates to have wide geographic distributions, but concluded that community-level differences between continents and the number of taxa restricted to a single continent were large enough to support the moderate endemicity hypothesis (Chao et al. 2006). Another study noted surprising similarities in the distribution patterns of ciliates and macrobiota in Chile (Campello-Nunes et al. 2022). Comprehensive analyses of freshwater diatom communities also supported the existence of distinct protist biota in different regions, including endemic species. The degree of taxon turnover between these biota is not only governed by ecological processes (Vyverman et al. 2007), as even when similar habitats are investigated, large regional differences in species composition have been found (Van de Vijver, Gremmen, and Beyens 2005; Pinseel et al. 2021; Verleyen et al. 2021). In an extreme case, 44% of all Antarctic diatom species were reported to be endemic to the Antarctic, with most of these also showing restricted distributions within Antarctica (Verleyen et al. 2021). Similarly, morphological analysis of fossil and extant freshwater diatom floras showed evidence for at least three flagship species/genera confined to the former Gondwanan continents of Antarctica, Australia (Tasmania), New Zealand and southern South America (Pinseel et al. 2021). Even though Gondwana almost certainly predates the origin of these diatom taxa, it represents strong evidence for regional dispersal limitation. Altogether, the above observations are attributed to historical factors. However, not all community-scale studies point to a distinct impact of history on protists communities. For instance, a global-scale morphology-based analysis on marine benthic flagellates suggested that community composition was determined by contemporary climate, but not by geographic distance, which was generally confirmed by molecular analyses (Azovsky, Tikhonenkov, and Mazei 2016). Another study on ciliates found regional endemicity levels of only 5%–7%, which is much lower than those for macrobiota (Azovsky and Mazei 2013).

Despite their tremendous value in charting protist biogeographies, well-curated, globally compiled morphology-based datasets remain rare. Such efforts usually require combining independently obtained datasets, typically generated by different analysts and consequently may contain multiple biases due to varying interpretations of species boundaries. This might be one explanation for the above-mentioned, seemingly different results reported by different authors. As these datasets are also pivotal for the much-needed integration of morphological and molecular data, the dwindling number of traditionally trained taxonomists (i.e., those using morphology) is a worrying development and in need of appropriate funding.

2.2 | Molecular Phylogenetics Uncovered Widespread (Pseudo)Cryptic Diversity in Protist Morphospecies

Despite valuable insights from morphology-based datasets, for many protists morphology holds little potential for species discrimination between closely related lineages. This is because many protist lineages have few distinctive morphological characteristics and can show considerable phenotypic plasticity which hampers correct species delimitation (Dolan, Pierce, and Bachy 2014; Verbruggen 2014; Mulot et al. 2017). Not surprisingly, extensive molecular phylogenetic analyses of protists uncovered (pseudo)cryptic diversity, that is, species-level diversity characterised by little or no morphological divergence (Slapeta, López-García, and Moreira 2006; Boo et al. 2010; Cai et al. 2020). Even in lineages with rich morphological features such as diatoms and coccolithophores, molecular phylogenetics revealed that (pseudo)cryptic diversity is common (Mann 1999; Amato, Kooistra, and Montresor 2019; Bendif et al. 2023). The discovery that many protist morphospecies comprise distinct clusters in molecular phylogenies spurred detailed statistical analyses of protist morphologies, for instance using geometric morphometric techniques (Kloster, Kauer, and Beszteri 2014). This showed that statistical analyses of morphological features can frequently discern distinct groups that were revealed by molecular techniques (Poulícková et al. 2010; Postel et al. 2020), although sometimes intralineage morphological variability was too large to confidently assign protist strains to lineages in a phylogeny (Pinseel et al. 2019). In other cases, more detailed microscopic techniques, like scanning electron microscopy, were able to reveal fine ultrastructural differences, showing subtle morphological differences between protist taxa that were previously overlooked (Round, Crawford, and Mann 1990; Mann 1999; Dagamac et al. 2017; Pinseel, Vanormelingen, et al. 2017). Even though both examples show that detailed morphological analyses remain highly valuable when delimiting protist species, these techniques are rarely applicable in high-throughput settings to, for instance, identify pseudocryptic lineages in the large sample numbers necessary to reveal protist distributions. That being said, recent developments in the field of protist morphometrics and automatic microscopy slide analysis provide a promising outlook to the future (Kloster et al. 2017, 2020). Similarly, morphometrics can uncover subtle but distinct protist morphologies also in the absence of molecular data, such as in fossil datasets (Kloster et al. 2018).

Frequently, (pseudo)cryptic diversity is associated with niche divergence and/or non-overlapping geographic distributions in protists (Darling et al. 2004; Katz et al. 2011; Heger, Mitchell, and Leander 2013; Škaloud and Rindi 2013; Souffreau, Vanormelingen, et al. 2013; Ishitani, Ujiié, and Takishita 2014; Singer et al. 2018, 2019; Pinseel et al. 2020). Also, co-existence of multiple closely related (pseudo)cryptic species has been reported (De Decker et al. 2018; Pinseel et al. 2020; Shchepin et al. 2021). In some cases, extensive analysis of cryptic lineages reveals unexpectedly high species-level diversity, such as for the terrestrial diatom complex *Pinnularia borealis* in which 126 putative species were detected using molecular techniques, with an estimated number of up to ~400 species globally (Pinseel et al. 2020). Under the ubiquity hypothesis, one would expect to find the same species in similar environments, yet in reality polar and temperate habitats on different continents are home to different species from the *P. borealis* complex, indicative of dispersal limitation. Indeed, analyses on historical biogeography suggested allopatric speciation to be the dominant mode of diversification in the *P. borealis* complex (Pinseel et al. 2020). It is too early to conclude to what extent this observation on *P. borealis* is the exception or the rule in protists, but it is likely that other extraordinarily diverse lineages remain to be discovered. However, charting such cryptic diversity can be challenging given that (i) few studies use standardised approaches, such as automated molecular species delimitation methods, to detect and define (pseudo)cryptic lineages and (ii) some of the typical marker genes used in phylogenetic studies (e.g., the nuclear encoded 18S rRNA, the plastid *rbcL*) sometimes lack sufficient resolution to distinguish recently diverged species (Kollár et al. 2019; Pinseel et al. 2020; Lara, Singer, and Geisen 2022). In the latter case, a focus on more rapidly evolving genes, such as mitochondrial ones (Alverson 2008) or whole-genome sequencing (Bendif et al. 2023) can still detect species boundaries. For instance, whole-genome sequencing on the common, cosmopolitan marine coccolithophore *Gephyrocapsa huxleyi* recently revealed three separate species that originated in the last ~140 ka (Bendif et al. 2023). Finally, phylogenetic data were in some cases complemented with assays on reproductive barriers, further confirming the existence of cryptic species-level diversity (Vanormelingen et al. 2008; Quijano-Scheggia et al. 2009), but also uncovering evidence for mating compatibility between distant populations, such as between Arctic and Antarctic ciliates (Di Giuseppe et al. 2011). Altogether, molecular phylogenies have further supported the existence of protist biogeographies and endemism (Darling, Kucera, and Wade 2007; De Wever et al. 2009; Pinseel et al. 2020; Škaloud et al. 2020), but also confirmed the widespread distribution of numerous protist taxa (Janik, Lado, and Ronikier 2020; Van de Vyver et al. 2022). It has to be mentioned that molecular phylogenetics is not a panacea and might lead to under- or over-splitting if sequence differences are not carefully interpreted in the light of additional evidence, or when too little, or too much weight is given to large or small sequence differences respectively (Leliaert et al. 2014; Kotyk, Bourland, and Soviš 2023). A polyphasic approach which uses data from various sources, from molecular data to morphology, ecology and (reproductive) behaviour, remains a robust way forward to delimit and define protist species (De Decker et al. 2018; Kollár et al. 2019; Kotyk, Bourland, and Soviš 2023). In this light, the high taxonomic resolution provided by whole-genome sequencing will likely become increasingly important in the future of protist taxonomy (Bendif et al. 2023).

2.3 | High-Throughput Environmental Sequencing as the New Standard Method in Protist Biogeography

High-throughput sequencing of eDNA, from metabarcoding to metatranscriptomics and metagenomics, is revolutionising the field, allowing us to describe the occurrence of diverse phyla simultaneously at large geographic scales and low cost, while bypassing the difficulties with standardisation and sampling depth associated with morphology-based inferences (Burki, Sandin, and Jamy 2021). To date, eDNA surveys have detected high levels of novel protist diversity in understudied environments or lineages (Stern et al. 2010; Mahé et al. 2017; Venter et al. 2017; Metz et al. 2023) and revealed the existence of distinct protist communities across ocean provinces, lakes or soils including regional endemism (Bates et al. 2013; Seeleuthner et al. 2018; Tytgat et al. 2023; Pierella Karlusich et al. 2024). Several eDNA studies showed that both local environmental factors and historical factors (i.e., geographic distance) structure protist communities (Bates et al. 2013; Boenigk et al. 2018; Tytgat et al. 2023). However, not all studies detected clear biogeographical patterns or an impact of history on protist communities. For instance, eDNA surveys on marine ciliates and flagellates mostly suggest widespread distributions and a dominant control of local environmental factors on community composition (Flegontova et al. 2016; Gimmler et al. 2016; Canals et al. 2020; Obiol, Muhovic, and Massana 2021), although sometimes additional work was able to detect an impact of geography (Flegontova et al. 2020). Such differences in the outcome between studies can be due to sample size, geographic coverage and scale, as well as methodological approaches. For instance, whereas marine ciliates are often considered a prime example of cosmopolitanism based on eDNA surveys (Gimmler et al. 2016; Canals et al. 2020), recent work that took into account single-nucleotide differences between operational taxonomic units (OTUs), suggests that restricted distributions are not uncommon in ciliates (Ganser et al. 2021).

Environmental sequencing comes with its own set of challenges, including incomplete reference databases, low taxonomic resolution and difficulties with linking abundance of sequence data to cell numbers in environmental samples (Santoferrara et al. 2020; Keck, Couton, and Altermatt 2022), although efforts are underway to address this (Kosakyan et al. 2015; Martin et al. 2022) (Box 2). To date, metabarcoding studies have heavily relied on V4 or V9-18S rRNA, because it allows to amplify the entire protist community at once. However, it is becoming increasingly clear that 18S does not provide species-level resolution in many protists (Pinseel et al. 2020; Lara, Singer, and Geisen 2022). In fact, small differences in 18S rRNA sequence similarity (e.g., 97%–99%) equate to several hundred thousand to many millions of years of evolution (Tytgat et al. 2023). For instance, we calculated that in the terrestrial diatom species complex *P. borealis*, a 1124 base pair region of 18S, that includes the V4 and V9 regions, evolves at a rate of about one substitution every 3.6 million years (Pinseel et al. 2020). Given that protist species can arise on timescales of just a few hundred thousand years (Theriot et al. 2006; Bendif et al. 2019, 2023; Filatov et al. 2021), this example underscores the limitations of 18S metabarcoding to unravel fine-grained biogeographical patterns and suggests that failure to detect biogeographical patterns in some 18S-metabarcoding studies does not necessarily equate the absence of protist biogeographies. To alleviate some of these issues, clade-specific protocols targeting more variable, faster evolving genes (Canesi and Rynearson 2016; Segawa et al. 2018; Singer et al. 2018; González-Miguéns et al. 2023) and long-read sequencing (Jamy et al. 2020, 2022) are being developed. In addition, metagenomics and metatranscriptomics permit high-resolution community-wide inventories without amplification bias (Salazar et al. 2019; Obiol et al. 2020; Oliverio et al. 2020), although interpreting the sheer volume of data remains challenging. Still, such approaches offer a promising future for unravelling fine-grained patterns of protist community composition and turnover in environmental samples. Finally, novel statistical approaches to analyse metabarcoding data might provide more powerful means to detect signals of history in protists communities. In a recent study, Tytgat et al. (2023) used extensive sampling over large geographical scales, combined with careful statistical analysis of 18S-metabarcoding data at different levels of sequence similarity to detect deep evolutionary divergences between Arctic and Antarctic lacustrine protist communities despite similar environmental conditions. Another promising development is the use of phylogenetic haplotype networks and automated molecular species delimitation methods in global metabarcoding efforts to simultaneously uncover taxonomically fine-grained patterns within genera or species complexes and their geographic ranges, which has revealed previously undetected species-level diversity (De Luca et al. 2021; Rimet et al. 2023).

2.4 | Protist Biogeography Through the Lens of the Fossil Record and Ancient DNA

Several protist lineages have excellent fossil records, especially in the marine environment, allowing to study community dynamics over millions of years of evolution, contained within often continuous sedimentary records. Numerous studies have investigated community turnover, in particular of marine foraminifera, radiolaria, coccolithophores and diatoms, showing strong linkage between climate and community dynamics (Matsuoka and Okada 1990; Lazarus et al. 2014; Crampton et al. 2016; Petrizzo et al. 2020; Trubovitz et al. 2020). Analysis of fossil marine diatom communities revealed that species were able to mitigate extinction risk by tracking temperature changes in the open ocean (Cermeño and Falkowski 2009; Cermeño et al. 2010; Cermeño 2012). In contrast, the majority of radiolaria species failed to track major changes in climate throughout the Neogene, but instead went extinct, suggesting major barriers to dispersal exist for this lineage (Trubovitz et al. 2020). It is important to note that fossil records cannot account for cryptic diversity and might thus underestimate the degree of community turnover and dispersal limitation. This is illustrated by recent, genome-scale work on globally dominant marine coccolithophores, which showed that geographic barriers to gene flow and thus dispersal limitation, shaped repeated species radiations throughout the Holocene (Bendif et al. 2019, 2023; Filatov et al. 2021). Similarly, dispersal limitation was also evident for marine foraminiferans, as revealed by phylogenetic analyses (Darling et al. 2004; Darling, Kucera, and Wade 2007).

Fossil records of freshwater environments are much less studied and except for ancient lakes, do not stretch much beyond the late Pliocene. For older geological time periods, data are scantier and lack continuity. Yet, the few available examples show interesting patterns, including a global biogeographical reorganisation of freshwater diatom floras in response to the late-Eocene end of 'greenhouse Earth' (Siver and Wolfe 2009) and a dramatic extinction wave of Antarctic diatoms in response to Miocene climate cooling (Pinseel et al. 2021). Lacustrine polar diatoms, and protists in general, likely never recovered from the latter event and/or the following Pleistocene glacial–interglacial cycles, as Arctic and Antarctic protist communities are highly distinct despite experiencing similar environmental conditions (Pinseel et al. 2021; Tytgat et al. 2023). These observations are suggestive of different constraints on marine and freshwater protist communities, with the latter possibly experiencing a more distinct, longer lasting impact of historical processes compared to the marine realm, although unlimited dispersal is also not a given in the marine environment (Darling, Kucera, and Wade 2007; Trubovitz et al. 2020). Indeed, diversification rate analyses on diatom phylogenies are indicative of increased speciation and extinction rates of freshwater diatoms relative to their marine counterparts (Nakov, Beaulieu, and Alverson 2019), suggesting higher levels of community turnover in freshwater than marine environments.

On more recent time scales, aDNA in sediment (De Schepper et al. 2019; Armbrecht et al. 2022) and ice (Segawa et al. 2023) cores offers excellent opportunities to study range dynamics and protist responses to regional drivers of environmental change. Our ability to recover aDNA is now rapidly progressing, with the oldest known records, which detected protist DNA, dating back to ~2 million years (Kjær et al. 2022). This opens exciting avenues for understanding historical drivers of protist community composition, as aDNA allows to study the entire protist community, including taxa that do not fossilise. Nevertheless, fossils will remain crucial for uncovering pre-Quaternary protist dynamics. It is thus imperative that the protist community works towards filling major gaps in the fossil record, as reports on freshwater protist fossils remain scarce, particularly in the Southern Hemisphere (Pinseel et al. 2021) and considerable uncertainty exists regarding the age and origin of many protist lineages (Bryłka et al. 2023, 2024). A better understanding of the fossil record will also be useful for improving time calibration of molecular phylogenies which is essential to understand the timing, rates and patterns of speciation and colonisation of new regions.

2.5 | Investigate Protist Diversity and Biogeography Through the Lens of Populations

Population-level approaches have great potential to reveal fine-grained patterns in protist distributions, including to what extent and why protist distributions range from very local scales (e.g., endemic species in ancient lakes) to cosmopolitan distributions. Most of our initial understanding of population structure in protists came from allozymes (Gallagher 1980) and later from Amplified Fragment Length Polymorphism and microsatellite studies (Sassenhagen et al. 2015; Van den Wyngaert et al. 2015; Godhe and Rynearson 2017). Recently, genome-wide single-nucleotide polymorphisms (SNPs) obtained via restriction site-associated DNA sequencing (RAD-seq), genome skimming, whole-genome sequencing or single-cell amplified genomes are opening up new avenues for population-level research (Craig et al. 2019; Postel et al. 2020; Rengefors et al. 2021; Gollnisch et al. 2023; Pinseel et al. 2023). Such studies revealed that the level of population differentiation varies considerably depending on the species and the investigated area, ranging from little-to-no population structure over relatively short distances (Evans, Kühn, and Hayes 2005), to surprisingly large population differentiation stretching from tens (Rengefors, Logares, and Laybourn-Parry 2012; Sefbom et al. 2018) to hundreds or thousands of kilometres (Evans et al. 2009; Casteleyn et al. 2010; Lowe et al. 2012; Sjöqvist et al. 2015; Pinseel et al. 2023). Moreover, whereas some population-level studies favour unlimited dispersal (Whittaker and Rynearson 2017), others report limits to gene flow in both marine and freshwater environments (Casteleyn et al. 2010; Lowe et al. 2012; Vanormelingen et al. 2015; Pinseel et al. 2023). These contrasting observations are in line with insights from the previously mentioned species-level studies and suggest that environment- or lineage-specific traits and/or processes determine which species (do not) have limited dispersal capacities.

Both marine and freshwater protist populations are characterised by relatively high levels of (within-population) genetic diversity (Godhe and Rynearson 2017; Lundholm et al. 2017) which are within the range of those reported for Metazoa, including insects and small mammals (Leffler et al. 2012; Pinseel et al. 2023). Growth experiments and transcriptome studies revealed that protist populations are equally diverse in phenotypic traits and their responses to their environment (Schaum et al. 2012; Ajani et al. 2021; Bishop et al. 2022; Pinseel et al. 2022). The occurrence and potential drivers of high levels of intraspecific variation in protist populations have been reviewed in detail elsewhere (Godhe and Rynearson 2017; Sjöqvist 2022; Ryderheim and Kiørboe 2024). Importantly, the scientific literature shows that substantial genetic and functional variation is present within protist species, thus laying the foundation for adaptation to environmental changes as well as future speciation events, which are both crucial for the establishment of biogeographical structuring over macroevolutionary timescales.

Despite the above-mentioned insights, population-level studies predominantly focus on common, culturable, mostly marine protists, precluding extrapolation of these insights across the protist tree of life which includes many poorly known lineages and taxa belonging to the rare biosphere taxa (Box 1). However, recent advances in single-cell population genomics opens up new opportunities for population-level research in understudied protists, including non-culturable taxa (Gollnisch et al. 2023; Pinseel et al. 2023). Another recent, promising development in the field is the use of metagenomics or metatranscriptomics to directly obtain SNPs from environmental samples (Le Gac et al. 2022; Nef et al. 2022), effectively bypassing the time-consuming and costly step of having to culture hundreds of strains for population-level research. However, this approach requires that alleles of closely

BOX 1 | The understudied majority.

A central factor that limits a holistic understanding of protist biogeography is the fact that not all phyla have received equal attention. The number of studies on different protist clades varies greatly, and within clades, some habitats are much better studied than others. Arguably the most thoroughly studied environments are the marine epipelagic and freshwater plankton and their dominant protists, such as diatoms and coccolithophores. In contrast, especially the marine benthos and terrestrial environments such as soils have received comparatively little interest, despite their global importance (Geisen et al. 2017). Geographically, most research focused on temperate, and to a lesser extent, polar, localities in the Northern Hemisphere, whereas arid and (sub)tropical areas, and the Southern Hemisphere in general, are much less covered. This discrepancy is apparent across community-, species- and population-level studies and from the availability of reference sequences and genomes, access to trait data, as well as the type of data that are generated. With exception of human parasites, another understudied group are parasitic and symbiotic protists, especially those that interact with microscopic invertebrates or other protists (Holt et al. 2022; Savage et al. 2023). Furthermore, many protists are not amenable to culturing. Although historically this has impeded their inclusion in molecular studies, single-cell techniques have come a long way and are increasingly applied for species- and population-level research (Hamilton, Lefebvre, and Bull 2015; Ruck et al. 2016; Seeleuthner et al. 2018; Gollnisch et al. 2023; Pinseel et al. 2023; Roberts et al. 2023). In addition, environmental sequencing opens new avenues for studying unculturable protists, the rare biosphere or understudied, difficult to access environments. For example, only recently did renewed interest in soil protists result in the first global-scale studies of their diversity and biogeography, revealing unprecedented species-level diversity (Lara et al. 2016; Oliverio et al. 2020; Pinseel et al. 2020; Metz et al. 2023). Similarly, metabarcoding of deep-ocean sediments revealed that eukaryotic diversity in these areas exceeds that of the plankton threefold (Cordier et al. 2022). Other studies found a high diversity of specialised protists in marine epibiotic biofilms (Kanjer et al. 2022). Finally, detailed morphological surveys of understudied environments continue to reveal novel protist species to this day (Pinseel, Van de Vijver, et al. 2017; Goeyers, Vitt, and Van de Vijver 2022). Clearly, this understudied majority has an exciting biogeography story to tell. Considering their immense phylogenetic diversity and global distribution among all major habitat types, it is not unlikely that different protist biogeographies will be uncovered, as well as diverse evolutionary histories among groups with different habitat preferences, life histories and ecologies.

related species sharing large similarities in their core genomes can be separated when calling SNPs from eDNA, which may be problematic for recently diverged taxa (Bendif et al. 2023). Moreover, there are still limitations in what can be done with SNPs obtained from eDNA. Their analysis relies on pool-seq software, which (i) generally assumes DNA of different individuals is represented in equimolar concentrations, (ii) requires relatively high coverage to reliably assess allele frequencies (preferably minimum 20–40×), which can be difficult to achieve for eDNA and (iii) needs information on the ploidy level (number of genotypes) for calculating population-level statistics, which is inherently unknown for environmental samples (Adams et al. 2019; Czech et al. 2022; Pinseel et al. 2023). Clearly, the protist community needs novel software tools that allow to fully leverage eDNA for population-level research. Given the strong interest of the eDNA field, it is to be expected that such tools will be developed in the foreseeable future. Yet, it remains to be seen whether this approach will be useful for protists that are not highly abundant, as SNPs of rare species might not reach a sufficiently high coverage following sequencing. Target capture, which enriches a sample for target DNA of interest could possibly alleviate this issue but this technique requires availability of a reference genome or transcriptome (Armbrecht et al. 2021; Pinseel et al. 2023).

2.6 | Beyond the Debate: Why and Where Are Protists More Prone to Cosmopolitan Versus Endemic Distributions

Altogether, a plethora of both morphological and molecular studies confirmed that protist biogeography is not black-and-white: protist communities appear to present a mixture of species with cosmopolitan as well as restricted distributions. Although this statement represents a straightforward summary of three decades of debate on protist distributions, it makes an important point: it shows that the field is ready to move beyond the *ubiquity* versus *moderate endemicity discourse* and instead ask *why* and *where* specific protist species and clades are more prone to cosmopolitan or endemic distributions. What is the relative importance of the contemporary environment and historical factors and how (and if relevant, why) does this differ between protist phyla? What combination of traits and environmental conditions makes for an endemic versus a cosmopolitan protist? Which phyla are more likely to be impacted by historical factors and dispersal limitation and harbour endemism? Which environments and specific geographic locations show the highest levels of protist endemism and do these differ among protist clades? To what extent are the relative contributions of the processes that shape organismal biogeography different between prokaryotes and protists and between protists and macro-organisms?

The current literature already provides partial answers to these questions. Even though most biogeographers now agree that historical factors contribute to shaping protist biogeography, local environment regularly explains most of the variation in protist communities (Hanson et al. 2012; Xu and Soininen 2019), although not always, such as in polar lacustrine protists (Verleyen et al. 2021; Tytgat et al. 2023). Several studies also suggest that the imprint of historical factors on protist communities are more regularly detected at larger than smaller geographic scales (Soininen 2007; Soininen et al. 2011; Hanson et al. 2012; Azovsky, Chertoprud, and Saburova 2022; Nemcova, Faturova, and Škaloud 2023) or in specific, geographically isolated environments, such as mountain ranges (Boenigk et al. 2018) and

BOX 2 | The way forward: Building and expanding reference phylogenies and databases of protist sequence, distributional and trait information.

Thanks to recent (ongoing) efforts, such as *Tara Oceans* and global soil protist initiatives (de Vargas et al. 2015; Oliverio et al. 2020); the protist community is beginning to be able to address global-scale questions on biogeography and trait evolution. Yet, current datasets have a strong focus on marine phytoplankton, highlighting the need to further expand databases with curated sequence, distributional and trait data across the protist tree of life, covering all continents, oceans and climate zones, as well as the full diversity of auto-, hetero- and mixotrophic lifestyles. This is important because—in contrast to animals and plants—many protist phyla are common in marine, freshwater and soil environments (Pinseel et al. 2020; Jamy et al. 2022; Roberts et al. 2023). In addition, increased efforts to generate well-sampled time-calibrated phylogenies for representative protist clades will help understand their biogeographical history and the evolutionary origins of their traits.

Reference databases of protist DNA and RNA

The structure and distribution of protist microbiomes can be documented without the need to identify sequences at a high taxonomic resolution, such as is the case for amplicon sequencing. This approach, however, constrains the nature of the hypotheses that can be tested, especially those requiring a good understanding of taxonomic identity and the link between sequence and phenotype. Reference databases that link protist DNA/RNA sequences with taxonomic classifications are thus essential to fully uncover the potential of eDNA sequencing efforts. To date, in particular the exploitation of metagenomic and metatranscriptomic data is still hampered by the scarcity of reference sequences as genomes and transcriptomes are not available for most protists (Santoferrara et al. 2020). Yet, both techniques are also part of the solution, as genomes can be assembled directly from environmental samples to obtain MAGs (metagenome-assembled genomes), which in turn can be used to expand reference databases (West et al. 2018; Delmont et al. 2022; Alexander et al. 2023). Even though reference databases for metabarcoding are more complete, they come with their own difficulties, including mislabelling, sequence errors and missing taxa and intraspecific variants (Keck, Couton, and Altermatt 2022). Clearly, curation and expansion of existing metabarcoding databases, such as PR2 for protist 18S rRNA (Guillou et al. 2013) and Diat.barcode for diatom *rbcL* (Rimet et al. 2019) will continue to be essential. With the use of new markers also comes the need for expanded or new reference databases, which will likely happen on a clade-by-clade basis, depending on the needs of different research groups (Pawlowski et al. 2012). EUKARYOME, a recently developed database for the entire rRNA operon from all eukaryotes, including the widely sequenced nuclear ribosomal 18S rRNA as well as the internal transcribed spacer (ITS) and 28S rRNA, is a particularly promising development (Tedersoo et al. 2024). A major advantage of EUKARYOME is that by including longer sequences in reference databases, it becomes easier to filter chimera's and taxonomically classify sequences from long-read metabarcoding efforts.

Trait and distributional databases for protists

Distributional data and trait databases are widely available for plants, animals and fungi (e.g., the Global Biodiversity Information Facility (GBIF) and TRY database for plant traits (Kattge et al. 2011)), in contrast to protists. This is at least partially because it is much more straight-forward to measure and quantify traits in macro-organisms, compared to single-celled organisms. Such distributional and trait databases are routinely used by biogeographers to unravel general patterns and rules concerning the biogeography of plants and animals. If we are to similarly move the field forward, it is paramount that trait data on protists will become easier to access and apply. In doing so, we can lean on resources developed outside of the protist community, such as the GeOMe repository which allows to attach geographic and ecological metadata with sequence data (Deck et al. 2017). Several recent initiatives for protists, including the metaPR2 database to classify eDNA sequences in major functional or phenotypic trait categories (Vaulot et al. 2022), a dataset on trophic mode of aquatic protists incorporated in WoRMS (Schneider et al. 2020) and a database on coccolithophore morphological traits (Sheward et al. 2024) are promising steps forward. In addition, even though measuring trait variation in protists is challenging, new techniques are regularly being developed, such as characterisation of plankton functional traits from image data (Orenstein et al. 2022). In addition, metatranscriptomics provides data on functional diversity and thus biological trait variation, of active protist communities, at an unprecedented scale (Geisen et al. 2015). For example, Martin et al. (2021) reported that environmental differences in the upper oceans of polar and non-polar regions strongly impacted gene activity in algal microbiomes. And Carradec et al. (2018) found that about half of the retrieved RNA sequences of marine eukaryotic plankton do not show any similarity with known proteins and many of these belong to novel gene families with restricted distributions in the ocean. It is clear from these examples that the metatranscriptome revolution opens a wide range of possibilities to understand the biogeography of protist traits, but is also challenged by unknown gene families and functions. Finally, it is paramount that taxonomic progress finds its way to reference databases and researchers working on understanding protist distributions, because failure to do so may bias biogeographic and evolutionary inferences (Alverson et al. 2011).

The need for well-sampled, time-calibrated phylogenies

For most protist clades we lack fairly complete time-calibrated molecular phylogenies, which stands in stark contrast to the resources available for plants, animals and fungi. Such phylogenies are however crucial to model trait variation, assess diversification rates and estimate historical biogeographical distributions. Given the tremendous diversity of protists, the high levels of (pseudo) cryptic diversity and the labor-intensive nature of field sampling and culturing, it is challenging to build fairly complete species-level molecular phylogenies of focal clades. Yet, opportunities are available for improving such resources, including single-cell sequencing, long-read metabarcoding and metagenomics. Although phylogenies for evolutionary meta-analyses have been built using partial 18S from environmental samples (Lewitus et al. 2018), such analyses are sensitive to spurious phylogenetic inferences (Hassler et al. 2022). In contrast, long-read metabarcoding provides more robust data for phylogenetic inference (Jamy et al. 2022).

might depend on organismal life form (Benito et al. 2018). For instance, a survey on soil protist diversity found that nutrient availability, and not spatial separation, was the main factor structuring communities over regional scales (Venter et al. 2017), whereas a global-scale study found clear imprints of geographic distance (Bates et al. 2013). Furthermore, the literature suggests that history might have a larger impact on protists compared to bacteria (Tytgat et al. 2023), yet a smaller impact on protists compared to macro-organisms (Soininen et al. 2011; Soininen 2012). This is further evidenced by the regular observation of lower slopes of distance–decay relationships in protists compared to macro-organisms (Hillebrand and Azovsky 2001; Bates et al. 2013; Macingo et al. 2019; Azovsky, Chertoprud, and Saburova 2022). It remains to be seen, however, how much of these observations reflect true differences between the biogeographies of protists and macro-organisms or are due to methodological constraints. It has to be noted that the vast majority of regional- or global-scale studies on protist biogeography, including those reporting weak distance–decay relationships, are based on morphological observations. Such datasets are sensitive to taxonomical interpretations, analyst bias and cannot account for cryptic diversity (cf. above). Similarly, even though metabarcoding is becoming increasingly popular to unravel regional and global patterns in protist biogeography, the standardised use of 18S rRNA means most studies are capturing protist diversity, at least partially, above the species level (Pinseel et al. 2020; Lara, Singer, and Geisen 2022). Upon applying great care to taxonomic harmonisation and fine-grained taxonomy in morphology-based datasets, or extensive molecular analyses of highly variable marker genes or whole-genomes, numerous studies revealed surprisingly high levels of endemism and/or previously unrecognised (pseudo)cryptic diversity, such as in chrysomonad algae (Boo et al. 2010), coccolithophores (Bendif et al. 2023), diatoms (Abarca et al. 2014; Pinseel et al. 2020; Verleyen et al. 2021; Jovanovska et al. 2023), foraminifera (Darling et al. 2004), green algae (Slapeta, López-García, and Moreira 2006; De Wever et al. 2009; Škaloud and Rindi 2013), red-snow algae (Segawa et al. 2018), testate amoebae (Singer et al. 2019; González-Miguéns et al. 2023) and tintinnid ciliates (Santoferrara et al. 2015). These observations have likely not been (fully) recognised in much of the large-scale analyses on protist biogeography that use morphology or 18S-metabarcoding. Given that cryptic diversity does not preclude cosmopolitan distributions of cryptic lineages (Bendif et al. 2023), future work should therefore assess if and to what extent our perception of protist biogeography has been shaped by taxonomical and methodological constraints.

It could be argued that some environments, such as the marine epipelagic or eutrophic lakes (Cermeño and Falkowski 2009; Trobajo et al. 2009), might be more prone to harbour cosmopolitan species. Several known hotspots for endemic plant and animal species have a large representation of endemic protist taxa, such as ancient lakes Baikal, Ohrid and Tanganyika, although it remains unclear how such endemic protist diversity is generated and maintained in these lake systems (Annenkova et al. 2015; Stelbrink et al. 2018; Jovanovska et al. 2023). Similarly, geographically isolated regions, such as the Antarctic Continent and sub-Antarctic islands (Verleyen et al. 2021), but also Tasmania and New Zealand (Vyverman et al. 1998; Pinseel et al. 2021) have been found to harbour many protist endemics. Although it is difficult to directly compare taxonomic ranks among phyla due to differences in divergence times (Nakov, Beaulieu, and Alverson 2018b), it seems that in protists, restricted distributions are mainly confined to the species and possibly genus level, while families and higher taxonomic ranks seem to have cosmopolitan distributions, like the 'wandering families' among land plants and mammals (Cox et al. 2020). That being said, it is likely that also on higher taxonomic levels, differences in the extent of cosmopolitanism versus endemism exist between different clades, as for instance many ciliates and flagellates appear to have global distributions (Azovsky, Tikhonenkov, and Mazei 2016; Azovsky et al. 2020; Gimmler et al. 2016; Canals et al. 2020; Ganser et al. 2021), whereas diatoms harbour multiple endemic genera (Vyverman et al. 2007; Pinseel et al. 2021). Traits, such as cell size, population size, tolerance to environmental extremes, reproductive strategy and resting stage formation are likely central to determining the relative contributions of environmental versus historical factors in shaping the biogeographies of different protists clades and thus who is more likely to exhibit cosmopolitan versus endemic distributions (Hillebrand and Azovsky 2001; Wilkinson et al. 2012; Azovsky et al. 2020; Pinseel et al. 2020; Richter et al. 2022). For instance, in the marine environment, a comprehensive eDNA survey showed that the global biogeographical provinces of smaller taxa ($< 20\,\mu$m) are governed mostly by local environmental conditions (e.g., nutrients), whereas the biogeography of larger taxa ($> 20\,\mu$m) is more strongly impacted by global-scale gradients (e.g., temperature) and oceanographic connectivity (Richter et al. 2022), indicative of size-dependent effects on protist biogeography.

Altogether, elucidating why some taxa are more apt to successful dispersal and colonisation, and hence showing wide geographical distributions, is fundamental to better comprehend protist biogeography. For most taxa and entire phyla, however, robust data on their geographical distribution are lacking (Box 1). While accurately documenting protist distributions is now within reach with the various recent molecular approaches outlined above, this endeavour will only succeed if attention is paid to carefully integrating datasets from different analysts and data sources. Researchers will need to account for the varying taxonomic resolutions of different marker genes and sequencing techniques and integrate information about protist morphologies, traits and molecular data. Crucial here is the development, expansion, digitisation and quality control of biocollections from various data sources (Box 2) (Ball-Damerow et al. 2019). Although not an easy task, such data integration holds the promise of global-scale meta-analyses at unprecedented taxonomical and spatial resolution. Meta-analyses will not only allow assessing species distributions across the protist tree of life in great detail, but will ultimately enable us to reveal general rules and patterns in protist biogeography, like it did for macrobiota (Holt et al. 2013; Tietje et al. 2022; Coelho et al. 2023). Such progress will also help us to better integrate data on both macro- and microbiota when defining global biogeographical realms, as previously attempted for the marine environment (Costello et al. 2017). In turn, this will lead to more holistic biodiversity assessments that take all life forms into account, which is particularly crucial in an era where biota worldwide are impacted by profound environmental change (Cavicchioli et al. 2019).

In what follows, we will discuss ways to better understand the processes that shape protist biogeographies.

3 | Processes That Shape Protist Biogeographies

Speciation, selection, dispersal and ecological drift are the four processes that determine the assembly and diversity of communities and thus the distribution of species (Vellend 2010). These four ecological processes are closely aligned with the four evolutionary processes that drive patterns in population genetics: mutation, selection, gene flow and genetic drift (Vellend 2010; Hanson et al. 2012). In macro-organisms, these processes have traditionally been studied largely independently. In the case of protists, with their often extremely large population sizes, short generation times and widely differing geographical distributions and dispersal abilities, we argue that studying species- and population-level processes simultaneously and over similar spatial scales could be especially rewarding to further our understanding of their biogeography.

3.1 | Disentangling the Roles of Selection, Dispersal and Drift

Considering the widely varying range size of protists, understanding their dispersal and colonisation capacity, modes and frequency is central to comprehending protist biogeography. Protist dispersal capabilities have mostly been studied indirectly, by investigating (i) patterns of endemism and community turnover over various geographic scales, (ii) patterns of genetic differentiation and gene flow between populations or (iii) phylogenetic inferences of long-distance dispersal and geographic isolation. Taken together, the results are mixed. Several studies neither detect dispersal limitation (Cermeño and Falkowski 2009; Whittaker and Rynearson 2017) nor distinct distance–decay relationships (Hillebrand and Azovsky 2001; Stock et al. 2013) or rejected the possibility of allopatric speciation (Fiore-Donno et al. 2011). Yet, several others revealed distinct isolation-by-distance or distance–decay relationships in both marine and freshwater protist populations and communities (Wetzel et al. 2012; Vanormelingen et al. 2015; Jamoneau et al. 2018; Lentendu et al. 2018; Holman et al. 2021), distinct protist assemblages in different regions despite similar environmental conditions (Bruni et al. 2023; Tytgat et al. 2023) and evidence for allopatric speciation and thus dispersal limitation (Singer et al. 2019; Pinseel et al. 2020). In several studies on marine protists, oceanographic circulation, and not distance, best explained gene flow between populations (Casabianca et al. 2012; Sjöqvist et al. 2015) and has also been suggested to increase the diversity in the marine rare biosphere (Villa Martín et al. 2020). In contrast, the population structure of the freshwater raphidophyte *Gonyostomum semen* was independent of lake connectivity (Sassenhagen et al. 2015).

Direct observations on protist dispersal come from field-based experiments and microscopic surveys, which showed that both abiotic (e.g., wind and water) and biotic (e.g., insects, birds and mammals) vectors can be of importance (Kristiansen 1996). This includes aeolian transport (Brown, Larson, and Bold 1964; Broady 1979; Wuthrich and Matthey 1980; Sharma, Rai, and Singh 2006; Genitsaris et al. 2014; Wanner et al. 2015; Jauss et al. 2021; Schulte et al. 2022) as well as biotic dispersal vectors such as insects, amphibians and birds (Schlichting and Speziale 1978; Atkinson 1980; Bharti et al. 2020; Cochak et al. 2021; Johansson, Kaasalainen, and Rikkinen 2021; Manning et al. 2021) or even sea turtles (Majewska et al. 2017). Colonisation success is often overlooked but essential to dispersal efficiency, as without colonisation, there will be no gene flow (Incagnone et al. 2015). For example, despite the high dispersal capacities of marine phytoplankton, resting spore-forming species have been hypothesized to maintain distinct population structuring on small spatial scales due to strong anchoring effects of well-adapted local populations, reducing successful gene flow between populations (Sundqvist et al. 2018). Altogether, protist dispersal might not be all that different from many macrobiota: mosses, for instance, show clear biogeographies, yet also have microscopically small stadia (spores) which might mediate long-distance dispersal over vast geographic distances (Muñoz et al. 2004; Foissner 2011; Biersma et al. 2017). That being said, unlimited dispersal is within the reach of protist species, especially in the marine environment (Cermeño and Falkowski 2009; Whittaker and Rynearson 2017; Koester et al. 2018). It would be particularly valuable to understand the dispersal routes and minimal dispersal frequencies necessary to maintain such global metapopulations, as well as the organismal traits that promote unlimited dispersal.

Given the high amenability of protists for common garden experiments, and their usually short generation times, controlled laboratory experiments, as well as field-based (microcosm) experiments, offer opportunities to study evolutionary processes such as selection, adaptation, drift and dispersal over ecological timescales (Altermatt et al. 2015; Bell 2010; Lachapelle, Reid, and Colegrave 2015; Schaum et al. 2018; Teittinen, Soininen, and Virta 2022). Laboratory experiments will be particularly useful when paired or complemented with well-designed field studies. Examples include null model approaches on eDNA, which already revealed that selection, drift and dispersal differently affect the community composition of bacteria and protists in marine and freshwater environments (Logares et al. 2018; Logares et al. 2020; Wu et al. 2018). Similarly, null model approaches revealed drift to be the dominant process shaping soil protist communities, but its relative strength depended on the organism's cell/body size and niche breadth (Aslani et al. 2022). Clearly, such studies offer a promising way forward to understanding the roles of selection, drift and dispersal in shaping protist biogeographies, including how these processes are impacted by and contribute to adaptation to environmental change (Collins, Boyd, and Doblin 2020). Crucial in this context is the need to infer the relative contributions of these processes, including speciation.

3.2 | Leveraging Fossil Data, Molecular Phylogenies and Whole Genomes to Study Speciation

The mode of speciation in protists has generally been investigated indirectly, by means of (time-calibrated) molecular phylogenies or fossil data. Using such methods, indications for sympatric speciation mainly come from marine environments (Lazarus et al. 1995) and (ancient) lakes (Theriot et al. 2006; Stelbrink et al. 2018). Several cases of sympatric species flocks suggest protists can be subject to (adaptive) radiations, like macro-organisms (Stelbrink et al. 2018; Jovanovska et al. 2023). Parapatric speciation has been detected along environmental gradients, such as different depths in the water column (Weiner et al. 2012). Some authors believe parapatric speciation to be the main speciation mode in protists, as it can be easily conceived that each species might consist of a constantly shifting mosaic of temporarily isolated (meta)populations, some of which can become fully reproductively isolated (Boo et al. 2010; Mann and Vanormelingen 2013). Although a consequence of the ubiquity hypothesis is that allopatric (and parapatric) speciation should be rare in protists, studies are increasingly finding evidence for allopatry in marine, freshwater and terrestrial protists, suggestive of effective barriers to gene flow imposed by dispersal limitation (Darling et al. 2004; Singer et al. 2019; Škaloud et al. 2019; Pinseel et al. 2020). Within this context, it has been proposed that protists with an intermediate capacity for dispersal, for example, due to an ability to survive adverse dispersal-associated conditions combined with relatively small census population sizes that generate only a limited number of migrants, are more likely to undergo allo- or parapatric speciation (Mann and Vanormelingen 2013; Pinseel et al. 2020). It is worth noting that the short generation times of protists might facilitate allo- or parapatric speciation as relatively little time, compared to macro-organisms, might be needed for genetic incompatibilities to arise between (temporarily) separated populations. Nevertheless, phylogenetic methods provide only indirect evidence for the mode of speciation and are highly dependent on sampling completeness (Box 2). For instance, even though many closely related (cryptic) protists identified in molecular phylogenies occur sympatrically (Beszteri, Acs, and Medlin 2005; Amato et al. 2007; Vanelslander et al. 2009), this is not direct evidence for sympatric speciation, as allo- or parapatric speciation followed by range expansion would create the same pattern. Demographic analyses (i.e., the reconstruction of genome evolution throughout time) of sibling species offers a promising route forward to investigate the tempo and modes of protist speciation in more detail. Specifically, demographic analyses allow to assess whether complete isolation contributed to speciation, and thus whether the speciation process happened in allo- or sympatric conditions. Given that demographic modelling relies on the availability of multiple nuclear genomes per species, which are costly and challenging to obtain, the technique is to date still rarely applied to protists. Yet, recent work on marine coccolithophores underscores the promising nature of demographic techniques, as it revealed that geographic isolation associated with Pleistocene glaciations drove speciation and extinction in present-day sympatric lineages (Bendif et al. 2019; Filatov et al. 2021). Other studies using phylogenetic techniques and fossil data of marine, freshwater and terrestrial photoautotrophic protists similarly suggested that major changes in global climate have strongly impacted diversification (Pinseel et al. 2020, 2021). Whether this equally applies to phyla with a heterotrophic or mixotrophic life history remains to be seen, but it is a strong case for the role of historical processes in shaping protist diversity and biogeography.

Above, we focused on the geography of speciation, but equally intriguing is the question what underlying drivers cause genome divergence in protists during the speciation process: (i) ecological speciation, during which speciation is the result of divergent adaptation to distinct environments or (ii) mutation-order speciation, during which divergence occurs in populations experiencing similar selection pressures. In vertebrates, it has been found that mutation-order speciation, usually with an allopatric phase, is the norm (Anderson and Weir 2022), but it is unclear whether this applies to protists as well. Within a scenario of allo- or parapatry, where populations of a species are temporarily isolated from each other, it is indeed conceivable that protists accumulate non-adaptive differences in their genomes, leading to genetic incompatibilities or other mechanisms of reproductive isolation which can prevent or reduce gene flow upon secondary contact. In an alternative scenario, the generally large dispersal capacities of many protists might allow for effective long-distance dispersal, increasing the chance that new colonisers experience environments vastly different from their source area, requiring rapid acclimation and adaptation to ensure (long-term) survival. In such a scenario, which is particularly likely for freshwater and soil environments, it is conceivable that ecological speciation would occur. Indeed, population genomic analyses of the dinoflagellate *Apocalathium* and the chrysomonad alga *Synura* revealed high potential for ecological speciation, especially over small geographic scales (Rengefors et al. 2024; Škaloud et al. 2024). However, in cases of long-distance dispersal, it can also be argued that effective dispersal rates will be low, implying that founder populations are small, thus experiencing substantial genetic drift and less effective natural selection than would be expected in larger populations, counteracting ecological speciation but increasing opportunities for mutation-order speciation. Studies focused on trait divergence of sibling lineages will be needed to examine the relative roles of mutation-order and ecological speciation and how this relates to, and differs between, protist lineages, habitat type and life history traits. An alternative route to speciation, which has received little attention in protists, is polyploidisation. It is unclear how (un)common polyploid speciation in protists is, but studies have shown evidence for past polyploidisation events across the protist tree of life (Aury et al. 2006; Parks et al. 2018). Related to the above information, studies focusing on genome evolution in protist radiations and cryptic clades remain rare, but provide a promising route forward to understanding the drivers and genomic signature of diversification and (adaptive) radiation in protists (Xiong et al. 2019; Roberts et al. 2024).

3.3 | Biogeographical Processes Through the Lens of Population Genomics

SNPs generated across the nuclear genome of multiple individuals provide the tools necessary to investigate processes shaping population structure by reconstructing demographic history and mode of speciation, as discussed previously (Filatov et al. 2021; Filatov 2023), to identify selection pressures involved in local adaptation (Nef et al. 2022; Pinseel et al. 2023) and to estimate the direction of gene flow within or between species (Rengefors et al. 2021; Çiftçi et al. 2022). Combined with targeted laboratory experiments designed to unravel adaptive potential, tempo of differentiation under selection and fitness of natural populations (Moerman et al. 2022; Sefbom et al. 2022), such studies can result in a better understanding of population-level processes and ultimately uncover the drivers of speciation and community dynamics at both the inter- and intra-specific level. Within this context, we believe it is essential to diversify this approach across auto-, hetero and mixotrophic protists from different habitat types and species with various population sizes to allow for comparative analyses. This is because freshwater and terrestrial protist populations are expected to be much smaller and less interconnected (Vanormelingen et al. 2015; Pinseel et al. 2020), and their habitats are generally ephemeral over geological time (Wetzel 2001), making them more vulnerable to genetic drift and extinction than their marine counterparts (Nakov, Beaulieu, and Alverson 2019). In contrast, the astronomically large population sizes of marine phytoplankton reduce the impact of drift and increase the efficiency of selection, allowing for rapid adaptation (Filatov 2023; Filatov and Kirkpatrick 2024).

A major challenge to population-level research relates to the lack of knowledge about several key population genomic parameters that are needed to identify the mode and timing of population divergence and speciation. For example, mutation rates are known for only a handful of protists (Krasovec, Sanchez-Brosseau, and Piganeau 2019; Krasovec, Rickaby, and Filatov 2020). Information on generation time and presence/absence as well as frequency of sexual reproduction is mostly missing (Lahr et al. 2011). This hampers our ability to fully exploit the power of population-level approaches and underscores the need to continue gathering such data through mutation accumulation experiments and field observations. In addition, a better comprehension of the role of genomic processes that might be common in protist diversification, such as mitotic recombination in diatoms (Bulankova et al. 2021), will be paramount to our understanding of their adaptive potential and ecological divergence. Finally, population genomic studies on macro-organisms are increasingly showing the importance of structural variants (SVs) in speciation and adaptation (Wellenreuther et al. 2019; Mérot et al. 2020). SVs have received little to no attention in protists, yet offer an exciting opportunity to further unravel the drivers of protist diversification and adaptation.

3.4 | Towards Incorporating Trait Variation and Biotic Interactions in Protist Biogeography

It has long been understood that lineage-specific traits affect the geographical distributions of plants and animals. Similarly, we expect trait variation to impact species distributions in protists by influencing how they interact with their environment, including their ability to survive adverse conditions, disperse, colonise and interact with other organisms. Indeed, protists exhibit a large variation in functional characteristics, such as reproductive strategies, ability to form resting stages/spores, cell size, growth rates and strategies (e.g., planktonic, benthic, epizoic and chain formation), trophic modes (e.g., autotrophic, heterotrophic and mixotrophic), habitat preferences (e.g., marine, freshwater, terrestrial, oligotrophic and eutrophic), resource utilisation (e.g., nitrogen fixation), population size (e.g., bloom-forming phytoplankton vs. rare biosphere protists) and particular behavioural characteristics. We argue that this huge variation in protist traits is similarly reflected in a wide variation of biogeographic patterns—from cosmopolitanism to narrow endemism, emerging from a differential impact of ecological versus historical processes.

The biogeography of protist traits has received most attention in the context of marine phytoplankton. For example, although marine microbes are to date not yet sufficiently integrated in climate forecasting (Tagliabue 2023), trait-based modelling has been applied to foster a better integration of marine plankton functional traits with biogeochemical cycling and to predict the response of plankton to global change (Follows et al. 2007; Barton et al. 2013). More recently, trait-based genomics has been shown to be a promising route forward to improve biogeochemical forecasting in the global oceans (Coles et al. 2017; Garcia et al. 2020). Yet, outside the realm of marine plankton such approaches are scarce and consequently our understanding of how life history and ecological traits affect the four processes that shape species- and population-level biogeographies in protists remains largely elusive. We argue that widening the taxonomic scope of trait modelling and trait–environment correlation analyses will be crucial to discover and define general rules on protist biogeography, including how protists diversify through space over time (Box 1). The few studies that expanded beyond the marine realm already yielded promising results. For example, phylogenetic analyses revealed that marine and freshwater diatom diversification rates varied with life history traits and habitat type (Nakov, Beaulieu, and Alverson 2018a; Nakov, Beaulieu, and Alverson 2019) and growth form has been found to affect distributions of stream diatoms (Passy 2007). A crucial step to expand such analyses would be the much needed development of global datasets of distributional, trait and phylogenetic data with broad taxonomic and geographic scope (Box 2). At the same time, these approaches should be complemented with studies of trait variation at the population level, considering the extraordinary genetic and phenotypic diversity of protist populations (Sjöqvist and Kremp 2016; Godhe and Rynearson 2017; Olofsson et al. 2019; Ajani et al. 2021; Bishop et al. 2022; Pinseel et al. 2022) and its potential role during niche expansion and contraction of species.

Researchers tend to measure physicochemical variables, such as temperature, pH, conductivity and nutrient availability, to assess the impact of the local environment on protist distributions. Yet, such parameters are at best a very rough representation of the environment as experienced by a protist cell, which might be reliant on spatially limited micronutrients or affected by daily or seasonal variations in environmental variables, which are seldomly measured. This suggests that even (superficially) highly similar environments might still harbour unmeasured environmental differences that affect protist distributions. Similarly, protist distributions are likely impacted by biotic interactions such as predator–prey interactions, symbiosis, parasitism and competition (Bjorbækmo et al. 2020). For example, protists exhibit close, both synergistic and antagonistic, associations with bacteria (Amin, Parker, and Armbrust 2012), which can affect protist community composition by altering the outcome of competitive interactions (Koedooder et al. 2019). Other studies have shown that symbiotic and predator–prey interactions affect protist diversity, size structure and behaviour, turnover in ecological niche and ultimately geographic distributions (Hamels et al. 2004; Bjærke et al. 2015; Faure et al. 2019; Kim et al. 2019; Selander et al. 2019; Abdullah Al et al. 2023). Correlation and network analyses on environmental sequencing data, as well as targeted laboratory experiments and single-cell sequencing will help to further uncover protist interactions and their potential impact on biogeographical patterns (Martinez-Garcia et al. 2012; Santoferrara et al. 2020; Boscaro et al. 2023). In addition, careful analysis of phylogenetic and fossil data can help to disentangle the impact of environmental factors and competition on protist community turnover (Jovanovska et al. 2022). Finally, while environmental and climatic forcing of community turnover has been observed globally in Holocene fossil records, much less is known about the resilience of local communities to such forcing and how this is affected by, among others, microbiome interactions.

3.5 | Cell Size, a Master Trait in Protist Biogeography

Protist morphologies impact how cells move and interact with their environment, which in turn can impact community composition and biogeographical patterns. Nevertheless, we understand little about the function of protist morphologies, which is surprising given that the field of functional morphology is a cornerstone in biology (Flaum and Prakash 2024). However, studies are increasingly showing evidence for adaptive morphological evolution (Škaloud et al. 2011) and a link between form and function (Macumber et al. 2020) in protists. There is at least one morphological trait that has received considerable attention because of its impact on diverse aspects of protist life: cell size (Finkel et al. 2009). Cell size impacts predator–prey interactions, nutrient acquisition and photophysiology (Key et al. 2009; Edwards et al. 2012; Sommer et al. 2016; Branco et al. 2020). As a consequence, cell size has been found to corroborate well with shifts in environmental changes and gradients over evolutionary timescales (Atkinson et al. 2003; Finkel et al. 2005, 2007), which might even drive different cell size optima between marine and freshwater environments (Litchman et al. 2009; Nakov et al. 2014). Similarly, cell size has been at the centre of the debate surrounding the ubiquity hypothesis and protist dispersal (Wilkinson 2002; Finlay 2002; Mitchell and Meisterfeld 2005). Protist taxa supporting smaller cells have been suggested to be more prone to long-distance dispersal because they tend to have larger population sizes that can generate more dispersal events and might remain airborne for longer (Wilkinson et al. 2012). Similarly, a global-scale integration of metabarcoding, metagenomics and imaging data from marine, planktonic habitats revealed evidence for size-dependent rates of phytoplankton transport, suggestive of stronger barriers to long-distance dispersal in large-celled versus small-celled plankton (Richter et al. 2022). This confirmed previous work that found that, in marine environments, small-celled flagellates show biogeographic distributions as predicted under the *ubiquity hypothesis* whereas large-celled ciliates are reminiscent of the *moderate endemicity hypothesis* (Azovsky et al. 2020). Also in soils, the degree to which community composition was impacted by local environmental conditions versus historical processes depended on cell/body size (Aslani et al. 2022).

Cell size alone is unlikely to be the sole factor that determines protist distributions (Mitchell and Meisterfeld 2005; Foissner 2007). We hypothesise that cell size interacts with population size, which is at least partially mediated through intrinsic growth rates and ecological traits in determining the dispersal capacity of protist taxa. Indeed, the ability of many protists to (not) form resting cells, cysts or spores (McQuoid and Hobson 1996; Lundholm et al. 2011; Bharti et al. 2020) as well as differences in environmental tolerance (Souffreau, Vanormelingen, Sabbe, et al. 2013; Pinseel et al. 2020) have been suggested to affect dispersal success. Similarly, the range of protist population sizes are many orders of magnitudes larger than those of macro-organisms. Especially marine phytoplankton can reach astronomically large population sizes (Filatov 2019). The intrinsic growth rate affecting the (effective) population size of a species plays a central role in its evolution, as population size directly affects the magnitude of genetic drift and thus the strength and efficiency of natural selection (Filatov and Kirkpatrick 2024). It is thus a priority in the field to better understand the links between protist population sizes, speciation and adaptation and dispersal (Filatov and Kirkpatrick 2024). For instance, whereas (vegetative cells of) terrestrial protists might be highly tolerant to environmental extremes, such as desiccation and freezing, which are encountered during long-distance airborne dispersal (Souffreau, Vanormelingen, Sabbe, et al. 2013; Stock et al. 2018; Hejduková et al. 2019), many terrestrial protists likely support much smaller populations than their aquatic counterparts, overall resulting in less dispersal events and a larger impact of genetic drift (Pinseel et al. 2020). In contrast, the possibly lower survival rates of freshwater taxa, such as planktonic algae, during airborne long-distance dispersal might be compensated by their larger population sizes that can supply a high number of dispersers (Pinseel et al. 2020). Similar expectations can be put forward within environments, where highly abundant versus rare biosphere protists might show distinctly different biogeographical patterns. The above examples illustrate the likely central role of population size in shaping protist communities and biogeographies. That being said, historical impacts can override intrinsic dispersal capacities, even in small-celled plankton. For instance, genome-scale analyses revealed that speciation in small-celled coccolithophores of the genus *Gephyrocapsa* occurred during periods of allopatry, imposed by the Pleistocene glacial–interglacial cycles (Bendif et al. 2019; Filatov et al. 2021). To further unravel the interactions between protist morphologies—cell size and beyond—and the other factors that shape protist biogeographies, a better understanding of the link between, on the one hand protist morphologies, and on the other hand function and behaviour, will be essential and will likely hinge on cutting-edge imaging technologies (Flaum and Prakash 2024).

3.6 | Life Cycles and Protist Biogeography

Protists comprise a wide diversity of different life cycles and for many protists taxa the exact mode of reproduction remains elusive even today (von Dassow and Montresor 2010). Sexual reproduction in protists can involve a single parental cell or two cells from opposite mating types and in some taxa (i.e., ciliates), sex, that is genetic exchange, is decoupled from reproduction, that is an increase in cell numbers and involves two to a hundred different mating types within a single species (Phadke and Zufall 2009; Kaczmarska et al. 2013). Furthermore, life cycle modifications affect functional variability in protist populations, which might not be regularly detected with standard molecular markers (von Dassow et al. 2015). How this diversity in life cycles and reproductive strategies impacts protists biogeographies remains unknown. It is however conceivable that the occurrence of, or mechanisms behind, sexual reproduction impact the emergence of reproductive barriers and thus the likelihood of speciation, which in turn contributes to shaping protist biogeographies over macroevolutionary timescales. The emergence of reproductive barriers can be enhanced by historical processes, such as during prolonged periods of geographic isolation imposed by climatological changes—providing a direct link between historical processes and protist biogeographies. Reproductive barriers can also emerge in sympatry, by the spread of reproductively isolating mutations under the Dobzhansky–Muller model (Dobzhansky 1937; Muller 1942; Filatov 2023). If sympatric speciation is combined with dispersal limitation and/or niche divergence, it can also contribute to the emergence of biogeographical patterns. It is possible that the complexity of the mating system determines, at least partially, how prone a lineage is to diversification and cosmopolitan versus endemic distributions. To give the example of diatoms: sexual reproduction in pennate diatoms hinges on a complex, multistage pheromone cascade which is used by opposite mating types to attract and interact with each other (Bilcke et al. 2020; Audoor et al. 2024). In turn, this suggests that numerous opportunities exist to evolve mating incompatibilities by random mutations that occur in genes involved in mating, at least as long as opposite mating types evolve in a compatible way (Mann and Vanormelingen 2013). Such complexity in mating strategies could be one reason why diatoms are not only one of the most diverse eukaryotic lineages (Mann and Vanormelingen 2013), but also prone to high levels of endemism (Verleyen et al. 2021).

It has been argued that in predominantly asexual clades, less opportunity for lineage divergence exists, which may result in less distinct biogeographies and lower levels of global species richness (Škaloud and Rindi 2013). Indeed, several presumed asexual taxa, such as the model diatom *Cyclotella nana* (*Thalassiosira pseudonana*) (Koester et al. 2018), have cosmopolitan distributions. That being said, at least some asexual organisms have been found to undergo diversification at similar rates as sexually reproducing biota (Fontaneto et al. 2007; Fontaneto, Boschetti, and Ricci 2008) and ecological divergence has been detected between closely related, sympatric, asexual protists (Škaloud and Rindi 2013). Such ecological divergence in asexual species flocks could be governed by mitotic recombination between homologous chromosomes, which enables more efficient adaptation without meiotic recombination (Maciver, Koutsogiannis, and de Obeso Fernández Del Valle 2019; Bulankova et al. 2021). Uniparental auxosporulation, which might or might not involve meiosis, in diatoms has also been linked to the emergence of 'microspecies', similar to apomictic angiosperms (Mann and Trobajo 2024). Even in lineages that were presumed to be asexual, such as amoebae, sex might be more frequent than originally thought (Lahr et al. 2011). Altogether, relatively little is known about the history and mechanisms of (sexual) reproduction in most protist lineages (Liang et al. 2020) and how it impacts diversification and distributions. If we are to better understand the impact of sex on protist biogeographies, we will first need to unravel the prevalence and frequency of sex across the protist tree of life and understand the molecular mechanisms behind it.

4 | The Role of Human Activities in Shaping Protist Biogeographies

Human activities have profoundly impacted all protist habitats. This includes direct effects ranging from, for example, eutrophication and pollution of waterways, lakes and coastal seas (Smol 2008) and drying of terrestrial environments (Swindles et al. 2019), to plastic pollution in the open ocean, which has been found to negatively affect picophytoplankton (Focardi et al. 2022). Indirect effects of human activities, such as global warming and atmospheric deposition of nitrogen, which can affect remote and seemingly pristine regions, also have profound impacts on the community structure of protists (Wolfe, Baron, and Cornett 2001; Mendes et al. 2023).

Human-mediated long-distance dispersal of protists could be a significant and potentially seriously underestimated source for protist range expansion on a global scale (Cariton and Geller 1993; Wilkinson 2010; Perrigo, Romeralo, and Baldauf 2012; Darling and Carlton 2018). Some of the most striking examples come from diatoms in rivers and lakes, for example, *Asterionella formosa* (Harper 1990), *Discostella asterocostata* (Alverson et al. 2021) and *Achnanthidium delmontii* (Buczkó et al. 2022), but also riverine dinoflagellates such as *Ceratium furcoides* (Macêdo et al. 2021). In another example, several species of the Southern Hemisphere testate amoebae genus *Nebela* were imported to the United Kingdom from New Zealand in *Sphagnum* for horticultural purposes (Smith and Wilkinson 2007; Wilkinson 2010). Similarly, vegetative cells and resting spores of marine protists, including toxic dinoflagellates capable of forming harmful algae blooms, have been known to be transported in the ballast water of ships, possibly already since the 1880s (Hallegraeff and Bolch 1992; Cariton and Geller 1993), and at least one marine diatom, *Coscinodiscus wailesii* is believed to have been introduced by human activities (Edwards et al. 2001). It is not clear how widespread human-mediated dispersal of protists is, and on which timescale it is acting, but if common, this could affect inferences on species distributions (cosmopolitan vs. endemic), historical biogeography and trait evolution. Given the small cell sizes of protists, it is conceivable that they are more likely to be subject to successful human-mediated dispersal than most plants and animals, but this will also be more difficult to detect. Indeed, despite the huge potential for human-mediated dispersal, and the numerous well-documented case studies, it remains challenging to disprove that invasive protists could in fact represent local and regional emergence from the rare biosphere related to environmental change. This is the case for the raphidophyte *G. semen* in boreal lakes (Hagman, Rohrlack, and Riise 2020) and whereas the nuisance diatom *Didymosphenia geminata* is invasive in New Zealand (Kilroy and Novis 2018) it is not in South America (Jones et al. 2019). Accurate knowledge on the past distribution patterns of protists is therefore required (Litchman 2010), which is evidently impeded by the previously mentioned challenges to study fossil and extant protist community structure. Deep sequencing of eDNA/aDNA in sediment cores may represent a promising avenue for addressing such issues in the future. Clearly, there is a better need to understand how past, present and future human activities impact protist community assembly and biogeographies and how this affects their roles in the healthy functioning of the planet, including biogeochemical cycling and climate change (Cavicchioli et al. 2019).

5 | Conclusions

There has never been a more exciting time to study the patterns of protist diversity and biogeography and the processes that shape them. The field is highly dynamic, rapidly progressing and is strongly benefitting from next-generation sequencing, which allows investigating protist communities, species and populations at an unprecedented scale and detail. This offers a unique opportunity to answer outstanding questions on protist biogeography. This is especially so because protists are highly amenable for experimental work on evolution and dispersal and in contrast to macro-organisms, entire protist populations and communities can be sequenced and characterised at once, allowing to study global patterns and in particular their response to environmental change. To reach this goal, the protist community needs to meet several challenges, foremost including a stronger focus on understudied habitats and protist lineages, inclusion of trait information and targeted field and experimental work aimed at unravelling the processes that drive protist biogeographies. Furthermore, progress will not be possible without continuous investment in expanding and managing the underlying resources and knowledge that are available to our community, including the development, expansion and curation of reference sequence databases and trait datasets, development of new sequencing protocols (e.g., variable marker genes) and techniques (e.g., population genomic techniques for environmental samples), collection of fundamental information on population genetic parameters (e.g., mutation rate, population size and generation time) and building well-sampled time-calibrated molecular phylogenies of lineages across the protist tree of life. Central to all this remains our understanding of species boundaries, indicating that even in the era of massive parallel sequencing, it will remain paramount to invest in taxonomic research that combines morphological, molecular, ecological, reproductive and behavioural data to characterise species boundaries and describe diversity, when needed aided by the in-depth resolution provided by whole-genome sequencing. If we are committed to leverage these challenges to our advantage, it truly will be a new dawn for protist biogeography.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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