

REVIEW

Investigating the effects of anthropogenic stressors on lake biota using sedimentary DNA

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Abstract

- Analyses of sedimentary DNA (*sedDNA*) have increased exponentially over the last decade and hold great potential to study the effects of anthropogenic stressors on lake biota over time.
- Herein, we synthesise the literature that has applied a *sedDNA* approach to track historical changes in lake biodiversity in response to anthropogenic impacts, with an emphasis on the past c. 200 years.
- We identified the following research themes that are of particular relevance: (1) eutrophication and climate change as key drivers of limnetic communities; (2) increasing homogenisation of limnetic communities across large spatial scales; and (3) the dynamics and effects of invasive species as traced in lake sediment archives.
- Altogether, this review highlights the potential of *sedDNA* to draw a more comprehensive picture of the response of lake biota to anthropogenic stressors, opening up new avenues in the field of paleoecology by unveiling a hidden

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historical biodiversity, building new paleo-indicators, and reflecting either taxonomic or functional attributes.

5. Broadly, *sedDNA* analyses provide new perspectives that can inform ecosystem management, conservation, and restoration by offering an approach to measure ecological integrity and vulnerability, as well as ecosystem functioning.

KEYWORDS

anthropogenic stressors, climate change, eutrophication, invasive species, sedimentary DNA

1 | INTRODUCTION

Over the past c. 200 years, coupled lake–catchment ecosystems around the world have been exposed to multiple stressors, which include pollution (e.g., nutrient enrichment), water flow modification (e.g., dams, drought, and storms), overexploitation of natural resources (e.g., deforestation, overfishing), and invasions by non-native species (Stendera et al., 2012). These stressors, which are caused or at least exacerbated by human activities, modify lake functioning and biodiversity with important consequences for ecosystem services (Walsh et al., 2016; WWF, 2020). Ongoing climate change as a consequence of human activities also impact lakes (Jane et al., 2021; O'Reilly et al., 2015), causing dramatic shifts in lake biota (Barbarossa et al., 2021; De Senerpont Domis et al., 2013). Environmental stressors can act over short or long-term scales (i.e., decades to centuries). Understanding the cumulative as well as relative impact of stressors requires time series studies that match the question of interest. Similarly, time series data are useful to assess the extent to which a lake maintains its reference ecological state when exposed to pressure (i.e., resilience) and shed light on transitions between ecosystem states.

Studies exploring long-term patterns in limnetic biological communities are essential to aid in understanding reference conditions and historical ranges of variability, and to assist in determining potential drivers of ecological change. However, the general lack of long-term monitoring data that span both pre- and post-disturbance periods makes it difficult to determine the nature and the timing of ecosystem changes. The paleolimnological approach circumvents these challenges by providing a long-term perspective and information about historical reference states (Smol, 2010). Studies based on classical paleolimnological indicators such as diatom frustules, sub-fossil chironomids, and cladoceran remains have provided important insights into the response of lake ecosystems to multiple stressors (Jenny et al., 2016; Perga et al., 2010). However, traditional paleolimnological proxies are limited to the few biological taxa that leave diagnostic morphological features, thereby impeding the assessment of long-term changes in overall biodiversity, tropho-dynamics, and ecosystem functioning.

The emergence of sedimentary DNA (*sedDNA*) analyses has allowed researchers to expand the paleolimnological toolbox and generate a holistic view of past freshwater ecosystems and their trajectories (Capo et al., 2021). *SedDNA* represents DNA from both living and deceased organisms found in the sediments. Mixed with the

DNA of sediment-living organisms, *sedDNA* from past organisms can reveal key information about the long-term trends in freshwater biodiversity and open new avenues to reconstruct biological time series more broadly (Capo et al., 2022; Gillings & Paulsen, 2014). In 2017, Domaizon et al. showed how the emerging field of *sedDNA* research offered new opportunities for researchers to: (1) track the introduction and spread of invasive species; (2) assess changes in the composition of biological communities; (3) infer long-term dynamics within ecological networks; and (4) aid in the development of tools to determine past changes in environmental conditions (e.g., transfer functions). A range of molecular methods have been applied to *sedDNA*, including quantitative polymerase chain reaction methods (qPCR, digital droplet PCR) and amplicon sequencing (or metabarcoding) to study the past abundance and diversity of aquatic organisms (Capo et al., 2021). Sequencing of all DNA fragments (metagenomics) and of taxa-specific DNA fragments (hybridisation capture) are now increasingly used to study the past genomic diversity of aquatic organisms using *sedDNA* with extended resolution (e.g., Armbrrecht et al., 2021; Garner et al., 2020; Lammers et al., 2021).

Our review synthesises knowledge from studies that have incorporated *sedDNA* to advance our understanding on the effects of anthropogenic stressors on lake biota over the last c. 200 years, a period of enhanced global human activities (Figure 1). We provide a comprehensive inventory of studies that have used *sedDNA* approaches to explore the influence of eutrophication, climate, and non-native species introduction on in-lake biological processes (Figure 2). Table 1 presents a synthesis of the biological changes detected using a *sedDNA* approach as a response to environmental stressors that occurred during the Anthropocene. As illustrated in Figure 1, these environmental perturbations are affecting lakes across multiple trophic levels through bottom-up and top-down effects; as such, the review is structured by trophic levels and aims to evaluate the knowledge acquired using the *sedDNA* approach over the last 2 decades of research.

2 | PHOTOTROPHIC ORGANISMS

2.1 | Cyanobacteria

The biomass of cyanobacteria has increased over the last centuries in many lakes worldwide as a consequence of increased

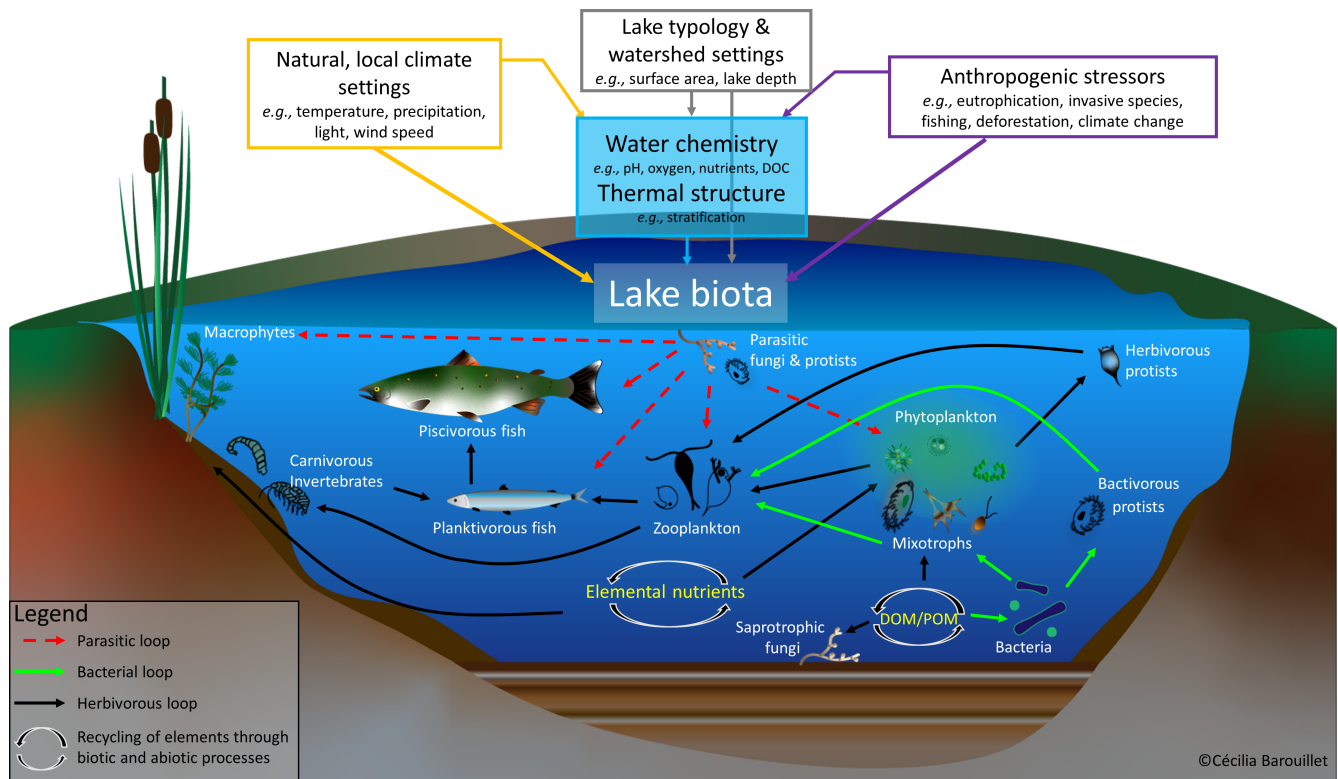


FIGURE 1 Illustration of lake trophic interactions and the direct and indirect (via modification of water chemistry and thermal structure) influence of anthropogenic and climate pressures on lake biota.

anthropogenic impact (Erratt et al., 2022; Huisman et al., 2018; Taranu et al., 2015; Yan et al., 2020). A shift in dominant phytoplankton towards cyanobacteria is of particular concern in lakes and reservoirs because some strains have the potential to synthesise toxic compounds (cyanotoxins), with deleterious effects on wildlife, domesticated animals, and humans (Chorus & Welker, 2021). Large cyanobacterial blooms impair ecosystem services (e.g., drinking water provisioning, recreational activities) and ecosystem functioning via the degradation of water quality (e.g., fish death due to oxygen depletion after cyanobacteria bloom events, reduction of biodiversity via the disruption of the food chain). Decades of laboratory experiments and empirical studies have helped identify external drivers that contribute to regulating cyanobacteria metabolism (including their toxin synthesis pathways) and favour their dominance in freshwaters (e.g., Chorus et al., 2021). Major environmental drivers include enhanced nutrient concentration (i.e., eutrophication) and high water temperatures (exacerbated by climate change) that can act synergistically to promote cyanobacteria dominance in aquatic environments (Chorus et al., 2021; Chorus & Welker, 2021; Paerl & Otten, 2013; Paerl & Paul, 2012). However, due to the paucity of long-term data the factors explaining diversity and inter-annual variability in cyanobacterial natural assemblages are not fully known.

Paleolimnological studies based on *sedDNA* have contributed to greatly improve our knowledge of timing and magnitude of shifts in cyanobacterial community composition, dominance, and

toxin synthesis potential over time periods that span both pre- and post- anthropogenic disturbance. These studies complement works based on other paleo-indicators such as photosynthetic pigments, biomarkers, and microfossils, and are useful to infer historical trends in cyanobacterial communities throughout the Anthropocene and beyond (e.g., Erratt et al., 2022; Monchamp et al., 2018; Picard et al., 2022; Tse et al., 2018).

2.1.1 | Long-term temporal changes in cyanobacterial communities driven by anthropogenic stressors

Following established methods from pioneer studies (Fernandez-Carazo et al., 2013; Savichtcheva et al., 2011), some of the earliest *sedDNA* studies on cyanobacteria population dynamics over the last c. 200 years focused on reconstructing the populations of single genera using cloning-sequencing or qPCR methods. The dynamics in populations of *Synechococcus* (order Synechococcales) and *Planktothrix* (order Oscillatoriales) changed over c. 100 years as a consequence of shifts in the lake's trophic status and climate warming (Domaizon et al., 2017; Savichtcheva et al., 2015). Another study based on qPCR analysis used cyanobacteria-specific primers targeting a region of the 16S rRNA gene to quantify temporal changes in cyanobacterial communities in five Canadian lakes within and outside a protected area (Quebec, Canada) (Pal et al., 2015). This study reports an increase in cyanobacteria

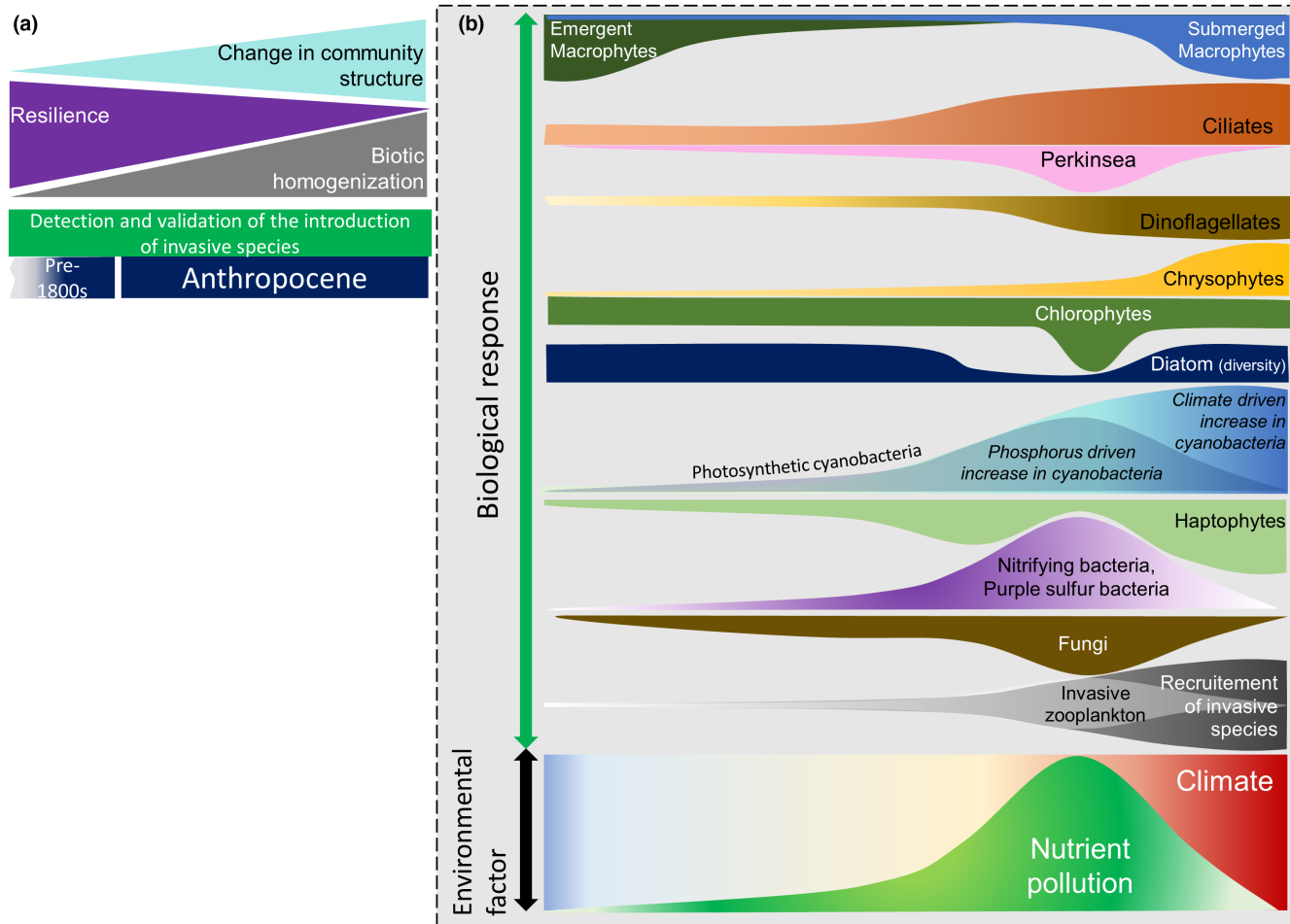


FIGURE 2 Schematics summarizing commonly observed trends in: (a) biological endpoints and insights gained from the *sedDNA* analysis of north temperate lake sediment cores; and (b) the biological response to eutrophication and/or climate recorded in lake sediment cores through *sedDNA* analysis. The width of the bands for the biological response illustrates a period of major changes for each biological group represented, either expressed as an increase in abundance, changes in community structure or in diversity.

abundance over the past 30 years in comparison with the historical average (past 150 years).

The development of high-throughput sequencing technologies (e.g., amplicon-based sequencing) has opened new possibilities for sequencing multiple taxa at the same time (metabarcoding) to reconstruct whole cyanobacterial communities from *sedDNA*. In some lakes, it was found that the cumulative impact of anthropogenic-driven nutrient input and reduction of lake-water level probably promoted the increase of cyanobacteria abundance since the 1980's (Yan et al., 2019; Zhang et al., 2021). In other lakes, climate change causing warming of surface waters and increasing stability of the water column (Monchamp et al., 2019), as well as a combination of warmer and wetter conditions (Erratt et al., 2022) were identified as important drivers of changes in cyanobacteria taxonomic composition.

Over the last 2 decades, a growing body of research based on *sedDNA* metabarcoding analyses has reported on the regional homogenisation of cyanobacterial communities across broad geographical scales, which is generally attributable to both recent changes in local conditions (mainly eutrophication) and global changes (climate

warming). A study by Monchamp et al. (2018) reported that the composition of cyanobacterial communities across 10 peri-alpine lakes had become more similar over the recent decades due to the combined influence of enhanced nutrient pollution (nitrogen and phosphorus) and increased water temperature (leading to increased duration and strength of lake thermal stratification). Other authors have also observed similar trends in the recent homogenisation of cyanobacterial communities (Cao et al., 2020) and in both cyanobacteria and eukaryotic phytoplankton communities (Huo et al., 2022; Zhang et al., 2021).

Aside from photosynthetic cyanobacteria, the temporal dynamics of recently described clades of non-photosynthetic cyanobacteria (Soo et al., 2015) have been investigated using *sedDNA* from temperate lake cores (Ibrahim et al., 2021; Salmaso et al., 2018). It was recently suggested that these ancestral cyanobacteria respond to different factors than the photosynthetic lineages (Monchamp et al., 2019), probably due to the fact that they have alternative metabolic pathways. Nwosu et al. (2021) further found that stronger lake circulation, as indicated by non-laminated sediments, favoured the deposition of the non-photosynthetic cyanobacteria

TABLE 1 Summary of the biological changes detected in *sed*DNA studies as a response to environmental changes.

Environmental factor	Direct influence	Factor of investigation	Biological group	Response	References				
Eutrophication	Lake water chemistry	Increase in phosphorus	Photosynthetic cyanobacteria	Change populations dynamics and cyanobacterial community composition	Domazon et al. (2017); Pal et al. (2015); Savichtcheva et al. (2015)				
				Increase in abundance	Yan et al. (2019); Zhang et al. (2021)				
				Homogenisation of communities	Monchamp et al. (2018)				
				Detection of Saxitoxin	Martínez de la Escalera et al. (2014)				
				cyanotoxin-synthesis genes	Microcystin	Monchamp et al., 2017; Pilon et al. (2019); Tse et al. (2018); Zastepa et al. (2017)			
				Anatoxin	Hobbs et al. (2021)				
				Relative abundance increases when [TP] >80 µg/L	Capo et al. (2016, 2017)				
				Increase in relative abundance, indicator of early warning signal	Capo et al. (2017)				
				Decline in diversity	Ibrahim et al. (2021)				
				Increase in relative abundance	Capo et al. (2017); Li et al. (2019); McCarthy et al. (2011)				
				Increase in relative abundance (when 20 < [TP] < 80 µg/L)	Capo et al. (2016, 2017); Ibrahim et al. (2021)				
				Increase in nitrifying bacteria and purple sulfur bacteria	Li et al. (2019); Liu et al. (2021); Shang and Shang (2005)				
				Increase in relative abundance	Capo et al. (2017)				
				Increase in relative abundance	Ibrahim et al. (2021)				
				Increase in diversity	Ibrahim et al. (2021)				
Climate change	Lake thermal structure	Increase in nitrogen	<i>Daphnia</i>	Increase in invasion potential: replacement of native <i>Daphnia</i> species by invasive <i>Daphnia</i> species	Brede et al. (2009); Hairston et al. (1999); Monchamp et al. (2017); Möst et al. (2015)				
				Change in community composition	Erratt et al. (2022); Monchamp et al. (2019)				
				Increase in abundance	Yan et al. (2019); Zhang et al. (2021)				
				Evidence of cyanotoxin-synthesis genes	Monchamp et al. (2017)				
				Homogenisation of communities	Cao et al. (2020); Huo et al. (2022); Monchamp et al. (2018); Zhang et al. (2021)				
				Increase in relative abundance	Capo et al. (2017)				
				Increase in anoxia-tolerant benthic ciliate	Barouillet et al. (2022)				
				Change in community composition, diversity, increase in submergent vegetation	Stoof-Leichsenring et al. (2022)				
				Increase in community composition, diversity	Capo et al. (2017)				
				Increase in community composition, diversity	Capo et al. (2017)				
				Decline in community composition, diversity	Capo et al. (2017)				
				Hydrodynamic	Increase in air temperature (indirect influence)	Decline in water levels	Macrophytes	Increase in relative abundance	Capo et al. (2017)
								Increase in community composition, diversity	Capo et al. (2017)
								Decline in community composition, diversity	Capo et al. (2017)

(Continues)

TABLE 1 (Continued)

Environmental factor	Direct influence	Factor of investigation	Biological group	Response	References
Catchment development	Dam	Waterflow modification	Dinoflagellates	Increase in relative abundance	McCarthy et al. (2011)
	Land use change		Fungi	Increase in diversity	Talas et al. (2021)
Industrial pollution	Underlying mechanism unclear		<i>Daphnia</i>	Invasion of <i>Daphnia curvirostris</i>	Duffy et al. (2000); Piscia et al. (2016); Turko et al. (2016)
Exotic species introduction			Fish	Validation of invasion, competition with or replacement of native species	Nelson-Chorney et al. (2019); Olajos et al. (2018); Stager et al. (2015)
Overall anthropogenic induce changes: land use, climate change, eutrophication (undetermined mechanisms or factors)			Overall microeukaryotes	Homogenisation of communities	Keck et al. (2020)
			Ciliates	Homogenisation of communities	Barouillet et al. (2022)
			Fungi	Increase in pelagic parasitic fungi	Talas et al. (2021)

clade Sericytochromatia, whereas lake bottom anoxia, as indicated by subrecent and recent laminated sediments, favoured the recovery of Melainabacteria DNA from sediments. The ecological role and significance of these ancestral clades of cyanobacteria remains to be investigated thoroughly in their environmental context.

2.1.2 | Long-term temporal changes in the toxic potential of cyanobacteria

Several *sedDNA* analyses have detected and quantified temporal changes in genes responsible for toxin synthesis by cyanobacteria from freshwater environments. In lakes, such studies have led to the identification of important patterns in potentially toxic cyanobacteria in relation to past changes in lake conditions, as summarised in Table 1. An increased abundance of cyanotoxin synthetase genes detected in lake sediments over recent decades has been attributed to major changes in lake trophic states. Saxitoxin-producing genes were found in sediment samples from the 21st century whereas they were absent in samples dated to the 19th century from a record collected in the subtropical freshwater Laguna Blanca (Martínez de la Escalera et al., 2014). Other studies revealed that legacy nutrient inputs into temperate lakes promoted an increase in the abundance of *Dolichospermum* sp. (i.e., a genus capable of producing anatoxins; Hobbs et al., 2021; Pilon et al., 2019). Disproportionate increases in toxin-synthetase gene concentration detected in *sedDNA* core samples dated to within the last century are consistent with findings obtained via classical paleolimnological tools (e.g., Tse et al., 2018) and surveys of water columns showing evidence for an increased occurrence of toxigenic species of cyanobacteria in many regions of the world (e.g., Rinta-Kanto et al., 2009).

2.2 | Eukaryotic phytoplankton

Lake eukaryotic microalgae are distributed in several lineages within the eukaryotic tree of life including the following dominant groups: chlorophytes, diatoms, chrysophytes, cryptophytes, and dinoflagellates (Adl et al., 2012; Burki et al., 2020). Eukaryotic microalgae are phylogenetically diverse and have different requirements for light intensity and nutrient levels (Wetzel, 2001). As illustrated by the functional classification of freshwater phytoplankton (Padišák et al., 2009; Reynolds et al., 2002), phytoplankton community composition provides a wealth of information on ecosystem dynamics. One general trend that emerged from the *sedDNA* analyses of 48 European lakes using a paired contemporary and pre-industrial sampling design (i.e., top-bottom study) is the relative increase in phototrophic and mixotrophic protists associated with recent anthropogenic changes (Keck et al., 2020). While the increasing abundance of cyanobacteria is often in the headlines (cf. previous section), other phytoplankton groups also appear to have been affected by human-induced changes over the past c. 200 years. Notably, the interplay between cyanobacterial and eukaryotic phytoplankton communities

is complex and strongly regulated by thermal stratification, mixing regime, and the biogeochemical balance of lakes (Posch et al., 2012). For instance, reducing phosphorus inputs can successfully reduce the occurrence of eukaryotic phytoplankton blooms; however, subsequent increase in nitrogen-to-phosphorus ratio may provide an advantage to the non-nitrogen-fixing cyanobacterium *Planktothrix rubescens* (Posch et al., 2012). Moreover, the introduction of new species may lead to imbalances in food webs and affect phytoplankton assemblages through top-down pressures (Leuven et al., 2017). As such, understanding the response of eukaryotic unicellular phototrophs to anthropogenic and other stressors in the global context of climate change is becoming increasingly important.

2.2.1 | Diatoms & chrysophytes

Diatoms and chrysophytes are highly sensitive to environmental change. As such, they serve as indicators to investigate the effects of changes in water chemistry, habitat, and thermal structure on lake ecosystem dynamics (Sandgren et al., 1995; Smol & Stoermer, 2010). For decades, most of the reconstructions of environmental changes derived from lake sediment cores were conducted using diatom frustules and chrysophytes scales and cysts. However, only a small proportion of the eukaryotic microalgae species bear silicious scales. Furthermore, the *morphospecies* identification of cysts has been linked to organisms in only a handful of taxa, which limits one's ability to draw ecological inferences (Smol, 2008). Despite these caveats, data based on diatom and chrysophyte microfossils have been used to reconstruct the long-term temporal variations of lake nutrients, metals concentrations and pH (e.g., Charles, 1990; Cumming et al., 2015).

Although chrysophyte DNA has been recovered from numerous sedimentary archives (e.g., Capo et al., 2016, 2017, 2019; Ibrahim et al., 2021; Keck et al., 2020), specific studies of chrysophyte population dynamics through *sedDNA* analysis are still sparse. In the perialpine lakes Bourget and Annecy, chrysophytes have been found to be favoured by low phosphorus concentrations and increasing temperatures (Capo et al., 2017); a trend that has been previously observed in limnological studies (e.g., Sandgren et al., 1995). More recently, analysis of DNA extracted from water column and sediment trap samples across a 3-year monthly time series showed that changes in chrysophytes were associated with several other physico-chemical and biological variables, including fluctuations in ammonia concentration (Gauthier et al., 2021).

Several studies combined the genetic approach with microscopic analysis to assess the long-term dynamic of diatom communities, while also exploring the similarities, differences and complementarity of the two methods (Anslan et al., 2022; Dulias et al., 2017; Epp et al., 2011; Gauthier et al., 2022; Huang et al., 2020; Kang et al., 2021; Stoof-Leichsenring et al., 2012; Stoof-Leichsenring, Dulias, et al., 2020; Stoof-Leichsenring, Pestryakova, et al., 2020). Beyond the methodological advancements, insights into the response of the diatom communities to environmental changes were

also gained from these analyses, including shifts in diatom community structure, diversity, and the occurrence of particular genetic lineages. Using a metabarcoding approach, Ibrahim et al. (2021) highlighted a decline in diatom diversity in Lake Constance (Germany) as a response to an increase in phosphorus concentrations, with a noticeable rebound when phosphorus concentrations later declined. However, this rebound in diversity also coincided with a change in the diatom assemblage and may be related to the presence of another stressor or biotic process. Interestingly, the early shift in the diatom assemblage detected in the paleo-records was not previously observed in the long-term water column phytoplankton time series.

SedDNA approaches reveal new information on the genetic plasticity of diatoms in response to environmental changes (Stoof-Leichsenring et al., 2014, 2015; Stoof-Leichsenring, Dulias, et al., 2020; Stoof-Leichsenring, Pestryakova, et al., 2020). The genetic structure of bloom-forming diatom *Skeletonema marinoi* was investigated using microsatellite markers applied on resurrected strains preserved in sediment for over c. 100 years (Härnström et al., 2011). This study showed that the dispersal potential and generation time do not have a large impact on the genetic structure of the populations, but rather the environmental conditions, such as the extreme eutrophication of the Mariager Fjord, were deemed more important. Supporting these results, analysis of the relatedness of diatom lineages in Siberian lakes along environmental gradients (i.e., across treeline transects) and across a large geographical and time (i.e., last 7,000 years) scales demonstrated that diatom-relatedness reflected patterns of environmental conditions through space and time rather than geographic distance (Stoof-Leichsenring et al., 2015).

2.2.2 | Chlorophytes

Chlorophytes, also known as green algae, do not leave many morphological diagnostic features in the sediments (with a few exceptions such as *Pediastrum* cell nets), and thus long-term reconstruction of this phytoplanktonic group largely depends on the availability of monitoring data, which are limited. To our knowledge, *sedDNA* studies specifically targeting chlorophytes are still rare (Fonseca et al., 2022). However, the reconstruction of the long-term dynamic of microbial eukaryotic communities was successful at recovering archived DNA of chlorophytes (Capo et al., 2016, 2017; Gauthier et al., 2022; Ibrahim et al., 2021), providing insight into the response of this specific group of algae to environmental change. In Lake Bourget (France), relative abundance of *Chlamydomonas* sp. was found to increase when phosphorus concentrations were greater than 80 µg/L (Capo et al., 2017). Interestingly, a complementary study combining *sedDNA* records from Lake Bourget (France) and Igaliku (Greenland) showed that chlorophytes were one of the phytoplankton groups with the highest relative abundance and highest OTU richness of the overall micro-eukaryotic communities, thus providing a new insight into their dominance in the phytoplankton over the last 100 years (Capo et al., 2016). Importantly, the data also highlighted a potential *unknown diversity* (or unreferenced

biodiversity), which underscores the need for further characterisation of micro-eukaryotes using both limnological and paleolimnological DNA approaches.

2.2.3 | Dinoflagellates and haptophytes

Dinoflagellates display various trophic ecologies as autotrophs, mixotrophs, and some heterotrophic species. Dinoflagellate blooms are most often observed in marine ecosystems, where they can cause important damage to the ecosystem (i.e., fish kill, release taste and odour compounds, reduce water treatment efficiency). Dinoflagellate blooms may also occur in tropical and subtropical freshwater reservoirs where they are becoming more frequent (Amorim & Moura, 2021). Although freshwater dinoflagellates are still understudied when compared to their marine counterparts, several *sedDNA* studies have highlighted their sensitivity to eutrophication. A 100-fold increase in dinoflagellates was observed in the eutrophic Lake Chao (China), concurrent with the establishment of a dam and an increase in nutrients inputs following industrial and agricultural development of the catchment (Li et al., 2019). Similarly, in the deep peri-alpine Lake Bourget (France), the cumulative increase in temperature and phosphorus concentration were associated with an increase in dominance of dinoflagellates (Capo et al., 2017). In contrast, the relative abundance of dinoflagellates from Lake Constance (Germany) did not increase during the eutrophication period but was favoured during lake re-oligotrophication (Ibrahim et al., 2021). Microscopic analyses and germination techniques coupled with single-cell large subunit ribosomal rDNA analysis of dinoflagellates cysts extracted from sediments revealed an increase in dinoflagellates concurrent with recent cultural eutrophication and land-use changes in Lake Huron (Great Lakes of North America) (McCarthy et al., 2011). Furthermore, the DNA analysis of the cysts from this study allowed for the identification of dominant cyst morphotypes (i.e., *Peridinium wisconsinense* Eddy, 1930 and *Peridinium willei*; Huitfeldt-Kaas, 1900) and demonstrated that an earlier increase in *P. willei* occurred at the expense of *P. wisconsinense* following anthropogenic disturbances of the catchment.

Other eukaryotic phytoplanktonic groups have been specifically investigated using *sedDNA* methods. Holocene records of *Isochrysis* (haptophytes) population dynamics of Kusai Lake (China) highlighted the sensitivity of these assemblages to climate-driven changes in nutrients, temperature, salinity, and light-intensity (Hou et al., 2015). The study demonstrated the strong influence of the Asian summer monsoon season and paleo-precipitations on the dominance of haptophytes populations relative to cyanobacteria populations, two algal groups commonly found in Tibetan lakes.

2.3 | Macrophytes

In shallow lakes, macrophytes play an important role in the dynamics of food webs and lake biogeochemistry. Macrophytes act as traps

that effectively sequester carbon and other elements (Brothers et al., 2013; Rooney et al., 2003). The loss of native submersed macrophytes is often a critical turning point in the eutrophication of a lake. For instance, the loss of macrophyte habitat can increase fish predation on zooplankton, with subsequent top-down effects, including the release of grazing pressure on the phytoplankton (Phillips et al., 2016). Increased oxygen-deficient conditions from yet-higher phytoplankton production exacerbate this phenomenon and reduce benthic invertebrate species.

Long-term time series of aquatic vegetation based on *sedDNA* can be used to track their responses to anthropogenic stressors with the potential to become indicators of environmental changes, although this work is still rare (Alsos et al., 2018, 2021; Heinecke et al., 2017; Stoof-Leichsenring et al., 2022). The reconstruction of the past terrestrial and aquatic vegetation over the Holocene period showed an increase in macrophyte dominance during periods when the water column was clearer in several lakes across Norway (Alsos et al., 2021). Additional *sedDNA* record specifically targeting submerged vegetation demonstrated the ability of using macrophytes as indicators of lake-water level changes (Heinecke et al., 2017). Changes in macrophyte diversity and community composition were also found to be sensitive to lake-hydrochemistry and climate variability (Stoof-Leichsenring et al., 2022), whereby submergent-dominated type of vegetation became more abundant when temperature and water conductivity increasing (following glacial runoff and evaporation in lakes from the Tibetan alpine zone).

3 | BEYOND OXYGENIC PHOTOTROPHS

3.1 | Bacteria and archaea

Bacteria and archaea thrive in both water column and sediments of most aquatic ecosystems. The more highly resolved taxonomic distribution and metabolism of bacteria and archaea are tightly related to environmental conditions (e.g., light, oxygen, nutrients, organic matter). Contributing as both primary producers and recycling of organic matter in trophic networks, these taxa maintain ecosystem productivity while being sensitive to natural and anthropogenic perturbations (Brasell et al., 2021; Cavicchioli et al., 2019; Qin et al., 2013). For instance, eutrophication can exacerbate the effect of climate warming on microbial methane emission in lakes (Davidson et al., 2018; Sepulveda-Jauregui et al., 2018). Likewise, lake trophic status and sediment redox conditions influence the denitrification potential of the microbial community, thus affecting the ability of a microbial community to mitigate increases in nitrogen loading (Small et al., 2016). Long *sedDNA* time series could help to understand the responses of lake heterotrophic prokaryotes to environmental stressors. One difficulty with such an approach is that the microbial DNA in sediments is a mix from sediment-living microorganisms and externally contributed microorganisms that have historically been deposited (Capo et al., 2022; Pearman et al., 2021).

3.1.1 | Composition of bacterial communities in sediments

Numerous studies have characterised the vertical distribution of microbial assemblages in lake sediments (Borrel et al., 2012; Han et al., 2020; Kadnikov et al., 2012; Ruuskanen et al., 2018; Vuillemin et al., 2018) but only a few used adequate sampling resolutions to relate microbial taxonomic composition to sediment biogeochemical properties (e.g., Wurzbacher et al., 2017). In general terms, surface sediments are dominated by members of the α -, β -, and γ -Proteobacteria, Bacteroidota, Verrucomicrobiota, Planctomycetota, Acidobacteriota, and Marine Group I Archaea while anoxic (subsurface) sediments are dominated by Chloroflexota, δ -Proteobacteria, Acetothermia, Aminicenantes, Bathyarchaeota, Lokiarchaeota, and Altiarchaeales (Borrel et al., 2012; Han et al., 2020; Kadnikov et al., 2012; Ruuskanen et al., 2018; Vuillemin et al., 2018). Typical depth profiles of sediment exhibited an electron acceptor sequence ($O_2 > NO_3^- > NO_2^- > Mn^{4+} > Fe^{3+} > SO_4^{2-} > CO_2$) with a thin layer of oxygen, nitrate, and nitrite depletion at the sediment surface, sulfate depletion after few cm, and with phosphorus, ammonium, and methane at deeper depths (Wurzbacher et al., 2017). This highly biologically active *successional organic matter degradation zone* in uppermost sediments receive large inputs of freshly produced bioavailable organic matter associated with high activity from members of Ignivibacteria, Sphingobacteria, and Flavobacterium (Bacteroidota). In deeper sediments, microbes such as Dehalococcales (Chloroflexota) and the Miscellaneous Crenarchaeotic Group seem to enter a stationary growth state due to a shortage of thermodynamically feasible electron acceptors. As a consequence, such taxa can stay viable and remain in relatively stable proportions for a very long time.

3.1.2 | Bacterial signal to assess past environmental perturbations

Li et al. (2019) investigated bacterial community change in a 150-year record from Lake Chao and revealed a 100-fold increase of taxa associated with nitrification (e.g., *Nitrospira*) since the 1960s, corresponding to the period of increased concentration of nitrogen and documented eutrophication (Li et al., 2019; Shang & Shang, 2005). Although increases in *Nitrospira* sp. have been associated with nitrification in Lake Chao (Li et al., 2019), higher contributions from *Nitrospira* sp. and lower contributions from Bacteroidota were evident in the oligotrophic Lake Lucerne, as well as shallow and medium lake depths of mesotrophic Lake Zurich compared to eutrophic lakes (Han et al., 2020). These results thus depict a more complex picture of the response of *Nitrospira* to nutrient levels. Liu et al. (2021) detected an increase of *Thiocapsa*, a group of purple sulfur bacteria, in sediment layers corresponding to the time of the accelerated eutrophication; however, the underlying mechanisms was unclear. A recent work by Han et al. (2020) have shown that the composition of the bacterial community, irrespective of sediment depth and age,

is separated by lake trophic state; however, the archaeal community became more similar regardless of trophic state in deeper and older sediment layers. The authors suggested that the trophic state at the time of sediment deposition affects the quality of the organic matter buried, and that this subsequently controlled the taxonomy and metabolic capacities of associated organotrophs. As such, the composition of bacterial communities from pre-eutrophication era of currently eutrophic lakes tend to be more similar to oligotrophic lakes than after the onset of eutrophication (Han et al., 2020). Supporting these results, links between lake trophic states and the taxonomic composition of bacterial communities from surface sediments have been reported in a nationwide study in New Zealand (Pearman et al., 2022). Methodological advances based on the comparison of water and sediment metagenomes (Garner et al., 2020) are expected to provide new insights into our understanding of the past versus active *sedDNA* signal from prokaryotes. Combined, all these pioneering studies provide compelling evidence that bacterial composition can be a useful proxy to infer ecosystem change in lakes, but also caution against uncritical interpretation of records of sediment sequence data.

3.2 | Heterotrophic protists

Heterotrophic protists, which include ciliates, amoeba, perkinsozoa, cercozoan, and oomycetes, are key components of aquatic systems (Sanders, 2009). They represent a diverse and abundant fraction of planktonic assemblages in both freshwater and marine environments (Debroas et al., 2017; Garner et al., 2022; Grossmann et al., 2016) where they play various ecological roles as predators, phagotrophs, saprotrophs, parasites, and mixotrophs (Lefranc et al., 2005; Mitra et al., 2016; Oikonomou et al., 2015; Singer et al., 2021). As part of the microbial loop, they participate in the remobilisation and recycling of carbon and nutrients in aquatic ecosystems (Pernthaler & Posch, 2009). Certain heterotrophic protists exert a strong grazing pressure with potential cascading effects on the planktonic and benthic food webs (Caron & Hutchins, 2013). In freshwaters, heterotrophic protists are the primary consumers of bacteria (Sanders, 2009; Sherr & Sherr, 2002) and shape the structure of microbial communities (Boenigk & Arndt, 2002; Lischke et al., 2016). As such, through their various ecological functions, they act as a hidden backbone of aquatic assemblages and provide resistance and resilience against disturbances (Sagova-Mareckova et al., 2021).

Despite their recognised importance in aquatic ecosystems, heterotrophic protists are often overlooked when studying the response of aquatic organisms to environmental changes, their photosynthetic counterparts being often in focus. Found in both pelagic and benthic zones, they are particularly interesting indicators, as the biological response to environmental perturbations such as deoxygenation (Jane et al., 2021; Jenny et al., 2016) is not limited to the photic zone of lakes. *SedDNA* analyses revealed that past environmental and anthropogenic changes strongly influence the composition of heterotrophic eukaryotic groups.

A general decline has been detected in the relative abundance of several groups of phagotrophic micropredators and saprotrophs, including amoebzoa, rhizaria, and stramenopiles from 48 lakes as a response to enhanced human activities in recent decades (Keck et al., 2020). *SedDNA* analyses also highlighted changes in ciliates and perkinsea groups as a response to eutrophication and changes in air temperature. As such, higher relative abundances of ciliates were recorded during periods of moderate increases in phosphorus concentrations in temperate Lake Bourget (Capo et al., 2016, 2017). Investigation in Lake Constance showed a similar increase in ciliate abundance in response to eutrophication (Ibrahim et al., 2021). In contrast, no clear changes have been observed in the relative abundance of heterotrophic protist groups of the eutrophic Lake Chao over the last 150 years (Li et al., 2019). Importantly, Lake Chao is shallow and has much higher phosphorus concentrations (>280 µg/L) than the deep peri-alpine lakes Bourget and Constance. Although more analyses are needed, these *sedDNA* records suggest that heterotrophic protist communities are sensitive to variation in phosphorus concentrations up until a certain threshold, at which assemblages might stabilise (in terms of diversity and relative abundance). A recent top–bottom *sedDNA* study comparing pre-industrial and modern periods revealed an increase in mixotrophic ciliates and facultative or obligate anaerobic ciliates related to increased anthropogenic pressures (Barouillet et al., 2022). Similarly, perkinsea appeared to be favoured by increased phosphorus concentrations but decreased with rising temperatures (Capo et al., 2017).

3.3 | Fungi

Exhibiting a large morphological diversity, from unicellular eukaryotes to macro-organisms, fungi are found in most aquatic ecosystems (Hawksworth & Lücking, 2017; Kagami et al., 2007; Wanasinghe et al., 2022). Despite their diversity and widespread distribution, knowledge about their ecological preferences and functional groups is still limited. Nonetheless, several studies have demonstrated that fungi are sensitive to environmental changes (e.g., Casadevall et al., 2019; Nnadi & Carter, 2021). Long-term changes in fungal communities using the *sedDNA* approach have been recently used to track catchment dynamics related to environmental changes (Talas et al., 2021; von Hippel et al., 2021). Using a fungal-specific assay, data on diverse fungal assemblages were retrieved from a series of lake sediment cores in Siberia (Seeber et al., 2022). In this case, most fungal sequences taxonomically annotated were from terrestrial taxa, thereby supporting the changes observed in fungi diversity and assemblage composition recovered from the sediment are closely associated to terrestrial vegetation changes. Changes in fungal assemblage composition and diversity as a response to eutrophication and climate change have also been investigated using a more universal *sedDNA* assay, targeting all eukaryotes (Capo et al., 2017; Ibrahim et al., 2021). While the sequences from these European sediment core studies had a lower taxonomic resolution than those generated with fungal-specific specific assay, fungi were generally found to increase with rising phosphorus

concentrations, and showed temperature and phosphorus increases could have an antagonistic effect on fungi assemblages. Interestingly, *sedDNA* analysis also revealed important insights into planktonic parasitic fungal communities such as relationships between chytrids and their *Planktothrix* hosts over a 35-year record of coexistence (Kyle et al., 2015). The seasonality of chytrids was also demonstrated when applying DNA analysis on sediment trap samples collected from a monomictic oligo-mesotrophic lake (Gauthier et al., 2021). The reconstruction of the fungal biodiversity of Lake Lielais Svetinu (Latvia) showed an increased richness of parasites associated with recent increased plankton blooms linked to human development of the catchment and climate shifts over 1,000 years (Talas et al., 2021). Given the importance of these fungal parasites in shaping the phytoplankton communities (Frenken et al., 2017), *sedDNA* can provide new innovative ways to advance knowledge on these understudied trophic interactions and their contribution to lake dynamics and their resilience to environmental changes.

3.4 | Zooplankton

Zooplankton occupy a pivotal position in lake food webs, positioned between predators (i.e., planktivorous fish) and primary producers (i.e., phytoplankton), and are thus impacted by both top-down and bottom-up pressures. As such, they can be used as indicators of changes in trophic and ecological dynamics of lakes related to anthropogenic stressors (e.g., nutrient enrichment and climate change; e.g., Jeppesen et al., 2009). Paleolimnological works based on counts of cladoceran remains have provided insights into ecosystem changes related to planktivorous fish populations, submerged macrophytes and lake production (Jeppesen et al., 2001). *SedDNA* opens new opportunities to study a wider range of zooplankton groups in paleolimnological studies, and also allows for long-term investigations of genetic diversity and variability of this diverse planktonic group.

3.4.1 | Resting egg banks archive ecological and evolutionary responses to anthropogenic impact

Many species of cladocerans, rotifers, and copepods are able to produce dormant forms as a resistance mechanism to survive harsh environmental conditions (Radzikowski, 2013). Among cladocerans, *Daphnia* is one of the most abundant zooplankton in freshwater lakes as it is a good source of food for planktivorous fishes (Leavitt et al., 1989; Paquette et al., 2022). For decades, past trajectories of *Daphnia* species have been investigated through genetic analysis of their resting eggs (Brede et al., 2009; Limburg & Weider, 2002; Mergey et al., 2006; Monchamp et al., 2017; Weider et al., 1997). For instance, Mergey et al. (2006) reconstructed the invasion history of a single asexual American *Daphnia* clone (hybrid *Daphnia pulex* × *Daphnia pulicaria*) following what appears as an accidental introduction of the American *D. pulex* in Africa c. 1920. The introduction

of the new hybrid was rapidly followed by the displacement of its native sibling species, probably through the African continent (based on surveys from 177 African standing water), reflecting this clone's adaptation to broad environmental gradients (Mergeay et al., 2006).

One of the main factors promoting lake invasions by exotic or non-native *Daphnia* around the globe is eutrophication. In Lake Constance (Germany), molecular analysis (i.e., ITS-RFLP, mitochondrial DNA, and microsatellite analyses) of sedimentary resting eggs demonstrated that anthropogenically-induced eutrophication facilitate changes in *Daphnia* assemblages through the interspecific hybridisation and introgression between the invasive *Daphnia galeata* and the native *Daphnia hyalina* (Brede et al., 2009). Molecular analysis of the resting egg from the invasive *D. pulicaria* also uncovered its historical genetic variation during the initial invasion (Möst et al., 2015), while Monchamp et al. (2017) revealed the invasion of *D. galeata* in two Swiss lakes during the peak of the eutrophication. Following the invasion, a *D. galeata* × *Daphnia longispina* hybrid became dominant over *D. longispina*. A growth experiment based on hatched dormant eggs of the invasive species of *Daphnia galeata* preserved in sediments of Lake Constance showed resistance of populations to dietary cyanobacteria during eutrophication era (Hairston et al., 1999). However, during the re-oligotrophication period that was accompanied by a decline in cyanobacterial biomass in Lake Constance, *Daphnia* genotypes showed a lower resistance to cyanobacteria, probably because of the high cost of maintaining resistance to cyanobacteria (Isanta-Navarro et al., 2021).

Additional paleolimnological studies based on genetic analyses of *Daphnia* resting eggs reported that invasions by non-native *Daphnia* were facilitated by other sources of chemical pollution (e.g., Hg, Pb). For example, in Lake Onondaga (New York), sequencing of the 12S ribosomal rRNA gene of mitochondrial DNA extracted from diapausing eggs revealed a past invasion of a Eurasian species, *Daphnia curvirostris*, at a time when there was increased chemical industry activity on the lake shore (Duffy et al., 2000). This exotic species eventually disappeared from the water column once the chemical pollution stopped. An experimental study also detected rapid adaptation in invasive *Daphnia* species to chemical pollution (Turko et al., 2016). In Lake Greifensee (Switzerland), the invasive *Daphnia galeata* acquired resistance to lead pollution, but once the lead stress was reduced, they showed a decline in resistance to this stress. Similar to paleolimnological studies on *Daphnia* resting eggs, several studies using rotifer resting eggs provide valuable insights into their population response to environmental change (Piscia et al., 2016) and history of genetic lineages in a geographical and climate context (Gómez et al., 2000). Molecular analysis targeting the mitochondrial gene coding for the cytochrome oxidase subunit 1 in resting eggs of the cosmopolitan rotifer *Brachionus plicatilis* revealed phylogenetic structure with distinct geographical distribution in lakes within the Iberian Peninsula (Gómez et al., 2000).

Altogether, zooplankton resting eggs (especially *Daphnia*) in sedimentary archives have been widely used as an effective tool to elucidate past population dynamics. However, genetic identification of sedimentary eggs is often unsuccessful owing to DNA degradation

(Faustová et al., 2004; Ishida et al., 2012; Tsugeki et al., 2021). Similarly, genetic analysis of rotifer using resting eggs is rarely conducted in paleoecological studies because their resting eggs are generally not well preserved (Epp et al., 2010; Merkt & Müller, 1999) and their identification via morphological characters is limited (Briski et al., 2011).

3.4.2 | Sedimentary DNA approach to reconstruct genetic diversity and population dynamics through environmental changes

As an alternative to extracting DNA from resting eggs or hatched individuals resurrected from the resting eggs, bulk *sedDNA* extractions can reveal temporal changes in abundances or genetic diversity of rotifers, copepods, and cladocerans. An early example came from Bissett et al. (2005) who detected copepod DNA from 9,950 year-old sediments in Antarctic lakes based on amplification and cloning of a c. 300-base pair variable region of the 18S and 28S rRNA genes. They identified several copepod species that matched modern populations, including the species *Paralabidocera antarctica* (family Acartiidae) that was detected in sediments c. 3,430 calibrated ¹⁴C year ago, but that was not found in more recent sediment samples or contemporary water samples. Moreover, Epp et al. (2015) detected several marine copepod DNA from sediments around 7,500 to 10,000 years ago, a period that corresponded to the marine and brackish conditions in a North Greenland lake. DNA of rotifers of the genus *Brachionus* extracted directly from bulk sediments of Lake Sonachi (Kenya) and analysed using a specific assay for the cytochrome oxidase subunit 1 gene revealed two phylogenetically distinct species and intraspecific population turnovers in response to a volcanic eruption and declining lake-water level (Epp et al., 2010). Furthermore, *D. galeata* and *D. pulicaria* populations were detected by qPCR analysis from Lake Biwa sedimentary archives spanning the last 100 years, and these DNA-based results were consistent with morphological time series data of their resting eggs (Tsugeki et al., 2022). Although zooplankton bulk *sedDNA* studies are still limited, these initial findings suggest that further development of such approaches will allow us to elucidate the long-term dynamics of a wide variety of zooplankton species and their ecological and evolutionary response to anthropogenic processes.

3.5 | Fish

Fish communities provide us with an integrated response of the whole lake ecosystem to environmental stressors given their elevated position in the food web and mobility among habitats. Traditional paleolimnological approaches have largely excluded fish due to a lack of preservation of tissues in sediment archives and the very large quantities needed to identify sparse subfossils. There are notable exceptions whereby an adequate number of fish macrofossils and scales have been obtained (e.g., Cohen et al., 2016;

Davidson et al., 2003; Reinthal et al., 2011), or where more indirect proxies have been used, such as zooplankton community structure or body size (e.g., Jeppesen et al., 2001), or carcass-derived $\delta^{15}\text{N}$ to track the population dynamic of anadromous fish (i.e., fish migrating from the sea to spawn in lakes and rivers; Finney et al., 2000). However, these proxies tend to have low taxonomic resolution, are temporally patchy and/or based on inferring changes through indirect approaches.

Studies employing *sedDNA* analytical techniques have highlighted their unique potential to evaluate historical changes in fish communities at greater temporal and taxonomic resolution (i.e., to species and genus level). To date, most *sedDNA* studies have focused on establishing and validating the identification of fish DNA (presence-absence data) in the sediment archive and correlating this to known records of fish presence in or introduction to a lake. Among the first studies to amplify fish DNA in sediment, Matisoo-Smith et al. (2008) recovered DNA from a sediment core that matched closely that of the native common bully (*Gobiomorphus cotidianus*) in a New Zealand lake. Fish *sedDNA* has since been used to track natural colonisations and introductions of fish in several lake environments. The *sedDNA* analysis of an Adirondack lake (USA) revealed that *invasive* yellow perch actually had been present for at least two millennia (Stager et al., 2015). Similarly, Nelson-Chorney et al. (2019) detected the presence of native westslope cutthroat trout (*Oncorhynchus clarkia lewisi*) and non-native cutthroat trout (*Oncorhynchus clarkii bouvieri*) in mountain lakes in Canada, corroborating historical reports of non-native trout introduction c. 1930. The colonisation history for whitefish (*Coregonus lavaretus* L.) was also inferred from Holocene-scale *sedDNA* records from Sweden where different trajectories were identified between the two study lakes (Olajos et al., 2018). Drawing on evidence from the marine environment, Kuwae et al. (2020) highlighted that DNA concentrations could be used to track abundances of three dominant fish species in Beppu Bay, Japan (anchovy, *Engraulis japonicus*, sardine, *Sardinops melanostictus*, and jack mackerel, *Trachurus japonicus*), as their data were coherent with historical capture time series. Nonetheless, extraction and amplification of fish DNA from lake sediment is often challenging (Capo et al., 2021; Eichmiller et al., 2014). Improvements in extraction methods and the application of newer sequencing technologies (e.g., droplet digital PCR) will probably allow for more fish *sedDNA* time series to be developed and thus investigators will be poised to link how environmental stressors affect fish communities over long-time scales.

4 | CONCLUSION

Advances in *sedDNA* studies over the last few decades have enabled investigators to tackle pressing ecological and environmental questions in aquatic systems. Since the review from Domaizon et al. (2017), the *sedDNA* scientific literature has flourished, bringing new insights into the natural dynamic and sensitivity of several understudied biological groups and the impacts

of multiple anthropogenic stressors. A few common trends were identified from these *sedDNA* studies, including some similarities in the pelagic community responses to eutrophication and climate change across various lakes, and the biotic homogenisation of limnetic communities. Altogether, these findings provide evidence that DNA molecules preserved in natural lake archives help draw a comprehensive portrait of the suite of responses of lake biota to anthropogenic stressors. Moreover, the *sedDNA* approach has been successfully applied to identify the timing and effects of the introduction of exotic species on native populations. Altogether, *sedDNA* studies have demonstrated the potential of some biological groups as new paleolimnological indicators of biological and functional changes (e.g., ciliates, macrophytes) as well as early warning signals. On a broader perspective, the *sedDNA* is expected to grow in the near future, yielding new perspectives for ecosystem management, conservation and restoration (Gillson et al., 2022; Watson & Medeiros, 2021). More specifically, *sedDNA* extends the field of paleoecology by offering a new lens of investigation, providing new information on understudied biological groups, historical biodiversity, and genetic variability.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception and design of the work, the drafting, revising of the work and final approval of the version to be published. All authors agreed to be accountable for all aspects of the work. C.B. prepared and design the figures and tables that were reviewed and approved by all authors.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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