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ORIGINAL ARTICLE

Sedimentary DNA records long-term changes in a lake bacterial community in response to varying nutrient availability

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Abstract

Microbial communities play important roles in lake ecosystems and are sensitive to environmental change. However, our understanding of their responses to long-term change such as eutrophication is limited, as long-term lake monitoring is rare, and traditional paleolimnological techniques (pigments and microfossils) are restricted to a low taxonomic resolution, or organisms with well-preserved structures. Sedimentary DNA (sedDNA) is a promising technique to reconstruct past microbial communities in sediments, but taphonomic processes and the ability of sedDNA to record bacterial pelagic history accurately are largely unknown. Here, we sequenced the 16S rRNA gene in triplicate sediment cores from Esthwaite Water (English Lake District) which has concurrent long-term monitoring and observational data. The sediment record spanned 113 years and included an episode of increased nutrient availability from the 1970s, followed by a more recent decline. Trends in bacterial community composition were broadly similar among the three sediment cores. Cyanobacterial richness in the sediment cores correlated significantly with that of cyanobacteria in a 65-year microscopy-based monitoring record, and some known pelagic bacterial taxa were detected in the sediment. sedDNA revealed distinct shifts in community composition in response to changing lake physicochemical conditions. The relative abundance of cyanobacteria closely reflected nutrient enrichment, and Proteobacteria, Bacteroidetes, and Verrucomicrobia were relatively more abundant in recent sediments, while Chloroflexi, Firmicutes, Acidobacteria, Nitrospirae, Spirochaetes, and Planctomycetes declined in more recent sediments. Following lake restoration efforts to reduce nutrient enrichment, the relative abundance of cyanobacteria returned to pre-1970 levels, but the bacterial community did not fully recover from the period of intense eutrophication within the time scale of our study. These results suggest that sedDNA is a valuable approach to reconstruct lake microbial community composition over the 100-year time scale studied, but an improved understanding of DNA deposition and degradation is required to further the application of sedDNA in paleolimnology.

KEYWORDS
bacteria, cyanobacteria, lake, palaeolimnology, sedDNA, time-series

1 | INTRODUCTION

Microbial communities form an integral component of lake ecosystems due to their diverse roles in nutrient cycling and position near the base of food webs (Newton et al., 2011). However, lake microbial communities are highly sensitive to environmental perturbations (Zingel et al., 2018), and many lakes worldwide are experiencing a complex mix of interacting pressures from the effects of human activities, such as nutrient enrichment and climate change (Birk et al., 2020). Eutrophication from increased nutrient pollution can change ecosystem dynamics, lead to a change and loss of biodiversity, and increase the frequency and severity of cyanobacterial blooms which can produce toxic compounds that are harmful to wildlife and humans (Battarbee et al., 2012). Climate change can exacerbate the effects of eutrophication, which further threatens the diverse biota that lakes support, and can have consequences for biogeochemical cycles (Davidson & Jeppesen, 2013; Richardson et al., 2019). Effective management of lakes is therefore crucial to maintain these important ecosystems, but relies on a comprehensive understanding of how lake microbial communities respond to environmental change.

Lake microbial community dynamics have previously been studied on relatively short temporal scales of less than 10 years (Rösel et al., 2012; Shade et al., 2007), but multidecadal time series are required to understand how communities respond to, and recover from, long-term drivers such as eutrophication and climate change. Such knowledge can inform predictions of how ecosystems may respond to future change, and provide a baseline for lake restoration (Bennion et al., 2011; Maberly & Elliott, 2012). However, long-term and high-resolution monitoring records for lakes are rare (Battarbee et al., 2012; Dong et al., 2012). Sediments can provide a long-term record of past communities, but traditional paleolimnological techniques are restricted to groups of organisms which leave well-preserved and morphologically distinct remains in sediments (Hobbs et al., 2010), or those whose abundance can be inferred from proxies such as pigments (Moorhouse et al., 2014).

Molecular-based techniques utilizing DNA preserved in lake sediments offer an opportunity to study a wider diversity of organisms with a higher taxonomic resolution compared to traditional paleolimnological techniques (Domaizon et al., 2017). DNA from living organisms is deposited in lake sediment where it is progressively buried and preserved over long periods of time. DNA extracted from different depths within sediment cores can therefore reflect the community present at the time of deposition, and the vertical organization of sedimentary DNA (sedDNA) can be used to reconstruct temporal patterns in community composition (Capo et al., 2021). Lake sedDNA has previously been used to investigate changes in the diversity and community composition of eukaryotic microbes and cyanobacteria in response to trophic status and climate warming over periods ranging between 100 and 2200 years (Capo et al., 2016; Domaizon et al., 2013; Ibrahim et al., 2020; Monchamp et al., 2016, 2019). Few sedDNA studies have focused on lake bacterial communities, but Li et al. (2019) demonstrated that sedDNA can be used to explore how different bacterial groups responded to nutrient and heavy metal pollution in a lake in China over a period of 150 years.

Previous sedDNA records for eukaryotic algae and cyanobacteria correlate with sediment core pigment records (Pal et al., 2015; Tse et al., 2018), and the community detected in the sediment closely reflects the phytoplankton community in the water column according to DNA sequencing (Capo et al., 2015) and microscopic analysis of pelagic communities (Monchamp et al., 2016). However, the extent to which sedimentary records represent the pelagic bacterial community is largely unknown. Due to their small size, bacteria may not deposit in the sediment efficiently, and those that do settle may be mostly particle-associated bacteria, whereas more buoyant cells could be flushed from the lake (Thupaki et al., 2013; Vuillemin et al., 2017). The contribution of the active, in situ sediment microbial community to the sedDNA signal compared to that deposited over time by the pelagic community is also poorly understood (Capo et al., 2021; Wurzbacher et al., 2017). The taphonomic processes which influence DNA preservation, such as oxidation, hydrolysis, decomposition by heterotrophs, and grazing by zooplankton, likely differ in the water column compared to that in the lake sediment (Giguet-Covex et al., 2019; Nwosu et al., 2021), and as a water-soluble molecule, free, extracellular DNA may be highly unstable in the water column (Mauvisseau et al., 2022). DNA originating from different sources may therefore experience different rates of degradation. The extent to which degradation of DNA over time may confound the sedDNA signal, and whether DNA from certain microbial taxa is more susceptible to degradation is relatively unknown (Boere et al., 2011). Furthermore, many palaeolimnology studies have used a single sediment core with the assumption that DNA is deposited in a homogenous manner in lakes, but whether different sediment cores show spatial heterogeneity is poorly understood (Capo et al., 2021). Lakes with detailed long-term monitoring and observational records offer an ideal opportunity to address these uncertainties and assess the reliability of sedDNA in palaeolimnology.

Our study is focused on Esthwaite Water, a lake in the Windermere catchment of the English Lake District. It is one of the best studied lakes in the world, as lake conditions have been continually monitored since 1945 and the long history of human activity in the catchment is well-documented (Dong et al., 2011). Prior to the 1970s, there was a gradual increase in nutrient concentrations in Esthwaite Water, following inputs from lowland pasture and fertilizer run-off, and sewage effluent from local villages (Talling &

Heaney, 1983). Nutrient enrichment in Esthwaite Water accelerated dramatically since the 1970s, with the construction of wastewater treatment works in 1973, followed by the establishment of a fish farm in the lake in 1981 (Dong et al., 2011). Esthwaite Water is one of the most nutrient-enriched lakes in the Lake District, and blooms of cyanobacteria have frequently been observed in recent decades (Dong et al., 2012). Efforts have since been made to reduce nutrient enrichment in the lake, with tertiary wastewater treatment initiated in 1986, closure of the fish farm in 2009, and further upgrades to the wastewater treatment works in 2010 (Dong et al., 2011; Maberly et al., 2011). However, continued release of phosphorus from sediments may delay recovery of the lake from this intense period of nutrient enrichment (Dong et al., 2012). Like other lakes worldwide (Maberly et al., 2020), Esthwaite Water is also increasingly influenced by climate change.

Eukaryotic algae and cyanobacteria in Esthwaite Water and the neighboring lakes in the Lake District have previously been studied using observational records (Feuchtmayr et al., 2012; Talling & Heaney, 2015; Thackeray et al., 2008). Lake sediment cores from Esthwaite Water have extended these records over longer time periods. Cyanobacterial and algal pigments have shown an overall increasing trend from 1800 to the 2000s (Moorhouse et al., 2017), and analysis of diatom frustules revealed distinct shifts in the diatom community over 1200 years (Dong et al., 2011). However, previous records have largely been limited to organisms such as diatoms which can be readily identified using traditional paleolimnological techniques (Bennion et al., 2000; Dong et al., 2011, 2012). The long-term temporal dynamics of other lake microorganisms, such as bacteria which do not leave well-preserved or morphologically distinct remains, are therefore poorly understood both in the Lake District (Rhodes et al., 2012), and globally (Billard et al., 2015; Thomas et al., 2019).

This study combines a lake sedDNA record of 113 years with detailed, long-term monitoring records to: (i) assess whether sedDNA is an effective and reliable tool to reconstruct past microbial community composition in lake sediments, (ii) investigate how the bacterial and cyanobacterial community have responded to past human activity and environmental change, and (iii) assess the resilience of lake microbial communities to lake restoration.

2 | MATERIALS AND METHODS

2.1 | Study site

Esthwaite Water (54° 21.56′ N, 2° 59.15′ W) is a relatively small lake in the Windermere catchment of the Lake District National Park, Cumbria, UK (Supplementary Information A, Figure S1). The lake has a surface area of 0.96 km^2, a volume of 6.7×10^6 m^3, mean and maximum depths of 6.9 m and 16 m, respectively, and an average retention time of 91 days. Esthwaite Water has a catchment area of 17 km^2, which is primarily comprised of improved grassland and broadleaf forest (Maberly et al., 2011). There is a well-documented history of human activities and intense eutrophication in Esthwaite Water and its catchment (Dong et al., 2011).

2.2 | Long-term lake monitoring

Physical, chemical, and biological conditions in Esthwaite Water have been continually monitored on a weekly or fortnightly basis since 1945 by the Freshwater Biological Association (FBA) until 1989, and then by the UK Centre for Ecology & Hydrology (UKCEH). The dataset used in this study covered the period from 1945 to 2015 (Maberly et al., 2017). Surface water samples and measurements, integrated over 0–5 m depth, were collected from the deepest point of Esthwaite Water, including surface water temperature, surface water pH, alkalinity, and the concentration of total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate-nitrogen (NO_3-N), ammonium-nitrogen (NH_4-N), and chlorophyll *a*. Winter SRP was calculated as the mean SRP from December to February because winter SRP represents phosphorus availability before substantial uptake in the lake (Dong et al., 2012; Sutcliffe et al., 1982). An annual mean was calculated for each variable measured (Supplementary Information B).

2.3 | Phytoplankton monitoring

Phytoplankton in Esthwaite Water was monitored on a weekly or fortnightly basis, and the record of cyanobacteria from 1945 to 2010 was used in this study. A sub-sample of each integrated depth water sample used for chemical analysis was preserved in Lugol's iodine and concentrated by sedimentation. Phytoplankton within these concentrated sub-samples were identified to the highest taxonomic level possible under a microscope, and their presence was recorded (Supplementary Information C). The mean morphospecies richness of cyanobacteria was then calculated for each year.

2.4 | Sediment coring

A HTH 90 mm diameter gravity corer (Pylonex, Sweden) was used to collect three 30 cm sediment cores. Prior to sampling, holes were drilled into the Perspex core tubes at 1 cm intervals and sealed with heavy-duty waterproof tape. All equipment were cleaned with sodium hypochlorite and Decon 90 cleaning agent, and thoroughly rinsed with deionized water before use. The three cores were collected from the deepest point of Esthwaite Water in 2016 and transported to a nearby laboratory managed by the FBA. To prevent contamination, sterile syringes were used to pierce the tape and extract sediment from the center of each core via the predrilled holes, starting from the top of the core and working downward. The sediment samples were stored in sterile Eppendorf tubes at −20°C prior to DNA extraction. A reference core, used for sediment chronology,

was collected from the deepest part of Esthwaite Water in 2014 with a gravity corer. This core was sectioned every 0.5 cm with the core extrusion kit, and each section was stored in sterile sample bags and then freeze-dried.

2.5 | Sediment core chronology

The freeze-dried sediments from the reference core were radiometrically dated at the Environmental Radioactivity Research Centre, University of Liverpool, UK, where they were analyzed for the radioactive isotopes, ^{210}Pb, ^{226}Ra, ^{137}Cs, and ^{241}Am, by direct gamma assay using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al., 1986, 1992). Radionuclide concentrations with depth for the reference core are given in Supplementary Information A, Table S1. Chronology of the reference sediment core was estimated by the sedimentation rate and ^{210}Pb dates calculated according to the CRS dating model. This model assumes a constant rate of supply of ^{210}Pb to the sediment and allows for a variable sedimentation rate (Appleby & Oldfield, 1978). The chronology, validated using ^{137}Cs dates as reference points which recorded radionuclide fallout incidents (Appleby, 2001), is presented in Supplementary Information A, Table S2. Sample depths for the reference core collected in 2014 were corrected to 2016 using the sedimentation rate to allow for comparison with the sediment cores collected in 2016 (Supplementary Information A, Table S3). The slope and intercept of the age-depth relationship as determined for the reference core (Supplementary Information A, Figure S2) was then used to estimate the age of each section of the three sediment cores used for DNA sequencing. Sample ages were rounded to the nearest calendar year, and the three sediment cores covered a combined period of 113 years from 1903 to 2016 (Supplementary Information A, Table S4).

2.6 | DNA extraction, PCR amplification and sequencing

DNA was extracted from the sediment core samples using the Qiagen DNeasy PowerSoil kit according to the manufacturer's protocol (Qiagen, Germany). The concentration and purity of the extracted DNA was checked using the NanoDrop 8000 spectrophotometer (Thermo Fisher Scientific, MA, U.S.). The V4 region of the 16S rRNA bacterial gene was amplified with primers, 515F (Forward: GTGYCAGCMGCCGCGGTAA) and 806R (Reverse: GGACTACNVGGGTWTCTAAT) (Walters et al., 2016). Each 50 µl PCR reaction contained 0.25 µl of 5 units µl^{-1} Taq DNA polymerase (Sigma-Aldrich, UK), 5 µl of 10x PCR reaction buffer, 0.5 µl of 20 mg ml^{-1} BSA (New England Biolabs, UK), 1 µl of a 10 mM dNTP mix (Bioline, UK), 40.05 µl of molecular grade water, 0.1 µl of the forward and reverse primers, and 3 µl of DNA. The PCR program was set to an initial denaturing temperature of 95°C for 2 min, followed by 30 cycles of 95°C for 15 s, an annealing temperature of 50°C for 30 s, an extension temperature of 72°C for 30 s, and then a final extension temperature of 72°C for 10 min. Successful PCR amplification was confirmed with an agarose gel. PCR product was purified with the Zymo DNA clean-up kit according to the manufacturer's protocol (Zymo Research, CA, U.S.).

Second step PCR was performed using a dual-indexing approach (Kozich et al., 2013), and 50 µl PCR reactions contained 0.25 µl of Taq DNA polymerase, 5 µl of PCR reaction buffer, 1 µl of dNTPs, 37.75 µl of molecular grade water, 5 µl of the indexing primers (Kozich et al., 2013), and 1 µl of purified PCR product from the first PCR step. The second step PCR program was set to an initial denaturing temperature of 95°C for 2 min, followed by 8 cycles of 95°C for 15 s, an annealing temperature of 50°C for 30 s, an extension temperature of 72°C for 30 s, and then a final extension temperature of 72°C for 10 min. Successful PCR amplification from the second PCR step was confirmed with an agarose gel.

PCR product from the second PCR step was normalized using the Invitrogen SequalPrep normalization kit according to the manufacturer's protocol (Thermo Fisher Scientific, MA, U.S.). All samples were pooled, and the concentration of pooled DNA was quantified using the Invitrogen Qubit dsDNA HS assay kit with the Qubit 3.0 fluorometer. The pooled amplicon library was denatured with NaOH, and combined with 4% denatured PhiX. The library was then diluted with HT1 buffer (Illumina, CA, U.S.), heat denatured at 96°C for 5 min, and immediately transferred to an ice bath. The denatured library was loaded and sequenced on the Illumina MiSeq Platform (250PE).

2.7 | Data processing

The sequences were quality filtered and adapters removed using TrimGalore (https://github.com/FelixKrueger/TrimGalore). The resulting quality-filtered reads were processed with R using the DADA2 pipeline (v1.14.1, Callahan et al., 2016) generating an amplicon sequence variant (ASV) abundance table. Each ASV was classified using the naive Bayesian classifier (Wang et al., 2007) against the SILVA database (v.132, Quast et al., 2012) for kingdom to species assignments. The sequences were rarefied to a uniform sequencing depth of 19,135 reads, and filtered based on taxonomy to include only bacteria and ASVs with more than 10 reads.

2.8 | Data analysis

Nonmetric multidimensional scaling (NMDS) based on a beta diversity Bray–Curtis dissimilarity matrix was performed to visualize variation in community composition in each sediment core with sample age and physicochemical conditions of the lake. The envfit function in the vegan R package (Oksanen et al., 2019) was used to fit vectors for these variables and identify which variables correlated significantly with the beta diversity dissimilarity matrix. Analysis of similarity (ANOSIM) with 999 permutations was used to determine the

degree of separation between the three sediment core communities. Alpha diversity in each sample was calculated as the Shannon diversity index, and long-term change in diversity and richness measured at the ASV level throughout the sediment cores was assessed by fitting a linear model of these measures against year.

To assess the ability of sedDNA to record the pelagic cyanobacterial community, ASV richness of cyanobacteria in the sediment was calculated and compared against morphospecies richness of cyanobacteria in the water column. To account for potential inaccuracies in the chronology of the sediment cores, the mean morphospecies richness of cyanobacteria in the water column was calculated for the year before, year of, and year after the corresponding sediment samples, and the mean ASV richness of cyanobacteria in the sediment was calculated for the three sediment core samples within this three-year period (Monchamp et al., 2016). As both measures of richness were dependent variables, a model II regression was fitted with the lmodel2 R package (Legendre, 2018).

To determine whether pelagic bacteria could be detected in the sedDNA record, the sedDNA sequences were compared against the FreshTrain database of known pelagic taxa using NCBI BLAST. This database is based on 1318 16S rRNA reference sequences of heterotrophic bacteria from temperate lake epilimnia (Newton et al., 2011; Rohwer et al., 2018) and is available at: https://github.com/McMahonLab/TaxAss. Matches were filtered at 97% identity, and taxonomy was assigned based on the Silva SSU v138 database available at: https://www.arb-silva.de/documentation/release-138.

ASV abundances were converted to relative abundances in each sample, and ASVs were grouped at the phylum level. The ten most abundant phyla were chosen for in-depth analysis. Generalized additive models (GAMs) were fitted for each phylum to visualize the main underlying patterns in relative abundance throughout the sediment cores. The GAMs were also used to assess the consistency of these relative abundance trends among cores. To do this, GAMs were fitted with a global smooth combining data for each phylum from all cores (assuming similar patterns of change in all three cores), and then fitted again with individual smooths for each core (allowing core-specific patterns). The Akaike Information Criterion (AIC) was then used to assess which model gave the best fit (Burnham & Anderson, 2002). For all GAMs, restricted maximum likelihood (REML) was used as the smoothness selection method. Relative abundance GAMs were fitted with error distributions from the beta family with a logit link, which is suitable for proportion data. GAMs were also used to visualize trends in ASV and morphospecies cyanobacterial richness, but with error distributions from the gamma family with a log link, which is suitable for positively skewed, non-negative data (Anderson et al., 2010; Simpson, 2018). Spearman's correlation was used to investigate the relationship between the relative abundance of each phylum and sample age and lake physicochemical conditions, and the results were presented as a heat map. All data analysis was performed in R version 4.0.2 (R Core Team, 2020) using vegan (Oksanen et al., 2019), phyloseq (McMurdie & Holmes, 2013), microeco (Liu et al., 2021), and mgcv (Wood, 2020) packages.

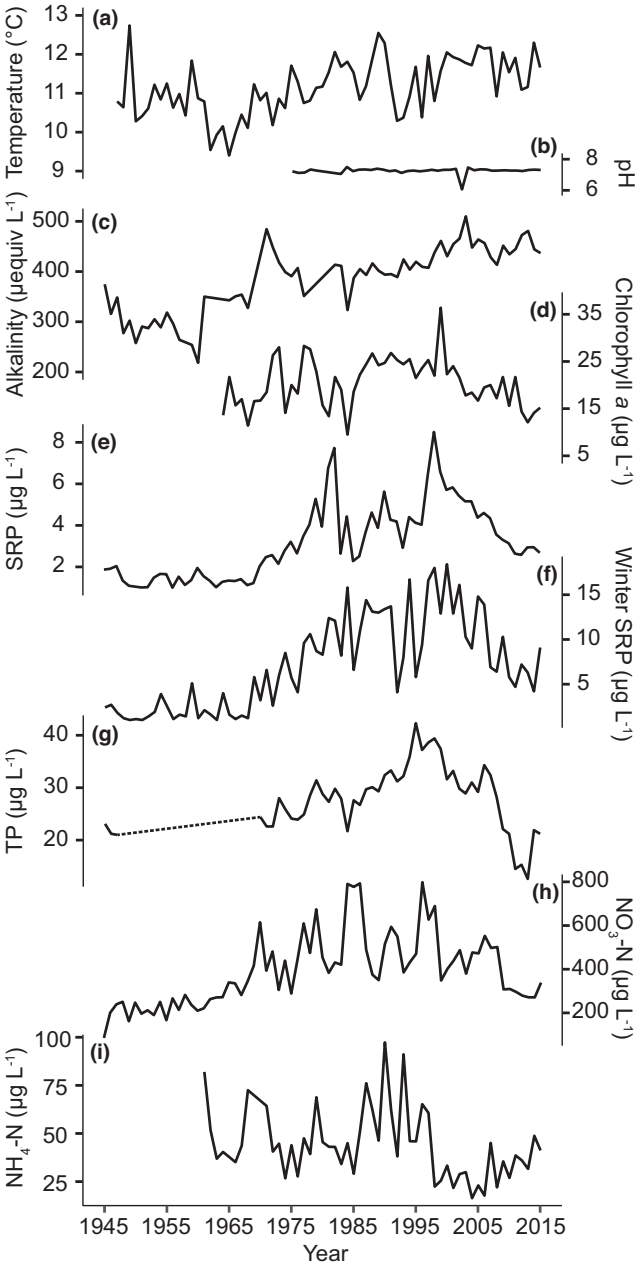

FIGURE 1 Mean annual conditions in Esthwaite Water between 1945 and 2016. (a) Surface water temperature, (b) surface water pH, (c) alkalinity, (d) chlorophyll *a*, (e) soluble reactive phosphorus (SRP), (f) winter SRP, (g) total phosphorus (TP), (h) nitrate-nitrogen (NO_3-N), and (i) ammonium-nitrogen (NH_4-N)

3 | RESULTS

3.1 | Long-term lake monitoring record

Over the 70-year period from 1945 to 2015, mean annual surface water temperature varied between 9.4°C and 12.7°C, and showed a general cooling trend until 1965, but then a warming trend to 2015 (Figure 1a). Mean annual alkalinity declined from 374.7 µequiv L^{-1} in 1945 to 218.3 µequiv L^{-1} in 1960, and then increased to 436.8 µequiv L^{-1} in 2015 (Figure 1b). Surface water pH was monitored from 1974

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to 2015 and was relatively consistent with a geometric mean pH of 7.3 ± 0.21 (*SD*) over this period (Figure 1c). Measurements of chlorophyll *a* began in 1964, and the mean annual concentration of chlorophyll *a* was highly variable but generally decreased from 26.7 μg L^{-1} in 1988 to 15.2 μg L^{-1} in 2015, with a large peak of 36.4 μg L^{-1} in 1999 (Figure 1d).

Phosphorus concentrations were measured as SRP (Figure 1e), winter SRP (Figure 1f) and TP (Figure 1g). From 1945 to 1969, SRP and winter SRP were relatively low, with a mean SRP over this period of 1.4 ± 0.3 μg L^{-1} and a mean winter SRP of 2.0 ± 1.3 μg L^{-1}. TP data were not available for this whole period, but the mean TP concentration was 21.8 ± 1.2 μg L^{-1} between 1945 and 1947. From 1970 to 2000, mean annual SRP and winter SRP increased. SRP peaked at 7.7 μg L^{-1} in 1982 and again at 8.5 μg L^{-1} in 1998, while winter SRP reached a peak of 18.4 μg L^{-1} in 2000. The mean annual TP concentration also showed an increasing trend from 1970 and peaked at 39.4 μg L^{-1} in 1998. From 2001 to 2015, mean annual SRP and winter SRP both showed decreasing trends to 2.7 μg L^{-1} and 9.1 μg L^{-1} in 2015, respectively. The mean annual TP concentration also decreased over this period to 12.6 μg L^{-1} in 2013, the lowest concentration observed since monitoring began in 1945.

The mean annual concentration of NO_3-N showed an increasing trend from 85.5 μg L^{-1} in 1945 to a peak of 790.6 μg L^{-1} in 1984, and then declined to 338.4 μg L^{-1} 2015 (Figure 1h). Monitoring of NH_4-N began in 1961, and there was a period of higher and more variable NH_4-N concentrations between 1986 and 1997, ranging between 45.9 μg L^{-1} and 97.3 μg L^{-1}, followed by a period of relatively lower NH_4-N between 1998 and 2015 when the concentration did not exceed 48.8 μg L^{-1} (Figure 1i).

3.2 | Bacterial community composition and diversity

The beta diversity dissimilarity matrix was most strongly and significantly structured by sample age (R^2 = 0.84, p < 0.001) and alkalinity (R^2 = 0.47, p < 0.001) according to the permutation test (Figure 2). Significant correlations were also identified with NO_3-N, winter SRP, TP (p < 0.01), chlorophyll *a* and SRP (p < 0.05) (Supplementary Information A, Table S5). The ANOSIM R value of 0.01 (p > 0.1) suggested a high degree of similarity between each of the three sediment core communities.

Shannon's diversity and richness for the whole community were relatively consistent throughout each sediment core with no significant change based on the linear regression tests (R^2 = 0.00, $F_{1,88}$ = 0.01, p > 0.1 for diversity and richness) (Figure 3a,b). Shannon's diversity ranged between 4.3 and 6.4, and richness ranged between 138 and 1429.

ASV richness of cyanobacteria in the sediment cores and morphospecies richness of cyanobacteria in the phytoplankton record both showed increasing trends from 1945 (Figure 4a), and there was a significant and positive correlation between ASV richness and morphospecies richness (R^2 = 0.60, $F_{1,15}$ = 23.53, p < 0.001)

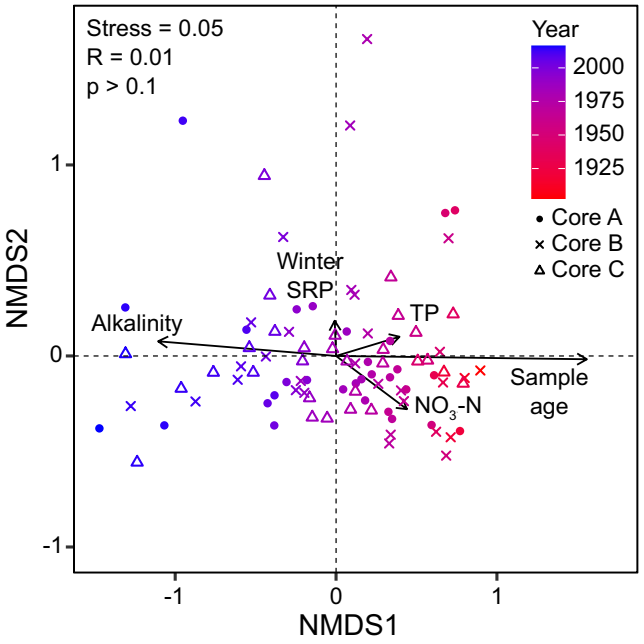

FIGURE 2 Nonmetric multidimensional scaling (NMDS) of Bray-Curtis community composition in three sediment cores. For clarity, only the strongest (R > 0.20) and most significant (p < 0.01) variables are displayed, including sample age, alkalinity, winter soluble reactive phosphorus (winter SRP), total phosphorus (TP), and nitrate-nitrogen (NO_3-N). ANOSIM R and P values are shown. The red to blue gradient indicates older to more recent sediment samples

(Figure 4b). The relationship was close to 1:1, but ASV richness was higher compared to morphospecies richness. Mean ASV richness in the sediment cores ranged between 3.0 and 11.3, while mean morphospecies richness in the water column ranged between 1.4 and 6.2.

3.3 | sedDNA record of known pelagic ASVs

There were 23 sedDNA ASVs that were a match (> 97% identity) with known pelagic bacterial taxa in the FreshTrain database, and 15 of these ASVs were assigned to Proteobacteria, three to Bacteroidetes, three to Verrucomicrobia, and two to Actinobacteria (Supplementary Information A, Table S6). These pelagic ASVs in the sedDNA record demonstrated distinct trends in relative abundance throughout the sediment cores, and selected ASVs which illustrate the range of trends observed are presented in Figure 5 (refer to Supplementary Information A, Figure S3 for remaining pelagic ASVs). The relative abundance of some pelagic ASVs increased over time, such as ASV 35 (*Methylobacter tundripaludum*) which increased from the 1930s to 2016 (Figure 5a), and ASV 948 (*Ferruginibacter*) which was not detected until the late 1990s, but increased throughout the 2000s (Figure 5b). Other pelagic ASVs had a distinct peak in relative abundance, such as ASV 290 (*Pseudarthrobacter*) which peaked from the 1960s (Figure 5c), and ASV 264 (*Terrimicrobium*) which increased

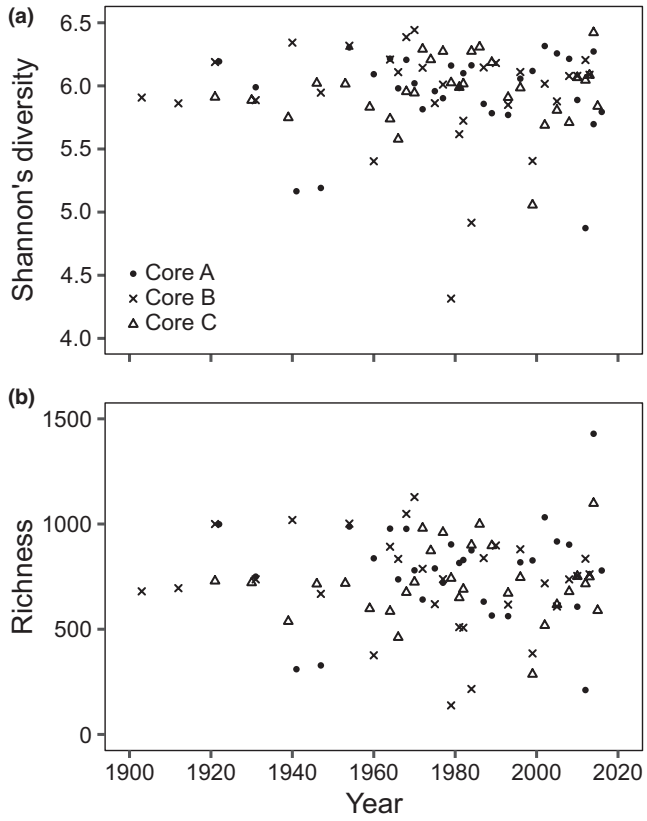

FIGURE 3 Shannon's diversity index (a) and richness (b) for the whole community throughout three sediment cores

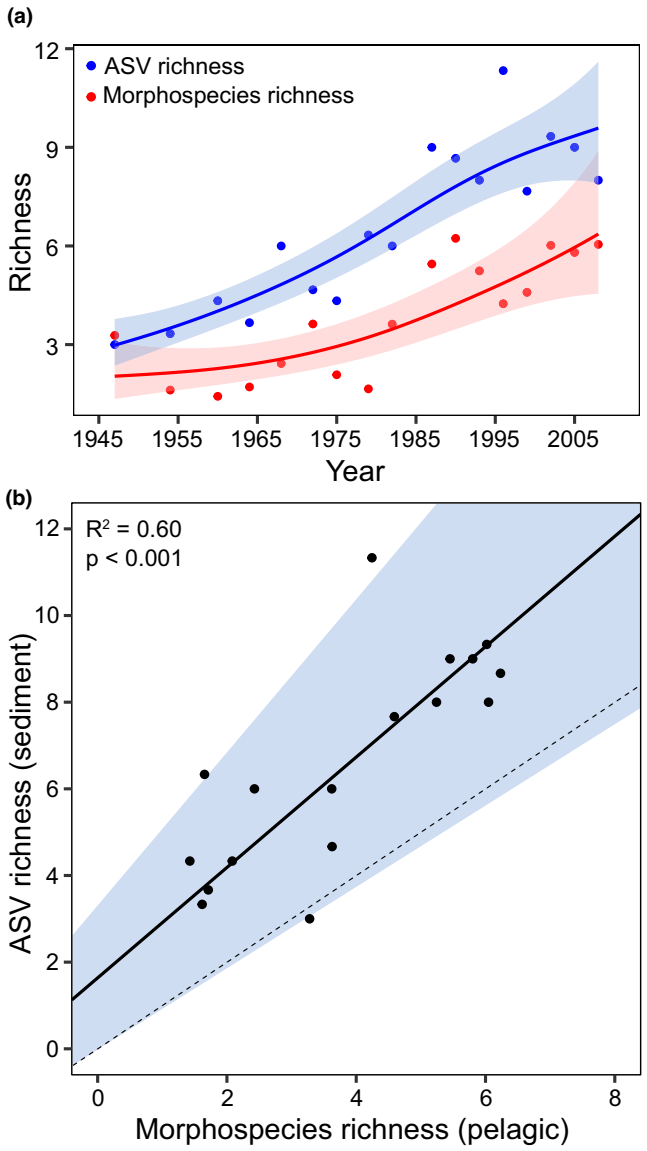

FIGURE 4 Generalized additive models (GAMs) of morphospecies richness of cyanobacteria in the water column and amplicon sequence variant (ASV) richness of cyanobacteria throughout the sediment cores (a), and correlation between morphospecies richness and ASV richness of cyanobacteria (b). Morphospecies richness is the running mean for three years, and ASV richness is the mean for three sediment core samples corresponding to the running mean. Dashed line shows the 1:1 relationship. Shaded area shows the 95% confidence interval

from 1960 to a peak in 1990, and then declined to 2016 (Figure 5d). ASV 52 (*Crenothrix*) showed a declining trend in relative abundance (Figure 5e), whereas ASV 72 (*Methylocystis*) had a more stable relative abundance over time (Figure 5f).

3.4 | sedDNA record of the lake bacterial community

Bacterial phyla showed distinct trends in relative abundance throughout the sediment cores (Figure 6). Each global (single-smoother) GAM revealed statistically significant down-core trends in relative abundance ($p < 0.001$), and associated statistics are presented in Supplementary Information A, Table S7. However, the AIC comparison suggested that core-specific smooths out-performed the global smooths for all phyla except Cyanobacteria and Verrucomicrobia (Supplementary Information A, Table S8). Core-specific trends in relative abundance were broadly similar, but with some variation in the size and timing of peaks for some phyla, most notably Nitrospirae which displayed a more linear trend in core A, but distinct peaks in cores B and C (Supplementary Information A, Figure S4–S13). For clarity, GAMs with a global smooth for all cores are presented in Figure 6, and are discussed below.

Proteobacteria comprised more than 25% of the community in each core section. The relative abundance of Proteobacteria was relatively stable between 1903 and 1950, but showed an increasing trend to 2016 (Figure 6a). Chloroflexi made up the second largest proportion of the community from 1903 to 1960, but there was a consistent decline in the relative abundance of Chloroflexi from the 1950s to 2016 (Figure 6b). The relative abundance of Firmicutes exceeded Chloroflexi in the 1960s, but displayed a general decreasing trend to 2016 (Figure 6c). The relative abundance of Bacteroidetes increased from 1970, and this group made up the second largest proportion of the community by 1990. Bacteroidetes then showed a slight decline in relative abundance from 2000 to 2016 (Figure 6d).

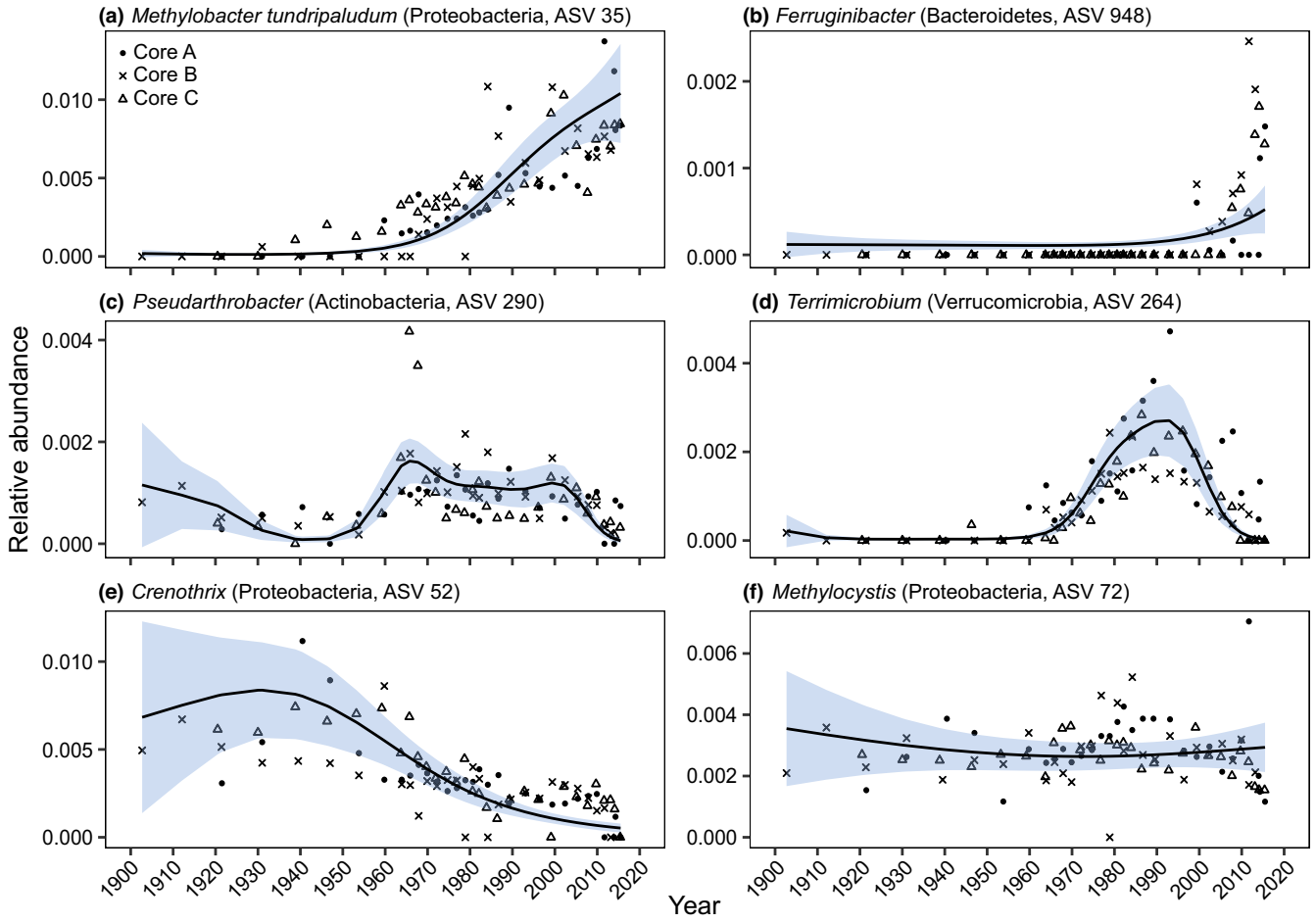

FIGURE 5 Generalized additive models (GAMs) of the relative abundance of selected pelagic ASVs throughout three sediment cores. Shaded area shows the 95% confidence interval. Note the different *y*-axis scales. (a) *Methylobacter tundripaludum* (b) *Ferruginibacter* (c) *Pseudarthrobacter* (d) *Terrimicrobium* (e) *Crenothrix* (f) *Methylocystis*

Other phyla that were present in the sediment cores at a lower relative abundance include Verrucomicrobia, which increased in relative abundance from 1950, and the rate of increase accelerated after 2000 (Figure 6). Acidobacteria showed a general decreasing trend in 2016 (Figure 6f). Cyanobacteria were at very low relative abundance (<0.001) in the sediment until the 1960s (Figure 6g). The relative abundance of Cyanobacteria then gradually increased to a peak in the 1990s before decreasing throughout the 2000s to 2016 when the relative abundance returned to a similar level to that in the 1960s. Nitrospirae declined between 1970 and 1990 (Figure 6h), and Spirochaetes and Planctomycetes both showed a general decreasing trend from 1903 to 2016 (Figure 6i,j).

3.5 | Correlations between bacterial phyla and lake conditions

Spearman's correlation was used to investigate the relationship between the relative abundance of each bacterial phylum and sample age and physicochemical conditions of the lake. The community could be divided into two groups based on their responses. With increasing sample age, the relative abundance of Proteobacteria, Verrucomicrobia, Bacteroidetes and Cyanobacteria significantly decreased ($p < 0.001$) (Figure 7 and Supplementary Information A, Table S9). Proteobacteria, Verrucomicrobia, Bacteroidetes, and Cyanobacteria also had a significant positive correlation with alkalinity, surface water temperature, SRP, and winter SRP ($p < 0.05$). The significant positive correlation between Cyanobacteria and SRP and winter SRP was relatively strong ($R_s = 0.69$, $p < 0.001$), and Cyanobacteria were the only phylum which had a significant and positive correlation with TP ($R_s = 0.74$, $p < 0.001$), chlorophyll *a* ($R_s = 0.58$, $p < 0.001$) and NO_3-N ($R_s = 0.54$, $p < 0.001$). With increasing sample age, the relative abundance of Planctomycetes, Nitrospirae, Firmicutes, Acidobacteria, Spirochaetes, and Chloroflexi significantly increased ($p < 0.001$), and these phyla had a significant negative correlation with alkalinity, surface water temperature, SRP, and winter SRP ($p < 0.05$). However, there was some significant cocorrelation among measures of physicochemical conditions (Supplementary Information A, Figure S14 and Table S10).

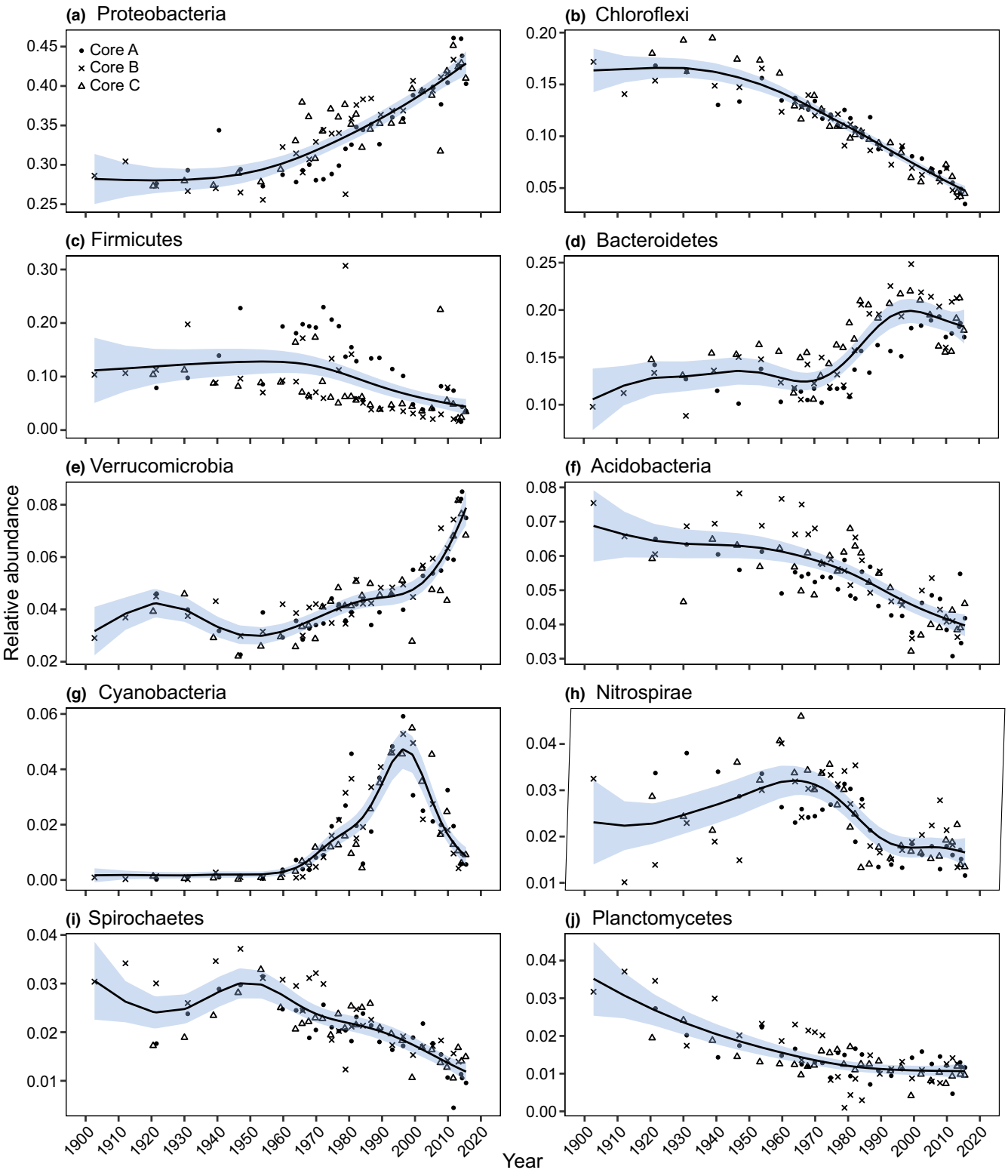

FIGURE 6 Generalized additive models (GAMs) of the relative abundance of bacterial phyla throughout three sediment cores. Shaded area shows the 95% confidence interval. Note the different *y*-axis scales. (a) Proteobacteria (b) Chloroflexi (c) Firmicutes (d) Bacteroidetes (e) Verrucomicrobia (f) Acidobacteria (g) Cyanobacteria (h) Nitrospirae (i) Spirochaetes (j) Planctomycetes.

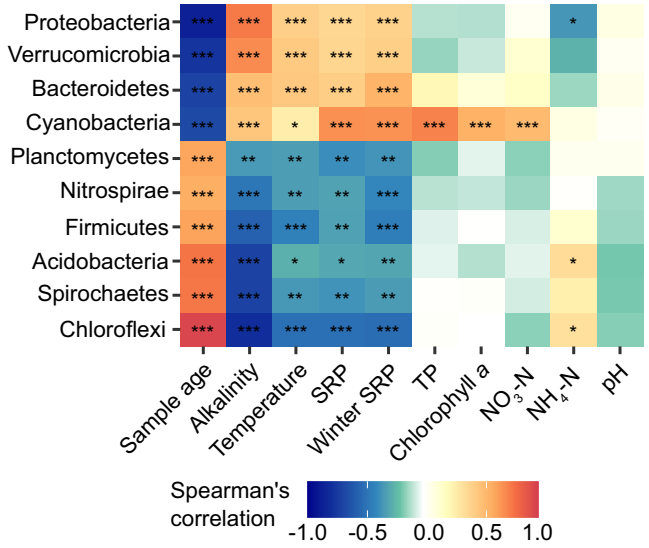

FIGURE 7 Correlations between the bacterial community and sample age and lake physicochemical conditions including alkalinity, surface water temperature, soluble reactive phosphorus (SRP), winter SRP, total phosphorus (TP), chlorophyll *a*, nitrate-nitrogen (NO_3-N), ammonium-nitrogen (NH_4-N), and surface water pH. Correlations are calculated using Spearman's correlation, where red shades indicate positive correlations, and blue shades indicate negative correlations (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$)

4 | DISCUSSION

4.1 | Eutrophication in Esthwaite Water

The 70-year monitoring record of nutrient concentrations in Esthwaite Water suggests substantial eutrophication which accelerated from the 1970s with the establishment of wastewater treatment works and fish farming in the lake in 1973 and 1981, respectively. Accelerated eutrophication in Esthwaite Water from the 1970s has previously been reported (Bennion et al., 2000; Dong et al., 2011; Maberly et al., 2011). Nutrient enrichment declined from the late 1990s, indicating that the tertiary wastewater treatment upgrade in 1986 successfully reduced some nutrient pollution, although the response may have been delayed because of continued phosphorus release from sediments and catchment run-off (Dong et al., 2011, 2012). The decreasing trend in nutrient enrichment continued following closure of the fish farm in 2009 and further upgrades to the wastewater treatment works in 2010. By 2015, the TP, SRP, and NO_3-N concentrations were similar to pre-1970.

4.2 | Consistency between sediment cores

Three sediment cores were collected from the deepest point of the lake to investigate spatial heterogeneity in the sedDNA signal. Each core recorded broadly similar trends in relative abundance, but slight variations were observed in the core-specific trends for some phyla. This could be a consequence of differing age-depth relationships for each core, or indicate that there was some spatial heterogeneity in the community between replicate cores. Pearman et al. (2021) concluded that a single core could adequately record trends in dominant bacteria. Billard et al. (2015) also demonstrated that the bacterial community was consistent between three lake sediment cores taken from the same sampling site, although from the much larger Lake Bourget, France. However, it has been reported that the microbial diversity of the littoral zone is often not well-represented in central sediment cores (Anderson, 2014). A single lake sediment core may therefore be sufficient to capture broad-scale temporal variation in microbial communities, but multiple cores may be valuable when finer-scale spatial and temporal trends are of interest.

4.3 | Effectiveness of sedDNA in describing pelagic communities

Although we did not have a concurrent DNA-based pelagic community dataset to compare the sedDNA communities against, the 65-year phytoplankton monitoring record for Esthwaite Water offered a rare opportunity to assess the ability of sedDNA to track changes in the pelagic cyanobacterial community over a long period of time. The increase over time in ASV richness of cyanobacteria in the sediment coincided with an increase in morphospecies richness of cyanobacteria in the water column, suggesting that this could largely be a response to changing lake conditions, such as nutrient enrichment, and not only loss of cyanobacterial DNA in older sediments. There was a significant positive correlation between ASV richness and morphospecies richness, supporting the use of sedDNA as a reliable measure of pelagic richness. Monchamp et al. (2016) also found a significant positive correlation between cyanobacterial richness in the sediment and water column when comparing sedDNA with a 35-year phytoplankton monitoring record for two temperate lakes. Similar to this study, richness as determined with sedDNA was slightly higher than that determined with microscopy in the water column, which could be expected because observational methods typically underestimate diversity compared to molecular methods (Monchamp et al., 2016; Olsen et al., 1986).

The FreshTrain database of known pelagic bacteria based on temperate lake epilimnia was used to determine whether sedDNA recorded known pelagic bacteria. There were 23 pelagic ASVs detected in the sedDNA record, and each ASV displayed a distinct trend in relative abundance, indicating that sedDNA could track the temporal dynamics of some pelagic bacteria. However, the 23 ASVs that were a match with the FreshTrain database were not diverse as only four different phyla were detected, and the majority were assigned to Proteobacteria. The number of known pelagic bacteria detected was a relatively small proportion of the total sedDNA community. This could suggest that only a proportion of the pelagic bacterial community deposit in the sediment, which could be expected to be mostly larger cells, or those which aggregate with organic material and other cells (Thupaki et al., 2013). Cells and extracellular DNA that are quickly adsorbed by particles and buried in sediment are better

protected from degradation, and rates of DNA degradation are typically higher in the water column compared to in the sediment (Nwosu et al., 2021). Surface water inputs may therefore be underrepresented in the sedDNA record compared to deeper water or sediment inputs. Furthermore, the FreshTrain database is based on a limited number of temperate lakes, most of which are located in North America (Rohwer et al., 2018), and it is likely that many more ASVs with pelagic lifestyles from Esthwaite Water may have been recorded by sedDNA but were not present in the FreshTrain database.

Differential degradation of DNA, either in the water column or during the sedimentation process, could limit the potential of sedDNA in palaeolimnology, but the extent of this is relatively unknown for bacterial DNA (Boere et al., 2011). Reduced diversity and the disappearance of some taxa in older sediments could indicate that DNA of certain taxa experience greater rates of degradation (Zhang et al., 2021). Diversity and richness for the whole community were relatively consistent throughout the sediment cores, suggesting substantial DNA degradation was not occurring. Many bacterial phyla also displayed contrasting trends in relative abundance that were not consistent with universal degradation of sedDNA through time. However, the relative abundance of cyanobacteria was low prior to 1960. Pigment records for Esthwaite Water suggest that cyanobacteria have increased from the 1800s (Moorhouse et al., 2017). Although cyanobacterial richness in the sedDNA record correlated significantly with that in the microscopy-based monitoring record from 1945, the low relative abundance of cyanobacteria in older sediments could be evidence that some postdepositional degradation occurred. Further research is therefore required to determine rates of DNA degradation in lacustrine systems, and to validate cyanobacterial and bacterial sedDNA records over longer periods of time.

The close agreement between cyanobacterial richness measured with sedDNA and that with microscopy, and the successful detection of some pelagic bacteria in the sedDNA record demonstrates that sedDNA has significant potential as a record of pelagic temporal dynamics. However, it must be considered that sedDNA may also record the temporal dynamics of the surface sediment community, and although heterotrophic bacterial activity is typically lower within lake sediments (Haglund et al., 2003), deep sediment communities could also contribute to the sedDNA record. These sediment bacterial communities may be less responsive to lake water conditions, and their distribution with depth may partly be a response to sediment conditions. sedDNA gives an indication of temporal bacterial community change, but further research is required to track the incorporation of DNA from different sources into the lake sediment, and to separate ancient DNA from that of metabolically active cells within the sediment.

4.4 | Community composition change

The sedDNA record revealed distinct shifts in cyanobacterial and bacterial community composition over 113 years, and several phyla underwent marked changes in their relative abundance during the period of intense eutrophication in Esthwaite Water between 1970 and the early 2000s. The relative abundance of cyanobacteria closely reflected changes in nutrient enrichment in the lake. Frequent cyanobacterial blooms have been observed during the period of intense eutrophication in Esthwaite Water (Dong et al., 2012), and photosynthetic pigments extracted from sediment cores in nearby Windermere and Blelham Tarn have also indicated an increase in cyanobacteria during periods of eutrophication from the 1970s (McGowan et al., 2012; Moorhouse et al., 2014). Eutrophication is a problem for many lakes worldwide, and previous sedDNA records from a large number of lakes have revealed an increase in cyanobacteria in response to past nutrient enrichment (Domaizon et al., 2013; Ibrahim et al., 2020; Monchamp et al., 2019; Zhang et al., 2021).

Proteobacteria made up the largest proportion of the community, and increased in relative abundance from older to more recent sediments. Proteobacteria are typically copiotrophic and often dominate lake bacterial communities (Newton et al., 2011). Using sedDNA, Li et al. (2019) also found a substantial increase in the relative abundance of Proteobacteria with increasing nutrient concentrations. However, Proteobacteria continued to increase after nutrient concentrations declined from the 2000s. Proteobacteria had a significant positive correlation with surface water temperature, and the relative abundance of Proteobacteria in bacterioplankton communities has previously been shown to increase with water temperature (He et al., 2017). Increasing water temperatures from 1965 onwards may therefore have contributed to the sustained increase in the relative abundance of Proteobacteria, although separation of potential drivers is complex as there were shared long-term trends between the physicochemical conditions.

The increase in the relative abundance of Bacteroidetes from 1970 to 2000 coincided with the period of accelerated eutrophication. Bacteroidetes have frequently been found to increase with nutrient concentrations, and are a major component of the bacterioplankton community associated with cyanobacterial blooms (De Figueiredo et al., 2007; Guedes et al., 2018). Many members of Bacteroidetes are chemoorganotrophs capable of metabolizing the complex extracellular polysaccharides produced by cyanobacteria, and so Bacteroidetes play an important role in carbon and nitrogen cycling in lakes (Cai et al., 2014). Similarly, Verrucomicrobia have previously been found in association with cyanobacterial blooms in eutrophic lakes and can metabolize complex polysaccharides (Cardman et al., 2014; Kiersztyn et al., 2019). Accelerated nutrient enrichment and a higher abundance of cyanobacteria may therefore have facilitated the increase in the relative abundance of Verrucomicrobia.

Other bacterial phyla declined over the period of accelerated eutrophication, such as Nitrospirae which dropped in relative abundance between 1970 and 1990 when nutrient concentrations were highest. Previous studies have also found that the relative abundance of Nitrospirae declined with increasing phosphorus (Liu et al., 2020; Xiong et al., 2012) and NH_4-N concentrations (Sun et al., 2020). Chloroflexi were relatively abundant from the 1900s but consistently declined over time. Increased turbidity

of water during eutrophication and cyanobacterial blooms may reduce light availability in the water column for photosynthetic members of Chloroflexi (Chen et al., 2015). The relative abundance of Acidobacteria also declined over time. Acidobacteria have previously been described as oligotrophic taxa (Huang et al., 2017), and many species have a preference for acidic environments (Xiong et al., 2012). At the deepest point, Esthwaite Water had a stable mean surface water pH of 7.3 ± 0.21. The neutral pH combined with nutrient enrichment may not have been optimal for the growth of Acidobacteria. Firmicutes form resistant endospores (Wunderlin et al., 2014), so the DNA of Firmicutes could be expected to be preserved more efficiently in the sediment compared to other bacterial phyla. However, the relative abundance of Firmicutes was not substantially higher in older sediments compared to other phyla, and this provides further evidence that DNA did not undergo significant differential degradation.

Planctomycetes and Spirochaetes were present at a relatively low abundance, each making up less than 0.4% of the bacterial community, and declined over time. Planctomycetes are usually present in lakes at a low relative abundance, and have slow growth rates and a delayed response to increased nutrient supply (Pollet et al., 2014). Previous studies have also found that Spirochaetes decreased with nutrient enrichment (Liu et al., 2014; Wan et al., 2017). However, many species of Spirochaetes are parasitic, and their abundance may also be related to the population dynamics of other organisms (Sitnikova et al., 2012).

Our results clearly demonstrate the potential for using sedDNA to make historical inferences of microbial community change. However, we acknowledge that, due to sediment accumulation rates, this technique is likely limited in its ability to discern intra-annual change, and short-term species turnover in response to environmental forcing. Furthermore, it is challenging to demonstrate causal linkages between environmental drivers and community change, given the inherent multidimensionality of lake ecosystem change. Physicochemical drivers, which may act on bacterial community composition, are, at these timescales, highly collinear. Here, we have adopted a correlative approach as a means of tentatively suggesting potential drivers of past change. While it is a commonly used metric, the use of relative abundance in paleolimnology can obscure temporal trends due to different groups showing reciprocal responses, potentially due to differential DNA degradation. Future studies should therefore aim to quantify absolute abundances of taxa for more accurate reconstructions of community responses.

4.5 | Recovery from eutrophication

Following the period of accelerated eutrophication from the 1970s, the relative abundance of cyanobacteria declined and returned to pre-1970 levels by 2016. The sedimentary record of cyanobacterial pigments in Esthwaite Water may also indicate some early signs of recovery from the 2000s (Moorhouse et al., 2017). Bacteroidetes, which increased over the period of accelerated eutrophication, began to decline from the 2000s, and Nitrospirae, which decreased over this period, showed a slight increase in relative abundance from the 2000s. This could indicate that the bacterial community has begun to gradually recover from intense eutrophication. However, although cyanobacteria declined relatively quickly, the relative abundance of other phyla such as Bacteroidetes remained higher in 2016 compared to pre-1970. Eutrophication and frequent blooms of cyanobacteria may have altered long-term functioning of the ecosystem, and cyanobacterial-derived polysaccharides could remain in the lake which other phyla such as Bacteroidetes and Verrucomicrobia may continue to metabolize. Climate warming could also delay complete recovery, as cyanobacteria and each bacterial phylum had a significant correlation with surface water temperature which has shown an increasing trend since 1965. The abundance of cyanobacteria has previously been found to increase with warming temperatures (Domaizon et al., 2013; Monchamp et al., 2018), and climate warming combined with eutrophication have been predicted to increase the frequency of cyanobacterial blooms in Esthwaite Water in the future (Elliott et al., 2010).

5 | CONCLUSIONS

Our results have shown that lake sedDNA can be used to infer past changes in cyanobacterial and bacterial community composition. The sedDNA record was validated by long-term monitoring of cyanobacterial richness in the water column, and successfully tracked some bacterial pelagic history. sedDNA recorded a substantial increase in cyanobacterial relative abundance during the period of intense eutrophication from the 1970s, and this was accompanied by shifts in bacterial community composition in response to changing physicochemical conditions of the lake. Lake restoration efforts appear to have been partially effective, as the relative abundance of cyanobacteria declined with reductions in nutrient enrichment. However, intense eutrophication and the increase in cyanobacteria may have substantially changed long-term ecosystem functioning, and climate warming could delay complete recovery of the lake. These changes in bacterial community composition could have implications for the role of lakes in carbon and nitrogen cycling. We have demonstrated the significant potential of bacterial sedDNA in paleolimnology, but further studies are required to identify the proportion of pelagic, benthic and sediment inputs, the taphonomic processes each source may be subject to, and the length of time over which sedDNA can act as a reliable record of lake microbial community dynamics.

AUTHOR CONTRIBUTIONS

SCM, SJT, DSR, and AA conceptualized the study and designed the methodology. AA and SJT performed the fieldwork. AA, HSG, and TG performed the lab work. ACT, HSG, DSR, and SJT contributed to data analysis. ACT wrote the original draft. SCM and SJT supervised AA, and DSR and JAB supervised ACT. All authors contributed to editing of the draft and approved the final version of the manuscript.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The sequencing data have been deposited with links to BioProject accession number PRJNA788262 in the NCBI BioProject database (http://www.ncbi.nlm.nih.gov/bioproject/788262). Annual means for the physicochemical variables used in this study, and the microscopy record of cyanobacteria are available in Supplementary Information B and C, respectively.

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