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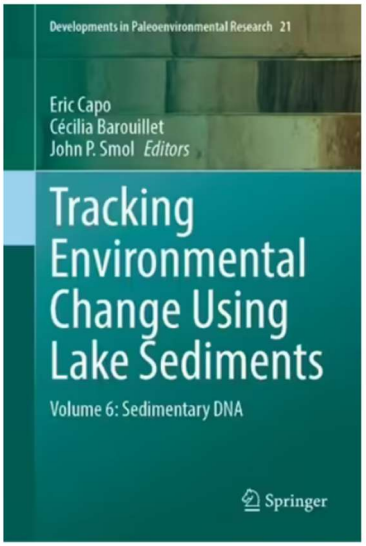

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4. BACTERIAL AND ARCHAEAL DNA FROM LAKE SEDIMENTS

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Introduction

Lake sediments as microbial niches and prokaryotic DNA repositories

Microorganisms are abundant and diverse in inland waters (Newton et al., 2011; Magnabosco et al., 2018; Bertilsson and Mehrshad, 2021), where they contribute significantly to global element fluxes through regulation of biogeochemical cycles. The distribution, density, and composition of microbial communities in aquatic sediments arise from multiple environmental processes that interactively create microbial niches. In contrast to the global ocean, where microbial taxa distributions are mainly affected by large-scale or global environmental factors, continental habitats are patchier and local processes such as geological and ecological events exert specific constraints on the assembly of microbial communities. Microorganisms recovered in lacustrine deposits are broadly assumed to reflect open aquatic ecosystems with typically high phylogenetic diversity and active metabolisms at the time of deposition, whereas at the pelagic-benthic transition zone, also called sediment-water interface, geochemical conditions drastically shift towards anoxia in the sediments. As sediments accumulate, microorganisms undergo growth-based selection paralleled by depletion of substrates. Thereby certain populations persist while communities are increasingly becoming confined, isolated and inactive. Because of this, the distribution of sedimentary bacterial and archaeal DNA is influenced and controlled by variable accumulation, turnover rates and preservation processes that act over short (seasonal, decadal) and longer (geologic) timescales.

Lacustrine sediments that accumulate over geologic timescales tend to form stratified archives that can reflect past regional climatic or local trophic conditions and biogeochemical processes, where specific microorganisms have thrived in response to, for example, resources, ecological processes and environmental constraints. Microbial responses to short-term environmental changes are currently a topic of increasing attention as anthropogenic disturbances have been found to alter aquatic conditions on a large scale (Jane et al. 2021). Because microbial communities drive key processes in biogeochemical cycles, they stand at the base of ecosystem functioning (Rousk and Bengston, 2014). Therefore, their physiological acclimation to environmental stress and feedback to higher trophic levels can help restore or, conversely, further degrade aquatic conditions and ecosystems. For instance, lakes act as significant components of the carbon pump as they accumulate large amounts of organic carbon in their sediments. Even if most lacustrine organic matter (OM) is terrestrial in origin and thereby assumed to be recalcitrant, sediment-dwelling prokaryotes have the potential to convert a significant but variable portion of this buried organic matter into methane and carbon dioxide that can be emitted to the atmosphere. Geochemical composition, physical regime, temperature, and sedimentation rate are some of the variables that exert significant influence on the pathways and rates of OM burial and degradation in lakes (Dean and Gorham, 1998; Mendonça et al., 2017). This significant role of microorganisms as OM degraders also pertains to more variable, sometimes extreme, lacustrine environments, such as soda lakes (Zorz et al., 2019), salt lakes (Vavourakis et al., 2018), volcanic lakes (İnceoğlu et al., 2015), thermokarst lakes (In't Zandt et al., 2020), as well as periglacial (Anesio et al., 2017), seasonally (Thomas et al., 2019) and permanently frozen (Li and Morgan-Kiss, 2019) lakes, or anthropogenically impacted systems, such as acidic mining lakes (Quatrini and Johnson, 2018).

Currently, there is no universal answer to the actual relationships between the presence of microorganisms in lacustrine systems and the physical and geochemical processes that characterize their sediments as microbial habitats. A thorough and spatially resolved characterization of sediment-living microorganisms in terms of abundance, diversity and metabolic traits can accordingly shed light on nutrient cycling, OM degradation and redox processes during burial and many other biogeochemical

processes. Compiling sedimentary DNA (sedDNA) data on lacustrine sediment microbiomes from a wide range of environmental and geochemical conditions will provide information on microbial ecosystem functioning in terms of core taxa, in response to anthropogenic perturbations and changing environmental conditions over recent geologic timescales.

In an effort to disentangle the significance and origin of prokaryotic sedDNA, this chapter describes taxonomic assemblages and metabolic traits of lacustrine microbiomes from source to sink and describe characteristic shifts in microbial functional guilds that develop during burial and subsequent sediment aging that shape the geochemical zonation. We further attempt to trace processes of microbial assembly and selection with increasing sediment age that foster an extant and persistently active, though less diverse, microbial biosphere even at great depths where thermodynamic conditions approach the limits for life. In order to correlate past physico-chemical processes in lakes to the stratigraphic distribution of microorganisms, we will also discuss specific methodological aspects that make best use of this prokaryotic sedDNA. We will briefly present an aseptic sampling strategy tailored for field operations and discuss how these can be efficiently adopted and modified to characterize extended sedDNA records. The chapter serves as an introduction for how prokaryotic sedDNA in lacustrine sediment archives can inform about biogeochemical cycles and their dynamic change over variable timescales.

Assembly of lake sediment microbiomes

Biogeographic patterns of microbial distribution in terms of presence, abundance, taxonomic diversity and functions principally arise from four basic environmental processes that shape microbial consortia (Hanson et al., 2012; Hanson, 2017). This includes adaptive emergence of new genetic variation in the environment under scrutiny by evolutionary processes (diversification); passive transport of viable microorganisms during watershed runoff or river flooding (dispersal); species interactions related to, for example, competition for resources such as nutrients, organic and inorganic substrates (selection); and stochastic changes in community composition resulting from isolation, turnover, and replacement of the active community, with reduction of genetic richness during burial (drift). The development and increased availability of high-throughput sequencing technologies over the last decade have broadened the field of ecology to now encompass the composition, phylogeny, biogeography as well as functional and metabolic attributes of the subsurface biosphere (Orsi et al., 2013; Salazar et al., 2019; Vuillemin et al., 2019a; 2020a; Pearman et al., 2022a). Advancing sequencing technologies now allow to build global catalogs of microbiomes and their communities across Earth, and to investigate in particular the subsurface biosphere and microbial dark matter (Thompson et al., 2017; Nayfach et al., 2021).

In the global ocean, microbial niches and biogeographical patterns are strongly influenced and controlled by large-scale hydrodynamic factors and isolation of water masses (DeLong and Pace, 2001; Sunagawa et al., 2015) and this also applies to the sediments in terms of distance from the shore, surface ocean productivity, and depositional rates and redox conditions (Kallmeyer et al., 2012; Hoshino et al., 2020). In comparison, continental habitats rather reflect the local history of geological events, resulting in a much more geographically constrained and dynamic biogeographical distribution patterns (Pavoine and Bonsall, 2011; Nemergut et al., 2011). In theory, sedDNA originates from multiple sources contributed from interconnected aquatic habitats, e.g. outflows, rivers, water column, shallow sediment (Zwart et al., 2002; Oliveira et al., 2015; Tang et al., 2020). Considering a series of climatic, hydrological, geochemical and depositional events, the combination of these four basic assembly processes exerts constraint on the composition and functions of microbial communities (Niño-Garcia et al., 2016; Paver et al., 2020), with selective environmental pressures determining the subsequent local growth of microorganisms (Lacap et al., 2011). Dispersed taxa that are either passively buried or

actively grow in lake sediments thereby represent a potential record of past source-to-sink processes, suggesting that the distribution of microbial features along lake stratigraphic deposits reflects broad ecological processes (Gugliandolo et al., 2016) and environmental changes (Pearman et al., 2020; 2023). By mapping the variability of lacustrine microbiomes across a wide range of environmental conditions, environmental "omics" can advance our understanding of microbial ecosystem functioning at both the local and global scale (Escalas et al., 2019). Ultimately, the systematic investigation of lacustrine microbiomes at the time of sampling and in their stratigraphic context (Hall et al., 2018) makes it possible to define core community subsets across very different lacustrine ecosystems (Gibbons and Gilbert, 2015; Ruiz-González et al., 2017).

Lacustrine stratigraphy and preservation of sedimentary DNA

In lacustrine ecosystems, sediments that accumulate over time can, at least in theory, reflect trophic conditions and biogeochemical processes at the time of deposition, i.e. conditions where specific microorganisms thrived in response to available resources and environmental constraints (Fig. 1A). Lacustrine sediments thereby record and reflect past and recent climatic conditions while providing at the same time a wide range of ecological niches for actively growing contemporary microorganisms. Geomicrobiological investigations of extensive lacustrine records recovered through scientific drilling supported the hypothesis that microbial features correlate with contrasting climatic and sedimentological context (Glombitza et al., 2013; Vuillemin et al., 2013a, 2016a; Holm et al., 2020). Because substrates accumulating in sediments exert selective pressure during the initial phase after deposition (Fig. 1A), in-lake processes underscoring the deposition of such substrates in essence define the degree to which the lake floor can be colonized by prokaryotes (Vuillemin et al., 2014a), thereby potentially defining microbial community shifts across different lacustrine environments and climatic periods (Ariztegui et al., 2015). Prokaryotic sedDNA can thus be developed into a novel biomarker for linking microbial communities and biogeochemical cycles in sediments to past ecological processes recorded by lacustrine archives (Garner et al., 2020).

For Holocene time series, lake ecosystem function and characteristics have been successfully reconstructed using ancient sources of eukaryotic planktonic DNA (Coolen et al., 2004; Capo et al., 2021a; Kisand et al., 2018), enabling backtracking of vegetation in the watershed (Parducci et al., 2015; 2017; Alsos et al., 2018), lake colonization by freshwater fishes (Nelson-Chorney et al., 2019), primary production in the water column (Stoof-Leichsenring et al., 2015) and recent anthropogenic influences on food webs (Li et al., 2019a; Barouillet et al., 2023). In comparison, prokaryotic sedDNA essentially originates from a combination of inputs from the catchment, primary production and microbial secondary production in the water column whereas sediments as a whole feature a combination of such imported allochthonous and autochthonous DNA alongside actively growing sediment microbiota (Fig. 1B). The direct impact of environmental change on the distribution and diversity of microbial communities in the lacustrine subsurface has been documented for the Late Glacial (Vuillemin et al., 2018a; Thomas et al., 2020), Holocene transition (Coolen et al., 2008; Møller et al., 2020) and in modern times, e.g. Medieval Climate Anomaly, Little Ice Age (Vuillemin et al., 2013a; Garcia-Lopez et al., 2021), with a special focus on the Anthropocene (Cai et al., 2018; Han et al., 2020). However, there are still challenges in accurately interpreting prokaryotic sedDNA in relation to the dynamic changes in lake communities (Barouillet et al., 2023). Because sediment archives encompass a living subsurface biosphere, the "ancient" prokaryotic sedDNA pool that they contain is constantly being degraded and recycled over time, and metabolic activities therein may skew our interpretations of the

stratigraphy (Fig. 1B). Different fractions of sedDNA are thereby subject to variable degrees of accumulation, turnover and preservation along lacustrine stratigraphic sequences.

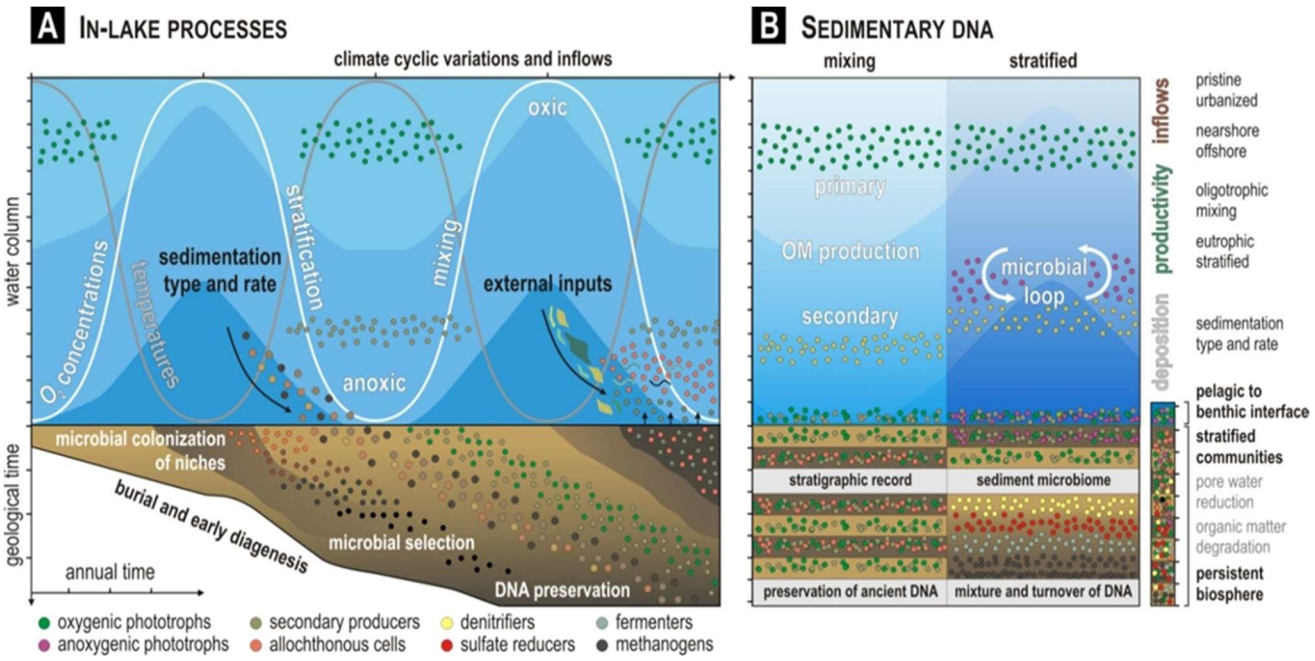

Figure 1. **Biotic and abiotic in-lake factors shaping sedimentary niches and their colonization by microbial communities over time. (A)** In-lake processes, such as seasonal variations in temperature, oxygen level, as well as external inflows, OM production, sedimentation rate and OM content will result in sediment strata that are differently colonized by microorganisms. **(B)** SedDNA accumulates over time from multiple environmental sources that, once identified, can be indicative of catchment, in-lake and sediment processes. External sources of DNA preserved in the sediment can be considered ancient and thereby of the same stratigraphic age as the sediment, whereas the degree of sediment colonization by resident microbial populations varies according to the substrate initially deposited in the corresponding layers (i.e. pore water ions, OM types). While substrate depletion results in selective survival of taxa, it also induces a replacement of living cells and turnover of sedDNA whose composition then gradually departs from the time of deposition.

Buried alive in lacustrine sediment archives

In lakes, depositional processes start with particle aggregation, flocculation and subsequent sinking of "lake snow" (Grossard and Simon, 1998). Pelagic OM aggregates are rapidly colonized and partially degraded by heterotrophic bacterial communities (Schweitzer et al., 2001) which tends to decrease the efficiency of carbon burial in lake sediments (Bižić-Ionescu et al., 2018). Depending on the regime, depth, and geochemical conditions of the water column, a succession of aerobic and anaerobic redox processes takes place during particle settling (Grossart et al. 1997; Lu et al, 2013; Li et al., 2021), resulting in early replacement of cells (Reiche et al., 2011) and DNA turnover (Torti et al., 2015). Prior knowledge of microbial diversity in the water column is thus key to discriminating allochthonous, and possibly ancient sources of sedDNA for environmental reconstructions, from those that are autochthonous to the sediment (Garner et al., 2020). Upon deposition at the sediment-water interface, local geochemical conditions exert selective pressure on the growth of microorganisms and thereby shape the composition of the viable microbial communities emerging and accumulating in the sediments. From the sediment-water interface down into the first layers of the sediment, microbial biomass production experiences an exponential reduction in cell density and generation times (Haglund et al., 2003). As sediments accumulate, microbial metabolism slows down along with a concomitant depletion of electron acceptors and decreasing reactivity of organic substrates (Jørgensen and Marshall, 2016). This gradual decrease in bioavailable substrates and cell generation times results in a

"depauperate horizon" (Wurzbacher et al., 2017) reflecting a selective change in community composition towards a so-called "deep biosphere assembly" (Walsh et al., 2016; Starnawski et al., 2017) that can still sustain metabolic activity over geologic timescales (Vuillemin et al., 2020a; 2020b).

Because prokaryotic sedDNA is a combination of ancient sources and active cells, uncertainties remain about the signal extractable from molecular inventories and the contribution of past and active communities to the sedimentary record (Stoeva et al., 2014; Pearman et al., 2022a). Depending on the changing metabolic constraints after sediment deposition and burial, prokaryotic sedDNA experiences different degrees of preservation depending on whether it persists intracellularly in living, albeit metabolically less active, and dormant cells (Ellegaard et al., 2020), or extracellularly after cell lysis as a free fraction or adsorbed to mineral surfaces (Torti et al., 2015; Vuillemin et al., 2017). Few studies have so far quantified the relative influence of initial environmental factors in regulating the final composition of total prokaryotic sedDNA in the sediment (Pearman et al., 2022b; Thorpe et al., 2022), and for lacustrine systems there is limited access to data for establishing a robust relationship between their environmental context and resident microbes that prevail over extended stratigraphic records (Ariztegui et al., 2015; Vuillemin et al., 2018b; Thomas et al., 2020).

Environmental fluctuations in lacustrine systems generate microheterogeneity and patchiness along the sediment stratigraphy, potentially contributing allochthonous sources of sedDNA and terrestrial OM in sporadic strata, or massively disrupting microbial structure at the lake floor (Brasell et al., 2021), possibly also modifying diffusion processes over sediment depth profiles. Extensive comparisons of community composition across sediment strata are thus required to benchmark the approach and evaluate whether sedDNA derived from prokaryotic organisms can be used to infer climatic and environmental conditions at the time of deposition (Bischoff et al., 2013; Holm et al., 2020; More et al., 2019). The parallel use of alternative (non-DNA) paleoenvironmental proxies is still recommended to identify and attribute prokaryotic sedDNA sources shaped by catchment or water body conditions at the time of deposition (Orsi et al., 2017; Vuillemin et al., 2016a, 2016b; More et al., 2019; 2021).

Taxonomic assemblages and metabolic guilds from source to sink

Allochthonous versus autochthonous microorganisms in lake sediments

Environmental processes: Dispersal, dormancy and resuscitation of microbial seed banks

Prokaryotic cells derived from terrestrial and aquatic sources are subject to different degrees of preservation and dormancy (Lennon and Jones, 2011) and often constitute a dominant fraction of sedDNA in aquatic systems (Aanderud et al., 2016; Vuillemin et al., 2017). Such microbial seed banks include active, viable but dormant cells, and resting stages (e.g. cysts, endospores, exospores, myxospores, akinetes), either transported as particulate OM from the catchment (e.g. soil bacteria) or emerging as planktonic aggregates (e.g. primary and secondary producers) that sink to the lake floor, that can be considered allochthonous from a sediment perspective (Tang et al., 2020). Dormant cells displaying sufficient metabolic flexibility can potentially be resuscitated outside of their preferred habitats and become active in the water column or sediment. The remaining dormant cells that are not resuscitated in the sediment environment only experience weak or no selection during burial (Lennon et al., 2021). Thus, microbial resting stages are ubiquitous in anoxic sediments (Wunderlin et al., 2014a), whereas dead cells and those that do not produce persistent resting stages typically lyse, senesce and in the process provide labile substrates for growth and expansion of active communities responsible for replacement processes (Wurzbacher et al., 2017; Pearman et al., 2021). For this reason,

microbiomes at the sediment-water interface are expected to initially reflect an open geochemical system that displays high phylogenetic diversity and metabolic activity. As the sediments become isolated and undergo aging, this diversity is purged and depleted (Martiny et al., 2006; Walsh et al., 2016).

To accurately link diverse microbial communities to their corresponding habitats and geochemical niches, a suite of functional marker genes (Fig. 2) reflective of metabolic traits and processes inherent to specific sediment settings or geochemical conditions can be investigated in parallel to taxonomic ribosomal RNA (rRNA) genes, enabling analysis of microbial guilds and ecological functional groups (Green et al., 2008). Since microbial guilds are never monophyletic (Boucher et al., 2003; Falkowski et al., 2008), taxonomic and functional genes are studied using a combination of amplicon sequencing, quantitative PCR (qPCR) assays, metagenomics (i.e. total DNA) and metatranscriptomics (i.e. total RNA) to characterize and quantify their functional diversity and ensure that the corresponding metabolic potential is present and realized (Perez-Garcia et al., 2016).

Starting with the watershed, members of the phyla Acidobacteriota, Actinobacteriota, Firmicutes and Verrucomicrobiota are all major components of the soil microbiome known to produce resting stages (Janssen et al., 2002; Paul et al., 2019). These persisting cells can be mobilized from terrestrial soils and hydrologically imported to lacustrine systems, especially during periods of high precipitation or floods (Crump et al., 2012; Ruiz-González et al., 2015). Although aerobic heterotrophs among remobilized resting stages often actively colonize planktonic aggregates in the water column, once deposited at the lake floor they undergo rapid replacement below the sediment-water interface to persist only as dormant cells, thus constituting rare taxa (Cardman et al., 2014; Ren et al., 2022). In contrast, allochthonous exospores (Actinobacteriota) and endospores (Firmicutes) from anaerobes imported and sedimented in lakes can only resuscitate in the deeper anoxic layers (Aüllo et al., 2013; Cupit et al., 2019). Furthermore, depending on OM productivity, light penetration, depth and redox zonation of the water column (Pearman et al., 2021), prokaryotic photoautotrophs (i.e. primary producers) can evolve both as planktonic and benthic colonies and settle actively at the lake floor (Pearman et al., 2022a). Akinete-forming Cyanobacteria (Ellegaard and Ribeiro, 2018) and obligate anaerobic Chlorobia (Gregersen et al., 2009) preserved in the sediment can later act as indicators of past productivity (Pearman et al., 2022b) and stratification events (Coolen and Overmann, 2007). It has been suggested that members of Planctomycetota genera (e.g. *Phycisphaera*, *Pirellula*) and other heterotrophs in the microbial loop act as secondary producers (e.g. Chloroflexota, Bacteroidia, Actinobacteriota) and scavengers of collapsing or senescent algal blooms (Lage and Bondoso, 2014), resulting in the overrepresentation of mixotrophs over phototrophs in the sedDNA pool (Kurilkina et al., 2016; Vuillemin et al., 2017). Moreover, oxic conditions at the lake floor allow benthic macro- and microfauna to bioturbate the sediments which highly increases replacement and turnover rates of sedDNA (Zeng et al., 2014). Although subsequent sediment anoxia selects against the main microbial populations seen in the water column, microaerobic and mixotrophs can nevertheless persist during the initial stage of burial and dwell over longer timescales, i.e. tens (Vuillemin et al., 2018a) or even hundreds of thousands of years (Thomas et al., 2020).

Taxonomy: Primary versus secondary producers in the microbial loop

Primary producers: In aquatic systems, Cyanobacteria are among the main prokaryotic primary producers that can be the cause of toxic blooms and create negative feedbacks on the water column, with excess ammonia release and oxygen depletion during bloom collapse and senescence (Huisman et al., 2018). Some important features among Cyanobacteria identified in sedDNA assemblages relate

to their lifestyle and ecology, including the capacity to fix nitrogen (i.e. diazotrophy), produce neurotoxins, perform both oxygenic and anoxygenic photosynthesis (i.e. with and without oxygen production), persist and grow under microoxic to sulfidic conditions (Hamilton et al., 2018; Block et al., 2021), and form colonies or akinetes (i.e. resting stages) (Legrand et al., 2016; Ellegaard and Ribeiro, 2018). Taxonomic analysis of cyanobacterial sedDNA has been used to determine shifts in lake salinity, such as the postglacial re-connection of the paleo-freshwater Antarctic Ace Lake and subsequent development of modern-day brackish conditions based on the first occurrence of the pelagic cyanobacterium *Synechococcus* strain Ace (Coolen et al., 2008). In stratified aquatic systems where light penetrates down to the chemocline (Gregersen et al., 2009; Storelli et al., 2013), anoxygenic aerobic and anaerobic phototrophs (purple sulfur, purple non-sulfur, green sulfur, green non-sulfur bacteria, Heliobacteriaceae) can actively grow under oxygen minimum, ferruginous and sulfidic conditions, oxidizing either dissolved iron or sulfur in close proximity to the chemocline (Madigan, 2003; Crowe et al., 2008). Accordingly, increased representation of sedDNA sequences preserved from taxa among green sulfur Chlorobia, green non-sulfur Chloroflexales, purple alphaproteobacterial Rhodobacteraceae or purple sulfur gammaproteobacterial Chromatiaceae can be indicative of water column stratification and shifts in salinity (Coolen and Overmann, 1998, 2007; Asao et al., 2011). Such assemblages of phototrophic taxa are known to constitute the upper layers of stromatolites and to form biofilms (Wong et al., 2015).

However, the mere presence of pigments involved in phototrophy does not necessarily imply a significant role in primary production as some pigment-producing bacteria (e.g. among Planctomycetota, Bacteroidia, Chloroflexota, Alphaproteobacteria) may be active as secondary producers in the microbial loop via photoheterotrophy and mixotrophy (Eiler, 2006). Phototrophy among prokaryotes rely on specific pigments used to harvest light at different wavelengths (Scheer, 2006), such as chlorophyll variants (*Chl-a*, *Chl-d*, *Chl-f*) and bacteriochlorophyll (*Bchl-a* to *Bchl-e*) (Suzuki et al., 1997). Some other pigments are associated exclusively with anoxygenic photosynthesis (*puf*M genes) (Pfennig and Trüper, 1992) and some of the genes encoding for these pigments can be compared to the corresponding fossil pigments along stratigraphic records (Leavitt and Hodgson 2001; Vuillemin et al., 2016a). Carbon fixation among phototrophs proceeds mostly via the Calvin-Benson-Bassham (CBB) cycle, with genes encoding the ribulose-1, 5-diphosphate carboxylase (*RuBisCO*) and some specific cytochromes (e.g. *cbbL*, *cbbS*) (Gibson et al., 2002). However, *RuBisCO* genes can also operate in chemoautotrophic dark carbon fixation in the absence of light (Canfield et al., 2005). To interpret the detection of such genes, one has to place observations in an environmental context and also consider taxonomic assignments (Hügler and Sievert, 2011). Additionally, while mixotrophs produce photoactive pigments, such as bacteriorhodopsins, proteorhodopsins and various carotenoids (Béjà et al., 2001; Eiler, 2006), they cannot use CO_2 as their sole carbon source.

Secondary producers: As OM aggregates from pelagic primary production sink through the water column, a microbial loop is established via mixotrophic and heterotrophic interactions that fuel a complex network of prokaryotes and protists (Ryszard et al., 2009; Xing et al., 2020). Depending on seasonal variations and trophic levels (Lewis 2009; Li and Morgan-Kiss, 2019), the microbial loop can drive intense nutrient cycling and heterotrophic processes leading, in turn, to rapid oxygen depletion in the hypolimnion. Subsequently, some taxonomic groups known to evolve as micro-aerobes can thrive in the oxycline - where oxygen concentrations are low - and settle at the sediment-water interface (Vuillemin et al., 2017) where they feed on sinking OM and reduced forms of nutrients diffusing out of the underlying sediment.

Some Planctomycetota (e.g. *Phycisphaera*, *Pirellula*, *Rhodopirellula*) are ubiquitous across a broad range of geochemical conditions (Storesund et al., 2020) and produce carotenoids that place them at the intersection between primary and secondary producers (Kallscheuer et al., 2019). These populations can anchor their cells to OM aggregates or form biofilms at the sediment-water interface (Lage and Bondoso, 2014), produce sulfatases involved in the degradation of complex sugars or derive energy from ammonia, either aerobically (i.e. nitrification) or anaerobically (i.e anammox). Finally, the Planctomycetota can form cysts in shallow sediments that persist long after burial (Wiegand et al., 2021).

Similar traits are reported for filamentous non-phototrophic Chloroflexota, including aerobic and facultative anaerobic representatives (e.g. *Nitrolancea*, *Caldilinea*) and obligate anaerobic taxa (e.g. *Anaerolinea*), displaying the ability to form biofilms, degrade biopolymers, and ferment carbohydrates and drive various nitrogen transformation processes (Speirs et al., 2019). These fermenters are known to thrive in shallow sediments.

The class Bacteroidia contains pelagic and benthic members, some of which producing photoactive pigments, degrading algal matter and assimilating carbohydrates via aerobic, microaerobic and anaerobic glycolysis (González et al., 2008; Dalcin Martins et al., 2021) - that play a key role in the turnover of sinking OM after algal blooms, potentially contributing to oxygen depletion in the water column (Vuillemin et al., 2022a). As micro-oxic conditions develop (100-60 μM), they can shift to micro-aerobic respiration with metabolic capacity for uptake of dissolved OM and anaplerotic reactions (i.e. non-autotrophic CO_2 fixation) replenishing the tricarboxylic acid (TCA) cycle (Fernández-Gómez et al., 2013; Krüger et al., 2019). Although they do not produce resting stages, some taxa can sustain activity and growth under anoxic conditions (Philipps et al., 2021) and persist in the sediment long after burial (e.g. *Pontibacter*, *Tenacibaculum*, *Imtechella*) (Vuillemin et al., 2022a). The protein-encoding genes superoxide dismutase (*sod*, i.e. H_2O disproportionation), and cytochrome-c oxidase (*cox*, i.e. aerobic respiration) are expressed during aerobic respiration, whereas those involved in cytochrome bd2 ubiquinol (*bd2*) and cytochrome cbb3-type (*cbb3*) oxidases are indicative of microaerobic respiration (Kalvelage et al., 2015).

Diazotrophs and nitrifiers: The ability to fix atmospheric nitrogen is carried out, mostly by Cyanobacteria, Actinobacteriota, Firmicutes and Alphaproteobacteria encoding by a complex of nitrogen fixation genes (*nif*) including homologous heterometal (Mo, V and Fe) nitrogenases responsible for the reduction of N_2 to NH_3 (Hu and Ribbe, 2015). Nitrifiers, which are known to thrive in soils, in the vicinity of oxyclines and oxic sediments (Vuillemin, 2023), constitute a metabolic guild involved in the recycling of inorganic fixed nitrogen (i.e. NH_4^+, NO_3^-, NO_2^-). By preventing a decrease in TN:TP ratio, this metabolic guild can adjust lake trophic status (Downing and McCauley, 1992), especially in systems with long residence time (They et al., 2017). Aerobic ammonia oxidizers are often considered to be chemolithoautotrophs although heterotrophy on dissolved organic carbon has also been observed (Aylward and Santoro, 2020). This metabolic guild includes several archaeal candidates among the class Nitrososphaeria, such as *Nitrosopumilus*, *Nitrososphaera*, *Nitrosotalea*, *Nitrosarchaeum* and *Nitrosomarinus* sp. (Jung et al., 2022), as well as genera among the Gammaproteobacteria, including *Nitrosomonas*, *Nitrosospira*, *Nitrosolobus*, *Nitrosovibrio* and *Nitrosococcus* sp. (Soliman and Eldyasti, 2018). Some well known nitrite oxidizers further include *Nitrospina*, *Nitrospira*, *Nitrococcus*, and *Nitrobacter* sp. among Nitrospinota, Nitrospirota, Gamma- and Alphaproteobacteria, respectively (Ge et al., 2015). Ammonia monooxygenase (*amo*) and nitrite oxidoreductase (*nxr*) (Rani et al., 2017; Kitzinger et al., 2020) are involved in aerobic nitrification (Fig. 2A).

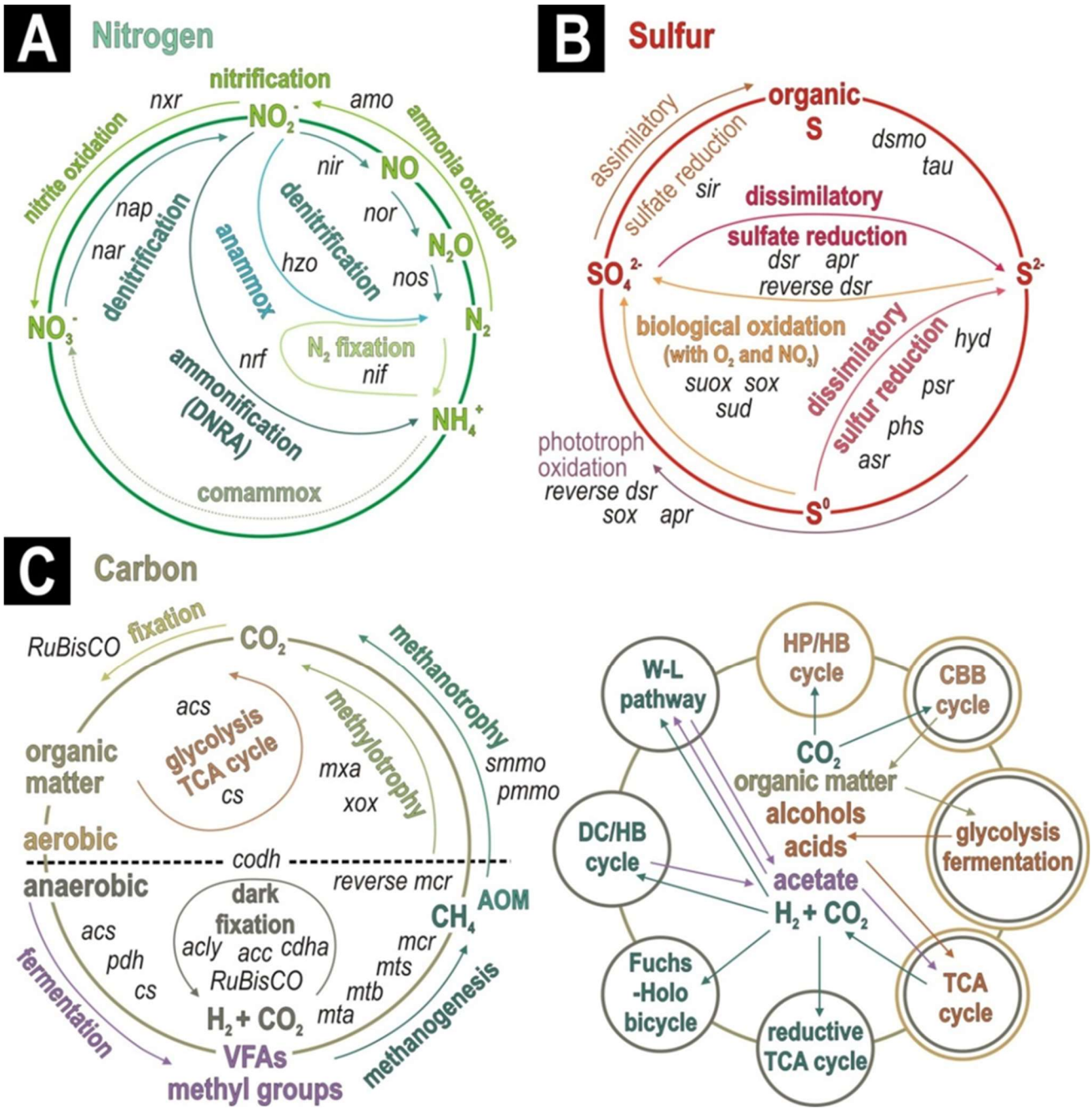

***Figure 2*. Biogeochemical cycling of nitrogen, sulfur and carbon and the main corresponding functional marker genes and pathways. (A)** Nitrogen cycling functional genes related to processes of nitrogen fixation (*nif*), nitrification (*amo*, *nxr*), anaerobic ammonia oxidation or anammox (*hzo*), dissimilatory nitrate reduction to ammonium (DNRA, *nrf*), and denitrification (*nar*, *nap*, *nir*, *nor*, *nos*). **(B)** Sulfur cycling functional genes related to processes of sulfur (*sox*, *suox*, *sud*, reverse *dsr*, *apr*) and organic sulfur (*dsmo*, *tau*) oxidation, assimilatory sulfite reduction (*sir*), dissimilatory sulfate (*dsr*, *apr*) and intermediate sulfur species reduction (*asr*, *phs*, *psr*, *hyd*). **(C)** Carbon cycling functional genes related to aerobic and anaerobic processes of carbon fixation (*RuBisCo*, *acly*, *acc*, *codh*, *cdha*), glycolysis and fermentation (*acs*, *cs*, *pdh*), methylotrophy (*mxa*, *xox*), methanotrophy (*smmo*, *pmmo*, reverse *mcr)* and methanogenesis (*mta*, *mtb*, *mts*, *mcr*), followed by metabolic pathways of autotrophic carbon fixation (Berg, 2011) including the light and dark Calvin-Benson-Bassham (CBB) cycle, the aerobic 3-hydroxypropionate/4-hydroxybutyrate (HP/HB) and anaerobic dicarboxylate/4-hydroxybutyrate (DC/HB) cycle, the reductive tricarboxylic acid (TCA) cycle, the Wood-Ljungdahl (W-L) pathway (i.e. acetogenesis, methanogenesis) and Fuchs-Holo (or 3-hydroxypropionate) bicycle that can be coupled to glycolysis, fermentation and TCA cycle via production and uptake of metabolic intermediates. For gene abbreviations and corresponding KEGG orthology, see Table 1.

Table 1. Marker gene subunits for nitrogen, sulfur and carbon cycling, their corresponding functional orthologs to the KEGG database, and published references for targeted primer amplification and identification in metagenomes.

Nitrogen cycling	***KEGG orthology***	***References for primers***
nifA: nitrogen fixation	K02585 to K02588	Pang et al. 2019
amoA: ammonia monooxygenase	K10944	Vuillemin et al. 2019a
nxrA: nitrite oxidoreductase	K00370-K00371	Rani et al. 2017
narG: nitrate reductase	K00367, K00370-K00371, K00373-K00374	Dong et al. 2009
napA: periplasmic nitrate reductase	K02567-K02568, K02570-K02571	Dong et al. 2009
nirS, nirK: copper-containing nitrite reductase	K00362-K00363, K00368, K15864	Braker et al. 2000
nrfA: ammonia-forming cytochrome nitrite reductase	K03385, K15876	Pang et al. 2019
norB: nitric oxide reductase	K04561, K02305, K02448, K04747, K04748	Heylen et al. 2007
nosZ: nitrous oxide reductase	K07218, K19342, K19339, K00376	McGuirl et al. 2001
hzo: hydrazine oxidoreductase (custom primers F1-R1)	K20935	Kong et al. 2013
nfsA, nfsB, snrA, nbzA, pnrA: nitroreductases	K15976, K10678, K10679	Roldán et al. 2008
Sulfur cycling	***KEGG orthology***	***References for primers***
suox: sulfite oxidase (no PCR primers)	K00387	Dahl, 2020
soxYZ: sulfur-oxidizing proteins	K17226, K17227	Dahl, 2020
sir: assimilatory sulfite reductase (no PCR primers)	K00392, K00380, K00381	Gisselmann et al. 1993
dsrA, dsrB: dissimilatory sulfite reductase	K11179 to K11181, K07236, K07237	Loy et al. 2009
aprA, aprB: adenylylsulfate reductase	K00394, K00395	Biderre-Petit et al. 2011
asrA: anaerobic sulfite reductase	K16950, K16951, K00385	Vuillemin et al. 2018b
phsA, psrA: thiosulfate/polysulfide reductase	K08352 to K08354	Wasmund et al. 2017
hydB: sulfhydrogenase	K17993 to K17995-K17996	Wasmund et al. 2017
dsmo: dimethylsulfoxide reductase (no PCR primers)	K07306 to K07308	Baltes et al. 2003
tauA: taurine dioxygenase	K02975, K19245	Wetzl et al. 2016
Methane cycling	***KEGG orthology***	***References for primers***
mxaF: methanol dehydrogenase	K23995	Heyer et al. 2002

xoxF: methanol dehydrogenase homologue	K23995	Taubert et al. 2015
pmmoA: particulate methane monooxygenase	K10944 to K10946	Inagaki et al. 2004
smmoX: soluble methane monooxygenase	K16157 to K16162	Heyer et al. 2002
mtaB: methanol CoM methyltransferase	K14080	Bose et al. 2008
mtbA: methylamine-specific CoM methyltransferase	K14082	Veit et al. 2005
mtsA: methylthiol-specific CoM methyltransferase	K16954	Tallant et al. 2001
mcrA: methyl-CoM reductase	K00399, K00401, K03421, K03422, K00402	Vuillemin et al. 2018b
Carbon assimilation pathway	***KEGG orthology***	***References for primers***
accA, accD: acetyl-CoA carboxylase	K01962, K01963	Freiberg et al. 2004
acsA: acetyl-CoA synthetase (glycolysis)	K01895	Gardner et al. 2006
cs: citrate synthase (TCA cycle) (*gtlA* primers)	K01647	Castro et al. 2012
acly: ATP-citrate lyase (reductive TCA cycle) (*aclA, AclB* primers)	K15230, K15231	Voordeckers et al. 2008
pdhA, pdhB: pyruvate dehydrogenase (fermentation)	K00161, K00162	Bao et al. 2021
codH: carbon monoxide dehydrogenase (W-L pathway) (CODHech primers)	K00198, K00193	Omae et al. 2021
cdhA, cdhB: acetyl-CoA synthase (W-L pathway)	K00192, K00194, K00197	Eggen et al. 1991
RuBisCO: ribulose-1,5-diphosphate oxidase (CBB cycle) (*cbbL primers*)	K01601-K01602	Chi et al. 2018

Stratified microbial communities in shallow subsurface sediments

Environmental processes: Imprints of successive respiration modes and fermentation

Although geochemical and depositional conditions exert initial control over the sedimentation and colonization of the lake bottom sediments by microorganisms (Fig. 1), selective growth of subpopulations on bioavailable substrates rapidly results in a mismatch between microbial characteristics and past lacustrine conditions during the early burial phase (Lacap et al., 2011). Pore water concentrations and availability of respiratory electron acceptors and other dissolved constituents, as well as the reactivity of sedimentary OM, are regarded as the main factors controlling the distribution and growth of microbial communities in aquatic subsurface sediments. As sediment accumulates and microorganisms are buried, the potential for exergonic metabolic reactions (i.e. Gibbs free energy) decreases with the sequential depletion of pore water oxidants during respiration (i.e. O_2, NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}, CO_3^{2-}) and the stepwise decomposition of bioavailable OM (McInerney et al., 2009). Expecting that microorganisms utilize the most energetically favorable respiratory electron acceptor available (Fig. 3A) and preferentially degrade the most labile OM sources (Fig. 3B), microbial communities stratify with respect to the gradual depletion of deposited substrates by "layering" metabolic guilds that experience selective growth over sediment depth profiles. The successive use of

electron acceptors during microbial respiration as well as their cryptic recycling (Fig. 3A) typically result in the strong vertical redox zonation within the sediment column (Frindte et al., 2015).

In anoxic habitats, stepwise degradation of labile OM can also proceed, but then by means of fermentation without the need for external electron acceptors. Such fermentative degradation of OM (McInerney et al., 2009) begins with hydrolysis (i.e. breakdown into soluble compounds), and goes on with acidogenesis (i.e. conversion into organic acids) and acetogenesis (i.e. conversion into acetate) coupled to methylotrophic and acetoclastic methanogenesis (i.e. substrate conversion into methane). Advanced stages of fermentation include heterotrophic dark carbon fixation via homoacetogenesis (Ryan et al., 2008) and hydrogenotrophic methanogenesis (Fig. 3B). These reactions lead to formation and buildup of volatile fatty acids (VFAs), dissolved inorganic carbon (DIC) and methane with concomitant accumulation of an array of increasingly oxidized substrates (i.e. alcohols, ketones, aldehydes, carboxylic acids) in the sediment (LaRowe and Van Cappellen, 2011).

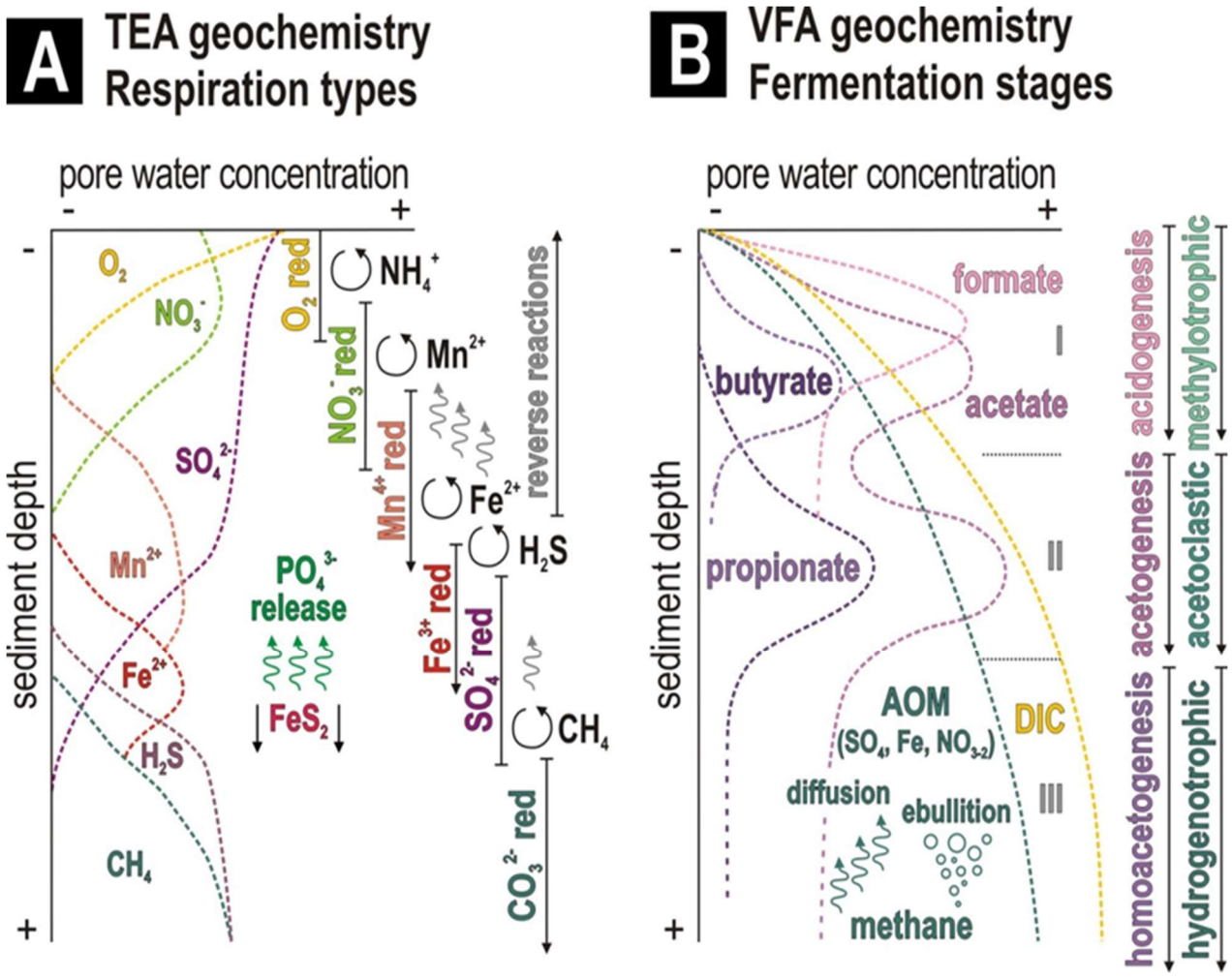

***Figure 3*. Idealized model of stratified sediment pore water geochemistry related to the respiration of terminal electron acceptors and anaerobic remineralization of organic matter.** (A) Successive respiratory use of terminal electron acceptors (TEA) according to available Gibbs free energy (i.e. O_2, NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}, CO_3^{2-}) leading to their gradual depletion in pore waters and increase in their reduced counterparts. Upward diffusion allows for reverse redox reactions (e.g. cryptic sulfur cycling, anaerobic oxidation of methane). (B) Fermentation stages involved in the production of volatile fatty acids (VFAs) as metabolic intermediates (I-III: acidogenesis, acetogenesis, homoacetogenesis), and paralleled methanogenic pathways (I-III: methylotrophic, acetoclastic, hydrogenotrophic) leading to stepwise remineralization of OM that results in buildup of methane and dissolved inorganic carbon (DIC) over depth. The increase and subsequent decrease of VFA concentrations with depth reflect their fermentative production and turnover mostly via syntrophy.

Fermentative decomposition of complex residual substrates (Wüst et al., 2009) can further proceed via cross-feeding on metabolic products (i.e. syntrophy). Syntrophs make use of fermentation byproducts as electron donors (LaRowe and Van Cappellen, 2011), and such metabolic partnerships arise from energetic constraints related to the depletion of labile OM (Orsi et al., 2020a). Syntrophic partnerships involve two or more interacting microbial populations whose complementary metabolisms enable the combined mineralization process to proceed and be thermodynamically favorable for all involved populations (Sieber et al., 2012). For example, syntrophic associations between fermenting bacteria and sulfate reducers, or methanogenic archaea, are based on the exchange of hydrogen between partners (Morris et al., 2013). The fermentative syntrophic metabolizer produces molecular hydrogen through substrate level phosphorylation (SLP) of VFAs (i.e. ATP production via fermentation) while the sulfate reducer, or methanogenic partner, consumes hydrogen (or formate) (Fig. 3B). Although interspecies hydrogen transfer is essential to syntrophs to make VFA fermentation energetically favorable, these reactions can also occur intracellularly without a syntrophic partner among homoacetogens (Wiechmann et al., 2020).

Charismatic microbial guilds in shallow sediments: Denitrifiers, sulfate reducers, syntrophs, methanogens

Denitrifiers: Denitrification starts in the oxycline and parallels the onset of anoxia. After oxygen has been depleted, denitrification is the second-most thermodynamically favorable respiratory process (Fig. 3A). This metabolism involves a stepwise reduction of NO_3^- to gaseous N_2O and N_2 as end products (Pessi et al., 2022). It is mediated by the respiratory (*nar*) and periplasmic (*nap*) nitrate reductase, nitrite reductase (*nir*), nitric oxide reductase (*nor*), and nitrous oxide reductase (*nos*) (Braker et al., 2000; Dong et al., 2009, Dalsgaard et al., 2014). The more reduced forms of inorganic nitrogen are respired in the final steps of denitrification (*nor*, *nos*) and result in a gaseous loss of fixed nitrogen (Einsle and Kroneck, 2004; Lam and Kuypers, 2011). Denitrifiers are common in soils, aquatic oxygen minimum zones, surface sediments and other oxygen depleted ecosystems (Tiedje, 1994). Many taxa among the Alphaproteobacteria can perform denitrification (e.g. *Paracoccus*, *Agrobacterium*, *Rhizobium*, *Azospirillum*, *Nitrobacter*), as well as within Gammaproteobacteria (e.g. *Nitrosomonas*, *Alcaligenes*, *Pseudomonas*, *Thiobacillus*, *Acidovorax*, *Limnobacter*) and Bacteroidia (e.g. *Flavobacterium*, *Cytophaga*, *Flexibacter*). It is important to note that this metabolic trait is not taxonomically conserved and can therefore not readily be inferred from taxonomic information. Dissimilatory nitrate reduction to ammonium (DNRA), or heterotrophic ammonification, often occurs concurrently with denitrification (Fig. 2A) and is encoded by the gene ammonia-forming cytochrome nitrite reductase (*nrf*) (Pang et al., 2019), while nitroreductases (*ntr*) mediate reduction of nitro-compounds (Roldán et al., 2008).

Sulfate reducers: Although the ability to use sulfate as a respiratory electron acceptor (sulfate reduction) is restricted to certain phylogenetic groups (Castro et al., 2000), many apparent sulfate reducers display metabolic flexibility and are also capable of fermentation to produce VFAs and hydrogen, thereby acting as important regulators of OM turnover (Plugge et al., 2011). Sulfate reducers are mostly affiliated with the phylum Desulfobacterota (e.g. *Desulfobacca*, *Desulfomonas*, *Desulfobacter*, *Desulfovibrio*, *Desulfococcus*, *Thermodesulfobacterium*), but also include some Firmicutes (e.g. *Desulfotomaculum*, *Desulfosporosinus*) and specific groups within the Nitrospirota (i.e. *Thermodesulfovibrio*), Thermodesulfobiota (i.e. *Thermodesulfobium*) and Halobacterota (i.e. *Archaeoglobus*) (Muyzer and Stams, 2008; Anantharaman et al., 2018). The canonical sequence of genes encoding proteins for respiratory reduction of sulfate to hydrogen sulfide (Fig. 2B; Table 1) is

dissimilatory sulfite reductase (*dsr*), adenylylsulfate reductase (*apr*), anaerobic sulfite reductase (*asr*), thiosulfate/polysulfide reductase (*phs*/*psr*) and sulfhydrogenase (*hyd*) (Wasmund et al., 2017).

Concomitant reactions of cryptic sulfur cycling and redox transformation of intermediate sulfur species (i.e. SO_3^{2-}, $S_2O_3^{2-}$, S_n^{2-}, S^0) are carried out by taxonomically and functionally diverse microorganisms, including denitrifiers and anoxygenic anaerobic phototrophs (van Vliet et al., 2021; Vigneron et al., 2021). Cryptic sulfur cycling is an enigmatic process in which intermediate sulfur species can be re-oxidized anaerobically, in theory in the presence of ferric iron (Holmkvist et al., 2011), via disproportion or "dismutase" (Fig. 2B). Some genes involved in the respiratory reduction of sulfur intermediates include the aforementioned genes: *asr* (i.e. SO_3^{2-}, sulfite), *phs* (i.e. $S_2O_3^{2-}$, thiosulfate), *psr* (i.e. S_n^{2-}, polysulfide chains), sulfhydrogenase (*hyd*) (i.e. S_n^{2-} and S^0, elemental sulfur). The metabolic functions driving sulfur dismutase in cryptic cycling remain unclear. Some genes involved in sulfur cycling have demonstrated reverse types, namely reverse sulfide dehydrogenase (*sud*), also known as bifurcating ferredoxin: NADP oxidoreductase or NADH-dependent reduced ferredoxin: NADP+ oxidoreductase (*nfn*) (Pereira et al., 2011), reverse dissimilatory reductase (*rdsr*), and reverse-acting adenylylsulfate reductase (*apr*) although they are mostly known to be expressed under (micro)aerobic conditions (Loy et al., 2009; Wasmund et al., 2017). The reduction of intermediate sulfur species with molecular hydrogen as electron donor is channeled via heterodisulfide reductase (*hdr*) as a hydrogenase with heme groups and iron-sulfur clusters (Hedderich et al., 1998). By being reversible (Bell et al, 2020), the confurcating-bifurcating electron transport chain involved in cryptic sulfur cycling can prevent the accumulation and precipitation of sulfide (Vuillemin et al., 2018b; Berg et al., 2019). However, because several genes involved in cryptic sulfur reactions are reversible and relate to aerobic or anaerobic functions, they are difficult to assign to a specific environmental context.

Syntrophs: Syntrophic partnerships consist of the "degraders" with fermenting capacity and the "consumers" that remove the excreted fermentation products (e.g. VFAs) so that the first part of the process can proceed with marginal gain of energy. The fermentative degraders are mostly found among Desulfobacterota (e.g. *Syntrophus*, *Geobacter*, *Smithella*, *Desulfovibrio*, *Syntrophothermus*, *Syntrophobacter*), Firmicutes (e.g. *Pelotomaculum*, *Sporotomaculum*, *Thermosyntropha*, *Ruminococcus*, *Syntrophomonas*, *Clostridium*) and some specific Crenarchaeota (i.e. *Ignicoccus*, *Pyrococcus*), anaerobic methanotrophic archaea (i.e. ANME I and II) and Chloroflexota (i.e. *Bellilinea*, *Longilinea*). The consumers that make use of hydrogen (or formate) produced in the first fermentation step are commonly sulfate reducers, methanogens and (homo)acetogens (McInerney et al., 2008; Morris et al., 2013). The consumption of VFAs (Fig. 3B) proceeds via acetate (i.e. $C_2H_3O_2^-$) kinase, propionate (i.e. $C_3H_5O_2^-$) kinase, butyrate (i.e. $C_4H_7O_2^-$) kinase and phosphotransacetylase which are all genes involved in the SLP of VFAs. Formate (i.e. CHO_2^-) is anaerobically oxidized via formate dehydrogenase (*fdh*). The redox complexes involved in interspecies electron transport are composed of several subunits and include, among others, the heterodisulfide reductase (*hdr*), NAD^+-reducing Ni-Fe hydrogenase (*hox*), with the Nuo and Rnf membrane complexes (McInerney et al., 2009; Yan and Ferry, 2018). However, the presence of these genes alone cannot robustly be used as markers for syntrophic metabolism.

In addition, hydrogenases catalyze the reversible oxidation of molecular hydrogen as energy and electron source that characterize many syntrophic associations. Metal-based and metal-free hydrogenases display specific sensitivity to the partial pressure of molecular hydrogen, and show different efficiencies in fermentative environments (Vignais et al., 2001) as increased hydrogen concentrations compromise certain hydrogenase activities (Skidmore et al., 2013). In order of decreasing sensitivity to hydrogen partial pressure, such hydrogenases include Fe-Fe hydrogenase

(*ddh*), Ni-Fe hydrogenase (*nfh*) with NAD-reducing hydrogenase (*hox*) used in oxidation of molecular hydrogen, and formate hydrogenlyase (*fhl*), coenzyme F420 reducing and non-reducing hydrogenase (*frh*), methyl-viologen hydrogenase (*mvh*) and heterodisulfide reductase (*hdr*) used in the production of molecular hydrogen.

Methanogens: Methanogens in lake sediments typically display succession patterns that reflect the type of carbon substrates that they assimilate (Fig. 3B) as well as their tolerance to pore water sulfate and chloride concentrations (Vuillemin et al., 2014b). In the presence of pore water sulfate, sulfate reducers can outcompete methanogens for hydrogen. This causes hydrogenotrophic methanogenesis (detailed below) to be depressed under saline and brackish conditions (Liu and Whitman, 2008), that can only prevail in sulfur-poor freshwater lakes or below the sulfate-methane transition zone (Borrel et al., 2011). Twenty species of archaea have been identified as methylotrophic methanogens (e.g. *Methanohalophilus*, *Methanolobus*, *Methanococcus*). This group relies on methyl compounds such as methanol, methylated amines or methylated sulfides as substrates to produce methane. Thirteen of these are obligate methylotrophs (e.g. *Methanosphaera*, *Methanomicrococcu*s, *Methanococcoides*, *Methanomassilicoccus*, *Methanomethylophilus*). There are furthermore 9 genera of acetoclastic methanogens (e.g. *Methanoregula*, *Methanosarcina*, *Methanoculleus*) that utilize acetate to produce methane, only one of which is an obligate acetotroph (i.e. *Methanothrix*). Syntrophic acetate oxidation can sometimes replace acetoclastic methanogenesis (Fig. 3B) followed by hydrogenotrophic methanogenesis or homoacetogenesis (Dyskma et al., 2020). Hydrogenotrophic methanogens (e.g. *Methanospirillum*, *Methanoregula*, *Methanoplanus*, *Methanopyrus*, *Methanocalculus*, *Methanothermobacter*) oxidize H_2 and reduce CO_3^{2-} to produce methane. Although often found in syntrophic partnerships, they do not depend on them. Among the hydrogenotrophic methanogens, 38 genera can also assimilate formate to form methane, i.e. formatotrophs (e.g. *Methanolinea*, *Methanobacterium*, *Methanococcus*). Some methanogens are capable of performing multiple alternative methanogenic pathways and hence cannot be placed into a single category (Garcia et al., 2000). Finally, some uncultivated clades display an unexpected potential for methane production (Evans et al., 2015), these include the Verstraetearcheota (Vanwonterghem et al., 2016) and certain clades of Bathyarchaeia (Berghuis et al., 2019), which are the only cases of methane metabolism identified outside the phyla Euryarchaeota and Halobacterota (Söllinger and Urich, 2019). Functional genes involved in methane production target specific carbon sources (e.g. methanol, methylamine, methylthiol) and can be used to discriminate fermentation stages (Figs. 2C and 3B), for instance the methanol coenzyme M methyltransferase (*mta*), methylamine-specific coenzyme M methyltransferase (*mtb*), and methylthiol-specific coenzyme M methyltransferase (*mts*) that are involved in methylotrophy, or the methyl-tetrahydromethanopterin coenzyme M methyltransferase (*mtr*) in hydrogenotrophy (Table 1). The final step leading to methane production and release from the cell corresponds to methyl-coenzyme M reductase (*mcr*). Because certain archaea hold a partial methanogenic Wood-Ljungdahl (W-L) pathway (Baker et al., 2016; Orsi et al., 2020b), the *mcr* genes are the only valid marker for microbial methane production (Morris et al., 2014).

Vertical distribution of microbial taxa in recent sediments from two geochemically distinct lakes

To reconstruct past lacustrine environmental conditions, the taxonomic composition of prokaryotic communities was investigated by producing 16S rRNA gene amplicon data from recently deposited sediment (down to 1.5 m) from two lakes with contrasting hydrological regimes and geochemical conditions (Fig. 4).

Lago di Cadagno is a crenogenic meromictic lake located in the Swiss Alps at 1,921 m elevation above sea level (asl) (Del Don et al., 2001). Submerged saline springs flowing through the evaporites of the fractured bedrock supply the lake with high concentrations of SO_4^{2-}, which is reduced by sulfate reducers creating anoxic, sulfidic conditions in the monimolimnion (Berg et al., 2016) and underlying sediments (Berg et al., 2022). The upper 1.5 m sediment profile represents the last 3,500 years (0.4 mm × $year^{-1}$) and is composed of pelagic muds and mixed terrestrial deposits (Wirth et al., 2013). The prokaryotic assemblage of Lago di Cadagno sediments (Fig. 4A) can be interpreted as taxa derived from soil runoff (e.g. Actinobacteriota, Acidobacteriota); the oxic photic overlying zone (e.g. Cyanobacteria) and the anoxic sulfidic photic zone (e.g. Chlorobia). In addition, the assemblage includes aerobic (e.g. Nitrospirota), microaerobic (e.g. Bacteroidia) and anaerobic heterotrophs (e.g. Nanoarchaeota, Patescibacteria, Planctomycetota). In the sediment, stratified microbial guilds related to contrasting respiratory types (Fig. 3A) are predominant, with a succession from denitrifiers (e.g. Alphaproteobacteria) to sulfate reducers, (e.g. Desulfobacterota) and a few methanogens that are tolerant to sulfate (e.g. Euryarchaeota) combined with fermenters providing molecular hydrogen for methanogenesis (e.g. Firmicutes). The vertical succession of fermenters implies a stepwise degradation of organic substrates through primary (e.g. Acetothermia, Aminicenantia) and secondary (e.g. Caldatribacteriota, Chloroflexota, Bathyarchaeia) fermentation (Fig. 4A).

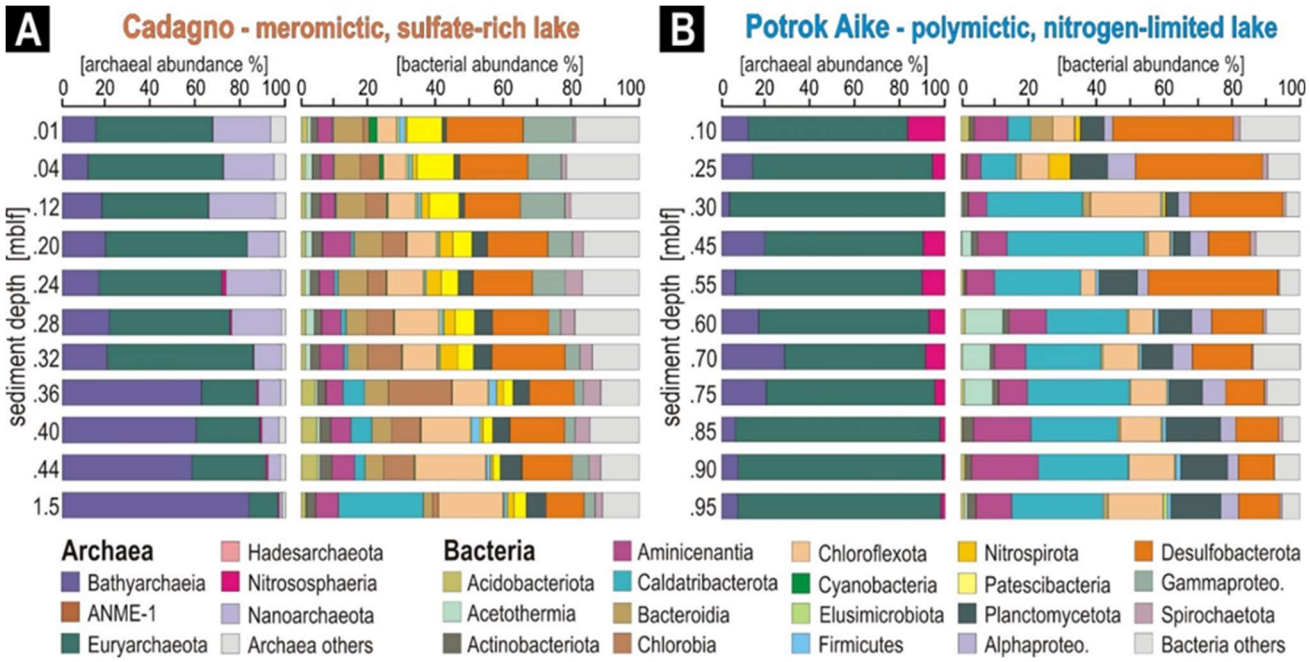

***Figure 4*. Layered microbial communities in surface sediments corresponding to contrasted lacustrine conditions. (A)** 16S rRNA gene diversity [relative %] for Archaea and Bacteria in the shallow sediment of Lago di Cadagno, a sulfate-rich permanently stratified alpine lake (modified after Berg et al., 2022). **(B)** 16S rRNA gene diversity [relative %] for Archaea and Bacteria in the shallow sediment of Laguna Potrok Aike, an endorheic, polymictic and nitrogen-limited maar lake (modified after Vuillemin et al., 2018a).

Laguna Potrok Aike is a maar lake located in Southern Patagonia, Argentina within the Pali Aike volcanic field. The steep morphology of this 100 m deep maar results in a pelagic-hemipelagic regime with frequent slumps and turbidites (Zolitschka et al., 2013). Due to the persistent influence of the Westerly winds on the study site, the lake is polymictic and the water column does not stratify in any season (Mayr et al., 2007) with mean annual temperatures between 4°C and 10°C. The basin is endorheic with nitrogen-limited oxic conditions down to the sediment-water interface, but oxygen penetration is restricted to the uppermost few millimeters (Vuillemin et al., 2013a). The top meter of

sediment was assessed to cover a period of 1,500 years (i.e 0.6 mm × $year^{-1}$). The prokaryotic assemblage of Laguna Potrok Aike (Fig. 4B) reflect the oligotrophic conditions of the water column, with taxa related to nitrogen recycling by nitrifiers under oxic (e.g. Nitrososphaeria, Nitrospirota) and microoxic (e.g. Planctomycetota) conditions and only a few aerobic heterotrophs from the water column (e.g. Bacteroidia). Apart from some terrigenous inputs (e.g. Acidobacteriota, Actinobacteriota), stratified guilds related to various respiratory guilds (Fig. 3A) are present, i.e. denitrifiers (e.g. Alphaproteobacteria), sulfate reducers, (e.g. Desulfobacterota). Due to the low salinity of this lake, the more thermodynamically favorable electron acceptors are depleted at shallow depths (ca. 40 cm) and methanogenesis prevails (e.g. Euryarchaeota) as a dominant process (Fig. 4B). The concomitant prokaryotic assemblage is mainly composed of primary (e.g. Acetothermia, Aminicenantia) and secondary (e.g. Chloroflexota, Bathyarchaeia) fermenters, some of which may be involved in syntrophic associations (e.g. Caldatribacteriota, Firmicutes) with hydrogenotrophic methanogens (Fig. 3B).

Together, the limited water depth and redox zonation in Lago di Cadagno promote the preservation of "ancient" sedDNA exogenous to the sediment, which can readily be discriminated from the active resident microbial populations. The related 16S rRNA gene abundances are indicative of specific subpopulations that allow inferences about past regime, redox stratification and type of sedimentation in the lake. Notable replacements and turnover of taxa exogenous to the sediment still occur within the upper meter of sediment. Finally, the lake salinity and related availability of favorable electron acceptors in the pore water allow sulfate reduction to be maintained deeper into the sediment profile, delaying the onset of fermentation and methanogenesis. In contrast, Laguna Potrok Aike's deep and constantly mixing oxic water column leaves little room for preservation of "ancient" sedDNA derived from planktonic sources. Fully oxic conditions allows for colonization of the sediment-water interface by aerobic heterotrophs, whereas the low salinity results in rapid depletion of pore water electron acceptors and promotes rapid transition to fermentation and hydrogenotrophic methanogenesis as the main processes in the sediment.

Slow growers and persistent prokaryotes in deep lake sediments

Environmental processes: Fermentation of residual substrates, necromass and DNA turnover

Microbial communities in deep lacustrine sediments are structured according to energy-conserving fermentative metabolisms along with the gradual depletion of pore water electron acceptors (Berg et al., 2022) and labile OM (Glombitza et al., 2013). Microbial cell densities experience an exponential decrease into the fermentation zone (Orsi et al., 2020a), resulting in a "depauperate horizon" (Wurzbacher et al., 2017) corresponding to a sharp decrease in microbial diversity, followed by a steady increase in taxonomic assemblages representing "persister" populations (Vuillemin et al., 2018a; Thomas et al., 2020) where starvation induces dormancy (Ellegaard et al., 2020). Metabolic features that exert selection of pre-adapted persisters seem to relate to their ability to drive secondary redox reactions for OM fermentation in substrate-limited sediment (Friese et al., 2021). These processes include hydrogen production (i.e hydrogenases) and electron bifurcation (i.e. cytochromes, flavins) used in heterotrophic dark carbon fixation (Santoro et al., 2013), such as in the W-L pathway, anaerobic dicarboxylate/4-hydroxybutyrate (DC/HB) cycle, or reductive TCA cycle (Fig. 2C). Although these metabolisms are similar to those involved in syntrophic associations (Conrad, 2020), it is not clear whether deep biosphere taxa actively collaborate in stepwise degradation of refractory OM via non-methanogenic interactions (Bertolet et al., 2019; Conrad et al., 2020) or alternatively persist opportunistically by making use of hydrolysed products (Orsi, 2018). Deep sediments accumulate

diagenetically altered and recalcitrant necromass over time (LaRowe and Van Cappellen 2011; Lever et al., 2015). The pool of OM is at least partially degraded and fermented by (homo)acetogenic bacteria (Vuillemin et al., 2020a, 2020b; Zemskaya et al., 2021), and in theory via fermentative Stickland reactions between amino acids that can serve as either electron donors or acceptors (de Vladar, 2012). While the energy yield from such reactions remains insufficient to produce a net increase in cellular biomass (Orsi et al., 2020a), such microbial activity sustained at the limit-to-life will result in turnover of microbial populations and sediment nucleic acids (Mhatre et al., 2019).

Depth profiles of 16S rRNA genes retrieved along lacustrine sequences spanning beyond the Last Glacial Maximum (i.e. sediment older than ca. 21 ka) are predominantly composed of yet-uncultivated fermenters and (homo)acetogenic degraders of complex organic carbon substrates (Fig. 5). Metabolic potential for heterotrophic dark carbon fixation (i.e homoacetogenesis, methanogenesis) is found in bacterial genomes from Aminicenantia, Elusimicrobiota, Chloroflexota (class Dehalococcoidia), and Caldatribacteriota, and archaeal genomes of Hadarchaeia and Bathyarchaeia which both display predicted metabolisms revolving around C_1 compounds (Colman et al., 2017). The distribution of metabolic traits across yet-uncultivated candidate clades and the evolutionary processes underlying them are incompletely resolved as even some core metabolic pathways (e.g. glycolysis, pentose phosphate pathway, pyruvate metabolism) are only partially predicted by phylogenetic relationships (Jaffe et al., 2020).

Populations that live and persist at the thermodynamic limit of life

We proceed to present candidate clades reported to be "persisters" in deep lake sediments, acknowledging that there could be metabolic diversification within each of these candidate phyla and classes whose metabolisms are only inferred from cultivation-independent metagenome-assembled genomes (Castelle and Banfield, 2018).

Aminicenantia: This class (phylum Acidobacteriota) features a metabolism that allows its taxa to only ferment proteinaceous substrates and sugars, albeit they can access a wide range of short and long-chain carbohydrates including chitin and cellulose via respiration of nitrite (Kadnikov et al., 2019). As anaerobic organotrophs, they act as initial degraders of buried biomass and OM, producing hydrogen and acetate as metabolic products. This clade tends to decrease in the microbial assemblage as it transits from fermentative stage I to II (Fig. 3B).

Caldatribacteriota: Members of this phylum perform complete anaerobic fermentative glycolysis (i.e. glycolysis, TCA cycle, SLP) and are putatively involved in syntrophic acetate oxidation in hydrocarbon-enriched environments (Liu et al., 2019). Its complex double membrane hinders diffusive loss of metabolites (e.g. VFAs, alcohols, aldehydes) out of the cell (Katayama et al., 2020). Its metabolic machinery includes a microcompartment that assists in secondary fermentation of aldehydes and conversion to pentose (Nobu et al., 2016) and a membrane complex for electron bifurcation that harnesses additional redox energy channeled through the W-L pathway (Vuillemin et al., 2020a). Altogether, this indicates that candidate clades among Caldatribacteriota can grow and sustain active populations in anoxic environments without a syntrophic partner. It is noteworthy that the Caldatribacteriota clade JS1 is the most abundant and widespread clade in oceanic anoxic sediments (Lee et al., 2018; Vuillemin et al., 2020a), whereas its presence in lake sediments is reported to be lower and variable (Chernitsyna et al., 2016; Vuillemin et al., 2018a; Panwar et al., 2020; Thomas et al., 2020).

Chloroflexota: Uncultured Chloroflexota in the class Dehalococcoidia are usually enriched in both anoxic subseafloor and lacustrine sediments. Metagenomic studies evidenced metabolic potential for fermenting highly oxidized and refractory OM, with hydrogen production (e.g. mvh) coupled to the W-L pathway and electron bifurcation to sustain primary fermentation and homoacetogenesis without the need for syntrophic H_2 consumption (Fincker et al., 2020; Vuillemin et al., 2020b). Their special cell membrane further allows this clade to persist in a dormant state.

Elusimicrobiota: Initially identified in the guts of insects (e.g. scarab, termite) where they act as fermenters of sugars and peptides (Herlemann et al., 2009), Elusimicrobiota are obligate anaerobes predicted to be capable of flexible heterotrophic and autotrophic lifestyles coupled with nitrate/nitrite respiration or fermentation of a variety of organic compounds, and homoacetogenesis with hydrogen and CO_2 as substrates (Méheust et al., 2020). Additional metabolic features include nitrogenase homologs that potentially enable them to fix nitrogen and thereby replenish the bioavailable nutrient pool under oligotrophic conditions (Lopez-Fernandez et al., 2018).

Hadarchaeota: First discovered in deep South-African gold mines (Takai et al., 2001), Hadarchaeota displays genome streamlining to mediate key geochemical processes in subsurface environments. They have genes putatively involved in degradation of short-chain alkanes, CO^- and H_2 oxidation, oxidation of VFAs and H_2 production associated with a partial W-L pathway (Wang et al., 2019). In the complex interactions of OM remineralization that characterize the fermentative zone (Orsi et al., 2020a), C_1 and C_2 compounds produced as fermentative by-products, such as formate, CO^-, and acetate, can be readily utilized by strictly anaerobic Hadarchaeota (Baker et al., 2016), potentially marking the lower boundary of syntrophic associations in the sediment.

Bathyarchaeia: As a generalistic class (phylum Crenarchaeota) that includes 17 subgroups, they are obligately found in anoxic sediments and are expected to anaerobically utilize a wide range of organic compounds, such as detrital proteins, carbohydrates, VFAs, aromatic compounds, short chain alkanes, methylated compounds (Zhou et al., 2018), and other refractory organic compounds such as lignin (Yu et al., 2018). In addition, they have inferred metabolic potential for hydrogen production, methanogenesis (Evans et al., 2015; Borrel et al., 2016; Berghuis et al., 2019) and homoacetogenesis (He et al., 2016) via the W-L pathway (Fig. 2C). This apparently allows them to dominate OM remineralization in deep sediment (Fig. 5) and efficiently drive heterotrophic dark carbon fixation (Feng et al., 2019). Consistently with their postulated hydrothermal origin (Feng et al., 2019), Bathyarchaeia also display metabolic capacity to use reduced sulfur.

Microorganisms involved in autotrophic and heterotrophic dark carbon fixation can make a considerable contribution to inorganic carbon fixation in lake sediments (Zhao et al., 2020). Genes involved in dark carbon fixation (Fig. 2C) include ATP-citrate lyase (*acly*) as the first step of the reductive TCA cycle (Kanao et al., 2001), ribulose-1,5-diphosphate carboxylase gene (RuBisCO) in the non-phototrophic CBB cycle, different carboxylases (Erb, 2011) used in mixotrophic DC/HP cycle and Fuchs-Holo bicycle, and several functional genes involved in the (homo)acetogenic W-L pathway from formyl-tetrahydrofolate synthetase (*fthfs*) to carbon monoxide dehydrogenase (*codh*). Metabolic mechanisms at the thermodynamic limits for life, such as secondary fermentations in the (homo)acetogenic W-L pathway, implement redox complexes (e.g. NADH, ferredoxin, flavins) for energy conservation via electron bifurcation (Schuchmann and Müller 2016; Buckel and Thauer, 2018). Electron bifurcation, combined with the reversible oxidation of molecular hydrogen (McInerney et al., 2009), is an indirect way of conserving redox energy by reducing protons to molecular hydrogen and makes use of it in heterotrophic dark carbon fixation (Lemaire et al., 2020). Some of the main

hydrogenases coupled with electron bifurcation (Vignais et al., 2001) are the heterodisulfide reductase (*hdr*), methyl-viologen reductase (*mvh*), coenzyme F420 reducing and non-reducing hydrogenase (*frh*), and in theory different L-amino acid dehydrogenases involved in fermentative Stickland reactions (de Vladar, 2012).

Prokaryotic assemblages of the deep biosphere persisting in lake sediments older than 50 ka

Geomicrobiological investigations of lacustrine sediment archives from ancient lakes has enabled characterization of the long and deeply buried biosphere in terms of cell concentrations (Vuillemin et al., 2014a; Kallmeyer et al., 2015), community composition (Vuillemin et al., 2018a; Thomas et al., 2020), and metabolic potential and activity (Glombitza et al., 2013; Vuillemin et al., 2018b; Friese et al., 2021). To illustrate the exploration of the lacustrine deep biosphere, we compared 16S rRNA gene diversities and cell densities in up to 500 ka old sediment profiles from four different lakes.

The stratigraphic sediment profile recovered from the 100 m deep maar Laguna Potrok Aike represents 51 ka years of sediment deposition (Zolitschka et al., 2013). Predicting functions based on identified taxa representative of respiration types, the 16S rRNA assemblages in the upper 10 m below lake floor (mblf) reflect successive replacement of denitrifiers (i.e. Alphaproteobacteria) with sulfate reducers (i.e. Desulfobacterota), and methanogens (i.e. Thermoplasmatota, Euryarchaeota) in syntrophic association with primary (i.e. Acetothermia, Aminicenantia) and secondary (e.g. Caldatribacteriota, Firmicutes) fermenters, generally trending towards homoacetogenesis (e.g. Chloroflexota). The Late Glacial transition around 10 mblf corresponds to a drastic shift in sedimentation types that resulted in less abundant and more refractory organic substrates in sediments of the glacial period (Vuillemin et al., 2014a, 2018a). This transition is accompanied by the increasing presence of a different microbial community predominantly composed of Bathyarchaeia, Hadarchaeota, and Elusimicrobiota with Aminicenantia, Caldatribacteriota and Dehalococcoidia persisting at slow metabolic rates throughout the sediment archive (Fig. 5A). Although intervals corresponding to gravity flows were systematically discarded, putative terrigenous inputs are still observed as sequences assigned to Acidobacteriota, Actinobacteriota and Bacteroidia (Fig. 5A).

Seated in ultramafic rocks on the Indonesian island of Sulawesi (Fig. 5B), Lake Towuti is a long-term stratified, 200 m deep tectonic basin. Lateritic weathering in the catchment delivers abundant iron oxides but very little sulfate to the lake, leading to ferruginous conditions that scavenge phosphorus from the water column. Its sedimentary column is estimated to span 1 Ma of depositional history with variable sedimentary rates (Russell et al., 2020), trophic state and redox conditions across wet and dry periods of the Quaternary (Vuillemin et al., 2022b). Given the lake's ferruginous chemistry and oxygen depletion below 130 m in the water column, Lake Towuti has an overall shortage of electron acceptors (i.e. oxygen, nitrate, sulfate) in its bottom waters (Vuillemin et al., 2016b). Thus, pore water electron acceptors are depleted even at shallow sediment depth (Vuillemin et al., 2016b, 2018b), leading to the emergence of taxonomic assemblages with fermentation as prominent features and methane as the final degradation product (Friese et al., 2021). This observation is surprising, as there are abundant minerals containing ferric iron. However, these minerals appear to be poorly reactive towards microbial reduction, contradicting the canonical sequence of electron acceptor use. The main initial microbial constituents reflecting metabolic guilds include sulfate reducers (e.g. Desulfobacterota, Nitrospirota) and methanogens (e.g. Euryarchaeota) in concomitance with primary fermenters (e.g. Firmicutes, Aminicenantia). Below 0.5 mblf, the taxonomic assemblage is predominantly composed of Bathyarchaeia, Hadarchaeota, Elusimicrobiota and Chloroflexota, with predicted metabolisms revolving around H_2, CO^-, formate and CH_4 (Colman et al., 2017). We propose that the main active

metabolic processes in sediments deeper than 2 mblf putatively include fermentation of proteinaceous substrates by Bathyarchaeia and recycling of excreted ammonium by Elusimicrobiota (Fig. 5B).

Lake Ohrid is an endorheic oligotrophic 288 m deep tectonic basin located in the Balkans mostly fed by karstic groundwater channels (Fig. 5C). The upper 200 m of the water column experience seasonal overturn, whereas the oxic bottom waters only mix on decadal scales and typically remain stratified due to strong salinity-induced density gradients. Its history is estimated to cover 1.2 Ma, with sedimentation rates that highly fluctuated across glacial-interglacial periods (Francke et al., 2016). The deep sediment record of Lake Ohrid displays a 16S rRNA gene diversity dominated by Caldatribacteriota, Bathyarchaeia and Dehalococcoidia, which is in accordance with processes expected to shape communities in substrate-limited and hundreds ka old anoxic sediments (Fig. 5C). The sporadic occurrence of gammaproteobacterial, cyanobacterial and putative soil representatives further suggests that some DNA sources that originated from the catchment and water column were preserved hundreds ka after burial, particularly in sediments corresponding to sudden deposits during dry glacial intervals (Thomas et al., 2020).

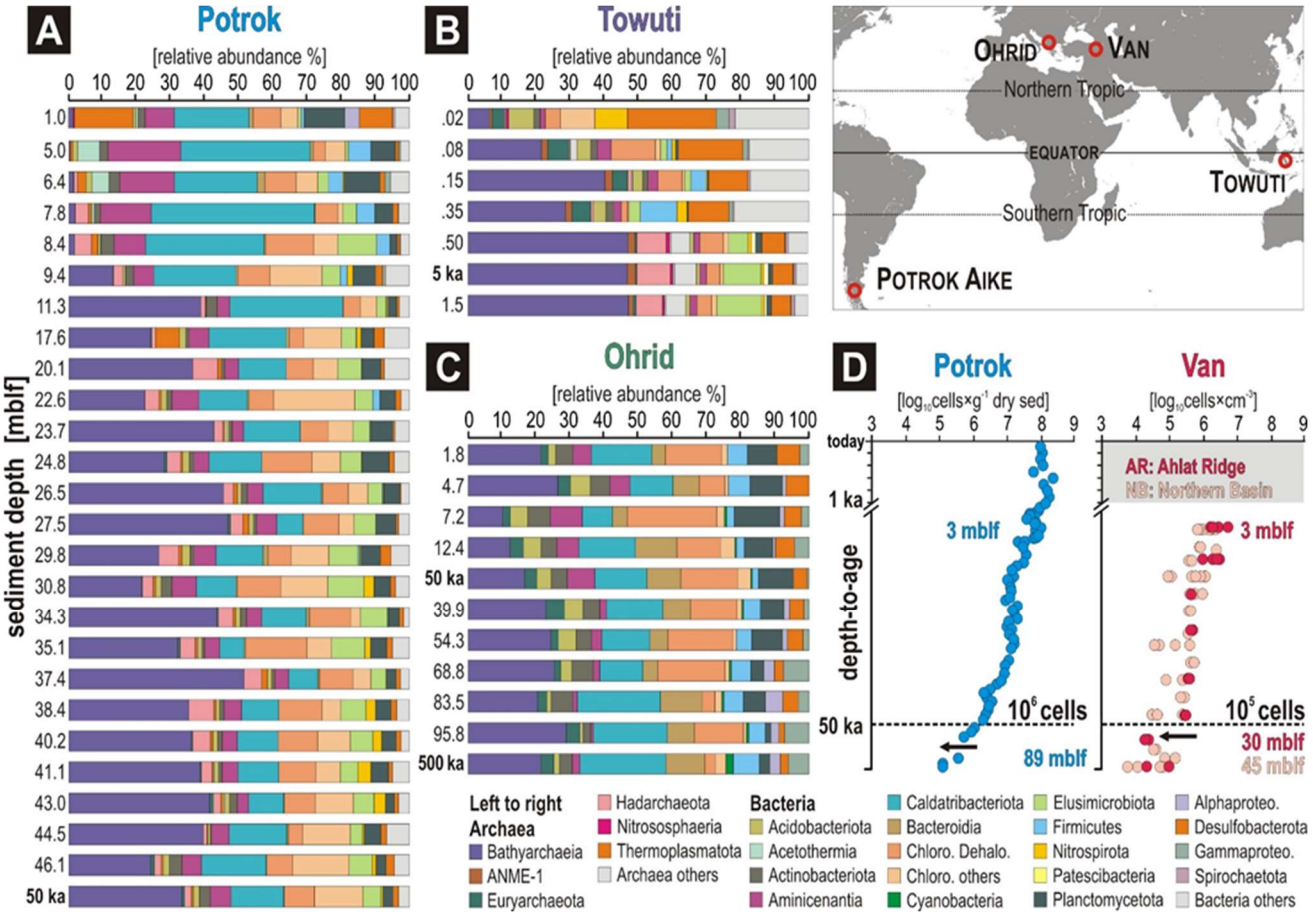

***Figure 5*. 16S rRNA gene taxonomic diversity and cell density in long-term sedimentary sediment archives from four different lakes retrieved by the International Continent Scientific Drilling Program (ICDP). (A)** 16S rRNA-based microbial community composition (relative abundance [%] at phylum level) in sediments of Laguna Potrok Aike, an endorheic nitrogen-limited and polymictic 100 m deep maar lake (after Vuillemin et al., 2018a). **(B)** 16S rRNA-based microbial community composition (relative abundance [%] at phylum level) in sediments of Lake Towuti, a ferruginous phosphorus-limited and stratified 200 m deep tectonic lake (after Vuillemin et al., 2018b). **(C)** 16S rRNA-based microbial community composition (relative abundance [%] at phylum level) in sediments of Lake Ohrid, an endorheic 288 m deep tectonic basin fed by underground karstic channels (after Thomas et al., 2020). **(D)** DAPI-stained total cell counts [$\log_{10}$ cells × g^{-1} dry sed] in sediments of Laguna Potrok Aike (after Vuillemin et al., 2014a) and SYBR Green-stained total cell counts [$\log_{10}$ cells × cm^{-3} wet sed] in sediments of Lake Van (after Kallmeyer et al., 2015).

Seated on the high plateau of far east Turkey, Lake Van is an endorheic 171 m deep soda lake. Due to hydrothermal activity in the catchment, the water column is strongly alkaline (pH 9.7). Although annual temperatures fluctuate between 25° and -12°C, the high salinity of the lake prevents freezing in winter. The stratigraphic sequence of the deeper of the two tectonic sub-basins is estimated to span 600 ka of climatic history, with a succession of finely laminated sediment, chemical varves and frequent tephra layers (Stockhecke et al., 2014). The differences in sedimentation rates across Lake Potrok Aike (1 mm $year^{-1}$), Towuti (0.22 mm $year^{-1}$), Ohrid (0.43 mm $year^{-1}$) and Van (0.4 mm $year^{-1}$) can account for discrepancies between sediment depth and age. Still in the case of Lake Potrok Aike and Lake Van (Kallmeyer et al., 2015), population cell densities experience a continuous decrease with depth and stabilize around 10^6 to 10^5 cells × cm^{-3} after some 50 ka years of burial (Fig. 5D).

These four case studies also show that sudden sediment deposition (e.g. turbidites, slumps, floods), especially during glacial periods, can result in enhanced preservation of DNA sources derived from the catchment and in-lake processes as increased sedimentation rates tend to disrupt stratified microbial communities and abort, or at least, hinder early diagenetic processes.

Anthropogenic expansion of adaptive and versatile ubiquists

The biogeochemical feedbacks of microbial communities on their respective ecosystems (Hall et al., 2018) are currently gaining attention, as pristine lakes are increasingly exposed to anthropogenic disturbances (Han et al., 2020; Jiang et al., 2017). Such perturbations may include land use (Kraemer et al., 2020; Pearman et al., 2022b) with increased nutrient or OM inputs (Wu et al., 2019) resulting in lake browning and eutrophication (Fiskal et al., 2019, 2021), as well as wastewater outfalls (McLellan et al., 2015) and oil spills (Zemskaya et al., 2015) delivering persistent organic pollutants (Morasch et al., 2010), heavy metals (Bravo et al., 2018) and potential pathogens (Chandran et al., 2011) across the watershed.

Microbial activities can have significant and variable impacts in pristine and human-impacted ecosystems (Hall et al., 2018), for instance by creating resilience to environmental perturbations (Shade et al., 2012a, 2012b), enabling on-site bioremediation (Aalto et al., 2018), or accelerating nutrient and metal release from sediments into the overlying waters (Sinkko et al., 2013). As eutrophication progresses and increases the flux of OM to the sediment, microbial processes produce specific metabolic solutes (e.g. N_2O, NH_4^+, PO_4^{3-}, H_2S, Fe^{2+}, CO_2, CH_4) that can potentially escape the sediment or diffuse across the sediment-water interface (Fig. 3). If such metabolites reach overlying waters, they could cause negative feedback that would further increase lake productivity (van Helmond et al., 2020) or enhance production of greenhouse gasses.

In contrast, pore water saturation can trigger precipitation of authigenic minerals that can help maintain stable water column conditions by promoting long-term sequestration of nutrients and metals in the sediment (Taylor and Boult, 2007; Vuillemin et al., 2013b, 2020b, 2022b; Berg et al., 2019). Since these effects are influenced by microbial community composition, it is necessary to study the link between lacustrine environmental conditions (Lewis, 2009), species distributions and mechanisms of selection (Bryanskaya et al., 2016). Thus, sedDNA surveys are necessary in order to understand microbial community assembly in emergent ecological niches (Mandakovic et al., 2018) and assess environmental resilience as pristine ecosystems transit to human-dominated ecosystems of the Anthropocene (Sun et al., 2017; Blanchette and Lund 2021; Fiskal et al., 2021).

Environmental processes: Pollutant loading, eutrophication, and excess nutrient

Sediment microbiomes downstream of urbanized catchments (Jiang et al., 2017; Han et al., 2020) are increasingly being used as models for elucidating how anthropogenic disturbances affect lacustrine habitats (Barouillet et al., 2023). Excessive nutrient inputs to lacustrine systems typically cause enhanced productivity in the water column, thereby increasing organic carbon sedimentation and promoting OM mineralization via organotrophic sulfate reduction, ammonification and methanogenesis at shallow sediment depths (Fiskal et al., 2019). Such redox conditions could invoke negative feedback in the overlying waters (Liikanen and Martikainen, 2003). The identification of core microbiomes, typically defined as the suite of populations consistently shared across variable microbial communities from similar habitats (i.e. adaptive ubiquists) (Shade and Handelsman, 2012; Ruiz-González et al., 2017), would facilitate a systematic assessment and monitoring of microbial assemblies that are characteristic for either pristine or resilient conditions (Yadav and Kour, 2018; Ji et al., 2019). This would help pinpoint populations and taxa that may be responsible for *in situ* bioremediation (i.e. bioremediators) or carry signals of human-impacted conditions (Gibbons and Gilbert 2015; Kato et al., 2018; Escalas et al., 2019; Wu et al., 2019).

Microbial mitigation of anthropogenic pressures: Sulfur and iron oxidizers, methylotrophs, methanotrophs, anammox bacteria, opportunists

Sulfur oxidizers: In organic-rich sediments, excess organotrophic sulfate reduction associated with limited iron reduction leads to an accumulation of H_2S in pore water with sediment sulfidization that can have potentially toxic effects. Specific taxa affiliated with Gammaproteobacteria (e.g. *Thioploca*, *Thiothrix*, *Beggiatoa*, *Thioglobus*, *Sulfuriflexus*, *Acidiferrobacter*, *Thiobacillus*) play important ecological roles in sulfide detoxification via sulfur oxidation coupled to autotrophic dark carbon fixation (i.e. chemolithoautotrophy) in the water column and at the sediment-water interface (Kojima et al., 2003; Lavik et al., 2009; Pjevac et al., 2015; Vuillemin et al., 2022a). Although sulfur oxidation is the prevalent process, the use of reduced forms of sulfur as electron donors by these taxa can also be coupled to DNRA, or ammonification. DNRA is a process in competition with canonical denitrification (Fig. 2A-B) that can potentially cause accumulation of excess ammonia in the system (Fernández et al., 2009). In acidic mining lakes (Lu et al., 2016; Quatrini and Johnson, 2018), some phototrophic sulfur bacteria (e.g. *Allochromatium*, *Ectothiorhodospira*) and bacterial candidates (e.g. *Acidithiobacillus*, *Ferrimicrobium*) are also capable of sustaining growth via sulfide, sulfur and iron oxidation to potentially drive in-lake neutralization and remediate groundwater pollution (Zak et al., 2021). Increased OM inputs to the sediment will stimulate mineralization coupled with sulfate reduction and methanogenesis. Excess sulfide buildup in the system can be mitigated under aerobic conditions by microbial expression of genes encoding the sulfite oxidase (*suox*) and periplasmic sulfur-oxidizing proteins (*sox*) as part of the sulfur oxidative pathway, as well as reverse dissimilatory sulfite reductase (*rdsr*), reversible adenylylsulfate reductase (*apr*) and reversible sulfide dehydrogenase (*sud*) (Dahl, 2020) also known as bifurcating ferredoxin: NADP oxidoreductase (*nfn*) (Pereira et al., 2011). However, it is not clearly established whether these genes are actively expressed in anaerobic sulfur oxidation under anoxic conditions (Orsi et al., 2016). Oxidation of organic forms of sulfur can aerobically take place by means of genes encoding taurine dioxygenase (*tauD*) and potentially via a heterodisulfide-like pathway. Under anoxic conditions, the dimethyl sulfoxide reductase (*dsmo*) encoding gene can potentially increase the production of toxic dimethyl sulfides, byproducts which can serve as substrates in producing methane via the methylthiol-specific coenzyme M methyltransferase (*mts*).

Iron oxidizers: Reduction of iron can cause excessive release of phosphorus from the sediment to the overlying waters (Gächter et al., 1988; Taylor and Boult, 2007) in association with solubilization of heavy metal ions accelerated by either reduction (e.g. Hg^{2+}, As^{3+}) or oxidation (e.g. U^{6+}, Se^{6+}, Cu^{2+}, Cr^{4+}). This is because many metals and nutrients tend to form complexes with ferric iron, and accordingly microbial iron oxidizers have the potential to mitigate pollutant releases from reduced sediments (Bravo et al., 2018; Kappler et al., 2021). Iron oxidizers are phylogenetically diverse and include scattered genera across diverse lineages of Proteobacteria (Hedrich et al., 2011) that thrive under variable environmental conditions (Singh et al., 2018). They display a certain degree of metabolic versatility, some being aerobic acidophiles (e.g. *Acidithiobacillus*, *Sideroxydans*), neutrophiles (e.g. *Leptothrix*, *Ferritrophicum*, *Gallionella*), phototrophs (e.g. *Rhodovulum*, *Rhodobacter*, *Rhodomicrobium*), or nitrate-dependent facultative anaerobes (e.g. *Paracoccus*, *Thermomonas*, *Azospira*). Iron oxidizers as a metabolic guild also include members of several other phyla (Emerson et al., 2010, 2013), including Actinobacteriota (e.g. *Acidimicrobium*, *Ferrimicrobium*, *Ferrithrix*), Firmicutes (e.g. *Alicyclobacillus*), Nitrospirota (e.g. *Leptospirillum*), and some archaeal clades that are mainly relevant to acid mining lakes. There is no clear functional marker gene for iron oxidation or reduction, which are metabolic processes involving complex redox cofactors, e.g. cytochromes, ferredoxins, iron-sulfur proteins and flavins (e.g. rubredoxins, riboflavins, rusticyanin), involved in electron transfer (Kappler et al., 2021). Some operons (i.e. *rus*, *petI*, *fox*) are clearly involved in iron oxidation and the corresponding iron respiratory transport chain, which include several subunits encoding the high potential iron sulfur (i.e. Fe_4S_4) protein (*Iro*) with different cytochrome oxidases (a, b, c) and variations of the related *cyc* and *cox* genes (Hedrich et al., 2011). Microbial reduction of metalloids is traceable via functional marker genes, such as arsenate reductase (i.e. glutaredoxin; *arsABC*) (Saltikov and Newman, 2003), selenite reductase (i.e. thioredoxin; *srrA-F*) (Wen et al., 2016) and mercury methylation via a corrinoid binding domain (*hgcA*) and a coupled ferredoxin (*hgcB*) (Parks et al., 2013).

Methylotrophs and methanotrophs: Canonical methylotrophs are obligate aerobes whose isolates have originally been classified based on membrane characteristics into gammaproteobacterial type I (e.g. *Methylococcus*, *Methylomonas*, *Methylobacter*, *Methylosarcina*, *Methylomicrobium*) or alphaproteobacterial type II (e.g. *Methylosinus*, *Methylocystis*, *Methylocella*). However, most methylotrophs are also facultative methanotrophs as they can use methane as a substrate in addition to a range of other reduced C_1 compounds (e.g. methanol, formate, alcohol, formaldehyde) (Higgins et al., 1981; McDonald et al., 2008). These facultative methane oxidizers can grow and survive under a broad range of environmental conditions with regards to, e.g. temperature, pH, and salinity, including the extremes (Trotsenko and Khmelenina, 2002). Substantial presence of this guild is expected to reflect high methane availability under oxic conditions, and thus potentially relate to increased productivity and stable methanogenic conditions with diffusive release from underlying sediments (Yang et al., 2016). Processes of anaerobic oxidation of methane (AOM) are performed with electron acceptors other than O_2. For instance, the anaerobic methanotrophic archaea (i.e. ANME groups) among the phylum Euryarchaeota can use SO_4^{2-} (Schubert et al., 2011), Fe^{3+} and Mn^{4+} (Yang et al., 2021) as electron acceptors. *Candidatus* Methanoperedens can also couple AOM processes to NO_3^- reduction (Haroon et al., 2013), while the bacterial candidate phylum Methylomirabilota mediates this process with NO_2^- (i.e. *Candidatus* Methylomirabilis) (Welte et al., 2016). Both aerobic and anaerobic methanotrophs are found in freshwater lake sediments but it is still not clear whether they play a significant role in mitigating emissions of the potent greenhouse gas methane to the atmosphere (Borrel et al., 2011; Norði et al., 2013; He et al., 2018). Methane escapes from anoxic sediments and can be oxidized aerobically

(Fig. 2C) in the water column or at the sediment-water interface by means of particulate (i.e. membrane bound) methane monooxygenase (*pmmo*) and soluble (i.e. cytoplasmic) methane monooxygenase (*smmo*) which both catalyze the oxidation of methane to methanol (Iguchi et al., 2010). Methane can also be oxidized anaerobically in the sediment via reverse methyl-coenzyme M reductase (*mcr*) which is the same enzyme as the one involved in methane production. Methylotrophic oxidation of other reduced C_1 compounds proceeds via genes encoding for instance methanol dehydrogenase (*mxa*), methanol dehydrogenase homologue (*xox*) and formate dehydrogenase (*fdh*).

Anammox bacteria: Microbial fermentation of proteins is the main source of the NH_4^+ released to pore water. Eleven candidates among the phylum Planctomycetota are known to perform anammox, a process where NO_2^- derived from either aerobic NH_4^+ oxidation or partial NO_3^- reduction is required. Under microoxic conditions, these candidates can play a significant role in removing excess NH_4^+ diffusing to the sediment-water interface (Kuenen, 2008), but can also result in production of nitrous oxide (N_2O), another potent greenhouse gas (Kuypers et al., 2005). They are affiliated with the genera *Kuenenia*, *Brocardia*, *Anammoxoglobus*, *Jettenia*, *Brasilis*, and *Scalindula* and display metabolic features, such as a membrane-bound organelle (i.e. anammoxosome), resistance to desiccation and long-term dormancy (Pereira et al., 2017; Zhu et al., 2019). Whereas nitrification (*amo*, *nxr*) only operates under aerobic conditions, anammox processes take place under microaerophilic conditions (Kong et al., 2013) via hydrazine oxidoreductase (*hzo*). The oxygen-sensitive conversion of organic and reduced nitrogen species in eutrophic systems is most effective under concomitant anaerobic oxidation and partial nitrification-denitrification (Hosseinlou et al., 2018), i.e. conditions where anammox can be combined with nitrite-nitrate dependent AOM (van Kessel et al., 2018). In contrast, aerobic chemolithoautotrophic sulfur oxidizers hold genes encoding ammonia-forming cytochrome nitrite reductase (*nrf*), which leads to the production and release of ammonia (i.e. DNRA), and thereby compete with the aforementioned processes. Otherwise, excess organic forms of nitrogen are commonly converted to ammonia via different aerobic ureases, cyanases, nitrilases and oxygen-insensitive nitroreductases (Vuillemin, 2023).

Opportunists: Opportunists are typically microbes that can sustain life from a number of resources and immediately take advantage of the opportunity to thrive when favorable conditions arise. Some opportunistic microaerophilic aerobes, or facultative anaerobes, found mostly within the Rhodobacterales among Alphaproteobacteria, Burkholderiales and Rhodocyclales in the class Gammaproteobacteria, or Pseudomonadales among Gammaproteobacteria, are metabolically versatile performing H_2 oxidation with oxalate (i.e. $C_2O_4^{2-}$) as a carbon source. They can make use of reduced metabolites diffusing across the sediment-water interface from underlying eutrophic sediments (e.g. HS^-, NH_4^+, CH_4, CO_3^-, H_2), remain viable long after burial and grow rapidly after even minor sediment exposure to oxygen (Vuillemin et al., 2010; Capo et al., 2021b). Many pathogens can survive in a dormant stage and be transported far downstream from e.g. wastewater treatment plants (Fisher et al., 2015; McLellan et al., 2015). Fecal matter from terrestrial and aquatic animals is also an important source of pathogenic fermenters to the sediment, including some Bacteroidia (e.g. *Prevotella*, *Porphyromonas*, *Rickenella*), Firmicutes (e.g. *Clostridium*, *Lachnospira*, *Trichococcus*, *Bacillus*), Gammaproteobacteria (e.g. *Aeromonas*, *Klebsiella*) and Campylobacterota (e.g. *Arcobacter*, *Campylobacter*). Depending on the features of the ecosystems in which these potentially pathogenic populations are imported, some of them can persist in impacted sediments where they contribute to enhanced mineralization (Haller et al., 2011; Han et al., 2020) or represent indicators of pollution gradients (Li et al., 2019b) or a potential health hazard (Chandran et al., 2011; McLellan et al., 2015;

Bai et al., 2022). Dissemination of sedDNA from feces also has specific applications in the field of microbial archaeology (Rampelli et al., 2021; Weyrich and Pérez, 2023).

Indicators of excess nutrient in lake sediments downstream urbanized catchments

Anthropogenic eutrophication downstream of urbanized catchments increases the amount of organic carbon deposited in lacustrine sediments (Anderson et al., 2014), which in turn shapes the redox chemistry and the degree of OM remineralization during shallow burial. Excessive microbial turnover of OM in the sediment can thereby result in increased sulfidization, ammonification and methanogenesis in the sediment, whereas metal reduction triggers nutrient releases from organic-rich sediments.

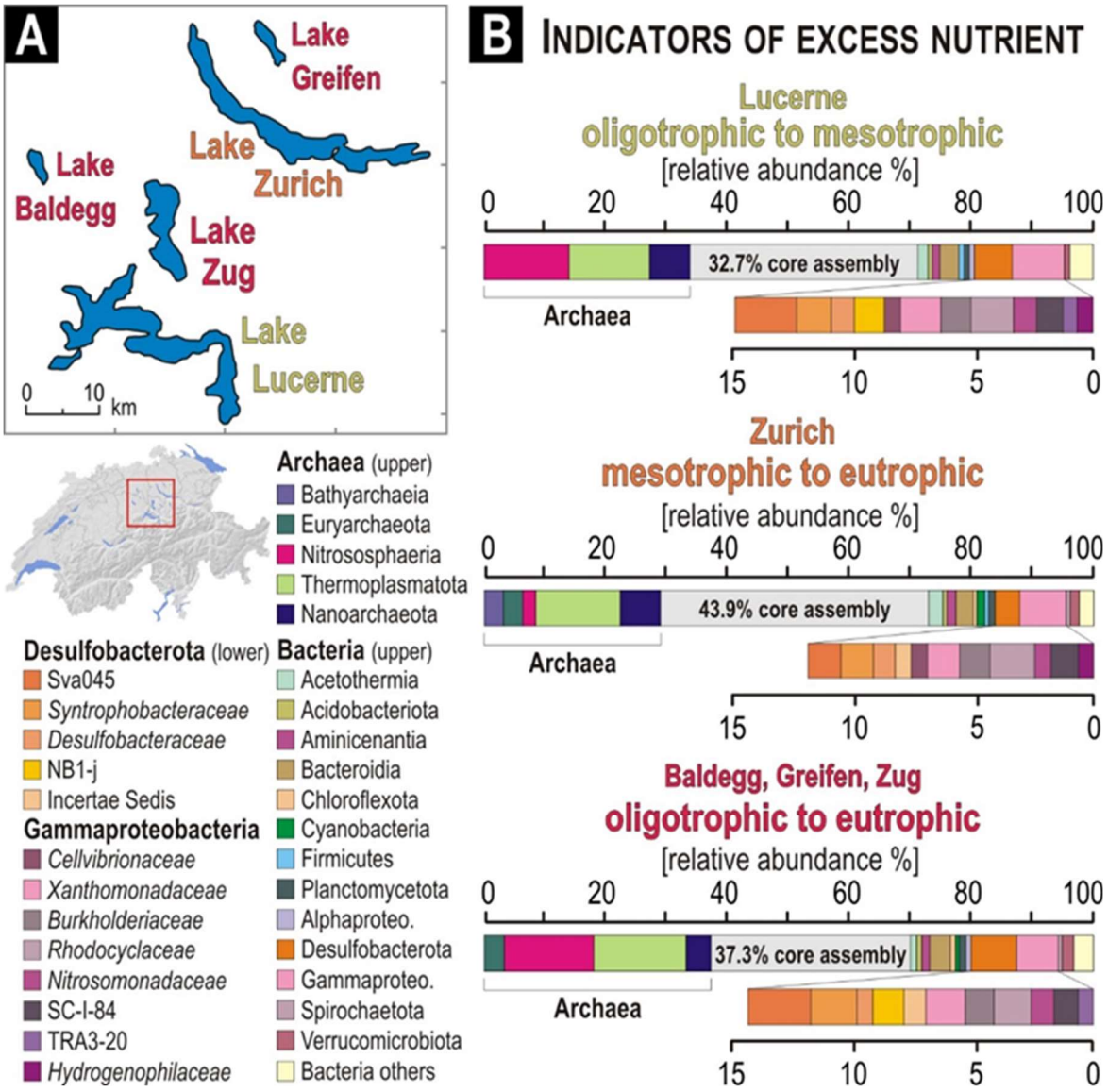

Figure 6. **Microbial indicators of excess nutrients in sediments of five Swiss lakes displaying increasing degrees of eutrophication. (A)** Geographic location of Lake Lucerne, Zurich, Zug, Greifen, and Baldegg. **(B)** 16S rRNA gene diversity of statistically relevant taxa putatively useful as proxies for tracing lake eutrophication over time (data from Han et al., 2020), with Desulfobacterota and Gammaproteobacteria enlarged in the lower bar charts. The nutrient gradient increases bottom to top in the sediment cores, reflecting an increase in sedimentary organic carbon related to anthropogenic influence over time. The most influential bacterial and archaeal groups in driving community differences between eutrophic Lake Greifen, Lake Baldegg and Lake Zug, mesotrophic Lake Zurich, and oligotrophic Lake Lucerne were identified via similarity percentages breakdown, correlation matrix of geochemistry and phylogeny, co-occurrence patterns and permutational multivariate variance (Han et al., 2020).

Five Swiss lakes displaying different degrees of increasing eutrophication over time (Fig. 5A) were investigated to trace the fate of aquatic OM loads (Fiskal et al., 2019, 2021) and decipher the role of microbial respiratory activities during shallow burial on increasingly OM-rich sediments over recent times (Han et al., 2020). Phylogenetic assemblages were analyzed statistically (i.e. similarity percentages breakdown, geochemistry and phylogeny correlation matrix, co-occurrence patterns, permutational multivariate analysis of variance) to sort out the taxa associated with permanent changes in microbial community structure (Fig. 6B).

Metabolic guilds that seem to thrive in increasingly eutrophic sediments (Fig. 5B) are nitrifiers (i.e. Nitrososphaeria, Gammaproteobacteria), methylotrophic methanogens (e.g. Euryarchaeota, Thermoplasmatota), sulfate reducers (i.e. Desulfobacterota) and ammonifying sulfur oxidizers (e.g. Gammaproteobacteria). Increasing preservation of putative planktonic sequences from the water column was observed along the eutrophication gradient, mostly affiliated with Cyanobacteria and Bacteroidia as well as anaerobic fermenters at shallow depth (e.g. Acetothermia, Aminicenantia). The main microbial drivers are found among the class Gammaproteobacteria that can make use of reduced metabolites diffusing from underlying anoxic sediments, e.g. oxidation of NH_4^+ and H_2S by *Nitrosomonadaceae*, and oxidation of both H_2 and CH_4 by *Hydrogenophilaceae*. The *Xanthomonadaceae* may include phytopathogenic populations feeding on algal blooms and nitrate reducers in the sediment. The bacterial assemblages that emerge from eutrophic conditions are apparently composed of several fast-growing opportunists which can disrupt syntrophic associations to short-cut the community core assemblage. This example raises questions on the actual resilience of sediment core microbiomes to anthropogenic disturbances over the long term.

Research perspectives and methodological considerations

Prokaryotic sedimentary DNA as an indicator of past and current environmental shifts

Whether prokaryotic DNA in the sediment can be used as a stratigraphic recording tool to inform us about past environmental changes and depositional conditions is still a matter of debate. A selection of proxies from sedDNA sequence data and gravity/piston/hydraulic coring techniques can foster novel multidisciplinary exploration of information preserved in sedimentary archives (Fig. 7). Such an approach would comprehensively integrate past climate and biogeochemical cycles and enable reconstruction of the dynamic roles of microbial activity in the water column and sediment, for instance in the climatic context of the last glacial-interglacial transition and the onset of the Anthropocene. A particularly exciting opportunity is the implementation of metagenomic, metatranscriptomic and metaproteomic approaches to the very extensive sedimentary archives retrieved from scientific drilling campaigns taking place over the last decades (Anselmetti et al., 2020). So far, such drilling has encompassed a collection of material from lakes displaying different geochemical conditions (Ariztegui et al., 2015; Kallmeyer et al., 2015), intensity of anthropogenic disturbances (Michas et al., 2017; Herold et al., 2020) and environmental management regimes along urbanization gradients (Blaser et al., 2016).

The implementation of high-throughput sequencing tools to paleolimnology can thus constitute a significant advance for stratigraphic studies and past environmental reconstructions. In depth characterization of planktonic and benthic microbial communities via a more complete inventory of taxonomic and functional marker genes presents a powerful and novel avenue for exploration of climatic time series along sedimentary records. The identification of microbial taxa and their related metabolic activities can potentially shed light on both in-lake and sediment nutrient cycling, OM

degradation and redox processes in relation to the deposited substrates. By tracing microbially mediated biogeochemical cycling in relation to physico-chemical processes and lacustrine endogenic conditions, one can shed new light on past climatic transitions and validate the reliability of parallel proxies used in environmental reconstructions of lake archives (e.g. lipids, minerals, isotope signals). Finally, metagenomic sequence data (i.e. total DNA) and metatranscriptomes (i.e. total RNA sequences) enable a broader assessment of metabolic potential and activities of sediment microbiomes at stratigraphic transitions and identification of key sequence signatures.

In the Anthropocene, lacustrine ecosystems are continuously exposed to increasing urbanization of their catchments and other disturbances, calling for efforts to monitor anthropogenic impacts (Picard et al., 2022; Barouillet et al., 2023) and the resilience of lacustrine microbiomes to such disturbances (Sun et al., 2017; Blanchette and Lund, 2021). Because microbial communities constitute the base of aquatic food webs, nutrient disequilibrium constitutes a major threat to the state of lacustrine ecosystems. By driving OM remineralization and redox processes in the shallow subsurface, microbial activities impact the sediment sorption capacities and thereby the long-term sequestration of pollutants. Compiled sedDNA studies targeting prokaryotic communities have shown the potential of integrating meta-omics methodology in limnogeology for *in situ* investigations of microbial processes. Such a combined approach could help us to study how global change brought by human-related impacts will influence lacustrine systems and what mitigation measures could be effective.

Meta-omics adapted to limnogeology and stratigraphic studies

Parallel field sampling for limnogeology and microbiology

Sediment sampling of gravity/piston/hydraulic cores is commonly processed for multidisciplinary approach of lacustrine archives integrating a series of climatic proxies (Ohlendorf et al., 2011). Here, we propose to routinely implement *in situ* aseptic protocols (e.g. Vuillemin et al., 2013a; Friese et al., 2017) that allows for combined studies of microbial systems and past climatic events (Fig. 7). Establishing controlled aseptic conditions on site is mandatory for any downstream analytical protocol that involves techniques based on PCR amplification and high-throughput sequencing of prokaryotic sedDNA (Capo et al., 2021b and references therein).

Using primer pairs that target specific marker genes for taxa or functions (Fig. 2; Table 1), qPCR assays can effectively profile lacustrine microbial communities in terms of depth distribution and abundance of these targets. Subsequent high-throughput sequencing of barcoded amplicons could subsequently validate the assays, whereas in depth sequencing of metagenomes and metatranscriptomes more quantitatively and broadly unravels the metabolic potential and gene expression patterns of entire prokaryotic communities. A multi-pronged characterization of prokaryotic genetic material via meta-omics can thereby provide a holistic understanding of aquatic ecosystems along stratigraphic records, and in this way revolutionize the conventional field of limnogeology. Here, we review some state-of-the-art techniques that allow for the characterization of the subsurface biosphere as well as ancient DNA sources, and share some opportunities and pitfalls with regards to the feasibility and accuracy of meta-omics targeted approaches applied to limnogeology.

Selective extractions of nucleic acid fractions

Applying some modifications to commercially available DNA extraction and purification kits can initially allow for the separation of specific fractions from the total sedDNA pool prior to PCR amplification.

Intra- and extracellular DNA extractions: sedDNA not enclosed in living cells may in some instances account for the largest fraction of the total pool of sedDNA, and includes molecules locked within dead cells, organic aggregates, adsorbed to mineral matrices, and viral DNA (Torti et al., 2015). Specific protocols allow for separate extraction of the genetic material enclosed in intact cells from the pool contained extracellularly (Corinaldesi et al., 2005; Alawi et al., 2014). Applying such protocols, one can refine the interpretation of prokaryotic sedDNA signals and their significance along stratigraphic sequences (Vuillemin et al., 2017). The principles for such DNA-partitioning methods is to retrieve the soluble extracellular DNA fraction from the extraction buffer, while cells are desorbed, put into flotation and concentrated into a pellet by centrifugation.

Ancient DNA: Ancient DNA preserved in sediments partially degrades and breaks into shorter DNA strands over time. Ancient DNA represents a relatively low percentage of the total extractable prokaryotic sedDNA. Furthermore, prokaryotic sedDNA experiences a constant turnover due to metabolic processes by the viable and active part of the sediment microbial community, making it hard to discriminate the recent from the ancient fraction (Capo et al., 2022), or assign a consistent stratigraphic age to taxa persisting in dormancy compared to those initially deposited as resting stages (Coolen and Overmann, 2007). Because of the typically very low biomass in ancient sediment samples, it is recommended to work in ultraclean lab facilities to minimize the potential for contamination and increase recovery of the true targets. DNA extraction replicates from low biomass samples can for example be pooled, or the volume of sediments and buffers can be scaled up and extracts can be concentrated using Amicon filters (Vuillemin et al., 2019, 2020). Hybridization capture techniques allow to focus metagenomic sequencing on specific biological targets (Beaudry et al., 2021), such as taxonomic and functional marker genes or metagenome-assembled genomes, with the possibility to bioinformatically identify DNA damage signals characteristic for ancient DNA (Armbrecht et al., 2021). This hybridization capture is performed by adding biotinylated baits that are complementary to the DNA sequences of interest prior to library synthesis to increase the proportion of the selected genomic regions in metagenomic libraries. Similarly, library preparation can be achieved from short fragments of single-stranded DNA using a biotinylated adapter oligonucleotide that have been tethered to magnetic beads for later recovery and amplification (Gansauge and Meyer, 2013). Cytosine deamination (observed as C-to-T transitions) is typically used to authenticate ancient sequences bearing characteristic DNA damage but it is important to keep in mind that computational filtering of ancient DNA leads to significant data loss (Borry et al., 2021; Pérez et al., 2022).

Endospore extractions: Endospore formation is a survival strategy found among Firmicutes. Although Firmicutes are one of the most frequently enriched and isolated groups in cultivation-based studies, they are often absent in molecular biodiversity inventories as their sedDNA remains locked in these resistant structures. Physical isolation of endospores from sediment samples can be used to specifically target endospore-forming bacteria, which can account for 5 to 20% of the combined community composition in total sedDNA extracts (Wunderlin et al., 2014b). The procedure includes a step where vegetative cells are lysed, followed by DNAse treatment that allow for subsequent filtration and enrichment of endospores from environmental sediment samples (Wunderlin et al., 2016). DNA is then extracted from the endospore enrichment by performing an enzymatic digestion directly on the filter. The relative abundance of bacteria with the potential to form endospores can be assessed via qPCR assays with primer pairs targeting the endosporulation-specific *spo0A* gene (Wunderlin et al., 2014a), and endospores can also be quantified based on the diagnostic biomarker dipicolinic acid (Wörmer et al., 2019).

RNA extractions: There are different commercially available extraction kits to recover RNA from frozen sediment samples, the critical step being the precipitation and efficient recovery of the RNA separate from inhibiting substances (Coolen and Orsi 2015; Vuillemin et al., 2020a; Orsi et al., 2020b). In low biomass samples, RNA extracts often remain below detection, even using high-sensitivity kits (Vuillemin et al., 2020b). To circumvent this issue, the initial amount of sample material and volume of extraction reagents can be scaled up. We discourage the use of RNAlater® solution to preserve samples in the field, as it is not adapted to sediment samples and often results in low nucleic acid yield and inhibition in later amplification stages (Rissanen et al., 2010). Instead, we recommend retrieving RNA from sediment minicores kept frozen at -80 °C after sectioning them into single use aliquots as this will minimize biases caused by repeated freezing-thawing. Once released from the cells, RNA molecules hydrolyse quickly and it may be prudent to perform transcription to synthesize the more stable complementary DNA (cDNA) prior to storage (Rosenow et al., 2001) or directly proceed with the preparation of metatranscriptomic libraries.

Activity rates: The incorporation of ^{3}H-thymidine into DNA (Kirschner and Velimirov, 1999) and ^{14}C-leucine into proteins (Fischer and Pusch, 1999) is a technique that allows monitoring bacterial secondary production in the aerobic zone. For anoxic sediments, specific process rates can be measured via sediment incubations with radiolabeled substrates, such as potential rates of sulfate reduction (Kallmeyer et al., 2004) or anaerobic oxidation of methane (Norði and Thamdrup, 2014). In deep sediments, modeling of D:L amino acid racemization rates allows inferring the distribution and turnover time of the deep biosphere in terms of living and dormant microbial biomass (Lomstein et al., 2012; Braun et al., 2017).

Negative control: In addition to *in situ* contamination controls (Kallmeyer, 2017), blank samples and mock communities are indispensable tools to identify and, if needed, also subtract DNA signals from ambient contamination in laboratories (e.g. airborne endospores, exospores, myxospores) (O'Sullivan et al., 2021) or extraction reagents (Glassing et al., 2016). These controls allow for later curation of the sequencing results (Pichler et al., 2018) as well as standardization and quality assurance of microbiome analysis (Tourlousse et al., 2022).

Targeted PCR assays for linking taxonomy to functions, fluorescence techniques

With the development of molecular probes based on the 16S rRNA and other functional marker genes (Table 1), qPCR and multiplex droplet digital PCR (Weisbrod et al., 2020) can be used to quantify and compare key features and populations within microbial communities, both with regards to taxonomic groups and functions (e.g. Fish et al., 2013; Alexander et al., 2015). A general technical difficulty in qPCR assays is the preparation and amplification of accurate and precise standard curves for all the primers used in targeting specific taxa and functional genes, as well as internal controls on amplification efficiency to compensate for coextracted inhibitors in different samples. Limits of detection are usually around 10^{2} to 10^{3} gene copies, depending on the dilution factor used (Boulter et al., 2016; Bender et al., 2018).

Taxonomic genes: Total sedDNA, which is comprised of both ancient and recent DNA from both eukaryotic and dormant/active prokaryotic material, can be superficially analyzed and compared by amplicon sequencing using primers that target universal 18S rRNA (eukaryotic) and 16S rRNA (prokaryotic) genes (e.g. Nichols et al., 2019; Capo et al., 2021b). The density and relative abundance of prokaryotic populations are primarily investigated using primers targeting the V4–V6 regions of the 16S rRNA gene, assuming a minor bias inherent to extraction and amplification efficiencies. However,

due to the variable number of 16S rRNA gene copies in genomes across phyla (Větrovský and Badrian, 2013), the use of such "universal" primer pairs can result in potential quantitative biases between the different clades studied (Starke et al., 2021). Primer pairs can also be designed *in silico* to target less conserved regions for a more selective identification of taxonomic groups (Morales and Holben 2009). For example, this can be done at the level of domains to compare the relative contribution of Bacteria and Archaea (Ye et al., 2012) with primers such as Arch519F-915R and Eub341F-534R, but also for more highly resolved populations (Narrowe et al., 2017). Taxonomic assignment of 16S rRNA gene amplicon sequences is commonly performed by grouping of recovered sequences into operational taxonomic units (OTUs) sharing an arbitrary level of sequence homology or unique amplicon sequence variants (ASVs). Representative sequences are then taxonomically assigned performing BLASTn searches against databases such as SILVA 16S rRNA small subunit (SSU) reference database (Pruesse et al., 2007; Quast et al., 2013).

Although cultivation-independent 16S rRNA gene surveys can be used to assess and compare the taxonomically diverse communities typical for sediments, they do not provide reliable information on the ecological functions of yet-uncultivated microorganisms or taxa with unresolved or variable functions (Macalady et al., 2013; Bier et al., 2015). Specific software (e.g. PICRUSt2, paprica) does at least in theory allow for reasonable predictions to be made about metabolism inferred from phylogeny and thereby describe the functionality of microbes in lacustrine ecosystems merely using taxonomic data (Douglas et al., 2020; Erazo et al., 2021). It should however be noted that such predictions critically depend on the availability of metabolically annotated reference genomes for functionally coherent target groups, and may thus be less well suited for sediments and other environments with a paucity of such reference data (i.e. where many organisms are uncultured and functionally undescribed).

After assessment of the community composition and as an alternative to the abovementioned approach, additional primer pairs targeting functional genes (Table 1) can be used to quantify the potential for specific processes related to biogeochemical cycling, and thereby indirectly associate taxonomy to functional traits. For instance, primers targeting different respiration types (Fig. 2), such as those involved in denitrification (i.e. *narG*, *napA*, *nirK*), sulfate reduction (i.e. *dsrAB*, *aprAB*), and methanogenesis (i.e. *mcrA*) can be amplified from the same DNA extracts to track the vertical distribution of microbial guilds and correlate them with the taxonomic assignment of 16S rRNA genes while avoiding inferences based on information obtained from their sometimes quite distantly related cultivated relatives.

Comparison with cell count techniques: Classic quantification of microbial biomass is usually achieved via cell counts by means of fluorescence microscopy, using different DNA stains, such as Acridine Orange (Parkes et al., 1994), 4',6'-Diamidin-2-phenylindol (DAPI) (Suzuki et al., 1993), and SYBR Green I (Kallmeyer et al., 2008). Optimizations of fluorescent microscopic cell enumeration protocols may include LIVE/DEAD cell counts to discriminate living from dead cells (Haglund et al., 2003), fluorescent *in situ* hybridization (FISH) with molecular probes targeting specific taxonomic groups (Moter and Göbel, 2000) and related protocols used to enhance the signal, e.g. catalyzed reporter deposition or CARD (Yamagushi et al., 2015), or detect metabolic activity, i.e. bioorthogonal non-canonical amino acid tagging or BONCAT (Hatzenpichler et al., 2014). Enumeration of microorganisms can be further streamlined using flow cytometry (Morono et al., 2013) and fluorescence-activated cell sorting (FACS) (Kalyuzhnaya et al., 2006). Although the respective shape of the downcore profiles is usually reliable, qPCR values and cell counts can easily be offset by orders of magnitude in the sediment (Lloyd et al., 2013).

Metagenomics and metatranscriptomics

High-throughput shotgun sequencing techniques can provide extensive information on the taxonomic identities and patterns of environmental occurrence of bacteria, archaea as well as viruses and eukaryotes (Rinke et al., 2013; Hug et al., 2016). Assigning metabolic functions to the phylogenetic diversity documented from the lacustrine subsurface does not always unravel cryptic interactions across metabolic guilds (Macalady et al., 2013), nor their actual metabolic activities in link to past trophic levels in the corresponding stratigraphic sequences (Ellegaard et al., 2020; Garner et al., 2020). Metagenomes and metatranscriptomes provide detailed insights into the genomic structure and metabolic potential and even activity of complex microbial communities (Vavourakis et al., 2018). The genetic potential of hitherto uncultivated microbial populations can be retrieved from shotgun metagenomes by reconstruction and analysis of metagenomic-assembled genomes (MAGs) (Solden et al., 2016; Jiao et al., 2021). The systematic and cumulative recovery of MAGs from different locations will in the longer run allow for pangenomic analyses of lacustrine microbiomes (Thompson et al., 2017; Nayfach et al., 2021), and such genomic resources will also facilitate and enable a population-centric interpretation of functional gene expression patterns via metatranscriptomics for a holistic understanding of the subsurface biosphere.

The critical role of read length: High-throughput sequencing can provide either short reads (2 ×150 bps, i.e. base pairs) that allow for rapid screening of functional genes in diverse microbial communities, or reads of intermediate length (2 × 300 bps) that are more effective for contig assembly (Knight et al., 2018). Contrary to ancient DNA that represents short fragments, longer reads are more likely to derive from intact cells for which a combination of DNA size selection long read sequencing technology (Oxford Nanopore, Pacific Biosciences) would allow the researcher to specifically target viable cells and rule out long-dead cells. The latter long-read technology is mainly feasible for low diversity samples where the aim could be to obtain reads that are long enough for MAG completion (Moss et al., 2020). Metagenomic sequencing of an environmental sample displaying a high taxonomic diversity may for example produce multiple fragmented bins, with potential chimeric edges and inclusions of false positive reads across bins. In searching gene expression, most of the initial RNA extracts are composed of non-coding ribosomal RNA (He et al., 2010). The reads assembled from metatranscriptomic libraries are then only analyzed in terms of messenger RNA, which is indicative of active protein synthesis and represents transcripts. A read length of < 300 bp is typically sufficient to identify such transcripts and a separate bioinformatic pipeline is needed to taxonomically assign them or map the transcripts back to the corresponding MAGs and SAGs. Similarly, in targeting ancient DNA, metagenomic assembly usually results in partial and less well supported bins due to the overall short read lengths of the fragmented DNA (Der Sarkissian et al., 2021). Because of the intrinsic nature of sedDNA and a necessity to optimize sequencing costs to the usefulness of the data, short reads are best suited for sediments, for which an alternative approach to the binning step can be applied (Key et al., 2017). In this case, the focus is rather on mining specific marker genes relevant to the studied environment, for instance by performing BlastP and taxonomic assignments against the corresponding functional gene database, e.g. FunGene (Fish et al., 2013).

On-site contamination control and core sampling

Gravity coring techniques allow for retrieval of undisturbed sediment-water interface and underlying fine grained sediment sequences from lakes (Weaver and Schultheiss, 1989). Given the lack of drilling fluids, the core samples are uncontaminated, except for possibly the outer few mm where some surface

material might be dragged down by the core barrel (Kallmeyer, 2017). These rims have to be scraped off under a protective atmosphere (e.g. glove bag, anaerobic chamber) using a sterile spatula.

In hydraulic drilling operations, it is almost impossible to maintain sterile conditions on site as the drill fluid itself contains surface microbes and other contaminants. Moreover, lake surface waters are usually pumped in the hydraulic system used to shoot core liners into the sediment, which can potentially result in a trans-contamination that is hardly detectable at the time of sampling and carried on in downstream analysis of the samples. The addition of tracer compounds or fluorescent tracer particles can then be used for identification and rejection of the parts of the hydraulic cores that were infiltrated by the drill fluid (Friese et al., 2017; Kallmeyer, 2017). Once retrieved, the sediment core liners from drilling operations can be subsampled on site according to a strategy that allows for successive core measurements of physico-chemical properties (Fig. 7A), retrieval of bottom waters and pore water samples with minimal exposure to ambient conditions (Fig. 7B), sediment material for sedDNA and sedRNA using sterile end-cut syringe minicores (Coolen et al., 2013) and ATP+ADP+AMP luminometer assays as an indication of living cell biomass (Vuillemin et al., 2010; Orsi, 2023). The stratigraphic description and subsampling for bulk parameters (Fig. 7C) can be performed according to standardized procedures (e.g. Ohlendorf et al., 2011). The sampling resolution across the sediment stratigraphy has to take into consideration factors, such as sedimentation rates, sample heterogeneity, and degree of sedDNA degradation with depth, and biological replicates are required (Pearman et al., 2021).

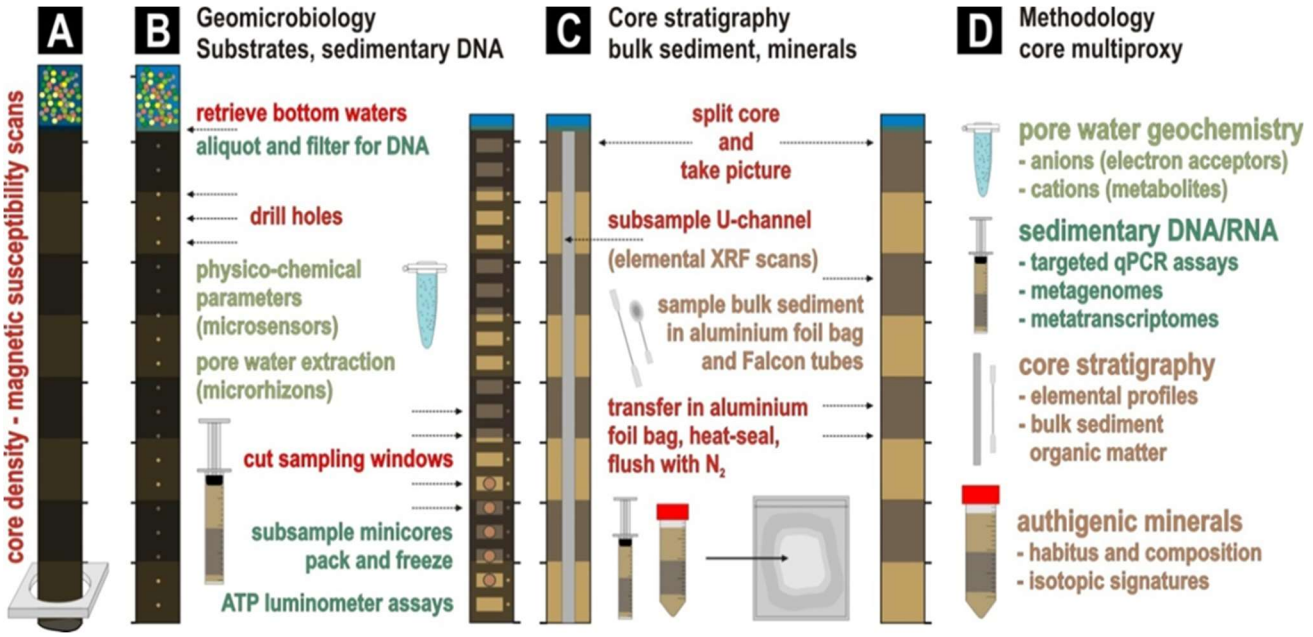

Figure 7. **Tentative implementation of an *in situ* aseptic protocol to the standardized strategy applied in lacustrine environmental studies. (A)** Core retrieval and core measurements of physico-chemical parameters; **(B)** perforation of holes, measurements of physico-chemical parameters using microsensors (e.g. TDS, resistivity, pH, O_2 concentrations), pore water extraction using rhizons or sediment peepers, aperture of sampling windows and subsampling for DNA/RNA extractions using sterile cut-off syringes (i.e. minicores), storage under protective atmosphere in hermetically sealed bags (or flash freezing in liquid N_2), and assessment of living cell biomass via ATP+ADP+AMP luminometer assays. At this point, the sampling windows can be taped; **(C)** core splitting and stratigraphic description, sampling of U-channels for stratigraphic profiles (e.g. paleomagnetism, X-ray fluorescence elemental profiles), sampling of bulk sediment (e.g. organic content, minerals); **(D)** this tentative sampling methodology includes physico-chemical parameters, geochemistry of pore water, sedDNA/RNA, elemental profiles on U-channels, characterization of OM and authigenic minerals in bulk sediment.

Summary

General microbial patterns of biogeography can be established based on sedDNA retrieved from diverse inland aquatic ecosystems, provided that certain variable environmental factors are taken into consideration in order to trace the admixture of prokaryotic sedDNA preserved in lacustrine sediments from source to sink. These include several watershed characteristics, such as climate and mineralogy in the catchment and degree of urbanization, which in turn determine the lake regime, productivity and geochemistry of the water body, redox conditions at the sediment-water interface, sedimentation rates and OM content over time.

Records of environmental conditions through the preservation of prokaryotic sedDNA will partially be obscured by the presence of a subsurface biosphere that remains active during burial. Sediment colonization and selective growth of specific sub-populations of the resident microbiomes are inherent to the substrates available in lacustrine deposits. Microbial guilds reflective of respiration types and OM decomposition usually go hand-in-hand with the geochemical gradient that develops in the sedimentary column during early diagenetic processes, but may also prevail in specific stratigraphic intervals. Thus, the correct attribution of prokaryotic sedDNA sources to an environmental context is essential for resolving past and modern ecosystem functioning. Because the succession of microbial taxa pre-adapted to gradual depletion of electron donors and acceptors is relatively well known, sources of sedDNA inherent to resident microbial communities can be discriminated and provide evidence of diagenetic processes during burial. In contrast, ancient sources of sedDNA that persist in microbially active sediments are exposed to a constant turnover, leading to preferential preservation of dormant stages over free sedDNA.

Bacteria and archaea are tremendously diverse, and therefore there is the need to rigorously assign their metabolic functions and assess their degree of activity along sediment archives. Beyond taxonomic surveys and geochemical profiling of the subsurface biosphere, novel procedures are being customized to sort, target, sequence and assemble sedDNA fragments of interest to unravel specific biogeochemical interactions in lacustrine ecosystems pertaining past and actual ecological changes at the local and global scale.

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