



Long-term perspectives on terrestrial and aquatic carbon cycling from palaeolimnology

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Lakes are active processors and collectors of carbon (C) and thus recognized as quantitatively important within the terrestrial C cycle. Better integration of palaeolimnology (lake sediment core analyses) with limnological C budgeting approaches has the potential to enhance understanding of lacustrine C processing and sequestration. Palaeolimnology simultaneously assimilates materials from across lake habitats, terrestrial watersheds, and airsheds to provide a uniquely broad overview of the terrestrial-atmospheric-aquatic linkages across different spatial scales. The examination of past changes over decadal–millennial timescales via palaeolimnology can inform understanding and prediction of future changes in C cycling. With a particular, but not exclusive, focus on northern latitudes we examine the methodological approaches of palaeolimnology, focusing on how relatively standard and well-tested techniques might be applied to address questions of relevance to the C cycle. We consider how palaeolimnology, limnology, and sedimentation studies might be linked to provide more quantitative and holistic estimates of lake C cycling and budgets. Finally, we use palaeolimnological examples to consider how changes such as terrestrial vegetation shifts, permafrost thaw, the formation of new lakes and reservoirs, hydrological modification of inorganic C processing, land use change, soil erosion and disruption to global nitrogen and phosphorus cycles might influence lake C cycling. © 2015 The Authors. *WIREs Water* published by Wiley Periodicals, Inc.

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INTRODUCTION

Quantification of the terrestrial carbon (C) cycle is paramount to understanding global climate change, and lakes, as ‘landscape chimneys,’ play a key role in terrestrial C processing.¹ Most lakes are considered to be net C sources to the atmosphere, emitting carbon dioxide (CO₂) and methane (CH₄), and are highly active C processing hotspots.^{1–4} Yet lakes also simultaneously sequester C in their sediments, comprising one of the largest stores of organic C (OC) on the continents.^{5–8} A major challenge therefore exists in trying to quantify relative rates of C evasion versus sequestration in lakes and the

influence this has on C fluxes from land, through river basins and to the ocean. Global estimates suggest that annual net lake C evasion exceeds sequestration and inland waters receive 1.9 PgC year⁻¹ from streams and rivers of which 0.2 PgC year⁻¹ accumulates as sediment, 0.8 PgC year⁻¹ is evaded to the atmosphere and 0.9 PgC year⁻¹ is delivered to the oceans,⁹ although the rates of C evasion in lakes⁴ and rivers¹⁰ might be higher. Therefore, the 'active pipe model' highlights that lakes are not simply passive vessels for C transport, but play a critical role in C processing of sufficient magnitude to alter regional C budgets.⁹ In this review, we outline the contribution that the long-term and integrative perspective offered by palaeolimnology can make in understanding the complex interplay of physical, chemical, and biological processes, which influence these C pathways in lakes.

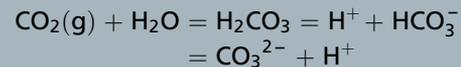
C within lake ecosystems can be separated into four major pools (Box 1). Dissolved inorganic C (DIC; as CO₂) may be fixed into organic form by autotrophs (through photosynthesis or chemosynthesis; autotrophy), and reciprocally organic C can be oxidized/mineralized through physical, chemical, and biological (e.g., respiration/heterotrophy) processes to CO₂ (aerobic conditions) or CH₄ (anaerobic conditions). The balance of these processes determines whether organic and inorganic C entering a lake is emitted to the atmosphere as a gas, incorporated into the particulate C pool to be collected in sedimentary deposits or exported downstream. Understanding how these processes will change in the future is key to calibrating the terrestrial C cycle.¹ One way to address this issue is to use the past as an analogue for future scenarios. Palaeolimnology, the investigation of lake sediments, provides a direct methodology for documenting C inventories in water bodies. Furthermore, through sediment proxies (Figure 1) it is possible to identify past changes in C flux from land to lake as well as gaining qualitative insights into the ways in which it is processed. Distinctive from most limnological approaches, which often focus solely on pelagic measurements (in the water column), palaeolimnology integrates C from all components of the catchment and lake ecosystem, including the benthos. Because benthic production accounts for a large proportion of primary productivity in many lakes,^{11,12} this integration has the potential to provide a more holistic overview of changes in whole-ecosystem C processing, which can be used to refine regional C budgets.¹³

One major unresolved question is how processing of terrestrial C within lakes and wetlands will alter with future global environmental change (GEC),

BOX 1

FORMS OF CARBON IN LAKE ECOSYSTEMS

Dissolved inorganic carbon (DIC): Carbon dioxide (CO₂) is the major DIC pool and either passes into lakes from the atmosphere, or is produced *in situ* by respiration and oxidation of organic material. When dissolved in water to form carbonic acid, it can dissociate as follows dependent on pH:



DIC links atmospheric and aquatic C pools.

Particulate inorganic carbon (PIC): PIC includes solid inorganic carbonate material, usually calcium carbonate (as aragonite or calcite). In lakes, PIC accumulates in sediments, but is sometimes found suspended in the water when mass production by phytoplankton causes 'whiting events.' PIC precipitation is common in lakes within carbonate-rich catchments and closed-basin lakes where salts accumulate. Charophytes may become encrusted in calcium carbonate deposits, or 'marl,' which can be a significant component of the lake sedimentary C pool.

Dissolved organic carbon (DOC): DOC includes molecules in water usually classified as <0.45 μm in size. Dissolved organic matter (DOM) is also used to describe organic material. Allochthonous DOM delivered to lakes is often brown-coloured (CDOM) deriving from partly decomposed terrestrial vegetation and soils including humic and fulvic acids, as well as lower molecular weight (Mr) compounds. Autochthonous DOC/DOM sources are usually lower Mr and colourless C compounds, released as metabolic byproducts by lake microbes and organisms. DOM is important in the terrestrial C cycle because it is highly mobile and can be utilized by heterotrophic bacteria as an energy source.

Particulate organic carbon (POC) (and particulate organic matter, POM) includes particles >45 μm, which exist in lakes either suspended in the water or collected in the lake bottom as sediments. Autochthonous POM may include living organisms such as bacteria, phytoplankton, zooplankton, and plants or detrital remains of decaying organisms. Allochthonous POM includes particulate matter such as vegetation remains and soil erosion washed into lakes and air-transported materials such as dust, pollen, and particulate contaminants.

because this may be an important feedback for greenhouse gas production or sequestration. Common approaches to this question use surveys across latitudinal gradients to understand how lakes process C within different biomes.^{14,15} This ‘space for time substitution’ approach can provide analogues for how lakes function within different climatic, edaphic, and biogeochemical circumstances, and thus guide likely trajectories of future change. Such approaches are, however, only achievable in areas with high lake density and so have been focused on northern latitudes, where the majority of lakes occur.¹⁶ Spatial surveys are only partially satisfactory for investigating C cycling because many other factors co-vary spatially, particularly between mid-high latitudes where the major climatic and vegetation transitions occur.^{4,17} For example, seasonal change in day length differs substantially between temperate-Arctic areas but most measurements of lake C processing have been conducted in boreal and temperate regions, which retain daylight during the winter and have greater anthropogenically derived nutrient burdens.¹⁸ The under ice period is important because heterotrophy dominates leading to major CH₄ degassing during the ice melt period,^{19–21} but little is known of under ice processes, particularly in Arctic lakes.²² Therefore, half or more of the annual lake C cycle within

the Earth’s most lake-rich regions is probably inadequately quantified.¹⁶ Where spatial comparisons have limitations for projecting future change in individual regions, the temporal approach of palaeolimnology has the potential to address some of these issues, especially when combined with comparisons across landscapes.^{23,24}

HOW CAN WE MEASURE ‘C CYCLING’ USING PALAEO LIMNOLOGY?

C cycling is a rather general term, but understanding the role of lakes within the terrestrial C cycle requires knowledge of lake C pools and the processes that alter relative shifts between them. Lake sediments sequentially archive material from the watershed, airshed (allochthonous), and lake environment (autochthonous) allowing direct comparison of how terrestrial, atmospheric, and aquatic processes are coupled through time (Figure 1). Although not implicitly process-based, well-designed palaeolimnological studies, which use a selection of well-chosen proxies are able to address many questions of relevance to C cycling. The section below focuses on routinely applied standard palaeolimnological techniques.

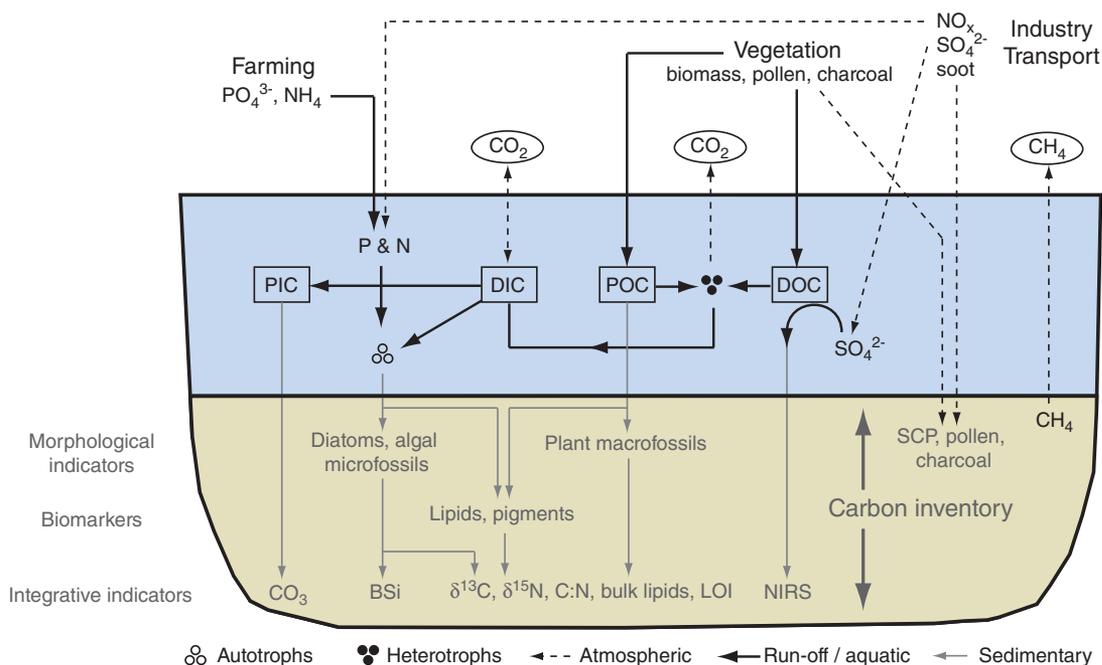


FIGURE 1 | Schematic showing the origin and processing pathways of commonly used palaeolimnological proxies in lake sediments (grey), including the influence of modifications by anthropogenic and natural processes (agriculture, fossil fuel combustion, and changes in terrestrial vegetation cover). Carbon (C) pools in lake waters (blue) include particulate inorganic C (PIC), dissolved inorganic C (DIC), particulate organic C (POC), and dissolved organic C (DOC).

C Inventories

Palaeolimnology can directly measure the amount of C sequestered within lacustrine basins (the C standing stock) and variability in past rates of C accumulation. Sedimentary C content can be estimated through by loss-on-ignition (LOI) after burning at 550°C (organic) and 925°C (carbonate) and correcting for C content,^{25,26} or via an elemental analyzer on acidified (to remove inorganic carbonates) or non-acidified sediments.²⁷ These straightforward methods estimate the relative C in organic and inorganic (usually carbonate) forms versus minerogenic material (including biogenic silica, BSi).²⁸ In areas where lake formation dates are known, regional estimates of lake C stocks are possible using lake morphometry and volumetric density-corrected calculations of sediment.^{5,29,30} Sediment cores dated using a combination of ²¹⁰Pb, ¹³⁷Cs, radiocarbon (¹⁴C) and other techniques can be used to quantify changes in the C accumulation rate (CAR), for an overview of changes in C processing over longer timescales.³¹ Most palaeolimnological studies are based on a single sediment core taken from the deepest central part of the basin where sediment focusing occurs (fine particles are preferentially deposited in deeper parts of the lake basin).³² Estimates of whole-basin CARs require correction for sediment focusing, which can be achieved in recent sediments using the ratio of sediment ²¹⁰Pb flux: regional atmospheric ²¹⁰Pb flux^{33,34} or through multiple coring.³⁵ Seismic surveys are informative in larger or deeper lake basins with heterogeneous sediment coverage,^{35–37} or where gas hydrates might be important for C budgets.³⁸

Morphological 'Fossil' Macro- And Microscopic Remains

Terrestrial pollen, spores, and plant macrofossils provide a relatively direct assessment of land vegetation cover³⁹ and, by inference, the presence of allochthonous C pools, soil development, and precipitation (Figure 1). Therefore, these proxies may be used to estimate the potential for changes in DOC runoff or soil erosion into lakes.^{40,41} Other allochthonous and wind-borne morphological remains indicative of processes relevant to C-cycling may derive from coal-fired power stations, which emit soot particles and pollutants,⁴² or from fires on land, which release charcoal into lake air- and watersheds.⁴³ Many autochthonous primary producers in lakes leave identifiable remains in sediments, especially diatoms (frustules), chrysophytes (cysts and scales), cyanobacteria (akinetes), dinoflagellates (cysts), and the chlorophyte alga *Pediastrum* (cell walls).⁴⁴ If fluxes are

quantified from dated cores a provisional estimate of changes in primary productivity of the source organism is possible.⁴⁵ However, sedimentary remains are only a remnant of the original community because of decomposition and differential preservation, and some remains such as cysts are formed during particular life stages.⁴⁶ Therefore, most estimates of past microfossil flux are used to infer relative measures of productivity changes through time rather than whole-basin estimates (c.f. Ref 32). Nevertheless, estimation of microfossil flux is a relatively straightforward but under-utilized technique to quantify variability in autochthonous C sequestration rates by individual groups of biota. Numerous primary and secondary consumers also leave sedimentary remains (e.g., chironomids, cladocera, oribatid mites, and sponge spicules⁴⁷). Indicator taxa tolerant to oxygen stress (e.g., *Chironomus*) can be used to infer hypolimnetic anoxia, which has implications for sediment C preservation and methanogenesis.⁴⁸ Using a combination of proxies it is possible to reconstruct paleo-food webs⁴⁹ to infer past changes in lake functioning. For example, major shifts between benthic and pelagic primary and secondary production in shallow lakes can infer changes in major habitats for autotrophic C production, processing and energy flows.^{50,51}

Biochemical Indicators of C Processing

Many morphological remains decompose before deposition in sediments and in these cases biochemical markers (biomarkers) may be used as sedimentary proxies.⁵² These may include chlorophyll and carotenoid pigments, indicative of certain algal and bacterial groups (e.g., cryptophytes and cyanobacteria) and used to estimate autochthonous primary production.⁵³ Some bacteriochlorophylls and carotenoids from obligate anaerobic photosynthetic bacteria (e.g., Chlorobiaceae and Chromatiaceae) can be used to infer anoxia, with associated implications for the preservation of sedimentary C. Other ultraviolet radiation (UVR)-screening pigments such as scytonemin and derivatives are produced by some microbes on exposure to UVR and so their production relative to other pigments can quantify water staining by CDOM.⁵⁴ Other lipid biomarkers include a range of hydrocarbons and carboxylic acids, alcohols, and ketones, which can be used as individual biomarkers, e.g., dinostanol (a sterol chlorin ester biomarker for dinoflagellates),⁵⁵ phenolic compounds from coniferous trees,⁵² hopanoid biomarkers from heterotrophic bacteria,^{56,57} archaeols from methanogenic archaea,^{58,59} and specific fatty acids and hopanoids

from CH₄-oxidizing bacteria.^{60,61} With the exception of chlorophyll and carotenoid pigments, many individual lipid biomarkers are present in low sedimentary concentrations however, which restricts their routine and high-resolution application in sediment analyses. As analytical techniques evolve and knowledge of affinities develops it is clear that organic geochemistry and emerging techniques such as ancient DNA will provide further insights into lake C processing.⁶²

Integrative Sedimentary Geochemistry

An alternative or complementary approach to specific biomarker methods is to use integrative measures on the OM fraction in sediments to evaluate broad shifts in source and process. The atomic ratio of carbon:nitrogen (C:N) is commonly used to infer the source of sediment OM because terrestrial material usually contains more C-rich cellulose and lignin than autochthonous algal material, which has a lower C:N ratio. Ratios of long (more common in terrestrial vegetation) and short chain (more common in aquatic organisms) alcohols and *n*-alkanes can be similarly compared to infer relative terrestrial fluxes.^{52,63} Near infra-red spectrometry (NIRS) is a nondestructive spectral measure of sediment properties, which correlates with water column DOC concentrations at the time of sediment deposition, although the basis of this correlation remains unclear.^{64,65} C stable isotopes are widely used in palaeolimnology and whilst the principles underlying isotopic fractionation are theoretically well understood, interpreting bulk (c.f. organism-specific) lake $\delta^{13}\text{C}$ ratios in sediment profiles requires thorough understanding of the lake-catchment system. Sedimentary $\delta^{13}\text{C}$ can be measured within the organic ($\delta^{13}\text{C}_{\text{org}}$) and inorganic ($\delta^{13}\text{C}_{\text{inorg}}$) sediment fractions and may record shifts in terrestrial/aquatic contributions to the lake basin and changes in process (including diagenesis).^{63,66} For example, $\delta^{13}\text{C}$ values in DIC fixed during photosynthesis may depend on lake-atmosphere CO₂ exchange, algal productivity rates, and decomposition of terrestrial OM into DIC, which is then incorporated into algal material.⁶⁷ DIC derived from CH₄-depleted $\delta^{13}\text{C}$ ratios may be effectively incorporated and preserved in the head capsules of chironomids^{68,69} and the $\delta^{13}\text{C}$ values of aquatic macrophyte remains have been used to reconstruct HCO₃⁻ concentrations.⁷⁰ Changes in catchment vegetation (e.g., C3 versus C4 plants) are also important drivers of sedimentary $\delta^{13}\text{C}_{\text{org}}$,⁷¹ but extraction of isotopes from isolated organic fractions such as leaf waxes can refine terrestrial vegetation

reconstructions.⁷² BSi analysis is a rapid alternative to microfossil analysis for quantifying sedimentary contributions from siliceous biota⁷³ and the fractionation of stable silicon isotopes $\delta^{30}\text{Si}$ can indicate palaeoproductivity.⁷⁴ Radiocarbon dating of terrestrial plant macrofossil and contemporary sediments frequently shows offset ages.⁷⁵ Whilst these discrepancies are regarded as troublesome for deriving accurate chronologies, they are informative of past lake water equilibration with atmospheric CO₂ and incorporation of 'old' C from the catchment (e.g., through permafrost melt), which can become incorporated into sedimentary OM.⁷⁶

QUANTITATIVE INTEGRATION OF PALAEO-LIMNOLOGY AND LIMNOLOGY

The previous examples describe how palaeolimnology can be used to directly quantify lake C inventories, CARs and changes in source materials accumulated in lake basins, and thus fill gaps in understanding of C sequestration and associated processes that are impossible to measure using limnological techniques⁸ (Figure 2). Improvements in the application of palaeolimnology might be achieved by a more critical consideration of sediment redistribution and focusing processes, which need to be accounted for when comparing sediment accumulation rates among different lakes.^{33,77} However, quantitative interpretation of palaeolimnology also requires stronger integration with limnology and sedimentation studies. Commonly, linkages between the sediment record and limnological conditions are established by correlating limnological conditions with sediments through space or time. Hence, in general, more C is sequestered in productive than unproductive lakes (c.f. 11 m of sediment in Denmark with 2 m Greenland over the Holocene^{31,78}). However, direct correlations between lake productivity and C sequestration are far too simplistic because they ignore the roles of allochthonous C delivery, the processes which cause decomposition and preservation of C in the water column and sediment focusing. Measurements in the water column and sediments can complement palaeolimnological observations to facilitate improved interpretations. Next, we explore how lake sediments are formed and the processes which change them during and after deposition to consider how this influences the interpretation of C cycling using palaeolimnology.

Sedimentation of C first requires production of particulate C that is composed of sources from inside

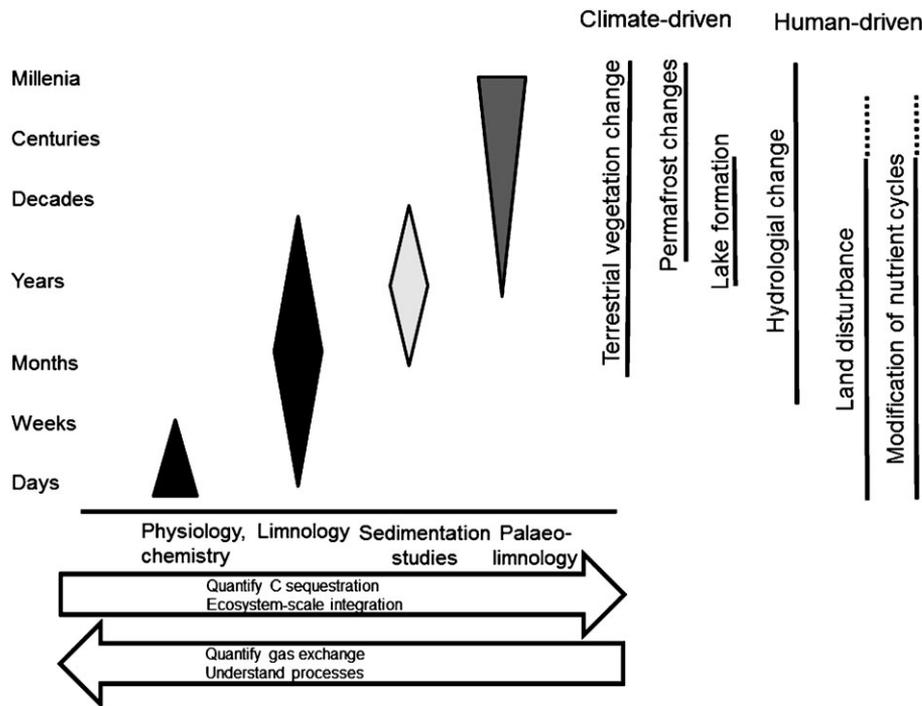


FIGURE 2 | Conceptual model illustrating how palaeolimnology integrates with other methodologies in quantification of terrestrial-aquatic carbon (C) cycling, and the elements that can be best quantified by each method (arrows). The breadth of the shapes indicates how widely the methodology has been applied at each timescale and the intensity of shading indicates the relative frequency that each type of technique has generally been applied. The majority of C cycling studies in lakes thus far have focused on physiological/chemical and limnological processes, although there are a growing number of palaeolimnological studies dedicated to this topic. In comparison there are fewer quantitative studies of C sedimentation using techniques such as sediment traps to understand whole lake C budgets; such studies are vital to bridge the gap between palaeo/limnological methods. Timescales of operation for a range of global environmental change processes discussed in the latter half of the review are presented for comparison.

and outside of the lake. Allochthonous POC can be a significant component in lake sediments from erodible catchments with organic soils,^{35,79} whereas in-lake production of POC depends strongly on the autotrophic–heterotrophic balance and food web processes. Up to 95% of DOC may be removed from lake pools by photochemical mineralization to CO₂, which in turn is influenced by physical processes such as lake mixing.^{80,81} It is not possible to directly measure the resulting gaseous emissions from lakes using palaeolimnology, but sediments provide a means of validating and guiding such limnological gas measurements. For example, sedimentary δ¹³C analyses might identify whether methanogenesis is important to the overall lake C budget to determine whether gas measurements, which may be temporally discontinuous, have effectively captured all relevant processes.^{68,82} Microbial processing of DOM also provides a pathway for POC (sediment) production because heterotrophic organisms utilize DOM as an energy source and are an important component of the POC pool, detectable by sedimentary C isotope

and other organic biomarker analyses.⁸³ Heterotrophic consumption of DOM releases nutrients (‘the microbial loop’), which can fertilize growth of autotrophic algal POC, but phototrophic productivity rates are moderated by light absorption by CDOM.⁴ Each of these POC sources is available for consumption and incorporation into higher parts of the lake food web.⁸⁴ These factors interact to determine the overall composition, abundance, and fate of the POC pool, and hence the sediment record that is ultimately preserved and detected by palaeolimnology.^{85,86}

Sedimentation studies demonstrate that only a small fraction of the C fixed or processed in lakes ends up in sediments.^{87,88} For example, approximately 90% of algal pigments and 85% of C is oxidized before leaving the epilimnion, so that ca. 6% of C reaches lake sediments.⁵² Models describe how lake depth and morphometry greatly influences these values because shorter sinking times for seston provide fewer opportunities for mineralization; thus incorporation of C should be most efficient and C sequestration rates should be greater in shallow

lakes.^{36,88,89} Counteracting this is the influence of bioturbation, resuspension, oxygenated sediment conditions, and generally faster flushing rates that exist in shallower lakes, which can enhance degradation after deposition, encourage export from the lake and reduce C burial efficiency.^{90–92} Lake morphometry is also important because C sequestration varies spatially within basins, with sediment focusing in the deeper areas distal from degradation pressures in the littoral zone.^{93,94} Such considerations are highly relevant for C budgets in lake-rich landscapes because most lakes globally are small and shallow.¹⁶ Benthic algal production usually exceeds planktonic production in shallow lakes but the relative influence that this has on C sequestration is poorly quantified.¹¹ Because some palaeolimnological proxies such as diatoms can indicate relative planktonic: benthic production, sediment core analyses provide a simple but, as yet, under-utilized means to quantify how benthic–pelagic balances influence net C sequestration.

Another important process to be considered is changes to the sediment record following deposition.⁸ Most sediment decomposition occurs in the first 5 years after deposition (e.g., around 20% of the C and 30% of the N is mineralized over this timescale).^{66,88,95} Selective loss of nitrogenous OM in the upper sediments reflects the lability of compounds such as proteins and chlorophylls in comparison to terrestrial materials such as lignins and cellulose.⁹⁶ Below this zone, the preservation of sedimentary OM is more stable,⁸⁸ and therefore many lake C sequestration studies exclude the less stable upper ca. 10 cm of sediment because it is unrepresentative.³³ Mineralization of C in lake sediments is positively correlated with lake temperature, with projected future temperature increases leading to a 4–27% decline in lake OC burial.⁹⁷ However, warming also increases the delivery of pelagic OC to sediments, which may offset a reduction in burial efficiency of OC from mineralization.⁸⁶ The importance of the sediment–water interface in methanogenesis is also becoming more widely recognized.⁸ In the light of these complex and interacting processes, palaeolimnology is able to integrate net C sequestration under different climatic conditions to provide an overview of likely C sequestration trajectories. For example, comparisons of Holocene sediment cores in an undisturbed region of Greenland show that mean CARs do not differ substantially between warmer and cooler periods, suggesting that although C production and mineralization rates might have changed, other factors that influence C sequestration (e.g., land to lake DOC flux, C production changes

associated with water level fluctuations) have compensated for them in this region.³¹ Holocene core surveys in Europe and North America similarly attribute fluctuations in CARs to land use rather than climate.³⁰ Therefore, whilst limnological measurements of DOC fluxes or gas/dissolved gas measurements can quantify land–water C fluxes on short-medium timescales,^{98–100} palaeolimnology can be used for long-term validation of lake C budgets. There is much scope for establishing the drivers and mechanisms of CAR variability using multiproxy palaeolimnology.

GEC AND THE C CYCLE

Many GEC processes that influence lakes and their watersheds operate on timescales that cannot be effectively addressed using ‘real-time’ physiological, limnological, or sedimentation measurements (Figure 2). Palaeolimnology can be used to understand GEC processes retrospectively where lake measurements do not exist and provide information on the decadal–millennial timescales relevant to many GEC processes. The next section considers possible future trends in C dynamics in lakes, with examples of how lake sediment records can be used to understand the fate of C within changing terrestrial–aquatic systems.

Climate-Driven Vegetation Changes

Climate change can alter the type and density of terrestrial vegetation cover¹⁰¹ with implications for the availability and quality of C transported (usually as DOC) from land to water.^{84,99,102} As the northward spread of shrubs into tundra regions indicates, vegetation biomes are changing and will continue to change with future warming.^{103–106} Climate also affects DOC delivery to lakes by altering precipitation and flow paths, which are themselves influenced by soil and vegetation development.^{85,107} These influences on C cycling are evident when comparing lakes over different biomes (Figure 3). Some of the differences in lake C processing described in Figure 3 can be detected in surface sediments of lakes collected across vegetation transitions indicating the potential for palaeolimnology. Pollen and macrofossils are well-established indicators of terrestrial vegetation used to identify vegetation assemblages on regional to continental scales.¹¹⁷ NIRS analysis of surface sediments demonstrates that DOC concentrations are lower in Swedish lakes above treeline (e.g., Figure 3(b)) compared to those with forested catchments where the DOC supply is more abundant

(Figure 3(a)).⁶⁵ In line with this observation, relative abundance of algal UVR-screening compounds are higher (clearer water) and C:N ratios lower (less terrestrially derived C) in surface sediments of lakes above treeline.¹¹⁸ Presence of tree cover appears to suppress autotrophic production (measured as sedimentary pigments) in lakes with forested catchments, because light is limited in brown-stained lakes.^{15,118,119} Lakes with limited catchment soil and vegetation development (e.g., Antarctic, High Arctic, and montane lakes; Figure 3(d)) often have extremely low DOC concentrations and UVR-screening pigments such as scytonemin can form a significant

proportion of the sedimentary pigment assemblage.^{115,120,121} These spatial surveys validate the utility of certain palaeolimnological proxies in detecting the presence and effects of vegetation cover around lakes.

Such spatial observations are reflected in temporal changes of sediment records. In montane lakes that have transitioned between forested and alpine conditions, scarcity of vegetation-derived DOC inhibits primary production through UVR damage during alpine periods.¹²² This response is more subtle in Swedish lakes at boreal-tundra treeline where low-intermediate DOC concentrations promote

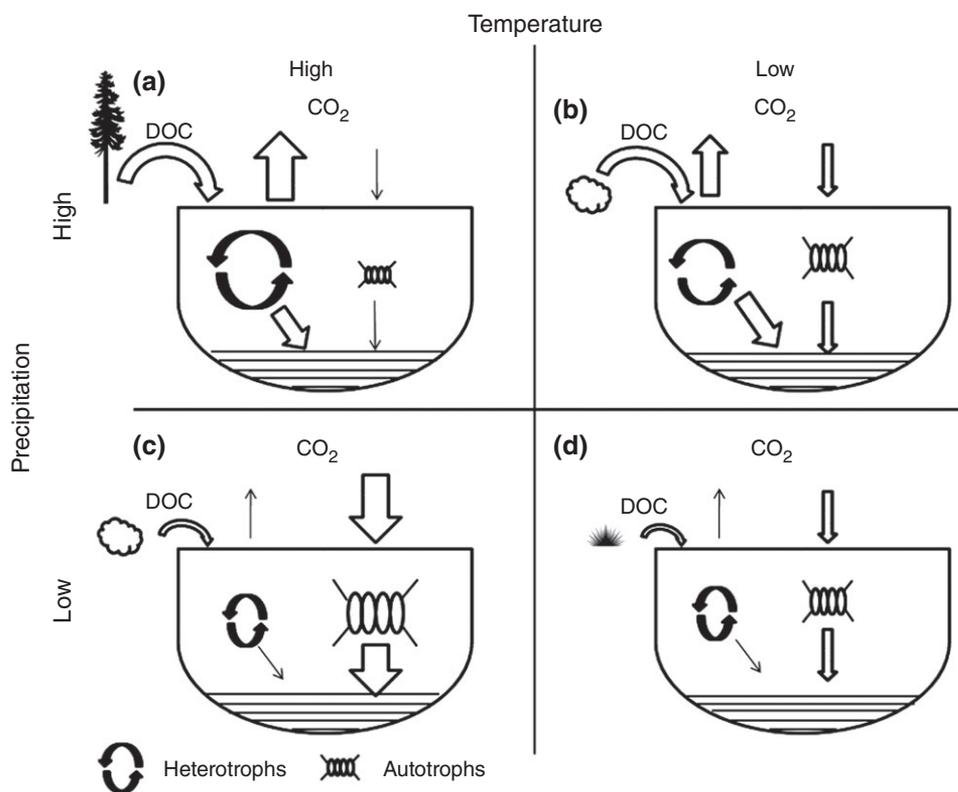


FIGURE 3 | Representation of how temperature and precipitation influence dissolved organic C (DOC) fluxes and processing within lakes and watersheds from mid-high latitudes during the summer ice-free growth periods of different climatic zones (after Ref 108). The size of the arrows indicates the relative flux or influence of each component. In 'humid and warm' boreal regions with forest cover (a) lakes are generally net heterotrophic because allochthonous DOC from terrestrial vegetation and soils is the dominant lakewater C pool, staining waters brown, limiting light penetration for autotrophic photosynthesis and providing an energy source for heterotrophs ('the microbial loop').^{4,98} (b) In cooler regions above treeline with high-moderate precipitation (e.g., shrub tundra, and tundra heath) where permafrost restricts DOC transport and low temperatures impede terrestrial vegetation decomposition,^{109,110} lake waters with intermediately colored with DOC¹¹¹ and lakes are usually weakly heterotrophic. (c) In areas of low precipitation with warm growth season temperatures (e.g., continental interiors with prairie/steppe or savannah vegetation), terrestrial vegetation growth and external DOC transport are limited by moisture availability, recalcitrant, and colorless DOC characterizes the lakewaters^{85,107,112} and dissolved inorganic C (DIC) is usually the most abundant C pool in waters¹¹³ leading to optimal conditions for autotrophic production. (d) In cold regions with low precipitation and minimal vegetation development (High Arctic, polar deserts, and Montane), allochthonous DOC sources are scarce and nutrients may strongly limit autotrophic processes with the C (and nutrient) budgets often supplemented by wind-blown dusts.¹¹⁴ Severe lack of DOC may limit algal growth through ultraviolet radiation damage.^{115,116} Note that the diagram represents only growth season conditions, and complete estimates lake autotrophy/heterotrophy must include the winter period which is usually ice-covered.

autotrophic production by increasing light availability, but due to greater baseline DOC abundance no UVR-screening pigments are produced.¹²³ Treeline changes in the Tamyr Peninsula, Russia increased land–lake fluxes of terrestrially derived C (with low $\delta^{13}\text{C}$ values) during warmer and more humid conditions in the earlier Holocene and increased autochthonous uptake of CO_2 (with high $\delta^{13}\text{C}$ values) when treeline retreated.¹²⁴ Similarly at Kharinei Lake (NE Russia), spruce forest expansion coincided with high NIRS-inferred DOC concentration in the water column and after tree-line retreat, optical transparency of the lake increased.¹²⁵ As well as promoting DOC delivery to lakes, enhanced precipitation promotes mire formation (inferred from pollen and peat studies) and both processes can control lake water total organic C (TOC), pH (inferred from diatoms), and color (inferred from NIRS).¹²⁶ Fire frequency (measured as charcoal) is also important in removing catchment vegetation and, despite temporary charcoal inputs, leads to lower lake-water TOC concentrations.¹²⁶ This and other studies suggest that the simple presence of vegetation is not always the primary driver of lake C processing. For example, shrub expansion in the Alaskan tundra had less influence on lake biota (diatoms and chironomids) than flooding caused by thermokarst expansion.¹²⁷ Fluxes of terrestrial DOC and POC (measured as C:N ratio and macrofossils of *Coenococcum*, *Sphagnum*, and *Empetrum*) in lakes from Greenland increased during the wetter Neoglacial conditions, but changes in lake C processing (as $\delta^{13}\text{C}$) were most pronounced where changes in lake hydrological balance (and hence C delivery) were greatest.⁴¹ Together, these palaeolimnological studies argue that precipitation/hydrology (delivery of DOC) might have a greater influence than vegetation cover (availability of DOC)¹²⁸ over lake C fluxes and processing,^{127,129} providing guidance on how conceptual models developed from spatial observations (Figure 3) might be further developed. To date, however, relatively few studies have explicitly linked these processes with lake C sequestration rates and this is an area where palaeolimnology could contribute further quantitative understanding.

Permafrost Thaw

In the next century, substantial near-surface permafrost degradation is projected to occur and thaw depth will increase.¹⁰⁶ Permafrost soils store immense amounts of frozen C, but warming threatens to activate that store.^{2,130–133} The presence of water bodies and wetland areas is a key control on C processing in

permafrost areas as it can shift frozen C sinks into C sources.^{134,135} Thermokarst ponds and lakes form on peaty soils or on Yedoma (deep deposits of ice-rich silt) across large parts of Siberia, Alaska, and Canada when thawing of frozen ground results in volume loss and mass failure of the land surface.¹³⁶ These water bodies are active sites for methanogenesis and CO_2 ebullition¹³⁷ and may have released sufficient quantities of CH_4 to influence global thermal forcing.^{138,139} However, over the past 15,000 years some estimates suggest that thaw lakes have buried more C than they emitted.^{95,140} Although much permafrost research has focused on C-rich areas of the Arctic and subarctic, many Arctic areas (e.g., High Arctic and polar deserts) currently have thinly developed soils due to exceptionally low temperatures, low productivity, and a lack of liquid water. In the High Arctic, as temperature increases and soils develop they are expected to become net CH_4 ¹⁴¹ and CO_2 ¹⁴² sinks. Consequently, the High Arctic has the potential to remain a strong C sink when other permafrost regions are transformed to a net C source as a result of future warming.¹⁴²

Permafrost thaw should increase the influx of C (DOC and POC) and other nutrients to lakes (Figure 3). Indeed, palaeolimnological records of $\delta^{13}\text{C}$ and organic $\delta^{15}\text{N}$ imply greater fluxes of N as well as C from soils into lakes when hydrological pathways are open.¹²⁴ Thermokarst processes that increase flooding cause greater DIC and N influx into lakes (as recorded by higher $\delta^{15}\text{N}_{\text{org}}$ and lower $\delta^{13}\text{C}_{\text{org}}$) leading to changes in aquatic biota.¹²⁷ In contrast with these predictions, limnological analyses show that lakes with thermokarst slumps are clearer and have lower nutrient concentrations than ones without slumps^{143,144} and palaeolimnology shows that periphytic diatom abundance and diversity increases after slumping suggesting that water gets clearer.¹⁴⁵ After formation of thermokarst ponds, DOC concentrations systematically decline and C pools in waters shift from soil-derived to autochthonous (algal-derived).¹¹¹ These studies suggest that there is no simple and synchronous lake response to permafrost melt and highlight the need for systematic regional-scale palaeolimnological investigations, although the issues for sediment dating in permafrost areas where ‘old C’ is actively redistributed need addressing.¹⁴⁶

Formation of New Lakes

Glacial recession, as projected over the next century¹⁰⁶ could form entire lake districts with exceptionally lake-rich landscapes. Palaeolimnology shows

that newly exposed land surfaces after glacial recession have very specific characteristics. Carbonate can be abundant in certain glacial deposits and weathering of this material is intense in the first few centuries after recession.^{147,148} Sediments deposited shortly after the formation of a small lake (SS2, South-west Greenland) are predominantly composed of carbonate because active weathering sequesters CO₂ as HCO₃⁻¹⁴⁹ resulting in very high (>30 gC m⁻² year⁻¹) CARs in this early period (Figure 4(a)). Newly created lake waters are usually ion-rich and, if receiving glacial meltwater, have a high loading of glacial flour leading to high minerogenic sedimentation rates.¹⁵² DOC is usually scarce because of the absence of terrestrial vegetation and thus the water is very UVR transparent with glacial flour scattering the light and creating an environment suited to cyanobacteria with UVR-screening pigments.^{122,150} Marl-secreting charophytes can thrive in these early postglacial base-rich conditions and diatom diversity is usually low.¹⁵³ This condition is reliant on the availability of alkaline glacial till material and may not characterize areas of noncarbonate geology or nonerosive glacial

regimes.^{154,155} Generally though, OC production shortly after lake inception is focused within benthic areas, and limited to specialized taxa but IC sequestration is often dominant. After this initial period of rapid inorganic C sequestration, which usually lasts a few centuries, soil development (dependent on climate) begins to influence lake C processing.^{148,156} Lake catchments in humid climates may develop thick peaty soils, which are a rich DOC source, but the delivery of C to lakes depends on hydrological pathways (e.g., permafrost presence, delivery of groundwater, and podzolization).¹⁵⁷ The consequences of this successional change are that lake water pH and calcium (Ca) concentrations usually decline whereas C and N increase.¹⁴⁷ Although the effects of this on overall C fluxes are unknown, it is clear from Lake SS2 that C sequestration declined fivefold after soil development (Figure 4(a)). Along with soil development, vegetation succession can influence C cycling by impeding sediment transport from land¹⁵⁸ and influencing N availability through presence of N₂-fixing plants such as alder.¹⁵⁹ There is great potential for the application of

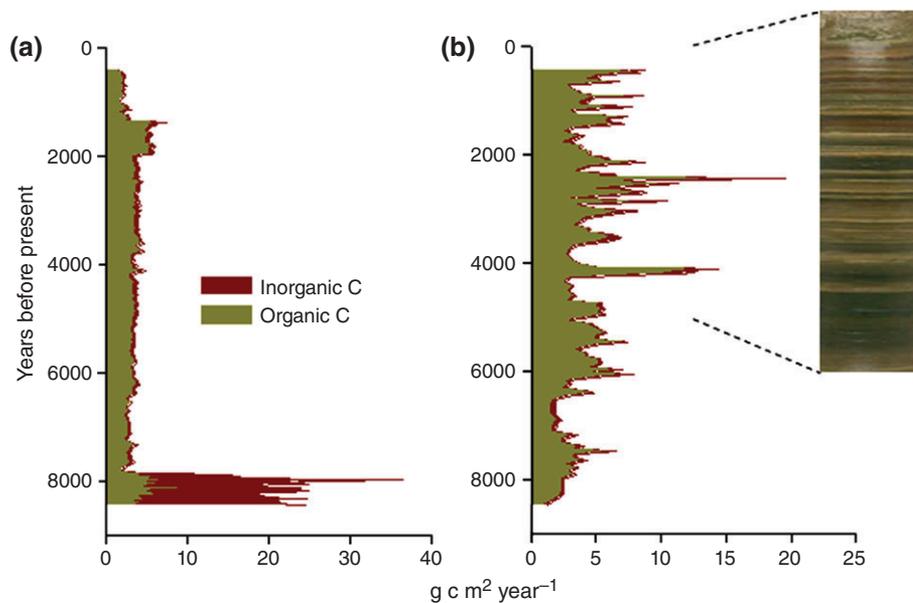


FIGURE 4 | Inorganic and organic carbon (C) accumulation rates (not focusing-corrected) over the past ca. 8000 years in (a) freshwater Lake SS2¹⁵⁰ and (b) closed-basin oligosaline lake Braya Sø,¹⁵¹ which are located with a few kilometers of each other in the Kangerlussuaq area of West Greenland. The high inorganic calcium carbonate deposition around 8000 years ago Lake SS2 sediments is most likely caused by intense weathering of carbonate minerals derived from glacial till, which declined when soils established. The absence of this feature in Braya Sø indicates heterogeneity of carbonate deposition in this area. Afterwards, mean uncorrected C accumulation rates (CARs) were similar in both lakes, but the much greater variability in Braya Sø is caused by fluctuations in water levels, and hence altered conditions for organic C production and deposition, including periods of anoxia in the bottom of the lake when autotrophic purple sulfur bacteria (that leave purple bands in the sediment—inset) were important in C processing. Distinct carbonate laminations in the Braya Sø sediments (inset) indicate periods of intense IC deposition, and yet IC is proportionally much less important than organic C in sediments of this lake. In both lakes, although there was a transition from warmer to cooler conditions ca. 4500 years ago, this had little impact on CARs; instead changes in the hydrological balance influenced CARs in Braya Sø, which is closed-basin and therefore hydrologically sensitive.

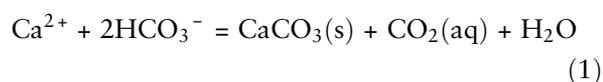
palaeolimnology to better understand links between C sequestration and lake–landscape ontogeny.¹⁶⁰

Palaeolimnology is also well placed to understand changes in C cycling within lakes and standing waters that are formed by nonglacial processes. Holocene connectivity between land and sea has altered through relative sea-level changes,¹⁶¹ including glacio-isostatic adjustments^{162,163} leading to isolation of lake basins from the sea. Most palaeolimnology studies to date have focused on reconstruction of past sea levels using isolation basins.¹⁶⁴ However, marine–freshwater transitions cause fundamental changes in ecosystem structure such as changes in water residence time and stratification, shifts in nutrient limitation, and major reorganization of biotic communities. Visible transitions in sediment stratigraphies show how sediments of isolation basins are more C-rich than marine basins,¹⁶⁵ and physical connectivity with the sea influences CARs in coastal fjords.¹⁶⁶ Globally, the damming of rivers created at least 1000 new reservoirs per year between 1950 and 1970¹⁶⁷ with hydroelectric reservoirs alone (20% of all reservoirs) now covering 3.4×10^5 km² of global land surface.¹⁶⁸ Future reservoir creation is acknowledged as one of the major drivers of changes in greenhouse gas fluxes between inland waters and the atmosphere,⁴ and damming has trapped 1–3 billion metric tons of C in reservoirs over the past 50 years.¹⁶⁹ Reservoirs can be a particularly important CH₄ source, especially in the tropics where they were created by flooding forests with C-rich soils.^{168,170} Reservoir sediment accumulation is strongly correlated with CH₄ production, highlighting a role for palaeolimnology in tracking potential changes in CH₄ fluxes.¹⁷¹ As reservoirs get older, intensity of C processing from the flooded terrestrial OM may subside and be replaced by autochthonous production, dependent on external nutrient supply.¹⁷² There is great potential to explore these ideas using palaeolimnology, but issues associated with heterogeneous sedimentation in the disturbed reservoir environments must be considered.^{173,174}

Hydrological Change and Inorganic C Processing

Inorganic C dynamics are important components of the C cycle in saline and hard-water lakes.^{4,175} Allochthonous IC sources to lakes usually depend on catchment geology and surficial deposits with groundwater inputs being important in limestone regions.^{176,177} Calcium carbonate (CaCO₃) can form directly from photosynthesis if soluble Ca²⁺ ions are present causing ‘lake whiting’ during phytoplankton

blooms (Eq. (1)). In this case, CaCO₃ precipitates around algal cells because the alkaline microenvironment caused by photosynthesis causes cells to act as nucleation sites.¹⁷⁸ This process is an effective vector for PIC deposition into sediments and can be enhanced during warmer years in some lakes.¹⁷⁹ Several types of aquatic plants are well known for CaCO₃ (marl) precipitation and can be important contributors to the sediment C sink.^{180,181} Inorganic precipitation and sedimentation of carbonates can also occur in lakes through simple concentration, which is common in closed-basin (endorheic) lakes that lack an outflow and become saline when there is a precipitation deficit¹⁵¹ (e.g., Figure 4(b)). Sustained CaCO₃ precipitation may cause lake waters to become dominated by sulfate rather than bicarbonate¹⁸² and this process also has implications for lake–atmosphere C fluxes because it causes CO₂ enhancement of lake water at high salinities¹⁸³:



These precipitation legacies preserved in lake sediments as PIC are useful in explaining present day patterns in water chemistry.¹⁸⁴ Saline lakes (>1000 μS cm⁻¹ conductivity and comprising one-fifth of the global lake surface area) are considered especially important in the C cycle¹⁸⁵ because CO₂ exchange with the atmosphere is chemically enhanced (up to threefold) by hydration reactions of CO₂ with hydroxide ions and water molecules in the lake boundary layer.¹⁸⁶

Palaeolimnology shows that past climate changes had a marked influence on IC cycling in many lakes, especially endorheic basins that are particularly responsive to climate.¹⁸⁷ Lake hydrological closure often leads to deposition of sediments that are more enriched in carbonates, as external sedimentary inputs decline.¹⁸⁸ However, higher relative abundance of IC may not necessarily translate to an increase in C sequestration rates (Figure 4). Concentration of lake waters through hydrological closure can increase carbonate sequestration and induce a switch from calcite to aragonite deposition as lake closure progresses,¹⁸⁹ but excessive evapoconcentration may cause a switch from carbonate to gypsum (CaSO₄·2H₂O).¹⁷⁷ In-lake processes such as meromixis and localized evaporation at lake margins can also affect ratios of calcite:gypsum deposition.¹⁸⁷ Transition from prairie to forest in North America around 4000 years ago led to the abrupt loss of annual carbonate-C laminations and predominantly

organic C burial in hydrologically closed lake basins.^{5,190} The converse transition from forest to prairie close to this region led to heavier $\delta^{13}\text{C}$ in sedimentary carbonates indicating that less DIC was derived from isotopically light terrestrial sources or lake primary producers.¹⁸⁹

Land Use Change and Soil Erosion

Soil erosion from humans has increased global river sediment transport by 2.3 ± 0.6 billion metric tons per year during the Anthropocene. However, land disturbance by humans has altered C sequestration in lake basins for millennia in many regions.^{85,191} It is apparent that over mid- to late-Holocene timescales humans can have a greater impact on sediment loads than climate.^{30,33,192} Agricultural development alters vegetation cover and hydrological pathways, e.g., via land drainage,¹⁹³ and so can directly influence DOC and POC fluxes to lakes.¹⁹⁴ For example, lakewater TOC concentrations in Sweden have been extensively influenced over the past ca. 500 years by changes in agricultural practices.^{195,196} Sediment delivery following major human impact can increase 5- to 10-fold.^{158,192} Although erosion of C-rich soils might enhance CARs in lakes, the relationship between lake C cycling and soil erosion is rarely this simple because erosion associated with the removal of forest cover often leads to minerogenic inwash (registered as higher sedimentation rates and lower sedimentary C content). Soil erosion is also often associated with eutrophication, which increases autochthonous OC production¹⁹⁴ (Figure 5). Therefore, abrupt increases in sediment accumulation rate often follow on from land disturbance, but it is unclear whether they result in increased CARs as much of the input is minerogenic.^{198–200} Many tropical regions are now experiencing major land disturbance associated with development which, when associated with intense monsoon rains, may have a significant influence on allochthonous POC loads.²⁰¹

A major indirect effect of land disturbance is that nutrients are more efficiently transferred from the land to lakes, and/or applied as fertilizers in intensive agricultural regimes. The resultant change in lake nutrient balances can fuel a greater proportion of algal-derived C as algal growth is fertilized (Figure 5).¹⁹⁷ Hence, OC and diatom accumulation rates increased after medieval land disturbances in Sweden.⁴⁵ Changes to land cover may also influence sediment C preservation because sediment laminations sometimes cease after removal of forest cover indicating greater physical mixing in the water column.^{202,203} In contrast, bottom-water anoxia may be

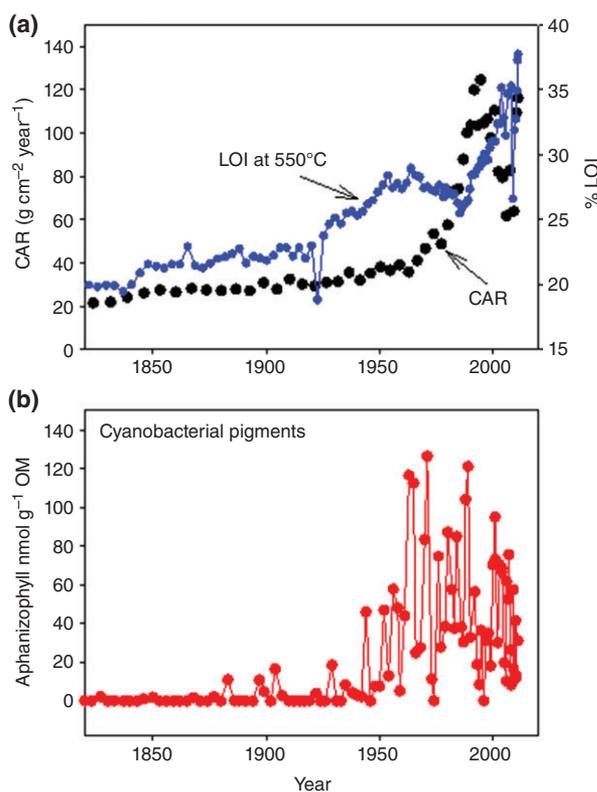


FIGURE 5 | Sediment core measurements from Blelham Tarn, a small lake in the English Lake District taken from¹⁹⁷ showing changes in (a) organic C (OC) burial rates (focusing-corrected) and loss-on-ignition (LOI) at 550°C as an estimate of the % organic content and (b) concentrations of the cyanobacterial pigment aphanizophyll expressed relative to the organic content of the sediment. The proportional increase in aphanizophyll relative to OM in the sediment indicates that cyanobacteria associated with lake eutrophication, became proportionally more important within the lake C budget after ca. 1950 when piped water and sewerage systems were installed in a village within the lake catchment. The general increase in C accumulation rate (CAR) started before 1950 and is associated with agricultural intensification, with peak CARs during the 1980–1990s associated with high livestock densities, and soil erosion. Soil erosion led to a decline in LOI, due to dilution of the %OM by minerogenic material, but the CARs show that it had the net effect of stimulating C burial, probably from enhanced eutrophication. The upper sediments have very high LOI, possibly due to incomplete C degradation, but also because of the decline in soil erosion when livestock densities were reduced.

initiated by lake catchment disturbance, as occurred with early native Iroquoian horticultural activity (AD 1268–1486) in North America.²⁰⁴ Meta-analysis of multiple sediment cores has shown that agricultural intensification has increased C sequestration rates up to eightfold in lakes from North America^{33,205} and Europe,³³ although increases in Europe have been sustained for longer throughout the 20th century. Therefore, in highly disturbed mid-latitude

regions (30–50°N), human-induced burial of C in lakes generally exceeds that driven by climatic changes.

Disruptions to Lake Biogeochemistry

The chemical balance of many lakes has been greatly altered by the delivery of human-derived pollutants during the Anthropocene.²⁰⁶ To service human population growth and urban expansion, lakes have been used as receptacles for sewage or sewage effluent.²⁰⁷ Unprocessed sewage has a high OM content and so may stimulate heterotrophic bacterial activity and CO₂ efflux from lakes. Secondary-treated sewage effluent has less OM but often remains enriched in nitrogen and phosphorus which fertilize autotrophic algal growth and so CO₂ uptake. The apparent benefit of enhancing C sequestration capability of lakes through fertilization is, however, offset by reduction in water quality and other ecosystem services,²⁰⁸ and the general resilience of lakes to be forced into net autotrophy.²⁰⁹ However, it is clear that relatively more sediment OM derives from autochthonous sources after lake fertilization²⁰⁰ (Figure 5). Increased sedimentation rates are a positive feedback for enhancement of OM preservation,⁸⁸ but severe sediment anoxia can lead to methanogenesis, which may cancel out the C sequestration benefits.^{210,211} In shallow lakes, fertilization can stimulate planktonic production at the expense of benthic plants and algae, which are very efficient C sequesterers.²¹² These compensatory whole-ecosystem effects are very difficult to monitor using standard limnological techniques and here sedimentary analyses can provide a useful overview.²¹³ Lake eutrophication can shift algal communities over longer timescales, as described by the Si depletion hypothesis,²¹⁴ whereby P fertilization initially stimulates diatom production and sedimentary C sequestration, but long-term burial of Si leads to eventual replacement of siliceous algae with cyanobacteria.³² As well as creating a water quality issue, little is known of the effects on mass C sequestration of such changes in algal communities.

Major modifications to the N cycle through fossil fuel combustion and artificial fertilizer production have led to the fertilization of many remote lakes through atmospheric deposition. Palaeolimnology has highlighted the widespread nature of this issue using ¹⁵N stable isotopes as tracers.^{215,216} It is estimated that 1.0–2.3 GtC year⁻¹ of terrestrial C storage may have been stimulated by anthropogenic increases in nitrogen deposition in the past century.²¹⁷ Lakes are not well integrated into this

estimate, despite the knowledge that N deposition can significantly modify lake ecology and, hence, C sequestration potential.^{218,219} Atmospheric pollution also causes acidification of surface waters in poorly buffered acid-sensitive regions,²²⁰ leaving strata of soot particles and metal pollution in lake sediments.^{42,221} Acidification makes lake waters more transparent because it coagulates, bleaches, and oxidizes colored DOM^{98,222} and therefore alters habitat availability for lake biota.^{223,224} Palaeolimnology shows how acidification-induced water clarity increases (traced using UVR pigments) lead to either expansion of benthic algal growth (increased C sequestration)²²⁵ or when acidification is extreme, suppression of algal production through UVR damage.²²⁶ Acidification can also lead to long-term Ca depletion in lakes, altering lake biota, with implications for OC and IC cycling.²²⁷ In recent decades, there is evidence for widespread lake water browning through increasing DOC concentrations, as lakes recover from acidification across North America and Europe.^{228,229} Understanding how such processes interact with the recovery of in-lake biota and other stressors will be critical in quantifying changes in lake C processing in the future.²³⁰

CONCLUSIONS

Many of the routine methods and techniques used in palaeolimnological studies can contribute to the interpretation of terrestrial-aquatic C cycling. Previous palaeolimnological studies applied to address other research questions are often of relevance to C cycling, and there is scope for further exploitation of this knowledge base. In comparison with limnological techniques, palaeolimnology has the specific advantages of being able to address questions on timescales of relevance to many GEC processes and of providing information that integrates spatially (habitat–lake–watershed–airshed) and temporally (annual–decadal). This integrative perspective is highly valuable in identifying which sources and processes might be quantitatively important to overall lake C budgets and in directing where limnological investigations need to be focused. Palaeolimnology techniques are well suited to quantifying C sequestration rates in lake basins but, unlike limnological techniques, cannot be used for directly estimating gas fluxes. However, closer integration of limnology and palaeolimnology together with quantitative sediment trap studies is key to providing holistic and quantitative understanding of lake C cycles and budgets and their relevance for earth system processes.

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