ENVIRONMENTAL STUDIES

Anthropogenic alteration of nutrient supply increases the global freshwater carbon sink

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Lakes have a disproportionate effect on the global carbon (C) cycle relative to their area, mediating C transfer from land to atmosphere, and burying organic-C in their sediments. The magnitude and temporal variability of C burial is, however, poorly constrained, and the degree to which humans have influenced lake C cycling through landscape alteration has not been systematically assessed. Here, we report global and biome specific trajectories of lake C sequestration based on 516 lakes and show that some lake C burial rates (i.e., those in tropical forest and grassland biomes) have quadrupled over the last 100 years. Global lake C-sequestration (~0.12 Pg year^{-1}) has increased by ~72 Tg year^{-1} since 1900, offsetting 20% of annual CO_2 freshwater emissions rising to ~30% if reservoirs are included and contributing to the residual continental C sink. Nutrient availability explains ~70% of the observed increase, while rising temperatures have a minimal effect.

INTRODUCTION

Filling gaps in the global C budget remains a critical aspect of understanding global biogeochemical change (*1*, *2*). Lakes act as integrators, sentinels, and regulators of climate change, and their sediments record disruption of key global biogeochemical cycles (principally, N and P but also S and Si) (*3*). Intimately linked to their catchments, lakes process large quantities of terrestrial C, much of which is degassed as CO_2 and CH_4 (*4*). The open-pipe model of lake C dynamics (*5*) has emphasized heterotrophic components of lake metabolism and systems in which net ecosystem respiration is greater than production. Although this is often true of boreal lakes (*6*), in other biomes, nutrient transfer associated with land-cover change (*7*) and agricultural intensification has increased lake production (autotrophy) and C burial rate (*8*–*10*). Estimates of CO_2 and CH_4 emissions have been revised extensively (*4*, *11*) and recently, reassessments of historic (*12*) global lake and reservoir C burial rates have been made (*13*). Yet, the global drivers of freshwater C sequestration and its temporal variability have not been systematically assessed.

Characterizing the temporal and spatial variability of lake C burial rates is critical for constraining the global C cycle, especially given widespread disruption of N and P cycles and their impact on lake primary production. In this study, we compare the trajectory of C burial rates across biomes over the last 100 to 150 years using a consistent methodology and accounting for spatial heterogeneity of sediment accumulation in individual lake basins. We applied a rigorous approach to site selection combined with a standardized correction for sediment focusing (see Materials and Methods). This resulted in the creation of a 516-lake database, representing the largest and most widely distributed coverage of organic-C burial rates. We coupled these data to a measure of global lake area (*14*) (fig. S1 and table S1) to yield a well-constrained global estimate of lake C sequestration over space and time. Although the distribution of the study lakes across the different biomes is uneven, in part because they were used initially to answer other research questions, the geographic sampling frequency adequately reflects the global distribution of lakes (see Materials and Methods and fig. S2). The uniformly treated data are presented as decadal global median burial rates and estimated individually for each of Earth's major biomes (*15*). We also supplement the calculations of lake burial rates with a first-order estimate of the temporal variability in carbon burial by reservoirs (as distinct from natural lakes) using global reservoir area over time from the GRanD database (*16*) and the most recent estimate of the global reservoir C burial rate (*13*).

RESULTS AND DISCUSSION

The total global C burial rate by lakes has increased from 0.05 [95% confidence interval (CI), 0.04 to 0.06] to 0.12 (95% CI, 0.09 to 0.16) Pg C year^{-1} over the last 100 years (Fig. 1A; see fig. S3 for biome-specific 95% CI through time), contributing an additional ~72 Tg annually to the global continental C sink. Across all biomes, burial rates have tripled, including ~4-fold increases in lakes in tropical grasslands and forests, reflecting high disturbance intensity during the 20th century in the tropics (*17*, *18*). Lake burial rates across biomes show nearly linear increases during the 20th century (Fig. 1B), with limited evidence of a more rapid increase associated with post–World War II industrialization (*19*).

Lakes in the boreal biome contribute the largest proportion to the global C burial rate (24%) due to their large areal coverage, but they are closely followed by lakes in tropical moist broadleaf (18%) and temperate broadleaf and mixed forests (16%) and lakes located in temperate grasslands and savannah (15%). These are all biomes that have been heavily affected by cultural landscape disturbance (*8*, *20*) (see below). Despite the large areal extent of tundra lakes, they contribute just 2% to the global total, because of their low C burial rate (3.1 g C m^{-2} year^{-1}). These rates may increase rapidly in the future as a result of the lateral transfer of organic-C from melting permafrost (*21*).

Although there have been localized hotspots of landscape change for millennia, the majority of the anthropogenic transformation of Earth's surface has occurred in the last 100 to 200 years (*22*), and rapid land-cover change since 1950 has resulted in increasing terrestrial C emissions (*23*). Consistent with recent definitions of the

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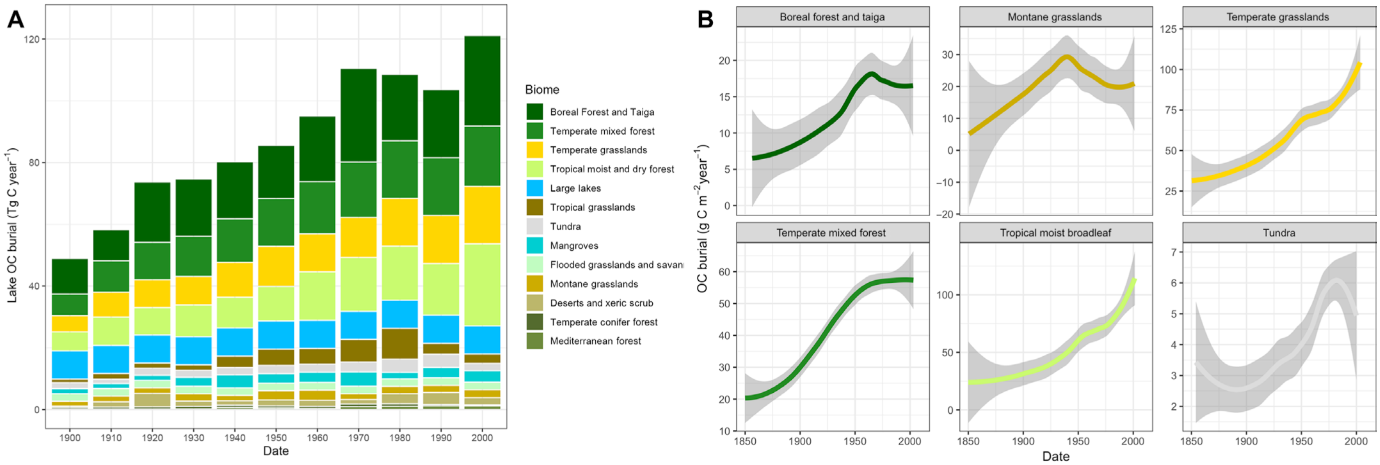

Fig. 1. Global distribution of annual lake organic-C burial rates. (**A**) Total organic-C burial rates by lakes over the last 100 years scaled by biome. (**B**) Comparative lake organic-C burial rates as LOWESS (locally weighted regression) curves with shaded 95% CI regions for selected biomes to show the variable trends in space and time. The number of lakes in each biome estimate is given in the table S2.

Anthropocene (*19*), most biomes show systematic increases in lake C burial from the late 19th century onward (Fig. 1B). Median lake C burial rates are high (46 to 88 g C m^{-2} $year^{-1}$) in those areas with intensive agriculture and substantial nutrient subsidies through fertilizer use (i.e., former temperate mixed forests and grasslands of Europe and North America), with a ~3-fold increase since the start of the 20th century. Not all individual lakes exhibit an increase in organic-C burial over the last 150 years, however, and some biomes show recent decreases. Montane grassland lakes, for example, show a steady increase from background rates of 6 g C m^{-2} $year^{-1}$ before 1900 but a decrease after 1940 (Fig. 1B), which may reflect marginalization of high-altitude agriculture in temperate biomes.

Global lake C sequestration is strongly correlated ($r = 0.9$) with disruption of the P cycle (Fig. 2B) during the 20th century, whereas the relationship with the global flux of reactive N plateaus at high rates of N loading (Fig. 2B). This suggests that the exponential increase in reactive N (*24*) is enhancing P limitation in lakes and is therefore not matched by a proportional increase in C burial, despite saturation of soils with P and increased P input to freshwaters (*25*). This divergence may be amplified with declining P availability globally, although continued disruption of the N cycle may offset this effect to some extent. Moreover, regional differences are likely, as many tropical lakes are N limited (*26*).

Using a multiple linear regression model based on contemporary temperature [mean annual temperature (MAT)] and fertilizer (N and P) use (see Materials and Methods), we predicted an increase in carbon burial by lakes of 52 Tg C $year^{-1}$ since 1900, which represents 72% of the observed change in the global lake dataset (Fig. 3B). The majority (70%) of this increase is explained solely by rising N and P fertilizer use (Fig. 2A) (*24*, *27*). Increasing atmospheric CO_2 concentration is unlikely to have affected aquatic production (and hence C sequestration), because lakes generally are supersaturated with respect to CO_2 during the ice-free season (*6*). The reduced fit of our predictive model to the data in the mid-20th century (Fig. 3B) can likely be attributed to the transfer of terrestrial C to lakes in association with land-cover changes (Fig. 2).

Contemporary organic-C burial rates increase latitudinally with increasing MAT to ~8°C before reaching a plateau (Fig. 3A), which suggests an initial temperature control on burial rates via increased aquatic production that is counteracted at higher temperatures by temperature-dependent respiratory losses. While there is a temperature effect on global aquatic primary production (*26*), the increase in burial rates from pre-1900 to post-1970 (Figs. 1A and 3B) is substantially greater than that attributable to regional temperature increases (*9*, *28*). This observation is supported by the inclusion of global temperature increase in the multiple regression modeling (Fig. 3B), which explained only ~4% of the rise in lake C burial since 1900. The pre-1900 burial rates for lakes located in the boreal zone and subtropical biomes (MAT range, 2° to 25°C) (Fig. 3A) are similar to one another (~10 to 15 g C m^{-2} $year^{-1}$), with the Arctic and Tropics representing the extremes (minimum and maximum are 3 to 30 g C m^{-2} $year^{-1}$, respectively). However, even these 19th century burial rates are likely elevated over a pre-Anthropocene background, which for boreal and temperate mixed-forest lakes is probably closer to long-term Holocene rates of ~5 g C m^{-2} $year^{-1}$ (*29*). Two notable exceptions from this trend include lakes from the Deserts and Xeric Scrub and Tundra biomes, which have been less influenced by fertilization due to the absence of arable land. MAT explained the greatest amount of variation (29 and 21%, respectively) of organic-C burial in these biomes (See table S3 for full biome-specific regression results).

Air temperature effects are difficult to disentangle from other global change processes that covary with latitude, including lateral transfer (erosion) of terrestrial C, increased autotrophic production from fertilizer use and associated nutrient runoff (*8*) (see above; Fig. 2), and elevated erosion rates, which reduce postdepositional mineralization through physical protection of sedimented organic matter. The latter effect is reflected in the high C burial rates of reservoirs (Fig. 3C), which were considered separately from natural lakes in more detail below.

These historic increases in lake C burial—driven, in part, by disruption of the major nutrient biogeochemical cycles—have been accompanied by alterations to surface hydrology, increased runoff (and erosion), and most notably, damming and reservoir construction. These changes all increase lateral C transfer and sequestration at the landscape scale. Although reservoir building has a long history

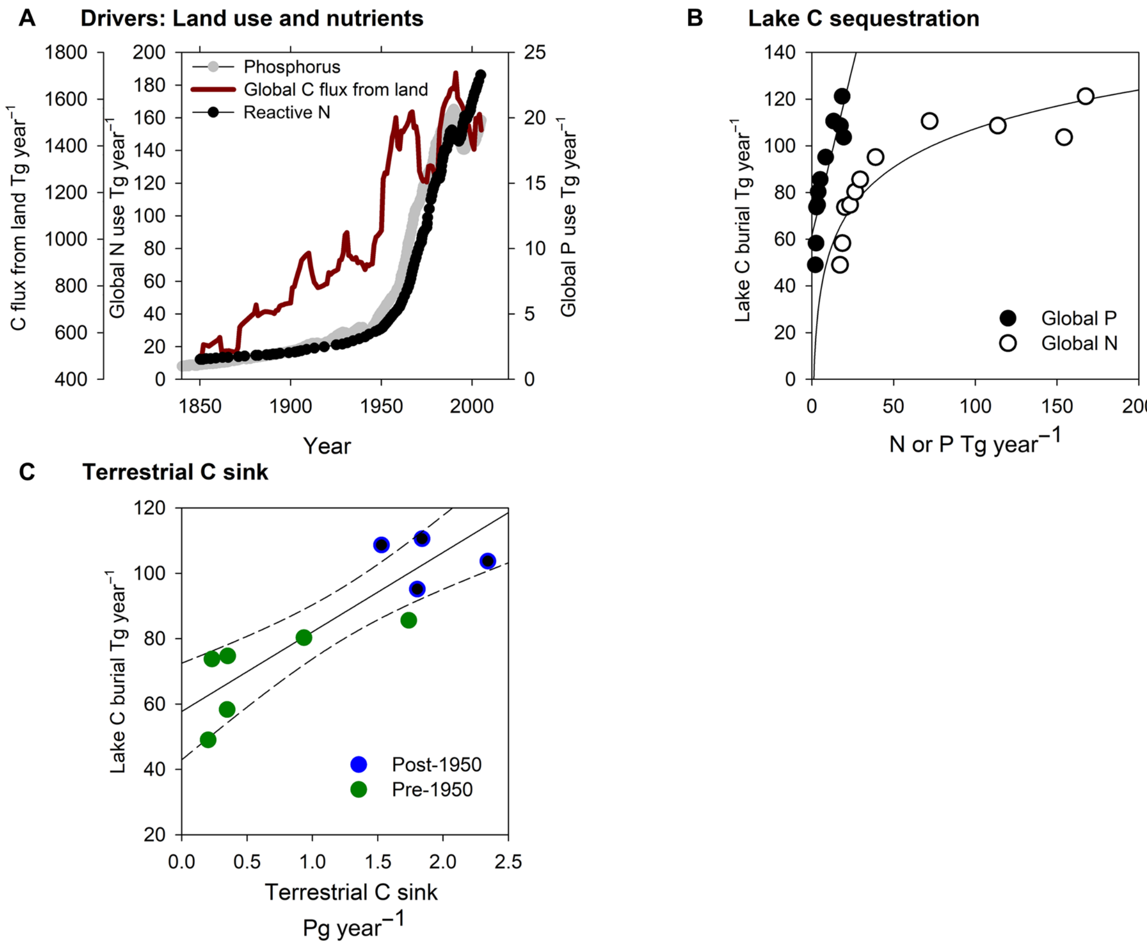

Fig. 2. Global drivers of organic-C burial and relevance to the terrestrial C sink. (**A**) Drivers of global environmental change that can affect lake C sequestration either through the promotion of primary production (key plant nutrients, such as reactive N and P) or via lateral transfer of terrestrial C due to land-cover change. Reactive N refers to that of which is biologically available. (**B**) Decadal lake C sequestration plotted against decadal mean global N and P use [from (A)], highlighting the strong linear relationship between phosphorus and lake C sequestration and the saturating relationship between nitrogen and C sequestration. (**C**) Decadal lake C sequestration plotted against the decadal total terrestrial C sink (note the contrasting units for each axis) derived from the Global C Project (www.globalcarbonproject.org), indicating that C sequestration by lakes contributes to the global terrestrial C sink [sensu Houghton (*23*)]. Pre- and post-1950 time periods are indicated. Sources for the biogeochemical drivers: (*23*, *24*, *27*).

dating back millennia, it increased markedly on a global scale after 1950 (*30*). Carbon burial rates generally are high in reservoirs as a result of catchment instability and high erosion rates. These high inputs [mean 239 g C m^{-2} $year^{-1}$ (*13*) or ~61 Tg $year^{-1}$ globally] due to catchment disturbance processes, coupled with their rapid areal expansion after 1950, nearly double the median total freshwater C burial rate (to 0.18 Pg $year^{-1}$) when combined across biomes (Fig. 3C). This combined lake and reservoir global burial rate is approximately 30% of annual lake CO_2 emission on a comparable areal basis (*4*). However, it is important to recognize that reservoir burial rates are presently poorly constrained in comparison to lakes (for example, they are uncorrected for sediment focusing), although they undoubtedly contribute substantially to aquatic C sequestration (Fig. 3C), particularly since 1950 with the major expansion of dam construction (*30*).

Although lateral transfer of terrestrial C is a natural process, mainly as dissolved organic-C, soil erosion rates have increased markedly owing to land-cover change (*31*), as exemplified by the estimated reservoir burial rate (Fig. 3C). Soil C is in a dynamic equilibrium with the atmosphere (although turnover times vary), but when transferred laterally and buried in lakes, this terrestrial-derived C is effectively removed from the short-term C cycle. Our estimate of the annual global lake and reservoir sequestration rate (0.18 Pg $year^{-1}$) is equivalent to the residual global forest C sink for the 1990s (*17*), which demonstrates that freshwaters play an important role in the integrated continental C cycle.

Beyond the impact of reservoir building and nutrient enrichment in cultural landscapes, our analysis shows that increases in aquatic C burial are occurring even in areas where there is limited land-cover change (i.e., boreal and tundra biomes) (see Fig. 2A), emphasizing the extent to which global development has resulted in fertilization of the biosphere (*32*). While land-use disruption of N and P cycles at regional and local scales is well documented (*22*), the results of the present study highlight the pervasive and integrated nature of anthropogenic environmental change on terrestrial and aquatic ecosystems (Fig. 2) through global disruption of biogeochemical cycles (*32*). Such global impacts include transboundary pollution by reactive nitrogen (derived from emissions from intensive agriculture

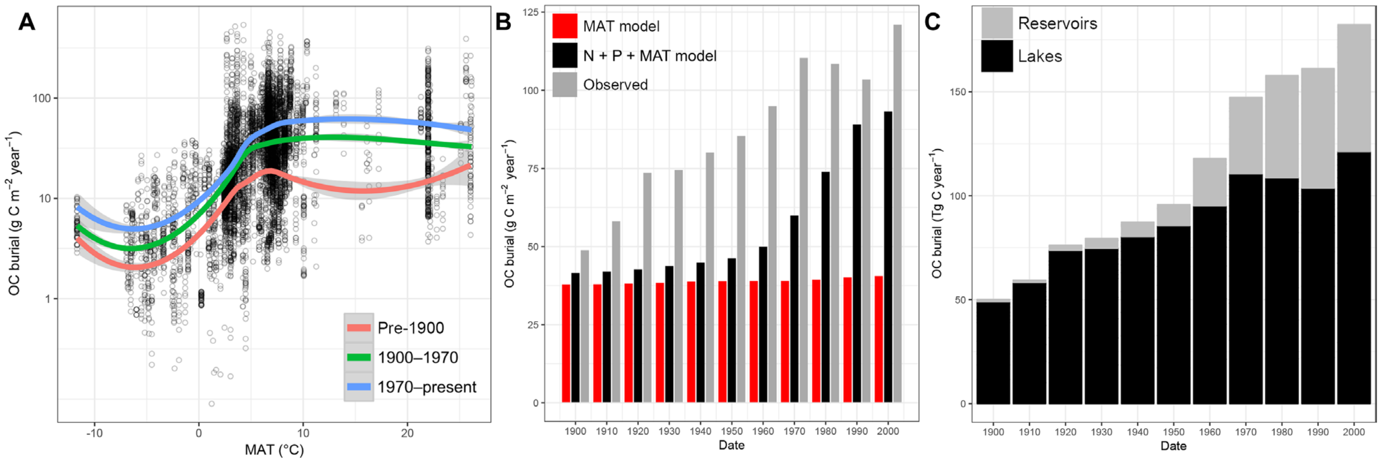

Fig. 3. Observed and predicted measurements of organic-C burial across space and time. (**A**) All C burial measurements for lakes included in this study versus the MAT of the site location. Lines represent LOWESS curves of this relationship with shaded 95% confidence regions, separated into three time intervals (pre-1900, pink; 1900–1970, green; and 1970 to present, blue). (**B**) Comparison of the global lake C burial rate and modeled C burial based on N and P availability and global temperature change during the period 1900 to 2000 (see the Supplementary Materials). The difference between modeled and measured lake C burial is attributable to terrestrial C from land-cover changes. (**C**) Global lake and reservoir C burial, by decade, from 1900 to present.

and industrial sources) (*24*). Although N-deposition rates are low (~1 kg N ha^{-1} $year^{-1}$ or less) when the recipient areas are far removed from the source areas, long-term chronic inputs to remote nutrient-poor systems increase ecosystem productivity (*33*), and its historic effect as has been previously inferred (*9*). Land-cover change, land-use intensification, and the deflation of agricultural soils with resultant long-range atmospheric transfer of nutrient-rich dusts also contribute to nutrient loading to remote lakes (*34*). The temporal reconstructions provided here offer a long-term perspective on the aquatic C cycle and highlight its variability and dynamic nature, both geographically and temporally at 10^2-year time scales. These results also demonstrate the importance of C sequestration in offsetting CO_2 emissions from lakes and reservoirs.

MATERIALS AND METHODS

Here, we summarize the approach taken to site selection and dataset compilation. The three critical criteria used in this process were availability of ^{210}Pb concentration, carbon or organic matter content in sediment cores, and lake geographic location. Because lake sediment studies are biased toward the temperate and boreal regions, major emphasis was given toward inclusion of the few extant studies that included the above criteria in underrepresented areas (see the "Geographical analyses" section).

Site selection

To ensure consistent dating and organic-C flux calculations across all sediment cores in this study, only records that had both ^{210}Pb and organic-C concentrations at approximately decadal resolutions for the last 100 years were selected. The initial dataset compilation was based on previous regional syntheses by Heathcote *et al.* (*9*, *20*) and Anderson *et al.* (*8*, *28*); however, these data represented less than half of Earth's major biomes. To address this, we conducted a literature review of other published ^{210}Pb-dated lake sediment records where sediment C content was measured.

The availability of ^{210}Pb concentrations (as opposed to only ^{210}Pb dates) was critical in terms of filtering the data because it was required to calculate a consistent sediment focusing correction across all sites. After this initial screening of data availability, we targeted other regional (i.e., multiple lakes) studies where ^{210}Pb concentrations were not published, but likely existed, with an emphasis on underrepresented geographic areas (i.e., the tropics and montane grasslands). We requested the raw data for these studies and included those who shared data as Globocarb data contributors for this study (see full authorship list at the end of the Acknowledgments). As a result of this dataset expansion, we compiled temporal trends in global organic-C burial rates from 438 previously published records from lake sediment studies combined with unpublished results from 78 additional lakes (see table S1 for a list of sources). Although it is not inclusive of all lake sediment core studies undertaken to date, primarily due the unavailability of raw data (notably ^{210}Pb concentrations), our total dataset of 516 lakes represents the largest synthesis of carbon burial fluxes in lakes to date.

Estimation of organic-C burial rates

Selected sediment records had a consistent methodology for calculating the age and organic-C content down the core (see above). In most cases, analyses were performed on the cores in 0.5- to 1-cm intervals. Organic-C content was estimated by loss on ignition (*35*). The age of sediment intervals was determined using ^{210}Pb, a naturally occurring radioisotope with a half-life of 22.3 years, following the constant rate of supply model (*36*). Because most burial rates are estimated on the basis of a single centrally located sediment core, we independently focus-corrected each core based on the ratio of the unsupported ^{210}Pb flux at the core site to the estimated regional average atmospheric ^{210}Pb flux (*37*). This method more accurately reflects the whole-basin sediment accumulation rate and takes into account uneven depositional patterns within a lake basin (*8*, *9*, *38*).

Literature values for organic-C burial lakes from the world's largest lakes (>1000 km^2) were used when available (see table S2). To minimize the influence of incomplete mineralization on our estimates, all sediment sections younger than 10 years (based on ^{210}Pb age) were excluded from the analysis (*9*, *39*). Median organic-C burial rates and nonparametric 95% CIs were calculated using a Mann-Whitney test.

Geographical analyses

The locations of all lakes were confirmed from either published coordinates or topographical maps using readily available satellite or aerial photography from Google Earth (Google Inc.). Climate data (MAT and annual precipitation) were derived from 30–arc sec interpolated averages spanning the period of 1950 to2000 available from the WORLDCLIM database (*40*) and extracted for each lake. Lakes were assigned to global biomes based on their location within The Nature Conservancy's Terrestrial Ecoregion polygons derived primarily from Olson *et al.* (*15*). The proportional areal distribution of lakes across global biomes was estimated from the Global Lakes and Wetlands Database, which only includes lakes with a surface area >0.1 km^2 (*41*). This proportion was then multiplied by the estimated global lake area (*14*) minus the known area of the world's 22 largest lakes and the global reservoir area (see table S2 for a list of biome-specific lake areas) (*16*). All geographical analyses were performed using the open-source software QuantumGIS, v.2.6.1 (*42*).

Since this study represents a synthesis of a large number of published and unpublished data (*n* = 516; see table 1), the selection of lakes was necessarily biased by data availability in the most studied biomes (e.g., boreal forest and mixed temperate forest). Furthermore, sampling sites were heterogeneously located across biomes due to the logistical reality of sampling lakes in sometimes remote areas. Some biomes are underrepresented in the sediment core dataset relative to their global distribution, for example, tropical lakes (see figs. S1 and S2). Southern South America, New Zealand, and the Antarctic are absent due to methodological constraints that make ^{210}Pb dating unreliable in this region due to low atmospheric fluxes of ^{210}Pb at high latitudes in the southern hemisphere (*43*). Despite this, the biomes with at least two or more sediment cores in this study represent 89% of global lake surface area (*41*), which includes independent literature-derived organic-C burial rates for the world's largest lakes (11% of global lake surface; see table S2). Given the disproportionately large areal extent of lakes in the boreal and temperate regions (58% of the global lake area, excluding the "Great Lakes"), it is important that these estimates be well constrained (i.e., the errors are lowest in the regions that contribute the most to the total global lake area) (see table S2).

Fertilizer use data were derived from 0.5–decimal degree interpolated averages of N and P fertilizer application spanning from 1994 to 2001; available online from NASA's Socioeconomic Data and Applications Center (SEDAC) (*44*–*46*).

Statistical analyses

For purposes of statistical comparison, organic-C burial rates were separated into two time periods (pre-1900 and 1970 to present) to represent the recently designated stratigraphic boundary between the Holocene and Anthropocene epochs (*19*). Differences in lake-specific averages for each time period were assessed via one-sided paired *t* tests for difference greater than zero. The direction of change over time was estimated as the slope of a linear regression over all observations for each lake. All data were $\log_{10}$-transformed for statistical analysis to conform to the assumption of normality. We used a space-for-time substitution to build our linear regression model for the effect of temperature and N + P fertilizer application on organic-C burial rates using our global C-burial dataset and the global interpolated geographical data listed above (see the Supplementary Materials). All statistical analyses were performed using the statistical software R (*47*).

Organic-C burial modeling: Temperature and nutrient predictors

We used a space-for-time substitution to develop linear regression models to predict organic-C burial over a gradient of MAT and fertilizer use (based on modeled nitrogen and phosphorus application rates). All explanatory variables for the regression models were based on globally interpolated datasets. For temperature, we used the 30–arc sec interpolated WORLDCLIM database (www.worldclim.org), which provides an average elevation-adjusted MAT from 1950 to 2000 (*40*). Nitrogen and phosphorus fertilizer application rates (kilogram per hectare) were based on the 0.5–decimal degree interpolated averages compiled by Potter *et al.* (*44*–*46*) based on a synthesis of national fertilizer use and cropping pattern statistics. These data are publicly available as part of NASA's SEDAC at http://sedac.ciesin.columbia.edu/data/collection/ferman-v1.

The above explanatory variables were compared to $\log_{10}$-transformed observations of organic-C burial from our global lakes dataset. MAT was compared to pre-1900 organic-C burial rates for the lakes to best isolate this signal from the rise of fertilizer use, which primarily occurred over the 20th century (*27*, *48*). Nitrogen and fertilizer application rates were compared to contemporary organic-C burial rates (1970 to present) for the same set of lakes; however, the *y* intercept from the pre-1900 temperature regression was used for the final predictive model to better represent true baseline conditions. Global predictions of organic-C burial rates were based on these regressions using global averages for fertilizer use (shown in Fig. 3A) and global average temperature data binned by decade (*27*, *48*).

Model selection

All three explanatory variables explained a significant amount of variation in organic-C burial rates. Although only a specific time period was used for the finalized model (pre-1900 for temperature and 1970 to present for N + P fertilizer use), this relationship was significant regardless of the time period chosen, and the slopes did not significantly differ. MAT explained 14% of the variance in organic-C burial ($F_{1,1671} = 257.4$, $P < 0.001$) and was modeled as

$$\text{Log}_{10}\,\text{organic-C burial} = \text{MAT} \times 0.03 + 0.905$$

P fertilizer use explained 25% of the variance in organic-C burial ($F_{1,1911} = 637.1$, $P < 0.001$) and was modeled as

$$\text{Log}_{10}\,\text{organic-C burial} = \text{P application} \times 0.04 + 0.905$$

N fertilizer use explained 28% of the variance in organic-C burial ($F_{1,1911} = 742.9$, $P < 0.001$) and was modeled as

$$\text{Log}_{10}\,\text{organic-C burial} = \text{N application} \times 0.009 + 0.905$$

When combined into a multiple regression model, these three explanatory variables collectively explained 44% of the variance in organic-C burial rates ($F_{3,1909} = 499.6$, $P < 0.001$)

$$\text{Log}_{10}\,\text{OCburial} = \text{MAT} \times 0.03 + \text{Papplication} \times 0.017 + \text{N application} \times 0.005 + 0.905$$

In addition to all predictors being significant individual predictors of organic-C burial, the full model had the lowest AIC (Akaike information criterion) score using both forward and backward selection of each parameter, indicating that it was the best performing and most parsimonious model.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/16/eaaw2145/DC1

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