

Organic carbon sink dynamics and carbon sink-source balance in global lakes during the Anthropocene

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Running title: lake carbon sink dynamics and sink-source balance

Key findings

1, The organic carbon sink dynamics and carbon source-sink balance in lakes are quantified with effect-size metrics, namely the organic carbon burial ratio and carbon balance ratio, respectively.

2, There is a decreasing latitudinal trend for organic carbon sink dynamics, while nonsignificant for carbon sink-source balance.

3, The organic carbon sink dynamics are mainly positively influenced by lake trophic state, while the carbon sink-source balance are primarily positively affected by lake catchment properties.

Abstract

The carbon burial and greenhouse gas emissions of lakes are pivotal in the global carbon cycle to offset or accelerate global warming. However, their balance or the magnitude of anthropogenic increase of carbon burial remains uncertain in global lakes. Here, we quantified the carbon sink dynamics and the sink-source balance in global lakes with effect size metrics, that is, the log-response ratio of organic carbon burial between post-1950 and pre-1900 periods and the carbon balance ratio between carbon burial and greenhouse gas emissions, respectively. The organic carbon burial ratios revealed an average increase of 2.44 times in carbon burial rates during the Anthropocene, while the carbon balance ratios were negative in 82.68% of lakes, indicating that most lakes had lower burial rates than emission rates and acted as carbon sources rather than carbon sinks. The organic carbon burial ratios exhibited a significantly decreasing latitudinal trend and were mainly influenced by its trophic state with the explained variation of 44.79%. They were also indirectly influenced by climate, lake morphometry and catchment properties through their interactions with the lake's trophic state. The carbon balance ratios however showed nonsignificant latitudinal trend. They were primarily affected by lake catchment properties with the explained variation of 26.21% and were also indirectly affected by climate variables via the interactions with catchment properties. Overall, our study highlights that human activities such as lake eutrophication and catchment changes have altered the carbon sink and source in global lakes during the Anthropocene, and are essential drivers for future evaluations of lake carbon budgets.

Keywords: organic carbon burial; greenhouse gas emission; carbon sink dynamics; carbon sink-source balance; anthropogenic activity

Glossary terms

Effect size metrics: The statistical metrics to quantify the magnitude and direction of the relationship between two sets of variables or groups. The log response ratio (LRR) is one of effect size statistics and is calculated as the log proportionate change in the means of a treatment and control group.

Organic carbon burial ratio: The organic carbon burial ratio is a log response ratio used to quantify the magnitude and direction of changes in lake organic carbon burial during the Anthropocene. For instance, the organic carbon burial ratio could be calculated for organic carbon burial between the pre-1900 and post-1950 periods. Positive values of the organic carbon burial ratio indicate an increase in organic carbon burial rates over time, while negative values suggest a decrease. A ratio of zero indicates no change in organic carbon burial rates.

Carbon balance ratio: A log response ratio that compares the difference between organic carbon burial and greenhouse gas (GHG) emissions, and measures the balance between carbon sink and source in a lake. A positive value of the carbon balance ratio indicates a higher carbon burial rate than carbon emission in a lake, resulting in a positive contribution to the regional carbon stock. Conversely, a negative value suggests that a lake has higher carbon emission rate than carbon burial, resulting in a negative contribution to the regional carbon stock. A ratio of zero indicates no contribution in carbon stock.

Organic carbon sink dynamics: The temporal changes in the burial or accumulation of organic carbon within lake sediments during a defined period. These dynamics can be quantified by the log response ratio as changes in the burial rates, either increasing or decreasing, over time, and indicate the potential contributions of a lake to regional carbon stock.

Carbon sink-source balance: The balance between carbon sink and source regulates the role of lakes in regional and global carbon budget. This balance could be quantified by the difference between organic carbon burial and gaseous carbon emissions in lake sediments.

Introduction

Lakes disproportionately affect the global carbon cycle relative to their area as a highly efficient carbon sink and an important source of greenhouse gases. Although lakes cover less than 4% of Earth's surface area, they have the potential to store approximately 25-50% of the total organic carbon that is buried in marine sediments (Verpoorter et al. 2014, Drake et al. 2017). Lakes are also an important source of greenhouse gases (GHG), which equals to nearly 20% of the whole global CO₂ fossil fuel emissions into Earth's atmosphere (DelSontro et al. 2018). Notably, the estimates of carbon sink and source in global lakes exhibited variability across different literatures (Fig. 1). For instance, organic carbon burial varies with nearly three times differences from 0.04 to 0.12 Pg C yr⁻¹ (Dean and Gorham 1998, Anderson et al. 2020). The CO₂ emissions vary with nearly six times differences from 0.11 to 0.64 Pg C yr⁻¹ (Cole et al. 2007, Aufdenkampe et al. 2011), while the CH₄ emissions show less variations with a range of 0.01 to 0.11 Pg C yr⁻¹ (Ehhalt 1974, Rosentreter et al. 2021). Whether lakes are net sinks or net sources for their regional carbon neutral roles is primarily determined by the balance between carbon burial and evasion to the atmosphere. However, such a balance (i.e., carbon sink-source balance) and the temporal variability of organic carbon burial (i.e., carbon sink dynamics) during the Anthropocene remain uncertain for global lakes.

Characterizing the temporal changes of carbon burial in lakes during the Anthropocene is critical to constrain the dynamics of global carbon stocks given the increasing and widespread human disturbance (Anderson et al. 2020). Lake organic carbon burial is promoted by climate warming and anthropogenic disturbance via increasing autochthonous production and inputs of allochthonous carbon from the catchments (Tranvik et al. 2009). For instance, the temperature at ecosystem level has a positive effect on lake organic carbon burial (Heathcote et al. 2015), while incubation experiments show decreased carbon burial in lakes with increasing temperature (Gudasz et al. 2010). The increasing organic carbon burial observed during the Anthropocene could not be fully explained by climate alone, and thus other environmental drivers, such as human-induced landscape changes, are proposed to be responsible (Heathcote et al. 2015). Anthropogenic activities, including land-cover change and extensive agriculture, could impact the organic carbon burial in lakes by causing eutrophication and increasing the inputs of terrestrially derived organic matter (Anderson et al. 2013, Dietz et al. 2015). Eutrophication, induced by excessive

126 nutrient input, could increase the amount of fresh organic carbon available for
127 subsequent depositional processes (Dong et al. 2012). For instance, eutrophication is
128 the primary driver of the elevated carbon burial rates in European lakes, as indicated
129 by the strong correlation between total phosphorus and the burial rates (Anderson et al.
130 2014). Nutrient enrichment could also promote heterotrophic bacterial activities and
131 alter the community composition of microbes and could further elevate the
132 mineralization of organic matters (Hu et al. 2022).

133 However, it remains largely unknown regarding the balance between carbon
134 burial and GHG emission in individual lakes, i.e., their role in regional carbon
135 budgets, and the major drivers behind these balances (Kortelainen et al. 2013). Such
136 carbon sink-source balance has been previously investigated in different terrestrial
137 and aquatic environments, such as forests, grasslands, arable lands, peatlands, and
138 oceans (Yang et al. 2008). For lake ecosystems, they are usually supersaturated in
139 CO₂, acting as net carbon sources to the atmosphere, but have large spatial variability
140 depending on latitude, climate, and lake types. For instance, the ratios of lake
141 emissions to burial in high-latitude regions are ten times higher in boreal lakes
142 compared to subarctic-arctic lakes (Lundin et al. 2015). The role of individual lakes
143 could be overlooked when comparing organic carbon burial to CO₂ emission at
144 regional scales, such as catchments based on a coastal segmentation (Raymond et al.
145 2013, Mendonca et al. 2017). Moreover, climate change and human activities such as
146 temperature and nutrient availability could significantly affect lake carbon sink-source
147 balance, but their impacts are generally understudied (Tranvik et al. 2009, Gudas et
148 al. 2015).

149 Under the combined influence of climate change and intensified anthropogenic
150 activities, lakes are playing more important roles in regulating the regional carbon
151 budgets by increasing carbon sedimentation and mediating the balance between
152 carbon sink and source. Here, we quantified carbon sink dynamics and carbon sink-
153 source balance and evaluated how they were influenced by multiple drivers in global
154 lakes. Specifically, we obtained organic carbon burial and CO₂ emission rates from
155 423 global lakes reported in previous literatures, including 286 lakes with long-term
156 carbon burial rates over the last 100-200 years (Table S1), and 137 lakes with
157 pairwise short-term carbon burial rates and contemporary CO₂ emission rates (Table
158 S2). We developed two effect size metrics, namely the carbon burial ratios and carbon
159 balance ratios, to quantify the carbon sink dynamics and carbon sink-source balance,

respectively. We further evaluated the relative importance of nature and anthropogenic drivers in explaining carbon sink dynamics and sink-source balance across global scales. These hierarchical drivers could be categorized as climate variables, lake morphometry, lake catchment properties, and lake trophic state (Fig. 2c). We expected that autochthonous and allochthonous productions, represented by the trophic state of the lake and the carbon inputs from the catchments, respectively, could strongly influence the carbon sink dynamics and sink-source balance. We further hypothesized that climate and lake morphometry could directly mediate the carbon sink dynamics and the sink-source balance, and could also have indirect influence through their interactions with lake trophic state and catchment properties. The syntheses of these hierarchical drivers could better illustrate the carbon sink dynamics and carbon sink-source balance in the global lakes and provide valuable insights into the mechanisms driving carbon cycling in lake ecosystems.

Methods

Data compilation of organic carbon burial and CO₂ emission rates

We compiled organic carbon burial and greenhouse gas emissions data from 423 global lakes, which mainly derived from published sources (Tables S1, 2). These lakes exhibit varying characteristics in latitude, climate, lake morphometry, lake catchment properties, and lake trophic state. This comprehensive dataset allows us to examine the relative importance of natural and anthropogenic drivers of lake carbon sink dynamics and carbon sink-source balances.

Our carbon burial dataset consisted of 286 distinct lakes observations of long-term (i.e., the last 100~200 years) sediment focusing corrected organic carbon burial rates, integrating both newly collected and previously published regional synthesis data (see Table S1 for a list of sources). To ensure consistent dating and organic carbon flux calculations across all sediment cores in this study, only records that had both ²¹⁰Pb and organic carbon concentrations at approximately decadal resolutions for the last 100 years were selected (Anderson et al. 2020). Our analysis relied exclusively on whole-system organic carbon burial rates (i.e., a single spatially resolved rate for each system), thus we used the average value if data on whole-system organic carbon burial from the same lake were available in different publications. Artificial reservoirs were excluded from this study due to their limited data of long-term organic carbon burial rates worldwide and their distinctive

characteristics compared to natural lakes. For instance, reservoirs could exhibit higher carbon burial due to catchment instability, high erosion rates, and more favorable conditions for organic carbon preservation (Mendonca et al. 2017, Anderson et al. 2020).

Our carbon burial-emission dataset included 142 pairwise data of CO₂ emission and organic carbon burial rates from 137 different lakes, which is the largest dataset available so far (see Table S2 for a list of sources). These lakes are widely distributed in spatial scales and represent most of Earth's major biomes (Figs. 2, S4). For CO₂ emissions across the air-water interface, we used the average value if data from the same lake were available in different publications. For carbon burial across sediment-water interface, we used short-term organic carbon burial rates, such as post-1950, to match the contemporary CO₂ emission if multiple estimates of burial rates for the same lake from different periods existed. However, it is challenging to obtain more data due to the heterogeneity of data sources for organic carbon burial and CO₂ emissions, and the lack of precise temporal alignment between these two variables.

Calculating organic carbon burial ratio and carbon balance ratio

Organic carbon burial rates were divided into three periods based on global anthropogenic activity before and after the beginning of the Anthropocene: pre-1900, 1900-1950, post-1950 (Steffen et al. 2007). We considered pre-1900 as background or very low disturbance, with limited global atmospheric emissions. Human population and industrialization increased during the transitory period of 1900-1950. We considered post-1950 as the modern period, reflecting the Post-World War II increase in both human population and industrialization.

We introduced an effect-size metric, the log-response carbon burial ratio, to quantify the magnitude and direction (i.e., positive, or negative) of lake organic carbon burial change during the Anthropocene. This ratio was calculated by comparing the modern rate of organic carbon burial (post-1950) to baseline value (pre-1900):

$$\text{Carbon burial ratio} = \text{LRR} \left(\frac{\text{post-1950}}{\text{pre-1900}} \right)$$

where pre-1900 and post-1950 are the organic carbon burial rates of lakes before 1900 and 1950 to present, respectively. Positive and negative values of organic carbon burial ratios indicate that organic carbon burial rates increase or decrease with time,

respectively, while zero organic carbon burial ratio suggests no temporal changes. Larger absolute burial ratio values indicate greater temporal changes in organic carbon burial rates within the two periods.

We further applied the log-response carbon balance ratios to investigate the role of each lake in regional carbon cycling. This ratio was calculated by comparing short-term organic carbon burial to contemporary CO₂ emissions:

$$\text{Carbon balance ratio} = \text{LRR} \left(\frac{\text{Carbon burial}}{\text{CO}_2 \text{ emission}} \right)$$

The carbon balance ratio is based on mass balance point of view, given that comparable amounts of carbon are buried in sediments and emitted as gas from lakes worldwide. It should be noted that the carbon balance ratios are employed as a preliminary evaluation of the role of lakes in regional carbon cycling. Although there is a lack of precise temporal alignment between carbon burial and CO₂ emissions, this approach represents one of the viable methods for comparing the two net vertical processes within lakes: evasion versus sedimentation (Ferland et al. 2014, Lundin et al. 2015, Mendonca et al. 2017). Specifically, lakes with positive carbon balance ratios indicate that carbon burial exceeds CO₂ emissions, acting as carbon sinks, while lakes with negative ratios indicate that carbon burial is lower than CO₂ emissions, acting as carbon sources. It should be noted that we excluded 15 lakes with negative CO₂ emission rates, which accounted for 10.95% of the 137 lakes. This is because it is not mathematically applicable to include negative CO₂ emissions in the carbon balance ratio calculation. Moreover, there is no need to apply the carbon balance ratios to quantify the carbon sink-source balance of the lakes with negative CO₂ emissions, because they are typically characterized as net autotrophic ecosystems and could be classified as carbon sinks, that is, higher CO₂ uptake by primary producers than the release via ecosystem respiration (Pacheco et al. 2014).

Data compilation of natural and anthropogenic drivers

Besides the carbon burial ratios and carbon balance ratios, the datasets also included natural and anthropogenic variables for each lake when available. A total of 11 explanatory variables were collected, including mean annual temperature (MAT), mean annual precipitation (MAP), lake area, mean average depth, maximum depth, nitrogen and phosphorus fertilizer use, Normalized Difference Vegetation Index (NDVI), chlorophyll *a*, total phosphorus (TP), and total nitrogen (TN). We

categorized these explanatory variables into four distinct groups, that is, climate variables (MAT and MAP), lake morphometry (lake area, mean average depth, and maximum depth), lake catchment properties (nitrogen and phosphorus fertilizer use and NDVI), and lake trophic state (chlorophyll *a*, TP, and TN) (Fig. 2c, Table S4).

The climate variables and lake morphometry were considered as natural drivers. For climate variables, we extracted MAT and MAP for each lake from previous literatures when available (Tables S1, 2). The unavailable climatic variables were derived by using latitude and longitude from Worldclim database version 2 for 1970-2000 with a spatial resolution of approximately 30 seconds (~1 km²) (Fick and Hijmans 2017). For lake morphometry, we extracted lake area, mean average depth, and maximum depth from previous literatures when available (Tables S1, 2). The unavailable variables were extracted from online repositories, such as Minnesota Pollution Control Agency (<https://www.pca.state.mn.us/>).

The lake catchment properties and lake trophic state were considered as anthropogenic drivers. For lake catchment properties, we included the nitrogen and phosphorus fertilizer use data and Normalized Difference Vegetation Index (NDVI) to quantify the impact of allochthonous carbon on the carbon sink dynamics and carbon sink-source balance in lakes. The fertilizer use data and NDVI, as indicators of terrestrial productivity in lake catchments, have been applied to predict organic carbon burial in lakes worldwide (Anderson et al. 2020) and greenhouse gas concentrations across boreal lakes (Valiente et al. 2022). Fertilizer application rates for each lake were derived by using latitude and longitude from 0.5-decimal degree interpolated averages of nitrogen and phosphorus fertilizer application spanning from 1994 to 2001 (Potter et al. 2010). These data are publicly available as part of NASA's Socioeconomic Data and Applications Center (SEDAC) at <http://sedac.ciesin.columbia.edu/data/collection/ferman-v1>. The average NDVI data for each lake from 2000 to 2023 was derived by using latitude and longitude from MODIS Terra Vegetation Indices MOD13Q1 v061 product (<https://lpdaac.usgs.gov/data/>). This product provides a temporal resolution of 16 days and a spatial resolution of 250 m (Didan 2021). For lake trophic state, we extracted chlorophyll *a*, TP and TN from previous literatures when available (Tables S1, 2). The unavailable variables were extracted from online repositories, such as Minnesota Pollution Control Agency (<https://www.pca.state.mn.us/>), and a database of chlorophyll *a* and water chemistry in freshwater lakes (Filazzola et al. 2020).

Statistical analysis

We conducted the linear models to explore the distribution patterns of carbon burial rates and CO₂ emission rates, and carbon burial ratios and carbon balance ratios along latitudinal gradients. We also conducted linear models to explore the relationships between the carbon burial ratios and carbon balance ratios and natural and anthropogenic variables. Prior to analyses, explanatory variables were log-transformed to improve normality when necessary. This analysis was performed using the R package “stats” V 4.2.2.

To further evaluate the key drivers of carbon burial ratios and carbon balance ratios, we employed random forest analysis (Breiman 2001) and structural equation modelling (SEM) (Grace et al. 2012). First, random forest analysis was conducted to quantify the relative importance of climatic variables, lake morphometry, lake catchment properties, and lake trophic state on carbon burial ratios and carbon balance ratios. The importance of each predictor variable was determined by evaluating the decrease in prediction accuracy (that is, increase in the mean square error between observations and out-of-bag predictions) when the data for that predictor were randomly permuted. The accuracy importance measure was computed for each tree and averaged over the forest (5000 trees). The contributions of predictor variables were scaled to sum to 100. This analysis was conducted using the R package randomForestSRC V3.2.2 (Ishwaran and Kogalur 2019).

Second, SEM (Grace et al. 2012) was used to explore the interactive effects of natural and anthropogenic drivers on carbon sink dynamics and carbon sink-source balance. The hypothesized links were developed based on our expectation that lake trophic state and lake catchment properties could strongly influence carbon sink dynamics and sink-source balance. We further expected that climate variables and lake morphometry could directly mediate the carbon sink dynamics and sink-source balance, and could also have indirect influence through their interactions with lake trophic state and catchment properties (Fig. 2c). Before modeling, all variables in the SEMs were z-score transformed to allow comparisons among multiple predictors and models. Consistent with previous studies (Grace et al. 2016), we used composite variables to capture the collective effects of climate variables, lake morphometry, lake catchment properties, and lake trophic state. The candidate observed indicators were shown in Table S4. The indicators for each composite were selected based on the multiple regressions for carbon burial ratios or carbon balance ratios (Table S5).

Based on all the hypothesized paths among composite variables (that is, full model; Fig. 2c), we examined all alternative models and chose the final model that met the model fit statistics with the low AIC value (Grace et al. 2010). The detailed modeling fit indices for all alternative models were provided in Table S6. We implemented SEMs using the R package lavaan V.0.6-15 (Rosseel 2012). It is worth noting that the sample size may vary across different analyses due to missing environmental data.

Results

Lake organic carbon burial and CO₂ emission rates

In the 286 global lakes, the organic carbon burial rates ranged from 0.01 to 223.30 g C m⁻² yr⁻¹ across individual lakes of all periods in three regions of China (n = 74), Europe (n = 73), and the USA (n = 139) (Fig. S1). Average organic carbon burial rates in China (9.53 g C m⁻² yr⁻¹) were nearly four times lower than those in Europe and the USA (40.94 and 35.16 g C m⁻² yr⁻¹, respectively). During the Anthropocene, organic carbon burial substantially increased from pre-1900 to post-1950, but also showed variations across the studied lakes. Specifically, the organic carbon burial rates increased averagely from 14.33 g C m⁻² yr⁻¹ for pre-1900 to 22.45 g C m⁻² yr⁻¹ for 1900-1950, and to 43.94 g C m⁻² yr⁻¹ for post-1950. The magnitude of the mean increase varied among regions: the lowest increase in burial rates of 9.04 g C m⁻² yr⁻¹ was observed in China, while the highest increase in burial rates of 39.61 g C m⁻² yr⁻¹ occurred in the Europe.

In the 137 global lakes, the carbon burial rates had a mean of 21.98 g C m⁻² yr⁻¹ and ranged from 0.01 to 204.40 g C m⁻² yr⁻¹, while the carbon emission rates, represented by CO₂, had an average of 60.26 g C m⁻² yr⁻¹ and a range of -97.10 to 411.71 g C m⁻² yr⁻¹ (Fig. 3b). The carbon burial rates, but not the carbon emission rates, in China (n = 48), Europe (n = 32), and the USA (n = 13) were significantly higher than those in other regions (n = 49), such as Africa, South America, and Oceania. However, non significant differences were observed in carbon burial and emission rates among China, Europe, and the USA (Figs. S2a, b). There was also no significant relationship between carbon burial and emission rates, but the CO₂ emissions showed relatively higher rates than the organic carbon burial (P < 0.001, Fig. S3).

Organic carbon burial ratio and carbon balance ratio across lakes

We developed the organic carbon burial ratios to quantify the lake carbon sink dynamics during the Anthropocene. The organic carbon burial ratios had a mean of 0.97 and ranged from -0.69 to 3.84 across individual lakes. These ratios indicated that the organic carbon burial rates increased on average 2.44 times from pre-1900 to post-1950. The carbon burial ratios were the highest with a mean value of 1.03 in the USA, which is significantly higher than those in Europe (mean 0.78). However, no significant differences observed between the burial ratios in the USA and China (mean 0.93) (Fig. S1d). The ratios between post-1950 and 1900-1950 were much lower (mean 0.50) than those between post-1950 and 1900-1950, supporting the enhanced carbon burial in many lakes due to accelerated eutrophication and increased sedimentation of organic matter in recent decades.

We further applied the carbon balance ratios to reflect the lake carbon sink-source balance. The carbon balance ratios had a mean of -1.60 and ranged from -5.90 to 3.28. The average ratios were highest in the USA (-0.59) and lowest in China (-1.93). The carbon balance ratios in Europe, with an average of -1.17, were significantly higher than those in China but showed nonsignificant difference with those in the USA. Negative carbon balance ratios were observed in 82.68 % of lakes, indicating carbon burial rates were lower than CO₂ emission rates. This suggests that most lakes are generally supersaturated in CO₂, acting as a carbon source rather than a sink in the regional carbon cycling.

The organic carbon burial ratios, but not the carbon balance ratios, showed predictable patterns along the latitudinal gradient. For the organic carbon burial ratios, there was a significantly decreasing trend towards high latitudes ($P < 0.05$, Fig. 3b), which was different from the burial rates for both periods of pre-1900 and post-1950 ($P < 0.05$, Fig. 3a). It is worth noting that the organic carbon burial ratios showed weaker variation than the burial rates along the latitudinal gradient, with a slope of -0.014 for the burial ratios, whereas the higher slopes of 0.403 and 1.171 for the burial rates during the pre-1900 and post-1950 periods, respectively. For the carbon balance ratios, however, there was no clear latitudinal pattern, with the pairwise carbon burial rates ($P > 0.05$) and the CO₂ emission rates ($P = 0.053$) also showed no significant relationship with latitude (Figs. 3c, d).

Drivers on organic carbon burial ratio and carbon balance ratio

We further examined the environmental drivers of the climate variables, lake catchment properties, lake morphometry, and lake trophic state for the organic carbon burial ratios and the carbon balance ratios (Fig. 4). The organic carbon burial ratios showed a significant relationship with key biogeochemical indicators of lake trophic state, including chlorophyll *a* ($r^2 = 0.11$) and total phosphorus (TP, $r^2 = 0.09$). Specifically, these ratios increased significantly with higher chlorophyll *a* and TP ($P < 0.05$). The burial ratios also had significant positive relationships with nitrogen and phosphorus fertilizer use ($r^2 = 0.08$ and 0.10 , respectively), but a negative relationship with normalized difference vegetation index (NDVI, $r^2 = 0.02$) in the catchment, indicating complex connections between organic carbon burial and terrestrial materials from surrounding catchments. Further, there was a positive relationship between carbon burial ratios and regional climate, such as mean annual temperature (MAT, $r^2 = 0.08$), which is consistent with their decreasing latitudinal pattern. However, lake morphometry, such as lake maximum depth, had a significant negative relationship with burial ratios with r^2 of 0.08 (Figs. 4a, S5a).

The carbon balance ratios were primarily linked to lake catchment properties and trophic state, such as nitrogen fertilizer application ($r^2 = 0.03$), chlorophyll *a* ($r^2 = 0.12$) and total nitrogen (TN, $r^2 = 0.07$). Meanwhile, the carbon balance ratios increased significantly with increases in MAT ($r^2 = 0.05$) and mean annual precipitation (MAP, $r^2 = 0.03$). However, there was no significant relationship between carbon balance ratios and lake morphometry, such as lake area, average depth, and maximum depth (Figs. 4b, S5b).

For the organic carbon burial ratios, the most important explanatory variable revealed by random forest models was chlorophyll *a*, which is usually a proxy for water quality and lake trophic state. Specifically, chlorophyll *a* accounted for 44.79% of the explained variations, followed by MAT (43.54%) and MAP (6.01%) (Fig. 5a). For the carbon balance ratios, the total relative contributions of climate factors (i.e., MAT and MAP) were predominantly 53.82%. The other explanatory variables included lake catchment properties and trophic state, such as nitrogen fertilizer application (26.21%) and chlorophyll *a* (14.47%) (Fig. 5b).

To quantify the interactive effects of the multiple environmental variables on the lake carbon sink dynamics and the carbon sink-source balance, we applied SEM to statistically synthesize their hypothesized relationships (Grace et al. 2012) (Fig. 2c).

Model performance statistics showed that the path analysis produced good models describing the carbon sink dynamics and carbon sink-source balance based on a nonsignificant Chi-square statistic, $RMSEA \leq 0.08$, and CFI and TLI values ≥ 0.95 (Table S6). These models explained 15.5% of lake carbon sink dynamics while 6.4% of variation carbon sink-source balance in the global lakes. It should be noted that the explained variations may not be as high as expected. This is largely because some potentially important variables, such as lake trophic state, are not available for each lake in literatures. Other variables, such as land-use change (Anderson et al. 2013, Dietz et al. 2015), may also influence the carbon sink dynamics and sink-source balance. We encourage future studies to include more comprehensive variables for better explaining the observed patterns in carbon sink dynamics and carbon sink-source balance.

The predictors showed divergent effects on lake carbon sink dynamics and sink-source balance regarding their influence strength and directions (Fig. 6, Table S7). For the carbon sink dynamics, the lake trophic state and catchment properties showed similar important direct effects on the carbon sink dynamics ($R = 0.221$ and 0.236 , respectively), while lake catchment properties had strong indirect effects ($R = 0.108$) and total indirect effects of 0.344 on carbon sink dynamics. Furthermore, we found that climate variables and lake morphometry also showed indirect influences on the carbon sink dynamics via the interactions with lake trophic state, with total indirect effects of 0.221 and 0.116 , respectively. For the carbon sink-source balance, lake catchment properties exhibited the most significant direct effect of 0.253 . The climate variables mainly showed indirect influences of 0.205 on the lake carbon balance via the interactions with catchment properties. Such divergent effects of multiple environmental variables were statistically supported by random forest analyses (Fig. 5). For instance, chlorophyll *a*, an indicator of lake trophic state, explained 44.79% of the carbon sink dynamics, while nitrogen fertilizer application, reflecting lake catchment properties, accounted for 26.21% of the carbon sink-source balance.

Discussion

Lakes become increasingly important for carbon burial especially under the joint effects of global warming and escalated anthropogenic activities (Tranvik et al. 2009, Heathcote et al. 2015). While the long-term storage of organic carbon is frequently documented (Heathcote and Downing 2012, Anderson et al. 2013, Anderson et al. 2020), there are few reports on the quantification of temporal changes in the organic carbon burial rates for individual lake on a global scale. It is also unclear how much greenhouse gas emissions could be offset by organic carbon burial in global lakes. This further limit our comprehensive understanding of the spatial distribution of the temporal changes in carbon burial and the balance between carbon burial and greenhouse gas emissions, and also the environmental factors that influence them. Here, we developed the carbon burial ratios to quantify the temporal changes in carbon burial, i.e., carbon sink dynamics. We then applied the carbon balance ratios to quantify the balance between carbon burial and CO₂ emissions, i.e., carbon sink dynamics. Finally, we constructed the statistical models with hierarchical drivers to explain the spatial patterns observed in these two metrics.

Carbon sink dynamics and carbon sink-source balance in lakes

Our study is among the very first ones to examine the temporal changes in organic carbon burial rates across global lakes, referred to as carbon sink dynamics, and further explore the environmental drivers underlying the temporal changes. The increased magnitude in burial rates from pre-1900 to post-1950 in China was lower than those observed in Europe and the USA. This may be attributed to the larger lake size of collected lakes in China compared to those in Europe and the USA, which might have reduced the impact of anthropogenic disturbance on the organic carbon burial rates (Wang et al. 2018). In addition, the lakes, located in Mongolia-Xinjiang Plateau and Qinghai-Tibetan Plateau in China, were relatively unaffected by anthropogenic activity, and exhibited a lower increased magnitude in burial rates (Wang et al. 2018). However, the increased ratios in burial rates of China, as indicated by the carbon burial ratios, were similar to those of the other regions (Fig. S1d). It should be noted that the above increased magnitudes are less comparable across lakes largely due to their differences in background burial rates across different regions worldwide. Thus, the carbon burial ratio, as an effect size metric that disregards the

background, could be used to directly compare the increasements of carbon burial rates of lakes worldwide.

The organic carbon burial ratios indicated that organic carbon burial rates have increased by average 2.44 times since 1900. The observed increase ratio in organic carbon burial is similar to those reported in another global study, which showed burial rates have tripled across all biomes over the last 100 years, while ~4-fold increases in lakes in tropical grasslands and forests (Anderson et al. 2020). However, the increase ratio is higher than the average values reported in previous studies, such as 1.58 in North America (Heathcote et al. 2015), 2.20 in Europe (Anderson et al. 2014), and 2.00 in China (Wang et al. 2018). Although our study focuses on the temporal changes in burial rates, the carbon burial ratio is comparable to the increased magnitude of organic carbon burial. For instance, the carbon burial in global lakes has increased from 0.05 to 0.12 Pg C yr⁻¹ (that is, 1.40-fold increase) over the last 100 years (Anderson et al. 2020), and inland waters have experienced an increase from 0.05 Pg C yr⁻¹ in the pre-industrial era to 0.15 Pg C yr⁻¹ at present (that is, 2.00-fold increase) (Regnier et al. 2022).

On average, the carbon balance ratios was -1.60 across the global lakes, which is similar to those of boreal and subarctic-arctic lakes in Scandinavia with a range from -1.39 to -4.45 and a mean of -3.40 (Kortelainen et al. 2013), but substantially lower than those for temperate lakes and reservoirs in Conterminous United States (mean = 0.33) (Clow et al. 2015). Furthermore, we found that the lakes in temperate biomes, such as temperate grasslands, savannas & shrublands exhibited relatively higher carbon balance ratios (Fig. S4). This phenomenon is consistent with the fact that temperate lakes are relatively effective at sequestering carbon (Clow et al. 2015). It should be noted that we considered the emissions of only CO₂, but not CH₄, in our calculation of the above ratios, which is mainly because CO₂ emissions are more readily available than CH₄ in literature, and CH₄ emission is less important in terms of only C units (Mendonca et al. 2017). Considering the stronger greenhouse effect of CH₄ (Bastviken et al. 2011) and the revealed carbon balance ratios, we expected that lakes should have a higher potential to act as sources for releasing carbon. Nevertheless, these results collectively suggest that there are substantial differences in lake carbon sink-source balance between biomes, and temperature lakes showed larger organic carbon burial.

Latitudinal patterns for the carbon burial ratios and carbon balance ratios

Towards higher latitudes, we observed a decrease in the temporal changes of organic carbon burial rates since 1900. This is supported by the fact that the organic carbon burial ratios between post-1950 and pre-1900 periods showed a significantly negative latitudinal trend across global lakes. Such a latitudinal pattern is rarely reported in previous literature for the temporal changes of organic carbon burial rates, except for the organic carbon burial rates (Heathcote et al. 2015, Anderson et al. 2020). For instance, the organic carbon burial rates are negatively correlated with latitude in a suite of northern lakes (Heathcote et al. 2015). When more lakes were included such as the low-latitude lakes from China, however, the carbon burial rates consistently showed increasing latitudinal trends for the global lakes in both periods of post-1950 and pre-1900 (Fig. 3a). These results suggest that there is a clear discrepancy in the geographical variations between the carbon burial rates and their temporal changes, and quantification of the temporal changes in carbon burial rate of each lake could provide novel information on how the lakes could contribute to the future regional carbon sink in a global scale.

In contrast, the carbon sink-source balance exhibited no clear latitudinal trends in the global lakes. This is supported by the nonsignificant relationship between latitude and the carbon balance ratios between carbon burial and CO₂ emissions rates (Fig. 3d). Such a latitudinal pattern is unexpected as there are previous reports frequently showing latitudinal differences in the balance between CO₂ emissions and carbon burial. For instance, when two regions are compared, the average ratio of emission to burial is substantially higher in boreal lakes than in subarctic-arctic lakes (Kortelainen et al. 2013, Lundin et al. 2015). However, when the global lakes were considered, such as including the tropical and temperate lakes, there were nonsignificant latitudinal trends for the carbon balance ratios (Fig. 3d). These results collectively suggest that in addition to climate variables, local factors such as the specific ecological and environmental conditions unique to each region could also be crucial drivers of carbon sink-source balance. It should be noted that the heterogeneity of data sources for organic carbon burial and CO₂ emissions may contribute to the nonsignificant latitudinal trends for the carbon balance ratios. The integration of a more comprehensive assessment of lake carbon burial and emissions, along with increased spatial and temporal coverage, is thus encouraged in future studies to enhance our understanding of carbon sink-source balance.

The effects of lake trophic state and climate on organic carbon sink dynamics

Organic carbon burial in lake sediments is generally controlled by three primary processes: autochthonous production, inputs of allochthonous carbon from the catchments and mineralization in both the water column and sediments (Cole et al. 2007). Across the global lakes, we find that the increased ratios in organic carbon burial were directly attributed to the increase in autochthonous production and indirectly influenced by the transport and subsequent accumulation of terrestrial organic matter to lake sediments.

Our results firstly indicate that the increased ratios of organic carbon burial rates were primarily driven by lake trophic state during the Anthropocene. This is supported by the positive relationships between organic carbon burial ratios and lake total phosphorus and chlorophyll *a* (Figs. 4a, S5a). It should be noted that carbon burial rates, rather than carbon burial ratios, are the focus in previous studies, but are also shown to be influenced by lake trophic state. For instance, the recent 10-year carbon burial rates and the mean burial rates during the period 1950-1990 were primarily driven by cultural eutrophication, i.e., total phosphorus, in European mesotrophic to eutrophic lakes (Anderson et al. 2014). The lake carbon burial rates for post-1950 were positively correlated with in-lake total phosphorus in Yunnan-Guizhou Plateau while with the total nitrogen in East Plain in China (Wang et al. 2018). Such effects of nutrients on carbon burial rates could be attributed to the enhanced autochthonous organic matter production due to the continuous increase of in-lake total phosphorus and the total nitrogen concentration and subsequent sedimentation (Pacheco et al. 2014). Collectively, we show here that lake trophic state could influence not only carbon burial rates but also the organic carbon burial changes since 1900, which is especially true regarding chlorophyll *a* (Figs. 4a, 5a), and indicates that lakes with higher trophic states would have higher organic carbon burial increases.

Secondly, the organic carbon burial ratios in lake sediments are also affected by the intensification of agricultural activities, such as fertilizer use in the lake catchment (Fig. 4a). This suggests that organic carbon burial ratios were not only a function of in-lake nutrient availability and primary productivity, but also affected by inputs of terrestrial carbon (Quinton et al. 2010). For instance, the lakes eutrophicated with fertile agricultural catchments accumulate more organic carbon than those in undeveloped catchments (Downing et al. 2008). The modern organic carbon burial

rates in Minnesotan lakes are primarily controlled by the intensification of agriculture in the catchment, but not climate (Anderson et al. 2013). Moreover, the increase in organic carbon burial rates observed at many lakes since the 1950s can be attributed to the increasing extent of arable land in lake catchments (Dong et al. 2012). Intensive agriculture is the main source of soil erosion with consequent transport of sediments, terrestrial organic carbon, and nutrients to inland waters (Quinton et al. 2010). This may therefore enhance organic carbon burial both directly through the high delivery and effective preservation of terrestrially derived organic carbon, and indirectly through nutrient enrichment (eutrophication) by stimulating aquatic productivity and thus the sedimentation of aquatic organic carbon (Heathcote and Downing 2012, Anderson et al. 2013, Pacheco et al. 2014). In contrast, the normalized difference vegetation index (NDVI) in the lake catchment displayed a distinct negative relationship with organic carbon burial ratios (Fig. S5a). This may be explained by the fact that extensive vegetation cover could reduce soil erosion and consequently decrease the amount of carbon eroded from the soil and delivered to aquatic ecosystems (Woo and Luk 1990). Moreover, the introduction and mixing of fresh organic matter into the lakes could stimulate microbial activity and facilitate the metabolism of more recalcitrant carbon via the priming effect (Fontaine et al. 2007, Doetterl et al. 2015, Doetterl et al. 2016), that is, labile dissolved organic carbon could stimulate decomposition of more refractory organic matter (Guenet et al. 2010). These effects may jointly reduce organic carbon burial in lake sediments, thus offsetting, to some extent, the effects of fertilizer use.

Finally, lake organic carbon burial ratios were also positively affected by climate variables, such as mean annual temperature. This is consistent with previous reports that the temperature at the regional scale exerts a weak but positive impact on lake organic carbon burial (Heathcote et al. 2015), although warmer water temperatures could lead to more mineralization and less organic carbon burial as suggested by experimental incubations of boreal lake sediments (Gudas et al. 2010). Temperature increase may result in enhanced aquatic primary productivity and increase the amount of organic carbon produced within lakes' basins (Maavara et al. 2017, Woods et al. 2020). Moreover, climate warming could exhibit stronger effect by disrupting catchment hydrological budgets and, consequently, affecting the delivery of both terrestrial carbon and nutrients to lakes (Weyhenmeyer and Karlsson 2009, Clark et al. 2010). However, lake organic carbon burial ratios were negatively affected by

lake morphometry, which is supported by the negative relationships between organic carbon burial ratios and lake maximum depth (Figs. 4a). This is consistent with the fact that shallower lakes could have greater burial efficiency at temperate and high latitudes (Alin and Johnson 2007).

The effects of lake catchment properties and climate on carbon sink-source balance

The carbon sink-source balance was primarily affected by lake catchment properties and climate variables. Since the carbon sink-source balance is quantified based on the comparison of organic carbon burial to CO₂ emissions, lake catchment properties and climate variables could influence the balance by affecting both organic carbon burial and CO₂ emissions. The application of nitrogen and phosphorus fertilizers could result in regional differences in nutrient availability, which appear to have influences on the carbon sink-source balance, as higher nutrient levels generally stimulate CO₂ fixation and net ecosystem production (Lundin et al. 2015). This would lead to a decrease in net CO₂ evasion and an increase in carbon accumulation in sediments (Kortelainen et al. 2013), thereby increasing carbon balance ratios. For instance, carbon accumulation has been shown to be very rapid, whereas pH is generally high resulting in relatively small CO₂ evasion in heavily loaded agricultural lakes (Downing et al. 2008, Balmer and Downing 2011). In addition, nitrogen fertilizer use may influence the carbon sink-source balance by increasing nitrogen deposition in lake sediments, as sediment nitrogen pool is positively linked to carbon accumulation/evasion ratio in boreal lakes (Kortelainen et al. 2013).

Climate variables, including temperature and precipitation, are also crucial variables that influence the carbon sink-source balance. Temperature could affect both the mineralization and burial of carbon by influencing aquatic respiration and primary production (Velthuis et al. 2018). Increasing temperature could stimulate algal growth and lead to the increase of primary production, thereby promoting the organic carbon burial in lake sediment (Heathcote and Downing 2012). It could also accelerate heterotrophic respiration rates, increase CO₂ emissions, and decrease the burial efficiency of organic matter after sedimentation (Gudas et al. 2010). The differential temperature dependence of photosynthesis and respiration may lead to the positive relationship between carbon balance ratios and mean annual temperature in our study (Fig. 4b). Temperature and precipitation also have an indirect effect on lake's carbon

cycle through their influence on terrestrial carbon fixation and the subsequent carbon leaching to the lake (Sobek et al. 2005). For instance, precipitation could increase terrestrial inputs of nutrients and organic matter (Greaver et al. 2016) that may further promote lake production, thus leading to an increase in carbon burial and a decrease CO₂ emission.

Implications

Several studies have linked development, land clearing, and the intensification of agriculture to increased soil erosion and transport of sediment, organic carbon, and nutrients to receiving water bodies (Anderson et al. 2013, Anderson et al. 2014). The nutrient transfer from land to surface waters will maintain elevated levels of lake productivity and carbon burial in the short term (Smith et al. 1999). As a result of these activities, organic carbon burial rates in lakes have increased on average 2.44 times during the Anthropocene, reflecting stimulation of autochthonous production by eutrophication and enhanced allochthonous inputs related to erosion and sedimentation (Alin and Johnson 2007). While rates of land-cover conversion have slowed in temperate regions, intensification of agriculture in less developed regions will continue to meet future food demands (Downing et al. 2006). These changes in cultural practices have caused substantial alterations to the global carbon cycle, with intensification of agriculture, soil erosion, and sedimentation contributing to a stronger aquatic carbon sink.

Climate change could alter lake primary production and stimulate CO₂ fixation, but it also may cause an increase in organic carbon mineralization rates. Meanwhile, warming trends may facilitate agricultural expansion within the high latitude regions, with associated impacts on lake carbon sink-source balances. High latitude regions are of special interest in a future climate warming scenario, as the surface air temperature increase is predicted to be amplified towards northern high latitudes (Serreze and Francis 2006), which would lead to strongly enhanced lake organic carbon burial. However, if also taking the higher emissions of CH₄ from lakes and its strong greenhouse forcing potential into account (Bastviken et al. 2011), we suggest that these effects could counteract the potential increased lake carbon sink capacity that potentially follows a warmer climate. A better understanding of interactions between these competing forces, and of linkages between terrestrial and aquatic carbon cycles,

is essential for improving global carbon cycle models that are used to project carbon budgets into the future.

Conclusions

Lakes play a critical role in the global carbon cycle by burying carbon in sediments and emitting greenhouse gas into the atmosphere. Lakes become increasingly important for carbon burial during the Anthropocene, but there has been little consideration of temporal change in organic carbon burial across global lakes. It also remains uncertain how much greenhouse gas emissions could be offset by organic carbon burial. In this study, we developed and applied effect-size metric carbon burial ratio and carbon balance ratio for each lake to quantify the temporal change of lake carbon burial and the balance between organic carbon burial and greenhouse gas emission, and the relative importance of natural and anthropogenic drivers. Our findings indicate that most lakes have consistently increased organic carbon burial during the Anthropocene but still exhibit lower organic carbon burial rates than carbon emission rates, acting as carbon sources rather than carbon sinks in the regional carbon cycling. Moreover, our results demonstrate that the lake trophic state exerts significant control over lake carbon sink dynamics, while lake catchment properties determine carbon sink-sources. These findings highlight the need of climate and anthropogenic-induced changes to be considered as integrated drivers of lake organic carbon burial and greenhouse gas emissions under global change.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets of global lake carbon burial and CO₂ emission rates collected in this study are available in the NODE (<https://www.biosino.org/node>) with access number OEP004967.

Author contributions

JW designed the study. FM and HW collected and analyzed the data with contributions from JW and AH. FM and JW finished the first draft. JW, AH and FM finalised the manuscript with contributions from KJ, BL, TG, and QW.

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Figure legends

Figure 1. The synthesis of organic carbon burial (a) and greenhouse gas emissions (b) in global lakes based on various literature sources. The inserted text indicates the first author and the publication year of the literature. The studies indicated by * are based on global lakes and reservoirs. The data and corresponding references presented in the figure can be found in Table S3.

Figure 2. The organic carbon burial rates and greenhouse gas emission rates across global lakes (a), computation of carbon burial ratios and carbon balance ratios (b), and hypothesized drivers and their pathways (c). (a) The map of global lakes with organic carbon burial and greenhouse gas emission rates. The color of the points represents lakes with long-term organic carbon burial rates over the past 100-200 years (red) and lakes with pairwise annual CO₂ emissions and short-term organic carbon burial rates during the Anthropocene (blue). (b) Schematic illustration of the quantification of carbon sink dynamics and carbon sink-source balance. (c) Hypothesized drivers and their pathways affecting lake carbon sink dynamics and carbon sink-source balance. Inset figure in (a) shows whittaker biome plot of lake locations, showing the mean annual temperature (MAT, °C) and mean annual precipitation (MAP, cm) for all 423 lakes. The comprehensive lists of collected data for this study are displayed in Table S1 and Table S2.

Figure 3. Geographic patterns of lake organic carbon burial and carbon emissions. (a) Organic carbon burial rates (g C m⁻² yr⁻¹) in lake sediments. Grey: the pre-1900 period; Black: the post-1950 period. (b) Carbon burial ratios between the two periods of post-1950 and pre-1900; (c) The pairwise organic carbon burial rates (g C m⁻² yr⁻¹) and greenhouse gas emissions rates (g C m⁻² yr⁻¹). Grey: carbon emission rates; Black: organic carbon burial rates. (d) Carbon balance ratios between organic carbon burial rates and carbon emissions rates. Solid lines represent statistically significant linear regression models ($P \leq 0.05$) and dashed lines represent nonsignificant linear regression models ($P > 0.05$).

Figure 4. Natural and anthropogenic drivers of organic carbon burial ratios and carbon balance ratios. The relationships between natural and anthropogenic drivers and carbon burial ratios (a) or carbon balance ratios (b) were visualized with linear regression models. MAT, MAP, N fertilizer use, Maximum depth, and Chlorophyll *a* were selected as representatives of the four environmental groups to investigate the relationship between environmental variables and ratios. The remaining environmental variables presented in Fig. S5. Solid lines represent statistically significant linear regression models ($P \leq 0.05$) and dashed lines represent nonsignificant linear regression models ($P > 0.05$). **(a)** Carbon burial ratios larger than zero (that is, over the horizontal dashed line) indicate that the organic carbon burial rates increased from pre-1900 to post-1950. **(b)** Carbon balance ratios with values above zero (that is, over the horizontal dashed line) indicate that organic carbon burial rates were larger than CO₂ emission rates. MAT: Mean annual temperature (°C); MAP: Mean annual precipitation (mm); N fertilizer: Nitrogen fertilizer use (kg/ha); Maximum depth: Lake maximum depth (m); Chlorophyll *a*: Water Chlorophyll *a* (µg/L).

Figure 5. Relative importance of predictor variables that influence carbon burial ratios (a) and carbon balance ratios (b) in random forest models. Predictor variables are colored by driver class: climate variables, lake catchment properties, lake morphometry and lake trophic state. MAT: Mean annual temperature (°C); MAP: Mean annual precipitation (mm); Nfertilizer: Nitrogen fertilizer use (kg/ha); WMD: Lake maximum depth (m); Chla: Water Chlorophyll *a* (µg/L); TP: Total phosphorus (µg/L).

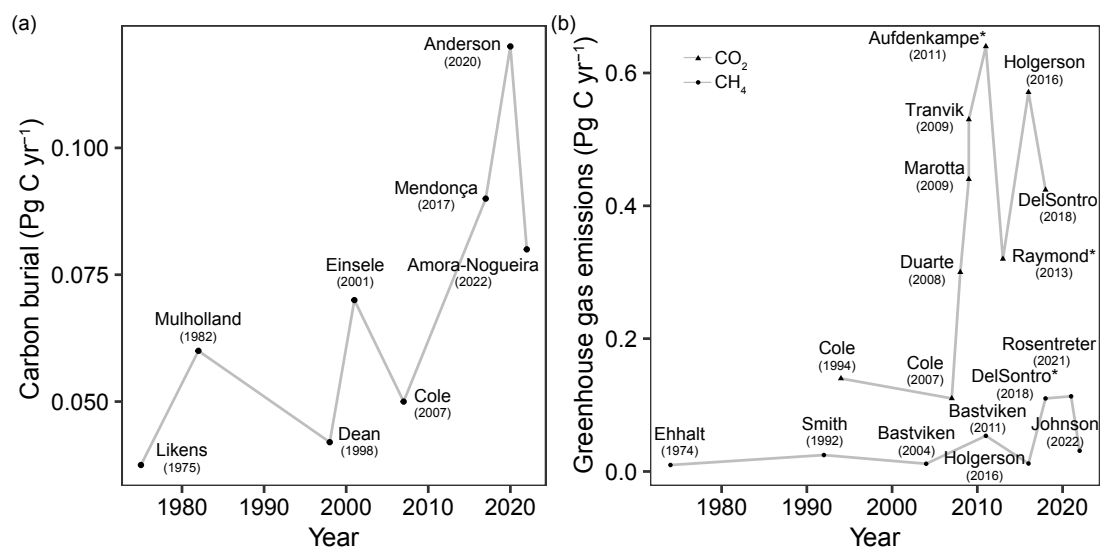
Figure 6. Structural equation models to explain carbon sink dynamics (a) and carbon sink-source balance (b). The carbon sink dynamics and carbon sink-source balance were quantified with carbon burial ratios and carbon balance ratios, respectively. Response variables are displayed within grey boxes and include carbon sink dynamics and carbon sink-source balance. Predictor variables are colored by driver class: climate variables, lake catchment properties, lake morphometry and lake trophic state. R^2 denotes the proportion of variance explained for endogenous variables. Arrows between variables represent statistically significant standardized

960 direct effects. Arrow widths and accompanying numbers are the relative effects (that
961 is, standardized path coefficients) of modeled relationships. Composite and observed
962 variables are indicated in ovals and rectangles, respectively. More details on the
963 model fit are summarized in Tables S6, 7.

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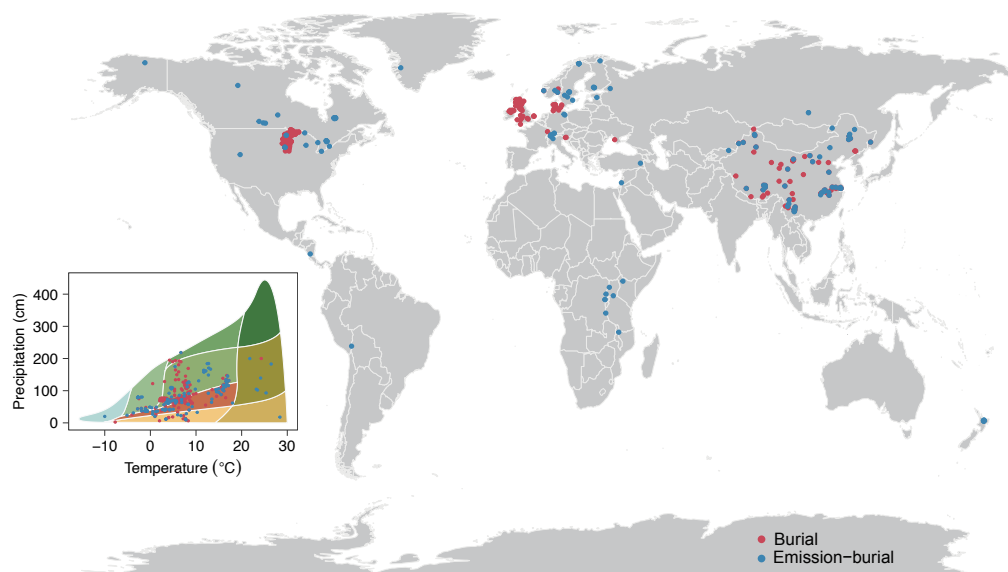
Figure 1



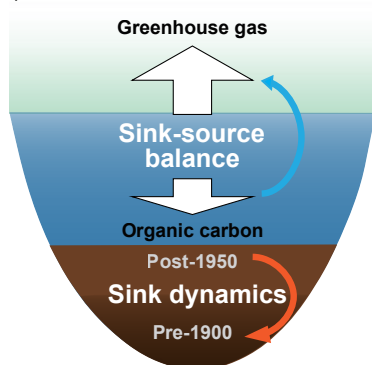
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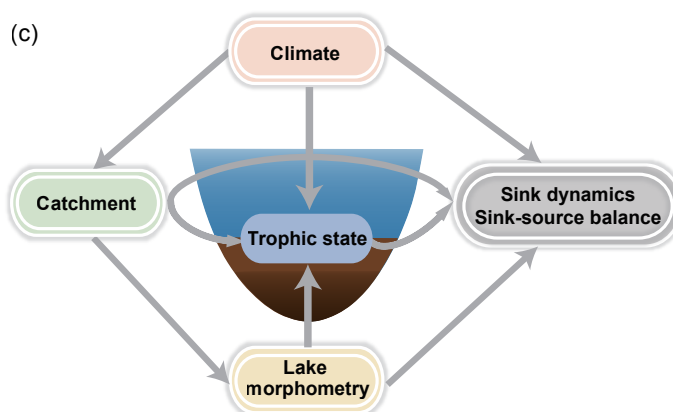
(a)



(b)

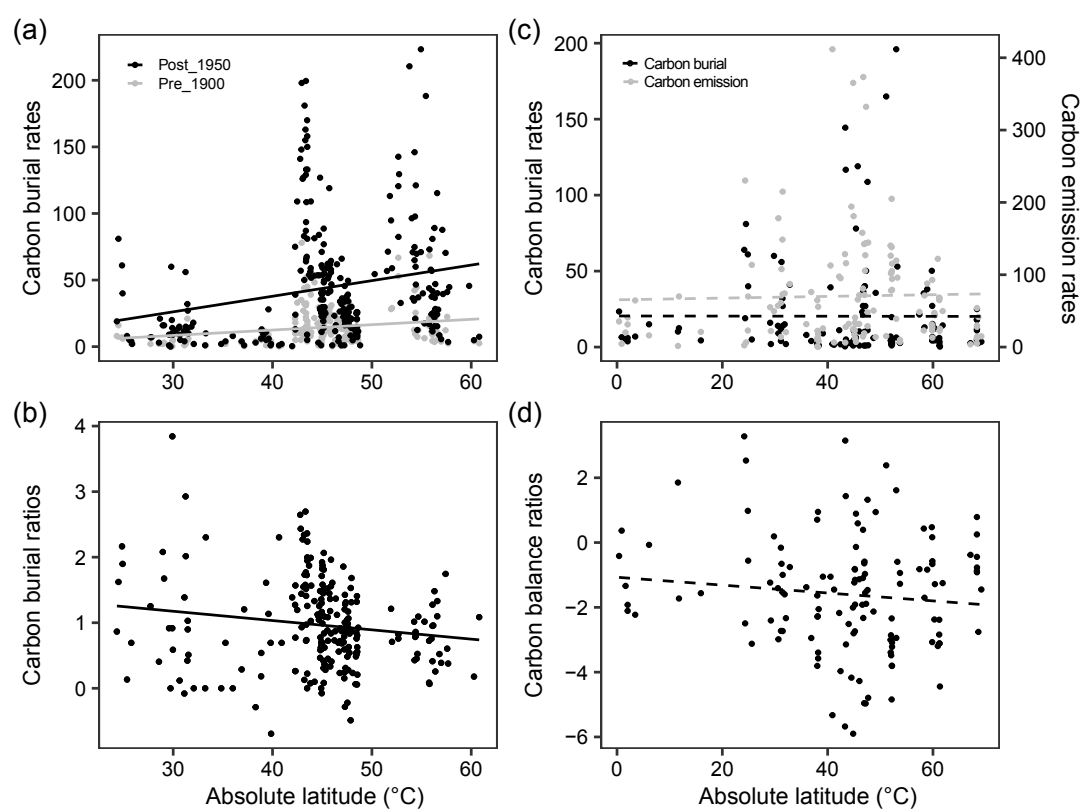


(c)



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Figure 3

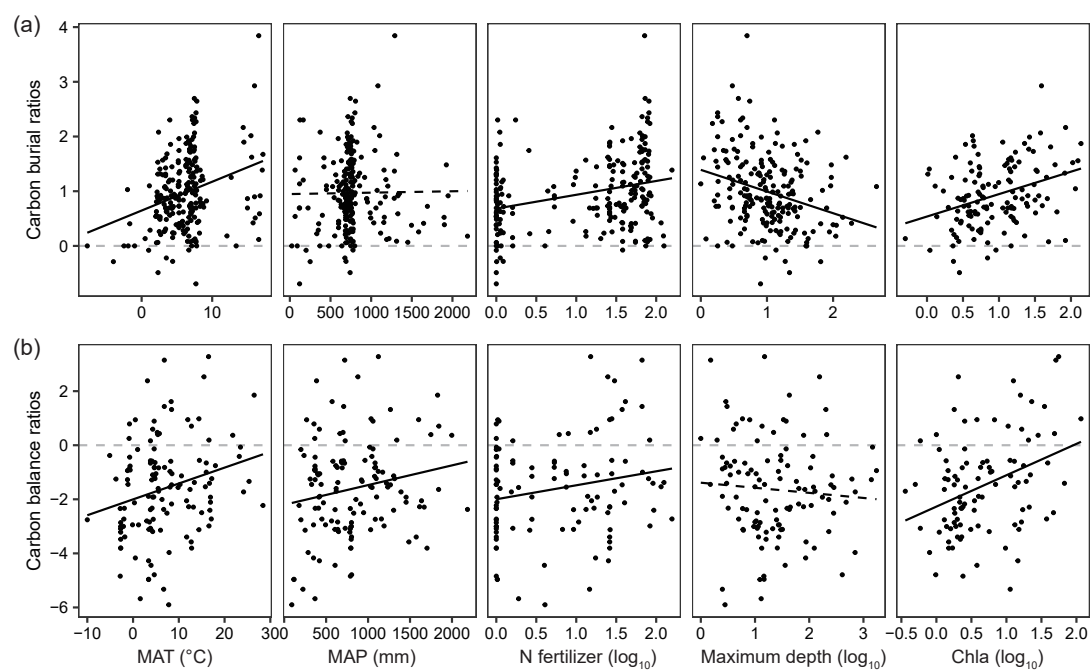


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Figure 4

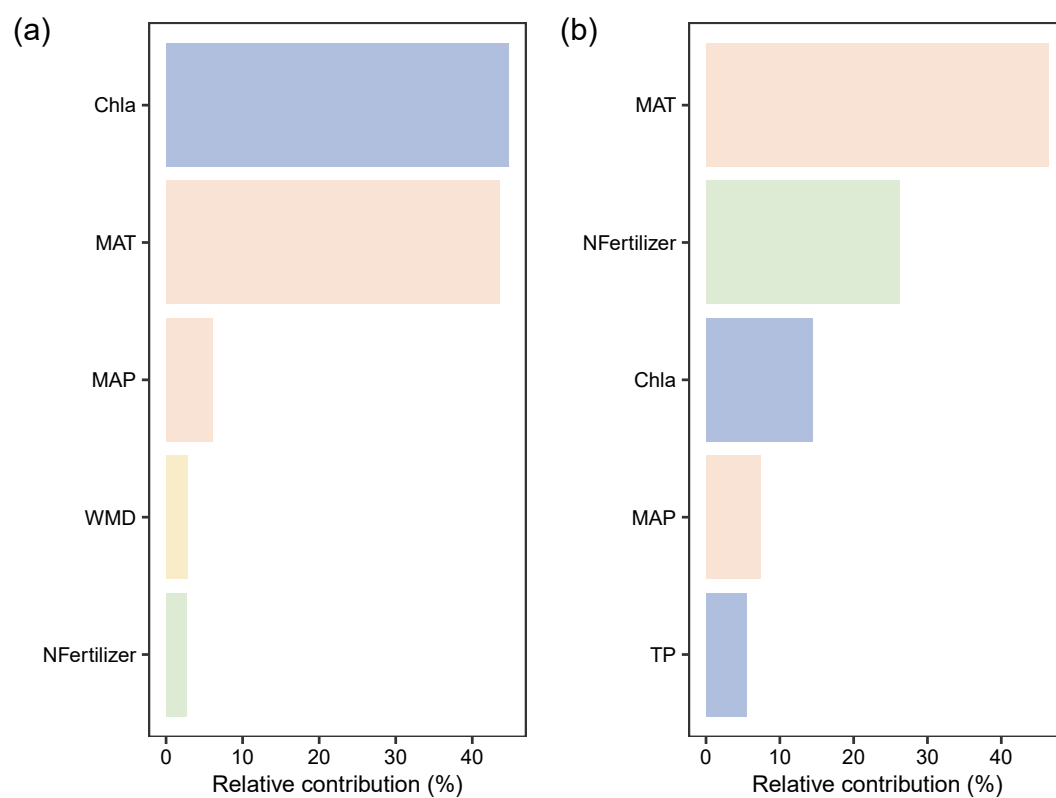


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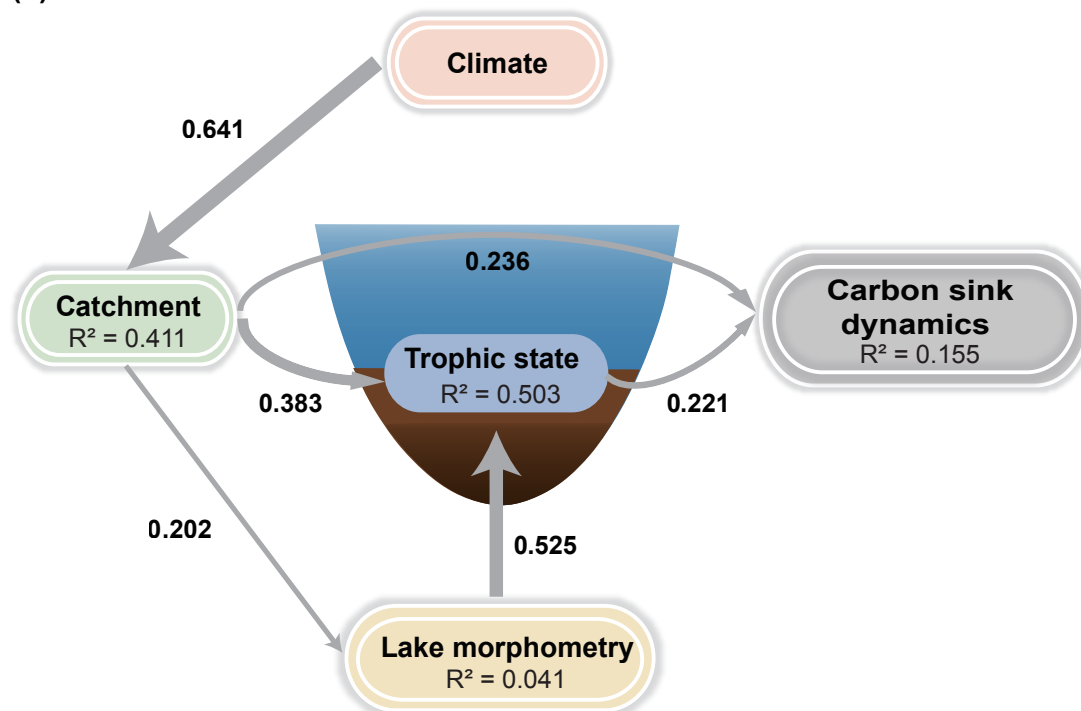
Figure 5



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979

(a)



(b)

