



Increasing Autochthonous Production in Inland Waters as a Contributor to the Missing Carbon Sink

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Accounting for the residual land sink (or missing carbon sink) has become a major budget focus for global carbon cycle modelers. If we are not able to account for the past and current sources and sinks, we cannot make accurate predictions about future storage of fossil fuel combustion emissions of carbon in the terrestrial biosphere. Here, we show that the autochthonous production (AP) in inland waters appears to have been strengthening in response to changes in climate and land use, as evidenced by decreasing CO₂ emissions from and increasing dissolved organic carbon storage and/or organic carbon burial in inland waters during recent decades. The increasing AP may be due chiefly to increasing aquatic photosynthesis caused by global warming and intensifying human activities. We estimate that the missing carbon sink associated with the strengthening AP in inland waters may range from 0.38 to 1.8 Gt C yr⁻¹ with large uncertainties. Our study stresses the potential role that AP may play in the further evolution of the global carbon cycle. Quantitative estimates of future freshwater AP effects on the carbon cycle may also help to guide the action needed to reduce carbon emissions, and increase carbon sinks in terrestrial aquatic ecosystems.

Keywords: inland waters, aquatic photosynthesis, global carbon cycle, climate change, land-use change, autochthonous production, missing carbon sink

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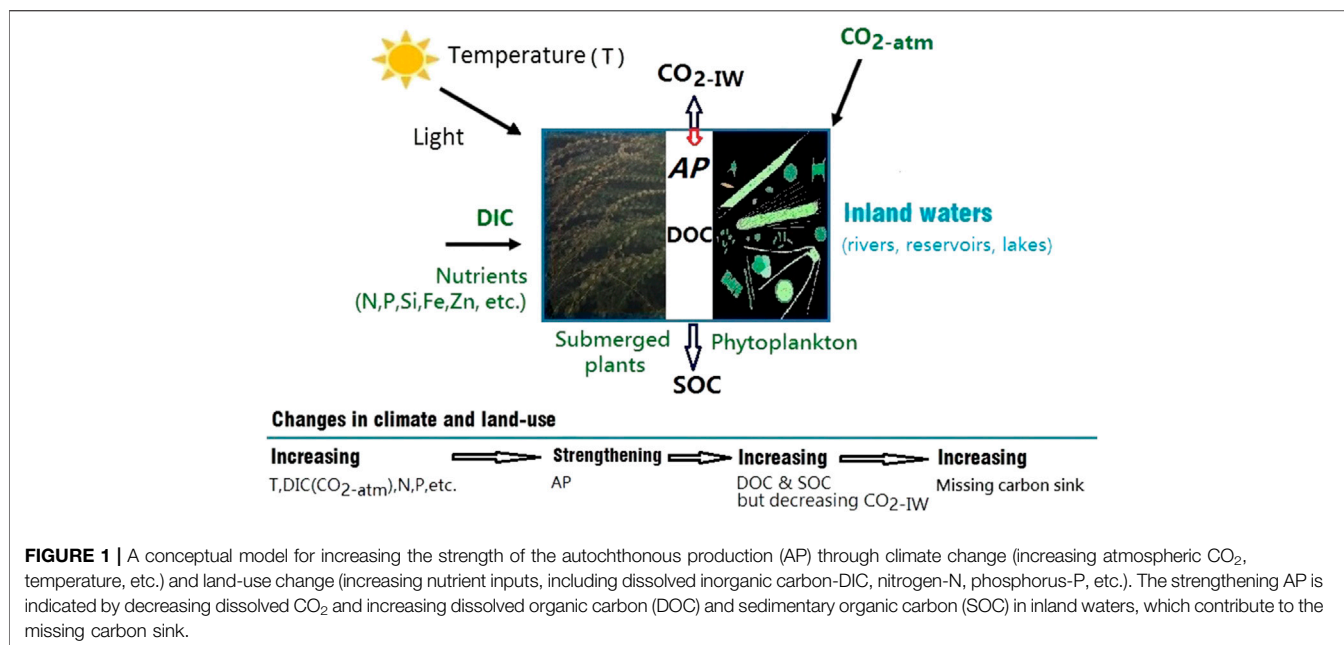
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INTRODUCTION

For the past three centuries CO₂ emissions from human activities, including the burning of fossil fuels and extensive land-use changes, have unbalanced the natural cyclical growth and rise of CO₂ in the atmosphere and the accumulation of CO₂ in the oceans (Broecker et al., 1979; Houghton et al., 1990; Tans et al., 1990; Houghton, 2003; Melnikov and O'Neill, 2006; Houghton, 2007; Ballantyne et al., 2012; Ciais et al., 2013; Houghton et al., 2018; Kirschbaum et al., 2019). This imbalance is recognized as the residual land sink (or missing carbon sink) in the global carbon cycle. The sink is estimated to amount to 2.5 ± 1.3 Gt C yr⁻¹ for the decade, 2002–2011 (Ciais et al., 2013). Various hypotheses have been proposed to explain it, the foremost among them being the finding that increased atmospheric CO₂ concentrations have boosted photosynthesis and the burial of carbon in terrestrial ecosystems (King et al., 1995; Kheshgi et al., 1996). Estimates of the biosphere's CO₂-enhanced drawdown, however, are much smaller than the missing carbon sink. There is evidence that nitrogen might be the cause (Schindler and Bayley, 1993). Over the last century human activity released more than twice as much nitrogen as in previous centuries. Nitrogen is the nutrient that most accelerates growth in forests (Vitousek et al., 1997). However, Nadelhoffer et al. (1999)



calculated that such larger nitrogen contributions increased the carbon flux by only 0.25 Gt C yr⁻¹ at most. Therefore, where the remainder of the missing carbon sink is hiding in the land has become a mystery (Broecker and Peng, 1998; Schindler, 1999). Liu et al. (2010) and Liu et al. (2018) have found the importance of the aquatic autochthonous production (AP) in CO₂ drawdown (or the missing carbon sink).

Here, we show that the AP (Figure 1) appears to have been strengthening in response to the changes of climate and land use, as evidenced by decreasing CO₂ emissions from and increasing dissolved organic carbon (DOC) storage and/or organic carbon (OC) burial in these waters during recent decades (Bianchi et al., 2004; Wang et al., 2007; Downing et al., 2008; Finlay et al., 2009; Sun et al., 2010; Heathcote and Downing, 2012; Anderson et al., 2013; Brothers et al., 2013; Anderson et al., 2014; Pacheco et al., 2014; Finlay et al., 2015; Ran et al., 2015; Wang et al., 2018; Anderson et al., 2020; He et al., 2020; Ran et al., 2021). There are also some studies that show there is no trend in CO₂ (Nydahl et al., 2017) and that increased lake OC burial is due to greater levels of terrestrial production (Heathcote et al., 2015). The reason for this may be that the former examples present the cases dominated by the organic carbon increase from aquatic production (with consumption of dissolved CO₂), which results in increasing OC but decreasing pCO₂ in inland waters, while the latter examples present the cases dominated by the OC increase from terrestrial sources, which results in increasing OC but increasing or no pCO₂ trends in inland waters. However, according to our thorough review the former positive-examples seems more universal (Anderson et al., 2020; Ran et al., 2021). We estimate that the missing carbon sink associated with the strengthening of the AP in inland water may range from 0.38 to 1.8 Gt C yr⁻¹. The considerable uncertainties here may be reduced in the future by integrating all terrestrial carbon cycling processes to better resolve the inland

waters carbon budgets (Cardille et al., 2007; Hanson et al., 2015). This study stresses the potential role that AP may play in the evolution of the global carbon cycle.

OVERVIEW OF THE INCREASING STRENGTH OF THE AP

The role of inland waters (particularly rivers, lakes and reservoirs) have only recently been integrated into the terrestrial carbon cycle. Cole et al. (2007) built a schematic budget for evaluating the contribution of terrestrial aquatic ecosystems to the global carbon cycle, using published data on gas exchange, sediment accumulation and carbon transportation for various different aquatic systems. They showed that inland waters receive 1.9 Gt C yr⁻¹ from terrestrial catchments, of which 0.2 Gt C yr⁻¹ is buried in their aquatic sediments, 0.8 Gt C yr⁻¹ is returned to the atmosphere in gas exchange and the remaining 0.9 Gt C yr⁻¹ is discharged into the sea. Therefore, almost twice as much carbon enters inland aquatic systems from the land as is delivered from them to the ocean. It is thus concluded that although the global area of inland waters is small, these freshwater aquatic systems can affect regional carbon balances. Tranvik et al. (2009) demonstrated that the global annual CO₂ emissions from inland waters to the atmosphere are of approximately the same magnitude as the CO₂ consumption by the oceans. They further show that the global storage of OC in terrestrial aquatic sediments surpasses organic carbon sequestration on the sea floor. This is because the rate of accumulation of sediments and their preservation are both higher in inland waters by a factor of about 50 (Einsele et al., 2001).

However, the carbon fluxes in inland waters are often assumed to remain unchanged regardless of the CO₂ level in the

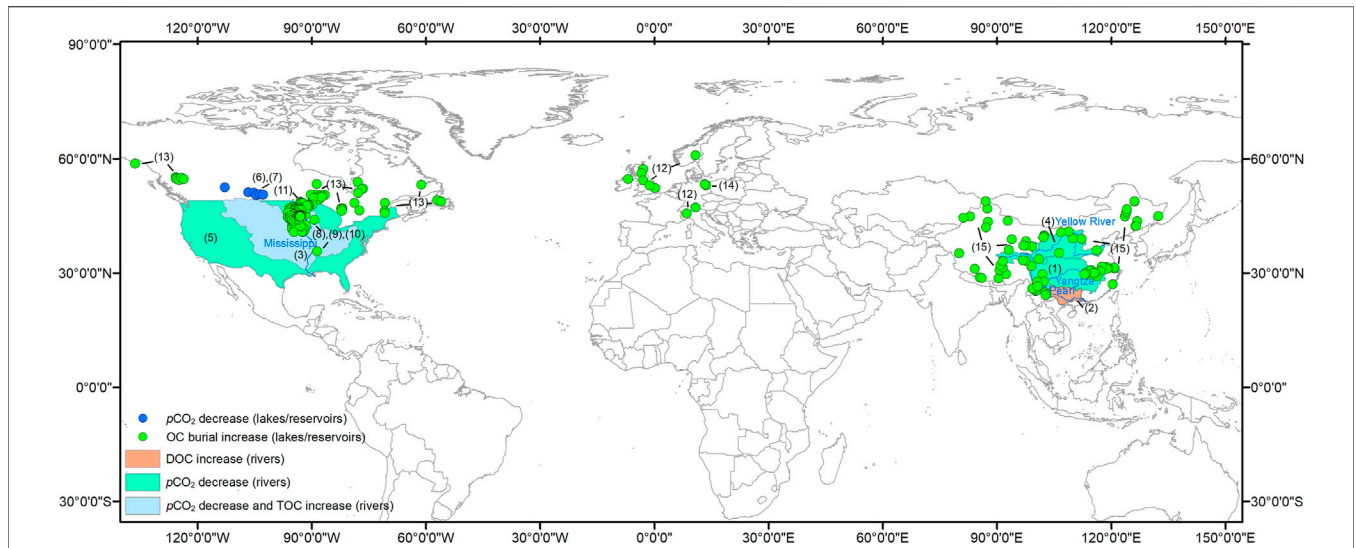


FIGURE 2 | Global distribution of inland waters (rivers, lakes or reservoirs) displaying strengthening of the AP [decreasing pCO₂ and/or increasing DOC/TOC (total OC) and OC burial]. The numbers on the map correspond to these selected references: (1) Wang et al., 2007; (2) Sun et al., 2010; (3) Bianchi et al., 2004; (4) Ran et al., 2015; (5) Jones et al., 2003; (6) Finlay et al., 2015; (7) Finlay et al., 2009; (8) Heathcote and Downing, 2012; (9) Downing et al., 2008; (10) Anderson et al., 2013; (11) Pacheco et al., 2014; (12) Anderson et al., 2014; (13) Heathcote et al., 2015; (14) Brothers et al., 2013; (15) Wang et al., 2018. Note: all of the study lakes are mid-latitude, northern hemisphere lakes, but not from the southern hemisphere or high latitude regions. The reason why 20–60°N lakes were the basis for the review is because this area is where there are the best long term records available.

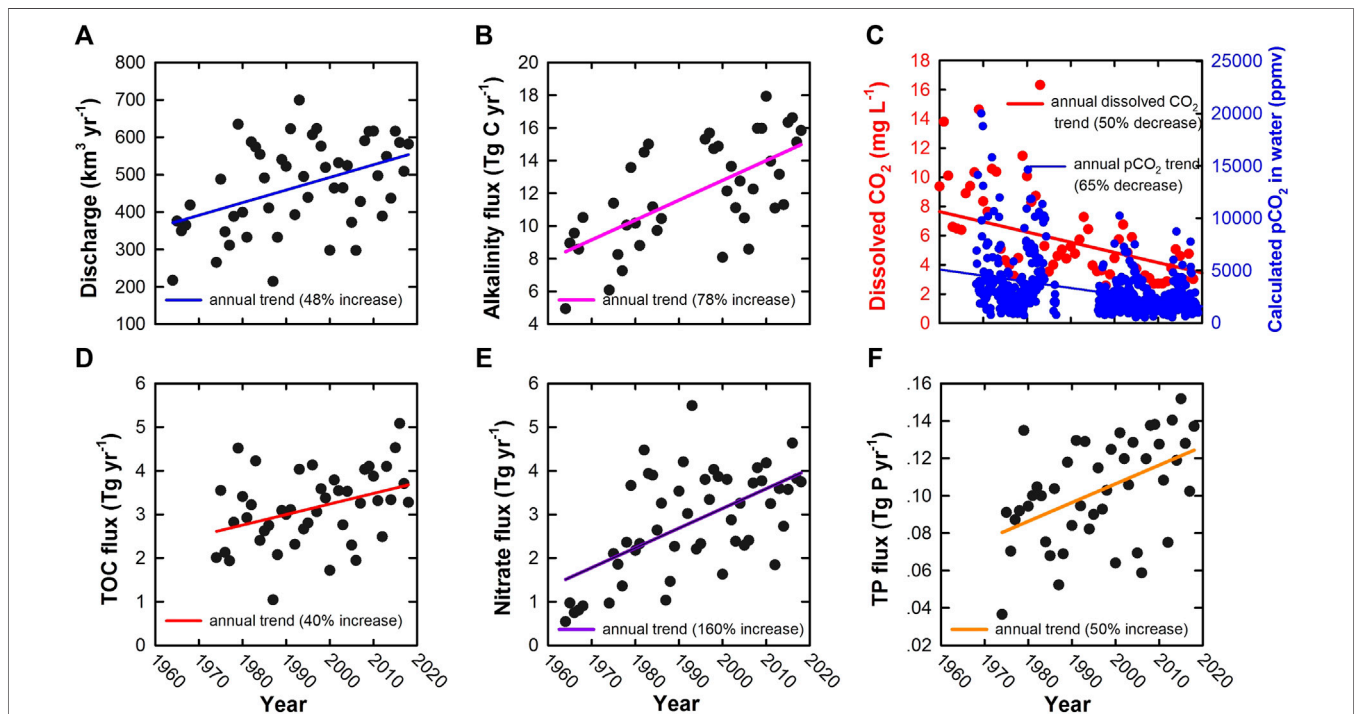
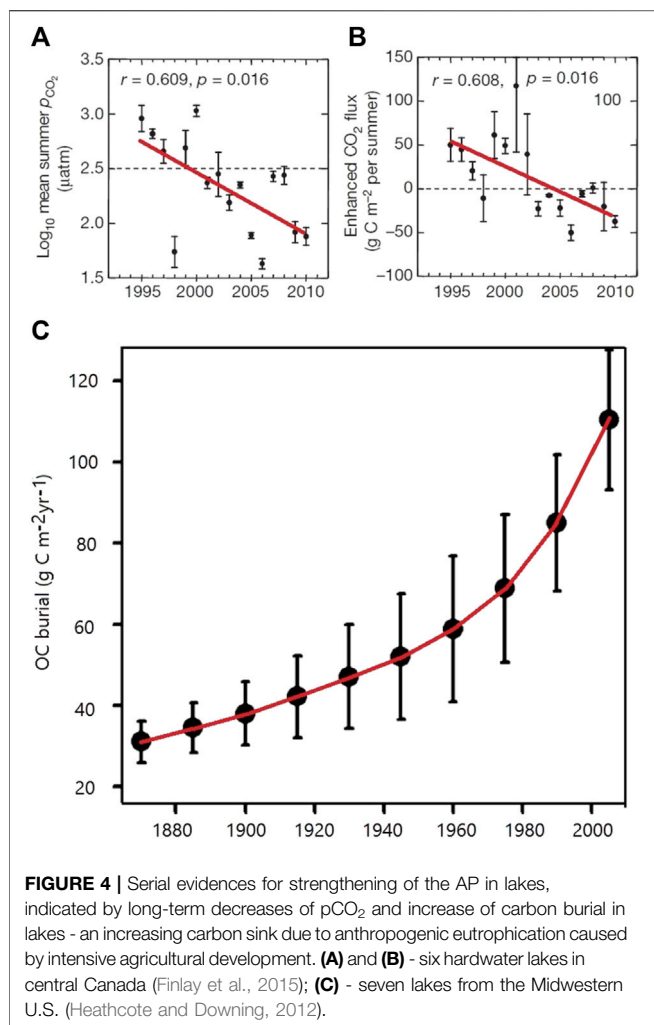


FIGURE 3 | Discharge and mass transport in the Mississippi River. Panels show time series of annual discharge of water (A); alkalinity flux (B); dissolved CO₂ and pCO₂ (C); TOC flux (D); Nitrate flux (E); and TP (total phosphorus) flux (F). All data are abstracted directly or calculated from the USGS Water Data for the Nation (<https://waterdata.usgs.gov/nwis>) at the St. Francisville USGS site 07373420. All depicted linear regression relationships are significant at the $p < 0.01$ level.



atmosphere (Sabine et al., 2004; Ciais et al., 2013). In addition, there is no quantitative differentiation of organic carbon flux sources between the allochthonous (terrestrial) and the autochthonous (formed in inland waters by the AP effect-Watson and Canuel, 2008; Liu et al., 2010; Yang et al., 2016; Liu et al., 2018) in these global studies. This impedes further understanding of the behaviour of the carbon cycle in inland waters and thus increases the uncertainty in global carbon budgeting.

Following a thorough review of previous publications, we have found that the AP in inland waters (Liu et al., 2010; Liu et al., 2018) appears to have been strengthening in response to the changes of climate and land-use (Figures 1, 2), as evidenced by decreasing CO_2 emissions from and increasing DOC storage and OC burial in inland waters during the past 60–150 years (e.g., Figures 3–5).

Carbon cycling in inland waters has been studied both in terms of the magnitude and global significance of carbon that is released to the atmosphere (Richey et al., 2002; Raymond et al., 2013) and that which is stored in the sediments (Mulholland and Elwood, 1982; Dean and Gorham, 1998; Stallard, 1998; Einsele et al., 2001). Interestingly, there have been few studies examining

whether measures of carbon release flux are directly related to how much carbon is being stored in sediments at the same time (Hanson et al., 2004). However, Flanagan et al. (2006) found that CO_2 saturation in water is inversely correlated with the rate of sedimentation, suggesting that calculation of CO_2 fluxes from inland waters should take this into consideration.

The AP has been recognized by oceanographers as the interaction between biota and sedimentation in the oceanic carbon cycle. Flanagan et al. (2006) thus thoroughly examined sedimentation types and rates and food web structure as factors controlling the saturation of CO_2 , and proposed a common framework for inland waters and marine ecosystems. Later, Knoll et al. (2013) described the regional significance of Ohio reservoirs for OC sequestration and CO_2 emissions, finding that the reservoirs bury up to four times more OC, and release less than 25% of the CO_2 , than predicted based on their area and recent global mean estimates in lentic ecosystems, which indicates that temperate hard-water reservoirs are important OC sinks rather than CO_2 sources.

Decrease in the CO_2 Degassing Flux in Inland Waters in Recent Decades

A decrease in CO_2 degassing flux seems to be a global phenomenon both in rivers (Wang et al., 2007; Ran et al., 2015; Ran et al., 2021) and lakes (Finlay et al., 2009; Finlay et al., 2015) (Figure 2), that is likely to be influenced by anthropogenic activity and climate change.

Jones et al. (2003) calculated the partial pressure of CO_2 ($p\text{CO}_2$) in 417 streams and rivers distributed across the contiguous United States over a 22 year period. They found that $p\text{CO}_2$ declined by 78.4 ppmv a^{-1} (or 58%) between 1973 and 1994. Although the leading cause for the decline was attributed to large-scale declines in terrestrial CO_2 production and import into aquatic ecosystems during this 22-year period, increased in-river primary production was likely a significant factor because it coincides with significantly increased oxygen saturation in the aquatic environment (Jones et al., 2003). For the Mississippi River (the largest in North America, draining an area of ~ 3 million km^2), we have found a similar decrease in $p\text{CO}_2$, about 65% in the last 50 years (Figure 3C). In addition, Finlay et al. (2015) found that hardwater lakes in the northern United States plains have shifted progressively from being substantial CO_2 sources in the mid-1990s to sequestering CO_2 by 2010 (Figures 4A,B), with a steady increase in annual mean pH. This decrease in CO_2 efflux and increase in pH were attributed to the atmospheric warming and nutrient-induced increase in aquatic photosynthesis.

In Asia, Wang et al. (2007) found that the dissolved CO_2 in the Yangtze River (the largest river in Eurasia, draining 1.8 million km^2) decreased greatly over the period, 1960–2000 (Figure 5B), together with a marked increase in nutrient concentrations (e.g., $>500\%$ increase in NO_3^- ; Figure 5C). They showed that although the discharge and DIC flux had remained essentially constant in the Yangtze, dissolved CO_2 was oversaturated wrt atmospheric CO_2 and its concentration had displayed a decreasing trend since the 1960s. This decrease in

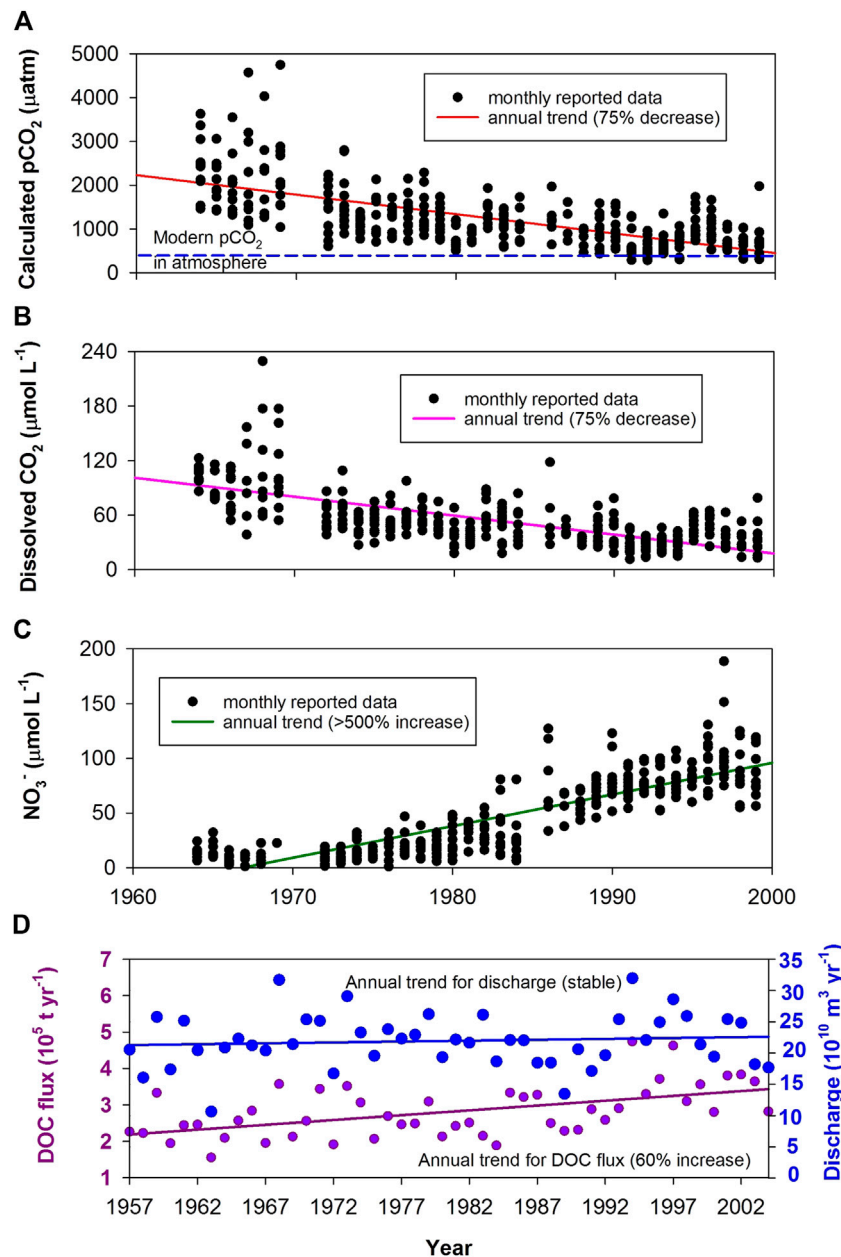


FIGURE 5 | Serial evidences for the increasing strength of the AP in rivers, indicated by long-term decreasing dissolved CO_2 and increasing DOC flux in two of China's bigger rivers as an increasing missing carbon sink is created by human activities that include reservoir/dam construction and domestic/agricultural effluents (increasing nutrient inputs, e.g., NO_3^-). **(A–C)** - Yangtze River (Wang et al., 2007); **(D)** - Xijiang River (Sun et al., 2010).

dissolved CO_2 concentrations was ascribed to variations in the riverine trophic level and stream damming activities in the Yangtze drainage basin. Due to substantial economic innovations (e.g., agriculture and industry development) across the Yangtze watershed, fertilizer applications and physical regulation have significantly altered the original state of the river. Its ecosystem and hydrological condition have been evolving toward the “lacustrine/reservoir” autotrophic type prevailing with plankton. Consequently, average CO_2 degassing flux from the river had declined by ~75% from the

1960s ($58.8 \text{ Mt C yr}^{-1}$) to the 1990s ($15.3 \text{ Mt C yr}^{-1}$; Wang et al., 2007).

Similar decreasing trends in $p\text{CO}_2$, 1950–2012, were also found in the Yellow River, China (the sixth longest river system in the world, draining ~ 0.8 million km^2). Ran et al. (2015) attributed this to flow regulation by dams that reduced turbidity and extended residence times, thus promoting photosynthesis of aquatic plants and reduced aqueous CO_2 concentrations. More recently, Ran et al. (2021) investigated seasonal and annual fluxes of CO_2 emissions from streams,

rivers, lakes, and reservoirs throughout China and quantify their changes over the past 3 decades. They found that the CO₂ emissions declined from $138 \pm 31 \text{ Tg C yr}^{-1}$ in the 1980s to $98 \pm 19 \text{ Tg C yr}^{-1}$ in the 2010s. They suggest that this unexpected decrease was driven by a combination of environmental alterations, including massive conversion of free-flowing rivers to reservoirs and widespread implementation of reforestation programs.

The Increase in DOC and OC Burial in Inland Waters in Recent Decades

As shown above, strengthening of the AP in recent decades has reduced the pCO₂ of inland waters due to the photosynthetic consumption of DIC (Liu et al., 2010; Yang et al., 2016; Liu et al., 2018) which, in turn, should increase the DOC concentration (Bianchi et al., 2004; Zhou et al., 2018) and the OC burial (Heathcote and Downing, 2012; Anderson et al., 2013; Brothers et al., 2013; Anderson et al., 2014; Pacheco et al., 2014; Heathcote et al., 2015; Radbourne et al., 2017; Anderson et al., 2020; He et al., 2020).

Reservoir building has resulted in lower velocities and turbidities in many rivers, improving the conditions for photosynthesis and thus contributing more DOC to global fresh waters (Sun et al., 2010). In addition, the increasing nutrient loadings from domestic and agricultural effluents worldwide may also have led to an increased contribution to the DOC flux (Figure 5D). Bianchi et al. (2004) have shown that autochthonous production in rivers may be more important as a source of DOC than previously believed. Increases in nutrient loading (Figures 3E,F) and decreases in suspended loads (because of dams) in the Mississippi River, as well as other large rivers around the world (e.g., Figure 5D), has resulted in significant changes in the sources and overall cycling of riverine DOC.

Heathcote and Downing (2012) evaluated changes in carbon burial rates in several natural lakes in the United States state of Iowa, where the watersheds have been severely altered over the past 150 years. Their remarkable findings (Figure 4C) show the increasing rates of carbon burial in these lakes as agricultural activity intensified. These rates before strong human activities are comparable to worldwide averages for nutrient-poor lakes. However, burial rates have increased to very high levels (up to $200 \text{ g C m}^{-2} \text{ yr}^{-1}$) following agricultural development in most other cases reported.

These studies suggest that anthropogenic change leads to higher OC burial rates by increasing autochthonous and allochthonous carbon fluxes, and that global carbon burial in lakes will become more significant with continuing eutrophication caused by human activities.

Anderson et al. (2013) further suggest that it is land-use change but not climate that causes increases in OC burial in lakes. Pacheco et al. (2014) suggest that, although lakes are important participants in global carbon cycle, the significance of their role may vary with the extent of anthropogenic eutrophication. Geographical regions with abundant surface water supplies can anticipate the development of highly

eutrophic lakes because they tend to be more polluted by agriculture and urbanization. They show that enhanced primary production in highly eutrophic lakes can be CO₂ sinks by taking up atmospheric CO₂ directly. These lakes transform both atmospheric CO₂ and DIC into OC, burying some proportion of it in bottom sediments and sending the remainder downstream. Moreover, eutrophication may reverse the role of oligotrophic lakes by enhancing their carbon sequestration ability to store OC (Pacheco et al., 2014). Throughout the course of transition from agriculture to urbanization, levels of eutrophication increase. At the same time, the expected large releases of CO₂ into the atmosphere from natural lakes decline substantially (cf. Figures 4A,B), and inland carbon sequestration (cf. Figure 4C) and enrichment of DOC in waters flowing to the sea (Figure 5D) are augmented. Therefore, these authors propose that the global carbon budget should take eutrophication into consideration due to its influence on lakes.

The nitrogen and phosphorus surplus from agriculture development and land use change is causing severe eutrophication in lowland lakes in Europe (Anderson et al., 2014). Although the eutrophication effects on local ecology are understood, their influence on OC burial in lakes and its temporal variation have not been well investigated. These authors also show that the carbon accumulation rate has been high through the 20th Century. Current rates have increased by at least four times compared to background estimates. Their study suggests that lowland European meso-to eutrophic lakes have had OC burial rates more than $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ over the past century. Heathcote et al. (2015) showed that the burial rates are up to fivefold compared with prior estimates. Although temperatures are higher their rise is not enough to explain the increase in burial. Therefore, other drivers including atmospherically deposited reactive nitrogen are involved.

In Asia, Wang et al. (2018) investigated the temporal-spatial pattern of OC sequestration in Chinese lakes since 1850. They found that the average post-1950 OC burial rates were significantly higher than the 1850–1900 rates. The magnitude of this increase was most marked in the subtropical lakes of the Eastern Plain and on the Yunnan-Guizhou Plateau where the post-1950 OC burial rates was about three times that of 1850–1900, due to the agricultural intensification and urban expansion in recent decades. Moreover, OC burial rates were significantly higher in the Eastern Plain than on the Mongolia-Xinjiang Plateau (Northeast China) for all time periods. Lake OC burial rates in Yunnan-Guizhou Plateau were significantly higher than rates in the Qinghai-Tibetan Plateau for the post-1950 period and in Mongolia-Xinjiang Plateau for 1850–1900. Regression analyses showed that the controls on lake OC burial rates varied among regions, with catchment climate variables being the most important regulators in Mongolia-Xinjiang Plateau and Qinghai-Tibetan Plateau, but the in-lake nutrient concentrations were more important in Yunnan-Guizhou Plateau and Eastern Plain. These results indicate that lakes will become increasingly important for OC burial under future global change scenarios, especially due to intensifying human activities.

In addition, Brothers et al. (2013) showed that a regime shift from macrophyte to phytoplankton domination boosted carbon burial in a shallow, eutrophic lake with no surface in-or outflows, where sedimentation rates are four times higher than 50 years ago. This change coincided with an ecological regime shift involving the complete loss of submerged macrophytes, leading to a more turbid, phytoplankton-dominated state. To determine if the carbon burial increase is caused by the transformation of carbon cycling pathways coincident with this regime shift, they compared the annual carbon balances of this turbid lake to a neighboring clean lake with similar nutrient concentrations and submerged macrophytes. Results showed that around 80% of the carbon input was buried permanently in the turbid lake sediments, but only 40% in the clean lake. The reason is that a turbid lake buries carbon more rapidly due to lower benthic carbon mineralization rates (Brothers et al., 2013). The latter were linked to a decline in benthic oxygen availability coinciding with the loss of submerged macrophytes. In contrast to previous assumptions that a regime shift to phytoplankton dominance decreases lake heterotrophy by boosting whole-lake primary production, their results suggest that an equivalent net metabolic shift may also result from lower carbon mineralization rates in shallow, turbid lakes. The widespread occurrence of such shifts thus may fundamentally alter the role of shallow lakes in the global carbon cycle, away from channeling terrestrial carbon to the atmosphere and towards burying increasing amounts of it (Brothers et al., 2013).

More recently, Anderson et al. (2020) have reported global and biome specific trajectories of lake C sequestration based on 516 lakes and showed that some lake C burial rates (i.e., those in tropical forest and grassland biomes) have quadrupled over the last 100 years. They found that global lake C-sequestration ($\sim 120 \text{ Tg year}^{-1}$) has increased by $\sim 72 \text{ Tg year}^{-1}$ since 1900, offsetting 20% of annual CO_2 freshwater emissions rising to $\sim 30\%$ if reservoirs are included and contributing to the residual continental C sink. They further indicated that nutrient availability explains $\sim 70\%$ of the observed increase, while rising temperatures have a minimal effect. In addition, though increased gross primary production (GPP) in rivers and streams is often accompanied by increased ecosystem respiration (ER) (Hosen et al., 2019), GPP increased more than ER especially during drought, even leading to temporary autotrophy, an otherwise rare event in the typically light-limited heterotrophic river main stem. With climate change, rivers and streams may become warmer and drought frequency and severity may increase. Such changes may increase autotrophy in rivers with broad implications for carbon cycling in aquatic ecosystems (Hosen et al., 2019).

IMPLICATIONS FOR ESTIMATIONS OF THE MISSING CARBON SINK

As shown above, the AP in inland waters has strengthened significantly in the recent past, indicated by decreasing CO_2 emissions and increasing DOC flux and OC burial (storage) in

world rivers, lakes and reservoirs (Figures 3–5). Both the decreasing CO_2 emissions and the increasing OC burial can be considered as missing carbon sinks, which will be estimated below.

Estimation of the Missing Carbon Sink Based on Decreasing CO_2 Emissions

Wang et al. (2007) have demonstrated that the average CO_2 degassing flux to the atmosphere from the Yangtze River declined by $\sim 75\%$ over the period from the 1960s to the 1990s. Jones et al. (2003) found that $p\text{CO}_2$ in 417 streams and rivers throughout the contiguous United States declined 58% from 1973 to 1994. For the Mississippi River, the decrease in dissolved CO_2 was also large, amounting up to 50% during the past 55 years from 1963 to 2018 [Figure 3, U.S. Geological Survey (USGS) site 07373420, near St. Francisville, LA; $30^\circ 45' 30''$, $91^\circ 23' 45''$, <https://waterdata.usgs.gov/nwis/>].

If we take 50% as the conservative estimate for the decrease in the CO_2 degassing flux in inland waters in these recent decades, with 2.1 Gt C yr^{-1} (Raymond et al., 2013) and $0.75 \text{ Gt C yr}^{-1}$ (Cole et al., 2007) as the maximum and minimum global CO_2 emissions from inland waters respectively, then a maximum value of 1.0 Gt C yr^{-1} and a minimum of $0.38 \text{ Gt C yr}^{-1}$ are obtained for the missing carbon sink. The role of the AP here needs to be determined quantitatively in the future by distinguishing between the decline in terrestrial CO_2 production plus import into aquatic ecosystems (Jones et al., 2003; Maberly et al., 2013; Campeau et al., 2019) and the decrease in CO_2 caused by increased AP (Wang et al., 2007; Ran et al., 2015; Ran et al., 2021).

Estimation of the Missing Carbon Sink Based on Increasing OC Burial

Anderson et al. (2013), Anderson et al. (2014), and Anderson et al. (2020) have shown that, compared to background estimates of OC burial, contemporary rates have increased at least three to fivefold.

If we take three-fold (Anderson et al., 2013) as the conservative estimate for the increase in OC burial flux in inland waters in the recent past, with 0.6 Gt C yr^{-1} (Tranvik et al., 2009) and 0.2 Gt C yr^{-1} (Cole et al., 2007) as maximum and minimum global OC burial rates in inland waters respectively, then a maximum of 1.8 Gt C yr^{-1} and a minimum of 0.6 Gt C yr^{-1} are obtained for the missing carbon sink, which are the same order of magnitude as those obtained above for the estimates of decreasing CO_2 emissions. This may indicate that it is highly likely that the increasing OC burial and decreasing CO_2 emissions are together due to the strengthening of the AP in inland waters, an important contributor to the missing carbon sink.

Finally, the persistence of autochthonous production derived organic carbon deserves short discussion here. It is commonly assumed that autochthonous organic carbon is easier to be decomposed. However, this depends on the environmental conditions (Gudasz et al., 2015; Katsev and Crowe, 2015; Guillemette et al., 2017; Huang et al., 2017; Radbourne et al., 2017). For example, Radbourne et al. (2017) found that most of

the autochthonous OC is preserved (similar to 95% of OC captured in the deep trap and 86% of the NEP in the contemporary system), which is contrary to the widely held assumption that this more labile, algal-dominated OC component is not well preserved in lake sediments. According to our study in Fuxian Lake, there was little change in the proportion of autochthonous OC, which accounted for more than 50% of OC during the past century (He et al., 2020). Similar results are obtained by Heatcote and Downing (2012) in a suite of natural lakes in the United States state of Iowa, and Huang et al. (2017) in western and northern Dianchi Lake, SW China.

CONCLUSION AND FUTURE RESEARCH DIRECTIONS

We have shown that the AP in inland waters appears to have been strengthening in response to global changes of climate and land use, as evidenced by decreasing CO₂ emissions from, and increasing DOC storage and OC burial in, inland waters during recent decades. We estimate that the missing carbon sink associated with this strengthening may range from 0.38 to 1.8 Gt C yr⁻¹. Our study stresses the potential role that the AP may play in the further evolution of the global carbon cycle. However, to determine quantitatively the role played by this mechanism, the following needs to be done in future work:

- 1) Treat changes in DIC (including pCO₂), DOC and buried OC simultaneously in a given inland water ecosystem to fully describe the AP effect

Although some global-scale studies have examined specific processes such as carbon burial and CO₂ exchange with the atmosphere, most studies of lake carbon cycling are from single systems, focus only on a specific habitat, and do not account for all of the major terms in OC budgets. Hence, most lake OC budgets are incomplete, leaving some key processes highly uncertain. To advance the analysis of the role of the inland waters in carbon cycling, ecosystem science needs a new generation of studies that confront these shortcomings (Cole et al., 2007; Battin et al., 2009; Tranvik et al., 2009; Hanson et al., 2015).

The future final quantification of the freshwater AP effect on the carbon cycle, therefore, should contribute to policies to reduce carbon emissions and increase carbon sinks in terrestrial aquatic ecosystems.

- 2) Monitor the long-term changes in these parameters to understand the AP responses to changes in climate and land use

Understanding the variability of DIC (including CO₂), DOC and OC burial through long-term studies is crucial to capture the patterns and drivers influencing sources of these components at scales relevant to decision-making (Jones et al., 2003; Raymond and Cole, 2003; Wang et al., 2007; Downing et al., 2008; Raymond et al., 2008; Finlay et al., 2009; Sun et al., 2010; Heathcote and

Downing, 2012; Finlay et al., 2015; Ran et al., 2015; Drake et al., 2018).

- 3) Partition between autochthonous and allochthonous OC in inland waters

Key problems in understanding OC budgets are the partitioning between autochthonous and allochthonous sources (Waterson and Canuel, 2008; Yang et al., 2016; Huang et al., 2017; Radbourne et al., 2017; Huang et al., 2018; He et al., 2020), resolving the spatial heterogeneity and temporal dynamics in inputs and their transformations, and measuring critical processes such as burial of OC at temporal scales suitable for resolving annual budgets (Hanson et al., 2015).

- 4) Understand the limitation of nutrients, especially CO₂, on the primary production or eutrophication in different inland waters

The unique property of CO₂ in the biosphere is its conversion to biomass through photosynthesis. The research interest in CO₂ as a key nutrient (King, 1970; Schindler and Fee 1973; Riebesell et al., 1993; Kaplan and Reinhold, 1999; Jansson et al., 2012; Low-Decarie et al., 2014; Kragh and Sand-Jensen, 2018; Zeng et al., 2019) is related to its ready global availability compared to other resources, especially phosphorus and nitrogen (Schindler, 1977; Smith et al., 1999). The limited role assigned to CO₂ in restricting productivity is based on the assumption that only a single nutrient can control it at any given time. However, Low-Decarie et al. (2015) suggest that CO₂ can function as a rate-limiting rather than a yield-limiting resource (phosphorus is a yield-limiting resource), and that it can interact with other resources in the co-limitation of productivity. CO₂ can limit the productivity of eutrophic lakes in cases where photosynthesis exceeds diffusive influx from the atmosphere (Kaplan and Reinhold, 1999). Jansson et al. (2012) found that even in lakes where phosphorus limitation is present, CO₂ supersaturation strengthens primary productivity ten times more than in the same system in equilibrium with the atmosphere.

In addition, CO₂ accessibility can be limited even when carbon is abundantly available in other forms (e.g., HCO₃⁻), as is the case in aqueous systems with high pH (Riebesell et al., 1993; Kragh and Sand-Jensen, 2018).

Furthermore, most marine and freshwater phytoplankton have inducible carbon concentration mechanisms that assist in raising CO₂ concentration at the site of photosynthesis (Kragh and Sand-Jensen, 2018).

- 5) Pay attention to the importance of aquatic community structure and composition in the AP process

The efficiency of the AP is a function of the physiology and community structure of the phytoplankton and submerged plants, which in turn are governed by the physical and chemical conditions of inland waters (Findlay and Kasian, 1987; Low-Decarie et al., 2011; Brothers et al., 2013; Low-Decarie et al., 2014; Low-Decarie et al., 2015; Basu and

Mackey, 2018). However, few studies have focused on the importance of aquatic community structure and composition to AP.

Since global change is projected to affect carbon and nutrient availability, temperature and light, a better understanding of how aquatic community structures will respond in the future is needed to gain knowledge about the AP and the capacity of the inland waters to function as both long-term and short-term sinks for atmospheric CO₂ (Low-Decarie et al., 2014; Shen et al., 2018).

6) Extend the geographical distribution of research areas to improve the AP data base

As is seen in **Figure 2**, though the decrease in CO₂ degassing flux and increase in DOC concentration and carbon burial seem to be global phenomena both in rivers and lakes/reservoirs influenced by anthropogenic activity and climate change, long-term monitoring and investigations need to be extended to wider geographical areas, not merely in Europe, Asia and North America as at present, but also to South America, Africa and Oceania to increase the world representativeness.

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AUTHOR CONTRIBUTIONS

ZL developed the research concept and wrote the manuscript. SZ and HY collected the data and generated the figures. All authors contributed to the revisions and approved the final version of this manuscript.

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