The study of carbon in inland waters—from isolated ecosystems to players in the global carbon cycle

Lars J. Tranvik 1,*, Jonathan J. Cole, 2 Yves T. Prairie 3

1Department of Ecology and Genetics/Limnology, Uppsala University, Uppsala, Sweden; 2Cary Institute of Ecosystem Studies, Millbrook, New York; 3UNESCO Chair in Global Environmental Change, Département des Sciences Biologiques, Université du Québec à Montréal, Montreal, Quebec, Canada

**Scientific Significance Statement**

This essay describes the evolution of our understanding of the carbon cycle of inland waters. Research has evolved from studies of individual lakes with limited attention to the surrounding landscapes, to a focus on how lakes are affected by external factors such as import of organic matter from the watershed, thereafter increasingly addressing how inland waters impact the carbon cycle beyond their own limits, for example by emission of gases to the atmosphere. Major steps are described toward the now widely applied concept of the aquatic “active pipe,” and the development of global quantification of inland water carbon cycling. Despite the great progress in understanding of the carbon cycle during the last decades, we argue that there is still a need for better integration of inland waters with other habitats in studies of carbon biogeochemistry.

Limnology, and in particular the study of the aquatic carbon cycle initially focused on lakes as isolated ecosystems. Later on, investigations followed of lakes as recipients. Current studies of inland water carbon cycling emphasizes fluxes in and out of lakes and other inland waters, in exchange with both upstream landscapes, downstream recipients, the atmosphere, and the long term sediment sink. This widening of scope has developed in a combination of fundamental science and research motivated by applied problems (e.g., effects of dams and climate change). Given that inland waters receive, process, emit and store carbon in globally significant quantities, we anticipate the field to continue this transition, and anthropogenic pressure on the environment to increasingly motivate carbon cycle research. In 2007, we (and other co-authors) published an article that introduced the idea of the “active pipe concept” for inland waters, which states that they are not passive conduits from soil to sea but instead divert large quantities of carbon to the atmosphere and to the sediment sink (Cole et al. 2007). Since the original presentation of the “active pipe,” there has been substantial progress in our understanding of the inland water carbon cycle and its role in the biogeo sphere. In this essay, we describe the evolution that has taken place in our field to not only study aquatic ecosystems as the complex microcosms bound by their basins that they definitely are, but also as active players in global cycles (Fig. 1); and, we describe some important anthropogenic effects on the

*Correspondence: lars.tranvik@ebc.uu.se

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“active pipe” as well as knowledge gaps that need to be addressed in future research.

Inland waters as microcosms, collectors, and reactors

The appearance of lakes as confined ecosystems has appealed to scientists since the beginning of limnology. Lakes were early referred to as microcosms (Forbes 1887). Although it was recognized that the conditions in lakes depend on the surrounding landscape, this connection initially received relatively limited attention. In his seminal introduction to limnology, Thienemann (1925) described the “geographic-hydrographic characteristics” of lakes with only minor focus on external factors. However, it was also early emphasized that lakes and their biota are shaped by their watersheds. Naumann (1932), in his “Fundamentals of Regional Limnology” presented a comprehensive account of lake types and their dependence on surroundings. He identified the role of organic matter import, and the carbon cycle was clearly addressed in terms of gas balances (i.e., how dissolved oxygen and carbon dioxide depend on autotrophic and heterotrophic metabolism). However, it was in the eutrophication literature that the lakes and catchments became inextricably linked, with the development of successful nutrient loading models (Vollenweider 1975), an approach that was subsequently transposed to carbon (e.g., Dillon and Molot 1997), and which has more recently expanded to regional, continental, and global scales (e.g., Raymond et al. 2013).

Lakes, streams, and rivers are recipients of matter and energy from the watershed and the atmosphere. The unidirectional study of lakes as recipients has been and remains a fertile approach. In paleolimnology, it enables the study of how lakes and surrounding ecosystems change through history, including anthropogenic impacts and relatively recent changes (Smol 2009). An example is the increasing interest in using lakes as sentinels of climate change, benefitting from ecological and biogeochemical shifts that may reflect patterns at larger scales (Williamson et al. 2009).

Ecological effects of inland waters in the upstream direction are less intuitive and have received less attention (Bar-tels et al. 2012). Although they may be of minute direct importance for biogeochemical fluxes, they may provide critical connections at critical times for supporting keystone species or apex consumers (Schindler and Smits 2017), e.g., via emerging insects subsidizing terrestrial insectivores (Vander Zanden and Gratton 2011).

From the study of in-lake carbon cycling to a global estimate of inland water gas emission

In the 1990s, it became increasingly evident that lakes are often heterotrophic. Dissolved organic carbon (DOC) is the most abundant form of organic carbon in most lakes, commonly dominated by terrestrial import. Pioneering studies in Finnish lakes suggested that allochthonous DOC provides a substantial subsidy to water column heterotrophs (Salonen et al. 1983), leading to substantial bacterial carrying capacity (Tranvik 1988), low production to respiration ratios (del Giorgio and Peters 1993), and net emission of carbon dioxide (Duarte and Prairie 2005). Photochemical reactions were also found to contribute to the mineralization of DOC (Granéli et al. 1996), further increasing the concentration of dissolved CO2. In addition to the bottom-up effects of allochthonous carbon, food web configuration was demonstrated to have the capacity to regulate the balance between heterotrophs and autotrophs, potentially even shifting lakes from being net sources to net sinks of atmospheric CO2 (Schindler et al. 1997).

In general, this era of lacustrine carbon cycle studies yielded rapid progress in understanding the patterns within and among lakes. Many studies were focused on the importance of allochthonous organic subsidies for food webs and metabolic balance (Jansson et al. 2000), but did not quantify water-atmosphere exchange per se. Hence, although the coupling to the atmosphere via under- or oversaturation of dissolved gases was evident and sometimes explicit, there were so far no essential attempts to test the hypothesis that inland waters contribute significantly to atmospheric carbon gases. The first suggestion came from work in the Arctic where Kling et al. (1991) showed that the emission of CO2 from lakes and rivers was significant to the regional C budget. Following this in a compilation of data from almost 2000 lakes with a world-wide distribution, Cole et al. (1994) demonstrated a wide range of CO2 saturation, with most sites being net sources of atmospheric CO2, and reported a global estimate of lake emission (0.14 Pg C yr^-1). Around
the same time, the potential role of reservoirs as sources of atmospheric methane was highlighted (Rudd et al. 1993), and global estimates began to emerge (e.g., St. Louis et al. 2000). Similarly, a global estimate of inland water methane emissions was presented (Bastviken et al. 2011), which further emphasized a significant role of inland waters in the global greenhouse gas balance.

Continued upscaling of inland water carbon cycling

Following Cole et al. (1994), a number of studies addressed gas emissions across large geographic scales, from both lakes and lotic ecosystems, further emphasizing supersaturation and outgassing. The ubiquity of CO₂ supersaturation and emissions across broad boreal regions was demonstrated for lakes (Sobek et al. 2003) as well as for streams and rivers (Teodoru et al. 2009; Crawford et al. 2014). Most of the carbon import to aquatic systems can be viewed ultimately as a loss of terrestrial primary production (Maberly et al. 2012; Magin et al. 2017), a fraction of which will be lost to the atmosphere. Richey et al. (2002) found that the loss of carbon to the atmosphere from rivers and wetlands of the Amazon basin was an order of magnitude larger than the downstream transport of organic carbon, suggesting that aquatic ecosystems are sites of particularly intense mineralization of organic matter. Similarly, in the boreal zone of Sweden, Algesten et al. (2003) found that only about half of the imported organic carbon made it to the sea, with outgassing being responsible for most of the loss.

In a study of streams and rivers of the conterminous U.S.A., Butman and Raymond (2011) demonstrated that running waters alone in this region export a substantial amount of CO₂ to the atmosphere. If extrapolated to similar latitudes around the world, such rates would amount to 0.5 Pg of CO₂-C emitted per year by lotic ecosystems. These stream emissions are largely the result of respiration in surrounding soils, which is kept in soil water but emitted to the atmosphere when it enters the stream networks.

Some open questions on pathways of carbon loss from the water column

Fluxes of carbon out of lakes include downstream transport, outgassing to the atmosphere, and diversion into the geosphere (i.e., burial in sediments, Hanson et al. 2015). Among those processes, gas evasion has received most attention. Although the inland water sediment burial C flux appears to be less than the corresponding gas evasion flux, its magnitude exceeds C burial in ocean sediments by several fold, despite the huge difference in area (e.g., Dean and Gorham 1998). The loss into sediments is poorly constrained and few estimates are available, although it has been recognized for a long time. Improved global estimates require geographic information that allows consideration of watershed characteristics and lake bathymetry and productivity (Ferland et al. 2012).

Rates of sedimentation of organic matter of terrestrial origin are high in boreal lakes dominated by allochthonous organic carbon. Still, there is no sufficient direct source of particles that correspond to the high rates of allochthonous sediment accumulation observed. This apparent discrepancy may be reconciled by flocculation of allochthonous DOC in the water column (von Wachenfeldt and Tranvik 2008), causing a continuous in situ production of particles sustaining the observed allochthonous sedimentation. Follow-up studies of this and other mechanisms supporting sedimentation and carbon burial are scarce.

Lake emissions are to a large extent the result of in-lake respiration of allochthonous organic matter, the rate of which depends on its reactivity and modulated by the local hydrological regime (Vachon et al. 2016). However, imported inorganic carbon from terrestrial respiration may also be important (Maberly et al. 2012). Weyhenmeyer et al. (2015) suggested that the balance of internal and external sources of CO₂ evasion are controlled by climate, whereby internally produced CO₂ is of higher importance in warmer lakes and at higher concentrations of DOC. The role of these different sources is still under debate.

Photochemistry appears to be a major cause of mineralization in some cases, particularly in shallow Arctic lakes and streams (Cory et al. 2014) and in some lakes (Dillon and Molot 1997), but may be of limited importance in highly colored waters (Groeneveld et al. 2016). A modeling study suggests that it may be of moderate significance in lakes in general, corresponding to about 10% of CO₂ emissions (Koehler et al. 2014), largely due to the limited penetration depth of light at wavelengths that cause photochemical reactions. Correct estimates of photochemical CO₂ production from inland waters depends on a number of critical factors, including the wavelength-dependent photochemical reactivity of DOC, wavelength-specific attenuation of light in the water column, and the intensity and spectrum of incoming solar radiation. Both measurements and calculations are challenging, which hampers progress on the role of photochemical reactions for carbon transformations. Intercalibration of laboratories and standardization of procedures are urgently needed.

Much of our understanding of the inland water carbon cycle build on research where organic matter is conceptualized as a homogeneous “black box,” typically divided only into dissolved and particulate fractions. In reality, natural organic carbon is a highly diverse mix of thousands of molecules of different properties. Additional insight into the fate of various moieties of DOC in the water column has been gained from optical properties (absorbance and fluorescence, Kothawala et al. 2014). The last few years, ultrahigh resolution mass spectrometry has been introduced to gain further insight into the characteristics of organic matter. These
techniques are only beginning to be exploited in aquatic carbon cycling studies (e.g., Kelleman et al. 2015).

**Mapping of inland waters to support carbon cycle upscaling and modeling**

To produce accurate global estimates of carbon stores and fluxes, a need for improved global inventories of inland waters has emerged. Existing estimates were considered uncertain, and incomplete in particular with respect to small water bodies, which typically exhibit intense carbon metabolism. Downing et al. (2006) used statistical extrapolation based on power law abundance-size relationships to produce an estimate that also includes small lakes with areas down to 0.1 ha. This extrapolation was later criticized (Seekell and Pace 2011) for uncertain and probable overestimation of small water bodies. More recently, global maps based on satellite imagery have been presented, which overcome some of the uncertainty of extrapolation (Verpoorter et al. 2014; Feng et al. 2015), also enabling the analysis of temporal change in the inland water coverage of the continents (Pekel et al. 2016). These new resources have a great potential to support improved estimates of inland water carbon cycling.

**Global integration**

The realization that inland waters are important agents of the global carbon cycle emerged out of the various observations of fluxes and transformations discussed above, and was manifested by Cole et al. (2007). The paper contrasted a traditional view of inland waters as a “passive pipe,” transporting carbon from land to sea, with a new concept of an “active pipe,” where internal processing result in retention of carbon by sediment burial as well as loss by evasion to the atmosphere (Fig. 2). Several papers followed and discussed the magnitude and implications of the “active pipe” (e.g., Aufdenkampe et al. 2011). Although the exact numbers are still poorly constrained and constantly under revision, there is a wide consensus that the recently conceptualized “active pipe” annually processes one or several Pg of C, which is of similar size to other major components of the global carbon cycle that have so far received more attention, such as the net terrestrial C sink and the uptake of CO₂ into the oceans (IPCC 2013).

The work of many research groups during these years constituted an important step toward the integration of inland water processes into the wider perspective of the global carbon cycle. Accordingly, the assessment reports of the Intergovernmental Panel of Climate Change moved from conceptualizing inland waters as a passive channel of carbon from the continents to the ocean in previous assessment reports, into a model that acknowledges that inland waters simultaneously act as conduits from land to sea, sediment carbon sinks, and sources of atmospheric CO₂ and CH₄ (IPCC 2013).

**Interactions of the inland water carbon cycle with climate change and other anthropogenic pressures**

A substantial change in the organic carbon of boreal regions is the browning of boreal lakes and streams during several decades, due to increased concentrations of colored allochthonous DOC. Several mechanisms have been suggested, not mutually exclusive, including changing hydrology, recovery from acidification making terrestrial organic carbon less mobile (Monteith et al. 2007), and changing forestry practices (Kritzberg 2017). With continued climate change precipitation patterns will adjust. Where runoff will rise, browning will continue, due to increased mobilization of organic matter from soils and decreasing water residence time in lakes, allowing less time for degradation before downstream transport (de Wit et al. 2016). Browning of lakes results in increased resources for heterotrophic microorganisms, but also causes decreased primary production due to enhanced light attenuation, with further negative impact on higher trophic levels (Karlsson et al. 2015).

Most lakes are supersaturated with CO₂, due to the mineralization of imported organic carbon as well as import of dissolved inorganic carbon (DIC). Hence, in the analysis of large sets of lakes, inorganic carbon has not been found to limit primary production (Hessen et al. 2017), and further increased atmospheric pCO₂ may not cause increased
primary production (Vogt et al. 2017). Still, in soft water waters with low concentrations of DOC and DIC, primary production may be hampered by carbon limitation (Hein 1997).

In addition to browning, climate change may invoke further alteration of the carbon cycle of inland waters. The CO₂ emission from hard-water prairie lakes of Canada have been observed to decrease, or even reverse into a carbon sink, along with warming, suggested to be a result of shorter duration of ice-cover and increased pH (Finlay et al. 2015).

The construction of dams is one of the largest infrastructure projects of mankind, resulting in the retention of huge amounts of water on the continents, and the extent of impounded areas is still on the rise (Zarfl et al. 2014). Although hydropower is considered a renewable resource, dams are not carbon neutral (Prairie et al. 2017). In particular in the tropics they are strong emitters of greenhouse gases (Barros et al. 2011). In addition, reservoirs accumulate large amounts of carbon in sediments (Mendonca et al. 2012) although the fraction of these sediments that would have been deposited elsewhere prior to damming is still unknown.

In addition to large dams, there appears to be a widespread increase in sediment burial. Heathcote et al. (2015) reported increasing sedimentation during the Holocene, and sedimentation has similarly increased in European lakes due to soil erosion (Kastowski et al. 2011). Eutrophication, including the construction of nutrient-rich agricultural ponds, result in further increased sediment C burial (Downing et al. 2008).

The role of inland waters in carbon cycling is clearly dependent on the occurrence of the inland waters themselves. Loss and gain of water bodies is expected to follow upon climate change, an already ongoing process. Permafrost thaw and the emergence of thermokarst lakes is an obvious example, which is likely to drastically modify carbon cycling (Schuur et al. 2015). Glacial retreat enhances the transport of organic carbon previously immobilized in ice, which impacts downstream carbon cycling (Singer et al. 2012).

**Outlook**

In the proposal to the U.S. National Center for Ecological Analysis and Synthesis to form the working group that later published the “active pipe concept” (Cole et al. 2007), we argued that traditionally compartmentalized areas of research need to be better integrated, to allow a holistic view of the carbon cycle. Now, a decade after the publication, there has been substantial progress in our understanding of the inland water carbon cycle and its role in the biogeo-sphere, and significant synergy from collaboration across fields. Still, research on the aquatic carbon cycle is conducted largely within a compartment isolated from similar studies of terrestrial ecosystems. We argue that improved communication between carbon biogeochemists with experience from different habitats (aquatic as well as terrestrial) is required to reach a unified understanding of the mechanisms controlling the pool sizes, transformations, and fluxes of carbon globally.

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