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Spatially Explicit, Regional-Scale Simulation of Lake Carbon Fluxes

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Key Points:
- Water and carbon fluxes for 3,675 lakes are simulated using a process-based model
- Lake carbon fluxes are well predicted by hydrologic characteristics, such as the fraction of hydrologic export as evaporation
- Seventy-eight percent of total CO_2 emissions for the region originate from external loads of dissolved inorganic carbon

Supporting Information:
- Supporting Information S1

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Abstract Lakes are areas of intense biogeochemical processing in the landscape, contributing significantly to the global carbon cycle despite their small areal coverage. However, current large-scale estimates of lake biogeochemical fluxes are all generated by multiplying a mean observed areal rate by regional or global lake surface area, which ignores important heterogeneous spatial and temporal processes that regulate lake carbon cycling. We have developed a process-based model that integrates core scientific knowledge in hydrology, biogeochemistry, and ecology that is specifically designed to be applied over large geographic regions to hindcast or forecast regional lake carbon fluxes. We used our model to simulate daily carbon fluxes and pools for 3,675 lakes in the Northern Highlands Lake District from 1980–2010 and produced spatial and seasonal patterns consistent with observations. Variabilities in lake carbon fluxes were well predicted by relatively simple hydrologic metrics, such as the fraction of hydrologic export as evaporation (FHEE). Overall, lakes with a high FHEE processed a greater percentage of carbon inputs in the simulations than lakes with a low FHEE, but low-FHEE lakes ultimately processed more total carbon because of greater carbon inputs. Large lakes with low FHEE and high external loading of dissolved inorganic carbon contributed most to total CO_2 emissions for the Northern Highlands Lake District, and our model estimated that 78% of total CO_2 emissions from lakes to the atmosphere originated from external loads of dissolved inorganic carbon. By better characterizing the unique biogeochemical processes for each individual lake, regional estimates of carbon fluxes are more accurately determined.

1. Introduction

Lakes and reservoirs process over half of the carbon received from the surrounding terrestrial landscape and have recently been included in models of the global carbon cycle (Cole et al., 2007; Intergovernmental Panel on Climate Change, 2013). Since this inclusion, there have been several revisions to estimates of global and regional lake carbon fluxes (Butman et al., 2016; Raymond et al., 2013; Tranvik et al., 2009), mainly owing to amendments of global lake surface area or modification of atmospheric gas exchange parameters. Based on these amendments, there has been an increasing awareness of the importance of lakes to the global carbon cycle (Drake et al., 2017). However, these "best estimate" models are all generated by multiplying a mean observed areal rate by regional or global lake surface area (Bastviken et al., 2011; Butman et al., 2016; Cole et al., 2007; Deemer et al., 2016; Einsele et al., 2001; Raymond et al., 2013; Tranvik et al., 2009). While perhaps a reasonable zeroth-order estimate, these models ignore important heterogeneous spatial and temporal processes that regulate lake carbon cycling, and their static nature renders them incapable of predicting how lake carbon cycling will change under future climate or land use scenarios.

Nonlinear interactions among lake hydrology, lake physics, inflowing constituent concentrations, and organisms produce carbon fluxes into and out of lake ecosystems. Hydrologic variation underpins spatial and temporal patterns of lake carbon cycling (del Giorgio & Peters, 1994; Dillon & Molot, 1997; Vachon & del Giorgio, 2014; Vachon et al., 2016; Zwart et al., 2017). For example, lakes with smaller watershed area-to-lake area (WA:LA) ratios generally process more of their carbon inputs internally rather than exporting downstream when compared to lakes with larger WA:LA for a given hydrologic residence time (HRT; Figure 1). This is because of the increased importance of evaporation to a lake's water budget for small WA:LA lakes. Since carbon does not leave with evaporated water, the elevated importance of evaporation to a lakes' hydrologic budget for small WA:LA lakes causes differential importance of flux pathways between water and carbon (Jones et al., 2018). Failure to consider the importance of evaporation to lakes' water budget might lead to dramatic misrepresentations of lake contributions to large-scale carbon cycles (Jones et al., 2018).

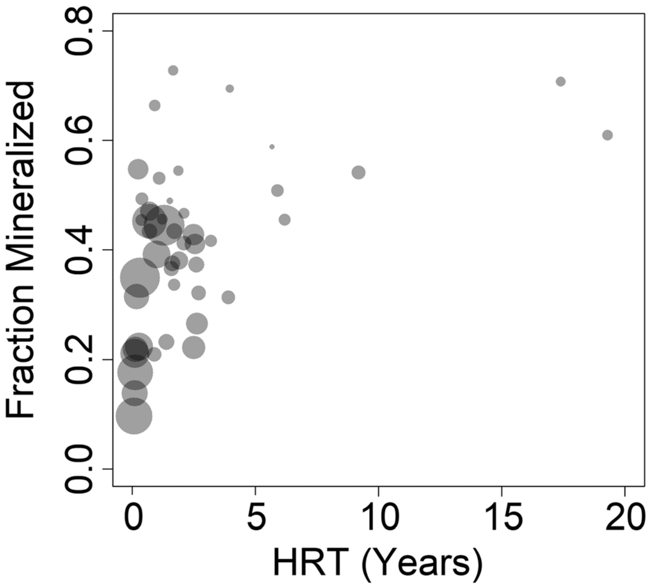

Figure 1. Fraction of incoming dissolved organic carbon mineralized within each lake for 48 net dissolved organic carbon sink lakes from Evans et al. (2017) was significantly positively related to hydrologic residence time (HRT) and negatively related to watershed area to lake area ratio (WA:LA; point size is $\log_{10}$(WA:LA); $p < 0.05$ for both $\log_{10}$ HRT and $\log_{10}$ WA:LA).

Temporal changes in hydrologic fluxes to lakes can have a large impact on lake carbon cycling. Extreme precipitation events, which are predicted to increase in intensity and frequency with climate change (Meehl et al., 2005; Min et al., 2011; Tebaldi et al., 2006; Westra et al., 2014), can account for a majority of annual watershed carbon and phosphorus flux to lakes (Carpenter et al., 2015; Zwart et al., 2017). Lakes act as "activated control points" on the landscape (Bernhardt et al., 2017), and the high carbon loading to lakes following extreme precipitation events alters light climate due to increased particulate and dissolved organic carbon concentrations (POC and DOC; Klug et al., 2012), enhance lake heterotrophy (Zwart et al., 2017), increase CO_2 emissions from lakes to the atmosphere (Vachon & del Giorgio, 2014), and elevate the mineralization rate of DOC (Zwart et al., 2017). However, lake hydrologic setting plays a modifying role in how lakes respond to extreme weather events. Lake morphology dictates the relative importance of internal regulation of $p\mathrm{CO}_2$ in response to extreme precipitation events (Vachon & del Giorgio, 2014), and lake HRT dictates a trade-off between DOC load and processing time, dampening the potential effect of large DOC loads on lake heterotrophy following storm events (Zwart et al., 2017). Thus, accurate scaling of lake carbon cycling likely requires consideration of temporally dynamic lake hydrologic regimes.

Current large-scale models do not take into account spatial and temporal dynamics in watershed constituent fluxes to lakes, which influence their carbon sequestration capacity. For example, conversion of lake watersheds to agriculture increases soil erosion and sediment loading to lakes (Downing et al., 2008; Kang et al., 2001) and enhances nutrient runoff that stimulates algal growth and subsequent sedimentation (Carpenter et al., 1998). Indeed, land use change toward agriculture in southern Minnesota resulted in a greater than twofold increase in lake sedimentation rates over the past 100 years, while relatively pristine northern Minnesotan lakes experienced little increase in sedimentation rates (Dietz et al., 2015). Despite sedimentation rates that vary over 2–3 orders of magnitude across lakes (Dietz et al., 2015; Downing et al., 2008; Ferland et al., 2012; Kastowski et al., 2011), best estimates of large-scale lake carbon burial are still based on areal average rates multiplied by lake surface area. To overcome this potential bias and yield more accurate estimates, lake carbon models at regional scales should account for heterogeneity in local watershed nutrient loading processes.

Current zeroth-order models have neglected complex interactions among lake hydrologic setting, watershed constituent loading, lake physics, and organismal physiology that regulate lake carbon cycling, which limits their capacity to forecast lake carbon cycling responses to future climate and land use scenarios. This knowledge gap presents a significant deficit in our understanding of large-scale lake ecosystem ecology and biogeochemical cycling. To fill this gap, we have developed a process-based model that leverages hydrologic, biogeochemical, and ecological knowledge capable of being applied over large geographic regions to hindcast and/or forecast lake carbon fluxes in response to global change scenarios. Using this model, we aim to answer the following questions: (1) How do lake carbon emission and burial rates vary across lakes within the region to which we applied our model? (2) What are the key regulators of lake carbon fluxes across lakes within our modeled region? And (3) at the regional scale, what are the aggregate lake carbon fluxes and how do the predictions of a spatially explicit model compare to previously applied zeroth-order models?

2. Methods

2.1. Model Overview and Domain

We have combined an existing integrated hydrologic model (composed of coupled surface, groundwater, and lake water balance models) developed specifically for this study (Hanson et al., 2018) with simple lake energy budget, constituent loading, and lake biogeochemical models to estimate regional lake carbon cycling dynamics, accounting for spatially explicit, local-scale processes. Our model is capable of estimating daily lake carbon pools and fluxes for thousands of lakes within a model domain and can in principle be applied in any region with sufficient forcing data. For this analysis, we chose to apply it to a lake-rich region located on the border of Wisconsin and Michigan, the Northern Highlands Lake District (NHLD), because of the wealth of validation data available, including long-term data sets from the North Temperate Lakes (NTL) Long-Term Ecological Research (Magnuson et al., 2006) and spatial surveys of lake physical, chemical, and biological characteristics (e.g., Eilers et al., 1983; Hanson et al., 2007; Lottig et al., 2012).

2.2. Coupled Surface Water and Groundwater Hydrology Model

The objective of the integrated hydrologic model is to simulate the water balance for each individual lake as a function of precipitation, evaporation, surface runoff (inflow and outflow), snow storage and melt, ice cover, and groundwater fluxes, based on meteorological forcings, land cover, and readily available geospatial information. The hydrologic model is described in greater detail by Hanson et al. (2018); however, we give a brief overview here to help orient the reader. The Variable Infiltration Capacity model (VIC) surface water model was originally developed as a land surface model for use in global circulation models and uses elevation, soil characteristics, and land cover data to determine the fate of precipitation falling on a given land area (Liang et al., 1994). VIC has been used at diverse spatial resolutions to model surface water dynamics at regional to global scales. VIC relies on daily meteorological forcings (precipitation, minimum and maximum air temperature, and average wind speed) and solves water and energy balances to generate daily estimates of groundwater recharge, runoff, and evapotranspiration for each 1/16th degree grid cell. Surface runoff (simulated as a depth) was scaled to each lake by estimating the WA of each lake in the model domain (see the supporting information for details on lake watershed delineation).

We used a simple, steady state groundwater model (GFLOW) to simulate regional groundwater head fields and groundwater fluxes to and from lakes in the model domain. GFLOW provides spatially explicit estimates of the direction and quantity of groundwater flow in and out of each lake in the model domain. GFLOW is built on an analytic element framework (Haitjema, 1995) and exploits established analytical solutions to the groundwater flow equations as well as the principle of linear superposition to calculate flows for arbitrarily complex landscapes. A major benefit of this method is that it can represent relatively large geographic regions at a fraction of the computational cost that other finite difference groundwater models require (e.g., MODFLOW; Harbaugh, 2005). The solution depends on lake elevations across the region (which provide boundary conditions), groundwater recharge rates (from VIC), and estimated regional hydraulic conductivities.

VIC and GFLOW were used to drive the dynamic lake water budget components of the model. Since there are no dynamic feedbacks to the VIC model, it was run once with appropriate model domain forcings and the VIC outputs are in turn used as forcings for GFLOW and the dynamic lake water budget model. The lake hydrologic budget was solved at a daily time step, and updated lake elevations were used to solve groundwater flow equations in GFLOW at a monthly time step.

2.3. Lake Energy Budget

We used lake energy mass balance equations from Lenters et al. (2005) and functions from the R package *LakeMetabolizer* (Winslow et al., 2016) to model epilimnetic lake water temperature during the open-water period at a daily time step. The lake energy mass balance accounts for the effect of inflows, outflows, entrainment, and surface heating and cooling on heat transfer in the epilimnion of each lake. The hypolimnion water temperature was kept constant at the mean hypolimnetic water temperature from the NTL lakes during open-water period (7 °C), and both the epilimnion and hypolimnion water temperature was set to 3 °C during ice cover. We modeled the depth of the epilimnion as a function of lake water light attenuation and lake surface area. Each lake had the potential to be completely mixed if the modeled epilimnion depth was the same as or exceeded the maximum lake depth, which is similar to other simple models distinguishing between stratified and fully mixed lakes (e.g., Lathrop & Lillie, 1980). Each lake was fully mixed during ice cover and fully mixed 10 days prior to ice on and 10 days following ice off. For more details on the lake energy budget, see the supporting information.

2.4. Watershed Constituent Loads

To estimate constituent loading to each lake from the surrounding watershed, we coupled the simulated water budgets described above with either median constituent concentrations from samples in the NHLD, or with a model relating watershed attributes to inflowing water constituent concentrations. The watershed constituent loading model estimates daily loads of DOC, dissolved inorganic carbon (DIC), terrestrial particulate organic matter (tPOC), and dissolved inorganic phosphorus (DIP) to each lake in the model domain. The impact of land cover on elemental loads to lakes is well documented (Webster et al., 2000). For example, bogs and other wetlands often supply large amounts of organic carbon to lakes and streams (Canham et al., 2004; Lottig et al., 2012). Given the strong influence of wetland land cover on stream DOC concentration in the region, we used the regression equation described in Lottig et al. (2012) for the relationship between inflowing DOC concentration and fraction of the lake watershed that was characterized as wetland using the 2006 National Land Cover Database (http://www.mrlc.gov/nlcd06_data.php). For all other constituents, we used median literature values from previous research conducted in the NHLD since there were no significant geospatial predictors of inflowing stream concentration. We multiplied surface water and groundwater fluxes by estimated constituent concentration to estimate daily hydrologic loads of DOC, DIC, tPOC, and DIP to each lake in the model domain. Constituent concentrations in the various types of water fluxes (e.g., groundwater, precipitation, and surface runoff) are given in Table S1.

In addition to hydrologic loads, we considered constituent loading via airborne deposition and diffusion from adjacent wetlands as these sources can be significant pathways of carbon loading to lakes (Hanson et al., 2014), especially during certain seasons (e.g., via leaf litter in Fall; Gasith & Hasler, 1976) or during strong winds and heavy rain events (Preston et al., 2008). We estimated daily adjacent wetland carbon and phosphorus loading as a function of lake perimeter and fraction of each lake's watershed that was characterized as wetland (Hanson et al., 2014). We estimated the airborne tPOC deposition as a function of daily wind speed and precipitation according to Preston et al. (2008), and autumn leaf fall into the lake as a function of lake perimeter (Gasith & Hasler, 1976; Hanson et al., 2014).

Alkalinity for each lake was modeled as a function of average groundwater and surface water flux into each lake and held constant throughout the model run. We fit a saturating relationship between our modeled groundwater and surface water fluxes and measured lake alkalinity from Hanson et al. (2007). Based on a survey of 275 lakes within and near our study region, lakes with significant groundwater and surface water fluxes have higher alkalinity compared to lakes that are more isolated hydrologically (Eilers et al., 1983). Throughout the model run, we calculate a dynamic pH and carbonate speciation (CO_2, HCO_3^-, and CO_3^{2-}) using each lakes' fixed alkalinity, daily epilimnetic DIC concentration, daily epilimnetic water temperature, and daily atmospheric pressure with the function *aquaenv* from the R package *AquaEnv* (Hofmann et al., 2010).

2.5. Lake Biogeochemical Model

The final objective of our model was to simulate CO_2 exchange with the atmosphere and burial of carbon in lake sediments. To achieve this, we coupled a simple lake carbon model with the water and energy budget models and the watershed constituent loading model described above. Driven by watershed inputs, meteorological data, and water temperature, our lake carbon model simulated key biogeochemical processes at a daily time step. Each lake was divided into two layers, the epilimnion (epi) and hypolimnion (hypo) with a modeled mixed layer depth as a function of LA and light attenuation. Biogeochemistry was represented by a set of 13 differential equations describing DIP (epi and hypo), DIC (epi and hypo), slow decomposing DOC (epi and hypo), fast decomposing DOC (epi and hypo), phytoplankton biomass (epi only), terrestrial-POC (epi and hypo), and autochthonous and allochthonous sediment carbon. Briefly, phytoplankton growth rates were based on phosphorus concentration and light availability (Vadeboncouer et al., 2008), water column respiration was represented as a sum of autotrophic and heterotrophic respiration (respiration of DOC), and sediment respiration was a function of sediment carbon content and type of sedimenting carbon (autochthonous or allochthonous). CO_2 exchange with the atmosphere was a function of the concentration gradient between the surface water and the atmosphere and modeled piston velocity described by Vachon and Prairie (2013). For details on the model differential equations, see the supporting information.

2.6. Model Simulation

We used the National Hydrography Dataset (NHD) to identify lakes within our model domain, the NHLD; however, due to inaccuracies in the NHD, particularly for small lakes (Soranno et al., 2015), we manually inspected each lake and reservoir within the NHLD, comparing the NHD classification with Google Earth Imagery and the Imagery Basemap in ArcGIS. We removed 1,803 waterbodies that we considered were not lakes (e.g., swimming pools, sections of rivers, shallow standing water in open land areas, retention ponds, and wetlands), and we added 251 lakes that were missing in the NHD but were present in the imagery. We modeled 3,692 lakes from 1980 to 2010 in the NHLD at a daily time step. We omitted 17 lakes from the final analysis due to unrealistic rates of carbon processing (e.g., negative fraction of carbon mineralized). All of the omitted lakes were small with large WA to LA ratio (lake size median = 1,159 m^2, range = 98–16,310 m^2; WA:LA median = 1,070, range = 168–2,676) and suffered from numerical integration issues during model runs due to extremely high water and carbon loads. This left us with a final data set of 3,675 lakes dynamically modeled in the NHLD.

2.7. Model Validation

We have validated the integrated hydrologic model for the NHLD as described in Hanson et al. (2018). To validate the within lake physical and biogeochemical dynamics generated by our model, we used time series data from the NTL Long-Term Ecological Research as well as spatial surveys conducted in the region (Hanson et al., 2007). The spatial survey data set from Hanson et al. (2007) was designed to be a representative sample of the full lake size distribution in the NHLD and is therefore a valuable data set with which to compare our model estimated constituent concentrations. For comparison to the NTL time series data, we adjusted the initial volumes of the seven modeled NTL lakes to the actual volumes reported by Hanson et al. (2014) to eliminate the effects of errors in lake volume estimates on simulations of in-lake constituent concentrations. Unfortunately, we do not have lake volume measurements for the lakes included in the spatial survey conducted by Hanson et al. (2007); thus, we do not adjust our estimated initial lake volumes for this model validation.

2.8. Comparison to Published Large-Scale Lake Carbon Models

We compare our regional estimates of total lake carbon emissions and burial to estimates derived from Cole et al. (2007) and Raymond et al. (2013). We scale the Cole et al. (2007) global estimate to our modeled LA by dividing their global evasion and burial rates by global LA used in that study (4.2 million km^2) and multiply the resulting annual areal rates by the LA we modeled in the NHLD. We also scale their global estimate of reservoir burial and emissions to the NHLD using the areal burial rate they cite from Dean and Gorham (1998) and the global emission rate divided by global reservoir surface area they used from St. Louis et al. (2000). Areal reservoir emission and burial rates were then applied to the NHD defined reservoirs (FType = 436) in the NHLD of which there were only 13 in our quality-controlled waterbody data set. We scale the global estimate of CO_2 emissions from lakes and reservoirs by Raymond et al. (2013) to the NHLD area by multiplying mean emission rates for each lake size bin defined by Raymond et al. (2013) to the area of each lake size bins in the NHLD. Since Raymond et al. (2013) did not distinguish between lakes and reservoirs, we could only scale one total estimate of natural lakes and reservoirs in the NHLD from this global carbon flux estimate.

The biogeochemistry model was run using the statistical software package R, and the code is available on GitHub at https://github.com/jzwart/NHLD_C_Model.

3. Results

3.1. Validation

Calibrating only to initial lake volume, our regional model produced seasonal dynamics of water temperature, constituent concentrations (DOC, DIC, soluble reactive phosphorus, TP, and pH), and phytoplankton biomass consistent with mean monthly observations from 1987 to 2010 of the seven NTL lakes (Figure 2). Generally, model estimated total phosphorus (TP) and chlorophyll (Chl) were highest during the summer months, which agreed with observations except for Crystal Lake (CR) and Sparkling Lake (SP), two low-nutrient lakes whose TP and Chl peaks were during the winter or early spring months. Model estimated DOC concentrations and pH were highest during the open-water period, which also agreed with observations except for the two bog lakes, Trout Bog (TB) and Crystal Bog (CB), whose peak DOC concentration and pH were highest during the winter. Soluble reactive phosphorus and DIC were lowest during the open-water period for both model estimated and observed concentrations. Model estimated epilimnetic water temperature produced seasonal

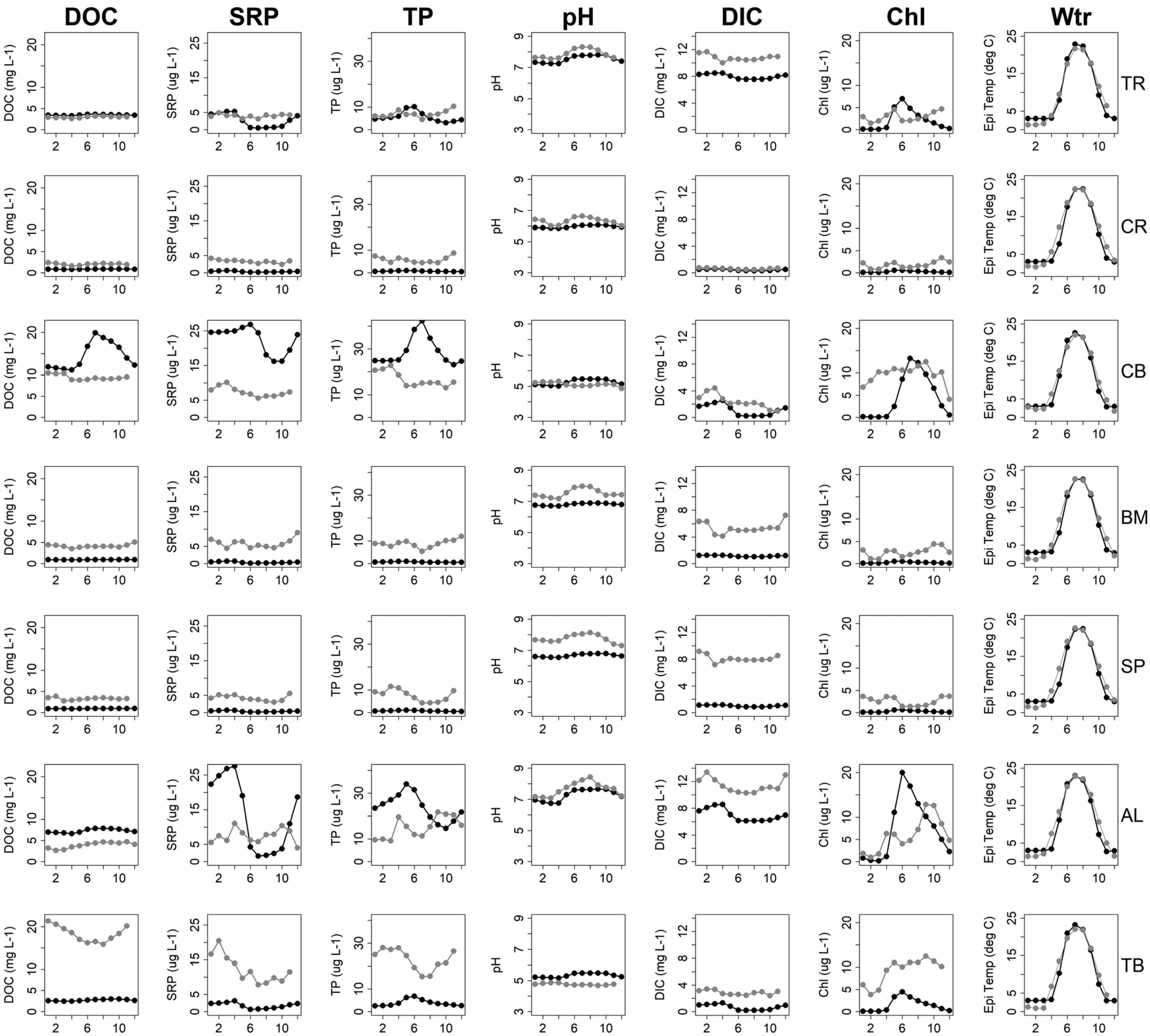

Figure 2. Mean monthly constituent concentrations from 1987 to 2010 for the seven North Temperate Lakes for both model estimates (black) and observations (grey). From left to right, columns are dissolved organic carbon (DOC), soluble reactive phosphorus (SRP), total phosphorus (TP), pH, dissolved inorganic carbon (DIC), chlorophyll-a (Chl), and epilimnetic water temperature (Wtr).

dynamics consistent with observations, although our model generally underestimated water temperature when averaged across the entire year.

Cumulative frequency distributions of modeled constituent concentrations during the open-water period for the NHLD also agreed with the spatial survey conducted by Hanson et al. (2007; Figure 3), although occasionally performed poorly for individual lakes (one-to-one inset plots for Figure 3). Model estimated DOC matched the distribution of observed DOC well with a modeled median DOC concentration of 6.5 mg/L and an observed median DOC concentration of 7.6 mg/L (Figure 3a). Model estimated alkalinity and DIC agreed with the Hanson et al. (2007) survey, however, tended to underestimate lakes with high DIC and alkalinity (modeled alkalinity median = 18.8 μEq/L; observed alkalinity median = 48.1 μEq/L; modeled DIC

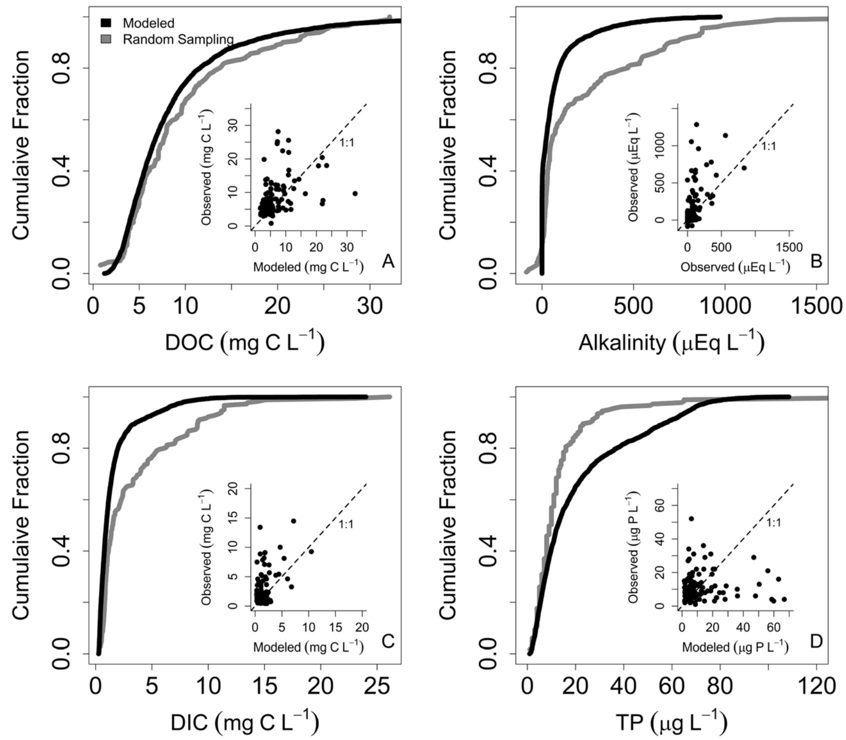

Figure 3. Distribution of long-term mean constituent concentrations from our model estimates (black, n = 3675) and observations from the Hanson et al. (2007) spatial survey (grey, n = 168). Inset are one-to-one plots of lakes for which both model estimated and observed states were available, where each point represents a lake (DOC n = 128; alkalinity n = 128; DIC n = 123; TP n = 128).

median = 1.3 mg /L; observed DIC median = 1.4 mg/L; Figures 3b and 3c). Our model slightly overestimated TP concentrations with a median concentration of 12.6 μg/L, while observed median concentration was 10.0 μg/L (Figure 3d).

3.2. Relationships Between Lake Size and Hydrologic Characteristics

Across the 3,675 lakes modeled in the NHLD, WA to LA ratio (Figure 4a) and fraction of hydrologic export in the form of evaporation (FHEE; Figure 4c) were uncorrelated with lake size (R^2 = 0.05 and R^2 = 0.004, respectively). Thus, these hydrologic characteristics were evenly distributed across all lake sizes. Large lakes tended to have somewhat longer HRTs (Figure 4b and Table 1; R^2 = 0.20), an effect that was driven primarily by greater lake volume in larger lakes rather than areal hydrologic load since areal hydrologic load was uncorrelated with lake size (R^2 = 0.003). FHEE was also evenly distributed across lake size (Figure 4c; R^2 = 0.004), and HRT was positively related to FHEE (Figure 4d; R^2 = 0.64).

3.3. Lake Carbon Processing Rates

Our model produced carbon-processing rates across the NHLD consistent with previous cross-system surveys. The fraction of DOC loaded from the watershed that was mineralized within each lake was positively related to HRT in a saturating relationship (Figure 5a). Watershed area to LA ratio (WA:LA) modified this relationship with HRT as WA:LA was negatively related to the fraction of DOC mineralized, and this pattern was consistent with previously published lake carbon budgets spanning similar WA:LA. Since low HRT lakes generally have higher loading rates of DOC from the watershed, DOC respiration rates were negatively related to HRT (Figure 5b), which results in a hydrologically mediated counterbalance between DOC respiration rates and fraction of DOC mineralized within the lake (Figure 5c).

FHEE was a strong indicator of the fraction of DOC mineralized within each lake and explained over 94% of the variation in fraction DOC mineralized (Figure 6a; $p < 0.001$, R^2 = 0.944). Areal carbon emission and burial

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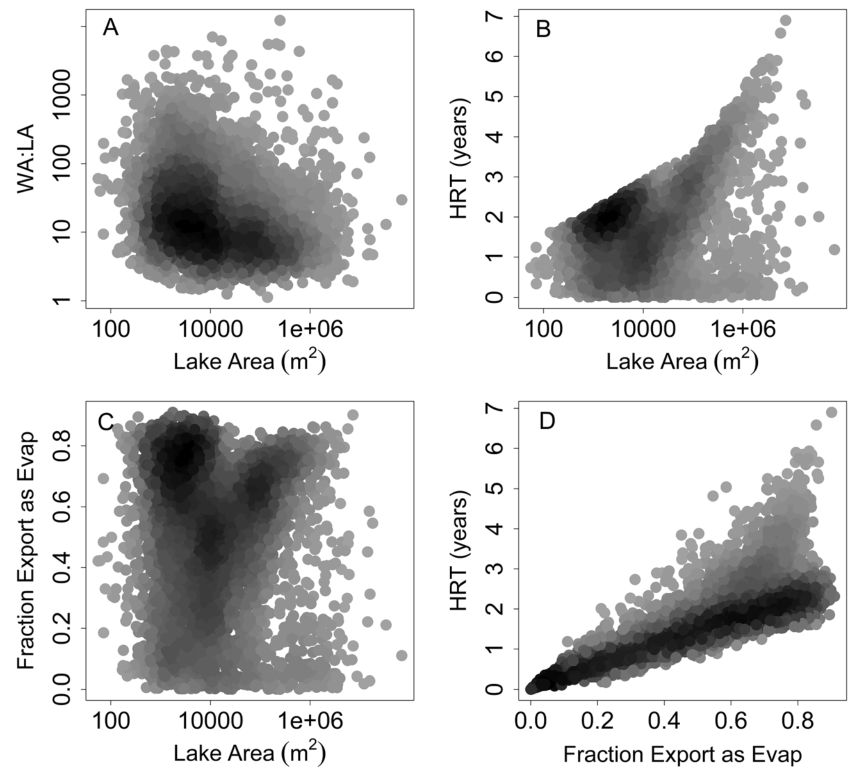

Figure 4. (a) Model estimated lake hydrologic characteristics plotted as a function of lake size. There was little relationship between lake area and watershed area to lake area (WA:LA; R^2 = 0.05). (b) Large lakes tended to have longer hydrologic residence times (HRT; R^2 = 0.20). (c) There was little relationship between lake area and the fraction of hydrologic export in the form of evaporation (fraction export as Evap; R^2 = 0.004). (d) Lakes with higher fraction of hydrologic export in the form of evaporation tended to have longer hydrologic residence times (R^2 = 0.64). The darker hues represent higher density of points based on a two-dimensional kernel density estimation using the function *heatscatter* in the R package *LSD*.

rates were comparable to previous observations in natural lakes in temperate regions and were negatively correlated with the FHEE (Figures 6b and 6c). The highest rates of emission and burial occurred in lakes that had FHEE near zero.

FHEE was also a strong predictor of whether lakes received more DIC from the watershed relative to DIC produced within the lake itself (DOC respiration + sediment respiration). The ratio of loaded:produced DIC was negatively related to the FHEE (Figure 7a). Although most lakes produced more DIC than they received DIC from the landscape (median loaded:produced DIC on a per lake basis = 0.70), 78.5% of total DIC loaded and produced (DOC mineralized + sediment respiration + DIC loaded) for the NHLD came from external loads of DIC, while 17.8% came from DOC mineralization, and 3.7% came from sediment respiration. This indicates that while the population of lakes in the NHLD is dominated by small lakes with higher internal than external loading of DIC, total lake CO_2 emissions for the NHLD are driven primarily by a handful of large lakes with very high external loading of DIC.

A majority of lakes in the NHLD were net heterotrophic (92.8%); however, even those lakes which were net autotrophic during the open-water period (green points in Figure 7b) emitted CO_2 to the atmosphere as a result of excess DIC loaded from the catchment, and these net autotrophic lakes contributed 5.0% of total CO_2 emissions from lakes in the NHLD.

3.4. Total Carbon Emissions and Burial for the NHLD

In aggregate, our model estimated that lakes in the NHLD emit 23.2 Gg C/year and bury 8.6 Gg C/year (Figure 8). This is similar to the Cole et al. (2007) global rates of natural lakes scaled to the NHLD lake surface area (emit 21.0 Gg C/year; bury 9.6 Gg C/year), but lower when reservoir rates are included in the scaling from

Table 1
Modeled Regional Lake Characteristics for the NHLD Split by Lake-Area Class, by Frequency, and Weighted by Lake Area

Area class (km^2)	Number of lakes	Total area (km^2)	Open-water k (m day^{-1})	Open-water pCO_2 (µatm)	Open-water pH	Annual emissions (g C · m^{-2} · $year^{-1}$)	Open-water emissions (g C · m^{-2} · $year^{-1}$)	Annual burial (g C · m^{-2} · $year^{-1}$)	Open-water burial (g C · m^{-2} · $year^{-1}$)	Fraction DOC mineralized	FHEE	HRT (days)	Open-water DOC turnover rate (day^{-1})	Annual DOC turnover rate (day^{-1})
<0.01	1,945	6.22	0.53	1,547.22	5.64	24.02	41.27	6.05	5.94	0.50	0.52	513	0.0022	0.0017
0.01–0.1	1,008	37.04	0.53	1,138.14	6.46	28.82	49.73	5.91	6.10	0.47	0.45	585	0.0022	0.0017
0.1–1	565	186.28	0.76	783.34	6.95	23.60	40.99	5.69	5.87	0.61	0.53	978	0.0020	0.0015
1–10	148	367.23	1.33	697.26	7.43	30.86	53.43	10.96	11.48	0.53	0.41	1016	0.0021	0.0016
>10	9	208.05	1.79	616.59	7.76	27.39	47.93	14.97	15.57	0.46	0.28	889	0.0021	0.0016
All by frequency	3,675	804.82	0.60	1,280.19	6.14	25.55	44.07	6.18	6.22	0.51	0.50	626	0.0022	0.0016
All by area	-	-	1.35	709.80	7.41	28.82	50.46	10.71	11.39	0.52	0.39	940	0.0021	0.0016

Note. We report mean rates of gas exchange (k), partial pressure of CO_2 (pCO_2), CO_2 emissions, carbon burial, fraction of dissolved organic carbon (DOC) mineralized within lakes, fraction of hydrologic export as evaporation (FHEE), hydrologic residence time (HRT), and dissolved organic carbon (DOC) turnover rate. For emission, burial, and turnover rates, we report both the mean annual rate and the mean rate for only the open-water period.

both the Cole et al. (2007) estimate (emit 36.0 Gg C/year; bury 19.3 Gg C/year) and the Raymond et al. (2013) estimate (emit 106.6 Gg C/year; no burial estimate). Since Raymond et al. (2013) did not consider ice cover duration in their annual emission estimate, as a point of comparison with this study, we also estimated regional carbon fluxes when using only open-water season carbon flux rates. When we only use open-water season emissions and burial rates scaled annually, our total annual emission estimate increased by 75% (emit 40.7 Gg C/year) and total burial increased by 7% (bury 9.2 Gg C/year). Thus, including ice cover in our integrated model is a crucial factor in estimating annual carbon fluxes, especially in the context of climate change.

Large lakes account for a vast majority of the carbon fluxes in the NHLD, as 90% of emissions and 90% of burial came from 7.5% and 4.2% of the lakes, respectively (Figure 9). Although most lakes' water budget were dominated by evaporation (median FHEE on a per lake basis = 0.54), 84% of all CO_2 emissions came from lakes below this median, indicating that relatively large lakes with large WA:LA contribute the most to total carbon fluxes for the region.

4. Discussion

Lakes are areas of intense biogeochemical processing and contribute significantly to global carbon cycling (Cole et al., 2007; Raymond et al., 2013; Tranvik et al., 2009). However, current global lake carbon flux estimates use zeroth-order models to scale up to global values, which ignore important heterogeneous spatial and temporal processes that regulate lake carbon cycling. This calls into question their accuracy. Some argue that scaling across space and time is the preeminent problem in ecology and biogeochemistry (e.g., Levin, 1992; Scholes, 2017), and scaling is obviously a key issue when estimating global biogeochemical fluxes. We argue that process-based models provide one of the most robust ways to deal with issues of scale. In this analysis, we used a spatially explicit, process-based model to scale to regional lake carbon fluxes by accounting for local heterogeneity in lake and landscape characteristics. We explored which lake and watershed characteristics regulate lake carbon cycling at the individual lake scale and for the whole region. Additionally, we compared our regional carbon flux estimates to recent large-scale carbon flux models scaled to the NHLD and hypothesized why these estimates differed or were similar.

4.1. Assessment of Hydrologic Characteristics as a Basis for Scaling Lake Carbon Fluxes

Simulated variation in hydrologic characteristics across lakes drove patterns in areal lake carbon fluxes, consistent with past empirical research and models. HRT has long been recognized as a governing variable for aquatic carbon fluxes (e.g., Curtis & Schindler, 1997; del Giorgio & Peters, 1994; Mulholland & Elwood, 1982) and continues to be a basis for understanding carbon flux dynamics across space (Catalán et al., 2016) and through time (Zwart et al., 2017). Our model demonstrates the importance of HRT in dictating carbon flux rates and fate of carbon loaded from the watershed, consistent with previous empirical research (Curtis & Schindler, 1997; del Giorgio & Peters, 1994) and models (Brett et al., 2012; Hanson et al., 2011; Jones et al., 2018; Vachon et al., 2016), which show that the fraction of DOC mineralized within the lake is positively related to lake HRT. However, there was also considerable variability in the fraction of DOC processed in lakes with HRTs between one and three years. Variability at this HRT has typically been explained by variability in DOC decay rates stemming from variation in quality of loaded DOC (e.g., Hanson et al., 2011). However, we show that variability in fraction of DOC mineralized at this HRT is more consistent with variability in lake hydrologic characteristics, specifically the FHEE. This regulation of fraction of DOC mineralized has also been demonstrated in empirical studies as WA:LA is significantly negatively related to the fraction of DOC mineralized after accounting for HRT (Figure 1). Since carbon does not leave with evaporated water, the elevated importance of evaporation to a lakes' hydrologic budget for low WA:LA lakes causes differential

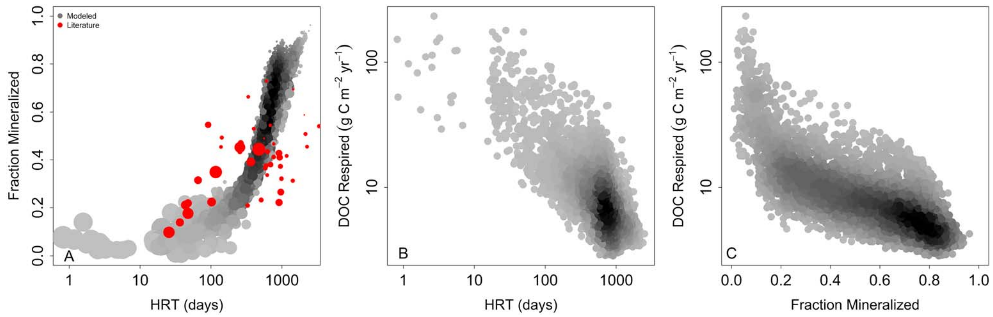

Figure 5. (a) Model estimated fraction of inflowing dissolved organic carbon (DOC) that is mineralized within each lake (fraction mineralized) was positively related to lake hydrologic residence time (HRT) and negatively related to watershed area to lake area ratio (WA:LA; point size is $\log_{10}$(WA:LA); $p < 0.05$ for both $\log_{10}$ HRT and $\log_{10}$ WA:LA). Previously published whole-lake DOC budgets from Evans et al. (2017, Figure 1) are plotted on top of the model estimates for comparison. (b) Model estimated areal rates of DOC respiration was negatively correlated to lake HRT, which created a HRT-induced trade-off between the DOC respiration rate and fraction of DOC mineralized in each lake (panel c). The darker hues represent higher density of points based on a two-dimensional kernel density estimation using the function *heatscatter* in the R package *LSD*.

importance of flux pathways between water and carbon, thus creating variable fraction of carbon mineralized across WA:LA despite similar HRT's. Since a majority of the lakes' water budget in the NHLD is dominated by evaporation (>50% of hydrologic budget is evaporation; n = 2022, 55% of all lakes), considering hydrologic pathways rather than simply HRT is likely important to appropriately scaling to regional lake carbon fluxes and export of carbon downstream.

FHEE is such a strong predictor of the fraction of DOC mineralized within a lake (explaining >94% of variation in our model estimates, >98% with lake mean depth as a covariate) because it summarizes both areal hydrologic flux from the watershed to the lake as well as the degree to which water and carbon are co-transported. Areal hydrologic load has been shown to be a strong predictor of the fraction of DOC mineralized within lakes since most of the hydrologic load, and therefore DOC load, is advected in lakes with high areal hydrologic load (Brett et al., 2012); however, this relationship needs to be tempered with the knowledge that a substantial portion of the water inputs leaves the lakes through evaporation, thus leaving the carbon behind in the lake to be processed or stored. This differential importance of flux pathways between water and carbon increases with FHEE. Mathematically, we can approximate FHEE as

$$\mathrm{FHEE} = \frac{\mathrm{evap}\times \mathrm{SA}}{(\mathrm{evap}\times \mathrm{SA} + Q_{\mathrm{out}})} = \frac{\mathrm{evap}\times \mathrm{SA}}{Q_{\mathrm{in}}} = \frac{\mathrm{evap}\times \frac{V}{\bar{z}}}{Q_{\mathrm{in}}} = \frac{\mathrm{evap}\times \mathrm{HRT}}{\bar{z}} \quad (1)$$

where evap is lake surface evaporation (m/day), SA is lake surface area (m^2), Q_{out} is nonevaporative water outflow (surface water and groundwater; m^3), Q_{in} is hydrologic load from the watershed (surface water and groundwater) and direct precipitation (m^3/day, where Q_{in} is approximately equal to Q_{out} + evap × SA in

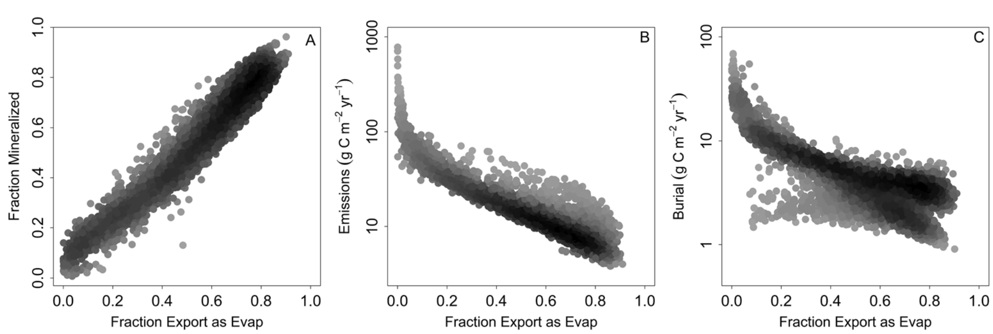

Figure 6. (a) Model estimated fraction of inflowing dissolved organic carbon that is mineralized within each lake (fraction mineralized) was strongly predicted by the fraction of hydrologic export occurring as evaporation. The fraction of export as evaporation was also negatively related to (b) areal carbon emissions and (c) burial. The darker hues represent higher density of points based on a two-dimensional kernel density estimation using the function *heatscatter* in the R package *LSD*.

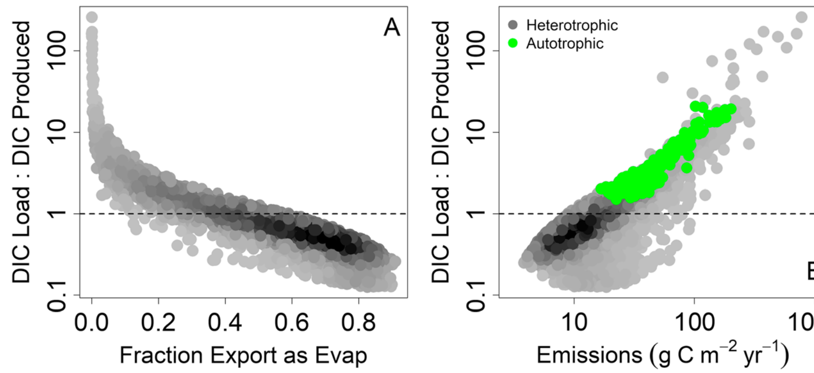

Figure 7. (a) Model estimated ratio of the externally loaded dissolved inorganic carbon (DIC) to DIC produced through lake respiration (DOC respiration + sediment respiration) as a function of the fraction of hydrologic export as evaporation. (b) The ratio of loaded DIC to DIC produced within the lake was positively related to areal carbon emissions. About 7.2% of the lakes were net autotrophic during the open-water period (GPP $>$ epilimnetic respiration; green points in panel b), and these lakes had a higher median areal emission rate compared to heterotrophic lakes. The darker hues represent higher density of points based on a two-dimensional kernel density estimation using the function *heatscatter* in the R package *LSD*.

the long-term mean), V is lake volume (m^3), $\bar{z}$ is lake mean depth (m), and *HRT* is HRT (days; $\frac{V}{Q_{in}}$). We can see that as hydrologic load (Q_{in}) decreases, HRT increases, and thus, FHEE increases (equation (1) and Figure 4d). The increased HRT with decreased hydrologic load increases the processing time of carbon within the lake; therefore, a larger fraction of loaded DOC is mineralized within the lake (e.g., Brett et al., 2012; Hanson et al., 2011). However, processing time of carbon in a lake can also change through changes in evaporation or mean depth for a given HRT (equation (1); see also Jones et al., 2018). Similar to an evapoconcentrating effect, as evaporation rate increases for a given HRT and mean depth, more carbon is left behind in the lake to be processed and the fraction of carbon mineralized within a lake increases. Therefore, FHEE encompasses two processes that influence the amount of time DOC spends within a lake, and both indicators are positively related to FHEE (Figure 4d).

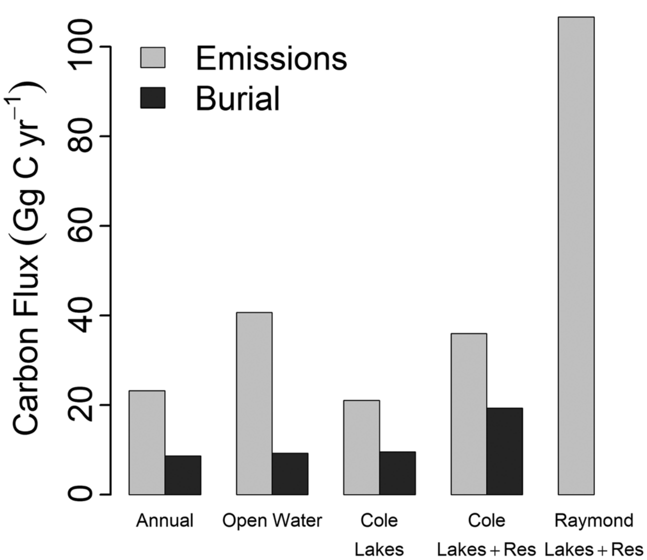

Figure 8. Aggregate annual lake carbon emissions and burial for the lakes we modeled in the NHLD when considering ice cover (annual) or by scaling open-water rates to annual emissions and burial (open water). We compare our spatially explicit model to previously published global carbon models (Cole et al., 2007; Raymond et al., 2013), which estimated rates for natural lakes (Cole Lakes) or natural lakes and reservoirs (Cole Lakes + Res; Raymond Lakes + Res). Neither Cole et al. nor Raymond et al. consider ice cover dynamics in their annually scaled fluxes.

Of course, the reactivity of inflowing carbon will also have an impact on the fraction of DOC that is mineralized within lakes. As mentioned above, variability in quality of inflowing DOC has been used to explain spatial differences in the fraction of carbon retained in lakes, where lakes with higher lability of inflowing carbon will mineralize a greater fraction than those with less lability of inflowing carbon at a given HRT (e.g., Hanson et al., 2011; Jones et al., 2018). More recently, modeling of a dynamic DOC mineralization rate dependent on HRT has improved the explanation of spatial variability in fraction of DOC mineralized across lakes (Vachon et al., 2016) and also improved estimates of in-lake DOC and CO_2 pools through time (Vachon et al., 2016). Although inflowing terrestrial carbon lability varies across the landscape (e.g., Berggren et al., 2010; Guillemette et al., 2013; Vachon et al., 2016), this variation is small compared to the hydrologic variability among lakes. And since the lability of in-lake carbon, and therefore mineralization rate of carbon, is an emergent property of inflowing terrestrial carbon quality and chemical residence time (e.g., Catalán et al., 2016; Mostovaya et al., 2016; Vachon et al., 2016), hydrologic variables alone can explain a majority of terrestrial carbon processing rates and fates within lakes. Indeed, our model-estimated long-term mean mineralization rates of DOC ranged from 0.0011 to 0.0055 day^{-1}, nearly spanning the range used to explain spatial variability in fraction DOC mineralized (Hanson et al., 2011). However, FHEE and mean depth alone still explained over 98% of the variability in fraction of DOC mineralized. This implies that simple physical constraints, which may be

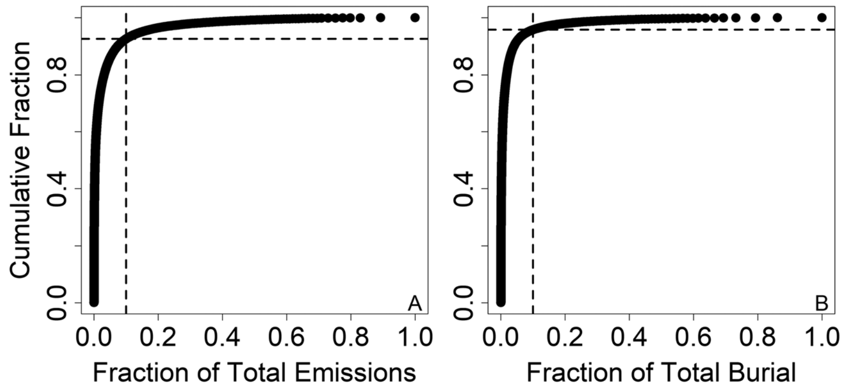

Figure 9. Cumulative fraction of lake contributions to total Northern Highlands Lake District (a) lake CO_2 emissions and (b) carbon burial. The vertical dashed lines indicate that 90% of Northern Highlands Lake District lake carbon emissions and burial are accounted for by 7.5% and 4.2% of the lakes, respectively (horizontal dashed lines).

approximated from geospatial analyses, can help researchers estimate the fraction of carbon buried or emitted by aquatic systems at large scales.

FHEE may also be used to approximate total lake carbon fluxes for a region as the fraction of export as evaporation was also negatively related to areal carbon emissions and burial in the NHLD (Figure 6). We would expect areal lake carbon emissions to be negatively related to the FHEE since lakes with low FHEE receive more terrestrial carbon from the watershed through high hydrologic loading (Q_{in}) and have a higher emergent mineralization rate of terrestrial carbon due to a more continuous supply of labile terrestrial carbon (Evans et al., 2017; Jones et al., 2018; Vachon et al., 2016). Previous research supports this model-derived relationship as respiration, and emission rates are often negatively related to lake HRT and thus also to FHEE (equation (1); e.g., Catalán et al., 2016; del Giorgio et al., 1999; Kelly et al., 2001; Rantakari & Kortelainen, 2005; Solomon et al., 2013; Zwart et al., 2017). Similarly, we would expect carbon burial to be negatively related to FHEE since lakes with low FHEE receive considerably more dissolved and particulate materials from the landscape such as terrestrial particulate organic carbon (tPOC) and phosphorus, which is necessary for phytoplankton productivity. Increased tPOC and phytoplankton biomass increases rates of carbon burial as tPOC and phytoplankton sediment out of the water column. The model is consistent with observations in this regard, because lakes with the largest watersheds typically have the highest carbon burial rates (Einsele et al., 2001; Mulholland & Elwood, 1982; Teodoru et al., 2012; Tranvik et al., 2009). However, we would not expect this relationship to hold when comparing across various regions, such as between agriculturally dominated landscapes versus more pristine environments, like the NHLD. Small, agricultural impoundments bury much more organic carbon in their sediments compared to relatively pristine lakes due to catchment soil erosion and algal production (Downing et al., 2008), and shifts toward agricultural land use has caused increased burial rates in Southern Minnesotan lakes over the past 100 years (Dietz et al., 2015). Our model also produced a strong relationship between TP concentrations and carbon burial rates (relationship not shown), consistent with observations from Dietz et al. (2015). However, variation in TP in our modeled lakes was driven by hydrologic characteristics as opposed to land use, thus creating a relationship between hydrologic metrics and carbon burial for our modeled region.

4.2. Externally Versus Internally Produced DIC

A vast majority of carbon emitted from the NHLD was from externally loaded inorganic carbon as opposed to internally produced (loaded DIC = 78% of all emissions), even though a majority of lakes produced more inorganic carbon within the lake than was exported to the lake from the surrounding watershed (65% of lakes' loaded, produced DIC was less than 1). This indicates that total lake CO_2 emission for the NHLD is driven primarily by a handful of large lakes with very high external loading of DIC. Additionally, lake hydrologic characteristics seem to be a driver of the importance of externally loaded DIC to regional CO_2 emissions since FHEE was a strongly related to both the source of DIC in the lake (externally versus internally produced) and the areal CO_2 emissions (Figures 6b and 7). This highlights the relatively quick venting of externally produced DIC compared to the longer time it takes for DOC to be mineralized to DIC and emitted as CO_2, indicating that externally loaded DIC is more sensitive to variation in hydrologic loading than internally produced DIC (Vachon & del Giorgio, 2014). Externally loaded DIC has been increasingly recognized in recent studies as an important flux contributing to total lake CO_2 emissions for a region (e.g., Maberly et al., 2013; Weyhenmeyer et al., 2015). Using a steady state model, McDonald et al. (2013) also highlighted the importance of externally loaded DIC to lake pCO_2 for >1,000 lakes sampled in the United States and Cardille et al. (2007) estimated the importance of loaded DIC to lake emissions within the NHLD using a different modeling framework. Our spatially explicit regional model provides further evidence for the importance of externally loaded DIC maintaining CO_2 supersaturation in lakes and thus CO_2 emissions from lakes to the atmosphere, even in low-alkalinity regions such as the NHLD.

Also consistent with previous research, our model estimated that 7.2% of the lakes in the NHLD are simultaneously autotrophic and net emitters of CO_2 to the atmosphere. This phenomenon has been described before, although the fraction of lakes we observed was slightly lower than reported by McDonald et al. (2013, 12%) and Bogard and del Giorgio (2016, 32%). Additionally, Wilkinson et al. (2016) observed net CO_2 emissions from lakes despite inducing and/or enhancing autotrophy following whole-lake nutrient additions. The lakes we modeled that were both net autotrophic and net emitters of CO_2 had a higher median emission rate than net heterotrophic lakes, due to the high external load of DIC (net autotrophic median emit: 44.7 g $C \cdot m^{-2} \cdot year^{-1}$; net heterotrophic median emit: 12.6 g $C \cdot m^{-2} \cdot year^{-1}$). This is similar to results obtained by Bogard and del Giorgio (2016), who observed that CO_2 emission rates were high for both net autotrophic and net heterotrophic lakes that emitted CO_2. However, their sampling time period was during the summer months, whereas our emission rates are integrated over the entire year, which includes high CO_2 emissions during the spring ice melt and fall mixis, and these periods can account for a majority of annual CO_2 emissions in some lakes in our simulation. This annual integration of CO_2 emissions may explain why our emission rates were higher for net autotrophic lakes compared to heterotrophic lakes, while Bogard and del Giorgio (2016) observed similar rates between the two lake types. However, more temporal sampling of CO_2 emissions, especially during spring and fall mixis in dimictic lakes, is needed for both net autotrophic and net heterotrophic lakes to either support or reject this pattern predicted by our model.

4.3. Scaling to Regional Lake Carbon Fluxes

We estimated lakes in the NHLD to emit 23.2 Gg C/year and bury 8.6 Gg C/year. These carbon flux rates were similar to the Cole et al. (2007) global rates of natural lakes scaled to the NHLD lake surface area, but slightly less than the Cole et al. (2007) estimate when reservoirs are included and much less than the Raymond et al. (2013). The NHLD is almost exclusively natural lakes, with only 13 out of the 3,675 lakes we modeled classified as reservoirs by the National Hydrography Dataset (FType = 436). Carbon emission and burial rates are much higher for reservoirs compared to natural lakes (Cole et al., 2007; Deemer et al., 2016; Tranvik et al., 2009). Therefore, it is not surprising that global estimates that do not distinguish between lake and reservoir carbon flux rates (e.g., Raymond et al., 2013) have a higher emission and burial rate when scaled to the NHLD LA than was predicted by our model.

Both Cole et al. (2007) and Raymond et al. (2013) do not consider ice cover in their scaling estimates, in part because measurement of the emissions shortly after ice out and during fall mixis in dimictic lakes is extremely difficult. Raymond et al. (2013) argued that the large emissions during ice out (Striegl et al., 2001; Striegl & Michmerhuizen, 1998) offsets the zero emissions during ice cover, and thus, it is reasonable to scale summertime emissions to annual rates. However, we estimated substantially lower regional emission rates when integrating emissions across the entire year as opposed to scaling open-water period emissions to annual rates (Figure 8). Therefore, temperate and boreal emission rates may be overestimated in current global-scale emission estimates that do not include ice cover duration and predicting how these regions' emissions respond to climatic change should include models that consider biogeochemical dynamics associated with ice cover.

Regional carbon fluxes were dominated by large lakes as >99% of carbon fluxes were accounted for by lakes larger than 1 ha, despite the median lake size being <1 ha (Figure 9). This overwhelming importance of large lakes to regional carbon fluxes has been documented before in temperate (Cardille et al., 2009) and arctic regions (Rocher-Ros et al., 2017). However, we also show that carbon fluxes scaled areally varied little across different lake size classes, which does not support recent hypotheses that small lakes emit and bury much more carbon areally than large lakes (e.g., Cardille et al., 2009; Holgerson & Raymond, 2016; however, see Kelly et al., 2001). Given the strong control of hydrologic characteristics on areal carbon flux rates (Figures 5–7), we think that the lack of relationship between areal carbon flux and lake size is driven by the lack of relationship between important hydrologic characteristics and lake size across the region (Figure 4). Additionally, areal emissions may be comparable between large and small lakes due to higher gas exchange coefficient (k) in larger lakes despite lower pCO_2 (Table 1). Indeed, Cardille et al. (2009) used a single gas flux rate across all lake sizes (0.5 m/day, one half to one third of the gas flux rate we estimate for the largest lakes in the NHLD; Table 1), which may be why they estimated lower areal carbon emissions in large lakes compared to small lakes with their model.

The lack of relationship between areal carbon flux and lake size could also be driven by low estimates of carbon loading to small lakes produced by our model. One area of uncertainty is the amount of carbon loaded to lakes from the immediate shoreline wetlands (Hanson et al., 2014, 2015). These loading rates are difficult to estimate since carbon flow paths from adjacent wetlands are diffuse and require extensive wetland monitoring (Watras et al., 2014) and/or confident estimates for the remaining pieces of a lake's water budget (Zwart et al., 2017). Furthermore, we relied on the 2006 National Land Cover Database (http://www.mrlc.gov/nlcd06_data.php) for characterizing land cover type within lakes' watersheds, which may mischaracterize watershed land cover for small lakes due to its spatial resolution (30 m). For this study, we used the mean wetland loading rate across all lakes used in the study by Hanson et al. (2014); however, we tested the sensitivity of our model results to this loading rate and land cover characterization by rerunning the model using the highest wetland loading rate estimated by Hanson et al. (2014) and by setting shoreline land cover of all lakes to 100% wetland. Although CO_2 emissions increased for the smallest lakes (<1 ha) with the increased wetland loading rate and 100% wetland shoreline, there was still no relationship between areal CO_2 emissions and lake size. This adds support to our conclusion that hydrologic variation across lakes, which is largely independent of lake size, rather than lake size alone has a stronger control on areal CO_2 emissions for this region; however, more research is needed on diffuse wetland carbon loading to help inform carbon loads to small lakes (Hanson et al., 2015).

4.4. Model Validation

Although our model preformed reasonably well when compared to regional characteristics of various lake constituent concentrations and seasonal dynamics when compared to time series, there were some discrepancies between our model estimates and observations. For example, our model underestimated constituent concentrations in TB, likely driven by too low inflowing concentration. Based on watershed land cover (17% wetland for TB from geospatial analysis), our model estimated TB to have an inflowing DOC concentration of only 7.1 mg/L while observations of in-lake DOC were between 15 and 20 mg/L. When we rerun our model with increased watershed land cover surrounding TB (80% wetland according to Hope et al., 1996), we achieve much better agreement between modeled and observed constituent concentrations (Figure S1). This indicates that improved information on forcing data for our model, such as land cover characterization, will likely improve model performance for specific lakes.

Although our modeled lake constituent concentrations were variable when compared to observations (one-to-one inset plots in Figure 3), it is unclear if this scatter around the one-to-one line has a meaningful effect on our regional-scale carbon flux estimates. This uncertainty in individual lake constituent concentrations may be due to our uncertainty in lake volume. For example, modeled lake volume ranged from less than one half to over twice the observed volume for lakes with known volumes, which essentially doubles or cuts in half in-lake constituent concentrations based on error in ecosystem size alone, assuming that the error is normally distributed. However, the effects of overpredicting lake volume, and thus constituent concentrations, in some lakes may cancel out the effects of underpredicting lake volume in other lakes, especially if regional distributions of modeled and observed concentrations are similar (cumulative fraction plots in Figure 3). Thus, our model may incorrectly estimate carbon fluxes for every individual lake while still estimating aggregate carbon flux for the region reasonably well. Ideally, lake volume would be known for every lake. But in the absence of known lake volumes, robust uncertainty analyses may help address the question whether uncertainty in lake volume significantly affects our ability to scale lake carbon fluxes for a region.

Regional carbon flux observations were limited for the NHLD; therefore, it was difficult to compare our model-estimated carbon emissions and burial to observations. However, our model estimated carbon burial and emissions were similar to broad-scale surveys of lakes conducted elsewhere. For example, a broad-scale survey of 183 European lakes reported that 14% of lakes had a burial rates greater than 10 g · m^{-2} · $year^{-1}$, which is similar to our model-estimated 13.6% lakes in the NHLD having burial rates greater than 10 g · m^{-2} · $year^{-1}$ (Kastowski et al., 2011). Our model-estimated pCO_2 were comparable to broad-scale surveys from Cole et al. (1994) and similar distributions to global scale analyses based on lake size where pCO_2 was negatively related to lake size bins (Table 1; Raymond et al., 2013). Additionally, model-estimated CO_2 emissions were similar to previous surveys of north temperate lakes (Bogard & del Giorgio, 2016; del Giorgio et al., 1999). These estimates of lake carbon emissions, burial, and export were constrained in our model by inputs of water and material fluxes from the landscape (Hanson et al., 2018). We think that this modeling approach is particularly promising for broad-scale biogeochemical studies because of the opportunity to link to terrestrial ecosystem models and estimate whole-region carbon budgets in response to global change (Buffam et al., 2011).

4.5. Biogeochemical Processes Omitted

Although our model includes many essential processes representing aquatic biogeochemistry, we omitted a number of processes to limit the number of state variables and make the model more computationally efficient. For example, our simple lake biogeochemical model does not include oxygen dynamics, benthic primary production, temperature-dependent sediment respiration, DOC flocculation, or photomineralization of DOC. Oxygen, temperature, and benthic primary production can impact organic carbon accumulation rates and burial efficiency (Ferland et al., 2014; Sobek et al., 2009, 2014). Modeled area-weighted average water temperature at the sediment-water interface during the open-ice period showed little variability across lakes (9.9–11.2 °C for 25th–75th percentiles), which meant that differences in temperature across lakes would have relatively little impact on C burial and sediment respiration rates across our modeled lakes. Even though we did not consider some dynamics that impact sediment respiration and burial (such as temperature and oxygen), carbon burial rates and burial efficiency varied substantially across lakes and were consistent with previous broad-scale analyses. Mean modeled burial efficiency was 55% and ranged from 32 to 89%, and the mean carbon burial rate was 6.2 g C · m^{-2} · $year^{-1}$ and ranged from 0.9 to 66 g C · m^{-2} · $year^{-1}$. These rates of C burial were consistent with previous surveys of lake C accumulation rates (Ferland et al., 2012, 2014; Kastowski et al., 2011), and burial efficiency rates were most similar to those observed under middle- to low-oxygen exposure times (Ferland et al., 2014; Sobek et al., 2009, 2014).

DOC flocculation and photomineralization were omitted from our model because this was a relatively small loss rate for DOC and small rate of POC sedimentation. The modeled median DOC loss through biological respiration was over 9 times higher than the flocculation rate reported by von Wachenfeldt et al. (2008), and our estimated POC sedimentation was 7 times higher than flocculated DOC sedimentation reported in von Wachenfeldt et al. (2008). Although some of the processes we omitted may be important for certain lakes, we think that our model captures many important aspects of broad-scale lake biogeochemistry due to the good agreement with broad-scale surveys of lake constituent concentrations (Figure 3) and consistency with previous observations of lake carbon emissions and burial.

5. Conclusions

Accurately scaling lake carbon fluxes is imperative given the global importance of lakes to the carbon cycle and projected climatic and land use changes that may alter lake carbon cycling dynamics in the future. Process-based models are one of the most robust ways to deal with issues of spatial and temporal scale by accurately capturing local-scale heterogeneity by leveraging physical, hydrological, and ecological knowledge. Through our spatially explicit, process-based model of lake carbon cycling, we add support to the existing literature that lake hydrologic characteristics strongly regulate lake carbon cycling. We show that one hydrologic metric in particular, the FHEE, can be used to predict important carbon processes and fluxes for our modeled region given that it summarizes both hydrologic loads from the watershed and the degree of decoupling between water and carbon cycles. Since hydrologic characteristics are evenly distributed across lake sizes, median areal lake carbon emissions and burial were similar for different lake sizes. Because of this, large lakes constitute an overwhelmingly large proportion of the total lake carbon flux for the region. Therefore, we conclude that accurately scaling lake carbon fluxes for a region must include accurate representation of lake hydrologic characteristics and that large lakes are most important to model accurately.

Acknowledgments
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