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Integrating aquatic and terrestrial components to construct a complete carbon budget for a north temperate lake district

ISHI BUFFAM*†, MONICA G. TURNER*, ANKUR R. DESAI‡, PAUL C. HANSON†, JAMES A. RUSAK§[1], NOAH R. LOTTIG§, EMILY H. STANLEY† and STEPHEN R. CARPENTER†

Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706, USA, †Center for Limnology, University of Wisconsin, Madison, WI 53706, USA, ‡Department of Atmospheric and Oceanic Sciences, University of Wisconsin, Madison, WI 53706, USA, §Center for Limnology, University of Wisconsin, Madison, Boulder Junction, WI 54512, USA

Abstract

The development of complete regional carbon (C) budgets for different biomes is an integral step in the effort to predict global response and potential feedbacks to a changing climate regime. Wetland and lake contributions to regional C cycling remain relatively uncertain despite recent research highlighting their importance. Using a combination of field surveys and tower-based carbon dioxide (CO_2) flux measurements, modeling, and published literature, we constructed a complete C budget for the Northern Highlands Lake District in northern Wisconsin/Michigan, a $\sim$6400 km^2 region rich in lakes and wetlands. This is one of the first regional C budgets to incorporate aquatic and terrestrial C cycling under the same framework. We divided the landscape into three major compartments (forests, wetlands, and surface waters) and quantified all major C fluxes into and out of those compartments, with a particular focus on atmospheric exchange but also including sedimentation in lakes and hydrologic fluxes. Landscape C storage was dominated by peat-containing wetlands and lake sediments, which make up only 20% and 13% of the landscape area, respectively, but contain >80% of the total fixed C pool (ca. 400 Tg). We estimated a current regional C accumulation of $1.1 \pm 0.1\ Tg\ yr^{-1}$, and the largest regional flux was forest net ecosystem exchange (NEE) into aggrading forests for a total of $1.0 \pm 0.1\ Tg\ yr^{-1}$. Mean wetland NEE ($0.12 \pm 0.06\ Tg\ yr^{-1}$ into wetlands), lake CO_2 emissions and riverine efflux (each ca. $0.03 \pm 0.01\ Tg\ yr^{-1}$) were smaller but of consequence to the overall budget. Hydrologic transport from uplands/wetlands to surface waters within the region was an important vector of terrestrial C. Regional C fluxes and pools would be misrepresented without inclusion of surface waters and wetlands, and C budgets in heterogeneous landscapes open opportunities to examine the sensitivities of important fluxes to changes in climate and land use/land cover.

Keywords: carbon budgets, carbon fluxes, carbon stocks, lake sediments, peatlands, surface–atmosphere fluxes, terrestrial–aquatic linkages

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Introduction

Lakes and wetlands process and store carbon (C) differently than uplands and may contribute substantially to C cycling at a range of spatial and temporal scales, yet few regional C budgets explicitly incorporate lakes and wetlands (Benoy *et al*., 2007). In spite of their relatively small areal coverage worldwide, lake sediments and wetland peat are globally appreciable C pools because of their often very high C density and long residence times (Mulholland & Elwood, 1982; Gorham, 1991; Downing *et al*., 2006; Cole *et al*., 2007). In addition, lake and peatland ecosystems respond differently than upland or ocean ecosystems to environmental perturbations including changes in climate. However, unlike ocean and upland systems they are not typically treated explicitly in global C models, and their potential response to climate change is complex and not yet well understood (Gorham, 1991; Schindler & Smol, 2006). Incorporation of surface waters and wetlands into regional and global C models would thus be a crucial next step, but as a part of building toward that goal we need to quantify the role of lakes and wetlands in C cycling for a range of biomes.

Regional sensitivities are important – whether regions/landscapes are net C sinks or sources, the magnitude of C storage, and vulnerability to change are all

[1]Present address: J. A. Rusak, Dorset Environmental Science Centre, Ontario Ministry of the Environment, Dorset, ON, Canada.

Correspondence: Ishi Buffam, Department of Zoology, University of Wisconsin-Madison, Birge Hall, 430 Lincoln Drive, Madison, WI 53706, USA, tel. + 1 608 265 8001, fax + 1 608 265 6320, e-mail: buffam@wisc.edu

valuable pieces of information that require a good understanding of the regional C budget. To date however, most C budget studies have been undertaken at fine spatial scales focusing on particular ecosystem types, primarily forest stands (e.g., Chen *et al*., 2004; Dunn *et al*., 2007; Baldocchi, 2008; Desai *et al*., 2008). C flux studies have been based on eddy-flux tower-based measurements, while forest C accumulation studies utilize productivity measurements and survey estimates of biomass (Turner *et al*., 1995; Kurz & Apps, 2006). Though rarer, ecosystem-specific C balances for individual lakes (Gasith, 1974; Likens, 1985; Dillon & Molot, 1997; Urban *et al*., 2005; Sobek *et al*., 2006) and wetlands (Billett *et al*., 2004; Roulet *et al*., 2007; Nilsson *et al*., 2008; Sulman *et al*., 2009) have also been undertaken. However, much less is known about the complete C balance of heterogeneous landscapes that include surface water elements as well as forest. Interactions among different landscape elements may give rise to complex behaviors in heterogeneous landscapes. In addition, relatively few budget studies have quantified hydrologic export of C from terrestrial watersheds, though this can be a sizeable contributor to annual net C balance (Christensen *et al*., 2007; Cole *et al*., 2007; Roulet *et al*., 2007; Nilsson *et al*., 2008). Billett *et al*. (2004) for example found that fluvial C losses equaled or exceeded terrestrial carbon dioxide (CO_2) uptake in a wetland-rich watershed.

Upscaling from individual surface water ecosystem measurements to biome (Molot & Dillon, 1996; Richey *et al*., 2002) and global (Cole *et al*., 2007; Battin *et al*., 2009; Tranvik *et al*., 2009) scales have suggested that surface freshwaters are a sizeable contributor to net C balance at these scales. At the intermediate regional (1000–10 000 km^2) scale, two recent studies have detailed ground-based measurements of the major components of the C cycle, including the freshwater component. In a $\sim$4000 km^2 subarctic Swedish catchment with total lake coverage ca. 14%, Christensen *et al*. (2007) found that lake surface–atmosphere exchange altered the total regional net C exchange by 12.5%, with an average areal efflux of C from lakes on par with net accumulation in other parts of the catchment. Small lakes were a particularly strong source of both CO_2 and CH_4. They also calculated that C accumulation in specific terrestrial vegetation compartments would be overestimated by anywhere from 15% to 98% if hydrological export of dissolved organic carbon (DOC) was not accounted for (Christensen *et al*., 2007), demonstrating the potential role of hydrological transport for landscape C budgets, and underlining the importance of the interaction of different landscape elements. Of the total terrestrial net uptake of C from the atmosphere in this subarctic landscape, 44% was exported to surface waters. Thus, the treatment of surface waters as C-neutral would result in an overestimation of landscape C sink strength by 44%.

In a study of similar spatial scale but with a smaller total lake coverage (3.5% by area), Jonsson *et al*. (2007) found in a boreal Swedish catchment that about 6% of the landscape's terrestrially produced C was exported to surface waters. In this boreal landscape with a well-developed river network, about half of that C was then exported to the sea, while half was evaded from lake and stream surfaces as CO_2; lake sedimentation and aquatic primary production rates were of little importance to regional C balance (Jonsson *et al*., 2007). These two studies highlight the potentially important and widely varying role that surface waters can play in current annual C fluxes, notwithstanding the central role they play in long-term C sequestration (Mulholland & Elwood, 1982). Similar studies performed in other regions and ecosystems worldwide are required to help fill the gap in understanding of C cycling at intermediate spatial scales in heterogeneous surface-water containing landscapes.

Here, we present a regional C budget for the Northern Highlands Lake District (NHLD), a $\sim$6400 km^2 lake-rich region of the north-central Midwest, USA, incorporating aquatic and terrestrial C cycles into a unified framework. All major C pools and fluxes and associated uncertainties have been estimated, with new measurements for peat wetlands and lakes of the region. We hypothesized that the surface waters in the NHLD would influence the regional net C balance at a level commensurate with their areal coverage, i.e., by about 13%. Peat in wetlands was expected to be the largest C pool, as found in other areas with substantial peatland coverage (e.g., Garnett *et al*., 2001; Beilman *et al*., 2008; Weishampel *et al*., 2009). Our study addressed three main questions: (1) How do C fluxes and pool sizes and vary among lakes, wetlands and forests of a north-temperate region? (2) By how much will an estimate of regional terrestrial C accumulation be biased if surface waters aren't explicitly considered? (3) What are the major remaining uncertainties in the regional C balance for this north-temperate region?

Study region

The NHLD of Wisconsin and Michigan (Fig. 1) is one of the most lake-rich regions of the world (Magnuson *et al*., 2006), and consists of a mosaic of lakes and wetlands interspersed in a mixed forest landscape. The central part of the region is a particularly lake-rich area of $\sim$6400 km^2, and is the focal area for this study. The bulk of the landscape is made up of mixed and hardwood forests (about 45% total by area) and a smaller

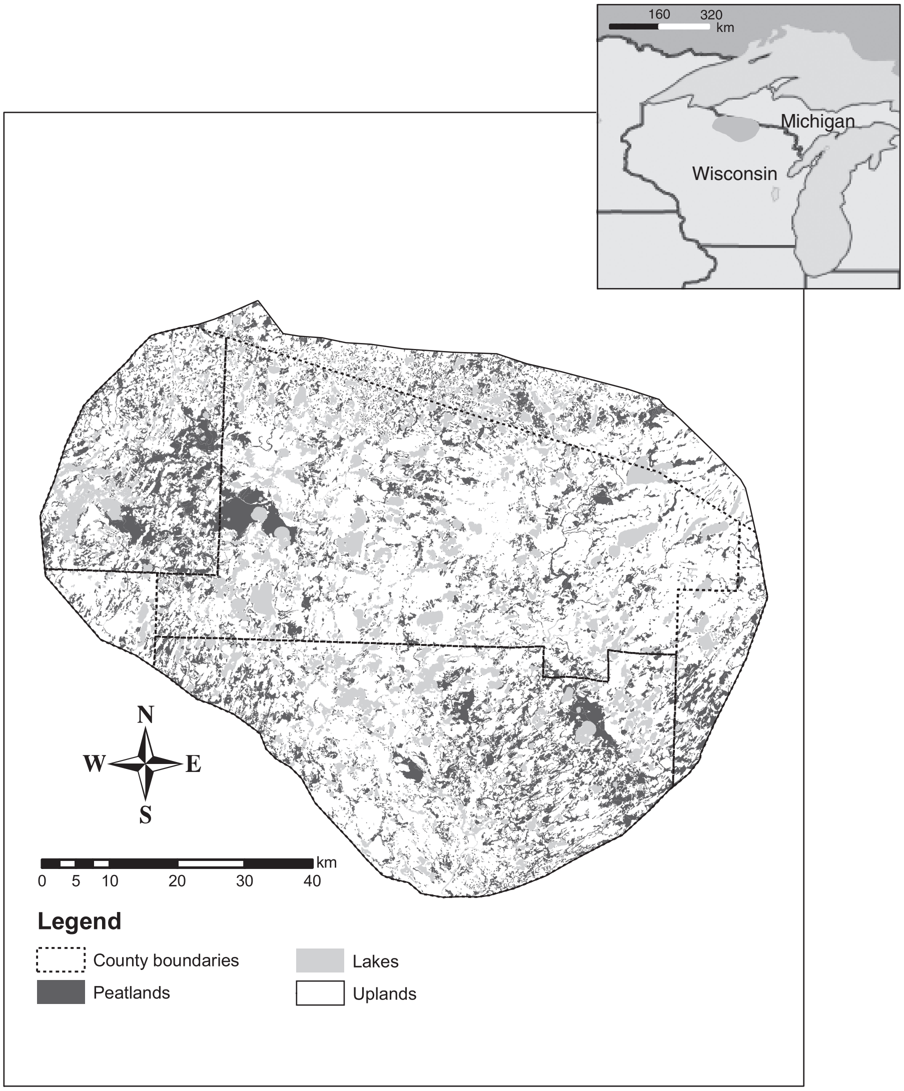

Fig. 1 Location of Northern Highlands Lake District study region in north central Wisconsin and Michigan, USA (inset), and land-cover map of the NHLD.

proportion of coniferous forest (~8% by area), with substantial coverage of wetlands (28%) and lakes (13%) while the remainder (~5% total by area) includes roads, small towns, agriculture and shrublands. Population density is low, averaging about 10 people km^{-2} (http://quickfacts.census.gov/qfd/). The entire region was largely deforested about 100 years ago, and consequently most forest stands are currently aggrading. The surface morphometry of the region was structured by the last deglaciation 10 000–15 000 years BP (Martin, 1965; Attig, 1985), which produced a pitted sandy outwash landscape (Curtis, 1959). Depressions in the low-relief sandy terrain (total range 450–580 m a.s.l.) were formed by melting ice-blocks, and many subsequently filled with water giving rise to numerous lakes. Currently, about 5000 open water bodies cover 13% of the surface area. The water bodies range in size from ponds of <0.1 ha to several lakes $>10\,km^2$, with a median are of <1 ha. Included among the largest lakes in the region are several man-made reservoirs, totaling 1.6% of the region by area. Discrete peat-containing wetlands (mostly forested) cover 20% of the surface area (NRCS, 2008), while nonpeat-forming wetlands cover 8% of the region by area. Many lakes and wetlands are linked together or fed by streams, and the major drainage basins in the NHLD are the Upper Wisconsin River, which drains approximately 45% of the region by area, and the Flambeau River basin, draining an additional 27%.

Methods

We estimated regional pool sizes and mean annual fluxes for the major ecosystem types (surface waters, wetlands, and forests) in the region using a combination of approaches. Where published values already exist at the regional scale, we combined values from the available literature. Where published data are available for individual sites in this or very similar regions, we scaled up with the help of a GIS and land cover/soil cover maps. Available data from the north temperate lake (NTL–LTER) database for lakes (http://lter.limnology.wisc.edu/), the NRCS database for soil C pools (NRCS, 2008), and the Ameriflux network for terrestrial fluxes (Desai *et al.*, 2008) were also used as a starting point for regional upscaling. Finally, gaps were filled with new measurements, including a field study of peatland C pool sizes (Buffam *et al.*, 2010). Further details of all pool and flux calculations are described below, with greater detail given for calculations involving new data and upscaling techniques. Calculations and statistical analyses were performed using R version 2.80 (R Foundation for Statistical Computing, 2008).

Terrestrial C pools

Forest vegetation, including uplands and forested wetlands. NHLD forest vegetation C was estimated by coupling US Forest Service Forest Inventory and Analysis (FIA) data on areal coverage of different forest stand types (http://fiatools.fs.fed.us/fiadb-downloads/datamart.html) for a 7230 km^2 rectangle approximating the NHLD region (bounded by 90.3°W, 88.9°W, 45.7°N, 46.3°N) with FIA-based data on mean C content of those forest stand types (http://ncasi.uml.edu/COLE/) within the seven-county region including the NHLD. The stand C content calculations are based on well-established allometric equations for aboveground biomass of live and dead trees (Jenkins *et al.*, 2003) and less secure estimates for tree roots (Jenkins *et al.*, 2003; Li *et al.*, 2003), understory vegetation, down dead wood, and forest floor/litter (Smith *et al.*, 2006). Calculations were performed separately for groups of mixed and hardwood forest stands (42% of region by area according to FIA), conifer stands (10.5% of area) and forested wetland stands (24% of area). An uncertainty in the total regional forest vegetation biomass of ± 10% was assumed for each group.

Forest soils. Using the NRCS soils map of the region (NRCS, 2008), soils were divided into two main categories: histosols and nonhistosols. Histosol C content was treated separately, described below in the wetland peat section. Nonhistosol soils were made up of 34 220 spatially discrete soil units for a total of 4289 km^2 or 67% of the NHLD region, the vast majority underlying upland forest. For each of the 293 distinct nonhistosol soil series found in the NHLD, carbon density (CD, in kg C m^{-2}) was calculated using the data from the SSURGO database (NRCS, 2008) together with the following equation:

$$\mathrm{CD} = \frac{1}{1000} R \sum_{j=1}^{n} \left[(z_\mathrm{t} - z_\mathrm{b})_j D_j \rho_j \right], \qquad (1)$$

where R is the C content (assumed to be $50 \pm 1\%$) of soil organic matter (OM), 1/1000 is a units conversion factor, n is the number of distinct soil layers categorized in the given soil series, z_t and z_b are depth below surface (m) of the top and bottom of soil layer j, D is the OM fraction (w/w) of soil layer j and ρ is the moist bulk density (g/cm^3) of soil layer j. The NRCS soil series data for this region typically goes down to a maximum depth of 1.52 m; we did not make any attempt to account for C in the deeper soils, except in the wetland histosols (peat) as described in a separate section below. The SSURGO database reports a range (high and low values) for both D and ρ for each soil layer. To obtain our mean estimate we used the average of the high and low values. For uncertainty estimates, we calculated an extreme high and low value of CD for each soil series, using Eqn (1) with the high or low values, respectively for both D and ρ for all soil layers. The distribution of potential CD values for each soil series was defined as a normal distribution with the extreme high and low values describing the 95% CI. Then, in a Monte Carlo simulation, each discrete soil unit in the NHLD ($N = 34\,220$) was assigned a CD value at random from the distribution for the appropriate soil series. The landscape total soil C was then summed, and the process repeated 10 000 times to explore the sensitivity of landscape soil C totals to uncertainty in individual soil series CD.

Wetland vegetation, open wetlands. In the absence of comprehensive surveys of wetland ground vegetation biomass in the region, values for shrubs and herbs were based on a compilation of literature on bogs and poor fens by Moore *et al.* (2002), and assuming that belowground biomass was half of aboveground biomass. *Sphagnum* biomass was estimated from a harvesting study in a Minnesota bog which found a mean biomass for active layer Sphagnum of 7.0 ± 2.0 kg ha^{-1} (Elling & Knighton, 1984). For upscaling Sphagnum biomass to the NHLD a regional mean *Sphagnum* coverage of 60 ± 8% (1 SE, $n = 21$) in peatlands was used (Buffam *et al.*, 2010). For all vegetation, dry biomass was assumed to be 50% C.

Wetland peat. Based on the distribution of histosols on the NRCS soils map, there are about 8000 discrete peat-containing wetlands covering 20% of the NHLD surface area, or 1259 km^2 (NRCS, 2008). These peatlands are dominated by areally small units (median size ca. 2 ha). Because NRCS soil survey data from this region only report on depths to 1.52 m, and often do not differentiate between histosol soil series containing shallow (<1.52 m) or deep (>1.52 m) peat of otherwise similar characteristics, these data were not sufficient to quantify the peat C pool. Instead, the size of the regional peat C pool was estimated using field surveys of 21 discrete peatlands which established a positive correlation between mean peat depth and a DEM-derived basin edge slope measurement, enabling upscaling to the region (Buffam *et al.*, 2010). A detailed description of the methods can be found in Buffam *et al.* (2010), but in short the mean depth was calculated from basin edge slope for each discrete peatland, and C content was estimated from mean characteristics of peat cores taken in the same study. Uncertainty in the regional estimate was calculated based on error in the edge slope vs. depth regression, as well as uncertainty in the peat C characteristics including bulk density.

Regional and terrestrial C fluxes

Regional precipitation. Mean precipitation DOC and dissolved inorganic carbon (DIC) concentrations were taken as 2 ± 1 and $1\,\mathrm{mg\,L^{-1}}$, respectively, after Cardille *et al*. (2007). Mean annual flux was estimated by multiplying these concentration values by the long-term (1989–2007) annual average precipitation amount of 602 ± 153 mm from the nearby Woodruff airport meteorological station (http://lter.limnology.wisc.edu).

Regional runoff. Because we lacked a detailed time series for C fluxes in rivers draining the NHLD, we accumulated all available published and unpublished data on DIC and DOC concentrations for rivers draining the NHLD. This dataset included one-time determinations of DIC and DOC concentrations in the Wisconsin River at multiple locations near the outlet of the NHLD region (E. Stanley, unpublished results) and the Tomahawk River (Lottig, 2009), and seasonal measurements of DOC in the Wolf and Flambeau Rivers that include concentrations during high and low flow periods (Shafer *et al*., 1997, 1999; Babiarz *et al*., 1998). These sites have drainage areas ranging from 189 to 3193 $\mathrm{km^2}$, with a similar parent geology and proportion of lakes, forests and wetlands to that of the NHLD region as a whole.

From this exercise we estimated ranges for flow-weighted mean concentrations of 5–15 $\mathrm{mg\,L^{-1}}$ for DOC, 5–10 $\mathrm{mg\,L^{-1}}$ for DIC, and 1–5 $\mathrm{mg\,L^{-1}}$ for POC for rivers exiting the NHLD. Summing these, the concentration estimate for flow-weighted mean C_{total} ($20.5 \pm 5.9\,\mathrm{mg\,L^{-1}}$) was multiplied by annual river runoff (20 year mean, 1989–2008) of 260 mm for the Wisconsin River at the USGS Tomahawk gauging station 05391000 (http://nwis.waterdata.usgs.gov/) to estimate regional hydrologic export of C. Here we assume that the specific (area-normalized) discharge for the region is well-represented by the runoff of the Wisconsin River, which at this gauging location drains a watershed of 1961 $\mathrm{km^2}$ of similar landcover (58% forest, 25% wetland, 10% lake) to the NHLD as a whole. Gauging stations for other intermediate sized ($>200\,\mathrm{km^2}$) rivers of the region give similar values for annual specific discharge for that time period, ranging from 244 mm (Iron River, USGS gauging station 04060500) to 306 mm (Flambeau River downstream of NHLD, USGS gauging station 05360500). Based on this spatial variability we assigned an uncertainty of $\pm$ 40 mm to the regional mean annual water runoff.

As data on riverine exports from the NHLD were limited, we investigated temporal patterns of DIC, DOC, and POC loads in the Popple River at a site ca. 35 km east of the eastern boundary of the NHLD as an indicator of possible variability and uncertainty in C exports from the NHLD. The Popple River site is the focus of intensive sampling for the USGS National Water Quality Assessment program (USGS gauging station 04063700). Detailed measurements of all forms of C were available and were sampled both regularly (approximately monthly) and during storm flows over several years. At 362 $\mathrm{km^2}$ the basin is smaller than the major NHLD drainage (the Wisconsin River) and has a lower coverage of lakes, but is similarly dominated by forests and wetlands and shares a similar parent geology.

Forest and wetland surface–atmosphere fluxes. For the forest and wetland surface–atmosphere exchange, we estimated mean annual fluxes for the period 1989–2007 using the Interannual Flux Tower Upscaling Experiment (IFUSE) regional C ecosystem approach (Desai *et al*., 2010). Direct observations of surface–atmosphere exchange of CO_2 measured by eddy covariance flux towers in the region were used to calibrate a simple ecosystem model (Desai, in press), which was then applied to an upscaling model to calculate regional sources and sinks of C in forest and wetland ecosystems. The C flux observations come from a set of 13 eddy covariance flux towers that are part of the Chequamegon Ecosystem–Atmosphere Study and also affiliated with the Ameriflux and Fluxnet consortia (Baldocchi, 2008; Desai *et al*., 2008). The direct observations, ecosystem model, upscaling model and uncertainty estimates are described in detail in Supporting Information Section S1.

Wetland CH_4 emissions. Northern peat-containing wetlands typically emit CH_4, with rates varying widely in time and space depending largely upon variation in water table depth and other variables including temperature and vegetation type (Moore & Roulet, 1993; Bridgham *et al*., 1995; Granberg *et al*., 2001). A range of 1–20 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ of CH_4 emissions was cited by Moore *et al*. (1998) for northern peatlands, and individual studies (Roulet *et al*., 2007; Nilsson *et al*., 2008) as well as large-scale estimates (Gorham, 1991) generally give values in this range. Recent chamber-based measurements of growing-season CH_4 emissions at three wetland sites in the NHLD region gave emissions values at the low end of this range: 0.06 $\mathrm{gC\,m^{-2}}$ for an Alder shrub fen, 0.3 $\mathrm{gC\,m^{-2}}$ for an Ericaceous bog, and 2.6 $\mathrm{gC\,m^{-2}}$ for a Graminoid fen (Cook *et al*., 2008). Lacking more numerous direct measurements of wetland CH_4 emissions in the region we assigned the range of 1–20 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, which acknowledges high uncertainty, to the peatlands of the NHLD.

Within-region terrestrial C subsidies to surface waters

Hydrologic export from forests and wetlands to surface waters. Hydrologic C fluxes from forest and wetland areas were estimated using a set of eight headwater streams distributed across the NHLD, including four streams with forested catchments (forest cover 88–95% of area) and four streams with wetland catchments (wetland cover 34–57% of area, forest cover >90% of the remainder). Annual stream DOC, DIC, and C_{TOT} (DOC + DIC) fluxes were estimated for water year 2008 for each of these streams (N. R. Lottig, unpublished results), and regressed against percent wetland cover in catchment. This equation was used to generate predictions of C export at 0% and 100% wetland, representing pure forest and pure wetland catchments, respectively. These estimates were then multiplied by the regional coverage of forest and wetland to give regional flux estimates. Uncertainty in the eight stream flux estimates, as well as the regression equation, were propagated in the regional estimate. The implicit assumption of this approach is that other terrestrial sources of hydrologic C flux aside from forest and wetland are insignificant in the measured catchments. This seems a reasonable assumption as these areas are rare (always $<10\%$ of catchment area) and they represent landscapes not known for high C export (primarily scrub/shrub and developed (open space), i.e. country roads).

Water year 2008 was a dry year in the region relative to the long-term mean. For the smaller ($<150\,km^2$) gauged USGS watersheds in the region, long-term (1989–2008) annual mean runoff averaged 1.175 ± 0.187 (SD, $N = 8$) times the water year 2008 runoff (http://waterdata.usgs.gov/nwis/). We applied this correction factor, with uncertainty, to the stream DOC and DIC fluxes estimated from water year 2008, and an additional error of $\pm 50\%$ acknowledging the uncertainty related to using a single year of concentration measurements rather than a long-term record for flux estimation.

Leaf litter and other aerial C fluxes from forests and wetlands to surface waters. Airborne inputs of OM to lakes have been measured infrequently, but several estimates exist for northern temperate lakes in forested landscapes. For the 26 ha Crampton Lake in the NHLD, direct measurements of summer particulate C deposition were made and indicated an average influx of $5\,mg\ C\,day^{-1}\,m^{-2}$ of lake area (Preston *et al*., 2008). Also within the NHLD, an estimate of particulate organic C inputs was generated for Peter, Paul and Tuesday lakes during an experimental addition of dissolved inorganic ^{13}C. For these three small (0.8–2.7 ha) lakes during summer, modeled allochthonous particulate organic C inputs ranged from 21 to $56\,mg\ C\,day^{-1}\,m^{-2}$ of lake area (Carpenter *et al*., 2005). Making the gross assumption that summer influx rate is representative of the entire year and the particulate allocthnonous C originates from the lake shore, this translates to an annual input ranging from 143 g C per meter of shoreline (Crampton Lake) to 466 g C per meter of shoreline (Tuesday Lake). This is similar to the annual estimates for Mirror Lake, New Hampshire of 354 g C per meter of shoreline (Likens, 1985), and for Lake Wingra (southern Wisconsin) of 320 g C per meter of shoreline (Gasith & Hasler, 1976), both of which include direct measurements of autumn leaf-fall inputs. Based on these ranges we estimated an annual airborne transfer of particulate organic C from forest to lakes of 150–450 g C per meter of shoreline with upland forest. A lower annual rate (100–300 g C per meter of shoreline) was assumed for forested wetlands, based on lower tree densities and the lack of deciduous trees, while open (unforested) wetlands were assumed to contribute negligibly to aerial C flux. For airborne particulate flux from forest to streams, we assumed the same transfer rate per meter of stream length as per meter of lake shoreline, multiplied by two to account for influx from both sides of the stream. These assumed rates are on the same order as those measured in Bear Brook, a 3 m wide overcanopied headwater stream in New Hampshire [$\sim$416 $g\,C\,yr^{-1}$ per meter of shoreline (Fisher & Likens, 1973)], and Fort River, a 14 m wide fourth order stream in Massachusetts [$\sim$942 $g\,C\,yr^{-1}$ per meter of shoreline (Fisher, 1977)].

Surface water C Pools and fluxes

Upscaling approach. For estimation of two pools (lake water column C pool, lake sediment C pool) and two fluxes (lake CO_2 surface–atmosphere exchange, and lake net sediment deposition rate) a similar approach was used. First, the target variable (C pool or flux) was measured/estimated for a small group of well-studied lakes. Second, we queried this small group of lakes for simple limnological parameters that were correlated with the target variable, and could be measured with relative ease during a single summer sampling. Third, these simple empirical models were used to predict the target variable for a group of 168 survey lakes, which were a random subset of NHLD lakes stratified in 20 bins by lake area (Hanson *et al*., 2007), and sampled once during summer 2004 (details of modeling approach in Supporting Information Section S2). During that survey many limnological measurements were made, but for this study the key measurements were Secchi depth and summer epilimnion [DOC], [DIC], pH, and calculated pCO_2. Finally, the modeled values were used to calculate a mean and standard deviation for each of the 20 lake area bins, and values from the respective distributions were randomly assigned to each of the $\sim$7000 lakes in the entire NHLD to generate a regional total pool/flux estimate. This assignment process was repeated 100 times in a Monte Carlo simulation and the resulting distribution of regional means was used to describe the uncertainty (95% CI) in upscaling from the 168 lakes to the entire region.

Representativeness of the intensively studied lakes. For estimating C pools/fluxes of the 168 lakes, we used models developed on a smaller number of lakes in the region for which detailed temporal and/or sediment records exist. These were primarily seven NTL–LTER lakes (http://lter.limnology.wisc.edu/, Magnuson *et al*., 2006) for which a $>$20-year record of approximately monthly measurements exist for a wide range of limnological variables, but also included several other lakes for which dated full sediment cores have been taken. The seven NTL–LTER lakes span a broad range of area (0.5–1608 ha), pH (annual means 4.8–7.9; summer means 4.8–8.4), DOC (annual means 2–19 $mg\,L^{-1}$; summer means 2–16 $mg\,L^{-1}$), DIC (annual means 0.6–11.1 $mg\,L^{-1}$; summer means 0.5–10.1 $mg\,L^{-1}$) and pCO_2 (annual means 727–2506 μatm; summer means 273–1576 μatm), all relevant factors for lake C cycling and CO_2 surface–atmosphere exchange. For all of these parameters except pCO_2, the range of values observed in the seven LTER lakes for lake size and summer chemistry span the major part of the range observed in a survey of hundreds of randomly selected NHLD lakes (Hanson *et al*., 2007). For pCO_2, the survey included many very small humic lakes with very high pCO_2 (median

1559 μatm, maximum 15 940 μatm) not found in the LTER lakes. This suggests very high local CO_2 efflux in some lakes, likely not well predicted by our empirical modeling approach. However, because of their small area (<6% of lake area in survey for lakes with summer $pCO_2 > 1576$ μatm) the uncertain estimates of CO_2 evasion from these lakes do not substantially influence the regional CO_2 efflux estimates.

For the NTL–LTER lakes with extensive measurements available, response variables used as the starting points for upscaling were determined by the following methods (details in Supporting Information Section S3). (1) Annual CO_2 surface–atmosphere exchange was calculated (Cole & Caraco, 1998) for the seven NTL–LTER lakes from a 19-year (1989–2007) time series of approximately monthly measurements of epilimnion DIC, pH and temperature together with daily measurements of wind speed. (2) Water column C pools were estimated for the seven NTL–LTER lakes from annual means of long-term (1986–2007) monthly mean epilimnion concentrations of DOC and DIC. (3) Mean sediment accumulation rate was measured in ^{210}Pb-dated sediment cores (using the section corresponding to 5–35 years before present) from nine lakes in the region, and used to calculate net C deposition rate. (4) Sediment C storage was estimated, with correction for sediment focusing, from total sediment depth at the deepest point in the cored basin of five lakes in the NHLD for which the entire Holocene sedimentary record was available. The center core sediment depths for these five lakes ranged from 2.5 to 17 m.

Lake CH_4 emissions. We applied simple equations relating CH_4 emissions to lake area developed with lakes from the NHLD and other northern regions (Bastviken *et al*., 2004), to the distribution of lake areas found in the NHLD. This analysis predicts CH_4 emissions from lakes in the NHLD averaging 3 g CH_4 C m^{-2} (of lake area) yr^{-1}, and an uncertainty of ± 50% was assumed.

CO_2 evasion from streams. As in many regions, stream CO_2 evasion measurements have rarely been made in the NHLD, but a recent random survey found NHLD streams are consistently supersaturated with respect to CO_2 with headwaters averaging 4000–6000 μatm and larger streams averaging about 700 μatm (Lottig, 2009). An estimate of stream and river CO_2 evasion was made based on this pCO_2 survey and assuming a regional mean exchange coefficient (k_{CO_2}) value of between 1 and 4 m day^{-1} (Raymond & Cole, 2001; Jonsson *et al*., 2007; Teodoru *et al*., 2009). This evasion rate was multiplied by the total area in each of these stream size categories based on the 1 : 24 000 streams and surface water bodies maps (Wisconsin Department of Natural Resources) to give regional estimates of flux.

Anthropogenic emissions – fossil fuel combustion

Fossil fuel emissions. We derived regional fossil-fuel CO_2 emissions from the Vulcan Project gridded emissions database (Gurney *et al*., 2009). Fossil fuel emissions in this database are computed from CO_2 emissions factors applied to most fuel types in the National Emissions Inventory air pollution data in addition to vehicle miles travelled, power production, and aircraft emissions databases. The Vulcan data are provided on an hourly 10 × 10 km resolution grid for the year 2002 and we extracted annual CO_2 emissions for the NHLD region from it. Uncertainty information was not available at the time, but we conservatively estimate it at ~10%. At the national scale, emissions compare well with independent coarse scale emission databases (Department of Energy Energy Information Administration data). Additionally, while interannual variability in fossil fuel emissions are typically small, there is a steady, upward trend. As such, the estimates for 2002 are likely an overestimate for years prior and underestimate for year following. To compensate, we scaled the 2002 annual NHLD emissions against a time series of total US fossil fuel emissions for 1989–2007 (Boden *et al*., 2009).

Mean C accumulation time

The mean time required to build up the pools of C in each of the three major regional ecosystem types (forest, wetland, and lake) was estimated [Eqn (2)]. For forests and wetland, net accumulation rate was calculated by difference from all measured fluxes, while for lakes the estimated net sedimentation rate was used. For this calculation, the assumption is that the net accumulation rate has been constant over the entire period of accumulation. This is unlikely to be the case, but the resulting value still provides useful information in discriminating between slow and fast accumulating pools.

$$t_{acc} = \frac{CP}{AR}, \tag{2}$$

where t_{acc} is mean accumulation time, CP is carbon pool size, and AR is net accumulation rate.

Results

A summary of the estimated C pools and fluxes for the region as a whole and for each of the three major ecosystem types can be found in Tables 1–5 and Fig. 2. Following is a more detailed description of each pool and flux together with uncertainty estimates. Pools are expressed both as the total for the region (units of Tg C) and as a density value normalized to the respective ecosystem type (units of Kg C m^{-2}). Fluxes are expressed likewise as regional total (Gg C yr^{-1}) and local flux strength (g C m^{-2} yr^{-1}).

Pools

Forest vegetation C pool. Conifer and hardwood forests gave similar mean total biomass values and the data were pooled into a single upland forest category. Using FIA data the NHLD upland forest biomass storage was estimated at 32–35 Tg C giving an average of 9.1–10.2 kg C m^{-2} in upland forested areas, consistent with published estimates for northern Wisconsin (Turner *et al.*, 1995; Rhemtulla, 2007). The forest vegetation pool is about half aboveground tree biomass (regional mean estimate $4.9\,kg\,C\,m^{-2}$), with contributions from roots, understory vegetation, dead wood, and forest floor litter (1.0, 0.9, 1.0, and $1.9\,kg\,C\,m^{-2}$, respectively).

Wetland vegetation C pool. Using FIA data the NHLD biomass storage in forested wetlands was estimated at 10–12 Tg C giving an average of $6.2–7.6\,kg\,C\,m^{-2}$. The forested wetland vegetation pool is less than half aboveground tree biomass (regional mean $2.7\,kg\,C\,m^{-2}$), with contributions from roots, understory vegetation, dead wood, and forest floor litter (0.5, 0.7, 0.7, and $2.3\,kg\,C\,m^{-2}$, respectively). For open (nonforested) wetlands, the total NHLD vegetation biomass was estimated at 0.7 ± 0.2 Tg C based on a value of $2.6 \pm 0.9\,kg\,C\,m^{-2}$ (Elling & Knighton, 1984; Moore *et al*., 2002). This was comprised primarily of *Sphagnum* (averaging $2.2 \pm 0.9\,kg\,C\,m^{-2}$) with an additional contribution from shrubs and herbs ($0.40 \pm 0.29\,kg\,C\,m^{-2}$).

Upland forest soil C pool. Using published soil series characteristics from NRCS soils maps (NRCS, 2008), we estimated a regional soil organic C storage of 30 ± 1.3 Tg C, corresponding to a mean soil C content of $8.7 \pm 0.4\,kg\,C\,m^{-2}$. This does not include OM from very deep soil horizons ca. 1.5 m or deeper, which fall outside the scope of NRCS surveys. Histosols (wetland peat soils, ~20% of regional area) are treated separately below.

Wetland peat C pool. Upscaling using the DEM-based regression described in Buffam *et al*. (2010) gave a mean C density of $115 \pm 15\,kg\,C\,m^{-2}$ in peatlands, based on a regional mean peat depth of 2.1 ± 0.2 m (95% CI). This amounts to a total regional pool size of 144 ± 21 Tg C.

Lake dissolved C pool. We estimated a mean lake dissolved C pool of 0.05–0.06 Tg C, based on an area-weighted regional mean lake depth of 5.2 ± 0.4 m (95% CI), and area-weighted annually averaged regional mean DOC and DIC concentrations of 4.7 and $7.4\,mg\,C\,L^{-1}$, respectively.

Lake sediment C pool. We estimated a regional mean lake sediment depth of 7.5–9.9 m, corresponding to a C storage of $89–301\,kg\,C\,m^{-2}$, for a total regional pool of 74–250 Tg C. The uncertainty in sediment depth reflects of the exploration of different groups of predictor variables (Secchi depth alone or Secchi depth + lake area + max lake depth) and three different upscaling methods for mapping the five lakes with sediment depth measurements onto the summer survey dataset (see Supporting Information Section S2). The additional uncertainty in C storage reflects uncertainty in sediment OC concentration and bulk density. Uncertainty related to upscaling from the summer survey to all lakes in the region using lake area was relatively small (mean 95% CI = $6.3\,kg\,C\,m^{-2}$).

Fluxes

Regional hydrologic fluxes. Precipitation influx of C was calculated at $1.2–2.4\,g\,C\,m^{-2}\,yr^{-1}$, and regional riverine outflow at $4–7\,g\,C\,m^{-2}\,yr^{-1}$. These correspond to regional totals of 8–15 and $23–45\,Gg\,C\,yr^{-1}$, respectively.

Forest surface–atmosphere fluxes. All forest types had a net uptake of CO_2, with mean annual net ecosystem exchange (NEE) estimated at $-116 \pm 50\,g\,C\,m^{-2}\,yr^{-1}$ for hardwood forests (25% of regional area), $-976 \pm 23\,g\,C\,m^{-2}\,yr^{-1}$ for conifer forests (7% of regional area), and $-247 \pm 29\,g\,C\,m^{-2}\,yr^{-1}$ for mixed forests (20% of regional area). The mean area-weighted respiration for all forests of the region was $648 \pm 18\,g\,C\,m^{-2}\,yr^{-1}$, and the mean gross primary production was $936 \pm 33\,g\,C\,m^{-2}\,yr^{-1}$, giving rise to a regional mean upland forest NEE of $-288 \pm 27\,g\,C\,m^{-2}\,yr^{-1}$. This corresponds to a regional total uptake of $994 \pm 94\,Gg\,C\,yr^{-1}$. Errors represent ecosystem model uncertainty (see Supporting Information Section S1).

Wetland surface–atmosphere fluxes. Wetlands had a net uptake of CO_2, with mean annual NEE estimated at $-65 \pm 11\,g\,C\,m^{-2}\,yr^{-1}$ for forested wetlands (23% of regional area) and $-89 \pm 37\,g\,C\,m^{-2}\,yr^{-1}$ for open wetlands (4% of regional area). The mean area-weighted respiration for all wetlands of the region was $-421 \pm 42\,g\,C\,m^{-2}\,yr^{-1}$, and the mean gross primary production was $490 \pm 23\,g\,C\,m^{-2}\,yr^{-1}$, giving rise to a regional mean wetland NEE of $-69 \pm 33\,g\,C\,m^{-2}\,yr^{-1}$. This corresponds to a regional total uptake of $124 \pm 59\,Gg\,C\,yr^{-1}$. Errors represent ecosystem model uncertainty (see Supporting Information Section S1).

Wetland CH_4 emissions. Based on a range of $1–20\,g\,C\,m^{-2}\,yr^{-1}$ in peat-containing wetlands, a total wetland CH_4 emission of $1–25\,Gg\,C\,yr^{-1}$ was estimated for the NHLD. The range reflects acknowledged uncertainty in the use of literature values for northern peatlands.

Lake surface–atmosphere CO_2 exchange. We estimated a regional lake surface CO_2 emission ranging from 25 to $39\,g\,C\,m^{-2}\,yr^{-1}$, for a regional total of $21–32\,Gg\,C\,yr^{-1}$. This net emission resulted from an annual mean gross

Table 1 Estimated C storage in different pools in the NHLD

Pool	Landscape	Areal coverage, km^2 (% of region)	Local pool density, best estimate (range) ($kg\,C\,m^{-2}$)	Regional pool size, best estimate (range) (Tg C)
Forest vegetation	Forest	3454 (54%)	9.7 (9.1–10.2)	33 (32–35)
Aboveground biomass	Forest	3454 (54%)	4.9 (4.4–5.4)	17 (15–19)
Roots	Forest	3454 (54%)	1.0 (0.9–1.1)	3.4 (3.0–3.7)
Understory vegetation	Forest	3454 (54%)	0.9 (0.8–1.0)	3.1 (2.8–3.4)
Dead wood	Forest	3454 (54%)	1.0 (0.9–1.1)	3.5 (3.1–3.8)
Forest floor (litter)	Forest	3454 (54%)	1.9 (1.7–2.1)	6.6 (5.9–7.2)
Forest soils	Forest	3454 (54%)	8.7 (8.3–9.1)	30 (29–31)
Wetland vegetation	Wetlands	1791 (28%)	6.3 (5.7–6.9)	11 (10–12)
Forested wetland vegetation	Forested wetlands	1535 (24%)	6.9 (6.2–7.6)	11 (10–12)
Open wetland vegetation	Open wetlands	256 (4%)	2.6 (1.7–3.5)	0.7 (0.4–0.9)
Peat	Peatlands	1279 (20%)	115 (100–130)	144 (123–165)
Lake water column DOC + DIC	Lake	832 (13%)	0.06 (0.06–0.07)	0.05 (0.05–0.06)
Lake sediments	Lake	832 (13%)	195 (89–301)	162 (74–250)
Whole region	Region	6397 (100%)		426 (336–516)

NHLD, Northern Highlands Lake District; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon.

Table 2 Estimated C fluxes into and out of the NHLD region

Regional fluxes	Landscape	Areal coverage, km^2 (% of region)	Local flux, best estimate (range) ($g\,C\,m^{-2}\,yr^{-1}$)	Total flux, best estimate (range) ($Gg\,C\,yr^{-1}$)
Forest NEE (in)	Forest	3454 (54%)	288 (261–315)	994 (900–1089)
Wetland NEE (in)	Wetland	1791 (28%)	69 (36–102)	124 (64–183)
Precipitation inputs	Region	6397 (100%)	1.8 (1.2–2.4)	12 (8–15)
Regional riverine runoff	Region	6397 (100%)	5 (4–7)	34 (23–45)
Lake CO_2 evasion	Lake	832 (13%)	32 (25–39)	27 (21–32)
Stream CO_2 evasion	Streams	29 (0.5%)	47 (10–84)	1.4 (0.3–2.4)
Lake CH4 emissions	Lake	832 (13%)	3 (1–4)	2.2 (1.1–3.3)
Wetland CH4 emissions	Peatland	1279 (20%)	10 (1–20)	13 (1–25)
Net accumulation*	Region	6397 (100%)		1053 (940–1165)
Fossil fuel emissions	Region	6397 (100%)	24 (22–26)	154 (138–169)

*Calculated as the sum of all regional fluxes except fossil fuel emissions.
NHLD, Northern Highlands Lake District; NEE, net ecosystem exchange.

efflux of 26–39 $g\,C\,m^{-2}\,yr^{-1}$ during periods of supersaturation, and mean gross influx of 0.6–1.4 $g\,C\,m^{-2}\,yr^{-1}$ during periods of undersaturation (midlate summer in some lakes). The range reflects results from the use of different groups of variables and three different upscaling methods for mapping the long-term LTER lakes dataset onto the summer survey dataset (Supporting Information Section S2). Uncertainty related to upscaling from the summer survey to all lakes in the region using lake area was relatively small (mean 95% CI = 1.3 $g\,C\,m^{-2}\,yr^{-1}$).

Stream CO_2 emissions. Stream CO_2 emission was estimated to be a locally substantial efflux at 80–330 $g\,C\,m^{-2}$ (of stream area) yr^{-1} for headwater (first and second order) streams, and 5–20 $g\,C\,m^{-2}\,yr^{-1}$ for larger streams and rivers. Because of the small area (about 0.1% of the landscape for headwater streams, and 0.4% for larger streams and rivers), the estimated total stream CO_2 evasion flux (1.4 ± 1.1 $Gg\,C\,yr^{-1}$) is about an order of magnitude smaller than the other major regional surface-water fluxes (runoff and lake CO_2 evasion).

Lake CH_4 emissions. A total lake CH_4 emission of 1.1–3.3 $Gg\,C\,yr^{-1}$ was estimated for the NHLD, which translates to an average emission of 1–4 $g\,C\,m^{-2}$ (of lake area) yr^{-1}. The range reflects uncertainty in the relationship between lake area and CH_4 emission generated for lakes of the region (Bastviken *et al*., 2004).

Table 3 Estimated C fluxes into and out of the upland forest areas of the NHLD

Forest fluxes	Landscape	Areal coverage, km^2 (% of region)	Local Flux, best estimate (range) ($g\,C\,m^{-2}\,yr^{-1}$)	Total Flux, best estimate (range) ($Gg\,C\,yr^{-1}$)
Forest NEE (in)	Forest	3454 (54%)	288 (261–315)	994 (900–1089)
Forest GPP	Forest	3454 (54%)	936 (903–969)	3233 (3119–3347)
Forest respiration	Forest	3454 (54%)	648 (630–666)	2238 (2176–2301)
Precipitation Inputs	Forest	3454 (54%)	1.8 (1.2–2.4)	6.2 (4.1–8.3)
Forest runoff	Forest	3454 (54%)	7 (3–11)	24 (10–37)
Forest DOC runoff	Forest	3454 (54%)	4.0 (1.5–6.6)	14 (5–23)
Forest DIC runoff	Forest	3454 (54%)	3.0 (1.3–4.8)	10 (4–17)
Leaf litter forests to surface waters	Forest–surface water interface	7805 km*	300 (150–450)†	2.3 (1.2–3.5)
Leaf litter forests to lakes	Forest–lake interface	4583 km*	300 (150–450)†	1.4 (0.7–2.1)
Leaf litter forests to streams	Forest–stream interface	3222 km*	300 (150–450)†	1.0 (0.5–1.4)
Net accumulation	Forest	3454 (54%)		968 (873–1063)

*Length of shoreline.
†Units of $g\,C\,m^{-1}$ of shoreline yr^{-1}.
NHLD, Northern Highlands Lake District; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; NEE, net ecosystem exchange; GPP, gross primary production.

Table 4 Estimated C fluxes into and out of the wetland areas of the NHLD

Wetland fluxes	Landscape	Areal coverage, km^2 (% of region)	Local flux, best estimate (range) ($g\,C\,m^{-2}\,yr^{-1}$)	Total flux, best estimate (range) ($Gg\,C\,yr^{-1}$)
Wetland NEE (in)	Wetland	1791 (28%)	69 (36–102)	124 (64–183)
Wetland GPP	Wetland	1791 (28%)	490 (467–513)	878 (836–919)
Wetland respiration	Wetland	1791 (28%)	421 (379–463)	754 (679–829)
Precipitation inputs	Wetland	1791 (28%)	1.8 (1.2–2.4)	3.2 (2.1–4.3)
Wetland runoff	Wetland	1791 (28%)	12 (3–20)	21 (5–37)
Wetland DOC runoff	Wetland	1791 (28%)	11 (2–20)	20 (4–35)
Wetland DIC runoff	Wetland	1791 (28%)	0.6 (−1.2–2.3)	1.0 (−2.2–4.2)
Leaf litter wetlands (forested) to surface waters	Wetland–surface water interface	3469 km*	200 (100–300)†	0.7 (0.3–1.0)
Leaf litter wetland (forested) to lakes	Wetland–lake interface	2037 km*	200 (100–300)†	0.4 (0.2–0.6)
Leaf litter wetland (forested) to streams	Wetland–stream interface	1432 km*	200 (100–300)†	0.3 (0.1–0.4)
Wetland CH4 emissions	Peatland	1279 (20%)	10 (1–20)	13 (1–25)
Net accumulation	Wetland	1791 (28%)		89 (27–152)

*Length of shoreline.
†Units of $g\,C\,m^{-1}$ of shoreline yr^{-1}.
NHLD, Northern Highlands Lake District; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; NEE, net ecosystem exchange; GPP, gross primary production.

Lake sedimentation rates. We estimated a mean regional lake sedimentation rate ranging from 14 to $39\,g\,C\,m^{-2}\,yr^{-1}$, for a regional total of 12–33 $Gg\,C\,yr^{-1}$. The range reflects results from the use of different groups of variables and three different upscaling methods for mapping the 9 lakes with deposition rate measurements onto the summer survey dataset (Supporting Information Section S2), as well as large uncertainty in sediment focusing ratio (Supporting Information Section S3, see also Lehman, 1975; Davis & Ford, 1982).

Hydrologic export from forests and wetlands to surface waters. We calculated a total dissolved C stream hydrologic export of $6.9 \pm 3.9\,g\,C\,m^{-2}\,yr^{-1}$ (±95% CI) for forested catchments, and $11.6 \pm 8.9\,g\,C\,m^{-2}\,yr^{-1}$ (±95% CI) for wetland catchments. For forests, stream DOC and DIC export are comparable with DOC making

Table 5 Estimated C fluxes into and out of the surface waters of the NHLD

Surface water fluxes	Landscape	Areal coverage, km^2 (% of region)	Local flux, best estimate (range) ($g\,C\,m^{-2}\,yr^{-1}$)	Total flux, best estimate (range) ($Gg\,C\,yr^{-1}$)
Precipitation inputs	Lakes + streams	861 (13.5%)	1.8 (1.2–2.4)	1.5 (1.0–2.0)
Forest runoff (in)	Lakes + streams	861 (13.5%)	28 (12–43)	24 (10–37)
Forest DOC runoff	Lakes + streams	861 (13.5%)	16 (6–26)	14 (5–23)
Forest DIC runoff	Lakes + streams	861 (13.5%)	12 (5–19)	10 (4–17)
Wetland runoff (in)	Lakes + streams	861 (13.5%)	24 (6–43)	21 (5–37)
Wetland DOC runoff	Lakes + streams	861 (13.5%)	23 (5–41)	20 (4–35)
Wetland DIC runoff	Lakes + streams	861 (13.5%)	1 (−3–5)	1 (−2–4)
Leaf litter forests to surface waters	Forest–surface water interface	7805 km*	300 (150–450)†	2.3 (1.2–3.5)
Leaf litter forests to lakes	Forest–lake interface	4583 km*	300 (150–450)†	1.4 (0.7–2.1)
Leaf litter forests to streams	Forest–stream interface	3222 km*	300 (150–450)†	1.0 (0.5–1.4)
Leaf litter wetlands (forested) to surface waters	Wetland–surface water interface	3469 km*	200 (100–300)†	0.7 (0.3–1.0)
Leaf litter wetland (forested) to lakes	Wetland–lake interface	2037 km*	200 (100–300)†	0.4 (0.2–0.6)
Leaf litter wetland (forested) to streams	Wetland–stream interface	1432 km*	200 (100–300)†	0.3 (0.1–0.4)
Surface water CO_2 evasion	Lakes + streams	861 (13.5%)	33 (26–39)	28 (22–34)
Lake CO_2 evasion	Lake	832 (13%)	32 (25–39)	27 (21–32)
Stream CO_2 evasion	Streams	29 (0.5%)	47 (10–84)	1.4 (0.3–2.4)
Lake CH4 emissions	Lake	832 (13%)	3 (1–4)	2.2 (1.1–3.3)
Regional riverine runoff (out)	Region	6397 (100%)	5 (4–7)	34 (23–45)
Net accumulation‡	Lake	832 (13%)		−15 (−40–9)
Sediment deposition	Lake	832 (13%)	20 (9–31)	17 (8–26)

*Length of shoreline.
†Units of $g\,C\,m^{-1}$ of shoreline yr^{-1}.
‡Calculated as the sum of all surface water fluxes except for sediment deposition, and assumed to accumulate in lakes only.
NHLD, Northern Highlands Lake District; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon.

up 57% of the total, while in wetlands DOC export makes up 95% of the total. When scaled up to the region, these amount to a lateral hydrologic export of $24 \pm 13\,Gg\,C\,yr^{-1}$ from forests, and $21 \pm 16\,Gg\,C\,yr^{-1}$ from wetlands.

Leaf litter and other aerial C fluxes from forests and wetlands to surface waters. In the NHLD there are a total of ~5000 lakes with a total shoreline of 7383 km, giving rise to an estimated airborne particulate transfer of 0.7–2.1 $Gg\,C\,yr^{-1}$ from upland forests to lakes, and 0.20–0.61 $Gg\,C\,yr^{-1}$ from forested wetlands to lakes. There are a total of 2595 km of stream and river length (DNR 1:24 000 map) giving rise to an estimated airborne particulate transfer of 0.5–1.5 $Gg\,yr^{-1}$ from upland forests to streams, and 0.15–0.47 $Gg\,C\,yr^{-1}$ from forested wetlands to streams.

Fossil fuel emissions. Measured regional fossil fuel emissions were $26\,g\,C\,m^{-2}\,yr^{-1}$ during 2002 (Gurney *et al.*, 2009), with an estimated average of $24 \pm 2.4\,g\,C\,m^{-2}\,yr^{-1}$ for the 20-year period of interest. This gives a total regional efflux of $154 \pm 15\,Gg\,C\,yr^{-1}$. Note that this represents local combustion of fossil fuels and does not account for transport of fossil fuels into the region, nor for local energy use derived from fossil fuel combustion outside the region.

Budget summary and mean C accumulation times

Combining all of the pools and fluxes into one framework (Tables 1 and 2, Fig. 2), it becomes apparent that peat and lake sediments are far and away the largest C pools in the NHLD, with best estimates of 144 ± 21 and 162 ± 88 Tg C, respectively. Upland soils (30 ± 1 Tg C) and forest biomass (33 ± 2 Tg C) are a much smaller component of the regional C storage in spite of covering >50% of the area. The total regional pool is estimated at 426 ± 90 Tg C. The calculated regional flux is $1.1 \pm 0.1\,Tg\,C\,yr^{-1}$ into the NHLD (i.e., C sink), with the flux ordering for the three main landcover types roughly inverse that of the pools (Fig. 2, Tables 1 and 2). Upland forest NEE is by far the largest net flux at $994 \pm 94\,Gg\,C\,yr^{-1}$ from the atmosphere into the forests. Wetland NEE contributes about 10% of the regional total exchange due to lower NEE and lower areal cover-

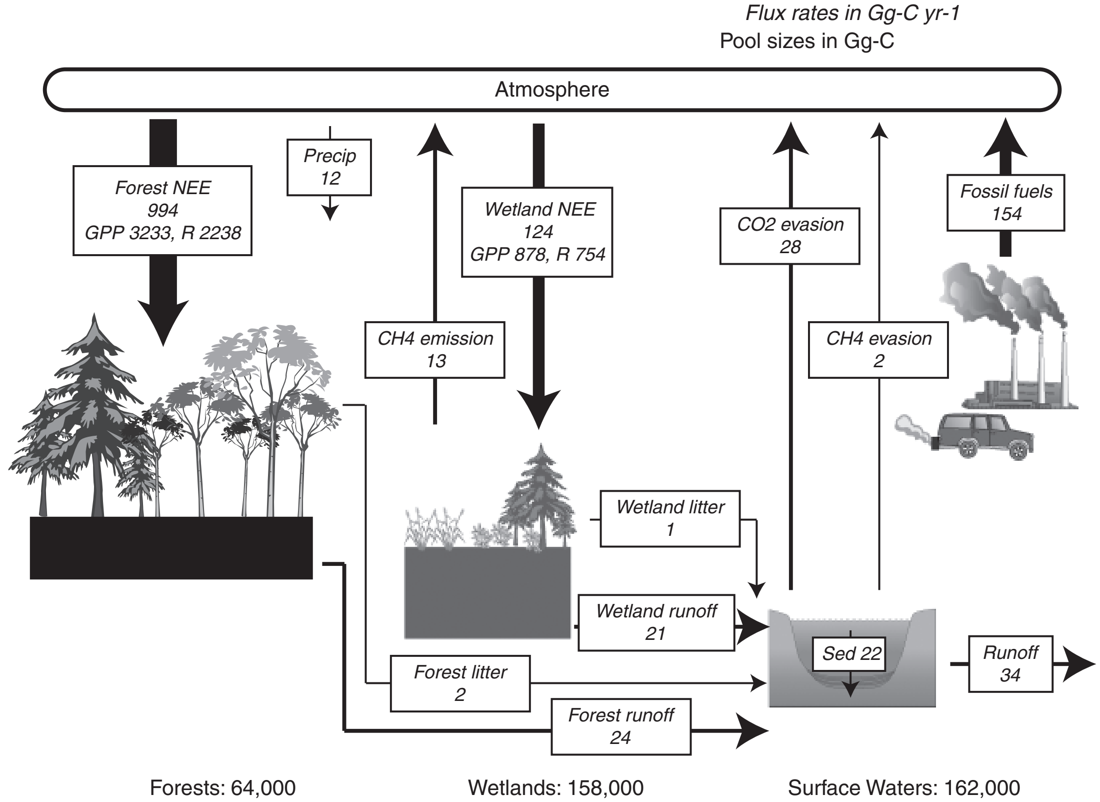

Fig. 2 Schematic showing the three major ecosystem types of the Northern Highlands Lake District (NHLD), along with best estimates of C flux rates and pool sizes. These estimates are associated with varying degrees of uncertainty (Tables 1–5). Forests make up 54% of the NHLD area, wetlands 28% (including 20% peatlands and 8% other wetlands), and lakes 13%. NEE, net ecosystem exchange; GPP, gross primary production; R, respiration.

age of wetlands relative to upland forests (Table 2). Lake CO_2 evasion contributes about 3% of the regional total net exchange. Precipitation flux into and hydrologic flux out of the NHLD are on the order of 1% and 3%, respectively, of the regional total net exchange.

The mismatch between pool sizes and current rates points to widely disparate mean C turnover times among wetlands, lakes, and forests of the region. Assuming current rates are representative of long-term rates, the estimated average time required to build up each major regional C pool was 65 years for forest, 1775 years for peat wetlands, and 7364 years for lake sediments.

Spatial distribution of C pools and fluxes on the landscape

Pools and fluxes of C were spatially heterogeneous at a range of spatial scales in the NHLD landscape. The most dense pools of C were peat in peatlands and sediments in lakes (Fig. 3b). Patches of relatively young coniferous forest gave by far the greatest local rates of influx of C into the land surface, while lakes gave rise to patches of C evasion, with smaller lakes having the highest evasion rates (Fig. 3c).

Discussion

Implications of magnitude and spatial variability of C pools and fluxes

By constructing a C budget we incorporated surface freshwaters, wetlands, and upland forests into a single framework. This framework establishes a context for C cycling research in this and other surface-water rich regions. An integrated view like this is needed to target research and management strategies in a parsimonious way.

We determined that the largest current-day annual land–atmosphere fluxes in the NHLD region are found in forests, which are aggrading. This rate is an order of magnitude higher than surface–atmosphere exchange in wetlands or surface waters (Fig. 2, Table 2). Thus the current behavior of the NHLD in terms of annual C

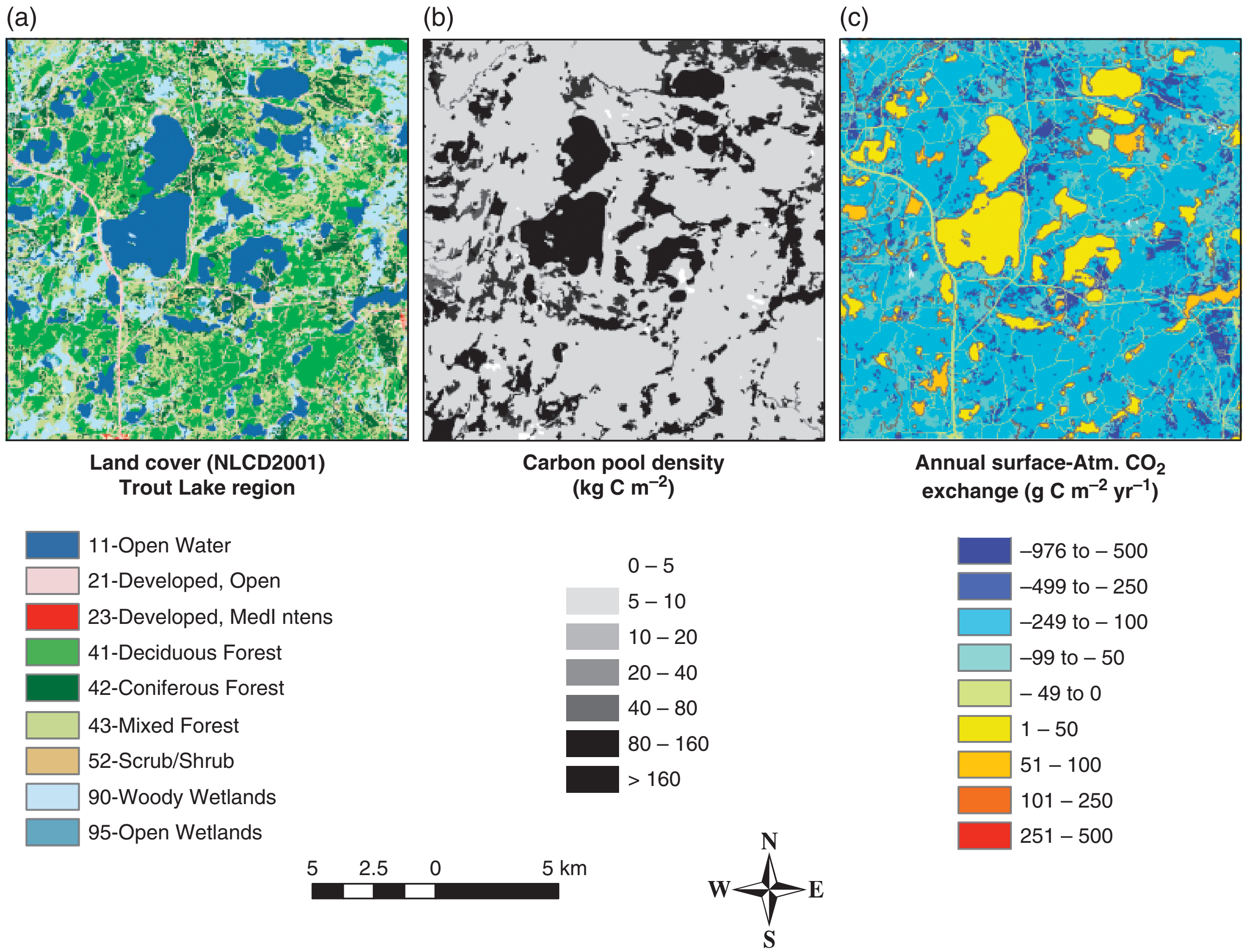

Fig. 3 Illustration of spatial variation of carbon pools and fluxes on the landscape, for an 18 × 18 km region around the Trout Lake Field Station. (a) Land cover. (b) Pool sizes were assigned by summing the soil/sediment C and vegetation C at a given location. This was achieved by combining the NRCS soils map for mineral soils and histosols (peatlands), the lakes map with modeled sediment pools, and the forest vegetation C pool using average values for each of three regional forest types from the USFS–FIA database. (c) Average annual surface–atmosphere fluxes are visualized by assigning the average value to each terrestrial 30 × 30 m pixel in the NLCD map according to category, while lake fluxes were assigned at random from the distribution of values for each lake size category as described in the text. The seven LTER lakes were assigned their measured long-term mean annual flux values. Positive values, flux into atmosphere; negative values, flux into land surface.

exchange can be roughly approximated by the behavior of the forests. In the short-term, management for increased forest productivity would increase the regional C sequestration. However, the largest C pools in the region are found in longer-term storage of peat and lake sediments (Fig. 2, Table 1). The disconnect between current rates and pool sizes implies very different turnover times in the different C pools within the region. Lake sediments and peatlands have accumulated over millennia, whereas most of the C in forests has accumulated during the past century as secondary succession followed large-scale deforestation for timber. These C accumulation rates will decrease as the forests approach climax, if they are allowed to do so. Otherwise, disturbances like fire or logging may again release C and reset the forest pool, though in the case of forest harvest, the fate of the wood must be considered (White *et al*., 2005). For long-term C sequestration, preservation of the peat and lake sediment pools may be more critical than encouraging forest growth.

Because peat and particularly lake sediments are long-term pools and much more stable than forest C, they are a critical component of the regional C picture. In our study, peat in peatlands was a major C store as expected (Buffam *et al*., 2010), but lake sediments were a similarly large, and more uncertain pool. In other North American regions with glacially formed lakes, mean lake sediment organic C accumulation rates vary from

15 to about $30\,g\,C\,m^{-2}\,yr^{-1}$ (Mulholland & Elwood, 1982; Dean & Gorham, 1998; Campbell *et al.*, 2000), i.e., about 150–300 $kg\,C\,m^{-2}$ assuming an average accumulation period of 10 000 years for the Holocene. Our estimate of $195 \pm 106\,kg\,C\,m^{-2}$ is uncertain but falls within this range, suggesting that the NHLD has similar long-term sedimentation rates and total pool sizes as other North American glacially-formed regions. Because of the high (13%) areal coverage of lakes in the NHLD, this C pool is on the same order as that of C in peat. Together, these two pools make up over 80% of the regional C store.

The patchwork of surface waters emitting CO_2 in the midst of a terrestrial landscape absorbing CO_2 implies connectivity between the terrestrial and aquatic systems. Since lakes are on balance accumulating sediment C as well, there is no internal source of C which could maintain the observed widespread lake and stream supersaturation in CO_2 (Cole *et al.*, 1994; Algesten *et al.*, 2004; Teodoru *et al.*, 2009; Wallin *et al.*, 2010). Thus, an allochthonous, terrestrial source of C is implicated for the surface waters in the NHLD and other similar systems. This source could be either organic C, which is subsequently mineralized in-lake, or direct inputs of inorganic C in groundwater, and likely includes both. The magnitude of C loading from uplands and wetlands to surface waters of the NHLD, and the strength and spatial extent of that connection has still not been well established. Connectivity may depend in large part on stream networks, which have not been as well studied as lakes in the region. New measurements in a random survey of streams across the region demonstrate a wide range of DOC and DIC concentrations up to 63 and 24 $mg\,L^{-1}$, respectively (Lottig, 2009), suggesting that streams may provide important conduits to lakes. Stream DOC concentration is positively correlated with wetland percentage (Gergel *et al.*, 1999; Lottig, 2009), demonstrating the coupling between watersheds and streams in the region.

The spatial heterogeneity in C density and surface–atmosphere flux throughout the landscape (Fig. 3) may be significant for some lateral fluxes of C. Although hydrologic and aolian transport of C from upland/wetland ecosystems into surface waters is quantitatively small on a regional basis relative to forest NEE, lake and stream ecosystems depend upon this linkage for their C cycling and metabolic activity (Fisher & Likens, 1973; Carpenter *et al.*, 2005). Much of the energy flow in surface waters depends ultimately on terrestrial C, thus changes in terrestrial systems may also alter aquatic C cycling and ecosystems. The spatial configuration of local C sources may thus be important. Spatial interactions among landscape components, which were not addressed in our analysis, could also create important feedbacks that could amplify or suppress fluxes from certain landscape components. Heterogeneity in forest patches, for instance, gives rise to heterogeneity in local air temperature regime which may feed back to influence local C accumulation rates (Robinson *et al.*, 2009). The importance of spatial heterogeneity for biogeochemical fluxes is still not well understood (Strayer *et al.*, 2003; Lovett *et al.*, 2005) and future research is needed to address these interactions.

While a thorough discussion of fossil fuel emissions is beyond the scope of this paper, we included estimates of such here for comparison and for inclusion within a complete atmospheric budget. Unlike biosphere-atmosphere fluxes, fossil fuel emissions are almost entirely produced by subsidy of external C (fossil fuels extracted outside the region such as automobile gasoline) that are then combusted locally. Consequently, they mostly do not directly impact local pools and fluxes of C. However, from the perspective of what the atmosphere senses (i.e., for tracer–transport inverse models), local emissions need to be considered. The low population density of the NHLD region gave rise to fossil fuel emissions that are relatively low, at least in comparison to the global scale where net fossil fuel CO_2 emissions are nearly four times the size of the biosphere net C sink (Houghton, 2007). Consequently, from the atmospheric perspective, the NHLD region is still a CO_2 sink even when fossil fuel emissions are considered. However, in terms of net fluxes, fossil fuel emissions are the second largest regional surface–atmosphere flux term after forest NEE, and unlike forest NEE, this term is likely to continue to increase with time at least in the near future (IPCC, 2007). Consideration of combustion elsewhere used to provide energy locally was not considered here, but is arguably a similarly large term that is relevant at least from a C management policy perspective.

Remaining sources of uncertainty

Substantial uncertainties and potential systematic errors remain in many components of the NHLD C budget, and these uncertainties highlight remaining critical knowledge gaps in this and other regions. Among the important pools, forest biomass and soil pool estimates are known from extensive datasets, many at a national scale. In the NHLD, the peat pool size is well constrained only because of a recent survey targeting regional mean peat depth (Buffam *et al.*, 2010). The largest uncertainty in this and many other lake-rich regions is storage in lake sediments. The uncertainty in lake sediment storage is related to uncertainty in maximum sediment depth, in mean/maximum depth ratio, and in mean C content of the sediment. In particular, there is a lack of generalizeable knowledge about the mean/maximum sediment depth ratio, which is related to the focusing of sediments in deeper areas of lakes (Lehman, 1975; Davis & Ford, 1982). For an individual lake, one should not expect to accurately predict mean depth from maximum depth or any single core (Davis & Ford, 1982), and even at a regional scale we estimate high uncertainty in this relationship. Technological advances in surveying techniques with for example ground-penetrating radar surveys of sediment depth possible from boats (J. A. Rusak, unpublished results, Buynevich & Fitzgerald, 2003) suggests hope for an increase in information on lake-wide sediment depth distributions. This would help greatly in reducing uncertainty in total sediment C storage.

Among the important fluxes, all groups still have substantial uncertainty, with the primary cause being relatively low numbers of sites with consistent measurements over multiple years. Interannual variability can be considerable (Hanson *et al*., 2006; Magnuson *et al*., 2006; Desai *et al*., 2010), thus short time periods are not adequate to characterize current rates, much less long-term responses to gradual environmental change. Ideally, long-term records would be obtained from a large random sample, but practical constraints may limit this approach. In the case of the NHLD, excellent long-term records are available for NTL–LTER lakes, which cover the regional range of values in several parameters relevant to C cycling. Nonetheless the small number of sites with long-term flux measurements has presented the greatest challenge to the upscaling exercise presented in this paper. This is also the most difficult to quantify and probably the largest source of uncertainty in upscaling to the region.

In moving forward, we recommend additional flux measurements in wetlands and reservoirs, for which there are currently few. These are crucial for understanding of landscape scale C cycling in the long term. The wetland fluxes in the NHLD were poorly constrained, despite being an important contributor to regional C exchange. They are also almost within the error range of being in balance with the atmosphere, due to high uncertainty in NEE, methane emissions, and hydrologic exports to surface waters. Research detailing complete annual hydrologic export of C, both surface and subsurface, from a range of wetland types is a clear need for the near future. Reservoirs make up about 1.6% of the regional area and for the purposes of this regional C budget we have assumed they behave as natural lakes of similar size. Studies of C cycling in reservoirs are rare relative to studies of natural lakes, but a recent review found CO_2 emissions in temperate reservoirs averaging about double those of natural lakes, and typically declining with age of the reservoir to reach a value near that of natural lakes after some decades (St Louis *et al*., 2000). Sediment C burial rates in reservoirs have been estimated at about an order of magnitude higher than those in natural lakes on a per area basis (Mulholland & Elwood, 1982; Dean & Gorham, 1998), but the fate of that buried C is not well known on timescales longer than a few decades, as it depends on the fate of the dam and reservoir (Cole *et al*., 2007).

One of the greatest sources of uncertainty in the surface water budget is the limited information on riverine C export from the region, in particular for DIC. Further, literature values of this riverine flux are limited and extremely variable. For example, DIC loads have been reported to be smaller than (Clair *et al*., 1994), greater than (Baker *et al*., 2008), or about the same (Hope *et al*., 1994) as DOC among different world regions. Limited available data for DOC adds additional uncertainty to C loss estimates from the NHLD. DOC concentrations and fluxes have been quantified in many streams and rivers throughout the world, and statistical models to estimate riverine export within and among regions are often strong (e.g., Aitkenhead & McDowell, 2000; Mulholland, 2003). However, there is also a wide range of DOC yields within and among regions. Aitkenhead & McDowell (2000) report the following averages based on an extensive literature review: peat/boreal mix $6\,g\,C\,m^{-2}\,yr^{-1}$, and northern mixed forest $5.2\,g\,C\,m^{-2}\,yr^{-1}$. These averages are similar to our estimated rate of $4–7\,g\,C\,m^{-2}\,yr^{-1}$ for *all* C fractions, of which half is DOC (Table 2).

The surface–atmosphere NEE fluxes estimated for forests and wetlands from the IFUSE approach used herein are sensitive to choice of flux towers used in model calibration and representativeness of these flux towers to the mean NEE for each land cover. A comparison of regional fluxes computed from IFUSE against three other independent regional flux estimates in a nearby region (Desai *et al*., 2010) shows that the IFUSE typically predicts more uptake (larger negative NEE) than methods based on inventory approaches or tracer–transport budgets and inversions, though often within the uncertainty bounds of each method. Further analysis has suggested that the mature hardwood forest flux towers used in the upscaling may not be representative of the range of variability in forest structure and C fluxes found in these kinds of forests (Desai *et al*., 2007). A more thorough investigation of C fluxes in other kinds of mature productive forests (e.g., mature aspen) is warranted. Forest inventory approaches for the Northern Highlands regions suggest a mean NEE that is smaller (less uptake) than the IFUSE, but still a significant sink in forests. It is also likely that the three wetland towers used to estimate wetland NEE (Supporting Information Section S1) are not sufficient to cover the range of fluxes found, given the large range in wetland vegetation types and the substantial C stocks in these systems across the region (Buffam et al., 2010).

Importance of accounting for surface waters in this and other regions

The C export from terrestrial ecosystems to surface waters in the NHLD ($\sim$16 g C m^{-2} land area yr^{-1}) is similar to the recently estimated global mean. The magnitude of the flux of C from terrestrial ecosystems to surface waters is not well constrained, but recent global estimates have ranged from 1.9 to 2.9 Pg C yr^{-1} (Cole et al., 2007; Battin et al., 2009; Tranvik et al., 2009), equivalent to 13–19 g C m^{-2} yr^{-1} averaged over the land surface of the earth. The fate of C upon reaching surface waters in the NHLD (34% CO_2 emissions, 27% sedimentation, 39% hydrologic export) was also in the same range as that estimated for the globe (44% CO_2 emissions, 22% sedimentation, 33% hydrologic export) (Battin et al., 2009).

In this region, the terrestrial C accumulation would be overestimated by $\sim$7% if export to surface waters was not included in the budget. Although this number may seem small, it is significant because it represents a persistent bias. Because surface waters almost invariably serve to remove/receive C from their terrestrial watersheds, any C budget that does not account for that loss will overestimate terrestrial C accumulation. In this study and two others of similar scale in the boreal and sub-arctic (Table 6), C export to surface waters varied only by a factor of two, while terrestrial NEE varied by over an order of magnitude (Christensen et al., 2007; Jonsson et al., 2007). The among-region variation in the proportional contribution of surface waters to regional C budgets is thus driven primarily by variation in terrestrial NEE, as opposed to variation in export of C to surface waters – and the NHLD, with growing secondary forest, has a relatively high NEE. At the global scale, recent estimates of C export to surface waters are similar to the total land accumulation rate ($\sim$2.2 Pg C yr^{-1}), thus at that scale terrestrial C accumulation would be overestimated by about 40–60% if the calculation was made by upscaling of local land–atmosphere exchange without taking into account C export to surface waters (Table 6, Battin et al., 2009).

Although there are few studies for comparison at the regional scale, we do not find evidence that the proportion of the landscape occupied by lakes is strongly correlated with total C export to surface waters, per unit area of land (Table 6). However, the ultimate fate of the exported C varies widely between systems dominated by lakes vs. systems dominated by riverine networks. With a high proportion of lakes in the landscape, C storage in sediment is a common pathway for C exported to surface waters (This study, Christensen et al., 2007) while in a stream-dominated landscape, hydrologic export of C is more important (Jonsson et al., 2007). In both lake-rich and lake-poor landscapes, CO_2 evasion to the atmosphere is another substantial fate of C exported to surface waters (This study, Christensen et al., 2007; Jonsson et al., 2007). The CO_2 evasion derives both from efflux of inorganic C from groundwater (surface waters as chimneys) and from the respiration of terrestrial organic C (surface waters as

Table 6 Comparison of the role of surface waters in C cycling for three studies featuring complete regional C budgets including surface waters, and an estimate for the globe

Biome	Subarctic Sweden	Boreal Sweden	North temperate WI, USA	Global land area
Study	Christensen et al. (2007)	Jonsson et al. (2007)	This study	Battin et al. (2009)
Area (km^2)	3955	3025	6400	1.5×10^8
% lakes by area	14	4	13	$\sim$3
Aquatic processing (gC m^{-2} yr^{-1})				
CO_2 efflux from lakes/streams	2.0	4.5	5.3 (4.2–6.5)	8
Hydrologic export	2.4	4.5	6.5 (4.4–8.6)	6
Sedimentation in lakes	2.3	0	4.2 (2.3–6.3)	4
Total	7	9	16 (13–19)	18
Terrestrial NEE (g C m^{-2} yr^{-1})*	15	139	213	30
Potential bias in NEE estimate (%)†	44	6	7 (6–9)	60

All fluxes are normalized to area of terrestrial watershed (i.e., not including lake area) for direct comparison with area-normalized terrestrial NEE. For the current study, best estimate and range are included.
*Includes uplands and wetlands.
†If surface waters are ignored in regional C budget.
NEE, net ecosystem exchange.

reactors) (Cardille *et al*., 2007; Cole *et al*., 2007). Because of the longer residence time in lakes as compared with river networks, it is likely that total in-system respiration of allochthonous organic material is higher in lakes, producing CO_2 and sponsoring much of lake CO_2 evasion. That terrestrial organic C is a source for lake respiration is supported by the positive correlation between lake DOC concentrations and CO_2 evasion in northern lakes (Algesten *et al*., 2004; Sobek *et al*., 2007). Whole-lake additions of ^{13}C also reveal substantial allochthonous subsidies of in-lake secondary production (Pace *et al*., 2004; Carpenter *et al*., 2005). Streams in contrast have short residence times and low surface areas but are often turbulent, thus providing loci for rapid evasion of terrestrially derived CO_2 (Billett *et al*., 2004). With both lakes and streams, the CO_2 loss should rightly be considered terrestrial C export (e.g., Kling *et al*., 1991), but would not typically be measured in traditional terrestrial NEE studies.

Summary

Ongoing changes in climate and biogeochemistry of C are important for understanding the earth system and for assessing options for managing the C cycle to mitigate climate change. However, the heterogeneity of C sinks and fluxes on complex landscapes still requires considerable research. By estimating a C budget for a diverse landscape with extensive cover of forest, wetlands, and lakes, we have shown that lakes and wetlands are significant long-term sinks whereas current fluxes are largest for forests. This budget provides a foundation, which can be built upon to include more complex interactions between different ecosystem types and landscape elements. The budget could also be used in the future to help identify which elements of the landscape are most likely to be most vulnerable to land use and climate change with respect to changes in C fluxes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Section S1. Forest and wetland surface-atmosphere fluxes: Detailed Methods.
Section S2. Modeling approach for upscaling lake C fluxes and pools to a group of 168 survey lakes.
Section S3. Starting point for lake C pools and fluxes: Detailed Methods.

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