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Sources and controls of organic carbon in lakes across the subarctic treeline

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Abstract Abundant northern lakes have an intrinsic role in the transport, sequestration, and mineralization of terrestrial organic carbon. The quantity and quality of this carbon control vital aquatic biogeochemical processes, and influence the metabolic balance of lakes with subsequent impact on the global carbon cycle. We measured concentrations and type of dissolved organic matter and elemental and stable isotopic composition of carbon and nitrogen in 31 subarctic lakes with varying catchment types across the treeline in northern Finland, integrating both the pelagic (lake water) and the benthic (surface sediments) carbon pools for a comprehensive understanding of landscape influence on aquatic carbon dynamics. Wetland cover was identified as the primary catchment control over the aquatic carbon pools, reflected particularly in the bio-optical properties of lake water. Landscape influence on sediment carbon content and composition, mirroring largely the structure and productivity of the aquatic communities, was primarily connected to allochthonous nutrient inputs fueling autotrophic production. Basin depth and benthic production were identified as important internal controls on the surface sediment geochemistry. Overall, our results suggest that shallow subarctic lakes will be particularly susceptible to climate-mediated changes in the export of terrestrial organic matter from wetlands. Whether the landscape influence will promote the channeling of terrestrial carbon into the atmosphere via aquatic ecosystems will strongly depend on the interplay between the biogeochemical characteristic of the allochthonous carbon inputs, terrestrial nutrient fluxes, and the depth of the recipient ecosystems.

Keywords Carbon · Colored dissolved organic matter · Sediment geochemistry · Stable isotopes · Subarctic lakes · Wetlands

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Introduction

Lakes and ponds are an essential component of the subarctic and arctic landscapes and act as sentinels of environmental change in the northern regions (Rautio et al. 2011; Smol 2015). Moreover, these lakes constitute an integral element in regional landscape-scale carbon balance, through conveying carbon from terrestrial environments into the atmosphere (Sobek and Tranvik 2005; Wilkinson et al. 2013; Sepulveda-Jauregui et al. 2015). Considering the vast abundance of small and shallow lakes across the Northern Hemisphere (Downing et al. 2006; Grosse et al. 2013), the channeling of carbon into the atmosphere via aquatic ecosystems is considered of global significance (Battin et al. 2009). The impact of the ongoing climate warming is expected to be most pronounced at high latitudes (Bekryaev et al. 2009) with a myriad of influences on the functioning of the sensitive aquatic ecosystems (Tranvik et al. 2009; Vonk et al. 2015). A key variable in these dynamics is organic carbon that is linked to several vital ecosystem functions via influences on biological production and on the physical and chemical properties of lakes (Snucins and Gunn 2000; Karlsson et al. 2009; Williamson et al. 2015). Dissolved organic matter (DOM) comprises a diversity of organic compounds that vary in their chemical characteristics and, consequently, in their functionality in lakes (Fellman et al. 2010). Colored dissolved organic matter (CDOM), derived primarily from terrestrial sources, is of particular significance as it governs the availability of light for photosynthesis, attenuates ultraviolet radiation (UV) in the water column, and fuels heterotrophic production (Pienitz and Vincent 2000; Sanders et al. 2015). Consequently, terrestrial organic carbon has a marked influence on lake metabolic processes and the balance between autotrophic and heterotrophic production in lakes, therefore controlling net aquatic carbon balance and carbon loss into the atmosphere (Jansson et al. 2008; Vonk et al. 2015).

The temperature-driven poleward movement of vegetation zones, permafrost degradation, and lengthened growing season combined with enhanced precipitation in polar regions (ACIA 2004; Harsch et al. 2009) are anticipated to increase the input of terrestrial DOM into lakes, with potential marked impact on their ecological functioning (Pienitz and Vincent 2000; Tranvik et al. 2009; Vonk et al. 2015). Moreover, the climate-mediated changes in the terrestrial ecosystems may have a major impact on regional carbon cycling. Here the role of lakes as conduits and reactors of terrestrial organic matter is of crucial importance, while studies on landscape-scale carbon balance have only recently began to incorporate the aquatic component. Previous research from ecotonal treeline lakes in the Fennoscandia (Korhola et al. 2002; Giesler et al. 2014) and across the Northern Hemisphere (Rühland et al. 2003; Seekell et al. 2014; Lapierre et al. 2015) have indicated a strong connection between catchment and limnology of shallow subarctic lakes. In particular, the presence of forest vegetation and wetlands have been commonly associated with increased supply of terrestrial organic matter. There are, however, few comprehensive regional studies examining landscape influence on organic carbon pools both in lake water and sediments, while the pelagic and the benthic environments together constitute an integral component in the climate-catchment-lake continuum (Vadeboncoeur et al. 2002; Buffam et al. 2011). Non-climatic factors, such as changes in atmospheric deposition chemistry, photochemical mineralization or land use, may further superimpose or interact with the climatic influences on DOM concentrations and quality (Solomon et al. 2015).

In this study, our primary objective was to examine landscape control over the water column and sediment organic carbon pools of subarctic lakes. For this aim, we examined the quantity and quality of organic matter in the lake water and surface sediments of 31 subarctic lakes in northern Finland, covering a gradient from catchments dominated by boreal forests to the treeless tundra, and to catchments with high wetland cover. We anticipate a shift in the quantity [dissolved organic carbon (DOC) concentrations, sediment organic carbon (C)] and quality [CDOM characteristics, isotopic composition of sediment C and nitrogen (N), C/N ratio] of organic matter in association with vegetation transformation across the treeline gradient. We further hypothesize that lakes with wetland influence are likely to contain larger amounts of CDOM in their waters and accumulate more carbon in their sediments related to the input of recalcitrant organic carbon from wetland soils. Through CDOM's influence on light availability for benthic primary production, it is also presumed that increased export of terrestrial organic matter affects the geochemical composition of the surface sediments. We discuss the potential impact of the projected global change scenarios on the carbon pools and ecological functioning of northern lake ecosystems, with particular regard to the shifting treeline position and wetland dynamics. By focusing on the interlink between the terrestrial and the aquatic realms and by examining both the pelagic and benthic carbon pools, we build towards an improved understanding of the responses of northern lake ecosystems to climate change and their role in regional and global carbon cycling.

Materials and methods

Study area

A regional lake set was selected along a treeline gradient from subarctic Finland (68–70°N), spanning from the northernmost extent of the boreal forest to the subarctic tundra (Fig. 1). Small-sized lakes (max lake area 13.3 ha, max depth 7.5 m) were chosen for comparability between sites and to represent the dominant type of lakes in the region. Lakes with variable catchment characteristics and limnological properties were selected to ensure wide range of organic carbon concentrations and quality.

The treeline ecotone in the northern Finnish Lapland encompasses a vegetation gradient from the boreal coniferous forest to the treeless tundra. The southern parts of the study area are characterized by boreal forests with either Scots pine (*Pinus sylvestris*), or mixed pine and birch as dominant tree species. Northwards, the vegetation shifts into mountain birch (*Betula pubescens* ssp. *czerepanovii*) woodland, and further, into treeless shrub tundra with patches of low-growing shrub birch (*Betula nana*). Higher up in the fells, treeless tundra dominates supporting mainly lichens and mosses. The treeline in the study area is formed by mountain birch that roughly follows the average-daily-maximum isotherm of 13.2 °C for four warmest summer months in the region (Odland 1996). The bedrock of the study area encompasses parts of the Lapland granulite belt and granite gneisses northeast. The soil cover is dominated by basal till and the soil layers are commonly very thin in the treeless tundra and elevated areas. Permafrost occurs discontinuously in the Lapland region and wetlands are highly abundant, comprising mostly minerotrophic fens. The region is characterized by subarctic climate, with a mean annual air temperature of ca. −2 °C and mean July air temperature of ca. 13 °C (Finnish Meteorological Institute), measured at the Utsjoki Kevo weather station (69°45′N, E 27°0′E). Mean annual precipitation in the region is ca. 450 mm. Owing to their remote locations, the studied lakes have been subjected to little human influence and may be considered pristine ecosystems.

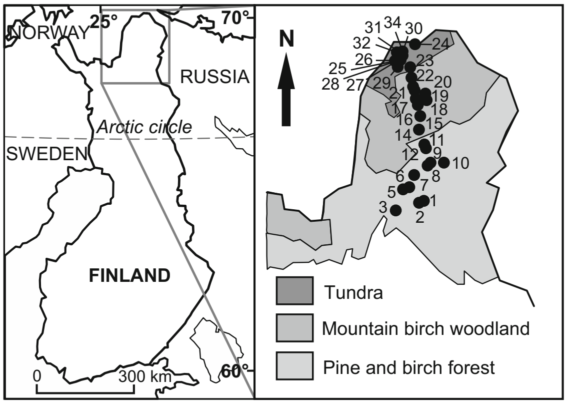


Fig. 1 Location of the study lakes in northern Finland across pine and birch forest, mountain birch woodland, and tundra ecotones. The *numbers* refer to lake number. Information on site characteristics is provided in Fig. 2 and Online Resource 1

Sampling and analyses

Catchment characterization, limnological *in situ* measurements and water and sediment sampling were performed at one time in late July 2014. The studied lakes are primarily shallow well-mixed water bodies that are likely isothermal throughout the ice-free period, yet a few deeper lakes may have experienced thermal stratification during sampling. Catchment parameters were obtained based on field observations and geospatial analysis using ArcGIS software, comprising locational (latitude, longitude, altitude), and physiogeographic and vegetational (catchment and basin morphometry, land cover, vegetation type) data. Catchment areas were delineated with ArcGIS 10.1 by Pour Point using Elevation model (10 m grid) provided by the National Land Survey of Finland. Aside from lake #28 situated within the catchment of lake #27, the lakes were located in their individual catchments. The studied sites encompass four forest vegetation types: boreal forest dominated by pine or pine and birch (n = 12), mountain birch woodland (n = 10), shrub tundra (n = 4), and treeless tundra (n = 5). As catchment influence is dependent on hydrologic connections between lake and the surrounding landscape (Xenopoulos et al. 2003, Soranno et al. 2015), the lakes were further divided into three hydrological types based on hydrologic connectivity: closed lakes (no stream inlets, n = 24 of which 6 were headwaters with a stream outlet), drainage lakes (with stream inlet and outlet, n = 2), and nested drainage lakes (with generally one lake or pond upstream, n = 5). Additionally, a number of catchment morphometric features were determined (Table 1), as the physical characteristics of the landscape often interact with other hydrological characteristics (e.g., flow pathways, water retention time) (Martin and Soranno 2006). Mean July air temperature for each site was interpolated from gridded monthly temperature data for years 1984–2013 made available by the Finnish Meteorological Institute.

Water samples were retrieved from the epilimnion (ca. 0.5 m) for the determination of DOC concentrations, a suite of carbon quality parameters, chlorophyll-*a* (CHLa), total phosphorus (TP) and total nitrogen (TN). The water samples were stored at 4 °C minimizing contact with air and light. Samples for DOC analysis (50 mL) were treated with 200 µL 2 M hydrochloric acid (HCl) on the field and filtered (45 µm) and analyzed with a Shimadzu Total Organic Carbon analyzer. The analysis was performed according to the European standard SFS-EN 1484 and the mean value of five parallel runs was used in data analyses. For spectrophotometric and spectrofluorometric measurements of carbon quality, 100 mL of lake water was filtered (0.7 µm) through pre-combusted GF/F filters into pre-combusted air-tight glass vials. Sample for lake #19 was frozen during storage and no reliable CDOM results could be obtained. Absorption coefficient at 320 nm (a_{320}) and specific UV absorbance (SUVA) were determined in dual-beam mode with Cary 100 UV–Vis spectrophotometer (Agilent) using a 10-cm quartz cuvette. Sample corrections were made against Milli-Q® water. The a_{320} values were used to indicate CDOM concentrations, and SUVA, representing DOC normalized absorbance at the wavelength 254 nm, to indicate the aromaticity of aquatic humic substances and to estimate the share of terrestrial organic carbon (Weishaar et al. 2003). Fluorescence index (FI) was further calculated to aid in differentiating between terrestrially and microbially derived fulvic acids. Simple fluorescence emission scans (400–700 nm) were performed with single excitation at 370 nm using a Cary Eclipse fluorescence spectrophotometer (Agilent), and FI was determined as the ratio of relative fluorescence emission intensities at 450 and 500 nm (McKnight et al. 2001). Additionally, excitation–emission matrices (EEM) were generated to study the

Table 1 Measured catchment, limnological and sediment properties, their units, and abbreviations

	Unit	Abbreviation
Catchment		
Latitude	°N	LAT
Longitude	°E	LONG
Altitude	m.a.s.l.	ALT
Catchment slope	m	SLOPE
Lake area	ha	LAKEa
Catchment area	ha	CATCHa
Drainage ratio	ratio	CAT/LA
Lake	%	LAKE
Forest	%	FRST
Wetland	%	WTLND
Tundra	%	TNDR
Mean July air temperature	°C	TEMP
Limnology		
Depth	m	DEPTH
Dissolved organic carbon	mg L^{-1}	DOC
Absorbance at 320 nm	m^{-1}	a_{320}
SUVA	mg C L^{-1} m^{-1}	SUVA
Fluorescence index	ratio	FI
CDOM components 1–4, 6	R.U.	HUMIC
CDOM components 5, 7, 8	R.U.	C5, C7, C8
Color	Pt mg L^{-1}	COLR
Total phosphorus	µg L^{-1}	TP
Total nitrogen	µg L^{-1}	TN
Chlorophyll-*a*	µg L^{-1}	CHLa
pH		pH
Water temperature	°C	
Sediment		
Loss-on-ignition	%	LOI
Carbon	%	C
Nitrogen	%	N
C/N (atomic ratio)	Ratio	C/N
$\delta^{13}C$	‰	$\delta^{13}C$
$\delta^{15}N$	‰	$\delta^{15}N$

distribution and intensities of different fluorescence components of DOM. EEM could not be obtained for lake #20. Excitation (220–450 nm) and emission (240–600 nm) wavelengths were measured spectrofluorometrically with 5 and 2 nm increments. Inner filter effect (McKnight et al. 2001), background scattering (Markager and Vincent 2000) and instrument-specific bias were corrected and the EEMs were standardized to Raman units (R.U.) (Stedmon et al. 2003). Rayleigh and Raman scattering were removed using MATLAB 2008b (Stedmon and Bro 2008). The DOM fluorescence signature was decomposed into individual components using parallel factor analysis (PARAFAC) model based on data from over 100 lakes across the boreal, subarctic and arctic regions of Finland, Canada and Greenland. For the determination of CHLa concentrations, 250 mL of water was filtered through GF/F filters that were subsequently freeze-dried and stored frozen until spectrophotometric and spectrofluorometric analysis. The analysis was performed following Nusch (1980) and corrections to remove bias caused by phaeopigments were done according to Yentsch and Menzel (1963). Final calculations for CHLa were done based on Jeffrey and Welschmeyer (1997). Lake-water TN and TP were analyzed from untreated 40 mL samples according to standards SFS-EN ISO 11905-1 and SFS-EN ISO 6878, respectively. Lake-water pH and color were determined with in situ with portable pH meter (Hanna Instruments © portable pH/EC/TDS/temperature meter) and water color meter (Hanna Color of Water Checker®) using a fixed wavelength LED (470 nm).

Surface sediments (0–2 cm) were sampled with a Limnos gravity corer from the deepest area in the basins (within the accumulation zone), with depths recorded using a portable depth meter (Speedtech Instruments, Great Falls, VA, USA). The samples were stored at 4 °C prior to physical and biogeochemical analyses. Loss-on-ignition (LOI) was measured to estimate the organic matter content of the sediments, determined as percentage weight loss after igniting the sediment samples at 550 °C for 2 h. The elemental concentrations (C, N) and stable isotopic composition of organic carbon and nitrogen (δ^{13}C, δ^{15}N) in bulk organic matter were analyzed from freeze-dried and homogenized sediments that were subjected to acid fumigation to remove carbonates. The δ^{13}C values and C/N ratio were used to track changes in the origin of the sediment organic matter, i.e. between autochthonous (benthic and pelagic), and allochthonous sources (Hecky and Hesslein 1995; Finlay and Kendall 2007). The δ^{15}N signature may yield information of both the origin and processing of organic matter, but was presumed to primarily reflect the source in the studied lakes, as is common in nitrogen poor lakes (Meyers 2003). For the carbonate removal, subsamples of ca. 30–200 mg were weighed into glass vials, moistened with Milli-Q® water, and placed inside a vacuum desiccator together with a beaker containing 100 mL of 12 M HCl. The samples were subjected to HCl vapor for 6 h after which the HCl beaker was removed and remaining HCl vapor was evacuated. The samples were dried at 60 °C and re-weighed to account for the mass change during fumigation, allowing the elemental proportions of organic carbon and nitrogen to be expressed in reference to the pre-acidified sediment weights (Ranmarine et al. 2011). The sediments were homogenized in the glass vials and subsamples of ca. 2 mg were weighed into 8 × 5 mm tin capsules for analysis. The elemental and stable isotopic analyses were performed using a FlashEA 1112 elemental analyzer coupled with a Thermo Finnigan DELTA plus Advantage mass spectrometer (Thermo Electron Corporation, Waltham, MA, USA). The stable isotopic values are expressed as the delta notation $\delta = R_{sample}/R_{standard} - 1) \times 1000$, where R equals ^{13}C/^{12}C or ^{15}N/^{14}N and the standards used were Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (AIR) for carbon and nitrogen, respectively.

Numerical analyses

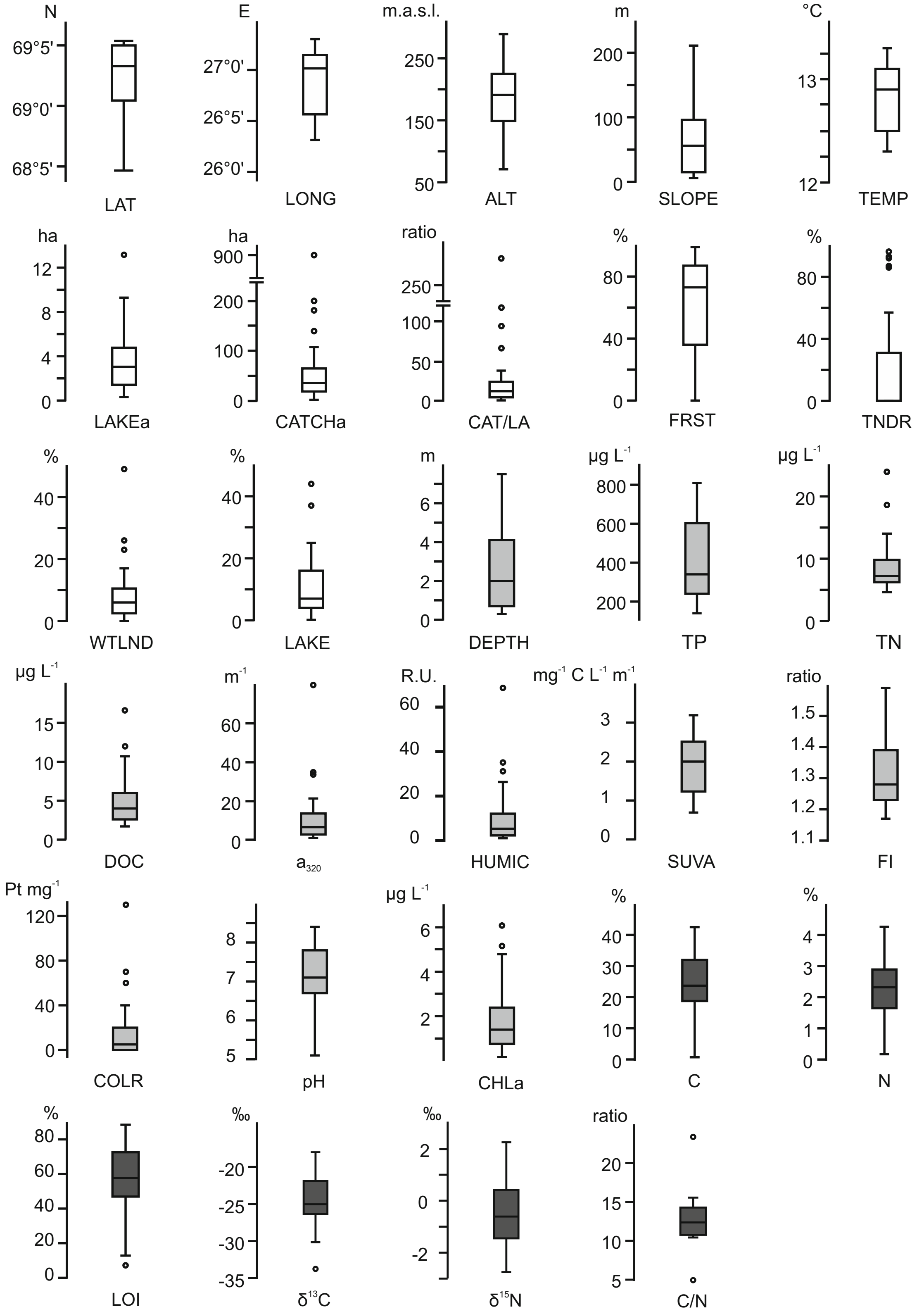
Permutational multivariate analysis of variance (PERMANOVA) was employed to test the influence of forest vegetation type as well as hydrological type on the limnology and sediment geochemistry of the lakes. Euclidean distance was used as the dissimilarity index and the number of permutations was set at 9999. Redundancy analysis (RDA), a direct gradient analysis, was used to examine variation in the quantity and quality of organic carbon in the lakes and their surface sediments across landscape gradients, using the limnological and sediment variables as response variables and the catchment characteristics as explanatory variables. RDA with forward selection was used to extract catchment variables that most strongly explain variation in the limnology and surface sediment geochemistry. The analysis was further performed to assess interconnections between the limnology and sediment geochemistry of the lakes, using the sediment properties as response variables and limnological characteristics as explanatory variables. Water column depth was included in both analyses as an explanatory variable. Prior to the analyses, data normality and bivariate relationships between all variables were assessed to identify potential data skewness and collinearity between variables. Data transformations (square root, log10) were performed where appropriate based on visual inspection of the data, and with skewness targeted at <±0.1 (Eriksson et al. 2001). For explanatory variables showing strong multicollinearity, only the variables considered most representative were included in the analyses. Accordingly, lake cover and catchment area as well as tundra cover were omitted from the first RDA due to high collinearity with drainage ratio and slope (strongly correlated with both lake cover and catchment area) and forest cover and temperature, respectively. Owing to strong multicollinearity between most of the limnological carbon and nutrient indices (DOC, a_{320}, HUMIC, SUVA, TP, TN, color), a preliminary RDA was performed to extract the variable that most strongly explains variation in the sediment geochemistry. Consequently, only TN was included in the final model. The transformed data were also used for pairwise correlations between the catchment parameters and the limnological and geochemical properties of the lakes and their sediments. The RDAs were performed with Canoco version 5.0 (Šmilauer and Lepš 2014). PAST 3 (Hammer et al. 2001) was used for the PERMANOVA.

Results

Organic carbon quantity and quality in water and surface sediments

Our data illustrate large range of variation in the quantity and quality of organic carbon in the studied lakes and their surface sediments (Fig. 2). Overall variation in the quantity of organic carbon in the lakes was large, with DOC concentrations ranging between 1.7 and 16.6 mg L^{-1} (median 4.0 mg L^{-1}). The composition of organic matter in the lakes, illustrated by the DOM optical indices, was similarly variable. The proxy for CDOM concentrations, a_{320}, ranged from 1.1 to 35.0 m^{-1} (median 6.1 m^{-1}), being strongly correlated with lake-water color (COLR) ($r = 0.96$, $p < 0.001$). PARAFAC identified eight fluorescence components of which five (C1–C4 and C6) had fluorescence characteristics commonly associated with humic terrigenous compounds (fluorescence peaks around 400–500 nm) originating from higher plants (Fellman et al. 2010). The remaining components C5, C7 and C8 had lower molecular weight and fluorescence peaks around 300–400 nm, resembling DOM from autochthonous production and microbial processes (Fellman et al. 2010). Of the three, C8 had a fluorescence signature typical of amino acids. The humic-like components C1–C4 and C6 were strongly correlated (all pairwise correlations $r > 0.69$, $p < 0.01$) and were pooled for numerical analyses (hereafter abbreviated as HUMIC). All three indices of transparency (a_{320}, COLR, HUMIC) were strongly skewed towards lower values, with most lakes characterized by clear and dilute waters. FI was negatively correlated with a_{320} ($r = -0.61$, $p < 0.01$) and the values (median 1.3) fell mostly within the range commonly associated with terrestrial fulvic acids (McKnight et al. 2001; Breton et al. 2009). The SUVA values (median 2.0 mg C L^{-1} m^{-1}) correspond with DOC aromaticity of ca. 17% (Weishaar et al. 2003) and were generally slightly lower than those observed by earlier studies in northern Fennoscandian ponds and lakes (Roiha et al. 2012; Olefeldt et al. 2013). Strong parallel variation with a_{320} and HUMIC ($r > 0.76$, $p < 0.001$) and negative correlation with FI ($r = -0.83$, $p < 0.001$) nevertheless suggest that SUVA reflects variation in the relative importance of terrestrial organic matter in the lake water. Similar to DOM quantity in the lake water, the C content of the surface sediments was variable (Fig. 2) ranging from 0.7 to 42.5% (median 23.7%). The sediment C content displayed strong parallel variation with the N and organic matter (LOI) contents in the surface sediment

Fig. 2 Boxplots presenting the minimum and maximum values ▶ (*whisker*), upper and lower quartiles (*box*) and median value (*line*) of the examined catchment (*white*), limnological (*light grey*), and sediment (*dark grey*) variables in the study lakes in northern Finland. Outliers are represented by *blank circles* and include all samples that exceed the inner fences, i.e., 1.5 × IQR (interquartile range) or more above Q3 (third quartile) or below Q1 (first quartile). List of abbreviations is included in Table 1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($r > 0.83, p < 0.001$). The C/N and δ^{13}C values varied between 4.9 and 20.0 (median 10.6) and −33.8 and −18.0‰ (median −25.0‰), respectively, indicative of a varied mixture of organic matter sources but prevalence of the autochthonous (benthic) signal in the surface sediments (Hecky and Hesslein 1995; Finlay and Kendall 2007). The δ^{15}N values were less variable, fluctuating between −2.8 and 2.3 (median −0.6‰). The negative values in majority of the lakes indicate the presence of nitrogen-fixing cyanobacteria (Meyers 2003) that commonly dominate the benthic communities of shallow northern lakes (Rautio et al. 2011).

Carbon variability across environmental gradients

No significant differences were found in the limnology and sediment geochemistry of the lakes between different forest vegetation types ($F = 2.30, p = 0.10$) nor between the three hydrological types ($F = 0.62$, $p = 0.56$), based on the PERMANOVA analyses. The variability in water and sediment carbon indices was rather due to environmental gradients that were related to catchment hydrology, geomorphology and soils properties, and to the productivity of the water bodies, respectively. The RDA identified wetland cover (WTLND) as the primary catchment control over organic carbon quantity and quality in the lake water (Table 2), with increasing concentrations of DOC and CDOM (as suggested by increasing a_{320} and SUVA, and declining FI) with increasing wetland cover in the catchment (Fig. 3). Wetland cover was also significantly correlated with all CDOM components ($r > 0.51$, $p < 0.05$), showing strongest connection to the protein-like component C8 ($r > 0.78$, $p < 0.001$). Increased allochthonous carbon inputs were also associated with elevated TP, TN, and CHLa concentrations in the lake water (Fig. 3). Additionally, depth was identified as an important explanatory variable showing an opposite pattern: declining carbon and nutrients along with increasing depth (Fig. 3; Table 2). The secondary RDA gradient was connected to several variables describing catchment and basin morphometry, in particular to drainage ratio (CAT/LA) (Fig. 3; Table 2). Increasing drainage ratio was associated with increasing SUVA and declining FI in the lake water, and declining sediment C, N and LOI. In total, the examined catchment variables and depth explained 54.0% of the variation in the limnology and sediment geochemistry of the studied lakes. The strong influence of wetland cover on various DOM indices in the lakes was also supported by pairwise correlations (Table 3).

The influence of landscape characteristics on surface sediment geochemistry was less conspicuous than with the concentrations and bio-optical characteristics of carbon in lake water (Fig. 3; Table 3), aside from elevated sediment C content in a few lakes with high wetland cover (>20%) and in lakes with low catchment slope and drainage ratio. The surface sediment geochemistry was more influenced by the limnological characteristics and lake depth than by the catchment variables. The RDA on sediment geochemistry suggested particularly strong influence of water column nutrients and production on the organic carbon content of the surface sediments, with increasing sediment C along with increasing TN and CHLa (Fig. 4; Table 4). With regard to TP and the carbon indices (DOC, a_{320}, SUVA) excluded from the model due to high collinearity with TN, pairwise correlations suggested a significant relationship for sediment C content with TP ($r = 0.47$, $p < 0.01$) and DOC ($r = 0.46$, $p < 0.01$). The secondary RDA axis divided the lakes along a depth gradient and was particularly strongly connected to the isotopic composition of the sediment organic matter, with increasing δ^{15}N and declining δ^{13}C along increasing depth. Overall, the limnological variables explained 51.1% of the variation in the sediment geochemistry of the lakes.

Table 2 Results from redundancy analysis (RDA) including catchment variables that significantly explain variation in the limnology and sediment geochemistry

	Explained variation (%)	Contribution (%)	Pseudo-F	*p*
WTLND	19.2	35.5	6.4	0.001
CAT/LA	9.0	16.6	3.2	0.006
DEPTH	7.7	14.3	3.0	0.036

List of abbreviations is included in Table 1

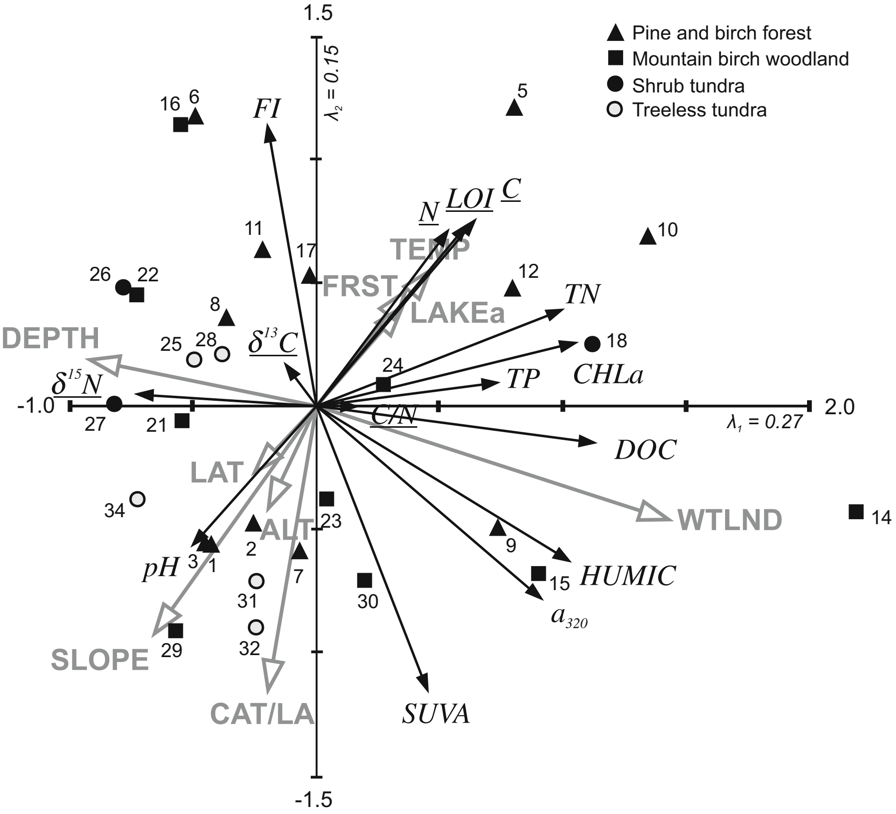

Fig. 3 Redundancy analysis (RDA) biplot on limnological and sediment properties (*black arrows*) in the 31 lakes in northern Finland, with catchment characteristics (*grey arrows*) as explanatory variables. Sediment variables are *underlined*. *Angles between arrows* represent correlations between variables. Projection of sites onto the *arrow lines* at right angle approximates the value of the respective variable. Variables that significantly explain variation in the limnology and sediment geochemistry are indicated in Table 2, and list of abbreviations is included in Table 1

Table 3 Statistically significant pairwise correlations between catchment characteristics and depth, and the quantity and quality of carbon in lake water and sediment

	Water								Sediment			
	DOC	a320	SUVA	FI	HUMIC	C5	C7	C8	C	N	LOI	δ^{15}N
WTLND	**0.78**	**0.70**	*0.49*		**0.70**	**0.56**	**0.50**	**0.78**				
TNDR										−0.42		
CAT/LA			**0.56**	*−0.53*					−0.41			
SLOPE									*−0.45*			
LAKE			**−0.61**	**0.60**					*0.48*		0.46	
CATCHa			*0.52*									
TEMP										*0.50*	0.40	
DEPTH					−0.44							**0.73**

Significance levels are indicated in bold ($p < 0.001$), italic ($p < 0.01$), and normal ($p < 0.05$), $r > 0.40$

List of abbreviations is included in Table 1

Discussion

Catchment controls on aquatic carbon pools

The studied lakes displayed a gradient from shallow and transparent oligotrophic ecosystems to strongly colored mesotrophic waters (Fig. 2), demonstrating the vast limnological diversity of northern freshwater ecosystems. The distribution of the lakes across limnological gradients was strongly connected to landscape features controlling variation in the sources and export of terrestrial organic matter. Our results

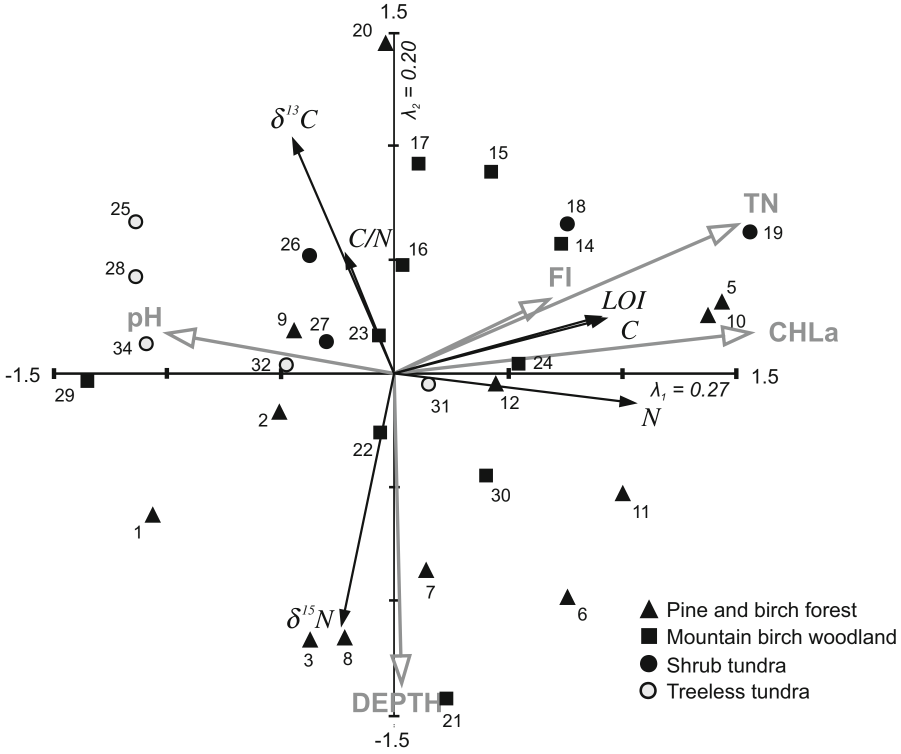

Fig. 4 Redundancy analysis (RDA) biplot on sediment properties (*black arrows*) in the 31 lakes in northern Finland, with limnological variables and depth (*grey arrows*) as explanatory variables. *Angles between arrows* represent correlations between variables. Projection of sites onto the *arrow lines* at right angle approximates the value of the respective variable. Variables that significantly explain variation in the sediment geochemistry are indicated in Table 4, and list of abbreviations is included in Table 1

Table 4 Results from redundancy analysis (RDA) including limnological variables that significantly explain variation in the sediment geochemistry

	Explained variation (%)	Contribution (%)	Pseudo-F	*p*
TN	18.6	36.3	6.4	0.001
DEPTH	12.1	23.7	4.7	0.001
CHLa	7.8	15.2	3.3	0.021
FI	6.6	12.9	3.0	0.039
pH	6.0	11.8	3.0	0.041

List of abbreviations is included in Table 1

thus underscore the tight coupling between northern lakes and their catchments (Kothawala et al. 2014; Lapierre et al. 2015), and their role in landscape-scale carbon cycling (Battin et al. 2009). The data analyses suggest that the quantity and quality of organic carbon in shallow subarctic lakes across the treeline are fundamentally controlled by the presence and extent of wetland vegetation (Fig. 3; Tables 2, 3). Northern wetlands contain extensive carbon storages (Gorham 1991), and their importance as suppliers of organic carbon into lakes has been well-established by earlier regional studies (e.g., Kortelainen 1993; Korhola et al. 2002; Buffam et al. 2011). A vast transregional comparison by Xenopoulos et al. (2003) similarly showed that wetland extent is a key factor controlling DOC concentrations in freshwater lakes across the Northern Hemisphere. However, their study also emphasized the importance of wetland type, as examination of lakes in the North American temperate forest region suggested that only forested wetlands were positively correlated with lake DOC. Overall, studies investigating the interaction between wetlands and lake ecosystems have had a strong boreal focus, and have generally only considered carbon quantity in lake water. The wetlands in our study region are typical of subarctic and arctic regions, comprising mostly moist minerotrophic fens supporting low-growing shrubs. Additionally, lacustrine or riverine marshes formed around the littoral margins of the lakes or their input streams were common in the studied sites. Although carbon sequestration by fens is typically lower than in bogs (Turunen et al. 2002), and despite that trees were small and sparsely present, our results indicate that the subarctic fens comprise important source of carbon and nutrients for the freshwaters in the region.

The pervasive influence of wetlands was further reflected in the quality of DOM (Fig. 3; Table 3) that largely determines its biogeochemical functionality in lakes. While DOC concentrations and DOM composition are not intrinsically coupled (Jaffé et al. 2008; Forsström et al. 2015), the quantity and quality of organic carbon often covary in lakes (e.g., Kothawala et al. 2014), as in the studied lake set (Fig. 5). The significant positive correlation of wetland cover with all CDOM components, and particularly with the protein-like component C8, suggests an influx of both aromatic humic and fulvic acids as well as more labile organic compounds with low molecular weight from the minerotrophic fens. This is in agreement with experimental studies showing that DOM from fen soils is characterized by lower aromaticity and molecular weight in comparison with other wetland and soil types (Fellman et al. 2008; Roehm et al. 2009). The elevated components C5, C7 and C8 may additionally indicate microbial processing of the terrestrial DOM or elevated autochthonous production in the lakes. The increased nutrient concentrations and CHLa in the water column along with increasing wetland cover (Fig. 3) further indicate enhanced nutrient loading from the fen soils fueling phytoplankton production in the lakes. Internal nutrient cycling may also contribute to the elevated nutrient concentrations and aquatic production as the lakes with high wetland cover were generally shallow (Fig. 3). While hypoxia (driving internal loading) is unlikely to occur in the shallow sediments during the ice free period due to efficient water column mixing, nutrients may be efficiently remobilized and distributed in the shallow water columns by sediment resuspension (Søndergaard et al. 2003). Aside from elevated sediment C contents in lakes with high (>20%) wetland cover (Online Resource 1), wetland influence on the quantity and quality of organic carbon in the surface sediments was small (Fig. 3; Table 3), suggesting importance of other environmental drivers on the sediment carbon pools (discussed below).

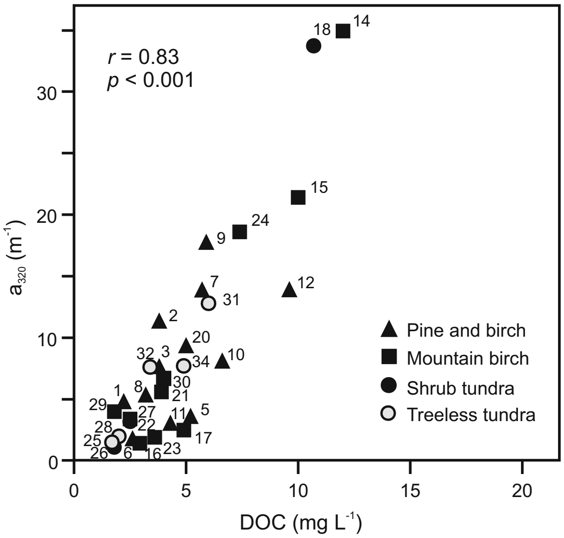

Fig. 5 Relationship between the concentrations of dissolved organic carbon (DOC) and colored dissolved organic matter (CDOM), as indicated by absorbance at 320 nm (a_{320}), in the 31 lakes in northern Finland

The latitudinal vegetation transition across the treeline, often reflected in the limnological characteristics of ecotonal lakes, had a surprisingly small effect on the limnology and sediment geochemistry of the studied lakes (Fig. 3). The elevated, rocky outcrops and low growing shrub vegetation in the treeless tundra presumably provide fewer sources of organic matter and nutrients to the lakes. Yet, regardless of the barren landscape, the organic carbon pools of the lakes in the treeless tundra (#28, 31–34) did not differ distinctly from those of the forested sites (Fig. 5). Our results are in contrast with several earlier studies from ecotonal regions, showing a distinct decline in the concentrations of organic carbon at the treeline (e.g., Korhola et al. 2002; Rühland et al. 2003; Roiha et al. 2012). A vast survey by Larsen et al. (2011) also showed that vegetation density was the most important predictor of DOC concentrations in Norwegian lakes across a wide latitudinal gradient, far exceeding the influence of other environmental gradients such as bog cover. We attribute this lack of clear distinction between the lakes situated in the treeless tundra and those in the forested catchments largely to the sedge

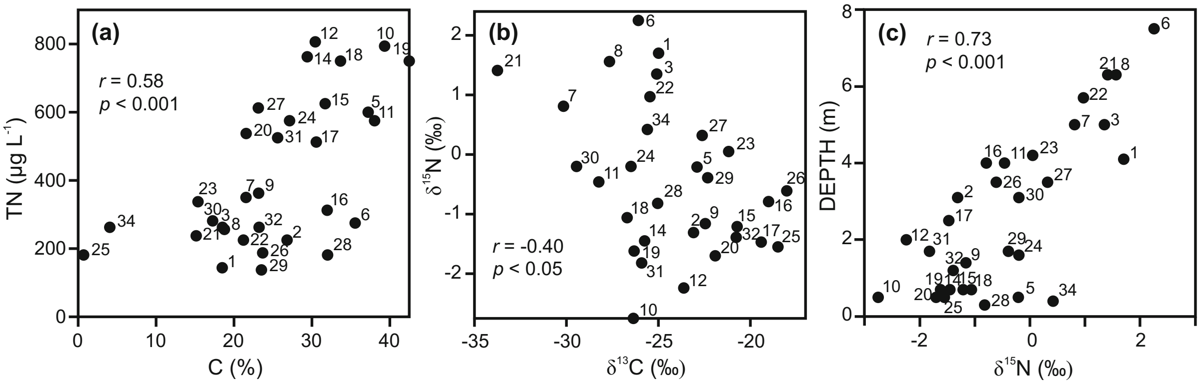

Fig. 6 Relationships between selected limnological and sediment variables in the 31 lakes in northern Finland, including **a** total nitrogen concentrations (TN) and sediment carbon content (C), **b** stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition of the sediments, and **c** depth and $\delta^{15}N$

and grass dominated peaty vegetation growing in the littoral margins of most of the tundra lakes, feeding organic carbon and nutrients into the lakes. As littoral marshes are a common feature of subarctic and arctic lakes, the pattern further highlights the pivotal importance of wetland vegetation in controlling aquatic carbon pools across the treeline. This result also lends support for the notion that local scale traits may have a comparatively larger influence on lake ecosystems than catchment scale characteristics (Soranno et al. 2015).

In addition to landscape characteristics that are controlled by climate, local factors such as catchment morphometry and hydrological pathways influence the quantity and quality of carbon in lakes. Such connections are often observed only at regional scale, while they may not appear in vast studies combining data on aquatic carbon pools across regions (Sobek et al. 2007). Hydrologic connectivity has a large influence on the transport of terrestrial organic matter into lake ecosystems (Martin and Soranno 2006; Read et al. 2015). We found no significant differences in the limnology and sediment geochemistry of the lakes when grouped based on surface water connections. This is probably largely attributable to the dominance of closed basins that ranged from mesotrophic wetland lakes to oligotrophic lakes in the treeless tundra. Instead, the limnology and sediment geochemistry of the lakes showed connections to several catchment morphometric features. The data analyses suggested particular influence of drainage ratio (Table 2) that covaried with other morphometric features (catchment slope, lake cover, lake and catchment area) (Fig. 3) and displayed a strong negative correlation with sediment C (Table 3). We suggest that this influence is essentially related to soil geomorphology and related variation in the relative importance of shallow and deep water pathways. Accordingly, a number of sites (#5, 6, 11, 16, 17) characterized by distinctly low drainage ratio, catchment area and catchment relief displayed consistent high sediment C contents (Fig. 6a) coupled with low values of SUVA, a_{320} and HUMIC, and high FI in the lake water (Fig. 3). All the lakes are situated in rocky or sandy outcrops with two of them (#5, 6) in aeolian dune fields (Kotilainen 2004) and the rest in the proximity of glaciofluvial deposits. We thus attribute the discrepancy between lake water carbon quality and sediment C content to groundwater influence, i.e., higher contribution of deep flow pathways relative to shallow. Organic carbon in groundwater has generally lower aromaticity and molecular weight than that derived from wetlands or forests (e.g., Olefeldt et al. 2013), related to selective adsorption of hydrophobic DOM fraction by mineral soils (Kalbitz et al. 2000). In concert, earlier research has associated groundwater influence with low SUVA (Olefeldt et al. 2013) and high FI values (McKnight et al. 2001). In support of our results, Olefeldt et al. (2013) found that the relative influence of wetland cover and groundwater discharge controlled the quantity and quality of allochthonous carbon in subarctic Swedish lakes, although the study did not consider sediment carbon pools. Our data suggests that, while resulting in lower aromaticity of organic carbon and higher transparency in the water column, the groundwater fed lakes may contain high sediment C pools. The geochemical composition of the sediments indicate no single source for the sediment organic matter, yet elevated nutrient concentrations (lakes #5, 11, 17, Fig. 6a) suggest that the groundwater flow may be feeding dissolved inorganic carbon (DIC) and nutrients into the lakes that fuel autochthonous production. The low DOM concentrations in the lake water could also partly be attributed to the low drainage ratio that is commonly associated with shorter water retention time in the catchment (less solutes) and higher in-lake processing of carbon (Kortelainen 1993; Sobek et al. 2007). The low catchment reliefs may further induce lower drainage of allochthonous DOM into the lakes, resulting in high light availability for primary production and thus in the generation of organic carbon contributing to the sediment carbon pools.

External and internal controls on surface sediment geochemistry

Surface sediments have an integral role in the functioning of shallow subarctic lakes, as benthic microbial production often forms the basis of food webs in these ecosystems, influencing benthic and pelagic energy flows, aquatic elemental cycles and carbon budgets (Rautio et al. 2011; Mariash et al. 2014). We examined controls on the distinct but tightly connected benthic and pelagic realms to better understand their differential responses to landscape transformations under the global change. Collectively, our data show that the sediment carbon pools are shaped by the combined influence of terrestrial nutrient and carbon transport, basin morphometry, and benthic production. Landscape influence on the sediment carbon pools was primarily mediated through allochthonous nutrient inputs that likely fuel autochthonous production in the lakes, as also suggested by the parallel increase in CHLa concentrations (Fig. 4; Table 4). The influence of increased water column nutrients and production were reflected particularly in the sediment C content (Figs. 4, 6a) implying increased biomass production in the lakes. The phytoplankton generally benefit more from increased nutrient loading relative to the benthic communities that are primarily restricted by light (Bonilla et al. 2005; Vadeboncoeur et al. 2008), although recent research suggests that the periphyton in arctic lakes may similarly be responsive to nutrient enrichment (Hogan et al. 2014). Most of the lakes influenced by terrestrial nutrient inputs displayed enriched δ^{13}C signatures (<-25‰) and depleted δ^{15}N typical of benthic production indicating dominance of the benthic community (Fig. 6b), likely attributable to higher availability of benthic habitats in the shallow water bodies. Nevertheless, a weak but significant negative correlation was found between CHLa and δ^{13}C ($r = -0.37$, $p > 0.05$), reflecting increased contribution of the ^{13}C depleted phytoplankton biomass (Finlay and Kendall 2007) to the sediments along increasing nutrient concentrations.

Underwater light climate is inherently connected to terrestrial carbon export, as DOM derived from allochthonous sources has commonly high aromaticity and light absorption capacity (Markager and Vincent 2000; Forsström et al. 2015). While reducing the availability of light for photosynthesis, terrestrial DOM may benefit aquatic communities not only via associated allochthonous nutrient inputs, but also by protecting from the harmful effects of ultraviolet radiation. Correspondingly, Nevalainen et al. (2015) showed that terrestrial organic carbon controls underwater UV exposure in lakes in the region, reflected in the photoprotective pigmentation of benthic microfauna. Our results conform with the view that primary production in alpine (Kissman et al. 2013) and clear arctic lakes where baseline DOC concentrations are low (Seekell et al. 2015a, b) may be most responsive to the allochthonous nutrient inputs, as suggested by the parallel increases in nutrient concentrations and CHLa with DOC in the studied lakes (Fig. 3). Even the most strongly colored lakes in our data set (COLR > 60 Pt mg^{-1}, #14, 18, 19) with DOC concentrations exceeding 10 mg L^{-1} displayed elevated CHLa concentrations (>3.6 mg L^{-1}) indicating increased phytoplankton production. In comparison, earlier studies (Seekell et al. 2015a, b) have suggested that light limitation by DOC may supersede the influence of increased nutrient availability for pelagic producers at lower DOC concentrations (4.8 mg L^{-1} and mean 5.96 mg L^{-1}, respectively). However, in contrast with the other shallow lakes receiving high terrestrial inputs from surrounding wetlands, these three lakes displayed δ^{13}C signatures deviating from the benthic signal (Fig. 6b), potentially implying suppressed benthic production under light limitation. Elevated C/N values in the lakes

(Online Resource 1), together with the depleted $\delta^{13}C$ signatures, additionally suggest increased contribution of flocculated terrestrial organic matter in the sediments (Meyers 2003; Finlay and Kendall 2007). The depleted $\delta^{15}N$ values instead contrast with the typical, slightly positive $\delta^{15}N$ values of terrestrial organic matter (Meyers 2003; Finlay and Kendall 2007). On the other hand, most of the studied lakes displayed depleted $\delta^{15}N$ values reflecting the contribution of light atmospheric nitrogen (fixed by benthic cyanobacteria) to the sediment N pools, and thus N poor terrestrial organic matter is likely to have a lower effect on the sediment $\delta^{15}N$ signature. Increasing terrestrial DOM inputs may also provide nutrient stimuli for heterotrophic microbial production (Forsström et al. 2013) and affect the balance between primary production and ecosystem respiration, with implications on aquatic carbon balance (Karlsson et al. 2005; Sanders et al. 2015). A shift from net autotrophy to heterotrophy has been estimated to take place at DOC concentrations above 5 mg L^{-1} (Jansson et al. 2000), yet, while several lakes exceeded this threshold value ($n = 11$, Fig. 5), we could not discern any unambiguous signs of increased heterotrophy based on the sediment geochemistry. This may partly be attributed to the biogeochemical characteristics of the allochthonous inputs, as DOM derived from fen soils (Fellman et al. 2008; Roehm et al. 2009) is often characterized by relatively low aromaticity and high biodegradability, and may thus have a less pronounced influence on underwater light attenuation and primary production. High substrate availability and light penetration in the shallow water columns may additionally enhance photochemical degradation of DOM in the lakes (Cory et al. 2015). Overall, the heterogeneity of the sediment signals in the studied lakes suggest that other environmental parameters, alongside the allochthonous carbon and nutrient fluxes, control light climate and nutrient regimes in the lakes.

Aside from the catchment influences, our results show that the sediment carbon pools are strongly connected to the depth of the water column (Fig. 4; Table 4). We suggest that the influence of depth, reflected particularly in the nitrogen isotopic composition of the sediments, is related to the combined influence of light attenuation as well as microbial processes in the water column and at the sediment-water interface. The increasing $\delta^{15}N$ along the depth gradient, coupled with consistent depleted $\delta^{13}C$ signatures ($<-25‰$) in lakes deeper than 5 m ($n = 6$) (Fig. 6b, c), indicate lower relative importance of light-limited benthic production (Finlay and Kendall 2007). Increasing depth was further connected with decreasing C/N ratio (Fig. 4) and showed no clear connection with phytoplankton production (estimated by CHLa), which implies a decline in the relative importance of benthic production, rather than any marked increase in allochthonous inputs or phytoplankton production along the depth gradient. In effect, the deeper lakes in our study were generally situated in rocky or sandy outcrops with lower availability of terrestrial CDOM, though mostly in forested rather than tundra catchments. Conversely, the lakes receiving high terrestrial inputs from surrounding wetlands were primarily very shallow and, thereby, the influence of CDOM on the benthic communities may be partially offset by depth. Our data thus indicate that the trade-off between nutrient and light availability related to terrestrial DOM inputs is strongly dependent on lake depth, consistent with recent studies (Karlsson et al. 2009; Seekell et al. 2015b). In addition to the potential light limitation on the benthic communities of the deepest lakes, the elevated $\delta^{15}N$ values may further indicate progressive enrichment of ^{15}N in the water column related to microbial degradation of the organic matter (Lehmann et al. 2002), and may also reflect higher trophic enrichment as deeper lakes are likely to sustain more complex food webs. In deeper lakes the bottom waters are also more prone to anoxia that may induce strongly positive $\delta\ ^{15}N$ values related to denitrification processes (Finlay and Kendall 2007). Majority of the shallow lake ecosystems in the studied lake set, whether influenced by terrestrial organic matter inputs or not, displayed a strong benthic signature. Our results both underline the notion that shallow northern lakes may support abundant benthic growth even when the overlying water column is poor in nutrients (Bonilla et al. 2005; Rautio et al. 2011) as well as demonstrate perseverance of the benthic community under increased loading of terrestrial organic matter and phytoplankton competition. Understanding of the benthic community dynamics has wider implications on overall ecosystem functioning as benthic primary production often forms the basis of the food webs in shallow northern lakes, affecting the composition of benthic (Luoto et al. 2016) and planktonic (Mariash et al. 2014) faunal communities and secondary production across all trophic levels (Karlsson et al. 2009).

Aquatic carbon pools under global change

Ecosystem responses to climate change are heterogeneous and a number of uncertainties hamper our attempts to predict the net impact of global change on the ecological functioning and carbon balance of lakes (Tranvik et al. 2009). Comprehensive regional data sets of aquatic carbon variability and associated environmental controls in sensitive ecotonal environments allow us to assess changes in the catchment-lake interaction and aquatic carbon dynamics under new environmental regimes imposed on by the ongoing climate change. Our results from lakes in the subarctic treeline underline the tight connection between the terrestrial and aquatic environments (Battin et al. 2009), and suggest that the most pronounced effects on the aquatic carbon pools and limnology of shallow northern lakes across the treeline will be mediated through wetland influence. Growing evidence suggests that the projected increases in humidity and temperature in the subarctic and arctic regions will severely impact the carbon storages in northern wetlands (Tranvik et al. 2009; Vonk et al. 2015), and may result in a substantial, sustained increase in carbon respiration from wetlands, particularly through the mobilization of subsurface carbon storages (Dorrepaal et al. 2009; Sepulveda-Jauregui et al. 2015). In the anaerobic conditions of wetlands, the decomposition of plant matter does not necessarily result in the direct release of carbon dioxide (CO_2), but rather in the generation of dissolved organic compounds that may be exported into aquatic ecosystems (Freeman et al. 2004) and may be indirectly released into the atmosphere via bacterial respiration (Roiha et al. 2015). Freeman et al. (2004) further suggested that northern fens may be particularly responsive to the effects of elevated CO_2 concentrations that stimulate terrestrial production and carbon release, as primary production in these systems is less constrained by nutrient limitation than in ombrotrophic wetlands. Our results show that the proposed increases in the export of terrestrial organic matter from northern fens may have a marked impact on lake-water bio-optical properties and nutrient regimes in subarctic lakes.

Despite the apparent influence of wetlands on DOM quantity and quality in lake water, examination of the sediment data with the limnological characteristics revealed a multitude of additional controls on resource availability at the base of the food web and on the quantity of organic carbon in the sediment carbon pools. Climate-driven increases in the export of organic matter from wetland soils are likely to reduce the availability of light for benthic autotrophic production that commonly dominates aquatic production in shallow northern lakes. In the studied lake ecosystems the benefit of allochthonous nutrient inputs largely outweighed the effects of light limitation, and the benthic community expressed resilience even under DOC concentrations that have been earlier associated with suppressed primary production. We attributed this to the specific biogeochemical characteristics of organic matter from fen soils (lower aromaticity) and to the confounding influence of the depth gradient (lower light extinction in shallow lakes). Our data analyses further illustrated the importance of hydrological pathways and soil characteristics as several lakes situated in catchments with distinct morphological characteristics and highly permeable soils, likely to receive larger share of groundwater discharge, showed elevated sediment C contents despite apparent low CDOM concentrations in the water column. Presumably, allochthonous nutrient inputs coupled with little shading by DOM promoted autotrophic production in the lakes. Olefeldt et al. (2013) suggested that increased precipitation in the subarctic region may increase the relative importance of deep relative to shallow flow paths, increasing the relative importance of lower aromaticity organic carbon in aquatic carbon pools. Consequently, changes in hydrology could partially offset the wetland influence on the bio-optical properties of the lakes and on the structure of the aquatic community. Overall, our data show that only part of the variability in aquatic organic carbon could have been captured if both the pelagic and benthic environments had not been considered. This notion is of importance both for modern limnological and paleoenvironmental studies of aquatic carbon dynamics and ecosystem functioning.

Conclusions

Our results underscore the tight coupling between the terrestrial and aquatic environment, as the terrestrial export of organic carbon was shown to exert strong control over the limnological characteristics of the studied lakes across the treeline gradient. The importance of integrating both the pelagic and the benthic environment in the analysis of aquatic carbon dynamics was further emphasized, allowing the identification of both external and internal drivers on the aquatic community structure and carbon pools. Our data suggest that landscape influence on the ecological functioning of subarctic lakes and their carbon dynamics is controlled by the combined effects of terrestrial carbon and nutrient fluxes, and that the influence is largely dependent on the quality of the allochthonous inputs as well as lake depth.

High-latitude ecosystems are likely to undergo major transformations under the climate change, yet, the mechanisms and potential positive and negative climate feedbacks are still not fully understood. For the global carbon balance, the fate of the vast carbon stocks in the northern wetlands is particularly significant. It is generally presumed that the export of organic carbon from terrestrial environments will increase in the northern regions with increasing temperatures and precipitation, underlining the importance of the aquatic carbon pathways. Through the tight catchment-lake coupling, climate change has the potential to trigger a positive feedback loop that accelerates the channeling of terrestrial carbon into the atmosphere via aquatic production and increasing heterotrophy. The present results build towards improved understanding of the link between the aquatic and terrestrial environments and associated influence on aquatic communities, providing also reference data for temporal studies on carbon dynamics under changing climate.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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