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SPECIAL ISSUE-LETTER

Vegetation transitions drive the autotrophy–heterotrophy balance in Arctic lakes

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Scientific Significance Statement

Warming of Arctic regions is shifting terrestrial vegetation ranges and altering lateral carbon transfer across landscapes, with implications for lake carbon balances (autotrophy vs. heterotrophy) in one of the most lake-dense regions on earth. Lake carbon research is strongly focused on boreal regions and so knowledge of terrestrial-aquatic linkages in high-latitudes crossing treeline-tundra environments is limited. This circum-Arctic paleolimnology study demonstrated that Arctic lakes undergo fundamental reorganizations of autotrophic communities as vegetation biomass in the watershed increases, toward mixotrophic dominance and indicating a relative shift from autotrophy to heterotrophy as the photic zone reduces due to increasing water color.

Abstract

"Arctic greening" will alter vegetation quantity and quality in northern watersheds, with possible consequences for lake metabolic balance. We used paleolimnology from six Arctic lakes in Greenland, Norway, and Alaska to develop a conceptual model describing how climate-driven shifts in terrestrial vegetation (spanning herb to boreal forest) influence lake autotrophic biomass (as chlorophyll and carotenoid pigments). Major autotrophic transitions occurred, including (1) optimal production of siliceous algae and cyanobacteria/chlorophytes at intermediate vegetation cover (dwarf shrub and *Betula*; dissolved organic carbon (DOC) range of 2–4 mg L^{-1}), below and above which UVR exposure (DOC; <2 mgL^{-1}) and light extinction (DOC; >4 mgL^{-1}), respectively limit algal biomass, (2) an increase in potentially mixotrophic cryptophytes with higher

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Author Contribution Statement: SMcG led the manuscript effort. NJA, MEE, VJ, PGL, SMcG came up with the research question and designed the study approach. SMcG conducted the statistical analyses. MvH and ST constructed the dating models. SMcG, NJA, MEE, EH, VJ, PGL, AL, NS, ST, MvH, EJW, EW conducted field sampling and lab analyses. SMcG wrote the paper with input from all authors.

Data Availability Statement: Data is available at https://catalogue.ceh.ac.uk/documents/1115ab47-3ccc-498c-8018-4682fa3a9bf0.

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

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forest cover and allochthonous carbon supply. Vegetation cover appears to influence lake autotrophs by changing influx of (colored) dissolved organic matter which has multiple interacting roles—as a photoprotectant—in light attenuation and in macronutrient (carbon, nitrogen) supply.

"Arctic greening" is the northward shift of vegetation biomes as climate warms and has led to increases in shrub cover in many tundra regions in recent decades (Walker et al. 2012). It is predicted that half of the vegetated areas in the Arctic will shift to a different physiognomic class as woody vegetation expands northwards (Pearson et al. 2013). As terrestrial vegetation is an important source of dissolved organic matter (DOM), concentrations of DOM in lakes are strongly influenced by watershed land cover (Cardille et al. 2007). Warming-induced vegetation changes in Arctic landscapes are accompanied by permafrost thaw, deepening of the active layer, and changes in hydrological transport and processing of carbon and nitrogen in Arctic watersheds (Walker et al. 2005; Walvoord and Striegl 2007; Tank et al. 2012). It is likely high that future Arctic vegetation shifts will influence carbon and nutrient fluxes to Arctic lakes, with probable consequences for lake metabolism. As one of the world's most lake-rich regions (Verpoorter et al. 2014) changes to Arctic lake metabolism could be significant for the terrestrial carbon cycle (Raymond et al. 2013; Wik et al. 2016).

Net autotrophy or heterotrophy (i.e., the metabolic balance) of lake ecosystems is determined by the relative rates of gross primary productivity vs. respiration (Karlsson et al. 2013; Kortelainen et al. 2013) and determines whether lakes are carbon sources or sinks. Most research has suggested that Arctic lakes are net heterotrophic; they emit more carbon dioxide to the atmosphere than they take up (Kling et al. 1992; Tranvik et al. 2009). The delivery of DOM to lakes is a key control on lake metabolism (Karlsson et al. 2009; Lapierre and del Giorgio 2012; Kritzberg et al. 2014) since it supplies organic carbon for heterotrophs and mixotrophs, pushing the metabolic balance of lakes toward net heterotrophy via respiration (Jansson et al. 2000; Kortelainen et al. 2013). DOM also supplies and binds nutrients which can be released by photolytic processes for autotrophic uptake and production (Kissman et al. 2013). Colored DOM (CDOM; humic substances) stains lake waters brown which can limit light penetration and restrict primary productivity (Karlsson et al. 2009). Conversely, because CDOM is a photoprotectant; ultraviolet radiation (UVR) damage may restrict primary productivity in lakes when CDOM is scarce (Sommaruga 2001; Harrison et al. 2015). Such processes may be important in Arctic lakes, which are strongly nutrient limited and often dominated by benthic production (Vadeboncoeur et al. 2003; Law et al. 2015). Therefore, influx of carbon to lakes may influence whether production is focused in benthic or pelagic areas of the lake (Rosén et al. 2009). These multiple functions of (C)DOM mean that relationships between dissolved organic carbon (DOC) and whole-lake production appear to be nonlinear; positive < 4.8 mg L^{-1} (driven by nutrient availability) and negative above this threshold (driven by light extinction; Seekell et al. 2015).

Climate-driven vegetation shifts occur over decadal-centennial timescales and are associated with characteristic successional, edaphic, biogeochemical, and hydrological processes (Walker et al. 2005; Engstrom and Fritz 2006; Tank et al. 2012). Tracking how such long-term and system-wide changes to biomes affect aquatic-terrestrial linkages is difficult using conventional monitoring or experimental techniques. However, past climate-driven shifts in vegetation during previously warmer periods (e.g., the Holocene Thermal Maximum) may be used as analogs for future warming scenarios and tested using paleolimnology (Reuss et al. 2010). Lake sediments collect carbon from the catchment and entire lake basin to provide a time-ordered and integrative overview of shifts in lake carbon balances (McGowan et al. 2016). Due to gravity, sediment focusing combines detritus from benthic and pelagic, littoral, and profundal zones into the deepest parts of the lake (Stone and Fritz 2006). As biomarkers of autotrophs, chlorophyll and carotenoid pigments in lake sediments estimate the proportion of autotrophically derived carbon that is buried in lake sediments (Leavitt et al. 2003). Expressed as a proportion of total sedimentary organic carbon, pigments provide a time-integrated index of whole-basin autotrophic biomass relative to carbon derived from other sources. Pigments can also identify dominant primary producer taxa, to provide information on where and how lake carbon is fixed (McGowan 2013). A separate group of UVR-protective or "sunscreen" pigments are produced by protists in low CDOM, UV-exposed environments. When UVR pigments preserved in sediments are expressed relative to total algal biomass, they provide an index of past UVR exposure (the UVR index of Leavitt et al. 1997). Pigment degradation processes are well understood and can provide information on autotrophic carbon burial and preservation vs. mineralization (Cuddington and Leavitt 1999).

We aimed to determine how past terrestrial vegetation transitions occurring in Arctic watersheds influenced lake metabolism over millennial timescales using paleolimnology. Because higher aboveground biomass and increasingly woody vegetation (herb → shrub tundra → boreal forest) will increase production of DOM and CDOM, we expected that it

Table 1. Information on (a) present day lake parameters including maximum lake depths (= coring depths), lake-water chemical variables including DIN (dissolved inorganic nitrogen), TP (total phosphorus) analyzed as outlined in Whiteford et al. (2016) and present vegetation types in the lake catchments; (b) mean (± SD) of sediment core parameters including LOI estimates of organic matter, with $\%C_{sed}$ either measured or estimated from LOI, and C/N_{sed} in organic matter for the entire core sequences. Organic carbon content (%C) of the sediments was calculated from a simple linear regression model with LOI and %C (503 sediment samples, r^2 0.931, $p < 0.001$) on a subset of sediment samples that were pre-acidified to remove carbonates and measured for C and N on an Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS).

	(a) Lake parameters										(b) Sediment cores	
Region	Lake name	Coring date	Latitude	Longitude	Depth (m)	Silicate mg L^{-1}	DIN μg L^{-1}	TP μg L^{-1}	DOC mg L^{-1}	Current vegetation type	LOI % $(\%C)_{sed}$ × estimate	C/N_{sed}
Greenland	AT1	April 2006	66°58′0.96″N	53°24′13.21″W	13.7	1.5	28	14	1.3	Herb	24 ± 6 (12 ± 4)	11 ± 1
	AT2	April 2013	66°58′24.10″N	53°23′34.93″W	11	1.2	23	5	0.9	Herb	20 ± 6 (10 ± 3)*	NA
Norway	Dalmutladdo	March 2014	69°11′23.42″N	20°43′55.70″E	4.75	4.8	N/A	7	6.5	*Betula*	37 ± 7 (18 ± 1)	15 ± 1
	NOR1	March 2014	69°11′53.27″N	20°42′42.768″E	4.35	2.3	120	0	10.5	*Betula*	62 ± 6 (27 ± 4)	15 ± 2
Alaska	Ruppert	July 2013	67°4′14.75″N	154°14′41.48″W	5.8	0.60	77	4	8.4	*Alnus*	27 ± 15 (16 ± 5)	13 ± 1
	Woody Bottom Pond	July 2013	67°4′33.64″N	154°13′52.97″W	4.25	0.65	40	6	6.2	*Alnus*	66 ± 9 (33 ± 5)	12 ± 1

would strongly influence lake autotrophs (and lake metabolism) via several mechanisms. Therefore, we tested three hypotheses: (1) Changes in light attenuation associated with CDOM influx will influence autotrophic production through UVR exposure (sparsely vegetated watersheds/low CDOM/low autotrophic production) and/or light limitation (forested watershed/high CDOM/low autotrophic production); (2) increasing influx of nutrients (primarily nitrogen) associated with allochthonous DOM will increase pelagic autotrophic biomass; (3) increasing influx of allochthonous carbon (forested catchments) will increase the production of mixotrophic algae. As these processes occur together, we expected that there might be synergistic or antagonistic effects.

Methods

We studied pairs of lakes in three Arctic regions (defined here as north of the Arctic circle) in Greenland, Norway, and Alaska, where past shifts in vegetation types, (i.e., plant functional types; Chapin et al. 1996) were well known (Table 1). We classified vegetation types to describe the biome shifts that had occurred in these lake catchments which spanned a gradient of terrestrial vegetation biomass (Supporting Information 1, Table S2). Our vegetation classes cover a broader range than the circumarctic tundra classes defined by Walker et al. (2005), to allow us to test scenarios of woody vegetation expansion. Sediment cores were collected from the lakes using piston or Russian corers. Successively deeper cores were joined together to create one complete sequence per lake, with the position of overlaps at core tops and bottoms being checked through matching visual sediment features and estimates of organic matter. Sedimentary organic matter (SOM) was estimated by loss-on-ignition (LOI; weight-loss from burning at 550°C; Meyers and Teranes 2001) (Table 1) at all sediment intervals for all core sequences except for Dalmutladdo (2 cm intervals). Missing LOI estimates for calculation of pigment concentrations (below) were calculated by interpolation between consecutive samples. A combination of macrofossil and pollen analysis in sediments (at a variety of sample resolutions), transposition of the timing of vegetation transitions between neighboring lakes (Lake AT1 transitions derived from macrofossil analyses in Lake AT2), and comparisons with published records were used to identify when vegetation transitions occurred in the core sequences. Full details are provided in Supporting Information 2.

New chronologies were constructed for sediment sequences for five lakes; for Lake AT1, the chronology published in Anderson et al. (2012) was used. Where possible, accelerated mass spectrometry (AMS) ^{14}C dating was conducted on terrestrial plant remains and, when unavailable, remains from aquatic macrophytes, moss, or bulk sediments were used (Supporting Information 3, Table S3). Samples were analyzed at the NERC Radiocarbon Facility, East Kilbride and low-mass samples at the Keck C Cycle AMS Lab, University of

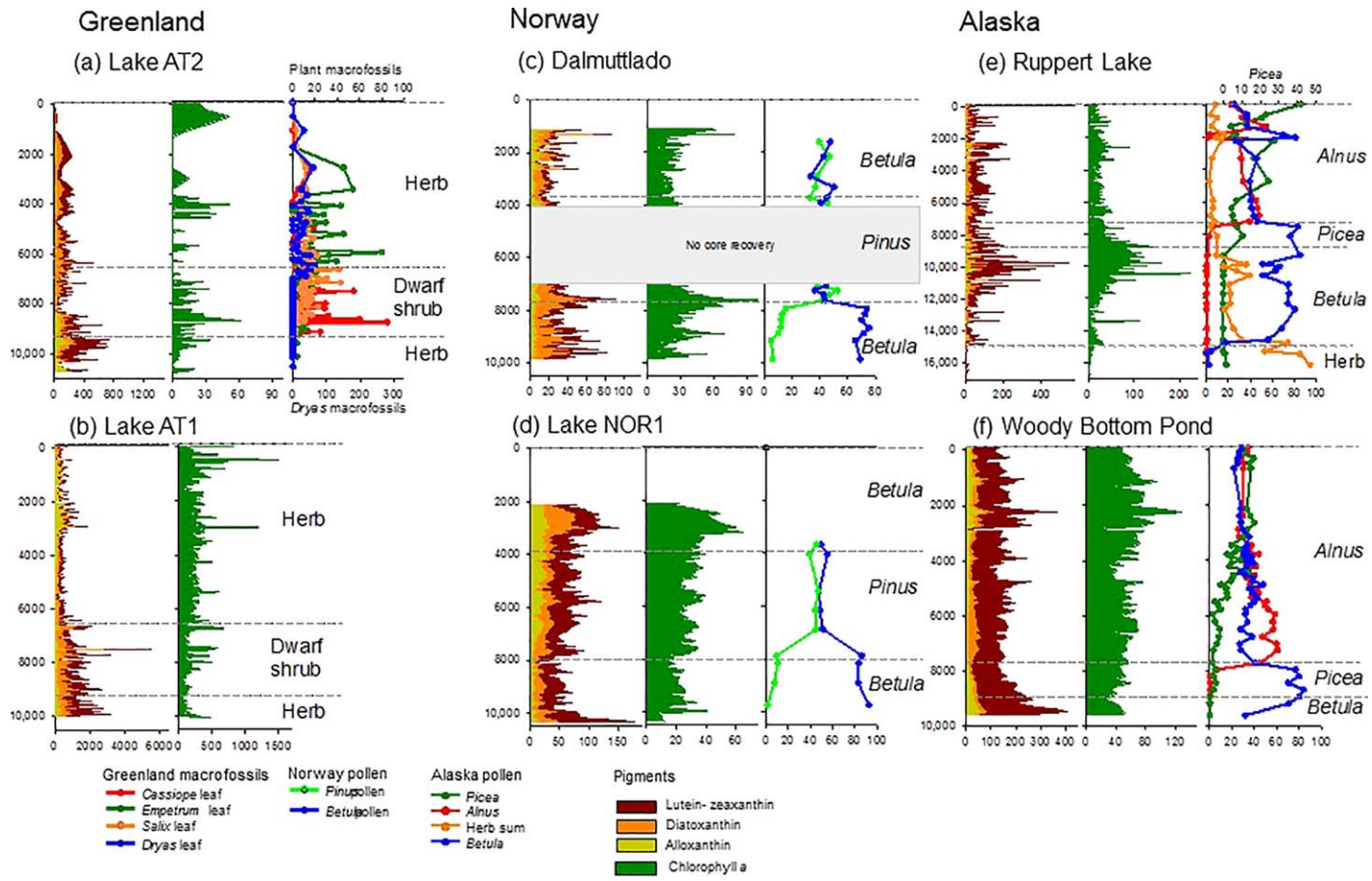


Fig. 1. Changes in algal carotenoids (left panel), Chl *a* (middle panel) (*n* moles g^{-1} OM), and pollen (%) or plant macrofossil (counts/100 mL) analyses (right panel) in lake sediment sequences, with estimated dates (in calibrated years BP). Horizontal gray lines indicate the boundaries of vegetation transitions.

California, Irvine. Ages were calibrated and age-depth models were created using Bacon version 2.2 for Mac, an R package using Bayesian modeling (Blaauw and Christen 2011) and the IntCal13 calibration curve (Reimer et al. 2013). Dates are given in calibrated years before present (BP). Dating models were further constrained using (1) a tephra layer from the Aniakchak Caldera-Forming Event II (3591 ± 3 BP), in both Alaskan lakes (Monteath et al. 2017); (2) pollen analysis of the well-established rise in *Alnus* pollen in Ruppert Lake (7565 ± 50 BP; Higuera et al. 2009) which was transferred to Woody Bottom Pond and (c) the initial occurrence (9245–10,044 BP) and rise (7056–7997 BP) of *Pinus* at Dalmutladdo (Bjune et al. 2004) which was transposed to NOR1.

Analysis of chlorophyll and carotenoid pigments by high-performance liquid chromatography (HPLC) was conducted at every level (1 cm resolution) along the entire core sequences following the methods in McGowan et al. (2012). Pigments were expressed relative to SOM as estimated by LOI (above). Four carotenoids were selected for analysis representing the most common aquatic photoautotrophs: cryptophytes (alloxanthin), siliceous algae including diatoms and chrysophytes (diatoxanthin), cyanobacteria (zeaxanthin), and chlorophytes (lutein). Lutein and zeaxanthin were inseparable using our HPLC system and so are reported together. Chlorophyll *a* was also selected because it is produced by all algae and higher plants and so is a measure of sedimentary burial of integrated autotrophic biomass. The UVR Index was calculated using the concentrations of a UVR-screening pigment described in Leavitt et al. (1997) relative to four dominant carotenoids: (UVR-screening compound/(alloxanthin + diatoxanthin + lutein + zeaxanthin)) × 100 to provide an index of UVR exposure.

Numerical analyses

Individual pigment time series from each lake sediment sequence were transformed to *z* scores (subtracted the mean and divided by the standard deviation) to standardize variance among pigments and among lakes. Pigment *z* scores were combined and split into zones corresponding to the vegetation type (shown in Fig. 1; see Supporting Information 1 and 2 for derivation and definitions of zones), and *z* scores of each vegetation zone were averaged to assess trends in

pigments across vegetation types. Differences in pigments among vegetation types were assessed using one-way ANOVA in SPSS with Bonferroni tests used to identify differences between vegetation pairs.

Results

The time span of the sedimentary records covered most of the Holocene in Greenland, Norway, and the Alaskan site Woody Bottom Pond; the late Pleistocene-Holocene in Ruppert Lake, Alaska (Fig. 1; Supporting Information 1, Table S2). The analysis identified vegetation transitions named here as herb → dwarf shrub → herb in Greenland (Fig. 1a,b), *Betula* → *Pinus* → *Betula* in Norway (Fig. 1c,d) and herb → *Betula* → *Picea* → *Alnus* in Ruppert Lake, Alaska with the final part of the sequence (*Betula* → *Picea* → *Alnus*) being recorded in Woody Bottom Pond (Fig. 1e,f). Vegetation shifts were accompanied by gradual changes in concentrations of Chl *a* and carotenoids (Fig. 1). Changes in pigments relative to vegetation transitions were gradual rather than abrupt, and there were long-term ontogenetic trajectories of change in pigment stratigraphies (Law et al. 2015). In general, periods of *Betula* expansion were associated with higher concentrations of carotenoid pigments in the sediment cores from Alaska and Norway (particularly pronounced in Lake NOR1; Fig. 1d) but this pattern was not universal (Fig. 1). Lakes in Norway had proportionally more carotenoids from cryptophytes and siliceous algae (alloxanthin and diatoxanthin) whereas lakes from Alaska had relatively greater contributions from chlorophytes and cyanobacteria (lutein-zeaxanthin) (Fig. 1).

UVR exposure in lakes (as indicated by the UVR index; Leavitt et al. 1997) was greatest in lakes with herbs, *Betula* and dwarf shrub with indications of sporadic UVR exposure during periods with *Alnus* (Fig. 2a). There was no production of UVR-screening pigments when *Pinus* or *Picea* were present. Comparisons among standardized pigment profiles indicated that boreal forest cover (*Pinus* and *Picea*) was associated with significantly more Chl *a* in sediments than the other vegetation categories ($p < 0.05$; Fig. 2b). *Pinus* catchment cover was associated with significantly more alloxanthin in sediments ($p < 0.05$) whereas during periods of herb and dwarf shrub presence there were lower quantities of this pigment in the SOM (Fig. 2c). Diatoxanthin from siliceous algae increased significantly ($p < 0.05$) during periods of dwarf shrub expansion and declined during herb cover, whereas concentrations were intermediate during *Betula*, *Alnus*, and *Pinus* phases (Fig. 2d). *Betula* and dwarf shrub expansion resulted in higher ($p < 0.05$) contributions of lutein-zeaxanthin to sediments than during periods of herb cover (Fig. 2e).

Discussion

The sediment cores span a broad range of Arctic vegetation types, from tundra to boreal forest, representing a

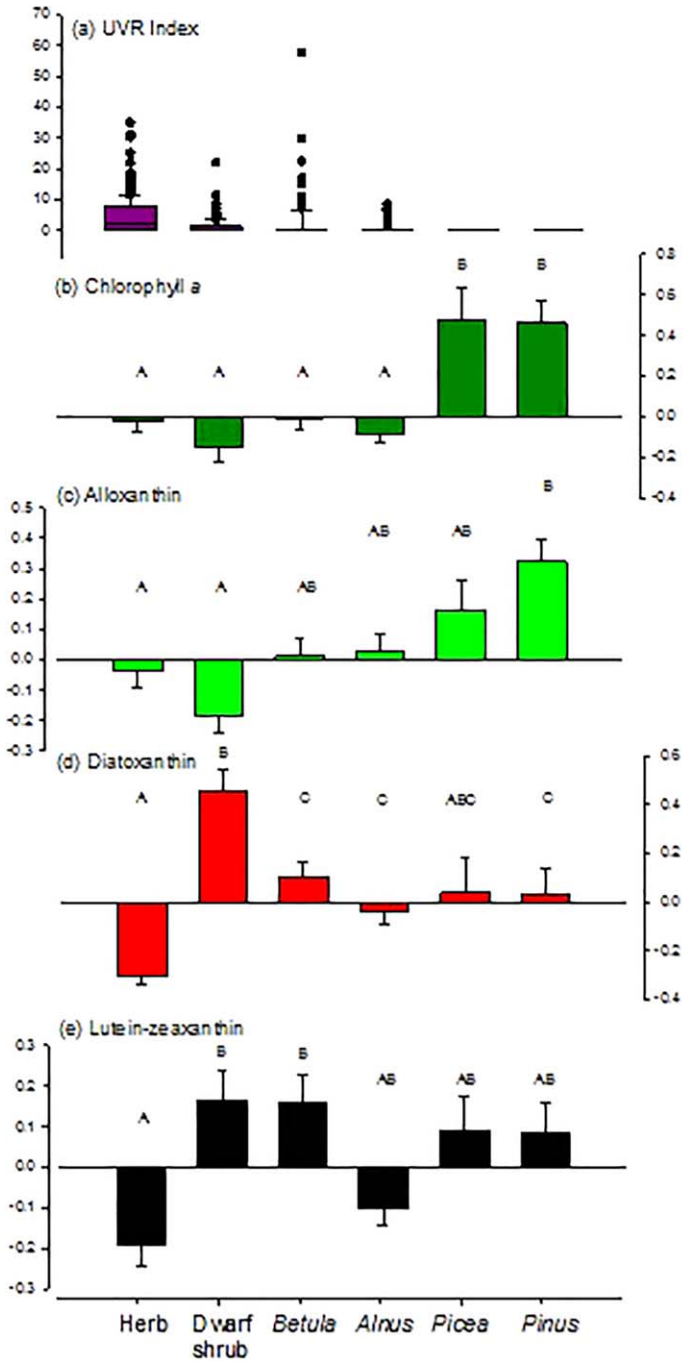
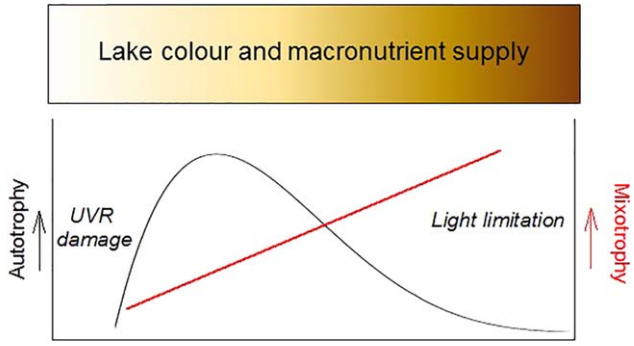


Fig. 2. The UVR index of water clarity (a; as in Leavitt et al., 1997) and *z* scores of pigments (+ SE) (b–e) from six lake sediment cores grouped by vegetation types as defined in Supporting Information 1, Table S2. The numbers of samples (*n*) derive from the data presented in Figure 1 and are summarized as Herb ($n = 384$, three lake sites, five time periods), Dwarf shrub ($n = 197$, 2 lake sites, 2 time periods), *Betula* (367 samples, 3 lake sites, 5 time periods), *Alnus* ($n = 269$, 2 lake sites, 2 time periods), *Picea* ($n = 46$, 2 lake sites, 2 time periods), *Pinus* ($n = 87$, 2 lake sites, 2 time periods). Differences among groups ($p < 0.05$) was assessed using one-way ANOVA with Bonferroni tests conducted on SPSS. Different letters indicate significant differences between groups.



	Herb	Dwarf shrub/ *Betula*	*Alnus*	Boreal forest
[DOC] mg L^{-1}	<2	2–4	4–8	>8

Fig. 3. Conceptual model predicting relative lake autotrophy and associated mechanisms across Arctic biomes, with the key vegetation transitions identified by the sedimentary analyses allocated typical DOC ranges based on values from the literature (Rouillard et al. 2011) and the measurements in Table 1.

gradient of increasing terrestrial biomass (from < 30–300 t ha^{-1} aboveground biomass; Supporting Information 1, Table S2), allowing us to comprehensively test the effects of changing watershed vegetation cover. The UVR index indicates that UVR exposure of lake photoautotrophs declined as vegetation biomass increased, with no UVR exposure indicated under coniferous forest (*Picea*, *Pinus*; Fig. 2a). Sedimentary pigments indicated major reorganizations of autotrophic community structure associated with different vegetation classes (Fig. 2). Carotenoids from siliceous algae and chlorophytes/cyanobacteria increased significantly during intermediate vegetation biomass (dwarf and *Betula* shrub tundra; Fig. 2d,e), suggesting that a unimodal model best describes relative shifts in autotrophic production of these algal groups along the gradient of vegetation types (Fig. 3). In contrast, alloxanthin (cryptophytes) and Chl *a* (all autotrophs) increased significantly when boreal forest cover was present (Fig. 2b,c), and declined when vegetation cover was sparse, indicating a more linear response to vegetation cover. These patterns were quite clear, despite inherent variability in the datasets which span a broad range of physiographic, edaphic, and ontogenetic circumstances. Therefore, while we note that these patterns require more rigorous experimental testing, they provide a useful preliminary overview for hypothesis testing and model development.

In agreement with our first hypothesis, lake autotrophic biomass appeared to be related to UVR exposure. Lakes located in sparsely vegetated catchments (herb) were more exposed to UVR (Leavitt et al. 1997) and had significantly lower concentrations of algal pigments, suggesting that UVR exposure might have restricted algal biomass (Leavitt et al. 2003; Harrison et al. 2015). It is well-established that lake waters in thinly vegetated catchments have low-CDOM concentrations and are highly transparent, although observations to date have been mostly confined to alpine (Rose et al. 2009) and Antarctic (Pienitz and Vincent 2000) rather than Arctic (Saulnier-Talbot et al. 2003) lakes. The lakes in this study are quite shallow (< 13.7 m; Table 1), with limited deepwater refuge from UVR exposure. The low concentrations of DOC (< 2 mg L^{-1}; Table 1) measured in the lakes from Greenland (herb cover in contemporary catchments) are within the sensitive range at which UVR penetration into lakes declines exponentially with respect to increasing DOC concentrations (Rose et al. 2009). Conversely, lakes located within forested areas are brown colored through CDOM influx which restricts the photic zone depth, reducing exposure of benthic areas, and restricting habitat for benthic cyanobacteria which are the main producers of UVR screening pigments (Leavitt et al. 1997). Therefore, our data supports the idea there is an optimal range of CDOM influx below and above which UVR exposure and light limitation respectively curtail production of siliceous algae and cyanobacteria/chlorophytes.

While the unimodal patterns exhibited by siliceous algae and cyanobacteria/chlorophyte groups are consistent with responses to light exposure, it is possible that nutrients bound in DOM and released by photolysis (hypothesis 2) could partly explain the patterns observed. Such mechanisms are likely to be important in Arctic lakes which are highly nutrient-limited (Whiteford et al. 2016). To further understand these patterns, we looked at proportions of planktonic (P) to benthic (B) diatom valves preserved in three of the sediment cores (Supporting Information 4, Fig. S4). If light availability was the primary driver of autotrophic communities, we expected that areal exposure of benthic habitats would increase under optimal light conditions and reduce the P : B ratios (Stone and Fritz 2006). During periods of maximum water transparency (herb cover) when UVR damage is likely to influence the ratios, diatom P : B ratios were low; benthic algal taxa are often common in UVR-exposed environments (Sommaruga 2001). However, during conditions of optimal light exposure (dwarf shrub cover; [DOC] 2–4 mg L^{-1}), P : B ratios were highest. The planktonic diatom *Discostella stelligera* increased during this period at Lake AT1 (Law et al. 2015). Therefore, the increase in autotrophic biomass might not be fully explained by littoral expansion and high phytobenthos production. Instead, a further explanation for this pattern is that DOM-influx under shrub tundra conditions supplied nutrients leading to an increase in planktonic algal biomass (Hansson et al. 1992; Vadeboncoeur et al. 2003; Rosén et al. 2009). The "alder rise" (transition from *Picea* to *Alnus*) in Alaska has been associated with increases in planktonic diatoms and linked to nitrogen supply (Perren et al. 2017), as observed in our

analyses (Supporting Information, Fig. S4). *Alnus* and *Dryas* are well-known nitrogen fixers and important for nutrient cycling in Arctic regions where nitrogen is generally scarce (Chapin et al. 1996). It is possible that the presence of these plants enhanced mineralization rates of labile soil C and reduced CDOM influx (Lavoie et al. 2011). This mechanism could partially explain the relative water clarity during *Alnus* and Herb zones and illustrates the potential for complex changes to DOM quantity and quality. Taken together, pigment and diatom evidence suggests that nutrient supply by DOM interacts with light conditions to influence autotrophic production in these lakes (Rosén et al. 2009; Seekell et al. 2015).

Our analyses also agree with our third hypothesis that lakes with greater catchment forest cover have more potentially mixotrophic taxa, recorded as significant increases in alloxanthin (a cryptophyte biomarker; Fig. 2c). The higher range of C : N ratios (Table 1) in the Alaska and Norway sediment cores supports the idea that allochthonous (colored) carbon sources were more prevalent in the forested lakes than in sites consistently covered in tundra (Greenland; lower C : N ratios within the algal-derived C range; Meyers and Teranes 2001). Cryptophytes are abundant in highly coloured boreal lakes and known to employ mixotrophy as a nutritional strategy (Lepistö and Rosenström 1998; Katechakis et al. 2005). As planktonic, motile protists they are well adapted to low light environments and a shallow photic zone. Thus, the patterns in alloxanthin (Fig. 2c), suggest a community shift toward motile algal groups, as vegetation biomass in the watershed increases, and we speculate that this was also associated with an increase in mixotrophy (Jansson et al. 2000). Patterns in Chl *a* were more similar to alloxanthin than the other pigments, which was rather unexpected because Chl *a* should provide an integrated measure of algal and cyanobacterial biomass. While it is possible that some Chl *a* could derive directly from terrestrial vegetation, allochthonous chlorophyll sources are usually only a minor component of lake pigment budgets due to decomposition during transport to the lake basin (Leavitt 1993). Chl *a* is more labile than most carotenoids (McGowan 2013) and the increases in sedimentary contributions associated with increases in water color are proposed to relate mainly to a combination of autochthonous production and preservation; water color limits the requirement for production of photoprotective accessory pigments (carotenoids) and reduces photo-oxidation of Chl *a* (Leavitt and Carpenter 1990). Photo-oxidation of organic matter is noted in many lakes and can influence water transparency (Osburn et al. 2001). Therefore, the Chl *a* patterns may indicate that pigments (and hence carbon) are buried more efficiently in highly colored lakes (Sobek et al. 2009).

The mechanisms proposed above provide logical explanations for the observed patterns, but it is inevitable in such a geographically dispersed long-term dataset that other factors might need to be considered. The effects of longer term landscape and lake ontogeny (succession) are relevant, because antecedent conditions including soil development have consequences for subsequent DOC and nutrient transfer to lakes (Engstrom et al. 2000; McGowan et al. 2008). Our statistical analyses attempted to remove long-term linear trends by using *z*-score transformation, but it is possible that some residual ontogenetic variance remains. However, because some vegetation zones (herb, *Betula*) associated with early periods of lake development were also present during later periods, our experimental design has countered ontogenetic effects as fully as possible, within the constraints of a paleolimnological study. Comparison among the sediment records also indicates different algal community composition among regions, with lower relative abundances of siliceous algae in Alaskan lakes, possibly related to the underlying limestone geology and lower silicate concentrations (Table 1). Terrestrial vegetation and permafrost soils are known to be important stores of silica, and it is possible that terrestrial vegetation cover regulated the supply of silica to lakes (Alfredsson et al. 2015). However, soil development is an inherent and inseparable property of vegetation biomes, which provides important contextual information on the effects of vegetation shifts. Despite these caveats, clear, significant, and ecologically sensible patterns were evident from the combination of six sediment records spanning vegetation zones.

Taken together, our results indicate that major changes in lake autotrophy : heterotrophy balance are likely along the vegetation gradients that we studied. Summarizing the pigment distributions alongside published and measured values of DOC, a conceptual model (Fig. 3) highlights that changes in the lake metabolic balance are most likely to occur in the lower ranges of lake DOC concentrations, i.e., < 4 mg L^{-1}, at the transition from herb to shrub tundra (< 2 mg L^{-1}) and shrub tundra to treeline (2–4 mg L^{-1}), close to Seekell's (2015) proposed threshold of 4.8 mg L^{-1}. Thus, although there has been a strong focus on boreal, subarctic, and thermokarst lake research, because of their importance for greenhouse gas emission and carbon storage (Walter et al. 2007; Karlsson et al. 2013), Arctic lakes which lie at this sensitive DOC transition zone, are probably most susceptible to net shifts in lake metabolic balance. While our sedimentary analyses cannot quantify the consequences for greenhouse gas fluxes, our conceptual model provides guidance for where such quantitative research efforts should be focused. The model developed from our results predicts that shifts in lake ecosystem carbon processing should tend toward increased autotrophy in sparsely vegetated (e.g., high Arctic) areas and heterotrophy in low Arctic tundra where woody vegetation biomass is increasing (Pearson et al. 2013). Accurate measures of rates of carbon efflux and burial in lakes across these transition zones are required to quantify the overall

importance of vegetation shifts within the broader Arctic terrestrial carbon cycle.

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