Spatial and temporal variability of algal community dynamics and productivity in floodplain wetlands along the Tanana River, Alaska

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Abstract: The boreal landscape is a mosaic of wetlands with distinct ecosystem properties. Algae are important for wetland functioning, but relatively little is known about the structure of algal communities among boreal wetlands. We documented spatial and temporal variability of algal community dynamics and productivity during a growing season in 6 wetlands (1 rich and 1 poor fen, 1 tussock, and 3 riverine marshes) in interior Alaska. Algal biomass and productivity were greater in the poor fen and a riverine marsh than in all other wetlands. Water depth and nutrients were significant predictors of benthic algal biomass and productivity among wetlands and were greatest immediately after the spring thaw and decreased during the growing season. Water depth and nutrients (N and P) explained the most variability in algal community structure. Algal community structure differed among wetlands, and temporal variation in environmental conditions was a significant predictor of the relative abundance of algal genera in individual wetlands. N_2-fixing cyanobacteria increased in abundance with a seasonal decline in water depth and nutrient concentrations. Our characterization of algal community dynamics and productivity in relation to environmental characteristics will help to forecast future wetland function in a changing boreal landscape.

Key words: algae, boreal, climate change, primary production, taxonomic composition, wetland

Algae are an integral component of wetland ecosystems (Robinson et al. 2000). Wetlands often lack a true phytoplankton assemblage, but benthic algae (including epiphytic forms) can be abundant because wetlands are shallow and have abundant submersed substrata available for colonization (Stanley et al. 2003). Algal material is easier than vascular plant material for grazers to ingest (Hart and Lovvorn 2003), making algae important for energy flow in wetland food webs (Hann et al. 2001, Rober et al. 2011). Their transformation of nutrients from inorganic to organic forms and the ability of cyanobacteria to fix atmospheric N_2 (DeLuca et al. 2002, Scott et al. 2005) make benthic algae important for nutrient cycling and retention in wetlands (Grimshaw et al. 1997). Despite the contribution of algae to wetland ecosystem processes and links between community structure and ecosystem function (Graham et al. 2009), research examining the factors that regulate algae in wetlands lags behind such research in other aquatic ecosystems. The paucity of information on wetland algae is particularly acute in boreal regions, where wetlands are abundant and likely to be affected by ongoing climate change.

Much of what is known about algal ecology in wetlands comes from work done in temperate (Robinson et al. 2000) and subtropical regions (Browder et al. 1994, Gaiser et al. 2011). Low-pH environments, such as those in temperate peatlands, tend to support green algae, particularly desmids (Greenwood and Lowe 2006). Cyanobacteria (blue–green algae) are tolerant of drought and commonly dominate algal communities in marginally moist or intermittent wetlands (Gottlieb et al. 2006). In the Florida Everglades, P concentrations <10 μg/L favor Ca-precipitating cyanobacteria and promote formation of marl sediments, a defining feature of the Everglades ecosystem (McCormick et al. 2001, Gaiser et al. 2006). Knowledge of the spatial patterns of algal communities and their interactions with biological and physical processes is needed to understand how environmental conditions affect ecosystem dynamics in wetlands.

Wetlands are a dominant feature on the boreal landscape, and they are diverse because of landscape position

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and variability in soil composition and hydrology. In the floodplains of large rivers, alternating cut-and-fill alluviation creates a habitat mosaic (Mouw et al. 2013) that includes shallow marshes with intermittent hydrology and dense stands of emergent macrophytes (Hall et al. 1994, Thormann and Bayley 1997). Interior wetlands are geologically older and are maintained by low evaporation rates and perennially (permafrost) and seasonally frozen ground, which impedes drainage and arrests decomposition (Schuur et al. 2013). These conditions facilitate accumulation of organic matter and the formation of peatlands (Wieder and Vitt 2006). As a consequence, peatlands make up ~¼ of the boreal land area (Wieder et al. 2006).

Conditions that favor wetland development across northern latitudes also make them susceptible to changes in climate (Schuur et al. 2013). In some areas of interior Alaska, wetlands are expanding because of hydrologic upwelling and meltwater runoff from the surrounding uplands (Osterkamp et al. 2000). In contrast, some wetland-rich areas are drying as a result of increased summer moisture deficits and drainage following permafrost thaw (Riordan et al. 2006, Roach et al. 2011). How these changes will affect aquatic ecosystems is debated (Carpenter et al. 1992, Flanagan et al. 2003), but consensus exists that processes related to climate warming (i.e., permafrost thawing, nutrient cycling) probably will increase algal primary production (Rouse et al. 1997). Except for small-scale experiments (Wyatt et al. 2010, 2012, Rober et al. 2013), few studies have been done on algal ecology in northern boreal wetlands. Larger-scale studies of algal ecology in boreal wetlands are needed to understand the spatial distribution of algae across the boreal landscape and to place experimental work within a larger spatial and temporal context.

Our goal was to relate patterns of algal productivity and community structure to the spatial and temporal variability of environmental conditions within wetlands of interior Alaska. Our objectives were to: 1) describe spatial and temporal patterns in the physical and chemical environment among wetlands, 2) characterize temporal variation in benthic algal biomass, productivity, and community structure among wetlands during a summer growing season, and 3) relate spatial and temporal variability of environmental conditions to algal community dynamics. We tested the hypothesis that algal productivity and community structure are heterogeneous across the boreal landscape and structured by environmental complexity that occurs in wetlands throughout time and space.

METHODS

Study sites

We conducted this study in the Tanana River floodplain just outside the Bonanza Creek Experimental Forest (35 km southeast of Fairbanks) in interior Alaska (Figs 1, 2). The Tanana River valley is 150 to 250 km south of the Arctic Circle and is part of the circumpolar band of boreal forest. The floodplain is in an intermontane plateau characterized by wide alluvium-covered lowlands with poorly drained shallow soils where fluvial deposition and erosion are annual disturbance events (Begét et al. 2006). The area is underlain by discontinuous permafrost and has large fluctuations in daylight with >21 h on June 21 and <3 h on December 21. The growing season is short (~135 d during May through August). This region has large fluctuations in average temperature (−23.5–16.3°C), a mean annual temperature of −2.9°C, and low levels of precipitation (269 mm/y) of which ~30% falls as snow (Hinzman et al. 2006).

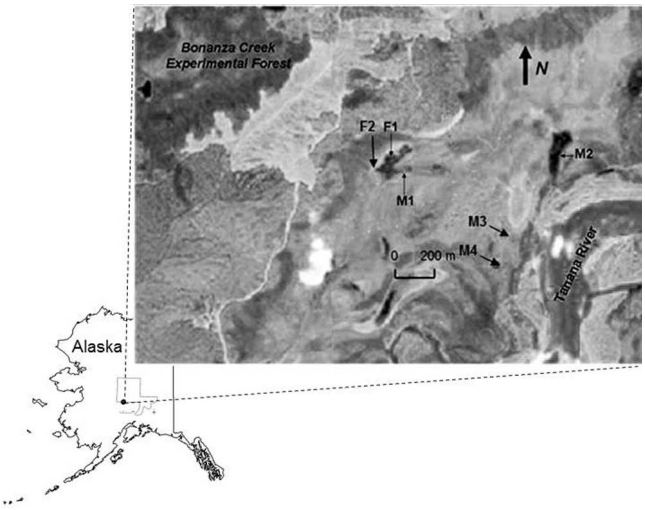

Figure 1. Aerial photograph showing the locations of the 6 wetland study sites.

We conducted field work to characterize the spatial and temporal variability in water depth, water chemistry, light attenuation, benthic algal biomass, productivity, and taxonomic composition in 6 wetland complexes, 2 peatlands and 4 marshes, in an expansive wetland mosaic along the Tanana River during the summer 2009 growing season (Figs 1, 2). The wetlands examined capture a range of physical and chemical conditions present in diverse peatland and marsh types that are characteristic of wetlands throughout boreal Alaska (Table 1). We used natural transitions in vegetation community structure and peat depth to distinguish wetland boundaries across the floodplain. Three wetlands used in our study (F1, M1, M2) were characterized by Kasischke et al. (2009) using remote sensing of vegetation and hydrology.

Wetlands M1, F1, and F2 are surrounded by lowland black spruce (*Picea mariana*) forest and shrub cover (*Andromeda polifolia*, *Gaultheria hispidula*, *Oxycoccus microcarpus*). Wetland F1 is a moderately rich fen that receives water from surface runoff, precipitation, and to a small extent, groundwater (Figs 1, 2). Vegetation is dominated

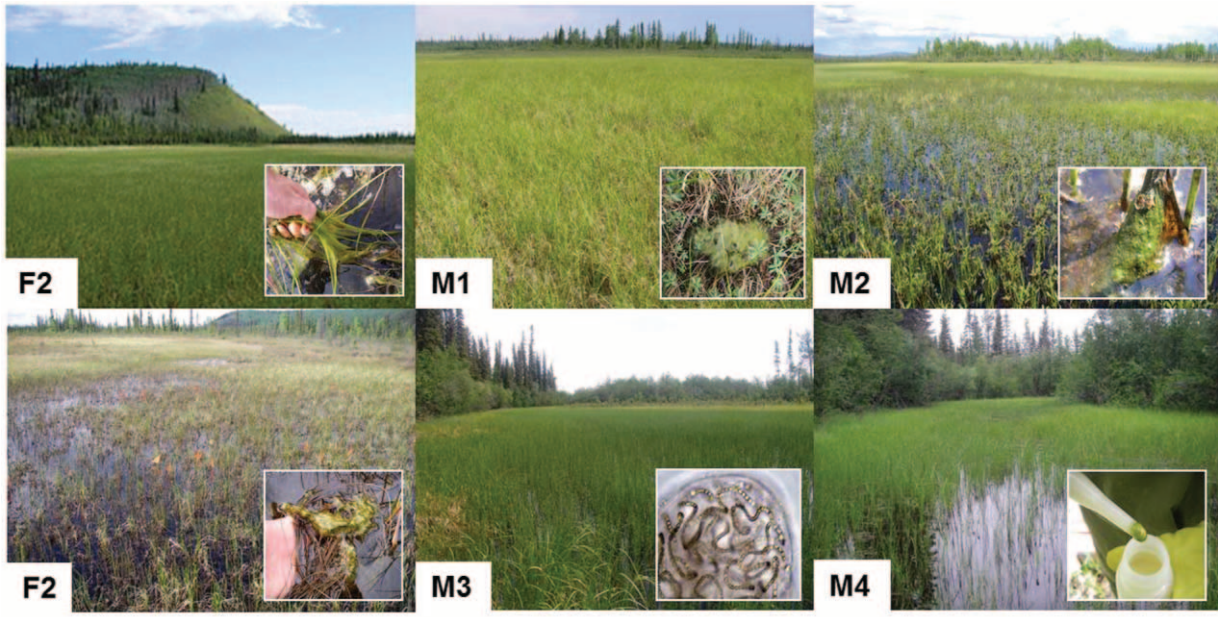

Figure 2. Images of the 6 wetland sites used in our study. F1 is a rich fen. F2 is a poor fen. M1 is a densely vegetated marsh with tussock grasses creating saturated hollows. M2 is a riverine marsh complex with several open water areas covered with floating macrophytes. M3 is a shallow riverine marsh dominated by *Equisetum fluviatile*. M4 is a shallow riverine marsh with diverse floating and emergent macrophytes. Insets show details of algae in each wetland.

by brown moss species, *Sphagnum*, and emergent vascular plants (*Carex utriculata*, *Equisetum* sp., and *Potentilla palustris*; Table 1). Peat thickness is >1 m. This wetland is part of the Alaska Peatland Experiment (APEX) described in detail by Turetsky et al. (2008). APEX is a large-scale experimental manipulation, but our samples were from a control plot with no manipulation. Wetland F2 is a peatland that receives water from surface flow and precipitation. It has a moss community composed of *Sphagnum* species (Table 1, Fig. 2), and is classified as a poor fen (National Wetlands Working Group 1997). F2 is ~100 m from F1 (Fig. 1) and is dominated by *Equisetum*, *C. utriculata*, and *P. palustris*. Peat thickness is >1 m.

Wetland M1 is ~50 m from F1 and F2 (Fig. 1), has <40 cm of peat, and is classified as a marsh (National Wetlands Working Group 1997). The dominant vegetation is short tussock grasses (*Carex* sp.), and intertussock spaces tend to be saturated with water (Fig. 2). No mosses are present (Table 1). Wetland M2 is in an abandoned oxbow ~300 m from the Tanana River (Fig. 1). It contains brown moss species but is classified as a marsh having <40 cm of peat (National Wetlands Working Group 1997). M2 is dominated by emergent vascular plants *Carex* sp. and *Equisetum* sp., and the floating macrophyte *Menyanthes trifoliate* (Table 1). This site has a thin layer of organic soil (~10 cm) on top of a mineral soil layer and undergoes extreme changes in hydrology, probably linked to river flow (Begét et al. 2006). Several open water pools are present within the marsh complex (Fig. 2). Wetland M3 is a shallow riverine marsh ~500 m from M2 and 50 m from the Tanana River. It is surrounded by alder (*Alnus* sp.), aspen (*Populus balsamifera*), and white spruce (*Picea glauca*) forest (Fig. 1). Vegetation in M3 consists almost entirely of *Equisetum fluviatile* (Fig. 2). Peat thickness is <40 cm, and mosses are absent (Table 1). Low levels of dissolved organic matter, probably linked to river connectivity, are present in the water column. Thus, M3 water is clearer than the tannin-enriched waters of the surrounding wetlands. Wetland M4 is a riverine marsh 100 m from M3 and the Tanana River (Fig. 1). M4 has diverse emergent vascular plants, including *E. fluviatile*, *C. utriculata*, *Sium suave*, *Sparganium angustifolium*, *Alisma plantago-aquatica*, and *Hippuris vulgaris* (Table 1). These dense stands of vegetation surround a shallow open-water pool with submerged *Utricularia intermedia* and *Ranunculus gmelinii* (Fig. 2). Peat thickness is <40 cm, and mosses are absent.

Sampling procedure

We sampled algae and water-chemistry variables weekly beginning in May, and then every 2 wk in July and August, or earlier if the water table fell below the soil or peat surface. We collected samples from 6 randomly selected locations along 25 to 100-m-long transects radiating out

Table 1. Description of wetland study sites and mean (ranges) of environmental variables over 12 wk during the 2009 summer growing season. Ranges illustrate seasonal change in environmental conditions and are arranged chronologically. TP = total P, TN = total N, SRP = soluble reactive P, DIN = dissolved inorganic N, DO = dissolved O_2, DOC = dissolved organic C, PAR = photosynthetically active radiation.

Characteristic	F1	F2	M1	M2	M3	M4
Wetland type	Rich fen	Poor fen	Tussock marsh	Riverine marsh	Riverine marsh	Riverine marsh
Peat thickness	>1 m	>1 m	<40 cm	<40 cm	<40 cm	<40 cm
Vascular plants	*Carex utriculata*, *Equisetum* sp., *Potentilla palustris*	*C. utriculata*, *Equisetum* sp., *P. palustris*	*Carex* sp.	*Carex* sp., *Equisetum* sp., *Menyanthes trifoliate*	*Equisetum fluviatile*	*E. fluviatile*, *C. utriculata*, *Sium suave*, *Sparganium angustifolium*, *Hippuris vulgaris*, *Utricularia intermedia*, *Ranunculus gmelinii*, *Alisma plantago-aquatica*
Mosses	brown moss, *Sphagnum*	*Sphagnum*	n/a	brown moss	n/a	n/a
TP (μg/L)	21.8 (6.4–33.3)	22.7 (19.8–25.9)	29.4 (21.1–41.7)	20.5 (8.81–1464.7)	29.5 (13.3–43.7)	25.2 (13.3–49.5)
TN (μg/L)	989.4 (876.9–1098.1)	1155.4 (967.9–1229.8)	1199.6 (1029.9–1560.3)	1403.8 (1221.1–1679.7)	682.4 (342.0–924.9)	744.5 (657.3–862.8)
SRP (μg/L)	1.38 (0–4.12)	2.45 (0–5.24)	3.10 (0–6.4)	1.85 (0.7–4.0)	3.28 (2.5–4.3)	1.93 (0.12–3.13)
DIN (μg/L)	11.6 (0.96–39.1)	7.77 (0–23.6)	33.0 (1.17–114.8)	18.6 (4.9–48.1)	12.9 (0–40.6)	4.99 (0–13.4)
Water depth (cm)	7.2 (10–0)	11.8 (39–0)	15.9 (42–0)	17.8 (29–4)	12.3 (25–0)	20.0 (45–0)
pH	5.53 (6.5– 4.61)	5.69 (5.84–5.48)	6.57 (6.5–6.6)	6.31 (6.18–6.72)	8.39 (8.28–8.61)	7.60 (7.4–7.8)
Water temperature (°C)	20.9 (15.4–25)	19.1 (15–25.1)	19.5 (18.5–20.1)	20.2 (18.2–20.9)	18.9 (18.0–19.25)	16.4 (14.7–18.2)
DO (mg/L)	12.1 (10.3–16.7)	9.80 (11.6–7.6)	6.70 (5.7–9.8)	6.79 (6.3–8.4)	12.5 (–)	9.23 (8.7–9.2)
DOC (mg/L)	28.7 (25.3–33.7)	47.9 (37.7–67.6)	35.3 (31.7–40)	40.7 (38.2–50.1)	10.8 (8.6–15.2)	13.95 (11.6–17.5)
PAR (μmol m^{-2} s^{-1})	713.5 (1154–424)	862.4 (1297–337)	357.8 (1114–66.4)	758.3 (1208–326.7)	556.7 (1433–117.7)	698.8 (1395–206.6)

from a central location in each wetland. Transect length varied among wetlands depending on wetland boundaries. On each sampling date, we collected benthic algae for estimates of biomass, productivity, and taxonomic composition. Each sample consisted of four 25-cm^2 subsamples collected from the peat surface when present, and the submersed portions of 4 stems of the dominant emergent macrophyte. We used a plastic syringe to remove algae from each 25-cm^2 quadrat until no loosely attached algae or biofilm remained (Wyatt et al. 2012). In cases where algae was attached to erect plant stems, we scraped the submersed portion of 4 stems clean with a plastic spoon and adjusted the surface area in calculations based on water depth, stem density, and the surface area of the plant stems measured with a caliper (Rober et al. 2013). We homogenized algal samples in 120 mL of water for analysis of chlorophyll *a*, ash-free dry mass (AFDM), and benthic algal abundance (algal cells/cm^2). We measured chlorophyll *a* (mg/m^2) from a subsample collected on a Whatman glass fiber filter (GF/F; Whatman, Maidstone, UK) with a Turner model 700 fluorometer (Turner Designs, Sunnyvale, California) after extraction with 90% ethanol and correction for phaeophytin (APHA 1998). We estimated AFDM (g/m^2) by drying samples at 105°C for 48 to 72 h and combusting them for 1 h at 500°C in preweighed Al pans to calculate the difference between dry mass and combusted mass, respectively (APHA 1998). We preserved a subsample in a 2% formalin solution for algal compositional analysis. We characterized algal taxonomic composition by counting and identifying ≥300 natural units/sample in a Palmer–Maloney nanoplankton counting chamber. We identified algae to genus at 400× magnification (Charles et al. 2002). When present, we counted heterocyst abundance as an indication of N_2-fixation capacity. We quantified benthic algal abundance (cells/cm^2) with the formula provided in Lowe and Laliberte (2006).

We estimated benthic algal productivity (mg C m^{-2} h^{-1}) by splitting a final portion of each homogenized sample into 2 separate biological O_2 demand (BOD) bottles and measuring changes in O_2 (McCormick et al. 1998). We filled each BOD bottle with filtered water from the wetland and recorded initial DO using a Hach HQ 40d luminescent DO probe (Hach Company, Loveland, Colorado). We wrapped one bottle from each set with Al foil for incubation in the dark. We incubated BOD bottles in situ at ~15 cm depth for 1 h between the approximate times of 1130 and 1330 h and recorded O_2 at the end of the incubation. Pre- and postincubation O_2 measurements from light and dark bottles were used to calculate net ecosystem productivity (NEP) of the algal biofilm and respiration, respectively. We calculated gross primary production (GPP) (Wetzel and Likens 2000) and converted GPP values into C units based on a C:O molar ratio of 0.375 and a photosynthetic quotient of 1.2 (Wetzel and Likens 2000).

We measured physical and chemical characteristics on each sampling date from the same 6 randomly selected locations used for algal collections. We measured water depth with a meter stick, and water temperature, DO, and pH with a calibrated model 556 YSI® Multi-Probe (YSI Incorporated, Yellow Springs, Ohio) at approximately the same time of day as productivity measurements to minimize variability associated with diurnal fluctuations. We filtered water for dissolved nutrient analysis through a 0.45-µm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, Massachusetts) into 120-mL sterile polyethylene bottles. We stored samples on ice until returning to the laboratory, where a portion of each filtered sample was analyzed for dissolved organic C (DOC) on a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, Maryland). The remaining portion of each sample was analyzed for dissolved inorganic N (DIN) as NO_3^- + NO_2^- with the Cd-reduction method on a Skalar® auto-analyzer (Skalar Analytical, Breda, Netherlands) and soluble reactive P (SRP) with the ascorbic acid colorimetric method using a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, UK) (APHA 1998). We collected whole-water samples in 120-mL sterile polyethylene bottles for analysis of total N (TN) and total P (TP), which were measured after oxidation with persulfate digestion, and 2nd-derivative ultraviolet (UV) spectroscopy and ascorbic acid methods, respectively (APHA 1998). We measured photosynthetically active radiation (PAR; µmol m^{-2} s^{-1}) in each plot 5 cm below the water surface using a Li-Cor submersible quantum sensor and LI-250 light meter (Li-Cor, Lincoln, Nebraska) attached to a 1-m pole to prevent disturbance of macrophytes.

Data analysis

We evaluated differences in algal abundance within and among wetlands and their interaction with environmental variables using general linear models in SPSS 18 (SPSS Inc., Chicago, Illinois). We evaluated differences in algal biomass and productivity among wetlands with repeated measures analysis of variance models (RM-GLM) with an adjusted Bonferroni significance level ($p < 0.016$) to preserve the experiment-wise Type I error rate and Tukey's test for post hoc comparison of means test. We used a bivariate Pearson correlation test to identify correlated environmental variables. We included water depth, TN, TP, PAR, and wetland site in a linear mixed model to predict changes in algal biomass and productivity, with the assumption that significantly correlated variables would respond similarly (Zar 2010). Prior to analysis, the distributions of continuous variables were $\log(x + 1)$-transformed, if necessary, to correct for nonnormal distribution and unequal variances among wetlands.

We evaluated differences in algal taxonomic composition among wetlands and sampling dates with a 2-way analysis of similarities (ANOSIM) test using PRIMER (version 5; PRIMER-E Ltd., Plymouth, UK). Analysis of similarities uses a dissimilarity matrix to test for statistically significant differences between ≥2 groups of sampling units. Therefore, if algal taxonomic composition differed among wetlands or sampling date, then among-wetland dissimilarities would be greater than within-wetland values. We used a canonical correspondence analysis (CCA) to evaluate temporal species–environment relationships among wetlands with PC-ORD (version 5; MjM Software, Gleneden Beach, Oregon). CCA axis scores were centered and optimized for genera. We used a Monte Carlo test to evaluate the relationship between matrices. We plotted sample scores that were linear combinations of species scores. We calculated algal taxonomic composition as a proportion of the total before analysis and included only taxa present at >5% relative abundance. We $\sqrt{(x)}$-transformed algal cell counts prior to ordination and ANOSIM to correct for nonnormal distribution and unequal variances.

RESULTS

Algal biomass and primary production

Algal biomass and productivity differed among wetlands and over time within wetlands. Measures of algal biomass and productivity were greater in the poor fen (F2) and riverine marsh complex (M2) than in the rich fen (F1), tussock marsh (M1), and shallow riverine marshes (M3, M4). Mean (± SE) chlorophyll *a* concentration (mg/m^2) was significantly greater in M2 (26.6 ± 7.8) than in other wetlands (RM-GLM, $F_{5,30} = 7.81$, $p \leq 0.028$; Fig. 3A), where values ranged from 2.5 ± 0.5 to 9.4 ± 3.6 and were not significantly different from each other ($p > 0.05$). Averaged across all wetlands, chlorophyll *a* was greatest during the early part of the growing season, peaked in mid-June, and decreased over the remainder of the growing season (Fig. 3E). AFDM (g/m^2) varied from 0.8 ± 0.1 to 5.47 ± 1.9 among wetlands and was greatest in F2 (RM-GLM, $F_{5,30} = 18.12$, $p \leq 0.009$; Fig. 3B), but the value in F2 was not different from the value in M2 (5.1 ± 1.4) ($p = 0.983$). Averaged across all wetlands, AFDM was greatest during the early part of the growing season and decreased over time (Fig. 3F). Benthic algal productivity (mg C m^{-2} h^{-1}) varied from 4.3 ± 0.78 to 32.8 ± 10.3 among wetlands and was nearly 2× greater in F2 (32.4 ± 3.63) and M2 (32.8 ± 10.3) than in the other wetlands (RM-GLM, $F_{5,30} = 7.47$, $p \leq 0.014$; Fig. 3C). Averaged across all wetlands, benthic algal productivity was greatest in early June and decreased over time (Fig. 3G). Algal cell density (10^4 cells/cm^2) was nearly 2× greater in M2 (36.6 ± 4.9) (RM-GLM, $F_{5,30} = 9.31$, $p \leq 0.0001$; Fig. 3D) than in all other wetlands, where values ranged from 1.2 ± 0.2 to 21.5 ± 3.4 and were not significantly different ($p > 0.05$). Averaged across all wetlands, algal cell density was greatest in mid-June and decreased over time until late July when cell density spiked because of a shift in taxonomic composition from large-celled filamentous green algae to small-celled cyanobacteria in F2 and M2 (Fig. 3H).

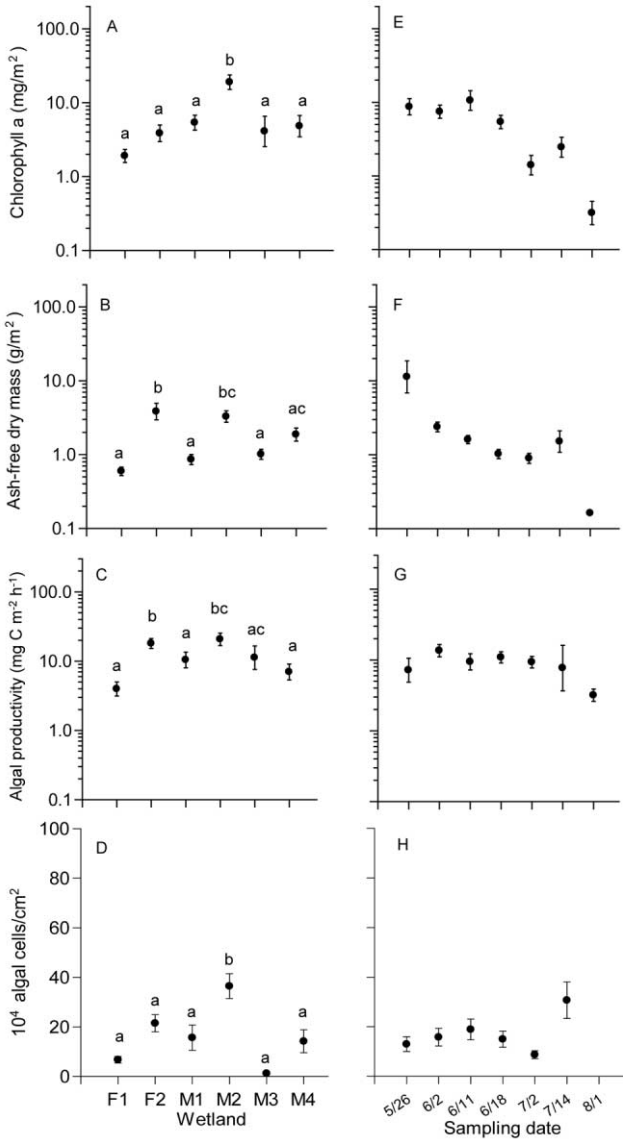

Figure 3. Mean (±1 SE) algal chlorophyll *a* concentration (A, E), ash-free dry mass (B, F), productivity (C, G), and cell density (D, H) in each wetland (A–D) and combined temporal change (E–H) during the summer 2009 growing season. Data are plotted on log-transformed axes. Dots with the same letter are not significantly different among sites. Dates are formatted m/dd.

Physical and chemical characteristics

Physical and chemical characteristics varied among wetlands and over time within wetlands. Mean TP varied only narrowly (20.5–29.5 μg/L) among wetlands (Table 1). Averaged across all wetlands, TP was lowest (10 μg/L) during

the early growing season (late May), peaked in mid to late June (30 μg/L), and decreased to ~20 μg/L for the remainder of the growing season (Fig. 4A). Mean TN concentration varied between 682.4–1403.8 μg/L among wetlands and was significantly greater in M2 than in the other wetlands (RM-GLM, $F_{5,240}$ = 209.9, p < 0.05; Table 1). Averaged across all wetlands, TN was relatively constant over the growing season (Fig. 4B). Inorganic forms of N and P (DIN and SRP) made up only a small fraction of total nutrient concentrations (TN and TP) (Table 1, Fig. 4C, D). Mean SRP concentration was <4 μg/L in all wetlands (Table 1) and decreased with time (Fig. 4D). Mean DIN was significantly greater in M1 (33 μg/L) than in all other wetlands, where values were ≤18.6 μg/L (RM-GLM, $F_{5,240}$ = 4.73, p < 0.05; Table 1). Averaged across all wetlands, DIN concentrations were relatively constant throughout the growing season (Fig. 4D). Nutrients (N and P) were the strongest predictors of AFDM (linear mixed model, $F_{5,68}$ = 45.3, p < 0.05).

Multivariate analyses indicated that benthic algal biomass and productivity were positively correlated with water depth in all wetlands indicating that seasonal change in water table is an important factor regulating boreal wetland algal communities. Water depth was greatest immediately after the spring thaw in all wetlands and decreased throughout the growing season until wetlands were dry (Table 1, Fig. 4E). Mean water depth was greater in the marshes (12.3–20 cm) than in the peatlands (7.2 and 11.8 cm) (Table 1). A linear mixed model indicated that wetland ($F_{5,69}$ = 45.3, p < 0.0001), time ($F_{6,226}$ = 22.6, p < 0.0001), and water depth ($F_{5,252}$ = 45.2, $p \leq 0.05$) were the strongest predictors of chlorophyll *a*, cell density, and productivity.

Environmental factors (pH, temperature, DO, DOC, and PAR) varied within and among wetlands, but they were not significant predictors of algal biomass or productivity (Fig. 4F–I). Mean pH was similar between peatland sites and was more acidic than in marshes (Table 1). Mean water temperature was similar among wetlands (Table 1) and increased throughout the growing season (Fig. 4G). Mean DO concentration was 2× greater in M3 and F1 (12 mg/L) than in M1 and M2 (6 mg/L) and was slightly higher than DO in F2 and M4 (9 mg/L) (Table 1). Averaged across all wetlands, DO concentrations were highest during peak algal abundance and decreased sharply over time (Fig. 4H). Mean DOC concentration was between 2 and 4× lower in wetlands closest to the Tanana River (M3 and M4) than in all other wetlands (Table 1). Mean PAR ranged from 357.8 to 862.4 μmol m^{-2} s^{-1} among wetlands

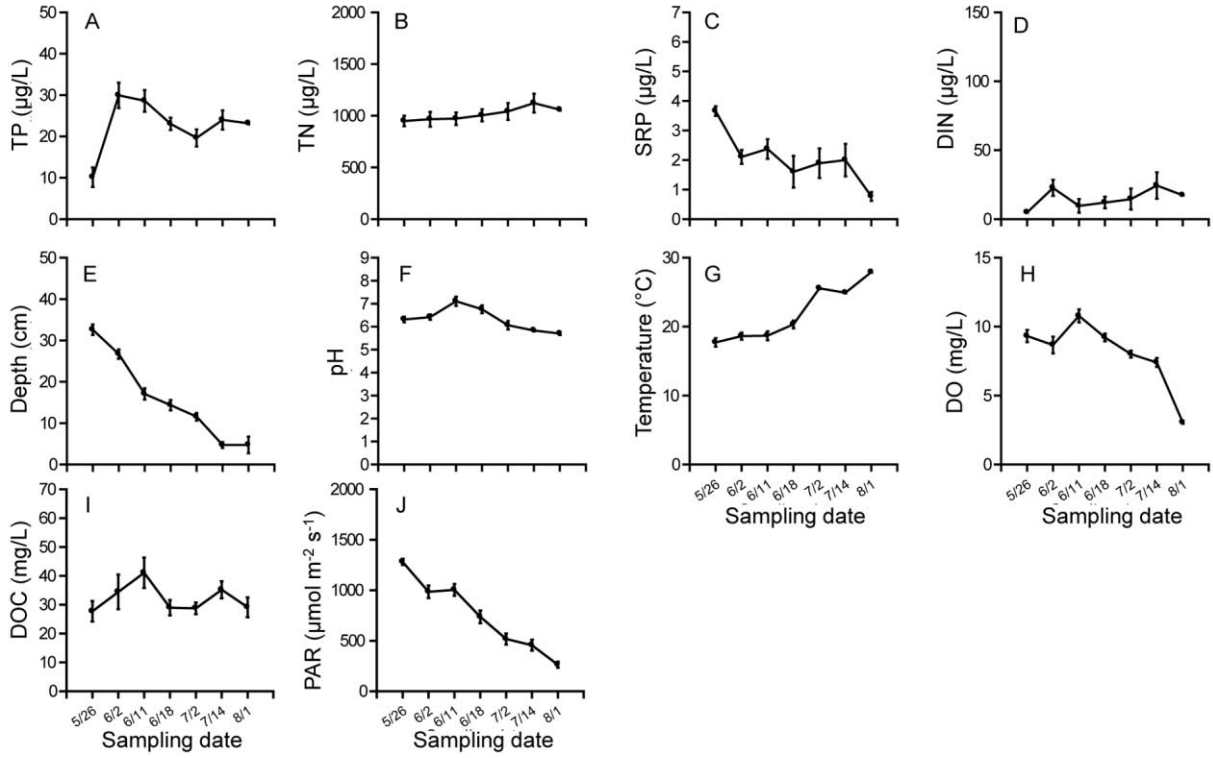

Figure 4. Mean (±1 SD) total P (TP) (A), total N (TN) (B), soluble reactive P (SRP) (C), dissolved inorganic N (DIN) (D), water depth (E), pH (F), water temperature (G), dissolved O_2 (DO) (H), dissolved organic C (DOC) (I), and photosynthetically active radiation (PAR) (J) in all wetlands during the summer 2009 growing season. Dates are formatted m/dd.

(Table 1) and decreased with increasing macrophyte growth throughout the growing season (Fig. 4J).

Algal taxonomic composition

Algal taxonomic composition was more similar within individual wetlands than among wetlands, and wetlands differed significantly from each other (ANOSIM, Global $R = 0.155$, $p = 0.015$) and over time (Global $R = 0.291$, $p = 0.001$). The higher Global R and correspondingly lower p-value for time indicate that temporal changes in taxonomic composition within each wetland were greater than differences among wetlands. The algal assemblage in all wetlands was composed of diverse green algae (Chlorophyta), cyanobacteria, Chrysophyta, and diatoms (Bacillariophyceae). Despite the presence of similar taxonomic groups, the proportion of individual genera varied over time and among wetland types. Across all sampling dates, 22 algal genera were present at >5% relative abundance in ≥1 wetland (Table 2). Chrysophyta, especially *Dinobryon*, and chain-forming desmids (Chlorophyta) *Bambusina* and *Desmidium* were present in greater abundances in peatlands (F1, F2), particularly the rich fen (F1), than in the marshes (Table 2). Filamentous green algae (*Microspora*, *Oedogonium*, *Spirogyra*, *Ulothrix*) and cyanobacteria, specifically N_2-fixing taxa (*Nostoc*, *Anabaena*, *Haplosiphon*), were abundant in peatlands and marshes (Table 2). N_2-fixing cyanobacteria became more abundant over the course of the growing season and the proportion of heterocysts increased from 3.4 ± 0.9% early in the growing season to 8.3 ± 0.7% as nutrient concentrations and the water table declined ($p = 0.01$). Diatoms did not contribute greatly to algal abundance, however *Tabellaria* was the dominant diatom in peatlands, particularly the rich fen (F1), whereas *Nitszchia* was more abundant in marshes, particularly M3 and M4 (Table 2).

Algal taxonomic composition was primarily influenced by water depth and time (CCA; Fig. 5). Algal taxonomic composition was equally influenced in direction and magnitude by TN and TP (Fig. 5). The effects of environmental variables that covaried with water depth (water tempera-

Table 2. Mean relative abundance of algal taxa in wetland sites over 12 wk during the summer 2009 growing season. Table includes only taxa with >5% relative abundance in ≥1 wetland site.

Algal division	Algal genus	F1	F2	M1	M2	M3	M4
Chrysophyta	*Dinobryon*	21.3	9.22	4.92	5.91	4.03	1.45
	Sum	21.3	9.22	4.92	5.91	4.03	1.45
Chlorophyta	*Bambusina*	6.34	9.52	4.81	1.37	0.10	1.05
	Desmidium	6.17	1.28	1.68	3.03	–	0.33
	Gloeocystis	7.51	9.19	8.73	5.95	9.10	5.28
	Microspora	3.31	15.9	2.76	0.39	1.99	0.86
	Oedogonium	5.73	5.42	4.21	2.31	3.85	4.66
	Palmella	–	0.22	3.28	–	6.87	9.05
	Radiofilium	8.77	0.41	3.02	–	1.69	1.18
	Sphaerocystis	5.34	2.59	2.92	1.41	1.07	1.96
	Spirogyra	2.11	5.09	0.60	0.39	1.03	5.88
	Ulothrix	3.34	2.51	5.37	3.73	4.33	28.6
	Sum	48.6	52.1	37.4	18.6	30.0	58.9
Cyanobacteria	*Anabaena*	3.64	7.28	2.86	36.1	–	6.72
	Aphanocapsa	17.5	5.15	14.9	4.67	2.66	–
	Calothrix	–	6.47	6.28	6.99	15.4	–
	Chroococcus	6.51	3.94	6.17	2.90	3.02	5.24
	Gloeocapsa	6.91	6.32	9.11	3.93	9.96	4.80
	Haplosiphon	6.34	7.71	0.50	17.2	–	–
	Merismopedia	6.09	2.78	12.0	5.23	–	–
	Nostoc	12.9	13.0	21.8	6.96	22.2	12.5
	Phormidium	1.33	–	–	10.2	–	–
	Sum	61.2	52.7	73.6	94.2	53.2	29.3
Diatoms	*Nitszchia*	0.82	0.22	0.83	2.02	7.00	5.68
	Tabellaria	7.83	2.46	2.84	2.00	–	–
	Sum	8.65	2.68	3.67	4.02	7.00	5.68

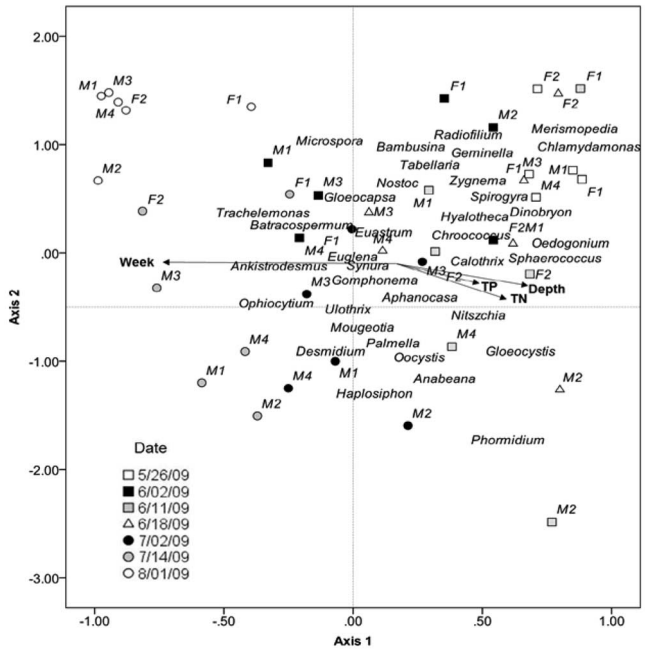

Figure 5. Canonical correspondence analysis (CCA) ordination illustrating the influence of environmental variables on algal community structure over successive sampling times and among wetlands (F1, F2, M1, M2, M3, M4). Arrows indicate the strength and direction of the correlation of environmental variables with the ordination axes. All symbols are labeled with the wetland site. Different symbols indicate week sampled during the growing season. Dates are formatted m/dd/yy.

ture, DO, pH) could not be separated from the influence of water depth, but probably influenced the algal community in a similar direction. DIN and SRP covaried with TN and TP and, therefore, probably have similar influence in direction, but potentially lower magnitude given that they contributed a small fraction of total nutrient concentrations (Table 1). PAR covaried with DOC because of tannins that reduce light penetration. However, PAR did not strongly contribute to the ordination so DOC probably does not influence algal taxonomic composition. Eigenvalues for the 1st, 2nd, and 3rd axes were 0.31, 0.122, and 0.079, and explained 23.9, 9.4, and 6.1% of the variability in the ordination, respectively, for a cumulative 39.3% of variance explained by the ordination (Fig. 5). The axes selected to describe the relationship of algal genera to environmental and temporal variation were significantly different than would be selected by chance alone (Monte Carlo test, $p = 0.001$).

DISCUSSION

Algal distribution and abundance is heterogeneous among boreal wetlands and varies in response to environmental complexity that occurs in space and time. Like in temperate (Goldsborough and Robinson 1996) and subtropical (McCormick et al. 1998) climates, algal communities were diverse and different among different wetland types (i.e., fens, marshes). Algal abundance and productivity varied considerably among wetlands and were related to variation in environmental conditions (i.e., hydrology, nutrient availability) during the summer growing season. Collectively, these findings support our hypothesis and suggest that environmental heterogeneity determines algal community structure among wetlands and that the timing of algal abundance and productivity within individual wetlands is governed mainly by temporal variation of environmental conditions. These findings suggest that algae-mediated functions in northern boreal wetlands probably will be altered by changes in environmental conditions associated with ongoing climate change.

Availability of N and P influenced algal community dynamics across the floodplain landscape despite expected variability in nutrient limitation among wetland types. Similar colimitation has been demonstrated in freshwater ecosystems globally (Francoeur 2001, Elser et al. 2007), which allows us to broaden the limited scope of previous work demonstrating N and P colimitation of wetlands within the Tanana River floodplain (Wyatt et al. 2010). Algal biomass and productivity were positively correlated with the timing of nutrient availability, were greatest immediately after the spring thaw, and decreased with nutrient depletion during the growing season. Understanding these timing mechanisms is important for future considerations of algal productivity with a changing climate. Currently, nutrient availability in northern latitude ecosystems is limited by slow rates of nutrient mineralization (Flanagan et al. 2003, Wrona et al. 2006). However, nutrient availability is projected to increase with soil weathering and decomposition of organic matter resulting from climate-change processes (Bridgham et al. 1995, Rouse et al. 1997). Nutrient inputs to boreal wetlands are likely to be minimal in comparison to inputs to aquatic ecosystems subject to eutrophication at lower latitudes (Gaiser et al. 2006, Scott and McCarthy 2010, Schindler 2012), but the algal response to nutrient concentrations <115 μg/L N and 7 μg/L P in our study suggests that even small increases in nutrient availability are likely to increase algal productivity and alter community structure in northern boreal wetlands.

Algal biomass and productivity were distinct among wetland types, but were positively correlated with water depth in all wetlands. Water depth is an important factor regulating algal structure and function in seasonally drawn-down marshes (Robinson et al. 1997a, b), naturally short- and long-hydroperiod Florida Everglades (Gottlieb et al. 2006), and during experimental water-table manipulation (both drought and flooding) in fens within the Tanana River floodplain (Rober et al. 2013). Given the consistency with which boreal wetlands experience drought during the growing season (Kane et al. 2010), water depth may have a par-

ticularly strong influence on the timing of algal productivity and community structure. Thus, we expect the algal contribution to wetland ecosystem processes to be greatest early in the growing season when standing water is above the soil surface and reduced as water depth decreases over time. Decreasing water depth may be caused by increased evaporative water loss with longer and drier growing seasons and by increasing temperature regimes that previously constrained water at the surface of permanently frozen soils (Serreze et al. 2000). Altered hydroperiod may have a particularly pronounced effect on algal communities in peatlands because water level is highly dependent on changes in rates of precipitation and evapotranspiration (Hinzman et al. 2006).

Algal productivity demonstrates the capacity for algae to contribute to C cycling in peatlands and marshes across northern boreal regions. When our measures of algal productivity are evaluated on an annual basis by converting hourly to daily measures, and then to annual values (based on 135-d ice-free period), mean algal productivity among all wetlands (30–235 g C m^{-2} y^{-1}) is in the lower range (0–500 g C m^{-2} y^{-1}) of values reported for temperate wetlands (reviewed by Goldsborough and Robinson 1996). During peak productivity, our annual estimates are below the lower range of productivity values reported for the subtropical Florida Everglades (300–600 g C m^{-2} y^{-1}; McCormick et al. 1998, Ewe et al. 2006). Algae are unlikely to contribute to long-term C storage, but our data provide information about the availability of algal production as a source of labile C for heterotrophic metabolism. Few researchers have evaluated the importance of algal productivity for heterotrophic metabolism in boreal wetlands, but C released by algae during laboratory incubations has been shown to be labile (Wyatt et al. 2012). Algal production may be an important source of C subsidies in peatlands where respiration is limited by the availability of labile organic matter (Bernot et al. 2010, Marcarelli et al. 2011).

Algal community structure differed among wetland types, and temporal variation in hydrology and nutrient availability within wetlands determined the relative abundance of individual genera within major algal groups. Filamentous green algae were most abundant early in the growing season, although the dominant genera varied among wetlands, and were replaced by cyanobacteria as water depth and nutrient concentrations declined following the spring thaw. The filamentous green algae, *Microspora*, *Oedogonium*, *Spirogyra*, and *Ulothrix*, were abundant in peatlands and marshes and often were found tangled among macrophyte stems and mosses. Large growths of filamentous green algae commonly appeared as grayish-white masses, probably because of infestation by fungal mycelia, which are important for the degradation of algal tissue (Yung et al. 1986). The widespread distribution and abundance of filamentous green algae among wetlands in our study suggest that they are tolerant of a range of environmental conditions and abundant at a relatively large spatial scale not detected in previous studies.

The abundance and distribution of N-fixing cyanobacteria in the rich fen (F1), riverine marsh (M2), and *Equisetum*-dominated marsh (M3) suggests that these taxa may be contributing to N inputs in peatlands and marshes in the Tanana River floodplain. The proportion of heterocyst-forming N_2-fixing cyanobacteria (i.e., *Nostoc*, *Anabaena*, *Haplosiphon*) increased as nutrient concentrations and the water table declined. This observation is consistent with greater abundance of N_2-fixing cyanobacteria in low-nutrient continuously saturated soils and during sustained periods of drought (Rober et al. 2013). The ability of these taxa to fix atmospheric N_2 enables them to survive in low-N environments (Scott et al. 2005) and has been described as the most important source of N to many arctic and boreal regions (Liengen 1999, Solheim et al. 2006). Our findings are consistent with previous research in a Swedish mire (Granhall and Selander 1973) and in feather mosses in the boreal forest (DeLuca et al. 2002), where similar taxa were associated with mosses and accounted for a high proportion of N input. The ability of N_2-fixing cyanobacteria to contribute to soil N may be particularly important in northern boreal regions where large quantities of nutrients are currently inaccessible because of the recalcitrant nature of organic matter. To our knowledge, the N-fixation potential of peatland cyanobacteria has not been quantified, but if N fixation were high, then nutrients made available by N-fixing cyanobacteria could increase moss and vascular plant production or, conversely, fuel nutrient-limited microbial decomposition.

Our characterization of algal community dynamics and productivity in relation to environmental conditions in boreal wetlands provides background information needed to inform future research and forecast changes in algal structure and function in a changing boreal landscape. Our study builds upon experimental evidence from individual boreal wetlands (Wyatt and Stevenson 2010, Rober et al. 2013), which broadens the applicability of previous findings to the larger landscape. Our results indicate that the contribution of algae to wetland ecosystem processes is likely to vary over time and among wetlands depending on differences in algal function related to taxonomic composition. Algal contribution to wetland ecosystem processes is likely to be most pronounced during the early part of the growing season immediately after seasonal ice thaw when algal biomass and productivity were greatest. Our results, in combination with data from Canadian prairie (Goldsborough and Robinson 1996, Robinson et al. 2000), subtropical (Browder et al. 1994, Gaiser et al. 2011, Hagerthey et al. 2012), and temperate (Wu and Mitsch 1998, Scott et al. 2005, Greenwood and Lowe 2006) wetlands, provide a foundation for understanding algal ecology across a wide

environmental gradient. Our study will facilitate across-ecosystem comparisons and inform ecological models designed to evaluate environmental controls on ecosystem function in anticipation of environmental change in the boreal forest.

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