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Carbon subsidies shift a northern peatland biofilm community towards heterotrophy in low but not high nutrient conditions

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Abstract

1. Producer–decomposer interactions within aquatic biofilms can range from mutualistic associations to competition depending on available resources. The outcomes of such interactions have implications for biogeochemical cycling and, as such, may be especially important in northern peatlands, which are a global carbon sink and are expected to experience changes in resource availability with climate change. The purpose of this study was to evaluate the effects of nutrients and organic carbon on the relative proportion of primary producers (microalgae) and heterotrophic decomposers (bacteria and fungi) during aquatic biofilm development in a boreal peatland. Given that decomposers are often better competitors for nutrients than primary producers in aquatic ecosystems, we predicted that labile carbon subsidies would shift the biofilm composition towards heterotrophy owing to the ability of decomposers to outcompete primary producers for available nutrients in the absence of carbon limitation.
2. We manipulated nutrients (nitrate and phosphate) and organic carbon (glucose) in a full factorial design using nutrient-diffusing substrates in an Alaskan fen.
3. Heterotrophic bacteria were limited by organic carbon and algae were limited by inorganic nutrients. However, the outcomes of competitive interactions depended on background nutrient levels. Heterotrophic bacteria were able to outcompete algae for available nutrients when organic carbon was elevated and nutrient levels remained low, but not when organic carbon and nutrients were both elevated through enrichment.
4. Fungal biomass was significantly lower in the presence of glucose alone, possibly owing to antagonistic interactions with heterotrophic bacteria. In contrast to bacteria, fungi were stimulated along with algae following nutrient enrichment.
5. The decoupling of algae and heterotrophic bacteria in the presence of glucose alone shifted the biofilm trophic status towards heterotrophy. This effect was overturned when nutrients were enriched along with glucose, owing to a subsequent increase in algal biomass in the absence of nutrient limitation.
6. By measuring individual components of the biofilm and obtaining data on the trophic status, we have begun to establish a link between resource availability and biofilm formation in northern peatlands. Our results show that labile carbon subsidies from outside sources have the potential to disrupt microbial coupling and shift

the metabolic balance in favour of heterotrophy. The extent to which this occurs in the future will probably depend on the timing and composition of bioavailable nutrients delivered to surface waters with environmental change (e.g. permafrost thaw).

KEYWORDS
algae, bacteria, carbon, climate change, fungi, nutrients, peatland

1 | INTRODUCTION

Biofilms are aggregates of autotrophic and heterotrophic microorganisms that form associations on surfaces in aquatic environments (Carr, Morin, & Chambers, 2005; Flemming & Wingender, 2010; Scott et al., 2008). In conditions where sufficient sunlight reaches submersed surfaces, algal members of the biofilm fix inorganic carbon into organic forms during photosynthesis. A portion of this photosynthetic product is released into the surrounding environment (Bertilsson & Jones, 2003) where it serves as a source of energy for heterotrophic microorganisms, including bacteria (Cole, 1982; Francoeur et al., 2020; Kuehn et al., 2014; Wyatt & Rober, 2020) and fungi (Halvorson et al., 2019; Kuehn et al., 2014; Wyatt et al., 2019). These decomposers, in turn, convert organic nutrients into inorganic forms, making them available for uptake by resource-limited algae (Daufresne & Loreau, 2001; Kuehn et al., 2014; Mesquita et al., 2019). This reciprocal exchange of resources forms the basis for microbial resource cycling in aquatic ecosystems and is generally considered to be the interaction upon which producer–decomposer coexistence within biofilms depends (Daufresne & Loreau, 2001).

Resource availability governs many aspects of aquatic biofilm formation (Kalscheur et al., 2012; Koedooder et al., 2019). The coexistence of primary producers and decomposers within the extracellular matrix requires that neither group competitively exclude the other from assimilating resources. Accordingly, differential limitation is an important factor for persistence of all biofilm communities. Primary producers in freshwater systems are often limited by the availability of inorganic nutrients, mainly nitrogen (N) and phosphorus (P) (Elser et al., 1990). Decomposers are often limited by organic carbon but may also be secondarily limited by nutrients (Burrows et al., 2017; Daufresne et al., 2008). Although decomposers are generally considered to be superior competitors over primary producers for available nutrients (Currie & Kalff, 1984a, 1984b; Joint et al., 2002; Liu et al., 2012), carbon limitation can result in decomposers depending on primary producers for organic carbon (Currie & Kalff, 1984b; Daufresne et al., 2008; Daufresne & Loreau, 2001; Wyatt & Turetsky, 2015).

Compared to our understanding of biofilm ecology in rivers (Battin et al., 2016; Bechtold et al., 2012; Wagner et al., 2017) and lakes (Ozersky et al., 2018; Wyatt et al., 2019), our knowledge of microbial interactions within wetlands is lacking (Halvorson et al., 2020). This knowledge gap is particularly evident in peatlands, a dominant wetland type at northern latitudes (Kolka et al., 2018). Northern peatlands are often characterised as nutrient poor ecosystems (Wieder, 2006). Plants that can tolerate low nutrient availability (e.g. mosses) produce litter that is slow to decompose (Moore & Basiliko, 2006). Over time, this results in an imbalance between primary production and decomposition, leading to the accumulation of organic matter as peat. While this paradigm represents dry conditions well, it does not fully represent periods of time when peatlands are inundated with water. Under these conditions, a biofilm develops on peat surface layers with the potential to influence aspects of biogeochemical cycling through active uptake and retention of nutrients (DeColibus et al., 2017). It also stands to reason that nutrient and carbon availability govern aspects of biofilm formation in northern peatlands by regulating competitive interactions within the biofilm matrix. Along with low nutrient availability, organic matter in peatland surface waters is comprised of high molecular weight compounds that are resistant to decomposition (Hansen et al., 2016). This may change in the future as permafrost thaw associated with climate warming is expected to transport bioavailable organic carbon and nutrients from previously frozen soils to surface waters across northern ecosystems (Abbott et al., 2014; Davis, 2001; Reyes & Lougheed, 2015; Wickland et al., 2018). Inputs of inorganic nutrients and labile organic matter may influence ecosystem processes in northern peatlands by regulating the composition and activities of microbial primary producers and decomposers that develop within biofilms on submerged peat surfaces.

For the most part, studies examining biofilm development in northern peatlands have focused on direct associations between algae and heterotrophic bacteria (e.g. DeColibus et al., 2017; Wyatt & Turetsky, 2015). To our knowledge, no study has examined producer–decomposer interactions across algae, bacteria, and fungi in northern peatlands and how these interactions respond to changes in resource availability expected with environmental change. Here, we manipulated inorganic nutrients (N and P in combination) and organic carbon (glucose) in a full factorial design using nutrient-diffusing substrates to examine the influence of nutrient and carbon subsidies on the formation of biofilms in a northern peatland. Overall, we hypothesised that differential nutrient limitation, where primary producers are limited by inorganic nutrients and decomposers are limited by labile organic matter, would promote stable coexistence between primary producers and decomposers. We predicted that nutrient enrichment would stimulate the growth of biofilm algae and that decomposer growth would be stimulated by labile organic carbon. We further predicted that organic carbon amendments would disrupt mutualist producer–decomposer interactions and shift the biofilm community in favour of decomposers.

2 | METHODS

2.1 | Study area and experimental design

This experiment was conducted in a fen peatland located within the Tanana River floodplain approximately 30 km southeast of Fairbanks, Alaska, U.S.A. (64°42N, 148°18W). This peatland has no tree cover and the plant community is composed of brown and *Sphagnum* mosses and emergent vascular plants (primarily *Equisetum fluviatile*, *Carex atherodes*, and *Potentilla palustris*). Mean (range) water-column concentrations (μg/L) of nitrate (NO_3^-) and phosphate (PO_4^-) are typically 11.6 (0.96–39.1) and 1.38 (0–4.12), respectively, and total phosphorus and total nitrogen are 21.8 (6.4–33.3) and 989.4 (876.9–1,098.1), respectively (Rober et al., 2014). The pH ranges from 5.5–6.9 during the summer growing season. Dissolved organic carbon (DOC) generally ranges between 15 and 50 mg/L (Gu & Wyatt, 2016). Topography at the site is flat with intermittent hydrology, ranging from 0–45 cm above the peat surface. We conducted the field experiment during a wet period when mean water depth at the site was 29.2 ± 4.5 cm. This region of interior Alaska experiences a short growing season (≤135 days/year) with >21 hr of daylight in June, which is when the experiment was conducted.

To examine the independent and interactive effects of nutrients and organic carbon on biofilm development, we made nutrient-diffusing substrates using 60-ml polyethylene canisters (Tank et al., 2017) filled with agar enriched with one of four treatment combinations (n = 4 for each treatment): no enrichment (control treatment), both N and P (NP treatment), glucose (G treatment), or a combination (NP + G treatment). Nutrients were added to an agar solution at a concentration of 0.5 mol/L of N and P (50.6 g/L KNO_3 and 68 g/L KH_2PO_4, respectively) (Tank et al., 2017). We manipulated carbon by adding 0.5 mol/L glucose (90.1 g/L). Our goal with enrichments was to alleviate resource limitation of the biofilm and we assumed that previously reported diffusion rates (Wyatt et al., 2015) would be growth saturating because they exceeded levels shown to alleviate resource limitation of other wetland biofilms (Wyatt & Turetsky, 2015). A 2.5-cm diameter circular hole was cut into the cap of each canister and a fritted glass disc was placed on top of the agar gel to serve as a substrate for biofilm growth and the caps were snapped shut (Figure 1). Inorganic substrates were used so that we could evaluate aspects of carbon limitation on the biofilm community without the confounding effects of substrate composition. The resulting nutrient-diffusing substrates were secured to segments of angle iron using all-purpose adhesive and suspended 10 cm below the water surface (Figure 1). Each section of angle iron (n = 4 for each treatment) contained three subsamples per treatment to allow one measurement per replicate of algal, bacterial, and fungal biomass. The experiment was left for 10 days (beginning on 17 June) to allow for biofilm colonisation. We expected that this period would allow us to observe biofilm development that is characteristic of intermittent peatlands while also minimising the potential for desiccation associated with variable hydrology observed within the larger fen complex (DeColibus et al., 2017).

Water temperature (°C) and light (as μmol photons m^{-2} s^{-1} photosynthetically active radiation) were collected using HOBOTEMP data loggers (Onset Computer Corporation, Cape Cod, MA, U.S.A.) at 4-hr intervals for the length of the experiment. On the day of deployment and on days 6 and 10 of the experiment, ancillary measures of water parameters were taken. Water samples were filtered through a 0.45-μm syringe-driven filter (Millipore Corporation, Bedford, MA, U.S.A.) into sterilised 120-ml Nalgene® bottles, frozen, and later analysed for nitrate and phosphate via high-pressure ion chromatography on a Dionex ICS-5000 system (Dionex Corporation, Sunnyvale, CA, U.S.A.) and for DOC using a Shimadzu TOC-L carbon analyser (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.). Water depth was measured using a metre stick and dissolved oxygen, water temperature, pH, and conductivity were measured using a Hach 40D portable multi meter (Hach, Loveland, CO, U.S.A.).

On day 10, the glass disc substrates were carefully removed from each canister using forceps to quantify biofilm colonisation. Separate discs for algal and fungal biomass were stored frozen and dark in 50-ml centrifuge tubes until analysis. Discs for bacterial counts were placed in plastic containers with 10 ml of spring water and scrubbed vigorously with sterile toothbrushes to remove adhesive bacteria. The resulting slurry was poured into 20-ml scintillation vials and preserved with a 10% formalin solution for later analysis of bacterial biomass and autotrophic index.

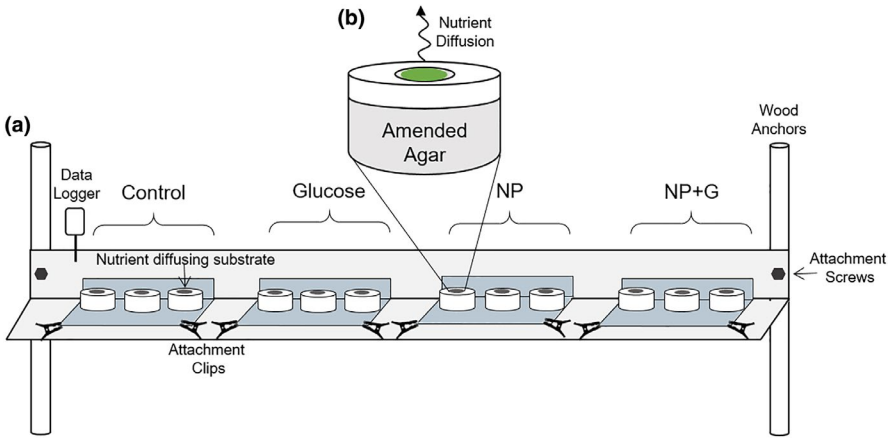

FIGURE 1 Schematic of the experimental design in the peatland depicting the arrangement of treatments and nutrient-diffusing substrate canisters (a). One replicate of each of the four treatments is represented per plank, with each replicate containing three subsamples. Four planks were deployed in the peatland (n = 4 for each treatment). Enlargement of 60-ml canister containing nutrient amended agar and topped with a porous glass disc substrate for biofilm colonisation (b) [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Biofilm analysis

Algal biomass was estimated using chlorophyll *a* as a commonly-accepted proxy (APHA, 1998). Chlorophyll *a* was extracted by submerging the glass discs in ethanol with all phases of analysis performed in the dark to prevent degradation. The glass discs were inundated with 15 ml of 95% ethanol directly in the 50-ml centrifuge tubes and left to extract at 4°C in the dark for 24 hr, after which the glass discs were removed and the resulting pigment extracts were allowed to reach room temperature prior to analysis. Spectrophotometric analysis was performed using a Cary 60 UV-Vis spectrophotometer (Agilent Technologies, Santa Clara, CA, U.S.A.). Sample absorbance was read at 665 and 750 nm, and then re-read at the same wavelengths 5 min after acidification with 2N HCl to correct for phaeophytin (APHA, 1998).

Bacterial biomass estimates were made using bacterial cell counts converted to carbon mass. The formalin-preserved samples were brought to equal volume using nanopure water and homogenised by vortex. An aliquot of each sample was stained using 4',6-diamidino-2-phenylindole to make bacterial cells fluorescent (Porter & Feig, 1980) and vacuum-filtered onto a 0.2 μm pore-size black filter (Whatman, Maidstone, U.K.). Bacterial cells were enumerated in the dark at 1,000× total magnification using epifluorescence microscopy on a Leica DM 1,000 microscope (Leica Microsystems, Buffalo Grove, IL, U.S.A.). Counts continued until ≥300 cells or 25 fields were enumerated (Ward & Johnson, 1996). Cell volume (μm^3) was calculated from measurements of length (*l*) and width (*w*) using the formula: $V = w^2/4 \times (l\text{-}w) \times \pi + w^3/6 \times \pi$ (Fry & Davies, 1985). Bacterial biovolume was then calculated by multiplying cell counts by mean cell volumes for each treatment replicate and converted to biomass using a conversion factor of 0.31 pg C cm^{-3} (Ward & Johnson, 1996).

Fungal biomass within biofilm samples was estimated using the concentrations of ergosterol, a membrane sterol in fungi (Gessner, 2005). Frozen substrates were lyophilised in the laboratory until dry, weighed, and placed into 10 ml of alcoholic KOH (0.8% KOH in HPLC grade methanol) and heated to 80°C for 30 min. The resultant crude extract was partitioned into n-pentane and evaporated to dryness with nitrogen gas. Dried ergosterol residues were resuspended in methanol and quantified using high-performance liquid chromatography (Kuehn et al., 2011; Su et al., 2015). Fungal biomass was then calculated using ergosterol concentrations and a conversion factor of 10 μg of ergosterol/mg fungal carbon, assuming 43% carbon in fungal dry mass (Kuehn, 2016).

An autotrophic index was calculated to evaluate the relative proportion of autotrophic and heterotrophic components within the biofilm (Steinman et al., 2006). A portion of each preserved sample was homogenised and emptied into pre-weighed aluminium weigh pans. Samples were dried at 105°C for at least 24 hr until weight was constant and then combusted in a muffle furnace at 500°C for 1 hr for the measurement of ash-free dry mass. Ash-free dry mass was then calculated by subtracting the ash weight from the dry weight and dividing by the surface area of the substrates. Autotrophic index was then calculated by dividing the ash-free dry mass of each sample by the concentration of chlorophyll *a* (Steinman et al., 2006). We used this index to evaluate the relative biomass of biofilm autotrophs and heterotrophs, where higher index values indicate a greater proportion of heterotrophic organisms in the microbial community (Bechtold et al., 2012; Steinman et al., 2006).

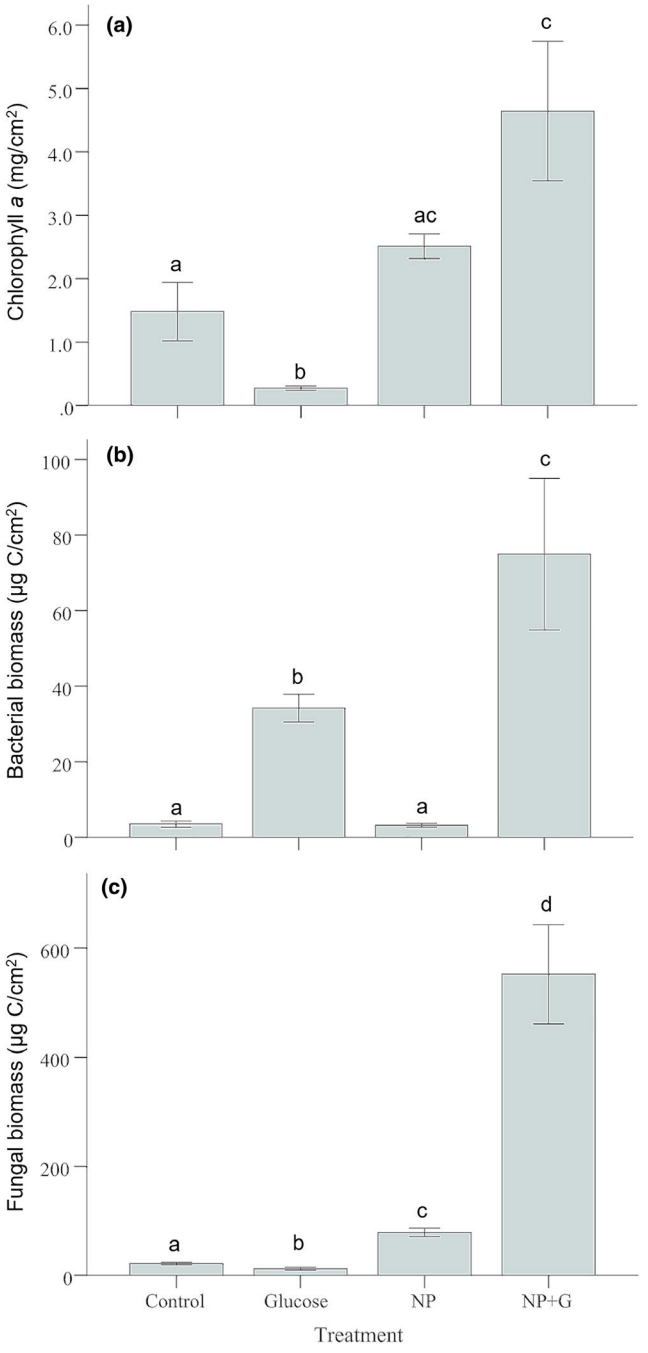

FIGURE 2 Comparison of biofilm (a) chlorophyll *a* (mg/cm^2), (b) bacterial biomass ($\mu g\ C/cm^2$), and (c) fungal biomass ($\mu g\ C/cm^2$) on nutrient diffusing substrates enriched with either agar only (control), glucose, nitrogen + phosphorus (NP), or a combination (NP + G). Bars are the mean of four replicates ± 1 SE. Significant differences are indicated by different letters ($p < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Statistical methods

Two-way general linear models were used to evaluate the independent and interactive effect of nutrients (enriched, unenriched) and glucose (enriched, unenriched) on chlorophyll *a*, bacterial biomass, fungal biomass, and autotrophic index. Where appropriate, data were log(x + 1)-transformed to correct for non-normal distribution of residuals. When significant differences among factor levels were detected ($p < 0.05$), *post hoc* least significant differences were used to discriminate between factor levels. Statistical analyses were performed using SPSS Statistics Version 20 (SPSS, Chicago, IL, U.S.A.).

3 | RESULTS

There was a significant interaction effect of nutrients and glucose on algal biomass ($F_{1,12} = 13.2$, $p = 0.003$; Figure 2a). Algal biomass was nearly 2-fold greater in the NP treatment compared to the control treatment but this difference was not statistically significant ($p = 0.08$). In contrast to nutrients, glucose alone had a negative effect on algae, reducing algal biomass by more than 5-fold compared to the control treatment ($p = 0.009$). A combination of glucose and nutrients (NP + G) significantly elevated algal biomass compared to glucose ($p < 0.001$) and control ($p = 0.009$) treatments.

Bacterial biomass was primarily limited by glucose and secondarily limited by nutrients. Glucose enrichment alone increased bacterial biomass 10-fold compared to the control treatment ($F_{1,12} = 200.6$, $p < 0.001$; Figure 2b). Nutrients alone did not stimulate bacterial biomass compared to the control treatment ($p = 0.09$). However, when combined with glucose (NP + G), nutrients further increased bacterial biomass more than 2-fold over glucose alone ($p = 0.02$).

There was a significant interaction effect of nutrients and glucose on fungal biomass ($F_{1,12} = 54.9$, $p < 0.001$; Figure 2c). Fungal biomass was significantly greater in the NP treatment compared to the control ($p < 0.001$). Glucose alone had a significantly negative effect on fungi, reducing biomass by nearly half compared to the control ($p = 0.02$). Fungal biomass showed the strongest response to a combination of nutrients and glucose (NP + G) and was significantly greater than with either glucose or nutrients alone ($p < 0.001$ for both).

There was a significant interactive effect of nutrients and glucose on autotrophic index ($F_{1,12} = 71.1$, $p < 0.001$; Figure 3). In contrast to nutrients alone (NP), which had no significant effect on overall autotrophic index ($p = 0.61$), autotrophic index was nearly 20 times greater (i.e. more heterotrophy) in the glucose treatment compared to the control ($p < 0.001$). Nutrients effectively neutralised the positive effect of glucose in the combination treatment (NP + G), significantly reducing the autotrophic index (i.e. less heterotrophy) compared to the glucose only treatment ($p < 0.001$) and resulting in values similar to the NP treatment ($p = 0.39$).

Environmental variables were relatively constant during the study period (Table S1). Mean (± *SE*) photosynthetically active radiation (μmol photons m^{-2} s^{-1}) was 565.2 ± 49.9 during daylight hours and mean daily water temperature was 18.3 ± 0.17°C. Water pH was slightly acidic (6.25 ± 0.12), dissolved oxygen measured 8.70 ± 0.16 mg/L, and conductivity was 32.3 ± 0.78 μS/cm. Dissolved nutrient concentrations in the water column (in the form of NO_3 and PO_4) were 15.7 ± 4.22 and 5.06 ± 1.24 μg/L, respectively. Mean DOC concentration at the site was 50.4 ± 0.47 mg/L.

4 | DISCUSSION

Boreal regions are experiencing a period of unprecedented climatic change that is expected to increase in severity over the next several decades (IPCC, 2013). The resulting changes such as permafrost degradation may alter the availability of limiting resources in peatlands by introducing nutrients and bioavailable carbon trapped within permafrost (Abbott et al., 2014; Davis, 2001; Reyes & Lougheed, 2015). Given that peatlands are widespread across the boreal landscape (Kolka et al., 2018) and store vast amounts

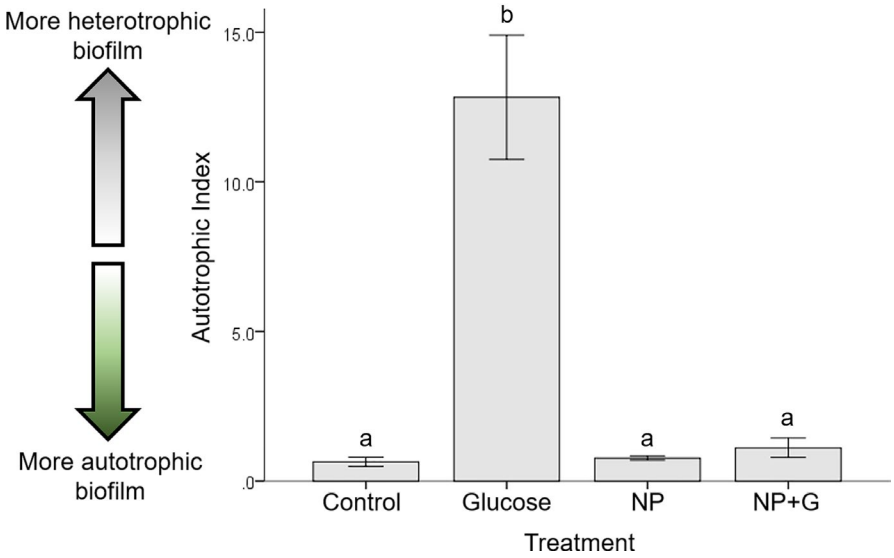

FIGURE 3 Comparison of biofilm autotrophic index (mg of ash-free dry mass cm^{-2} mg chlorophyll a^{-1}) on nutrient diffusing substrates enriched with either agar (control), glucose, nitrogen + phosphorus (NP), or a combination (NP + G). The autotrophic index is a measure of the ratio of total biofilm biomass to chlorophyll *a*, where larger values for the index indicate more heterotrophic biomass relative to autotrophic biomass. Bars are the mean of four replicates ± 1 *SE*. Significant differences are indicated by different letters ($p < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

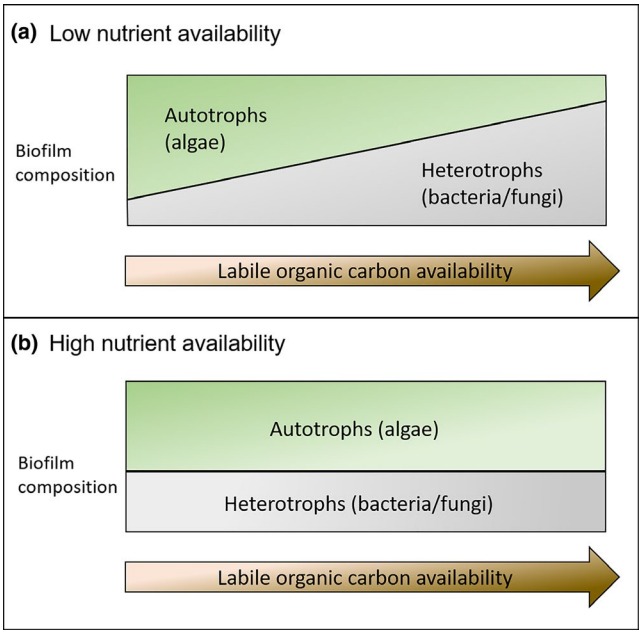

FIGURE 4 Conceptual diagram showing the relative proportion of autotrophs and heterotrophs in peatland biofilms in relation to the availability of labile organic carbon. In conditions of low nutrient availability (a), increasing labile organic carbon shifts the biofilm composition to heterotrophy owing to the ability for heterotrophs to outcompete autotrophs for available nutrients in the absence of carbon limitation. This shift does not occur in high nutrient environments (b) because nutrient levels surpass the combined energetic requirements of autotrophs and heterotrophs; instead, elevated levels of algal biomass maintain an autotrophic biofilm (i.e. a low autotrophic index value) even in the presence of carbon amendments [Colour figure can be viewed at wileyonlinelibrary.com]

of terrestrial carbon (Gorham, 1991) it is crucial that we better understand the role that biofilms play in regulating peatland energy flow and how resource inputs may alter biofilm development. Accordingly, our study was designed to examine how nutrients and labile carbon affect the relative proportion of primary producers and decomposers during peatland biofilm formation. Our overarching hypothesis that carbon subsidies would allow decomposers to outcompete primary producers for nutrients was supported in some conditions. In general, organic carbon subsidies did have an important role in determining competitive outcomes among the biofilm community. However, the extent to which carbon subsidies regulated community membership depended on background nutrient levels. In this respect, our study adds support to the carbon limitation hypothesis (Currie & Kalff, 1984b; Daufresne & Loreau, 2001) as a tool for understanding microbial interactions in boreal peatlands but notes that nutrient levels are a crucial factor in mediating microbial interactions and possible competitive exclusion (Figure 4).

Nutrient limitation of benthic algae has been documented in a variety of systems including streams (Ziegler & Lyon, 2010), lakes (Ozersky et al., 2018), and wetlands (Cooper et al., 2016). Algae in freshwater ecosystems are often co-limited by both N and P (Elser et al., 1990), and these nutrients have been shown to relieve nutrient limitation of benthic algae within wetlands located along the Tanana River floodplain (Wyatt & Turetsky, 2015). It was not our goal to evaluate nutrient limitation of algae but instead to elevate levels of N and P such that these nutrients were not constraining primary production during biofilm development. This aspect of our experiment was successful, as algal biomass was elevated in the presence of nutrient enrichment. Interestingly, algal biomass was further stimulated when glucose was added along with nutrients, probably owing to increased nutrient mineralisation generated by elevated decomposer communities within the surrounding microbial landscape (Naeem et al., 2000).

We expected that decomposers would be limited by organic carbon and that decomposer biomass would be stimulated by carbon subsidies. Although levels of dissolved organic matter in northern peatlands can exceed 50 mg/L (Gu & Wyatt, 2016), heterotrophic bacteria are often limited by available carbon in these ecosystems (e.g. Wyatt & Turetsky, 2015) owing to the composition of highly processed natural organic matter that is resistant to further decomposition (Hansen et al., 2016). In contrast to our expectations, elevated levels of algal biomass in the presence of nutrient enrichment did not stimulate heterotrophic bacteria. This result was somewhat surprising given that bacteria responded positively to glucose enrichment (with and without nutrients) and that algae have been shown to stimulate bacteria across a wide range of aquatic ecosystems (Kuehn et al., 2014; Scott & Doyle, 2006; Seymour et al., 2017), including northern peatlands (Wyatt & Rober, 2020; Wyatt & Turetsky, 2015). Our results show that bacteria were limited by labile carbon, but carbon limitation was not alleviated in the presence of algae, possibly owing to a combination of slow carbon release by algae in the presence of nutrient enrichment (Wyatt et al., 2014) and high energetic requirements of heterotrophic bacteria (Jansson, 1993). Detecting aspects of the latter would require metabolic measures, including bacterial production and respiration rates, in addition to estimates of biomass reported in our study. Although algae and bacteria compete for the same inorganic nutrients (Bratbak & Thingstad, 1985), competitive exclusion by algae is an unlikely explanation given that nutrient enrichment alone does not typically stimulate heterotrophic bacteria in northern peatlands, even in the dark without algae (Wyatt & Turetsky, 2015). It is more probable that bacterial growth was negatively affected by antagonistic interactions with fungi, a condition that has been demonstrated in other studies (Gulis & Suberkropp, 2003; Mille-Lindblom et al., 2006), although most were conducted in the absence of algae.

Heterotrophic bacteria were able to outcompete both algae and fungi in the presence of carbon enrichment when nutrient levels were low but not when both nutrients and organic carbon were elevated simultaneously. This finding is similar to other studies showing that heterotrophic bacteria have an affinity for nutrient resources (Currie & Kalff, 1984a) and can competitively exclude algae for available nutrients when background nutrient levels are low (Jansson, 1993; Joint et al., 2002). In cases where close associations between algae and heterotrophic bacteria continue to occur (Scott et al., 2008; Scott & Doyle, 2006), it is assumed that bacteria are

dependent on the photosynthetic products from the algae (Wyatt & Turetsky, 2015). Our results show that algae and heterotrophic bacteria were in fact uncoupled when carbon limitation was alleviated by outside sources (Bechtold et al., 2012; Klug, 2005; Stets & Cotner, 2008; Wyatt et al., 2019). The reduction of fungi in the presence of glucose alone suggests that heterotrophic bacteria may also be superior competitors for highly labile carbon. A similar result was reported in the nearshore area of an alpine lake where bacteria were able to outcompete fungi for labile carbon substrates but not for more recalcitrant carbon sources (Wyatt et al., 2019). This finding suggests that carbon quality may determine competitive outcomes among the heterotrophic biofilm community, in which case labile allochthonous carbon inputs would favour heterotrophic bacteria over fungi in northern peatlands. Given the importance of fungi as early-process decomposers (Kuehn, 2016), such a shift in biofilm structure could have important implications for ecosystem processes in northern peatlands, especially those associated with the breakdown of more recalcitrant organic matter.

In contrast to heterotrophic bacteria, fungal biomass was stimulated in the presence of nutrient enrichment alone. Nutrient limitation of fungi has been widely reported in benthic ecosystems, often on woody debris with high lignin to nitrogen ratios (e.g. Tank & Dodds, 2003; Tank & Webster, 1998). In addition to alleviating nutrient limitation, elevated levels of fungal biomass in the NP treatment may have been due in part to a positive association with algae. Although this aspect of producer–decomposer coupling has not been previously reported in northern peatlands, aquatic fungi are known to have close associations with algae in other freshwater ecosystems (Danger et al., 2013; Francoeur et al., 2020; Kuehn et al., 2014). For example, the fungal response to nutrients was much more subdued when algae were excluded by blocking sunlight in a lake biofilm (Wyatt et al., 2019). Similarly, fungal growth and production were lower on plant litter where algal photosynthesis was experimentally inhibited in a temperate wetland (Francoeur et al., 2020). The ability of fungi but not bacteria to respond to nutrient enrichment is interesting as it points to possible antagonistic interactions between these two competitors in the presence of algae. This outcome indicates that fungi were able to outcompete bacteria for algal carbon, highlighting the need to include estimates of fungal growth and production in studies aimed to evaluate aspects of biofilm development in northern peatlands.

Resource availability governed the balance between autotrophs and heterotrophs during peatland biofilm formation. The ratio of total biofilm biomass to chlorophyll *a* (i.e. autotrophic index; Steinman et al., 2006) in our study remained at relatively low levels in all treatments (i.e. a consistent degree of autotrophy; Bechtold et al., 2012) except in the glucose treatment where values were substantially elevated. This finding highlights the decoupling between algae and heterotrophic bacteria observed in the presence of glucose alone and demonstrates the ability for labile carbon subsidies to shift the biofilm community to be more heterotrophic (Figure 4a). The autotrophic index did not differ significantly between conditions where nutrients were enriched with and without glucose. This result shows that elevated levels of algal biomass maintained an autotrophic biofilm (i.e. low autotrophic index value) even in conditions of elevated heterotrophic biomass (i.e. NP + G treatment). This is important to note because many peatland-rich landscapes in northern regions are expected to experience more frequent flooding in the future (Douglas et al., 2020; Grosse et al., 2016). The type of biofilm that develops during periods of inundation will probably depend on the composition of resources delivered to surface waters with precipitation regime shifts and permafrost thaw (Abbott et al., 2014; Wickland et al., 2018). If conditions favour elevated nutrient levels along with carbon subsidies, our results show that peatland biofilms may be buffered against heterotrophy by an increase in algal biomass (Figure 4b). The ability for shifts in biofilm composition (i.e. low/high autotrophic index) to impact peatland ecosystem metabolism is not known but will probably depend on a combination of factors, including microbial production rates in the presence of available resources.

The climate of boreal regions is expected to shift drastically in the coming decades and these shifts will almost certainly affect resource supplies within surface waters, including peatlands. Given these circumstances, our aim was to establish connections between resource availability and biofilm formation. We successfully determined the conditions under which algal–bacterial mutualism may uncouple and impact the trophic status of the biofilm and showed that algal–fungal associations, as well as antagonistic decomposer interactions, probably play an underappreciated role in peatland biofilm formation. In doing so, our results provide a snapshot of biofilm development during the short periods of inundation that occur in floodplain peatlands across the boreal landscape. To place our study within a predictive context, it will be important for future studies to evaluate how natural organic compounds will affect biofilm communities. For example, it is not yet clear how changes in plant communities, such as those occurring in response to warmer temperatures or more variable hydrology (Churchill et al., 2015) , will alter the composition of organic matter available for heterotrophic microorganisms. It is also important to note our biofilm response variables focused mainly on estimates of autotrophic and heterotrophic biomass using fixed carbon conversions for bacteria and fungi. While these proxies, along with their derivative (i.e. autotrophic index), are sufficient to show relative shifts in biofilm composition, there are limitations to this approach including a possible overestimation of heterotrophic biomass in cases of carbon limitation (Vrede et al., 2002). Future work should address this by evaluating additional metrics, including aspects of biofilm metabolism and community structure. Doing so will provide a more accurate evaluation of biofilm structure and bring our collective knowledge of these ecosystems to a level more proportionate to their importance as global biogeochemical hotspots.

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AUTHOR CONTRIBUTION

J.M.M. and K.H.W. conceived the ideas and designed methodology and experimental approaches; J.M.M. collected the data and enumerated heterotrophic bacteria; K.A.K. led the fungal analysis; J.M.M. led the writing of the manuscript and all authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the public domain via the Bonanza Creek Data Catalog (https://www.lter.uaf.edu/data/data-catalog).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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