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RESEARCH ARTICLE OPEN ACCESS

Legacy Effects of Plant Community Structure Are Manifested in Microbial Biofilm Development With Consequences for Ecosystem CO_2 Emissions

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Received: 22 July 2024 | **Revised:** 29 October 2024 | **Accepted:** 1 November 2024

Funding: This research was supported by the National Science Foundation grants DEB-2141285 (to K.W. and A.R.) and DEB LTREB-2011286 (to K.W. and A.R.), and DEB LTREB-2011257 (to E.K. and M.T.). The Bonanza Creek Long-Term Ecological Research Program was funded by USDA Forest Service, Pacific Northwest Research Station grant RJVA-PNW-01-JV-11261952-231 and National Science Foundation grant DEB-1636476.

Keywords: aquatic biofilm | climate change | hydrology | microbial coupling | peatland | photoautotroph | plant subsidies | water table manipulation

ABSTRACT

To better understand linkages between hydrology and ecosystem carbon flux in northern aquatic ecosystems, we evaluated the relationship between plant communities, biofilm development, and carbon dioxide (CO_2) exchange following long-term changes in hydrology in an Alaskan fen. We quantified seasonal variation in biofilm composition and CO_2 exchange in response to lowered and raised water table position (relative to a control) during years with varying levels of background dissolved organic carbon (DOC). We then used nutrient-diffusing substrates (NDS) to evaluate cause–effect relationships between changes in plant subsidies (i.e., leachates) and biofilm composition among water table treatments. We found that background DOC concentration determined whether plant subsidies promoted net autotrophy or heterotrophy on NDS. In conditions where background DOC was $\leq 40\,\mathrm{mg\,L^{-1}}$, plant subsidies promoted an autotrophic biofilm. Conversely, when background DOC concentration was $\geq 50\,\mathrm{mg\,L^{-1}}$, plant subsidies promoted heterotrophy. Greater light attenuation associated with elevated levels of DOC may have overwhelmed the stimulatory effect of nutrients on autotrophic microbes by constraining photosynthesis while simultaneously allowing heterotrophs to outcompete autotrophs for available nutrients. At the ecosystem level, conditions that favored an autotrophic biofilm resulted in net CO_2 uptake among all water table treatments, whereas the site was a net source of CO_2 to the atmosphere in conditions that supported greater heterotrophy. Taken together, these findings show that hydrologic history interacts with changes in dominant plant functional groups to alter biofilm composition, which has consequences for ecosystem CO_2 exchange.

1 | Introduction

Microbial biofilms are comprised of autotrophic and heterotrophic microorganisms that play a key role in aquatic ecosystem function. Heterotrophic biofilms are responsible for releasing large amounts of carbon dioxide (CO_2) to the atmosphere (Battin et al. 2016; DelVecchia et al. 2019), whereas autotrophic biofilms can increase CO_2 uptake when primary production exceeds heterotrophic respiration (Hamard et al. 2021; Wyatt et al. 2021). The overall influence of biofilm

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Global Change Biology, 2024; 30:e17603
https://doi.org/10.1111/gcb.17603

composition on ecosystem carbon flux can be determined by food web interactions (Atwood et al. 2015; Wyatt et al. 2021; Zheng et al. 2023) as well as microscale interactions that involve the exchange of nutrients and organic matter among microorganisms, including species of algae, bacteria, and fungi (Halvorson et al. 2019; Wyatt et al. 2021; Jassey, Walcker, et al. 2022; Rober et al. 2023). These interactions can range from competitive to cooperative depending on background levels of nutrients and organic matter (Stets and Cotner 2008; Wyatt et al. 2019; Myers, Kuehn, and Wyatt 2021; Weaver and Jones 2022). Autotrophs rely on heterotrophs to recycle nutrients and heterotrophs rely on autotrophs for carbon subsidies produced during photosynthesis (Stets and Cotner 2008; Kuehn et al. 2014; Halvorson, Wyatt, and Kuehn 2020), allowing them to coexist. However, when carbon limitation is alleviated, heterotrophs tend to be better competitors than autotrophs for inorganic nutrients (Wyatt et al. 2019; Myers, Kuehn, and Wyatt 2021; Weaver and Jones 2022), suggesting that carbon limitation prevents competitive exclusion of autotrophs in low nutrient environments. Therefore, external inputs of limiting resources (nutrients or organic carbon subsidies) can alter the proportion of autotrophic and heterotrophic components of the biofilm with consequences for net CO_2 exchange (Rober et al. 2023).

Biofilm composition and metabolism are influenced by differences in hydrologically mediated environmental conditions (Wyatt et al. 2012; Rober et al. 2013; DeColibus et al. 2017). This is particularly evident in northern peatlands where open-water areas are intermittent, resulting in both wet and dry phases in the same location at different points in time (Euskirchen et al. 2020). Biogeochemical cycling tends to be enhanced at the interface of wet and dry phases (Bernhardt et al. 2017), and chemical cycling is anticipated to increase in magnitude in northern peatlands owing to more variable hydrologic conditions (Wickland et al. 2018). Previous studies have demonstrated that hydrologically induced nutrient inputs enhance biofilm productivity (Wyatt et al. 2012), especially the autotrophic biofilm (i.e., algae) (DeColibus et al. 2017).

While variable hydroperiods have been linked to accelerated CO_2 efflux from temporary aquatic ecosystems via enhanced heterotrophic decomposition (DelVecchia et al. 2019), research has shown that elevated autotrophic biofilm production can offset increases in CO_2 emissions during periods of inundation (Kane et al. 2021; Wyatt et al. 2021). For example, in studies simulating nutrient release from permafrost thaw, it was estimated that nutrient enrichment could increase peatland CO_2 emissions by ~300 g CO_2 m^{-2} y^{-1} in the absence of a counterbalance from algal photosynthesis (Wyatt et al. 2021; Rober et al. 2023). Likewise, Hamard et al. (2021) found that autotrophic microbes in peatlands can take up as much CO_2 per year (~75 Mega Tons) as is anticipated to be lost due to climate change. The magnitude of this effect highlights the potential importance of autotrophic biofilms as regulators of net ecosystem carbon exchange in northern peatlands, and suggests that the presence or absence of autotrophic biofilms could determine whether an individual peatland is a carbon source or sink (Jassey, Walcker, et al. 2022). Nevertheless, exactly how autotrophic biofilm production will influence peatland carbon storage is not yet clear. This is because altered hydrologic regimes (e.g., inundation frequency and duration) are also causing shifts in plant functional groups, which have the potential to influence biofilm development.

The dominant plant functional groups commonly found in boreal peatlands include mosses, sedges, horsetails, and shrubs (Rupp et al. 2019), but altered hydrologic regimes associated with ongoing climate change are causing shifts in plant functional groups across northern peatland landscapes (Laiho et al. 2003; Potvin et al. 2014; Churchill et al. 2015; McPartland et al. 2019; Zhang et al. 2024). Most notable has been a reduction in moss dominance in favor of vascular plants (Fenner et al. 2007; Dieleman et al. 2014; Hobbie et al. 2017). Plants contribute to the organic matter pool by leaching photosynthetic products into the water column following senescence (Robroek et al. 2016). Therefore, plant communities that dominate biomass production during one growing season may regulate aquatic biofilm development during the subsequent growing season as a legacy effect. Nutrient availability and organic matter quality vary among peatland plants and some plants provide subsidies that are more labile than others (Dorrepaal, Cornelissen, and Aerts 2007; Ward et al. 2015; Sahar et al. 2022). Therefore, shifts in plant community structure have the potential to influence biofilm composition by altering the amount and composition of resource subsidies available to biofilm microorganisms following senescence (Zhao, Xing, and Wu 2017; Rober et al. 2023). Relatively few studies have tested the effect of shifting plant community structure on peatland microbial communities (Robroek et al. 2015; Hough et al. 2022; Buttler et al. 2023). As a result, it is difficult to predict how shifts in plant functional groups, such as those occurring with altered hydrologic regimes, will influence the carbon balance of northern peatlands.

The goal of this study was to evaluate the influence of vegetation change occurring with long-term changes in water table position on the proportion of autotrophic and heterotrophic components of the biofilm and associated CO_2 flux. This study was conducted at the Alaska Peatland Experiment (APEX) site, a large-scale water table manipulation experiment simulating drought and flooding conditions relative to a control. Prior to the initiation of the APEX site in 2005, there were no significant differences in water table position or vegetation composition among experimental plots (Turetsky et al. 2008). However, the vegetation structure of each of these plots has changed from the beginning of the study up to present day as a result of the water table manipulation (Rupp et al. 2019). Most notable has been an increase in shrub cover (e.g., *Potentilla*) in response to drier conditions, with subsequent reductions in moss dominance (e.g., *Sphagnum*) (Churchill et al. 2015), while wetter conditions favor increased sedge cover (e.g., *Carex*) (McPartland et al. 2019; Rupp et al. 2019). However, previous research has not been able to disentangle the effects of water table from vegetation on biogeochemical measurements (Kane et al. 2021). We tested the hypothesis that drainage history interacts with changes in dominant plant functional groups to alter the proportion of microbial autotrophs vs. heterotrophs, which have consequences for net carbon balance. We quantified seasonal variation in the autotrophic and heterotrophic components of the biofilm and CO_2 exchange in response to lowered and raised water table positions relative to a control unmanipulated plot, over three consecutive growing seasons. We then evaluated cause–effect relationships between changes in plant subsidies and biofilm composition by experimentally manipulating the composition of plant leachates available to the biofilm using nutrient-diffusing substrates (NDS). Using NDS allowed us to emulate changes in the dominant plant cover type within each water table plot on a small scale with less disturbance, thereby methodologically separating vegetation from hydrologic controls on biofilm composition. We then linked changes in biofilm composition (i.e., autotrophy vs. heterotrophy) associated with different plant leachates to outcomes of CO_2 flux in APEX plots to evaluate how variation in biofilm trophic status would affect carbon emissions.

2 | Materials and Methods

2.1 | Study Site

The APEX study site is a rich fen located approximately 35 km southeast of Fairbanks, Alaska (64.7ºN, 148.32ºW). APEX is associated with the Bonanza Creek Long Term Ecological Research Program and the vegetation and climate characteristics of this site have been described in detail elsewhere (Churchill et al. 2015; Olefeldt et al. 2017; Euskirchen et al. 2020, 2024). APEX is made up of three 30 m × 40 m experimental plots positioned 25 m apart and outlined by a raised boardwalk to prevent disturbance of the peat surface during regular sampling. Water table is manipulated within experimental plots throughout the growing season (approximately June–September) (Chivers et al. 2009). Drought conditions (lowered water table treatment) are maintained by a series of drainage canals that divert water away from the lowered treatment plot to reduce water table position below the control plot (ambient). Flooding conditions (raised water table treatment) are maintained by solar-powered bilge pumps that increase water table position above the control (Turetsky et al. 2008). The goal of the APEX experiment was to maintain lowered and raised water table positions relative to the control while allowing for the natural seasonal variability in water table position at this site. However, it was not possible to experimentally manipulate water table position during periods of natural flooding, including years when flooding (water table > 40 cm above peat surface) persisted for the entire growing season (2013, 2014, 2016, 2017, 2018, 2020, 2022, and 2023; Euskirchen et al. 2024). Sampling for this study was conducted May–June in 2021 and May–August in both 2022 and 2023 and data are available in the Bonanza Creek Data Catalog (Wyatt and Bonanza Creek 2024). Across all treatments, water table dropped below the peat surface at the end of 2021 and re-flooded in 2022, whereas flooding was sustained across 2022 and 2023 (Figure 1), resulting in differences in the background concentration of dissolved organic carbon (DOC) among years.

2.2 | Seasonal Variation in Biofilm Composition

To capture seasonal variation in biofilm composition among water table treatments, we quantified the autotrophic and heterotrophic components of the biofilm weekly during each summer growing season. Microbial biofilm was sampled at six locations within each of the three water table plots and each sample was a composite collected from four senesced *Carex utriculata* stems (each 10 cm in length) within a 1 m^2 area (Kane et al. 2021). The microbial biofilm was removed from substrates with a toothbrush and the resulting slurry was homogenized and split for analysis of chlorophyll *a* and ash-free dry mass (AFDM).

Biofilm chlorophyll *a*, AFDM, and autotrophic index (AI) were used to evaluate how the ratio of autotrophs to heterotrophs

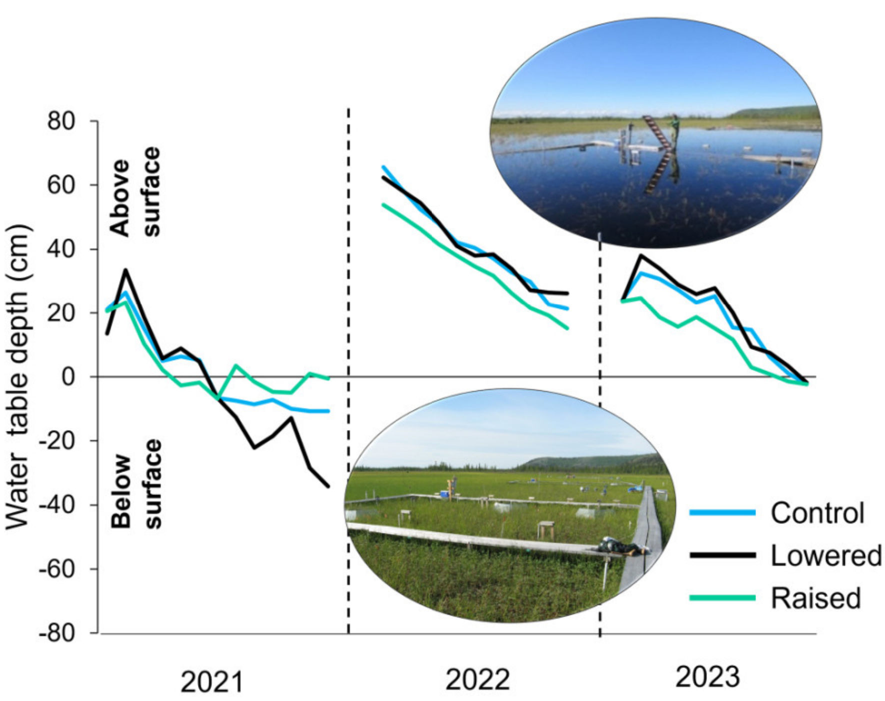

FIGURE 1 | Water table position among control, lowered, and raised water table treatments 2021–2023. Positive values indicate water table position above the peat surface. Inset photographs depict the site while flooded (top) and when the water table was below the surface of the peat (bottom).

vary among water table treatments over time (Steinman, Lamberti, and Leavitt 2006). Autotrophic biofilm colonization was quantified as chlorophyll *a* (a proxy for algal biomass) from a subsample collected on a 0.7-μm glass fiber filter (GF/F; Whatman, Maidstone, UK) following 24 h extraction with 90% ethanol in the dark. Chlorophyll *a* concentration was measured from the extract with a Cary 60 UV–Vis spectrophotometer (Agilent Technologies, Santa Clara, CA, USA) at 665 and 750 nm after acidification to correct for phaeopigments (APHA (American Public Health Association) 2005). A separate aliquot was poured into pre-weighed aluminum pans, dried at 105°C for 24 h and then ashed at 500°C for 1 h for measures of dry and ash mass, respectively, which were used to determine AFDM (APHA (American Public Health Association) 2005). An AI was used to quantify the ratio of autotrophs to heterotrophs among treatments. Autotrophic index is determined by dividing AFDM (a measure of the total autotrophic and heterotrophic biomass accumulated) by the concentration of chlorophyll *a* (a measure of algal biomass) using standard methods (APHA (American Public Health Association) 2005). Lower values of the index indicate a higher proportion of autotrophy in the microbial community (Bechtold et al. 2012).

2.3 | Gas Flux Measurements

Gas flux (i.e., CO_2) was measured within each water table treatment (within plot $n = 3$) in the same location as, but prior to, harvesting stems for biofilm collection (described above). Flux measurements were collected only during flooded conditions (i.e., when there was a saturated photic zone for aquatic biofilm development) using a floating chamber (Kane et al. 2021). This resulted in 2 sampling campaigns in 2021, 10 in 2022, and 6 in 2023. Water depth was similar among water table treatments at the time of sampling (i.e., flooded across all treatments) in either year. The floating chamber was constructed from a clear polycarbonate plastic bucket (18.9 L) with Styrofoam floatation around the base and one CPU fan inside for air circulation. This design allows for the measure of CO_2 flux in the airspace above the water. The floating chamber was equipped with an airlock to equilibrate pressure. Temperature, relative humidity, and photosynthetically active radiation (PAR) were logged continuously with a PP Systems TRP-1 sensor mounted within the clear floating chamber. The CO_2 flux rate ($\mu g\ CO_2\ m^{-2}\, s^{-1}$) was calculated as the slope of the linear relationship between headspace CO_2 concentration and time using a portable infrared gas analyzer (IRGA; PP Systems EGM-4, Amesbury, MA, USA). Net ecosystem exchange (NEE) was measured under ambient light conditions and positive NEE values indicated carbon release to the atmosphere while negative values indicated carbon uptake. For annual estimates of the biofilm contribution to CO_2 flux, we converted NEE values to $g\ CO_2\ m^{-2}\ y^{-1}$ by converting seconds to days assuming the average 21 h d^{-1} of sunlight available for biofilm photosynthesis (Hinzman et al. 2006). We then converted NEE from days to years based on the growing season length of 135 days for the study site (Hinzman et al. 2006). Outside of this timeframe, environmental conditions constrain biofilm production. Floating chamber measurements were conducted within water table treatments from a small inflatable boat or by wading along the established boardwalk network.

2.4 | Nutrient-Diffusing Substrate Experimental Design

We used NDS to evaluate the independent and interactive effects of drainage history and different plant carbon sources on biofilm composition in a full factorial design (Figure S1). Prior to the initiation of the study, plant leachates were collected from dried peatland plants and lyophilized (freeze-dried) before use in NDS. Above-ground biomass of three vascular plant genera (*Carex*, *Potentilla*, and *Equisetum*) were collected from peatlands near the study site and dried for 48 h at 60°C in a drying oven. Leachates were produced by leaching dried plant material from each genus in beakers containing 1500 mL of nanopure water for 12 h. The resulting leachate was filtered through a fine metal sieve to remove large particulate debris before being lyophilized using a Labconco Freezone 6 benchtop freeze dryer (Labconco, Kansas City, MO, USA) for approximately 48 h. All leachates used to produce NDS were from the same batch of freeze-dried plant extracts. Analysis of leachates was conducted to determine the chemical composition and concentration of dissolved organic matter (standardized per gram of dry mass) for each plant type and have been reported in detail elsewhere (Table 1; Rober et al. 2023).

NDS were constructed using 60 mL polyethylene canisters filled with agar + one of three plant leachates (3 g L^{-1}; *Carex*, *Potentilla*, and *Equisetum*) or a control with agar only. Leachate amendments were selected to emulate natural carbon and nutrient levels upon release (Rober et al. 2023). Canisters were topped with a fritted glass disc, providing an inorganic substrate for biofilm colonization (Tank et al. 2017). Inorganic substrates were used so that we could evaluate the influence of plant leachates, a source of organic carbon, on the biofilm community without the confounding effects of substrate composition. Each disc was held in place by a tight-fitting cap with

TABLE 1 | Nutrient and carbon composition of plant subsidies.

	Potentilla		*Equisetum*		*Carex*	
Plant leachate composition	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Dissolved organic carbon (DOC; mg L^{-1})	111.3	1.31	125.7	0.16	69.6	2.62
Total dissolved nitrogen (TDN; mg L^{-1})	1.14	0.04	3.42	0.05	2.57	0.14
Phosphate (PO_4; mg L^{-1})	1.80	0.18	2.44	0.08	1.51	0.11

a 2.5-cm-diameter circular hole cut from the center to allow for biofilm growth. Replicate NDS ($n = 4$) of each leachate treatment (*Carex*, *Potentilla*, *Equisetum*, or agar-only control) were secured to pieces of angle iron using all-purpose adhesive and one bar of each leachate treatment was submersed 10 cm below the water surface in each water table treatment (Figure S1). The experiment was left for 3 weeks (beginning on June 3, 2021, June 16, 2022, and June 4, 2023) to allow for biofilm colonization. Biofilm chlorophyll *a*, AFDM, and AI were used (as described above) to evaluate how the ratio of autotrophs to heterotrophs vary among NDS.

2.5 | Sampling and Analytical Methods

Physiochemical conditions were measured within each water table plot during biofilm collection and gas flux measurements. Water depth (cm) was measured with a meter stick and measurements of water temperature (°C), pH, conductivity (μS), and dissolved oxygen (DO; mg L^{-1}) were made with a Hach model 40d multiprobe (Hach Company, Loveland, CO, USA). Photosynthetically active radiation ($\mu mol\, m^{-2} s^{-1}$) was measured at approximately 10 cm below the water surface in each plot using a Li-Cor submersible quantum sensor and LI-250 light meter (Li-Cor, Lincoln, NE, USA) attached to a 1-m pole to prevent disturbance of macrophytes. Water samples for dissolved nutrient analysis and DOC were collected with a syringe and filtered through a 0.45-μm filter (Millipore Corporation, Bedford, MA, USA) into 60 mL acid-washed polyethylene bottles. Dissolved nutrient samples were stored on ice in the field and frozen until analysis for nitrate (NO_3; mg L^{-1}) and PO_4 (mg L^{-1}) using ion chromatography (Dionex Corporation, Sunnyvale, CA, USA). Dissolved organic carbon (mg L^{-1}) and TDN (mg L^{-1}) were analyzed using a Shimadzu TOC-V carbon analyzer with a TN unit (Shimadzu Scientific Instruments, Columbia, MD, USA). A subsample of filtered samples was analyzed for ultraviolet absorption at 254 nm using an Agilent Cary 60 UV–VIS spectrophotometer (Agilent Technologies, Santa Clara, CA, USA). Specific UV absorbance at 254 nm ($SUVA_{254}$) was calculated by dividing ultraviolet absorption at 254 nm by DOC concentration for an estimate of aromatic content and molecular weight.

2.6 | Statistical Analysis

A repeated measures multivariate general linear model (rmGLM) was used to evaluate the effect of sampling date and water table treatment on physical and chemical conditions. Seasonal and annual variation in AI, chlorophyll *a*, AFDM, and CO_2 flux among water table treatments were evaluated using general linear mixed effect models (GLMM) with sampling date as a random effect, water table treatment as a fixed effect, and physical and chemical characteristics as covariates to determine which environmental variables were the best predictors of variation among treatments. The effect of plant subsidies on biofilm composition (measured as AI) within water table treatments was evaluated using a nested GLM. Autotrophic index was log transformed prior to analysis to correct for non-normal distribution and unequal variance among treatments. When GLMs indicated significant differences among treatments, Tukey's post hoc comparison of means tests were used to discriminate between treatments. Linear regression analysis was used to evaluate the relationship between biofilm composition (measured as log-transformed AI) and net ecosystem CO_2 exchange (NEE) among water table treatments. Linear regression analysis with and without broken line modeling was used to evaluate the relationship between mean biofilm composition (measured as AI) and background DOC concentration among NDS plant subsidy treatments. Statistical analyses were performed with SPSS 29 (IBM Statistics, Chicago, IL, USA).

3 | Results

3.1 | Physical and Chemical Predictors of Biofilm Composition

Physical and chemical conditions were influenced by sampling date (rmGLM $F_{153,\, 1008} = 6.9$, $p < 0.001$) alone and in combination with water table treatment (rmGLM $F_{306,\, 2040} = 2.05$, $p < 0.001$; Table S1 and Figure S2). Both DOC ($p = 0.002$) and TDN ($p < 0.001$) were significant predictors of AI, whereas PAR was a significant predictor of chlorophyll *a* ($p = 0.03$), and NO_3 was a significant predictor of AFDM ($p = 0.009$). On average, DOC (mean ± SD) was lower in 2021 (32.7 ± 0.67) and 2023 (39.1 ± 0.59) and ranged from 24.1 to 53.8 mg L^{-1} compared to 2022 (56.4 ± 0.64) when DOC ranged from 41.8 to 76.6 mg L^{-1} (rmGLM $F_{17,104} = 790.9$, $p < 0.001$). Predictors TDN, PAR, and NO_3 were highly variable within and between study years and not significantly different among water table treatments ($p \geq 0.15$). TDN ranged from 0.03 to 0.24 mg L^{-1}, PAR ranged from 46 to 82 $\mu mol\, m^{-2} s^{-1}$, and NO_3 ranged from 0.08 to 0.59 mg L^{-1} within and between study years. Environmental parameters that were not significant predictors of biofilm dynamics included water depth, water temperature, conductivity, pH, SUVA, DO, and PO_4 (Figure S2). Water depth was greatest at the start of each sampling year and declined over the growing season (Figure 1). Overall water depth above the peat surface was shallower in 2021 (21.6 ± 1.66) and 2023 (17.8 ± 0.75) and ranged from 41 to 1 cm compared to 2022 (39.0 ± 0.84) when water depth ranged between 66.5 and 17.5 cm. Water temperature (°C) was highly variable throughout each growing season but remained within the range of 12.5–26.2 during each year of study. Conductivity (μS) increased over sampling years and was greater in 2023 (60.1 ± 2.51) than 2021 (43.4 ± 0.35) or 2022 (56.7 ± 0.89) (rmGLM $F_{17,104} = 973.4$, $p < 0.001$). pH declined over the growing season in 2021 and 2023 and ranged from 5.1–10.5 but was relatively consistent throughout 2022 ranging between 5.4 and 7.3. Specific UV absorbance was highly variable within and between study years and ranged from 1.73 to 4.9 L mg $C^{-1} m^{-2}$. The concentration of DO (mg L^{-1}) declined over the growing season during each year of study with a maximum ranging between 7.44 and 9.05 across study years and a minimum ranging from 0.18 to 1.64. Overall PO_4 (mg L^{-1}) was more elevated in 2022 (0.14 ± 0.005) than 2021 (0.03 ± 0.002) or 2023 (0.02 ± 0.002).

3.2 | Relationship Between Variation in Biofilm Composition and CO_2 Emissions

Differences in biofilm composition among study years influenced the direction of CO_2 exchange across water table treatments ($r^2 = 0.29$, $F_{1,53} = 21.2$, $p \leq 0.001$; Figure 2). Biofilm composition varied annually (GLMM $F_{14,129} = 5.75$, $p < 0.001$)

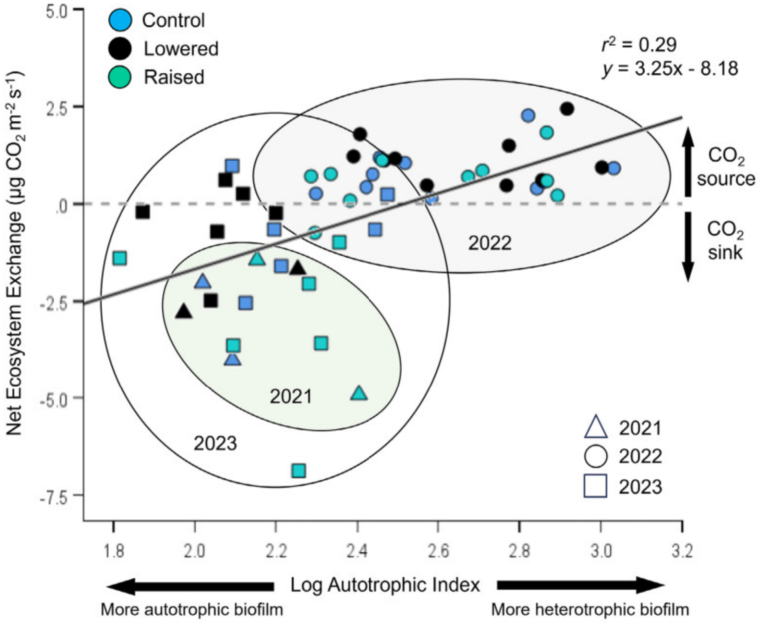

FIGURE 2 | Relationship between mean biofilm composition (measured as log-transformed autotrophic index; AI) and mean net ecosystem CO_2 exchange (NEE) among water table treatments over the 3 years of study. Lower values of AI indicate a higher proportion of autotrophy in the microbial community. Negative values of NEE indicate CO_2 uptake and positive NEE indicate CO_2 release to the atmosphere. Water table treatments are indicated by symbol color and years are indicated by symbol shape.

but was similar among water table treatments during each year of study (GLMM $F_{2,139} = 0.07$, $p = 0.93$; Figure 3a). The overall mean of AI was lower (more autotrophic) in 2021 (154.5 ± 17.6) and 2023 (157.4 ± 8.11) but was higher (more heterotrophic) in 2022 (482.7 ± 25.3) (Figures 3a and S3). Conditions that favored autotrophic biofilm development corresponded with lower values of NEE (greater CO_2 uptake) across water table treatments, whereas the site was a net source of CO_2 to the atmosphere in conditions that supported greater heterotrophy (Figure 3b). Uptake of CO_2 was consistently greater in the raised water table treatment compared to the control or lowered treatments, though differences were only significant during 2023 ($p \leq 0.03$; Figure 3b).

3.3 | Effects of Plant Subsidies on Biofilm Composition

Biofilm composition was significantly influenced by plant subsidies (GLM $F_{3,108} = 7.46$, $p < 0.001$) alone and in combination with water table treatment (GLM $F_{6,108} = 7.31$, $p < 0.001$). Water table treatment alone did not have a significant effect on biofilm composition (GLM $F_{2,108} = 1.81$, $p = 0.17$). On average, plant subsidies promoted a more autotrophic biofilm (decreased AI) among water table treatments when background concentrations of DOC were ≤ 40 mg L^{-1}, whereas when background DOC concentrations were ≥ 50 mg L^{-1}, plant subsidies promoted a more heterotrophic biofilm (increased AI) compared to the agar-only control (Figure 4). The biofilm response to individual plant subsidies was also influenced by background DOC concentration (Figure 5a,b). *Equisetum* subsidies were the most strongly influenced by background DOC ($r^2 = 0.68$, $p \leq 0.001$), followed by *Carex* ($r^2 = 0.52$, $p \leq 0.001$), and the least influenced was *Potentilla* subsidies ($r^2 = 0.20$, $p = 0.006$). Biofilm composition in the agar-only control was not influenced by background DOC concentration ($r^2 = 0.03$, $p = 0.29$) and was not different among water table treatments or study year ($p \geq 0.21$; Figure 5a). Background DOC had a stronger effect on AI among all plant subsidies when DOC was ≥ 50 mg L^{-1} ($r^2 = 0.26$) than when DOC was ≤ 40 mg L^{-1} ($r^2 = 0.006$; Figure 5b).

The biofilm response to individual plant subsidies was not consistent across water table treatments or years (Figure 6). Plant subsidies promoted a more autotrophic biofilm (decreased AI) among all three water table treatments in 2021 and 2023. Under ambient water table conditions (control treatment), both *Equisetum* and *Potentilla* subsidies promoted a more autotrophic biofilm (lower AI) compared to the agar-only control in 2021 ($p \leq 0.04$) whereas *Carex* subsidies promoted a more autotrophic biofilm in 2023 ($p = 0.01$). In the lowered water table treatment, all plant subsidies had lower AI than the agar-only control in 2021 ($p \leq 0.02$) and AI was significantly different among *Carex*, *Equisetum*, and *Potentilla* subsidies ($p \leq 0.03$), with *Potentilla* subsidies resulting in the lowest AI. *Carex* subsidies resulted in the lowest AI compared to the agar-only control in 2023 ($p = 0.003$) but neither *Equisetum* nor *Potentilla* subsidies were different from the control ($p \geq 0.32$). In the raised water table treatment, both *Carex* and *Equisetum* subsidies reduced AI relative to the agar-only control in both 2021 and 2023 ($p \leq 0.004$), but *Equisetum* resulted in the greatest reduction in AI in 2021 ($p \leq 0.001$) and was not significantly different from *Carex* in 2023 ($p = 0.18$; Figure 6).

Plant subsidies promoted a more heterotrophic biofilm (increased AI) among all three water table treatments in 2022 (Figure 6). In both the control and lowered water table treatments, *Carex* and *Equisetum* subsidies promoted a more

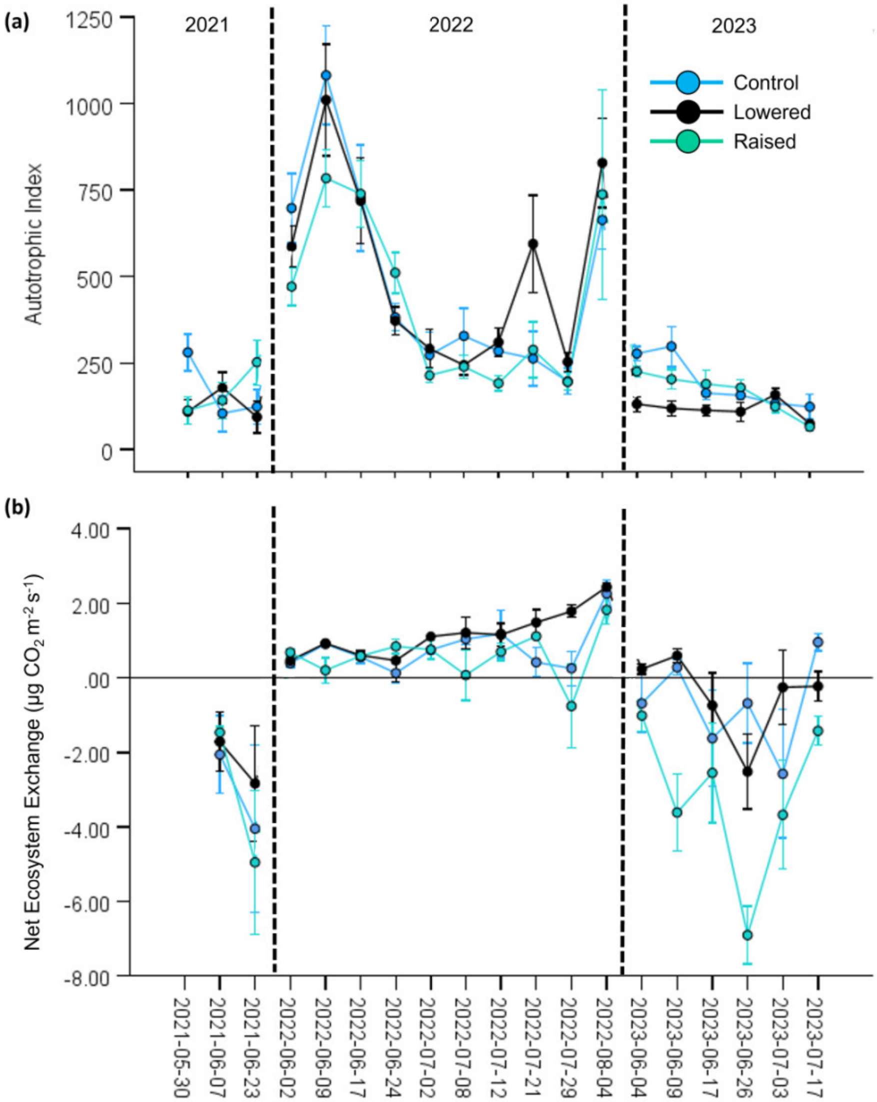

FIGURE 3 | Seasonal and annual variation in (a) autotrophic index and (b) CO_2 flux among control, lowered, and raised water table treatments over time.

heterotrophic biofilm than the agar-only control ($p \leq 0.03$), but the effect of *Equisetum* subsidies on AI was twofold greater in the lowered water table treatment compared to ambient (control) water table conditions ($p = 0.005$). In the raised water table treatment, *Equisetum* subsidies resulted in the greatest increase in AI relative to any other plant type ($p \leq 0.01$). Neither *Carex* or *Potentilla* subsidies resulted in biofilm composition significantly different than the agar-only control ($p \geq 0.11$; Figure 6).

4 | Discussion

Our research shows that changes in plant community composition and water chemistry expected with climate change will interact to influence microbial-mediated CO_2 emissions in northern peatlands. We found that background DOC concentration determined the magnitude to which plant subsidies regulated competitive interactions within the microbial community. For example, when background DOC was $\leq 40\,\mathrm{mg\,L^{-1}}$, plant subsidies supported an autotrophic biofilm. Conversely, when background DOC was $\geq 50\,\mathrm{mg\,L^{-1}}$, plant subsidies supported a heterotrophic biofilm. We found a similar response of the biofilm to background DOC among water table treatments. Conditions that supported autotrophic biofilm production resulted in net CO_2 uptake, whereas the site was a net source of CO_2 to the atmosphere in conditions that supported greater heterotrophy. In both scenarios, it appears that the biofilm was responding more to nutrients, rather than carbon, from the plant subsidies (Rober et al. 2023). In the absence of nutrient additions (i.e., agar-only control), background DOC did not alter biofilm composition across water table treatments or years of study. Previous research in these systems has shown that heterotrophs are co-limited by nutrients and carbon (Wyatt and Turetsky 2015; Myers, Kuehn, and Wyatt 2021; Rober et al. 2023). Collectively, these findings suggest that the biofilm was unable to respond to carbon inputs owing to nutrient limitation. These findings support our hypothesis that hydrologic history interacts with changes in dominant plant functional groups to determine the relative proportion

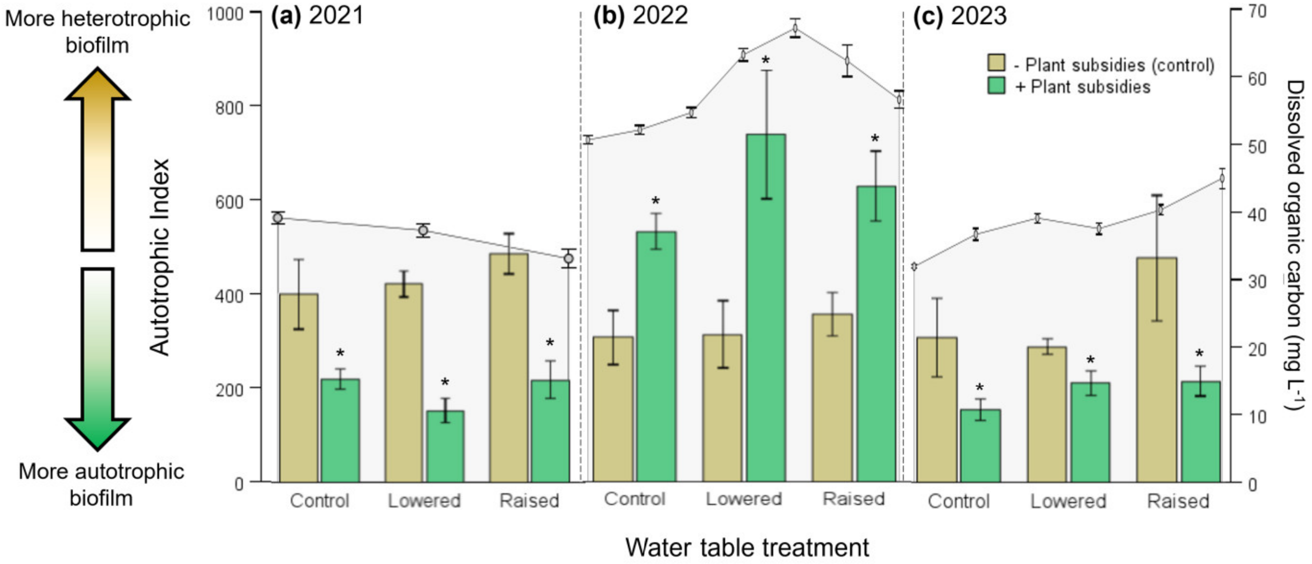

FIGURE 4 | Comparison of biofilm autotrophic index (AI; first *y*-axis) on nutrient-diffusing substrates without plant subsidies (agar-only control) or with plant subsidies (i.e., average of all subsidies) in relation to background dissolved organic carbon concentration (grey shading; second *y*-axis) among water table treatments. Sampling years are separated by a dashed line. Asterisks indicate significant differences between AI in the presence or absence of plant subsidies within each water table treatment.

of autotrophs and heterotrophs in the microbial community of this northern peatland—the results of which may have consequences for ecosystem carbon storage.

Light limitation of autotrophs in darker water may account for the observed differences in biofilm composition in response to annual variation in DOC. Comparison of light attenuation among peatlands with varying DOC concentration has revealed that photosynthetically active radiation is reduced to 30% of available light by increasing DOC concentration from 28 to 50 $\mathrm{mg\,L^{-1}}$ or an increase in water depth from 16 to 45 cm (Gu and Wyatt 2016). Further, light limitation associated with humic waters (i.e., browning) can inhibit the positive relationship typically observed between increasing nutrient levels and algal production (Karlsson et al. 2009; Gu and Wyatt 2016). We found that light availability was reduced by 20% on average (maximum 55%) during the heterotrophic year (2022) compared 14% (maximum 32%) during the autotrophic years (2021 and 2023). This was likely due to a combination of greater water depth and elevated DOC levels observed during the heterotrophic year. These findings may explain the observed switch between autotrophy and heterotrophy in response to plant subsidies among years with variable background DOC. As measures of organic matter quality (i.e., SUVA) were similar among study years (3–3.5 $\mathrm{L\,mg\,C^{-1}\,m^{-1}}$), it does not appear that the composition of the organic matter was different, which is consistent with findings from Kane et al. (2021). This reduces the possibility that lower quality carbon substrates made it difficult for heterotrophs to use available DOC during the autotrophic years. Furthermore, in a previous study evaluating heterotrophy with and without autotrophs, we found that in the dark (without algal photosynthesis), plant subsidies increased heterotrophic biofilm production and consequently CO_2 emissions (Rober et al. 2023). Taken together these findings suggest that higher background DOC concentrations (in 2022) caused light limitation of autotrophs (similar to dark treatments in Rober et al. 2023), allowing heterotrophs to use available nutrients. The extent to which autotrophic biofilms are able to buffer peatlands against net heterotrophy more broadly may depend on the composition of resources delivered to surface waters with variable hydrology and warming soil conditions (Kendrick et al. 2018; Wickland et al. 2018; Weaver and Jones 2022; Rieb et al. 2024) as well as the changing physical aspects of northern peatlands (Euskirchen et al. 2024), all of which influence concentrations of dissolved organic matter (Kane et al. 2010; Cory and Kling 2018). We might expect greater light attenuation associated with increasing levels of dissolved organic matter to overwhelm the stimulatory effect of nutrients on autotrophic microbes by constraining photosynthesis, favoring heterotrophy and increasing CO_2 emissions.

Given that some plant subsidies are more labile than others (Rupp et al. 2019; Sahar et al. 2022; Wilson et al. 2022; Rober et al. 2023), we anticipated that shifts in plant functional groups from long-term water table manipulation would alter the composition of dissolved organic matter and in turn affect biofilm composition. For example, in the raised water table treatment, where shrub abundance has declined, we expected the biofilm to respond more strongly to either experimental reintroductions of *Potentilla* subsidies or conversely, to sedges (i.e., *Carex*), which are favored under wetter conditions (e.g., home-field advantage hypothesis; Strickland et al. 2009). However, we did not see a consistent pattern of variation among plant subsidies. In fact, all plant subsidies alleviated nutrient limitation of the biofilm community. However, the extent to which the microbial biofilm could use these nutrients was regulated by background DOC concentration. For instance, the influence of *Carex* subsidies on biofilm composition ($r^2 = 0.52$) was more strongly influenced by background DOC than *Potentilla* ($r^2 = 0.20$). These plant types are favored under wetter (*Carex*) and drier (*Potentilla*) conditions, suggesting that elevated levels of DOC could interact with plant subsidies to influence the carbon sink strength of the system. Notably, the composition

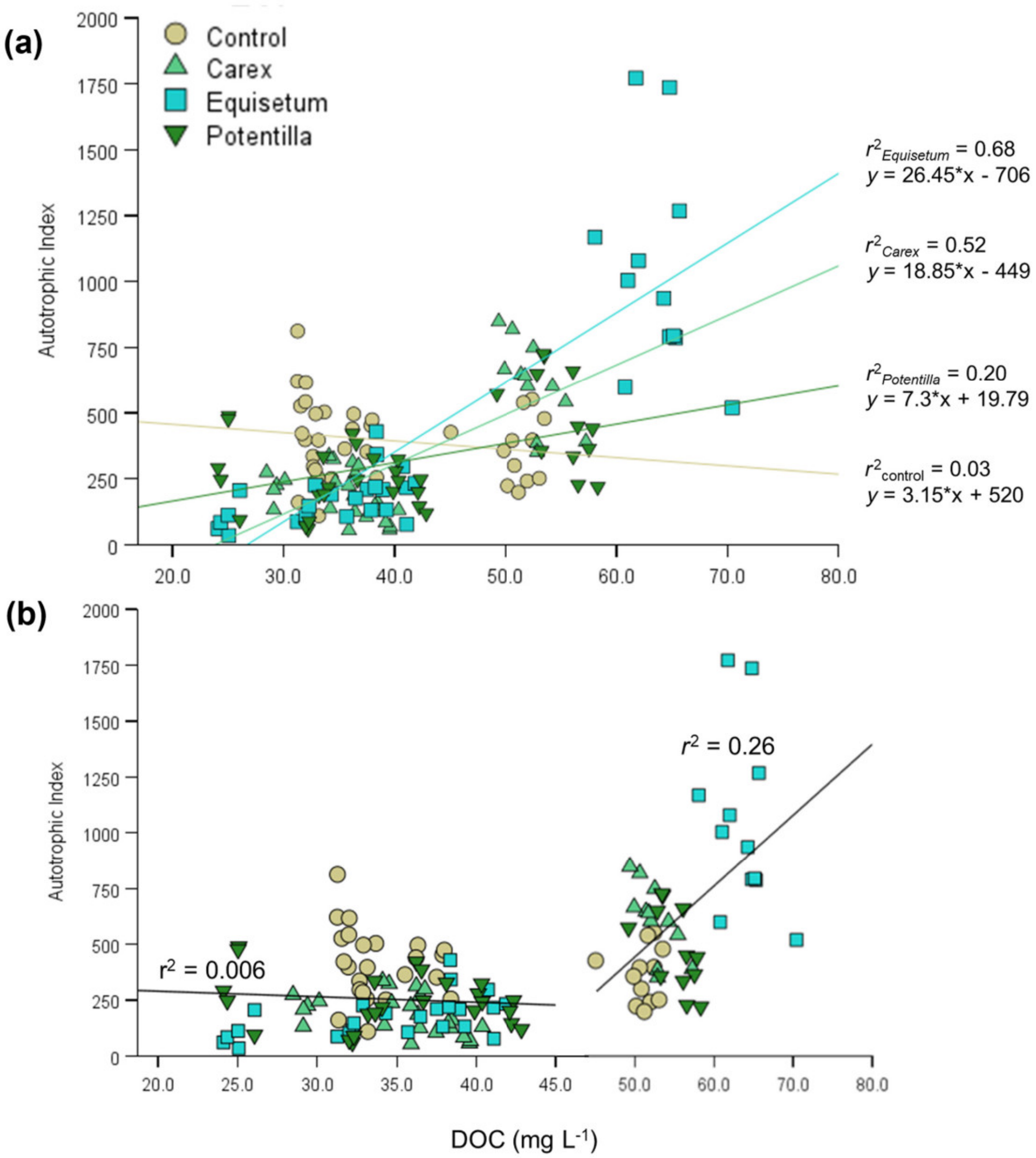

FIGURE 5 | Linear regression of relationship between mean biofilm composition (measured as autotrophic index; AI) and background DOC concentration (a) among plant subsidy treatments and (b) with broken line model showing overall relationship when DOC is ≤ 40 mg L^{-1} or ≥ 50 mg L^{-1}.

and quality of plant leaf leachates typically differs from root leachates (Robroek et al. 2016; Wilson et al. 2022) and the chemical composition of leaf and root tissue can respond to drought in opposing directions (Gargallo-Garriga et al. 2014). Therefore, we might expect leachate composition to not only vary among plant types, but also over time and in response to drought frequency and severity.

Differences in the magnitude of CO_2 fixed during years with autotrophic versus heterotrophic biofilms suggests that the presence or absence of an autotrophic biofilm could determine whether an individual peatland is a carbon source or sink. During years with net autotrophic biofilm production, the mean of all NEE values indicated that our site was a net sink of CO_2, taking up an average of 1.5–2.8 μg CO_2 m^{-2}s^{-1} (maximum 8 μg CO_2 m^{-2}s^{-1}). Yet, when conditions supported heterotrophic biofilm development (i.e., mean of NEE values during 2022), the site contributed an average of 0.85 μg CO_2 m^{-2}s^{-1} (maximum 2.98 μg CO_2 m^{-2}s^{-1}). When we compare the biofilm contribution to CO_2 flux as annual NEE (assuming 21 h d^{-1} sunlight during a 135-day growing season for the study site), we see that in the absence of autotrophic microbes, our site contributed on average 8.65 ± 0.90 g CO_2 m^{-2} y^{-1}. However, when algae were present to offset heterotrophic metabolism, our site took up on average 15.0 ± 3.21–29.0 ± 6.02 g CO_2 m^{-2} y^{-1}. Interestingly, the raised water table treatment was the strongest sink for CO_2 among experimental plots (taking up on average 32.7 g CO_2 m^{-2} y^{-1}), which is notable because the raised treatment has also shifted toward sedge dominance (e.g., *Carex*), which we show to support autotrophy. It is important to note that other primary producers (e.g., plants) or processes such as photomineralization (Cory et al. 2014) or microbial transformation of DOC (Rieb et al. 2024) could have influenced CO_2 flux in this study and it would be interesting to consider their contribution in future investigations. In this region of Alaska, open-water areas are expanding (Douglas,

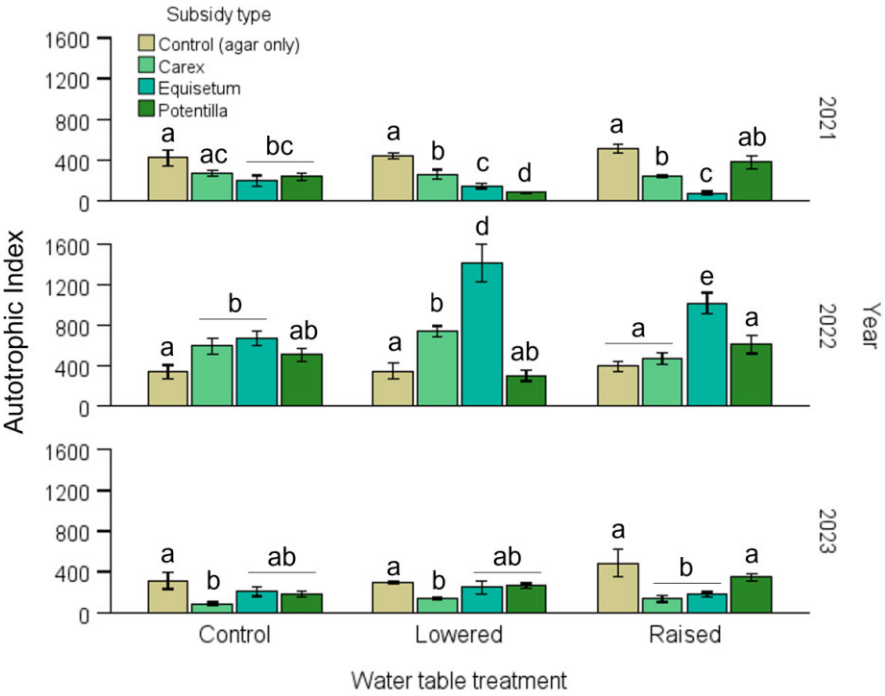

FIGURE 6 | Annual variation in biofilm autotrophic index (mean ± 1 SE; $n=4$) on nutrient-diffusing substrates enriched with either agar only (control), *Carex, Equisetum*, or *Potentilla* subsidies within control, lowered, and raised water table treatments. Lower values of AI indicate a higher proportion of autotrophy in the microbial community. Pairwise comparisons are within-year differences and bars with the same letter are not significantly different among treatments ($\alpha = 0.05$).

Turetsky, and Koven 2020), resulting in the release of between 13 and 59 g CO_2 m^{-2} y^{-1} (Euskirchen et al. 2024). Our findings add to a growing body of literature demonstrating the extent to which carbon fixation by autotrophic microbes contributes to the whole ecosystem carbon fixation (Wyatt et al. 2021; Jassey et al. 2022; Rober et al. 2023).

4.1 | Conclusion

Despite an extensive literature on the quantitative and qualitative aspects of peatland primary producers on belowground processes (Zak and Kling 2006; Ward et al. 2015; Fofana et al. 2022), we know very little about the effects of plant exudates on other primary producers (i.e., algae) and associated heterotrophic communities in the surrounding aquatic environment. We found that plant subsidies influenced biofilm development. Owing to the ability for plants to release nutrients along with carbon subsidies, nutrient-rich subsidies alleviated biofilm nutrient limitation and increased algal biomass, but only when DOC was $< 50\,\mathrm{mg\,L^{-1}}$. In conditions that supported autotrophic biofilm the site was a net sink for CO_2, suggesting that algal photosynthesis mitigated CO_2 emissions associated with heterotrophic respiration. Although heterotrophic members of the biofilm are typically better competitors for nutrients than algae (Stets and Cotner 2008), they coexist owing to the need for labile subsidies provided by the algae (Halvorson, Wyatt, and Kuehn 2020). With increasing background levels of DOC, heterotrophic microorganisms were able to outcompete algae for available nutrients. In this condition, algae were no longer available to mitigate the effects of heterotrophic respiration leading to greater CO_2 emissions from the system.

Author Contributions

Kevin H. Wyatt: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, supervision, writing – original draft, writing – review and editing. **Jillian Cieslik:** methodology. **Catherine M. Dieleman:** methodology, writing – review and editing. **Evan S. Kane:** conceptualization, funding acquisition, project administration, supervision, writing – review and editing. **Allison R. Rober:** conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, supervision, visualization, writing – review and editing. **Barrett Sullivan:** investigation, methodology. **Merritt R. Turetsky:** conceptualization, funding acquisition, project administration, writing – review and editing.

Acknowledgments

This research was supported by the National Science Foundation grants DEB-2141285 (to K.W. and A.R.) and DEB LTREB-2011286 (to K.W. and A.R.), and DEB LTREB-2011257 (to E.K. and M.T.). The Bonanza Creek Long-Term Ecological Research Program was funded by USDA Forest Service, Pacific Northwest Research Station grant RJVA-PNW-01-JV-11261952-231 and National Science Foundation grant DEB-1636476.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Environmental Data Initiative Portal at https://doi.org/10.6073/pasta/ef7951ef65ed82755c37623071a00923.

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Supporting Information

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