

LETTER

Trophic interactions regulate peatland carbon cycling

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Abstract

Peatlands are the most efficient natural ecosystems for long-term storage of atmospheric carbon. Our understanding of peatland carbon cycling is based entirely on bottom-up controls regulated by low nutrient availability. Recent studies have shown that top-down controls through predator-prey dynamics can influence ecosystem function, yet this has not been evaluated in peatlands to date. Here, we used a combination of nutrient enrichment and trophic-level manipulation to test the hypothesis that interactions between nutrient availability (bottom-up) and predation (top-down) influence peatland carbon fluxes. Elevated nutrients stimulated bacterial biomass and organic matter decomposition. In the absence of top-down regulation, carbon dioxide (CO₂) respiration driven by greater decomposition was offset by elevated algal productivity. Herbivores accelerated CO₂ emissions by removing algal biomass, while predators indirectly reduced CO₂ emissions by muting herbivory in a trophic cascade. This study demonstrates that trophic interactions can mitigate CO₂ emissions associated with elevated nutrient levels in northern peatlands.

Keywords

Algae, carbon dioxide, climate change, decomposition, food web, net ecosystem exchange, nutrients, predator, trophic cascade, zoogeographical effects.

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INTRODUCTION

Feedbacks between food-web structure and the form and availability of nutrients have the potential to influence ecosystem processes such as the production and subsequent decomposition of organic matter (Atwood *et al.* 2015a; Hammerschlag *et al.* 2019; Schmitz & Leroux 2020). Primary production in many ecosystems is nutrient-limited, usually by nitrogen (N) or phosphorus (P), and nutrient limitation of primary production can be propagated to higher trophic levels (Elser *et al.* 2000; Buchkowski *et al.* 2019). There is growing evidence that higher trophic levels in both terrestrial and aquatic food webs, in turn, can exert important control on nutrient availability, with consequences for primary productivity and other aspects of ecosystem carbon cycling (Estes *et al.* 2011; Schmitz *et al.* 2014, 2018; Limberger *et al.* 2019). In grasslands for example, predators limit the access of herbivores to plant material, resulting in a trophic cascade and greater primary productivity and carbon dioxide (CO₂) uptake within the ecosystem (Strickland *et al.* 2013). Examples from freshwater ecosystems are sparse, but trends point to the potential for predators to influence CO₂ emissions from lakes (Schindler *et al.* 1997) and more recently, from ponds and streams (Atwood *et al.* 2013, 2015a), where predators can substantially reduce CO₂ emissions if they control the density or foraging activities of herbivores and indirectly increase the biomass of lower trophic levels in a trophic cascade. These results imply that our ability to predict ecosystem processes, such as carbon inputs and losses, may be dependent on the outcome of

complex trophic interactions, including the direct and indirect effects of predators on food-web structure (Schmitz & Leroux 2020).

Northern peatlands are an important global carbon reservoir and their ability to store carbon in the future will depend in part on their response to environmental change (Schuur & Abbott 2011; Loisel *et al.* 2017). Because of their anaerobic status and thick organic soil layers that lock up significant amounts of nutrients, northern peatlands are nutrient poor ecosystems. Peatlands typically are dominated by mosses that can tolerate low nutrient availability and tend to form litter that decomposes slowly, thereby creating a positive feedback with peat accumulation rates (Turetsky 2003; Belyea & Malmer 2004). Owing to their low nutritional value, the dominant vegetation that forms surface peat layers (e.g. mosses) is thought to provide minimal support for higher trophic levels (van Duinen *et al.* 2013). This longstanding view has given primacy to bottom-up (resource limitation) over top-down (consumer regulated) drivers of ecosystem functioning in northern peatlands. However, conditions associated with ongoing climate change, including permafrost thaw and more variable hydrology (Jorgenson *et al.* 2001; Stewart *et al.* 2013), are expected to accelerate nutrient mineralisation and N and P levels across northern ecosystems (Reyes & Loughheed 2015; Wickland *et al.* 2018). In general, food-web theory predicts that herbivores and predators (i.e. top-down forces) will play an increasingly important role in regulating ecosystem processes in conditions with elevated nutrient availability (Schindler *et al.* 1997; Estes *et al.* 2011; McCann *et al.* 2021). However, no

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efforts to date have evaluated the role of animals in mediating carbon cycling through trophic interactions in northern peatlands.

Like most wetlands, northern peatlands are often inundated with water during the summer growing season (Euskirchen *et al.* 2019). Shallow pools are a common feature of northern peatlands (Pelletier *et al.* 2014) and the distribution of open-water areas are expanding in some regions owing to permafrost degradation and changes in precipitation patterns (Jorgenson *et al.* 2001; Douglas *et al.* 2020). During periods of inundation, which can span multiple growing seasons (Euskirchen *et al.* 2019), aquatic biofilms that include microbial primary producers (algae) and decomposers (heterotrophic bacteria) develop on peat surface layers (DeColibus *et al.* 2017). Primary producers and decomposers can vary in relative abundance within the biofilm, but the overall metabolic balance of peatland biofilms has been shown to favour autotrophy (Myers *et al.* 2021). As a consequence, biofilms make significant contributions to above ground primary productivity in peatlands (Rober *et al.* 2014). Furthermore, elevated nutrient availability associated with more variable hydrology is expected to alleviate bottom-up constraints on biofilm production (Wyatt *et al.* 2012), with a net effect of greater CO₂ uptake (Kane *et al.* 2021). In contrast to peatland plants, biofilms are rapidly consumed by herbivores (DeColibus *et al.* 2017), making this energy pathway potentially more susceptible to trophic regulation than a strictly detritus-based system.

Our primary research objective was to determine if wet phases or more nutrient-rich conditions would increase the trophic regulation of peatland carbon cycling (Fig. 1). Since recalcitrant plant material like moss tissue is not expected to be impacted by trophic regulation, here we focused on the biofilm that develops on peat surface layers during periods of inundation (Wyatt *et al.* 2012). We conducted a mesocosm experiment that included a full factorial combination of nutrient enrichment and trophic-level manipulation (herbivore and predator exclusion) during consecutive wet growing seasons in an Alaskan fen to test the hypothesis that interactions between nutrient availability (bottom-up effects) and predation (top-down effects) influence food-web structure and carbon cycling in northern peatlands (Fig. 1). We predicted that under low nutrient availability, biofilm biomass would be constrained and decomposition would be regulated by detrital pathways. We predicted that increasing nutrient availability would promote biofilm development and the transfer of energy to herbivores. If there was sufficient herbivore biomass, we predicted that predators would release the biofilm from top-down regulation by herbivores and under this trophic cascade, elevated biofilm biomass was anticipated to offset CO₂ emissions associated with enhanced plant-litter decomposition (Fig. 1).

MATERIAL AND METHODS

Study site

Nutrient availability and food-web structure were manipulated inside mesocosms in a moderate-rich fen located within the

Tanana River floodplain approximately 35 km southwest of Fairbanks, Alaska, USA (64°42' N, 148°18' W). The fen is affiliated with the Alaska Peatland Experiment (APEX), just outside the Bonanza Creek Experimental Forest. This region experiences a short growing season (≤ 135 d) with > 21 h d⁻¹ sunlight in June (Hinzman *et al.* 2006). The fen has little topographic variability and peat depth exceeds 1 m at the center of the site. The fen lacks trees and the plant community is composed of *Carex atherodes* (Sprengel), *Equisetum fluviatile* (Linnaeus), *Potentilla palustris* (Linnaeus), and *Sphagnum* moss species. Water depth varies interannually, ranging from 0 to 45 cm above the peat surface. Water-column concentrations of nitrate (NO₃⁻) and phosphate (PO₄⁻) are typically < 23 and $5 \mu\text{g L}^{-1}$, respectively, and pH ranges from 5.5 to 6.9 during the summer growing season (Rober *et al.* 2014). During periods of inundation, a three-tiered aquatic food web develops that consists of biofilm, herbivores, and predatory macroinvertebrates (most of which are insect larvae). Owing to prolonged periods of drought or freezing, these peatland environments are naturally fishless.

Experimental design

The open-water area of the fen was partitioned into 'enriched' and 'unenriched' sections (each approximately 30 m² in size) by an impermeable polyethylene curtain (Fig. 2). The curtain was installed through the center of the fen as a fence that was anchored to the bottom and floating at the surface to prohibit the exchange of nutrients between enriched and unenriched treatments. A raised boardwalk was installed on each side of the curtain partition to prevent disturbance during experimental set-up and regular sampling (Fig. 2). Once the boardwalks were in place, a second impermeable polyethylene curtain was installed on each side of the center partition to further prevent the movement of nutrients between enriched and unenriched treatments (Fig. 2). The curtains and boardwalks were installed approximately one week prior to nutrient enrichment and maintained throughout the duration of the two-year study. The nutrient 'enriched' treatments were made by amending half of the fen (i.e. one side of the curtain partition) with a granulose slow-release fertiliser (Osmocote, Scotts® Company, Marysville, OH, USA). Nutrients were applied by evenly spreading fertiliser pellets (N:P molar ratio = 16:3) with a broadcast spreader at the beginning of each growing season (two weeks prior to manipulating the food web) and then again after 6 weeks to sustain elevated nutrient levels for the duration of the experiment (O'Connor & Donohue 2012). Biofilm development within this fen complex is co-limited by N and P (Wyatt *et al.* 2015) and biofilm nutrient limitation is alleviated by the release of these nutrients during re-flooding events (DeColibus *et al.* 2017). Our goal with enrichments was to elevate nutrients above levels known to be growth limiting for biofilms within this context (Borchardt 1996) and to be in line with those of other studies aimed to simulate future conditions, such as nutrient release from permafrost thaw (Reyes & Loughheed 2015). The unenriched area of the fen was maintained at ambient nutrient conditions. Measures of water-column nutrient levels were made three times throughout each study year to confirm that

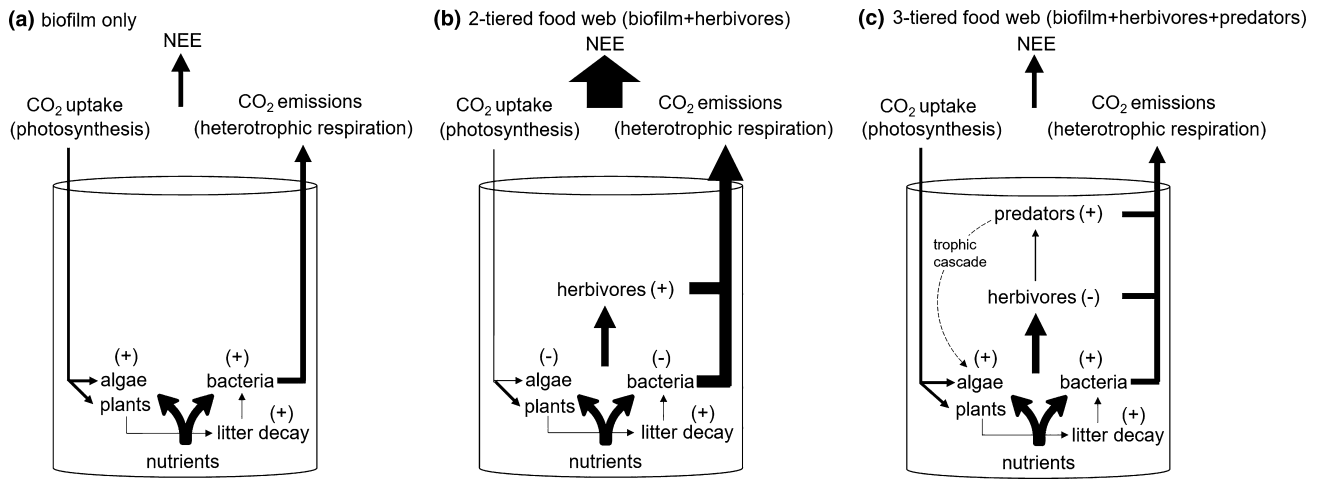


Figure 1 Conceptual diagram illustrating the ability for higher trophic levels to mediate peatland carbon emissions in conditions of enhanced nutrient availability. Predicted net effects of nutrient enrichment (bottom-up forces) and food-web manipulation (top-down forces) on community composition are depicted by + or – symbols, where + symbols indicate an overall increase and – symbols indicate an overall decrease in each food web compartment. Solid arrows represent carbon flux between trophic compartments and the uptake of CO₂ by photosynthesis and release of CO₂ by heterotrophic respiration. Arrow thickness represents the magnitude of trophic-level manipulation on CO₂ flux. Dashed arrows represent indirect effects of predators (e.g. trophic cascade) on the biofilm. Compared to dry surfaces, which typically act as a carbon sink, open water areas of northern peatlands often operate as a source of carbon to the atmosphere. Therefore, we anticipated that net ecosystem exchange (NEE) would be positive across all treatment combinations (i.e. CO₂ source), but emissions would be reduced in treatments with elevated algal photosynthesis. We predicted that (a) Greater decomposition in the presence of elevated nutrient availability would increase NEE, but the magnitude of the effect could be subdued by a simultaneous increase in autotrophic biofilm development in the absence of top-down regulation by herbivores. (b) Nutrients would continue to support litter decay within the reduced microbial community compared to treatments without nutrients, but consumption of algal biomass by herbivores would increase NEE by reducing photosynthetic activity. (c) Predators would indirectly increase algal biomass and reduce NEE by muting herbivory in a trophic cascade.

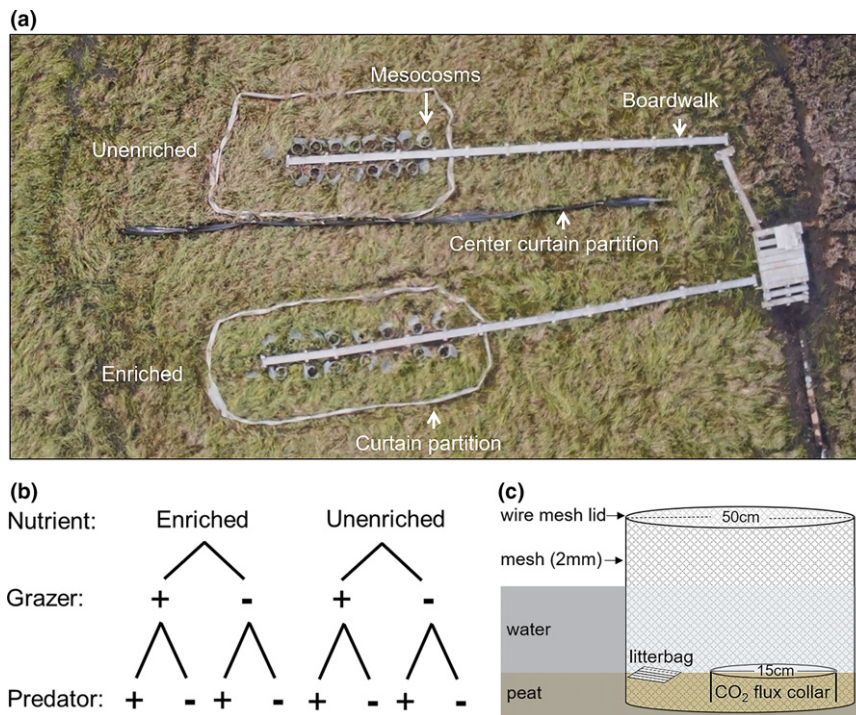


Figure 2 Aerial photograph of boreal peatland study site examining bottom-up (nutrient limitation) and top-down (consumers) regulation of CO₂ flux (a). Nutrients, grazers, and predators were manipulated in a full factorial design (b) inside mesocosm enclosures (c).

nutrients were elevated in the enriched treatment but not within the unenriched treatment.

Cylinder mesocosms (50 cm in diameter) constructed of welded-wire mesh were evenly spaced throughout the fen so

that each treatment (enriched, unenriched) had 16 enclosures for food-web manipulation (Fig. 2). Mesocosms were wrapped with porous transparent mesh (2 mm pore size) and pushed into the peat so that each enclosure extended approximately

15 cm above the water surface (Wyatt & Turetsky 2015). This porous mesocosm design made it possible to manipulate the food web while also facilitating the natural exchange of nutrients and water with the surrounding environment. These conditions allowed us to maintain similar nutrient levels among enclosures within the enriched section and observe the effects of variable biofilm development resulting from trophic dynamics on CO₂ flux. Each mesocosm contained pre-cut plant stems (*C. atherodes*; 10 cm length) as standard substratum for measures of biofilm colonisation. A stainless steel metal collar (15 cm in diameter) was inserted into the peat within each mesocosm for measures of ecosystem CO₂ uptake and losses (Fig. 2). Baseline physical and chemical characteristics showed no differences in vegetation structure or gas fluxes among experimental enclosures prior to manipulation.

Each mesocosm contained a litterbag to quantify slower ecosystem processes associated with plant-litter decomposition over the two-year study (Straková *et al.* 2012). Litterbags were constructed of nylon mesh (0.5 mm) and each bag contained 1 g of dried dead *C. atherodes* stems for measures of litter mass loss (Bärlocher 2005). Litterbags were constantly inundated during our study which should have minimised inaccuracies associated with air-drying (Taylor 1998) and the integrity of the litterbags did not appear to be compromised by the freeze-thaw cycle. We positioned litterbags horizontally on the peat surface where the plant litter would fall and naturally be decomposing (Straková *et al.* 2012).

Within each respective nutrient treatment (enriched, unenriched), mesocosm enclosures were assigned to one of four trophic-level manipulations: both grazer and predator exclusion (biofilm only treatment), grazer exclusion (+predator treatment), predator exclusion (+grazer treatment), or ambient conditions (+grazer + predator treatment) ($n = 4$ of each treatment; Fig. 2). Mesocosms were arranged using a randomised block design so that no two of the same treatment (i.e. trophic-level manipulation) occurred next to each other within each respective nutrient treatment. Grazer access to the biofilm was manipulated by manually removing grazers (grazer exclusion) and predator access to grazers was manipulated by manually removing predators (predator exclusion) (O'Connor & Donohue 2012; Amundrud & Srivastava 2016). Both grazers and predators were manually removed from grazer and predator exclusion treatments, whereas all trophic levels were present in the + grazer + predator treatment (i.e. ambient conditions). Owing to the naturally three-tiered food web present in our study system (DeColibus *et al.* 2017), the + grazer + predator treatment allowed us to evaluate the potential for a trophic cascade to influence CO₂ flux, where predation limits herbivory and indirectly promotes greater CO₂ uptake by reducing the consumptive effects of herbivores on algal biomass (Fig. 1). We expected that removing grazers in the + predator treatment would allow us to better evaluate the relative importance of the predator effects on grazing in the + grazer + predator treatment. The + predator treatment also allowed us to account for potential positive indirect effects of predators on primary production through consumer driven nutrient recycling (Buchkowski *et al.* 2019) or regulate CO₂ flux through detrital pathways (Atwood *et al.* 2013, 2014a). Mesocosms were lidded with wire mesh (2 mm mesh

size) to prohibit predatory fishing spiders from either entering predator exclusion treatments or escaping grazer exclusion treatments (Fig. 2). After mesocosms were installed, we inspected each enclosure to ensure that natural abundances of consumers were maintained among treatments (i.e. 4-6 snails (*Lymnaea*), 3-4 tadpole shrimp (Notostraca), 2-3 wood frog tadpoles (*Lithobates sylvaticus*; LeConte), 1-3 odonata (dragonfly and damselfly larvae), 1-2 diving beetle larvae (Dytiscidae), 1 fishing spider (*Dolomedes striatus*; Giebel) per m²) based on field observations (DeColibus *et al.* 2017). Organisms smaller than the mesh size (2 mm) of our mesocosm enclosures were present at natural densities. Owing to low visibility associated with the dark fen water and the flocculent nature of the submersed peat surface, it was not possible to track consumer abundance over time. Instead, we recorded visual observations (presence/absence) of the consumer community to confirm that manipulations were sustained throughout the duration of the two-year study. The aquatic biofilm was allowed to colonise substrates in response to the experimental manipulation for the duration of the aquatic growing season in 2017 and 2018 (i.e. while water covered the peat surface). This resulted in 50 days of colonisation in 2017 (7 June – 27 July) and 47 days in 2018 (15 June – 1 August).

Sample collection and analysis

Autotrophic biofilm colonisation was quantified as chlorophyll *a*. Four plant stems were collected from each mesocosm with forceps and the biofilm was removed by vigorously scraping and brushing (DeColibus *et al.* 2017). The length and width of each stem was measured and the surface area was adjusted in subsequent area-specific calculations of biomass accumulation. The detached biofilm was transported (1 h) to the lab in a dark cooler with ice where it was immediately filtered onto a glass fibre filter (0.7 µm GF/F Whatman, Springfield Mill, UK), placed into a 20-mL centrifuge tube with 90% ethanol, and steeped in a dark refrigerator overnight. Chlorophyll *a* was measured from the extract with a Shimadzu UVmini-1240 spectrophotometer (Shimadzu Corporation, Kyoto, Japan) at 665 and 750 nm following standard methods (APHA 1998).

Bacterial biomass was quantified by direct counts using epifluorescence microscopy. The biofilm was detached from a separate set of four stems as described above. The detached biofilm was preserved in a 2% formalin solution and bacteria were enumerated within two months of collection by staining an aliquot of the homogenised sample with 4', 6-diamino-2-phenylindole (DAPI) (Porter & Feig 1980). The stained aliquots were filtered onto a 0.2-µm pore-size black filter (OSMONIC INC., Livermore, CA, USA) and a minimum of 300 cells or 25 fields were counted per filter at 1000X magnification using a Leica DM 4000 light microscope with fluorescence. Bacterial biomass was calculated by a bacterial abundance/biomass conversion factor of 35 fg C cell⁻¹ (Theil-Nielsen & Søndergaard 1998).

To quantify ecosystem carbon inputs and losses, CO₂ (net ecosystem exchange under light conditions, ecosystem respiration under dark conditions) was collected using an infrared gas analyzer (IRGA; Amesbury, MA, USA). Ecosystem CO₂

flux was measured at the same time as biofilm collection using a CYP-4 canopy assimilation chamber (PP Systems, Amesbury, MA, USA) placed on a stainless steel metal collar within each mesocosm and sealed with a neoprene gasket. The CO₂ flux rate (g CO₂ m⁻² h⁻¹) was calculated as the slope of the linear relationship between CO₂ concentration in the headspace and time. Net ecosystem exchange (NEE) measurements were collected under ambient light conditions and positive NEE values indicated carbon release to the atmosphere (Chivers *et al.* 2009). Ecosystem respiration (ER) measurements were collected under dark conditions by covering the chamber (following a 1-min venting period) with a dark shroud that blocked light from entering the chamber.

Litterbags were collected from each mesocosm after two years to quantify the long-term effects of nutrient enrichment on plant-litter decomposition in the upper peat layers (Straková *et al.* 2012). After recovery, litterbags were transported (<1 h) to the laboratory where the content was cleaned over a 1 mm sieve to remove ingrowth materials, dried at 60 °C for 48 h, ashed at 500 °C, and reweighed to calculate ash-free dry mass. Plant litter mass loss was used as a proxy for decomposition and was calculated as the difference between the initial and final mass (Bärlocher 2005).

Physiochemical conditions were measured within each mesocosm during biofilm and gas flux measurements. Water depth (cm) was measured with a meter stick. Measurements of water temperature (°C), pH, conductivity (µS), and dissolved oxygen (DO; mg L⁻¹) were made with a Hach model 40 d multiprobe (Hach Company, Loveland, CO, USA). Photosynthetically active radiation (PAR; µmol photons m⁻² s⁻¹) was measured approximately 5 cm above the peat surface with a Li-Cor submersible quantum sensor and LI-250 light meter (Li-Cor, Lincoln, NE, USA). Water samples for dissolved nutrient analysis and organic carbon (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 NO₃⁻ and PO₄⁻ with an ion chromatograph (Dionex Corporation, Sunnyvale, CA, USA) (APHA 1998). Dissolved organic carbon was analysed using a Shimadzu TOC analyzer (Shimadzu Corp., Columbia, MD, USA).

STATISTICAL ANALYSES

Three-way general linear models (GLM) were used to evaluate the effect of food-web structure (+/- grazers and +/- predators) with and without nutrient enrichment on algal biomass, bacterial biomass, and CO₂ flux (ER, NEE). A three-way GLM was used to evaluate the effect of trophic-level manipulation and nutrient enrichment on plant-litter decomposition. A multivariate GLM was used to evaluate differences in physiochemical characteristics between enriched and unenriched treatments. When GLM indicated significant differences among treatments, Tukey's post-hoc comparison of means tests were used to discriminate between treatments. Statistical analyses were performed with SPSS 20 (IBM Statistics, Chicago, IL, USA).

RESULTS

Physiochemical characteristics

Environmental conditions were similar between enriched and unenriched sections of the fen except for aspects related to the experimental nutrient manipulation. Nutrient concentrations (NO₃⁻, PO₄⁻) in enriched treatments were significantly greater than unenriched treatments ($P < 0.0001$; Table 1). Both pH and DO were consistently elevated in enriched treatments likely owing to the uptake of inorganic carbon and the release of oxygen during photosynthesis (associated with elevated algal biomass) ($P \leq 0.0001$). Water depth, temperature, conductivity, PAR, and DOC were similar between enriched and unenriched treatments ($P \geq 0.78$).

Biofilm development

Biofilm response to nutrient enrichment was regulated by trophic dynamics (Fig. 3a and b). In the presence of nutrients, algal and bacterial biomass were significantly elevated compared to unenriched treatments (Table S1). Algal biomass was most elevated in treatments where both grazers and predators were excluded compared to all other treatment combinations ($P < 0.0001$), but was not significantly different from the predator-only treatment ($P = 0.14$; Fig. 3a). Grazing in the absence of a predator (+grazer treatment) reduced algal biomass 3-fold compared to ambient (+grazer + predator treatment) where grazers were present but their access to the biofilm was reduced by predation (i.e. a trophic cascade) ($P \leq 0.0001$; Fig. 3a). The presence of a trophic cascade in the + grazer +predator treatment weakened the effect of grazing, thereby maintaining an intermediate level of algal biomass compared to treatments with biofilm only (grazer and predator excluded) ($P = 0.02$) or grazers only ($P = 0.001$; Fig. 3a). Patterns of bacterial biomass were similar to the algae but bacteria responded more strongly to nutrient enrichment than the presence or absence of a predator (Table S1). Bacterial biomass was reduced by grazing, but the reduction was not significantly different from ambient

Table 1 Physiochemical characteristics of the fen site and mean, standard error (SE), and standard deviation (SD) over two years of experimental manipulation. Different letter superscripts indicate significant differences between enriched and unenriched treatments ($\alpha = 0.05$)

Characteristic	Enriched			Unenriched		
	Mean	SE	SD	Mean	SE	SD
Water depth (cm)	15.7 ^a	1.20	6.76	15.9 ^a	1.23	6.88
Water temperature (°C)	20.8 ^a	0.32	1.82	20.7 ^a	0.37	2.08
Conductivity (µS)	27.4 ^a	0.71	4.01	27.7 ^a	0.53	3.00
PAR (µmol cm ² s ⁻¹)	377.7 ^a	20.2	114.3	383.1 ^a	19.5	110.3
pH	6.03 ^a	0.11	0.60	5.29 ^b	0.05	0.29
DO (mg L ⁻¹)	5.95 ^a	0.39	2.20	3.60 ^b	0.32	1.81
NO ₃ ⁻ (µg L ⁻¹)	464.0 ^a	26.8	131.1	28.5 ^b	4.45	21.8
PO ₄ ⁻ (µg L ⁻¹)	123.7 ^a	7.92	38.8	7.79 ^b	1.12	5.48
DOC (mg L ⁻¹)	38.2 ^a	1.74	9.87	38.8 ^a	1.66	9.39

Note PAR, photosynthetically active radiation, DO, dissolved oxygen, NO₃⁻, nitrate, PO₄⁻, phosphate, DOC, dissolved organic carbon.

(+grazer + predator treatment) ($P = 0.12$; Fig. 3b). Trophic-level manipulation had little effect on algal (Fig. 3a) or bacterial (Fig. 3b) biomass under nutrient limited (unenriched) conditions, as both components of the biofilm were in low abundance (Table S1).

Ecosystem carbon exchange

Trophic-level manipulation mitigated the effects of nutrient enrichment on ecosystem CO_2 flux (Table S1). Conditions

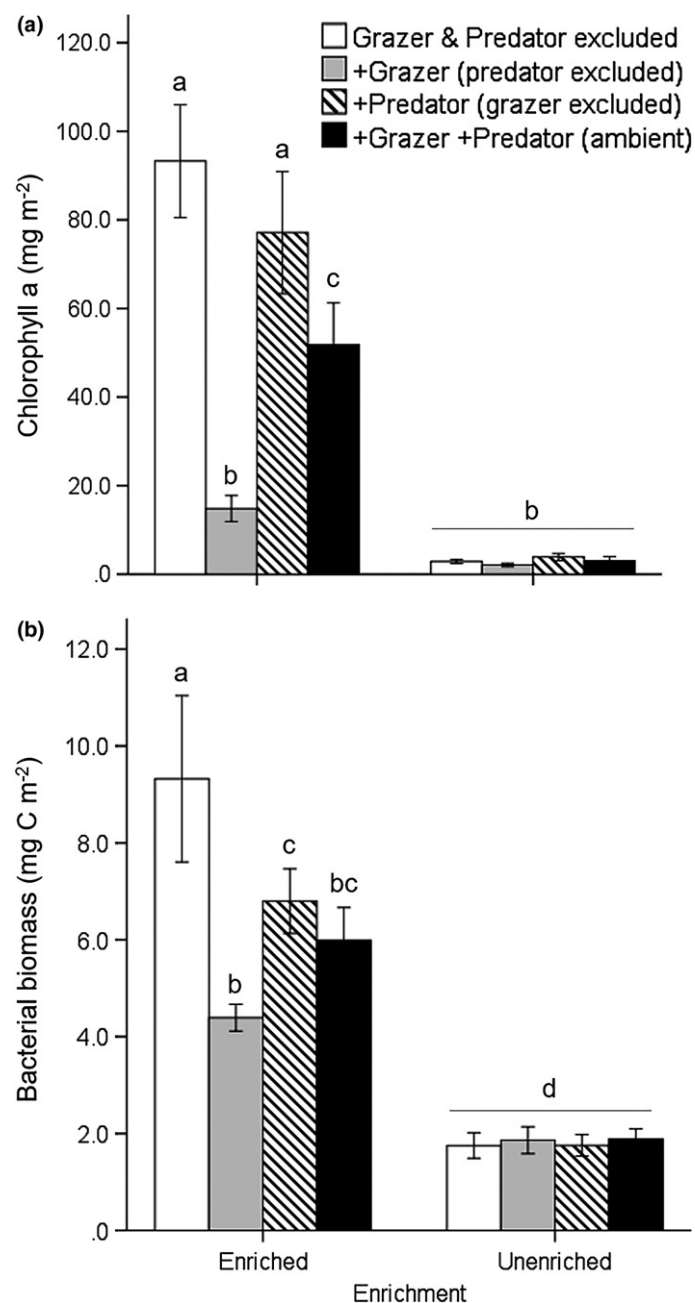


Figure 3 Mean ± 1 SE ($n = 8$) algal biomass measured as chlorophyll a concentration (a) and bacterial biomass (b) among grazer and predator exclusion treatments with and without nutrient enrichment. Bars with the same letter are not significantly different among treatments ($\alpha = 0.05$).

that favoured elevated algal biomass (i.e. nutrient enrichment in combination with grazer exclusion or reduced grazing via predation) promoted CO_2 uptake, whereas reductions in algal biomass by herbivory increased CO_2 emissions (Fig. 4). A trophic cascade in the + grazer +predator treatment (i.e. predators reduced the consumptive effects of herbivores on algal biomass) significantly reduced ER compared to the + grazer treatment, where ER was most elevated despite having reduced biofilm ($P = 0.01$; Fig. 4a). Net ecosystem exchange was positive across all treatment combinations (i.e. CO_2 source), but emissions were significantly lower in treatments with elevated algal biomass compared to the + grazer treatment ($P \leq 0.0001$; Fig. 4b). Trophic-level manipulation had little effect on CO_2 flux under nutrient limited (unenriched) conditions where heterotrophic respiration of CO_2 dominated all flux measurements (ER, NEE) (Fig. 4, Table S1).

Decomposition

Nutrient enrichment but not trophic-level manipulation influenced plant-litter decomposition. Organic matter loss was significantly greater in enriched treatments compared to unenriched treatments, where organic matter loss was nearly 70% compared to 50%, respectively (Fig. 5, Table S1). Organic matter loss was similar among trophic-level manipulations with and without nutrient enrichment (Fig. 5, Table S1).

DISCUSSION

This study shows that animals, through their direct and indirect interactions, regulate ecosystem carbon exchange in northern peatlands. The significant increase in algae with nutrient enrichment and subsequent decline in the presence of herbivores, supports our hypothesis that wetter more nutrient-rich conditions – anticipated to become more common in Alaskan fens with climate change – will promote biofilm development and the transfer of energy to consumers. Furthermore, we found that by releasing basal resources from top-down regulation (i.e. biofilm consumption by herbivores), predators indirectly promoted CO_2 uptake, supporting our hypothesis that a trophic cascade can reduce CO_2 emissions (i.e. NEE) from peatland surface waters. Under low nutrient availability, trophic-level manipulation had a minimal effect on biofilm development and CO_2 flux measurements. This finding supports our hypothesis that energy flow is constrained in conditions of low nutrient availability. Collectively, this study shows that trophic interactions can mitigate NEE (i.e. the carbon sink potential of the ecosystem) following elevated nutrient levels in peatlands during periods of saturation typical in our study region.

Consumption of the biofilm by herbivores accelerated CO_2 emissions in the presence of nutrient enrichment. A reduction of biofilm biomass in a two-tier food web is consistent with trophic theory where, in the absence of a higher predator, herbivores are free to consume any increase in basal resources that may be stimulated by nutrient enrichment (Hairston *et al.* 1960; Persson *et al.* 2001). The ability of herbivores to

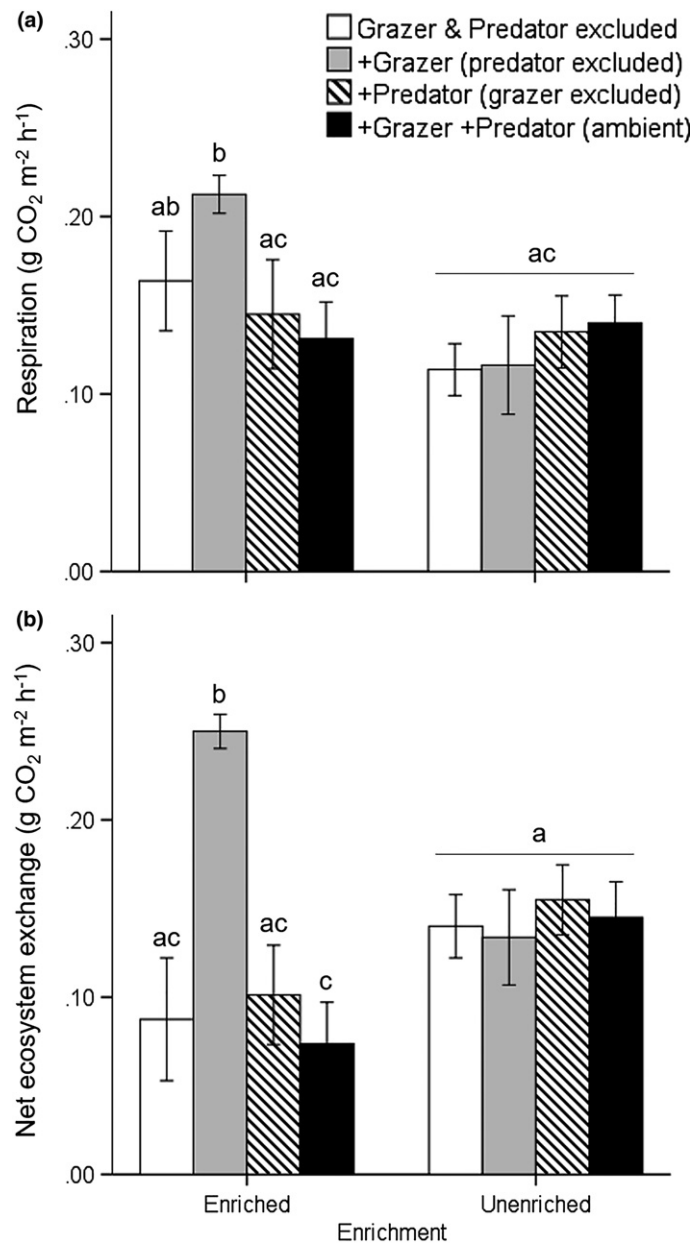


Figure 4 Mean \pm 1 SE ($n = 8$) ecosystem respiration (a), and net ecosystem exchange (b) among grazer and predator exclusion treatments with and without nutrient enrichment. Bars with the same letter are not significantly different among treatments ($\alpha = 0.05$).

maintain low levels of biofilm biomass, even in the presence of greater resource availability, has been widely reported in other environments (Hillebrand 2009; O'Connor & Donohue 2012; Rober *et al.* 2015). Our results show that by removing the biofilm, which was primarily autotrophic (Myers *et al.* 2021), the net effect of herbivory was an increase in NEE from saturated peat surface layers. These results are consistent with research showing that the loss or removal of top predators (i.e. a decrease in the number of trophic levels) results in lower carbon storage capacity across a range of other ecosystems (Estes *et al.* 2011; Atwood *et al.* 2015b; Schmitz *et al.* 2018; Hunter *et al.* 2019). These findings also provide valuable

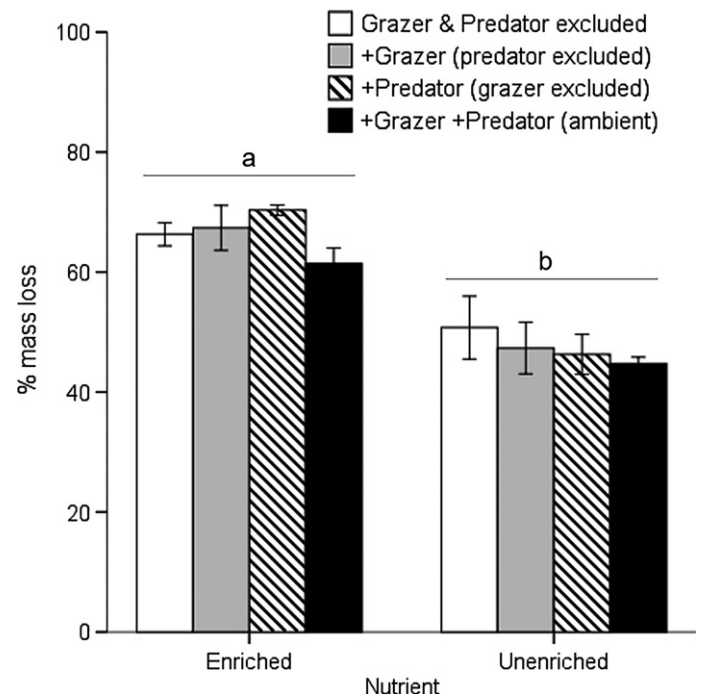


Figure 5 Plant-litter decomposition measured as % mass loss (mean \pm 1 SE; $n = 4$) among grazer and predator exclusion treatments with and without nutrient enrichment. Bars with the same letter are not significantly different among treatments ($\alpha = 0.05$).

insight into the role of aquatic herbivores in peatland food-web dynamics and suggests that in the absence of a predator guild, peatland herbivores can increase CO₂ emissions through consumption of aquatic primary production.

Consistent with our expectations, predators indirectly increased biofilm biomass and reduced CO₂ emissions by muting herbivory in a trophic cascade. The magnitude of the indirect effect of predators on CO₂ emissions is consistent with research from other aquatic ecosystems where predators have been shown to reduce CO₂ emissions by 46–137% through their direct interactions with prey and indirect interactions with lower trophic levels (Atwood *et al.* 2013, 2014a,b). The capacity to capture the indirect effects of predators on NEE over two years was remarkable given that the + grazer + predator treatment was essentially the intact natural ecosystem. By maintaining the natural aquatic community, our aim was to capture the net outcome of direct (consumptive) and indirect (nonconsumptive) effects of predators (Atwood *et al.* 2014a; Amundrud & Srivastava 2016), as well as weak and strong trophic linkages (McCann *et al.* 2021) on NEE. Although this approach does not allow for inference regarding specific mechanisms at play (e.g. trait mediated cascades; Trussell *et al.* 2008; Leroux *et al.* 2012), it has revealed the functional significance of a grazer food chain that until now has been assumed to be of minor importance to peatland carbon cycling. Following the literature, we would expect for predators to play an increasingly important role in peatland biogeochemical processes by regulating primary production and decomposition in conditions of elevated nutrient availability (Schindler *et al.* 1997; Estes *et al.* 2011). Our results

confirm these expectations and show that predators can mitigate the effects of enhanced nutrient availability on net ecosystem carbon exchange – highlighting a mechanism by which one of the world's largest carbon reservoirs may be buffered against greenhouse-gas emissions.

Northern peatlands experience wet phases via inundation or flooding that can occur both seasonally and interannually. It is broadly documented that conditions of elevated nutrient availability can stimulate organic matter decomposition in both wet and dry phases (Bragazza *et al.* 2006; Bubier *et al.* 2007). A unique feature of this study is that we show that elevated CO₂ emissions associated with enhanced decomposition (i.e. plant litter decay by bacteria) during the wet phase can be offset by autotrophic biofilm development. Given that algal biomass was present at different levels within the enriched treatments (i.e. owing to trophic regulation) while organic matter loss remained relatively constant, we were able to evaluate how hotspots of algal photosynthesis can mitigate the positive effects of nutrient enrichment on NEE. Because algae and bacteria occur in such close association, it was plausible that elevated levels of algal biomass might actually promote CO₂ respiration owing to higher rates of organic matter decomposition associated carbon subsidies from algal sources (Wyatt & Rober 2020). Although we did observe an increase in bacterial biomass in treatments with elevated algae, CO₂ emissions were reduced when compared to treatments with less algae. This finding indicates that carbon uptake by algal photosynthesis was greater than heterotrophic respiration associated with inputs of labile algal subsidies (Liang *et al.* 2018). When we compare annual estimates of NEE (assuming 21 h d⁻¹ sunlight during a 135 d growing season for the study site; Hinzman *et al.* 2006) between nutrient treatments where the biofilm was removed by grazing (NEE > 700 g CO₂ m⁻² y⁻¹) and treatments without nutrients (NEE > 400 g CO₂ m⁻² year⁻¹) we see that nutrient enrichment could stimulate bacterial decomposition and increase CO₂ emissions by approximately 300 g CO₂ m⁻² y⁻¹ in the absence of a counterbalance from algal photosynthesis. By releasing algae from grazing pressure in a trophic cascade, the indirect effect of predators reduced NEE to approximately 200 g CO₂ m⁻² year⁻¹, which not only mitigated CO₂ emissions associated with nutrient inputs, but reduced NEE to levels below the unenriched treatments. The magnitude of this effect (*c.* 500 g CO₂ m⁻² year⁻¹) highlights the importance of autotrophic members of the biofilm as regulators of NEE during wet periods in northern peatlands. Considering that open water areas of northern peatlands release 23–419 g CO₂ m⁻² year⁻¹ (Waddington & Roulet 2000; Pelletier *et al.* 2014), animal effects could determine whether an individual peatland is a carbon source or sink following nutrient enrichment.

Our study was designed to evaluate animal controls on peatland carbon dynamics during periods of sustained inundation, which have become increasingly common in boreal regions over the past decade (Douglas *et al.* 2020). It is also likely that more variable precipitation regimes (Stewart *et al.*, 2013) will exacerbate the intermittent nature of peatland hydrology, with more frequent events of both wet and dry periods (e.g. Euskirchen *et al.* 2019). While our study shows

that wetter conditions will likely increase trophic regulation of NEE, more frequent or extended periods of drought may restrict top-down forces by limiting the development of higher trophic levels (e.g. Amundrud & Srivastava 2019). Exploring linkages between wet and dry phases, especially as they relate to timing, will be an important next step toward meaningful predictions of climate-change impacts on peatland food webs and to developing a conceptual understanding of exactly how dominant carbon-cycle processes will be altered by dramatically changing water tables expected for the boreal region.

CONCLUSION

This study addresses recent calls in the literature to systematically examine the role of animals and their trophic interactions in regulating the carbon cycle (Schmitz & Leroux 2020) and does so in an ecosystem where changes in carbon flux could have implications for the global carbon cycle (Schoor & Abbott 2011; Loisel *et al.* 2017). While previous studies have shown that animal effects can regulate individual processes associated with carbon dynamics (i.e. ER, photosynthesis), there is still an incomplete understanding of whether or not they contribute to regulating net ecosystem carbon uptake and storage (Schmitz & Leroux 2020). By disassembling a grazer food chain, we show that animals, through trophic interactions, contribute to the carbon sink potential (i.e. net ecosystem carbon exchange) of a northern peatland ecosystem. Specifically, our results show that: (1) in the absence of top-down regulation (i.e. consumption by herbivores), elevated levels of biofilm biomass offset CO₂ emissions associated with greater organic matter decomposition, (2) herbivory accelerated nutrient-enhanced CO₂ respiration by reducing biofilm biomass, and (3) predators indirectly increased biofilm biomass and reduced NEE by muting herbivory (either directly through consumption or indirectly through fear) in a trophic cascade. Our results challenge the long-standing notion that energy flow in northern peatlands is restricted by detrital pathways and highlights the need to consider animal food-chain interactions with biogeochemistry (i.e. zoogeochimical effects) in carbon cycle models aimed to predict how global change will affect net ecosystem carbon uptake and storage.

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AUTHOR CONTRIBUTIONS

KHW, KSM, ARR, and MRT designed the study. Data were collected and analysed by KHW and ARR. KHW led the writing of the manuscript and all authors edited the manuscript.

DATA AVAILABILITY STATEMENT

The data from this manuscript are available in the Dryad Digital Repository, <https://doi.org/10.5061/dryad.d51c5b028>

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