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Vulnerability of wetland soil carbon stocks to climate warming in the perhumid coastal temperate rainforest

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Abstract The perhumid coastal temperate rainforest (PCTR) of southeast Alaska has some of the densest soil organic carbon (SOC) stocks in the world (>300 Mg C ha^{-1}) but the fate of this SOC with continued warming remains largely unknown. We quantified dissolved organic carbon (DOC) and carbon dioxide (CO_2) yields from four different wetland types (rich fen, poor fen, forested wetland and cedar wetland) using controlled laboratory incubations of surface (10 cm) and subsurface (25 cm) soils incubated at 8 and 15 °C for 37 weeks. Furthermore, we used fluorescence characterization of DOC and laboratory bioassays to assess how climate-induced soil warming may impact the quality and bioavailability of DOC delivered to fluvial systems. Soil temperature was the strongest control on SOC turnover, with wetland type and soil depth less important in controlling CO_2 flux and extractable DOC. The high temperature incubation increased average CO_2 yield by ~40 and ~25% for DOC suggesting PCTR soils contain a sizeable pool of readily biodegradable SOC that can be mineralized to DOC and CO_2 with future climate warming. Fluxes of CO_2 were positively correlated to both extractable DOC and percent bioavailable DOC during the last few months of the incubation suggesting mineralization of SOC to DOC is a strong control of soil respiration rates. Whether the net result is increased export of either carbon form will depend on the balance between the land to water transport of DOC and the ability of soil microbial communities to mineralize DOC to CO_2.

Keywords Dissolved organic carbon · Carbon dioxide · Soil organic carbon turnover · Soil respiration · Dissolved organic carbon bioavailability

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Introduction

High latitude northern ecosystems have warmed significantly over the last 100 years (Chapin et al. 2000) and considerable effort has been directed toward understanding how this warming is altering ecosystem carbon cycling (Schuur et al. 2009; McGuire et al. 2009; Hartley et al. 2012). Northern ecosystems contain roughly half of the global soil carbon stock (Schuur et al. 2009; Tarnocai et al. 2009) and therefore relatively modest changes in the soil carbon flux to the atmosphere from this region could influence the global carbon cycle. Northern peatland soils store much of this carbon (>30% of the global soil carbon) making these carbon dense ecosystems especially important for modulating climate change (Tarnocai et al. 2009). Extensive soil carbon has accumulated in northern peatlands during the Holocene because of low temperatures and persistent soil saturation (Hobbie et al. 2000; Grosse et al. 2011), both of which are expected to change measurably in the coming century (McGuire et al. 2000).

The dynamics of carbon cycling along high latitude coastal margins, such as the perhumid coastal temperate rainforest (PCTR) of southeast Alaska and British Columbia, are less well understood relative to boreal and arctic ecosystems despite containing some of the densest terrestrial carbon stocks in the world (Johnson et al. 2011). Wetlands occupy >20% of the total land area of the PCTR and soil carbon densities in this region can exceed 600 Mg ha^{-1} (Johnson et al. 2011). Preliminary estimates of net ecosystem carbon sequestration in the PCTR range from 1.0 to 1.8 Mg ha^{-1} - $year^{-1}$ (D'Amore et al. 2015b). However, enhanced SOC mineralization with a warmer climate may render this large soil carbon stock vulnerable to destabilization. Thus, the PCTR may transform from an ecosystem that sequesters organic carbon to one with enhanced decomposition under future climate regimes.

Many carbon balance studies in terrestrial ecosystems do not include lateral carbon fluxes and focus on quantifying vertical carbon dioxide (CO_2) exchange because lateral carbon loss is thought to be a minor contributor to the net ecosystem carbon balance (e.g., Trumbore 2006). However, lateral carbon loss can be a significant component of the net ecosystem carbon balance in northern wetlands (Worrall et al. 2003, 2009; Billett et al. 2010; Evans et al. 2016). Dissolved organic carbon (DOC) is one of the main forms of fluvial carbon loss from terrestrial ecosystems and export from northern wetlands typically ranges from 10 to 30 g m^{-2} $year^{-1}$ (Worrall et al. 2003, 2009; Billett et al. 2010). However, in the PCTR, abundant precipitation and frequent soil flushing results in wetland DOC fluxes as large as 50 g C m^{-2} $year^{-1}$ (D'Amore et al. 2015a), placing these values in the upper range of DOC export from forested and wetlands streams (Aitkenhead and McDowell 2000; Ågren et al. 2007; Moore et al. 2011; Oliver et al. 2017). As a result, fluvial carbon fluxes in this region may account for a substantial (>40%) component of total ecosystem carbon export. These findings underscore the importance of developing an understanding of the fundamental controls on carbon fluxes from wetland soils to both the atmosphere and inland waters to predicting the response of PCTR carbon stocks to climate warming.

To determine the potential vulnerability of northern PCTR soil carbon stocks to climate warming, we quantified DOC and CO_2 production from four different wetland types (rich fen, poor fen, forested wetland and cedar forested wetland) using controlled laboratory incubations of surface (10 cm) and subsurface (25 cm) soils incubated at 8 and 15 °C for 37 weeks. This design allowed us to partition organic matter mineralization into lateral and vertical carbon loss vectors as DOC and CO_2 and evaluate the interactive impacts of climate (temperature) and land cover (wetland type) on soil carbon losses. We further used fluorescence characterization of dissolved organic matter (DOM) and laboratory bioassays to assess how climate warming may impact the quality and bioavailability of DOM delivered to fluvial systems. Our overarching hypothesis was that CO_2 fluxes would be more responsive to temperature and differences across wetland type than DOC fluxes, which would be more strongly related to differences in soil carbon content associated with soil depth.

Methods

Study sites

Soils used in the laboratory incubations were collected from the northern PCTR near Juneau, Alaska. The cool, maritime climate of Juneau receives approximately 1800 mm of precipitation at sea level. Much of this precipitation falls as rain during the autumn (September through November) and as snow at upper

elevations in the Coast Mountains during the winter (December through March). Numerous glacial epochs combined with the cool, wet climate have created a diverse landscape containing heavily incised watersheds with steep slopes but also extensive lowlands with water-logged peatlands and coniferous forest.

Five replicate sites were sampled within each of four common wetland types (4 wetland types × 5 replicate sites) in southeast Alaska: poor fen, rich fen, forested wetland and cedar wetland. All wetland types were acidic (soil pH <4.7) and characterized by the accumulation of organic matter (% carbon >31%) due to frequent near-surface soil saturation and cool temperatures in the region (Table 1). Poor fens have moderate to well-decomposed peat accumulations >2 m deep with vegetation consisting of *Sphagnum* mosses (*Sphagnum* spp.), ericaceous shrubs, sedges (*Carex* spp.), and shore pine (*Pinus contorta* var. *contorta*). Forested wetlands are typical of the raised peatland swamp with 0.4–0.7 m deep peat overlaying glacial till. Forested wetland vegetation consists of *Sphagnum* mosses (*Sphagnum* spp.), skunk cabbage (*Lysichiton americanus*), blueberry (*Vaccinium* spp.) with an overstory of mainly western hemlock (*T. heterophylla*) and to a lesser extent Sitka spruce (*P. sitchensis*). Rich fens are minerotrophic peatlands that have more robust growth and slightly higher pH than poor fen and forested wetlands and are dominated by forbs and graminoids (*Carex* spp.) with varying coverage of sphagnum mosses (*Sphagnum* spp.) and *Alnus* spp. (i.e. common along the margins of these sites). Cedar wetlands have similar vegetation as forested wetlands but are dominated by yellow cedar (*Chamaecyparis nootkatensis*), although mountain hemlock (*T. mertensiana*) can be common.

Laboratory incubations

Soils were collected from surface (~10 cm) and subsurface (~25 cm) soils in each site and incubated in the laboratory at 8 and 15 °C for 37 weeks. Sampling for DOC and CO_2 occurred at the onset of incubations and after 1 (CO_2 only), 4, 8, 12, 17, 20, 25 and 37 weeks. The 15 °C incubations were designed to represent the rapid decomposition possible under the projected end-of-century climate warming scenario for the region (Shanley et al. 2015) while the low temperature or 8 °C incubations represent average summer soil temperatures in the region's wetlands (D'Amore et al. 2015a). Surface soils for incubations were collected from intermittently saturated or hydrologically active wetland soil layers and subsurface soils were collected from the permanently saturated (<20 cm) or hydrologically inactive wetland soil layers (D'Amore et al. 2015a). Water filled pore space (calculated according to Haney and Haney 2010) for the surface and subsurface soil for all four wetland types averaged together was 84 ± 5% and 97 ± 7%, respectively.

One soil core approximately 30 cm deep and 50 cm wide was excavated within each wetland site. Approximately 5 cm of the surface vegetation layer for each core was removed and a ~200 g subsample of the soil core was sampled for both soil depths (10 and 25 cm). Soils were placed in polyethylene freezer bags and immediately transferred to the laboratory and stored in the refrigerator for less than two days before the start of the incubations. Soil samples were hand-mixed using latex gloves to remove woody debris and large root masses and sieved, un-dried using a 2 mm sieve. Approximately 50 g of wet soil was added to the filter units (Falcon cups; Nadelhoffer 1990) with upper and lower chambers separated by pre-combusted

Table 1 Mean (n = 5, ±1 SE) soil characteristics for the four wetland types used in laboratory incubations

Site	Soil depth (cm)	C (%)	N (%)	C:N	pH	BD
Forested wetland	10	40.3 (4.5)	1.4 (0.3)	32.7 (7.3)	3.9 (0.1)	0.2 (0.1)
Forested wetland	25	36.8 (6.8)	1.4 (0.3)	26.4 (2.2)	3.9 (0.1)	0.2 (0.1)
Cedar	10	39.3 (4.3)	1.1 (0.1)	36.3 (6.6)	4.3 (0.4)	0.3 (0.1)
Cedar	25	31.7 (5.3)	0.8 (0.1)	42.3 (8.4)	4.5 (0.4)	0.4 (0.2)
Poor fen	10	43.5 (0.9)	1.4 (0.2)	35.3 (6.2)	4.0 (0.1)	0.1 (0.1)
Poor fen	25	47.6 (0.5)	2.0 (0.2)	25.4 (3.2)	3.9 (0.1)	0.1 (0.1)
Rich fen	10	36.5 (1.1)	2.0 (0.1)	18.3 (0.7)	4.7 (0.3)	0.1 (0.1)
Rich fen	25	40.9 (3.1)	2.2 (0.1)	18.9 (1.0)	4.5 (0.2)	0.2 (0.1)

BD stands for bulk density (g cm^{-3})

Whatman GF/D filters (2.7 μm pore size). The filter units were modified using venting clamps, stopcocks, septa and tygon tubing and incubated in low–temperature ovens. During the incubations, soil moisture was periodically re-adjusted to initial moisture content by re-weighing the filter unit and adding deionized water if necessary.

Fluxes of CO_2 were determined by measuring CO_2 accumulation in the headspace of the upper chamber of the filter unit over a 4 h period of time. Initially, vent clamps were closed and the entire filter unit was purged with CO_2 free air. Air was collected for CO_2 analysis from the upper chamber after 4 h using a 5 mL glass syringe through a septum. Concentrations of CO_2 were immediately determined with an LI-COR infrared gas analyzer. To perform DOC extractions, venting clamps were closed on the filter units and 100 mL of deionized water was added and allowed to equilibrate overnight (20–24 h). Filter units were suctioned until approximately 100 mL of the extractant was collected. The collected extractant was immediately filtered through a pre-combusted (450 °C for 4 h) Whatman GF/F filter (0.7 μm nominal pore size) into pre-combusted (450 °C for 4 h) glass vials. After extractions were completed, venting clamps were opened to permit gas exchange and filter units were returned to the incubating ovens.

Laboratory methods

Soil pH, % C and N, bulk density and gravimetric water content were determined on all soil samples. Bulk density was measured on 125 cm^3 samples collected from soil pit surfaces that were weighed while wet, dried and reported as a dry weight per unit volume (g cm^3). Soil pH was measured on a 2:1 slurry of Milli-Q water to moist soil. Gravimetric water content was calculated on duplicate subsamples of moist soil dried at 100 °C to a constant weight. The difference in the total soil weight (i.e. wet weight minus dry weight) was used to determine gravimetric water content. For soil total C and N analysis, soil subsamples were dried at 60 °C, ground in a tungsten analytical blade grinder and concentrations were determined by combustion on a Leco CN analyzer. Concentrations of DOC (non-purgeable organic carbon analysis) were determined by high-temperature combustion using a Shimadzu TOC-V-CSH analyzer.

Three replicate leachate samples for each wetland type (3 out of the 5 replicates) were randomly selected for fluorescence characterization and bioavailability assays to determine the chemical quality and bioavailability of DOM. Before fluorescence characterization, water samples were filtered through a 0.45 μm nylon filter (Pall Acrodisc) and allowed to warm to room temperature. Next, ultraviolet absorbance at 254 nm was measured on a Genesys 5 spectrophotometer to determine if sample dilution was necessary to minimize inner filter effects (Green and Blough 1994). Dissolved organic matter fluorescence (different sample aliquot than was used for UV absorbance) was measured on a Fluoromax-4 (Jobin–Yvon Horiba) scanning fluorometer. Excitation–emission matrices (EEMs) were collected by measuring fluorescence intensity across excitation wavelengths from 240 to 450 nm at 5 nm increments and emission wavelengths from 300 to 600 nm at 2 nm increments. All EEMs were corrected for instrument bias and Raman normalized using the area under the water Raman peak at excitation 350 nm.

Biodegradable DOC (BDOC) was determined as the difference in DOC before and after a 4 week laboratory incubation (Fellman et al. 2008). Water samples were initially filtered through a 0.2 μm nylon filter (Pall Acrodisc), a bacterial inoculum was added and samples were incubated at room temperature in the dark. After 28 days, the solution was re-filtered through a 0.2 μm filter, DOC was re-measured and BDOC was calculated as the difference in sample DOC before and after 28 days. The bacterial inoculum was prepared from extra water collected from each wetland type that was filtered through a Whatman GF/D filter (2.7 μm nominal pore size).

Carbon flux estimation

Previous laboratory incubation studies have shown that DOC production is controlled by the frequency of leaching and the volume of water used in soil extractions because leaching of water removes a substantial portion of the soil DOC pool (McDowell and Likens 1988; Neff and Hooper 2002). Concentrations of DOC therefore represent the potentially soluble fraction of organic matter at a given time as opposed to a flux per unit time (Neff and Hooper 2002). Although we present extractable DOC for each time period as well as cumulative extractable DOC

(summation of DOC concentrations only on days when soil leaching occurred), these concentrations should be interpreted cautiously because they are only useful for comparing across treatments but not for estimating actual field fluxes. Fluxes of CO_2 are more easily estimated between sample dates. Thus, we present cumulative CO_2 flux (summation of CO_2 fluxes) on days when soil leaching occurred as well as the total fractional loss of carbon from soils through CO_2 evasion for the duration of the incubations using a linear interpolation to estimate CO_2 flux on days when measurements were not made.

Statistical analyses

We used parallel factor analysis (PARAFAC) to decompose the EEMs into individual fluorescence components using the PLS_toolbox 7.9 (Eigenvector Research Inc.) in MATLAB. Rayleigh and Raman scatter were removed from the EEMs prior to modeling. Our PARAFAC model identified a total of five fluorescence components (4 humic-like and 1 traditionally defined as protein-like) and was validated using split-half analysis (Fig. S1; Stedmon et al. 2003). Fluorescence components were reported as a percent relative contribution determined from the maximum fluorescence intensity of each component divided by the total fluorescence of all the modeled PARAFAC components within a sample.

The spectral characteristics of the five fluorescence components were similar to those of other studies in freshwater environments (Jaffé et al. 2008; Fellman et al. 2010; Inamdar et al. 2012). Humic-like components 1–4 have emission maxima wavelengths greater than 420 nm and are generally recognized to originate mainly from terrestrial plant and soil organic matter (Coble 1996; Stedmon and Markager 2005; Stubbins et al. 2014). The fluorescence characteristics of protein-like component 5 (Ex = 275 nm, Em = 342 nm) were similar to those of the aromatic amino acid tryptophan (Coble 1996; Stedmon and Markager 2005). However, recent evidence suggests that the specific moieties associated with protein-like fluorescence are actually nitrogen-depleted, but the aromatics associated with its fluorescence are nitrogen-enriched (Stubbins et al. 2014). We refer to this component as "protein-like" to be consistent with the existing body of fluorescence research rather than associate it with proteinaceous DOM. Here, we focus our analysis on protein-like fluorescence only because we are interested in inferring potential DOM function (typically related to bioavailability, Guillemette and del Giorgio 2011; Cory and Kaplan 2012) within the soil waters.

We designed a randomized factorial experiment to test for the effects of wetland type, soil temperature (8 and 15 °C), soil depth (10 and 25 cm) and their interaction on concentrations of CO_2 and DOC. Each combination of temperature and depth was independently replicated five times, and each of these replicates was measured seven times (8 times for CO_2) over a 37-week period. The influence of these factors on concentrations of CO_2 and DOC was tested using a linear mixed-effects model (SAS Proc Mixed procedure SAS, V.9.4). Correlations in SPSS software were calculated where appropriate, and if necessary, data were log transformed to meet normality and equal variance assumptions.

Results

Effects of wetland type, temperature, soil depth and time on fluxes of CO_2 and extractable DOC

Extractable DOC across the whole incubation period did not differ among the four wetland types ($F_{3,67} = 1.00$, $p = 0.398$) or with soil depth ($F_{1,67} = 0.11$, $p = 0.744$) even though mean DOC concentrations at 10 cm were ~30% greater than at 25 cm (Fig. 1a–d). However, there was a significant interaction in extractable DOC between wetland type and soil depth ($F_{3,67} = 2.81$, $p = 0.046$). This interaction was likely driven by the poor fens, which had the highest extractable DOC of all wetland types at 25 cm (1.0 mg C g^{-1} soil C; mean of all other sites 0.5 mg C g^{-1} soil C) but not in surface soils (0.8 mg C g^{-1} soil C; mean of all other sites 0.7 mg C g^{-1} soil C). Incubation temperature strongly controlled extractable DOC across sites and at both soil depths, with ~25% greater concentrations at the higher versus lower temperatures ($F_{1,67} = 7.12$, $p = 0.010$). The greater DOC extracted at 15 °C did not vary in its interaction term with either wetland type ($F_{3,67} = 0.95$, $p = 0.421$) or soil depth ($F_{1,67} = 2.23$, $p = 0.140$). Extractable DOC concentrations did not change significantly across the length of the incubations for all sites ($F_{1,553} = 1.51$, $p = 0.220$). However, there was a significant interaction between incubation length and wetland type ($F_{3,553} = 7.14$,

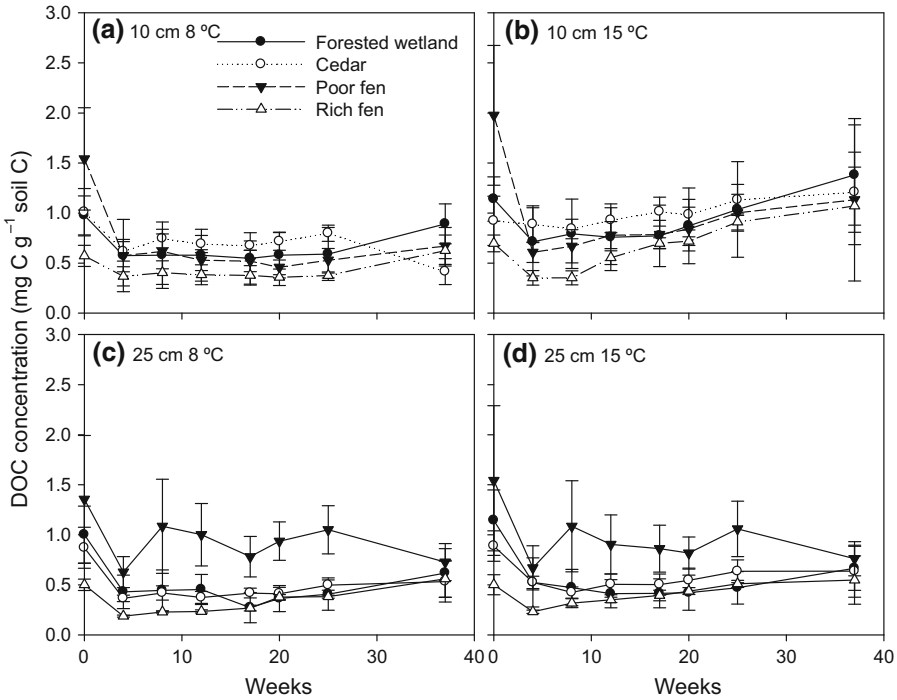

Fig. 1 Mean (n = 5, ±1 SE) extractable dissolved organic carbon (DOC) concentration for the four wetland types collected at 10 and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

$p < 0.001$) that was likely driven by the 2–4 fold increase in extractable DOC over time in rich fen sites.

Cumulative extractable DOC ranged from 2.7 to 7.9 mg C g^{-1} soil C, with mean concentrations greatest in poor fen sites (mean of 7.1 mg C g^{-1} soil C) and in the 10 cm versus 25 cm (~20% greater) soil depths (Fig. 2a–d). In poor fen sites at 25 cm soil depth, cumulative extractable DOC increased steadily for most of the incubation period resulting in nearly a two-fold greater total extractable DOC than the other wetland types by the end of the incubations. This is in contrast to the rich fens, which consistently had the lowest cumulative extractable DOC across soil depth and incubation temperature. Incubation temperature also influenced cumulative extractable DOC, with ~40% greater concentrations at 15 °C relative to 8 °C at 10 cm soil depth. However, the 15 °C incubations resulted in only slightly higher cumulative extractable DOC (~10%) at 25 cm soil depth.

Fluxes of CO_2 were similar to DOC in that there was no difference among wetland types ($F_{3,67} = 2.17$, $p = 0.100$), soil depth ($F_{1,67} = 1.25$, $p = 0.269$) or their interaction term ($F_{3,67} = 2.35$, $p = 0.080$) showing high within-site variability, particularly in rich fen and forested wetland sites (Fig. 3a–d). There was a significant difference in CO_2 flux between 8 and 15 °C ($F_{1,67} = 35.56$, $p < 0.001$). The 15 °C incubation increased average CO_2 yield by ~40% compared to the 8 °C incubation showing greater sensitivity to temperature than for DOC. Fluxes of CO_2 did not differ with incubation length ($F_{1,634} = 0.58$, $p = 0.446$), although the highest fluxes generally occurred during the initial and one week time periods in all sites except poor fens. This resulted in a significant interaction for CO_2 flux between incubation length and wetland type ($F_{3,634} = 20.02$, $p < 0.001$. In the most extreme case, CO_2 flux decreased nearly two-fold in the cedar wetlands between weeks 1 and 4.

Cumulative CO_2 flux ranged from 3.8 to 12.8 mg C g^{-1} soil C across all sites, with larger average yields of 8.0 mg C g^{-1} soil C d^{-1} in surface soils compared to subsurface yields of 5.3 mg C g soil C d^{-1} (Fig. 2a–d). Warmer incubation temperature also influenced cumulative CO_2 flux, with yields ~40% greater in the 15 °C treatment relative to 8 °C. Overall, as much as 29% (mean of 12%) of SOC under current soil temperatures was mineralized to CO_2 by the end of the incubations (~8 months), with the rich fens and cedar wetlands showing the highest potential for SOC turnover (Table 2). Under the future climate warming scenario (15 °C), mean SOC turnover through mineralization to CO_2 increased to 19% (Table 2).

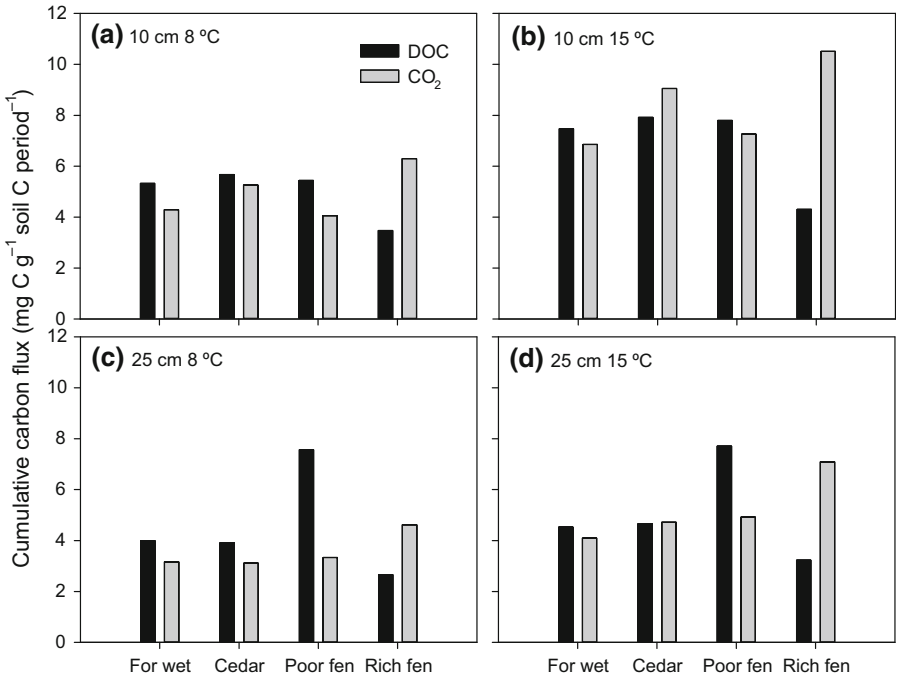

Fig. 2 Mean (n = 5) cumulative extractable dissolved organic carbon (DOC) and CO_2 flux for the four wetland types collected at 10 and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

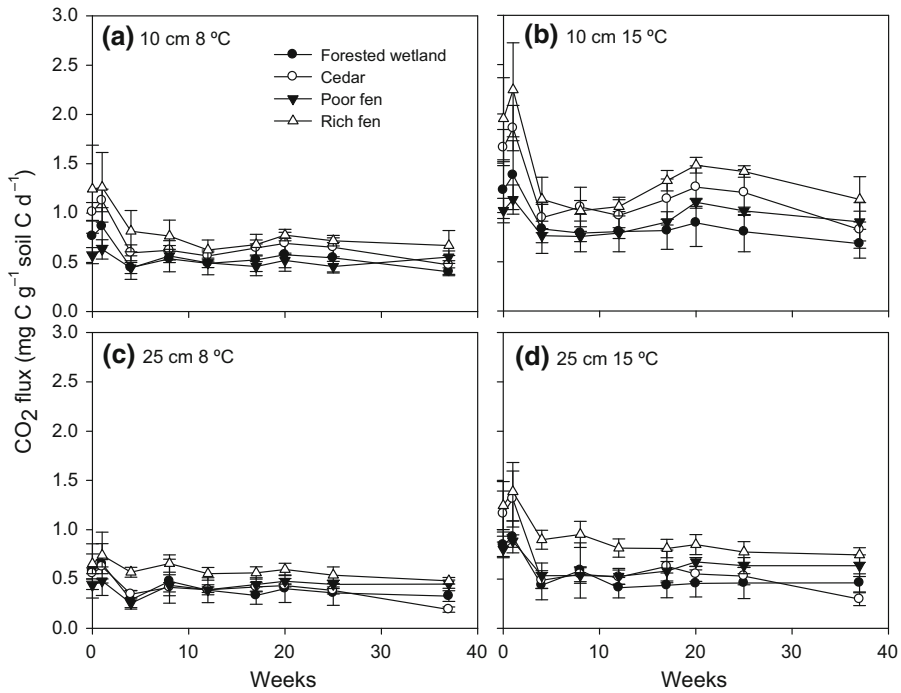

Fig. 3 Mean (n = 5, ±1 SE) CO_2 flux for the four wetland types collected at 10 and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

The temporal trends in CO_2 flux and extractable DOC across the incubations differed leading to shifts in the ratio of CO_2 to DOC (Fig. 4). In particular, average CO_2:DOC in forested wetland sites more than doubled between the initial and 17 week measurements as a result of the low

extractable DOC observed following the initiation extractions. In contrast, average CO_2:DOC in the rich fens decreased two-fold between the 4th week and final period of measurement, due to the sharp decline in CO_2 flux in these sites across the measurement period.

The relationship between carbon flux and soil characteristics (e.g., bulk density) was examined at each measurement period to assess whether the primary controls on CO_2 and DOC production were similar across the incubation period. Carbon flux at any of the time periods was not correlated with initial soil pH, soil N (%) or bulk density (all $p > 0.05$), but extractable DOC was related (all $p < 0.05$) to soil C:N and soil C (%) for all time periods except week 37. There was no relationship between CO_2 flux and extractable DOC (all $r^2 < 0.11$, $p > 0.21$, Fig. 5a–d) during the first 12 weeks of the incubation. However, the two carbon loss vectors were positively related between weeks 17 and 37 (all $r^2 > 0.27$, $p < 0.040$, Fig. 5e–h).

Effects of wetland type, temperature, soil depth and time on DOM bioavailability and fluorescence characteristics

Percent bioavailable DOC ranged from <1 to 34% across the incubations showing high variability within-sites as well with incubation length (Fig. 6a–d). Percent BDOC varied widely across the incubations, which resulted in no significant difference with wetland type ($F_{3,35} = 0.00$, $p = 0.999$), soil depth ($F_{1,35} = 0.63$, $p = 0.432$), incubation temperature ($F_{1,35} = 0.07$, $p = 0.793$), incubation length ($F_{1,234} = 1.01$, $p = 0.315$) or any of their interaction terms. However, percent BDOC was generally highest during the initial extractions followed by an overall decrease throughout the remainder of the incubations. Furthermore, percent BDOC was unrelated to CO_2 flux during the first 17 weeks but was positively correlated for weeks 20 and 37 (Fig. S2).

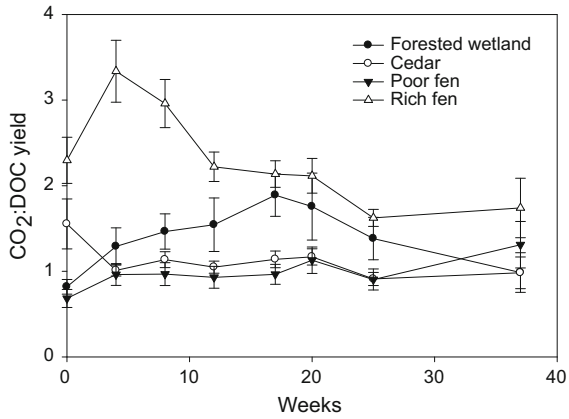

Fig. 4 Mean (±1 SE) CO_2:DOC for the four wetland types collected at 10 and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

The percent contribution of protein-like fluorescence, as determined from the PARAFAC-EEM approach, ranged from 0.1 to 15.3% of total DOM fluorescence (Fig. 7a–d). Percent protein-like fluorescence did not differ with wetland type ($F_{3,35} = 0.36$, $p = 0.782$), soil depth ($F_{1,35} = 0.90$, $p = 0.350$), incubation temperature ($F_{1,35} = 0.98$, $p = 0.329$) or any of their interaction terms. All sites showed pronounced declines (>50%) in protein-like fluorescence across the length of the incubations, with the largest decreases observed between the initial (mean of 11.7% for all sites together) and 4 week extractions (mean of 4.4% for all sites together). This temporal pattern in protein-like fluorescence resulted in a significant decrease with incubation length ($F_{1,230} = 7.08$, $p = 0.008$). Protein-like fluorescence

Table 2 Mean (n = 5, ±1 SE) fractional loss of carbon for the four wetland types

Values are expressed as the cumulative percentage of soil organic carbon respired to CO_2 for the 8 month incubations

Site	Soil depth (cm)	Incubation temp 8 °C	Incubation temp 15 °C
Forested wetland	10	14.3 (3.7)	22.2 (5.9)
Forested wetland	25	9.4 (3.5)	11.5 (3.9)
Cedar	10	16.8 (2.2)	28.4 (5.0)
Cedar	25	10.1 (1.0)	14.7 (2.6)
Poor fen	10	12.1 (1.3)	21.6 (1.5)
Poor fen	25	9.3 (1.3)	13.8 (2.2)
Rich fen	10	17.6 (3.4)	25.4 (3.9)
Rich fen	25	12.9 (2.5)	18.9 (4.1)

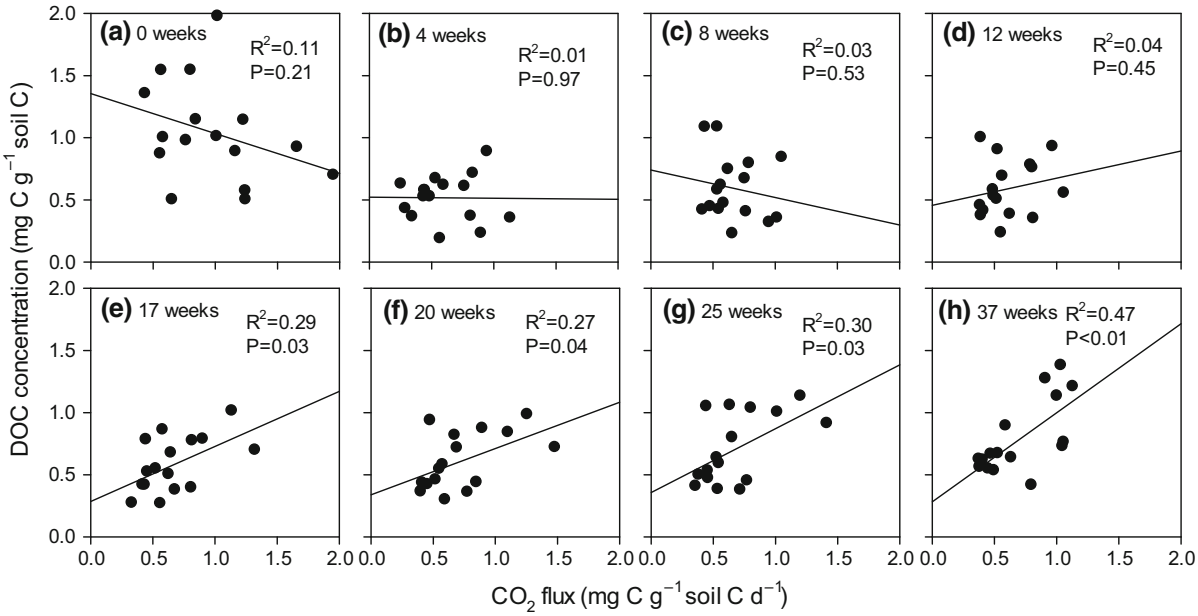

Fig. 5 Regressions of mean CO_2 flux and mean extractable dissolved organic carbon (DOC) for the four wetland types collected at 10 cm and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

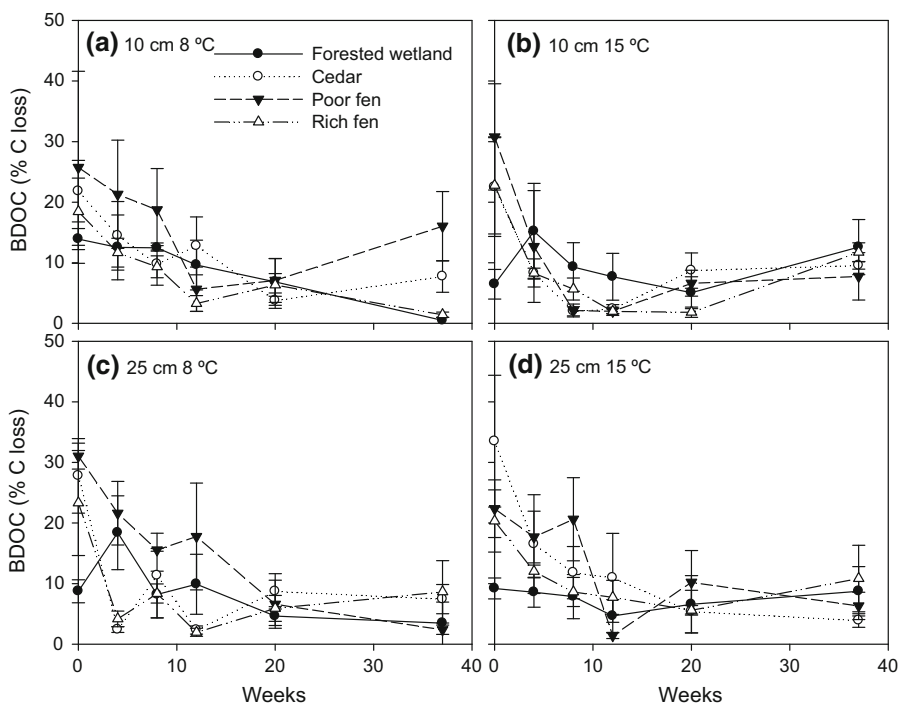

Fig. 6 Mean (n = 3, ±1 SE) percent biodegradable dissolved organic carbon (BDOC) for the four wetland types collected at 10 and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

did vary significantly in its interaction with wetland type and incubation length ($F_{3,230} = 6.55$, $p < 0.001$). In poor fen and cedar wetlands, mean percent protein-like fluorescence decreased to less than 1% in weeks 25 and 37 while it remained above 2.5% in the forested wetland and rich fen sites. Overall, protein-like

fluorescence was positively correlated to percent BDOC for all sites together throughout the incubations ($r^2 = 0.45$, $p < 0.001$, Fig. S3).

Discussion

Soil organic carbon decomposition in PCTR wetland soils

Wetland soils in the PCTR contain SOC stocks on the order of 4.6 Pg C (Mishra and Riley 2012), with some of the highest densities (600 Mg C ha^{-1}) reported on Earth (Johnson et al. 2011). There are extensive estimates for SOC turnover in northern, high latitude ecosystems (Hobbie et al. 2002; Nilsson et al. 2008; Chivers et al. 2009), although little is known about decomposition of this massive carbon stock in PCTR soils. Our laboratory results indicate that a substantial proportion of soil carbon in PCTR wetlands is readily mineralizable to CO_2 under both current (max = 29%, mean = 12%) and future (max = 43%, mean = 19%) climate scenarios. These findings suggest that PCTR soils contain a sizeable pool of readily biodegradable SOC that may be mineralized to CO_2 either directly or via the leaching and lateral export of DOC with future climate warming.

Laboratory incubations have been used extensively as a relative measure of SOC turnover and to determine the potential vulnerability of SOC stocks to climate warming (Bridgham et al. 1998; Neff and Hooper 2002; Conant et al. 2008). It is important to consider that our potential rates of SOC turnover are not necessarily representative of normal field conditions. For instance, soil moisture content was kept near constant throughout the incubations but water table levels in PCTR wetlands vary dramatically over the growing season (D'Amore et al. 2010). These frequent fluctuations in soil water table levels promote SOC mineralization and high production and flux of DOC from PCTR wetlands (D'Amore et al. 2015a). Thus, our results are conservative and should be interpreted with caution and not be treated in absolute terms. However, our estimates of DOC and CO_2 flux are useful for identifying local controls (e.g., soil pH, bulk density) and/or potential hotspots (i.e. particular wetland type) for SOC turnover in a region that is characterized by high variability in land cover and environmental conditions.

Our finding that soil temperature was the dominant control on CO_2 and DOC production is consistent with other studies of forested and wetland ecosystems (Subke et al. 2003; Bengtson et al. 2005; Clark et al.

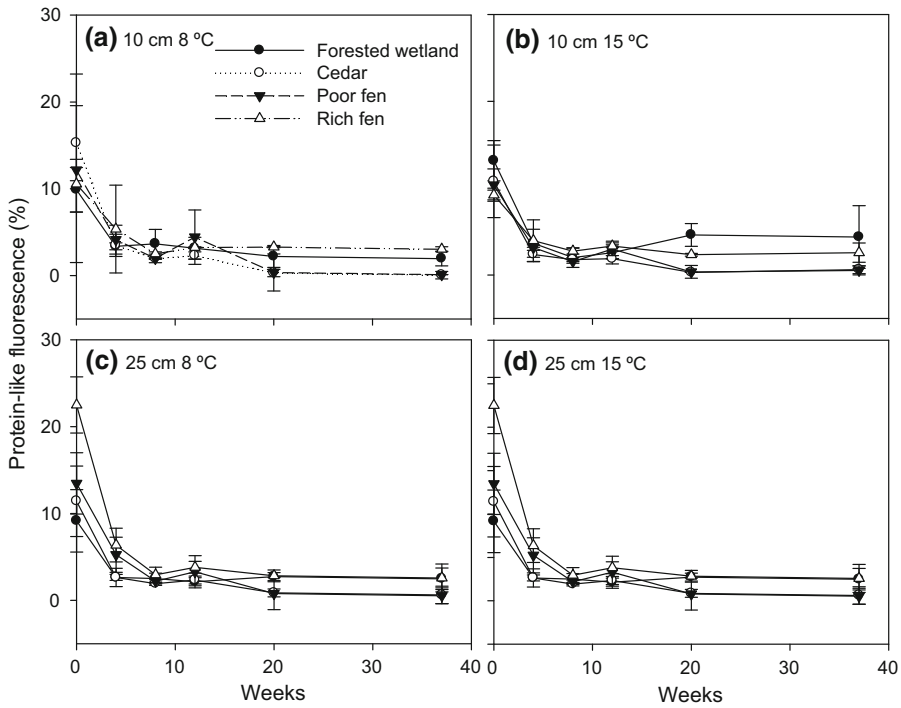

Fig. 7 Mean (n = 3, ±1 SE) percent contribution of protein-like fluorescence for the four wetland types collected at 10 and 25 cm depths and incubated at 8 and 15 °C across the 37 week laboratory incubations

2009; Chivers et al. 2009) showing that microbial activity is tightly regulated by temperature and that increased temperature would likely enhance the breakdown of SOC and subsequent release of CO_2 and DOC. Although our results show that SOC turnover did not significantly vary with substrate type (i.e. wetland type and soil depth), we did observe significant interactions between CO_2 flux and extractable DOC, wetland type and incubation length. One possible reason for these findings is that all four wetland types contain small labile pools of organic matter that turnover at similar rates. However, as SOC decomposition progresses over time and initial labile pools of organic matter become exhausted, there is a transition to a substrate-level dependence where SOC decomposition rates decrease and local controls unique to each wetland type (e.g., organic matter quality, bulk density) become more important controls on decomposition rates. These findings are consistent with traditional models of SOC turnover such as Century (Parton et al. 2010) or RothC (Jenkinson and Coleman 2008) that are based on the premise that SOC can be divided into pools or fractions that vary in their rate of turnover.

Soil C:N was a strong predictor of SOC turnover with ratios positively correlated to extractable DOC. Although soil C:N can be useful for predicting stream DOC export at the watershed scale (Aitkenhead and McDowell 2000; Aitkenhead-Peterson et al. 2005), these findings were somewhat surprising given that SOC content was consistently high relative to soil organic nitrogen content across wetland types and that increased soil nitrogen content typically accelerates SOC mineralization (Melillo et al. 1982; Hobbie 2000). A possible reason for this relationship is that soil microbes may be degrading larger amounts of SOC than necessary to satisfy their nitrogen requirements (Gödde et al. 1996; Schimel and Weintraub 2003). This waste respiration typically occurs with soil organic matter C:N above 30, which is similar to our average reported here (C:N = 29) across all sites.

Wetland carbon yields and DOC quality and bioavailability

Fluxes of CO_2 and extractable DOC were significantly correlated between weeks 17 and 37 but not during the first 12 weeks of the incubation. A tight correlation between CO_2 and DOC has been observed in some laboratory incubations (Gödde et al. 1996; Neff and Hooper 2002; Moore et al. 2008) but not others (reviewed by Neff and Asner 2001). During the initial extractions, extractable DOC may be derived from microbial breakdown of SOC and through the leaching of previously existing pools of soluble organic matter. This multi-source generation of DOC contrasts with CO_2, which originates mainly from microbial breakdown of SOC. The strong coupling that develops between DOC and CO_2 production after week 12 probably reflects the depletion of previously existing pools of soluble SOC being replaced by microbial breakdown as the main source of DOC, as observed in other incubation studies (Magill and Aber 2000; Kim et al. 2014). Overall, these findings highlight that DOC production is not always directly related to SOC turnover and other factors such as soil hydrologic regime (D'Amore et al. 2010; Hribljan et al. 2014), plant productivity (Kane et al. 2014) and soil biochemical properties influence wetland DOC yields.

Studies of northern peatland (Pastor et al. 2003) and forested ecosystems (Bengtson and Bengtsson 2007) highlight the importance of microbial degradation of SOC and subsequent solubilization to DOC in controlling soil respiration rates, especially under elevated temperature. As a result, DOC bioavailability and microbial activity will largely determine whether it is exported through leaching or mineralized to CO_2 in the soil profile. Our finding that soil C:N ratios were not related to CO_2 flux together with the temporal pattern in the relationship between CO_2 and DOC yield (Fig. 6) supports previous studies suggesting that solubilization of mineralized SOC to DOC is a strong control of soil respiration rates. Furthermore, CO_2 fluxes were positively correlated to percent BDOC between weeks 20 and 37. These results reinforce the importance of DOC production rather than concentration (higher DOC concentrations earlier in the incubations when no correlation between BDOC and CO_2 was observed) for controlling soil respiration rates (Bengtsson et al. 2003; Schimel and Weintraub 2003).

The high temperature incubation increased average CO_2 yield by ~40% compared to ~25% for DOC across all sites. These results are consistent with the idea that soil CO_2 flux is more sensitive to increasing temperature than DOC (Gödde et al. 1996; Neff and Hooper 2002; Moore et al. 2008). The result of this differential response in carbon flux to temperature is a shift in the ratio between CO_2 and DOC over the

duration of the incubations, although the proportional contribution of CO_2 to carbon loss was generally greater for all sites. In particular, the CO_2:DOC in rich fens was on average more than two-fold greater than the average for the other wetland types. A possible reason for this observation is previous research in the PCTR has shown that soil waters in rich fens contain large pools (as much as 40% of total DOC pool) of readily degradable DOC (Fellman et al. 2008). The lower BDOC values reported here for the rich fens (average of 10%) together with the observed relationship between percent BDOC and CO_2 flux suggests that a substantial amount of DOC may be readily converted to CO_2 in rich fens as well as the other wetland ecosystems.

Percent BDOC and protein-like fluorescence were significantly correlated for the duration of the incubations confirming the importance of DOC quality in controlling carbon uptake by microbial communities (Volk et al. 1997; Findlay et al. 2003; Wollheim et al. 2015). Incubation temperature and soil depth did not significantly influence protein-like fluorescence and percent BDOC, although there was a clear trend toward decreased percent BDOC and percent protein-like fluorescence over the incubations. These results suggest that high uptake of readily available carbon by soil microbes is reducing pools of bioavailable DOC, which is consistent with the observed relationship between percent BDOC and CO_2 flux. Our findings are in contrast to a temperature manipulation study of a poor fen in northern Michigan that observed a significant increase in DOC bioavailability in heated soil plots that was attributed to enhanced release of bioavailable organic compounds by plant roots and plant–microbe interactions within the rhizosphere (Kane et al. 2014). One possible reason for these contrasting findings is that the continual release of bioavailable DOC from plant roots and plant–microbe interactions, as hypothesized to occur in the heated soil plots, did not occur in our study because the laboratory soil incubations did not include live plants. These findings suggest that future climate-induced shifts in SOC turnover will not only alter wetland carbon balances but also wetland-stream linkages (Dawson et al. 2004; Fellman et al. 2009) through shifts in the quality and magnitude of bioavailable DOC delivered to downstream ecosystems.

Carbon loss from PCTR wetland soils

Our finding that SOC mineralization to CO_2 was generally the main pathway for SOC turnover and that this process demonstrates a strong sensitivity to temperature suggests that CO_2 is likely to become an increasingly important vector for carbon loss from PCTR wetlands with a warming climate. On the other hand, annual precipitation is expected to increase in the region (Shanley et al. 2015), which could result in more frequently elevated water tables and increased runoff via storm events depending upon the intensity of this additional precipitation. The export of DOC from wetlands is controlled largely by variability in runoff rather than any effect of soil water DOC concentration (Pastor et al. 2003; Nilsson et al. 2008; Moore et al. 2013). Thus, increased annual precipitation in the PCTR will likely enhance wetland DOC export to aquatic ecosystems because greater flow through highly conductive surface horizons will decrease soil residence times for DOC and reduce the opportunity for soil microbes to mineralize DOC to CO_2. Furthermore, increasing air temperature and altered soil hydrologic regimes will likely impact DOC bioavailability (Hribljan et al. 2014; Kane et al. 2014). Given the tight control DOC production has on rates of soil respiration (Pastor et al. 2003; Bengtson and Bengtsson 2007), future climate-induced changes in DOC bioavailability would play a strong role in determining whether carbon is lost via runoff or as CO_2 exchange with the atmosphere following SOC mineralization.

Solubilization of SOC to DOC contributed on average 34–54% of carbon production for each of the eight sampling dates, which is consistent with other studies showing that DOC export can account for more than half of lateral carbon flux from wetlands (Müller et al. 2015; Leach et al. 2016). Moreover, lateral export of DOC may be particularly important to wetland carbon budgets in humid ecoregions like the tropics and the PCTR where abundant precipitation leads to saturated soils and frequent hydrologic flushing of carbon-dense soils. Previous research from PCTR and tropical peatlands has shown that area-weighted DOC export from these ecosystems is among the highest in the world (Moore et al. 2011, 2013; D'Amore et al. 2015a; Oliver et al. 2017). Our findings and those of others (Nilsson et al. 2008; Billett et al. 2010; Moore et al. 2013) reinforce the importance of

lateral DOC export as a carbon loss pathway that should be included in terrestrial ecosystem carbon budgets. Failure to include DOC production and loss in the wetland carbon balance could result in considerable overestimation of the terrestrial carbon sink as well as impact estimates of wetland greenhouse gas fluxes occurring via the oxidation of DOC to CO_2 and potentially methane.

Overall, our findings indicate that PCTR wetland soils contain a sizeable pool of biodegradable SOC that is similar in magnitude to other high latitude northern ecosystems (Neff and Hooper 2002) and may be vulnerable to future climate warming. Soil temperature was the strongest control on wetland SOC turnover, with wetland type and soil depth less important in controlling fluxes of CO_2 and extractable DOC. Thus, both DOC and CO_2 production will likely increase if PCTR wetland soils warm with projected increases in regional air temperature (Shanley et al. 2015). The pathway of future SOC losses will depend on shifts in the balance between fluvial DOC export and rate at which soil microbial communities are able to mineralize DOC to CO_2. As a result, future increases in fluvial DOC export could result from either enhanced SOC turnover and leaching or a decrease in the efficiency of microbial mineralization of DOC to CO_2. The fact that the DOC and CO_2 loss pathways are interconnected suggests that fluvial DOC flux or CO_2 flux to the atmosphere should not be used as stand-alone indicators of enhanced SOC turnover or changes in the overall wetland carbon balance. Instead, detailed studies quantifying both lateral and vertical carbon exchange over a range of hydro-climatic conditions are necessary to determine the potential impacts of climate change on carbon cycling in wetland soils.

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