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Key Points:

- Waterbody size and shape have strong nonlinear effects on CO₂, with the highest concentrations in small, complex, waterbodies
- Dissolved organic carbon quantity and composition are the most important drivers of CH₄ concentrations in waterbodies
- Wildfires increase the sensitivity of waterbody CO₂ and CH₄ concentrations to degraded permafrost in upstream watersheds

Supporting Information:

Supporting Information may be found in the online version of this article.

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Using Machine Learning to Predict Inland Aquatic CO₂ and CH₄ Concentrations and the Effects of Wildfires in the Yukon-Kuskokwim Delta, Alaska

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Abstract Climate change is causing an intensification in tundra fires across the Arctic, including the unprecedented 2015 fires in the Yukon-Kuskokwim (YK) Delta. The YK Delta contains extensive surface waters (~33% cover) and significant quantities of organic carbon, much of which is stored in vulnerable permafrost. Inland aquatic ecosystems act as hot-spots for landscape CO₂ and CH₄ emissions and likely represent a significant component of the Arctic carbon balance, yet aquatic fluxes of CO₂ and CH₄ are also some of the most uncertain. We measured dissolved CH₄ and CO₂ concentrations ($n = 364$), in surface waters from different types of waterbodies during summers from 2016 to 2019. We used Sentinel-2 multispectral imagery to classify landcover types and area burned in contributing watersheds. We develop a model using machine learning to assess how waterbody properties (size, shape, and landscape properties), environmental conditions (O₂, temperature), and surface water chemistry (dissolved organic carbon composition, nutrient concentrations) help predict in situ observations of CH₄ and CO₂ concentrations across deltaic waterbodies. CO₂ concentrations were negatively related to waterbody size and positively related to waterbody edge effects. CH₄ concentrations were primarily related to organic matter quantity and composition. Waterbodies in burned watersheds appeared to be less carbon limited and had longer soil water residence times than in unburned watersheds. Our results illustrate the importance of small lakes for regional carbon emissions and demonstrate the need for a mechanistic understanding of the drivers of greenhouse gasses in small waterbodies.

1. Introduction

The Arctic stores vast quantities of carbon in soil and permafrost, perennially frozen ground, that is sequestered from the active carbon cycle. Approximately twice as much carbon is stored in permafrost globally as is currently in the entire atmosphere (Hugelius et al., 2014, 2020). The Arctic is now warming at an accelerated rate and recent research has shown that increasing emissions of CH₄ and CO₂ from ecosystems is causing the Arctic to switch from a net sink to a net source of carbon to the atmosphere in some locations (Belshe et al., 2013; Schuur et al., 2015; Virkkala et al., 2021; Watts et al., 2021). As permafrost thaws, modern soil and permafrost-derived carbon is then decomposed by soil microorganisms and respired as carbon dioxide (CO₂) or methane (CH₄), which are either emitted to the atmosphere directly, or transported through landscapes via ground and surface waters to inland waterbodies (Schuur et al., 2008, 2015). Globally, inland aquatic waterbodies receive approximately 2–3 Pg-C yr⁻¹ from terrestrial landscapes, of which 0.8–2.1 Pg-C yr⁻¹ is thought to be processed and emitted to the atmosphere as CO₂ (Cole et al., 2007; Raymond et al., 2013; Tranvik et al., 2009). This makes inland aquatic CO₂ emissions comparable to those estimated from global land use change (IPCC, 2013). Inland aquatic waterbodies can also act as globally significant sources of CH₄ to the atmosphere. CH₄ has 25-times the global warming potential of CO₂ over a 100-year time period (Boucher et al., 2009). Methane emissions from inland waters are estimated at 0.65 Pg of C yr⁻¹ (CO₂-eq), which is 25% of the global estimated land greenhouse gas sink (Bastviken et al., 2011). Despite the potentially pivotal role of inland aquatic ecosystems in the global carbon budgets, the uncertainty in inland aquatic fluxes is of the same magnitude as the fluxes themselves (Raymond et al., 2013; Regnier et al., 2013).

In high-latitudes, the inland water carbon emissions are particularly important because lateral carbon transport plays an outsized role in terrestrial carbon cycling (Chapin & Woodwell, 2006; Tranvik et al., 2009). As much as twenty-percent of terrestrial net ecosystem productivity is transferred to aquatic environments as dissolved

inorganic carbon (Kling et al., 1991; Stackpoole et al., 2017). The distribution of waterbodies in high-latitudes is dominated by small waterbodies ($<0.001\text{ km}^2$), which are the highest potential emitters of CO_2 and CH_4 to the atmosphere. These small water bodies are also the most difficult to accurately map, and, therefore, they are often not considered in “bottom-up” scaling estimates (Holgerson & Raymond, 2016; Hotchkiss et al., 2015; Muster et al., 2019; Thornton et al., 2016). One exception, a recent bottom-up meta-analysis found aquatic emissions contribute up to 50% of global methane emissions (Rosentreter et al., 2021). In this study, lakes were the second largest contributor behind freshwater wetlands, with approximately 50% of lake emissions coming from the smallest waterbodies ($<0.001\text{ km}^2$) and 62% of lake emissions coming from those under 0.01 km^2 . It is critical to reduce uncertainty in inland aquatic carbon fluxes and predict whether carbon is emitted as CH_4 or CO_2 to understand feedbacks to climate.

Wildfire frequency and severity are also increasing in high latitudes, with both direct (i.e., CH_4 and CO_2 emissions from combustion) and indirect (e.g., decreases in soil respiration but an increase in permafrost thaw) feedbacks to climate (Boby et al., 2010; Bond-Lamberty et al., 2007, 2004; Kasischke et al., 2010; Mack et al., 2008). Wildfires and permafrost thaw can affect landscape-level carbon dynamics in the Arctic through changing vegetation, energy balance, soil respiration, and hydrology (Alexander et al., 2018; Dooley & Treseder, 2011; Helbig et al., 2016; Jiang et al., 2017). Landscape-level processes can have consequences for waterbodies through influence over lateral transport, in turn regulating the quality and quantity of dissolved carbon and the availability of limiting nutrients as well as environmental conditions such as water temperature, oxygen content, and pH (Abbott et al., 2021; Hutchins et al., 2020; Vonk et al., 2015). Wildfires and permafrost thaw also affect the extent and distribution of waterbodies through both the formation of new waterbodies from permafrost subsidence and the draining of existing waterbodies from deepening thaw (Brown et al., 2015; Jorgenson et al., 2010; Jorgenson & Osterkamp, 2005; Minsley et al., 2016; Walvoord & Kurylyk, 2016).

Aquatic carbon dynamics are regulated at a hierarchy of scales, ranging from regional climate and substrate characteristics, to watershed-level vegetation, landscape connectivity, and disturbance, and internal processes (Lapierre & del Giorgio, 2012; Toming et al., 2020). The complex mechanisms that influence dissolved CO_2 and CH_4 in waterbodies make modeling inland aquatic carbon fluxes difficult, regardless of the type of model used. This complexity is a large reason for the uncertainty in inland aquatic carbon emissions, as many estimates are based on scaling average fluxes by lake size or simple linear regression models with one or two drivers that leave large amounts of variance unexplained. Interpreting the role of wildfire can be particularly challenging, as the effects of wildfires interact with nonlinear mechanisms operating at multiple scales (Hutchins et al., 2020).

The Yukon-Kuskokwim (YK) Delta is an ideal ecosystem to study the hierarchical mechanisms driving carbon cycling in permafrost landscapes. The YK Delta, the largest wetland on the west coast of North America ($\sim 1 \times 10^5\text{ km}^2$), is subarctic tundra underlain by discontinuous permafrost, but near surface permafrost temperatures are near the point of thaw ($\sim 1\text{ m}$ depth; S.M. Natali, unpublished data). YK Delta is subject to frequent wildfires, but more area burned in the YK Delta in 2015 than in the previous five decades combined (BLM-AICC Alaska Wildland Fire Maps). Atmospheric inverse models of the circumpolar Arctic and high latitudes using airborne CO_2 and CH_4 data have shown the YK Delta to be a regional hotspot of CO_2 and CH_4 emissions (Chang et al., 2014; Chen et al., 2015; Commane et al., 2017; Miller et al., 2016), but there have been few on the ground measurements of fluxes to properly identify and attribute the specific ecosystems and mechanisms contributing to these fluxes (Bartlett et al., 1992; Fan et al., 1992).

In order to evaluate the relationship between wildfires and inland aquatic carbon in the YK Delta, we require an approach that can accommodate the complex effects of fire and the potentially hierarchical and nonlinear functional relationships. In this study, we used boosted regression tree models to investigate environmental variables influencing dissolved CO_2 and CH_4 in surface waters from wetlands and small waterbodies in the YK Delta in Alaska. We evaluated the effect of fire on drivers of CO_2 and CH_4 in waterbodies by training separate boosted regression tree models for burned and unburned watersheds. We used the relative influence of a suite of drivers to rank which variable can best explain the variability in CO_2 and CH_4 , including environmental variables (e.g., dissolved oxygen, temperature, pH), waterbody size and shape, watershed landscape characteristics (e.g., average slope, percent cover burned area), and waterbody chemistry (e.g., dissolved organic carbon (DOC) concentration and composition, NH_4^+ , NO_3^- , PO_4^{3-}). We described the relationship between the most important drivers and dissolved CO_2 and CH_4 to (a) examine implications for process-based models and scaling waterbody CO_2 and

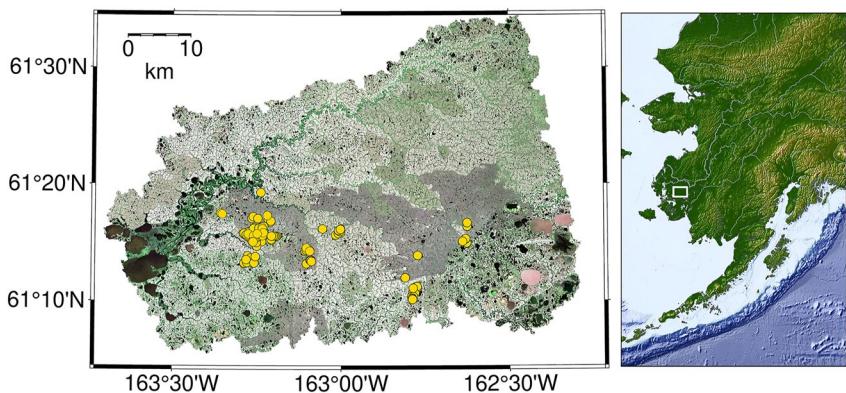


Figure 1. Yukon Kuskokwim Delta of Alaska (left), study region (inset). Sentinel-2 10 m resolution RGB imagery of the study region (right). Surface water sample locations from 2016 to 2019 are depicted as yellow points.

CH₄, and (b) examine how the processes controlling CO₂ and CH₄ relationships between landscapes and aquatic ecosystems may be altered under a warming climate (e.g., increased wildfire).

2. Materials and Methods

2.1. Site Description

This study was conducted in the central-interior of the YK Delta of Alaska, a subarctic tundra region underlain by discontinuous permafrost (Figure 1). The study region was located near the Kuka Creek fires of 2015 (N 61.26°, W 163.25°), about 90 km NW of Bethel, AK, and about 110 km inland from the coast. Average air temperatures in Bethel, AK are −0.4°C annually, 12.4°C in summer (June, July and August), −12.2°C in winter (December, January, and February), and above freezing from May–October (National Weather Service; Bethel area, 1981–2020). Average annual precipitation is 480 mm, with 188 mm falling in summer on average. Thaw depths were 30–40 cm in June and July 2016–2017, and 60–70 cm in September 2016. Organic layer horizons were deep, ranging from 30–75 cm at the surface. Lakes cover approximately one third of the region and range in area from several m² to several km². Lake depths were typically uniformly shallow (<2 m) and well-mixed. The remaining landscape is a patchwork of raised peat plateaus and low-lying wetlands, with elevation varying from 11–35 m above sea level. Vegetation on the peat plateaus can be characterized as dwarf shrub lichen tundra, with various lichen species and *Sphagnum fuscum* dominant by biomass. Other common plants include *Betula nana*, *Empetrum nigrum*, *Oxycoccus microcarpus*, *Rhododendron subarcticum*, *Rubus chamaemorus*, *Vaccinium uliginosum*, *Vaccinium viti-idaea*, and graminoids including *Eriophorum angustifolium*, and *Eriophorum vaginatum*.

2.2. Sample Collection and Processing

2.2.1. Water Sample Collection

Surface water samples ($n = 364$) were collected across 4 years of field campaigns (2016–2019). Of these surface water samples, $n = 294$ were analyzed for dissolved CH₄ and $n = 235$ for dissolved CO₂ from 201 distinct waterbodies. Several waterbodies were sampled in multiple years and the largest water bodies were sampled in multiple locations. Approximately 45% of the waterbodies sampled were lakes, 40% of the waterbodies sampled were fen surface waters, and the remainder of the waterbodies sampled were streams, small ponds, and surface waters on peat plateaus. While there are some clear differences between lakes, streams, and fens for example, many waterbodies exist on a continuum between such designations and these categories do not capture that complexity. Samples were collected between mid-June and mid-July. Surface water samples were immediately filtered through pre-combusted GF/F filters (Whatman nominal pore-size ~0.7 µm), portioned into sample-rinsed 20-ml polycarbonate containers, stored in the dark at ~4°C, and frozen within 48 hr until subsequent analyses.

2.2.2. Dissolved Gas Collection and Analysis

For each sample observation, three dissolved gas measurements were collected simultaneously and processed individually, with their average reported as the observation. Dissolved gases were collected by a headspace-equilibration method. For each triplicate, 30 ml of bubble-free surface water was slowly drawn into a syringe. Next 30 ml of ambient air was drawn and the syringe sealed. Each syringe was vigorously shaken for exactly 1 min while maintained at the temperature of the waterbody sampled. After equilibration, the headspace was injected into evacuated, double septum, vials until slightly over-pressurized. The gas vials were shipped to Woodwell Climate Research Center and analyzed for CH₄ and CO₂ concentrations using a Shimadzu GC-2014 gas chromatograph within several weeks of collection. Additional gas vials were injected in the field with ambient air to correct for the introduced headspace concentrations. Additional gas vials were injected in the field with standard gasses, and the accurate recovery of these concentrations was used to verify the integrity of gas vials during transportation. Dissolved gas concentrations were corrected for solubility using the water temperature and air pressure at the time of equilibration. Surface water temperature, pressure, dissolved oxygen (% and mg/L), and pH were measured using a YSI Pro-Plus multiparameter instrument. The YSI probes were calibrated daily using NIST standards (pH 4 and 7). Dissolved CH₄ gas samples were analyzed for stable carbon isotopic composition at Northumbria University using a Delta V Plus IRMS interfaced to a Trace Gas Pre-Concentrator and Gas Bench (Thermo Scientific). Dissolved CH₄ isotopic signatures were corrected for atmospheric mixing during headspace equilibration assuming global mean surface atmospheric $\delta^{13}\text{C}$ -CH₄ of $-47.2\text{\textperthousand}$ (Warwick et al., 2016).

2.2.3. Water Sample Chemistry

Surface water samples were analyzed for DOC and total dissolved nitrogen concentrations using a Shimadzu TOC-VCPh at the Woodwell Climate Research Center. Nutrient concentrations, including phosphate, nitrate, and ammonium, were analyzed colorimetrically on an Astoria-Pacific autoanalyzer at the Woodwell Climate Research Center. Nitrate concentrations were often below levels of detection, and henceforth we report dissolved inorganic nitrogen as the sum of ammonium and nitrate concentrations. Chromophoric dissolved organic matter (DOM) was measured on surface water samples using a Shimadzu UV-Vis spectrophotometer measuring absorbance across 200–800 nm wavelengths at 1 nm resolution. Specific UV absorbance at 254 nm (SUVA) and the DOM slope ratio (S_R) were then calculated as in Helms et al. (2008) as indicators of carbon composition and lability. The slope ratio of DOM is inversely related to the average molecular weight of DOM; a higher slope ratio indicates lower bulk molecular weight, which is commonly a more labile carbon source for decomposition (Helms et al., 2008). SUVA is directly related to average DOM aromaticity, which usually corresponds to higher contributions of biologically unreactive carbon sources (Helms et al., 2008).

2.3. Geospatial Waterbody and Watershed Analyses

We used remote sensing to quantify watershed characteristics that might be related to unmeasured landscape variables (e.g., watershed thaw depth), hydrologic variables (e.g., water residence time) and unmeasured reactants (e.g., black carbon, organic-phosphorus). Map figures were created using Generic Mapping Tools (Wessel et al., 2019).

2.3.1. Watershed Imagery Processing

To evaluate the role of watershed inputs and landscape connectivity on dissolved CO₂ and CH₄ concentrations, we delineated watersheds for each sampling location using the SAGA “Upslope area” algorithm in QGIS with a 2-m resolution digital elevation model (Porter et al., 2018). Level-2A Sentinel-2, 10-m resolution, multispectral surface reflectance imagery was used to provide information on vegetation, landcover, and surface water. The surface reflectance imagery was a composite of cloud-free imagery from 2017 to 2019 within 2 weeks of most sample collection dates (early July). The surface reflectance imagery was used to calculate the Normalized Difference Water Index (NDWI) and Normalized Difference Vegetation Index (NDVI), metrics of canopy or soil moisture and vegetation productivity. We calculated slope and elevation from the digital elevation model. We then determined the average of each derived index by sample watershed to include as potential drivers in modeling dissolved CO₂ and CH₄. The composite imagery and derived indices were made using Google Earth Engine.

Table 1
Boosted Regression Tree Model Fit and Predictive Ability

Model	Number of variables	Number of observations	R ²	Variance predicted (%)	RMSE (log μM)
CO ₂ Unburned	13	93	0.94	79%	0.55
CO ₂ Burned	15	142	0.87	61%	0.73
CH ₄ Unburned	17	121	0.88	52%	0.28
CH ₄ Burned	18	166	0.79	36%	0.47

Note. Coefficient of determination (R^2) from a linear regression of modeled and observed log concentrations. Variance explained (%) and root mean square error (RMSE) from predictive deviance of 10-fold cross validations.

2.3.2. Landcover Mapping

We created a 10-m resolution landcover map for the region of interest to determine the presence and abundance of various terrestrial, wetland, surface waterbodies, and disturbed areas in sample watersheds (Figure S1 in Supporting Information S1). We used an unsupervised k-means algorithm (Google Earth Engine, “wekaKMeans”) with the surface reflectance raw bands, derived bands (NDWI, NDVI), slope, and elevation as inputs for the classification. The Alaska Interagency Coordination Center historical wildfire database was used for wildfire delineations. Wildfires in the region of interest included fire scars from the 1970s, 1990s, and early 2000s, collectively designated as “old fires,” and fire scars from the large area burned in 2015. First, the region of interest was divided into unburned, old fire scars, and 2015 fire scars, and the classification algorithm was run separately for each. We used an initial number of classes “k” higher than the number of known landcover types in order to capture the variability in the driving layers,

then later grouped similar classes produced by the k-means algorithm. For example, the unburned classification identified three classes grouped as terrestrial peat plateau tundra and two wetland classes merged as peatland fens. The final landcover classes for unburned areas include terrestrial peat plateau, peat plateau edges, degraded peat plateau (i.e., from permafrost thaw), fens, and surface water. The final landcover classes for old fire scars and 2015 fire scars include peat plateau, degraded peat plateau, fens, and surface water. We calculated the total area and percent area of each landcover type and burned area by sample watershed to include as potential drivers in modeling dissolved CO₂ and CH₄. Landcover accuracy was assessed using 350 randomly stratified points from the region of interest. The classifications at these points were compared to higher resolution (Worldview-2) imagery using Google Earth Engine and reclassified using expert assessment. We used a confusion matrix to assess the balanced accuracy of each classification, which ranged from 0.75 to 0.99 (Figure S2 in Supporting Information S1) (Clewley et al., 2015).

2.3.3. Waterbody Shape

To determine the effects of waterbody shape on dissolved CO₂ and CH₄, we calculated the area and perimeter of every surface waterbody in the region of interest using object-based image analysis in Google Earth Engine. Each sample location with a large enough waterbody to be detected was then assigned the corresponding area, perimeter, and area:perimeter ratio. The waterbody shape data were mostly only available for sample locations classified as lakes, as the amount of surface water in fens, streams, and plateau ponds was often too small to detect at 10 m resolution.

2.4. Statistical Analysis

We used boosted regression tree models to predict dissolved CO₂ and CH₄ and explore the effect of fire on the relationships between potential drivers and CO₂ and CH₄. Boosted regression tree (also called gradient boosting) is a form of machine learning developed from the decision tree family of models combined with a boosting algorithm. Recent studies have used machine learning approaches to create statistical models with greater accuracy in predicting ocean surface dissolved CO₂ and DOC in inland waterbodies (Chen et al., 2019; Toming et al., 2020). These models have higher accuracy because they allow for complex interactions and non-linear relationships, which often better capture the mechanisms involved. All boosted regression tree models were fit using the “gbm” function in the gbm package in R v.3.6.1, and model results were investigated using the “ice” function in the ICEbox package in R v.3.6.1. Model fit was investigate by linear regression (“lm” function in R) between observed dissolved gas concentrations and the predicted dissolved gas concentrations from the boosted regression tree model results. Both dissolved CO₂ and CH₄ concentrations were log-transformed to achieve normality which was assessed using QQ-norm plots (“qqnorm” function in R).

2.4.1. Driver Selection and Model Structure

In order to capture potentially disparate effects of fire on the drivers of dissolved CO₂ and CH₄, we split the data set into observations with mostly unburned watersheds (<10% burn area) and burned watersheds (>10% burn area) and modeled them separately (Table 1). The majority of watersheds affected by fire were only partially

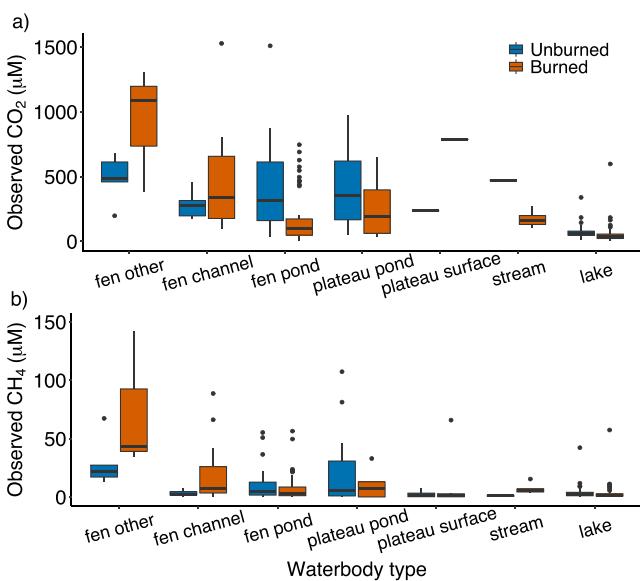


Figure 2. Observed dissolved gas concentrations for CO₂ (a) and CH₄ (b) by waterbody type and separated into unburned (blue) and burned (orange) watersheds. The lower and upper hinges correspond to the first and third quartiles, the whiskers extend to 1.5 times the interquartile range, with outliers indicated as points.

and $\geq 1,000$ trees. We saw no substantial difference in the model when increasing tree complexity to 3. We used 10-fold cross-validation to tune the number of trees and drop variables to avoid over-fitting. We used deviance as a loss function, a goodness-of-fit metric (D) related to the difference in log-likelihoods of the fitted model (L_m) and a perfect model (L_s) according to $D = -2 \left(\log \left(\frac{L_m}{L_s} \right) \right)$. We computed the predictive ability of each model as the percent improvement of predictive deviance using 10-fold cross-validation over the null model, which can be interpreted as the percent variance explained when predicting to new data. Model goodness-of-fit was evaluated as the R^2 of a linear regression between observed and fitted CH₄ or CO₂ concentrations. To estimate model stability, each boosted regression tree model was run 10 times with different random seeds using a different subset of observations to train each model.

2.4.3. Model Interpretation

An advantage of boosted regression tree models compared to other machine learning algorithms is the interpretability of the model results. The relative importance of each predictor variable can be calculated from the number of times it is selected for splitting in a decision tree, weighted by the improvement of the model caused by its inclusion, and then averaged over all trees in the final model. Variable relative importance is scaled to sum to 100. Individual conditional expectation plots and partial dependence plots are useful for visualizing heterogeneity in responses, interactions between predictors, and the average response to a predictor. Each line of an individual conditional expectation plot is calculated by varying the predictor of interest across the range of values in the training data set, while holding all other variables constant for that observation (Goldstein et al., 2015). Partial dependence plots are the average predicted response across observations of individual conditional expectation plots. We smoothed individual expectation and partial dependence plots using the loess method and set the x -axis limits to truncate the 10th and 90th percentile of observations to avoid over-interpretation (Goldstein et al., 2015). All partial dependence and individual conditional expectation plots are centered on 0 µM predicted CH₄ or CO₂.

3. Results and Discussion

Waterbody dissolved CO₂ and CH₄ concentrations in the YK Delta were similar on average to those found in other studies of lakes in Alaska and the Northwest Territories of Canada, although we observed a wider range and greater variability for both CO₂ and CH₄ (Figure 2; Cunada et al., 2018; Stackpoole et al., 2017; Townsend-Small

burned and few watersheds were completely within the 2015 Kuka Creek fire scar. Varying the cutoff from >0% watershed area burned through 33% area burned had little effect on model fitting or results. Dissolved CO₂ and CH₄ were log transformed to achieve normality. Several possible variables were excluded from the model due to strong correlations (Pearson correlation >0.7) with other drivers. While boosted regression tree models can accommodate correlated predictor variables, interpretations of variable importance are difficult in such circumstances. For example, watershed average NDWI and NDVI correlate strongly, so we chose to retain NDWI as it can also serve as a proxy for soil moisture which has direct consequences for CO₂ and CH₄ production. Dissolved organic nitrogen concentration was excluded due to the high correlation with DOC concentration. The classified percent area of landcover types in the watersheds necessarily sum to one and are therefore often highly correlated. We included only the landcover types that are expected to be more ecologically important.

2.4.2. Model Training

Boosted regression tree model training was performed using the “gbm.step” function from the dismo package in R v.3.6.1 following the procedure in Elith et al. (2008). We used a learning rate and bag fraction of 0.005 and 0.65 respectively, which are within the optimum ranges. Changes in the learning rate and bag fraction had little effect on model performance. We used a tree complexity of 2, allowing for two-way interactions between predictors. Small sample sizes for boosted regression tree models, such as the data set in this study, are generally best modeled with tree complexity two or three

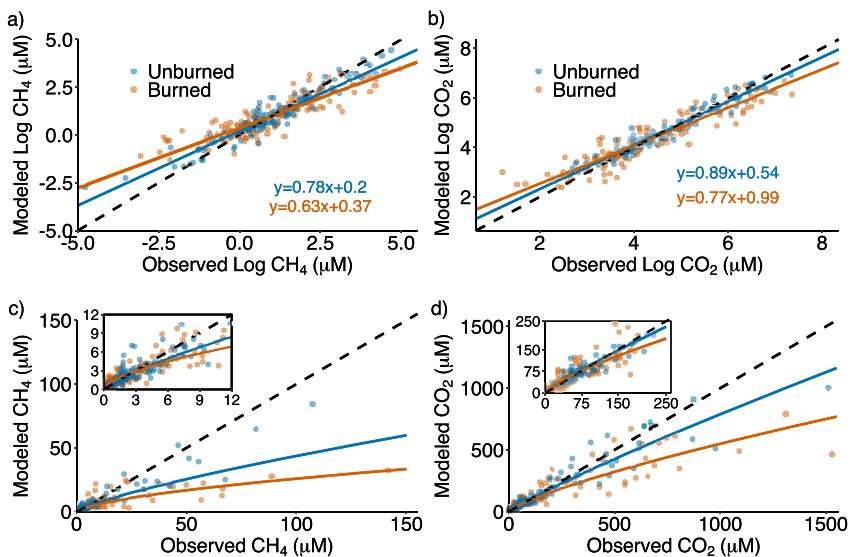


Figure 3. Modeled and observed dissolved gas concentrations for CH₄ (a and c) and CO₂ (b and d), unburned (blue) and burned (orange). Model goodness-of-fit shown using log-transformed data (a and b) and un-transformed data (c and d). One-to-one lines are the dashed lines, and linear regressions of fit are solid blue for unburned and orange for burned.

et al., 2017). Both the differences in CO₂ and CH₄ concentrations between waterbody types and the variability within waterbodies tended to be greater than the effects of fire on CO₂ and CH₄ concentrations (Figure 2). The effects of fire were inconsistent across waterbody types: for some fen surface waters, burned watersheds had higher CH₄ concentrations, but for lakes in burned watersheds, CH₄ concentrations were lower than in unburned watersheds. The boosted regression tree models predicted 79% and 52% of the observed variability in dissolved CO₂ and CH₄, respectively in waterbodies from unburned watersheds, and predicted 61% and 36% of dissolved CO₂ and CH₄ in waterbodies from recently burned watersheds (Table 1).

3.1. Model Performance

The boosted regression tree models developed for burned and unburned watersheds were able to accurately model and predict dissolved CO₂ and CH₄ in waterbodies. Model fit was better for CO₂ than CH₄ and better for unburned than burned watersheds. The final number of variables retained in each model ranged from 13 to 18 (Table 1). The goodness-of-fits for all models were excellent, with R^2 ranging from 0.79 to 0.94 (Table 1). Because the observations were log-transformed and the slopes of fit were all less than one (0.63–0.89), predicted values are conservative and in particular underestimated high concentrations of dissolved CO₂ and CH₄ (Figure 3). Model predictive ability (percent deviance explained) was better for aquatic systems within unburned than burned watersheds (Table 1). This disparity in performance could reflect processes that are important for regulating waterbody dissolved CO₂ and CH₄ in burned watersheds that were not measured in this study, such as increased thaw depths. Alternatively, a larger sample size might be needed for increased predictive performance for burned watersheds due to the range in contributing watershed area burned or heterogeneity in fire severity.

3.2. Drivers of Dissolved CO₂ and CH₄ in Waterbodies

3.2.1. Effects of Waterbody Shape

Waterbody size and complexity of waterbody shape were the largest drivers of dissolved CO₂ and contributed 45% and 25% relative influence in unburned and burned watershed models respectively (Figure 4a). Waterbody shape variables contributed to explaining a small but significant portion (4%–5%) of CH₄ models (Figure 4b). We observed that smaller waterbodies had higher predicted dissolved CO₂ and CH₄ (Figures 4, 5b and 5d), which is consistent with the global pattern (Holgerson & Raymond, 2016). Higher dissolved CH₄ and CO₂ in small lakes have been attributed to high edge or sediment to water volume ratios and more frequent mixing of the water column (Bastviken et al., 2008). Predicted dissolved CH₄ and CO₂ increased as the area: perimeter ratio

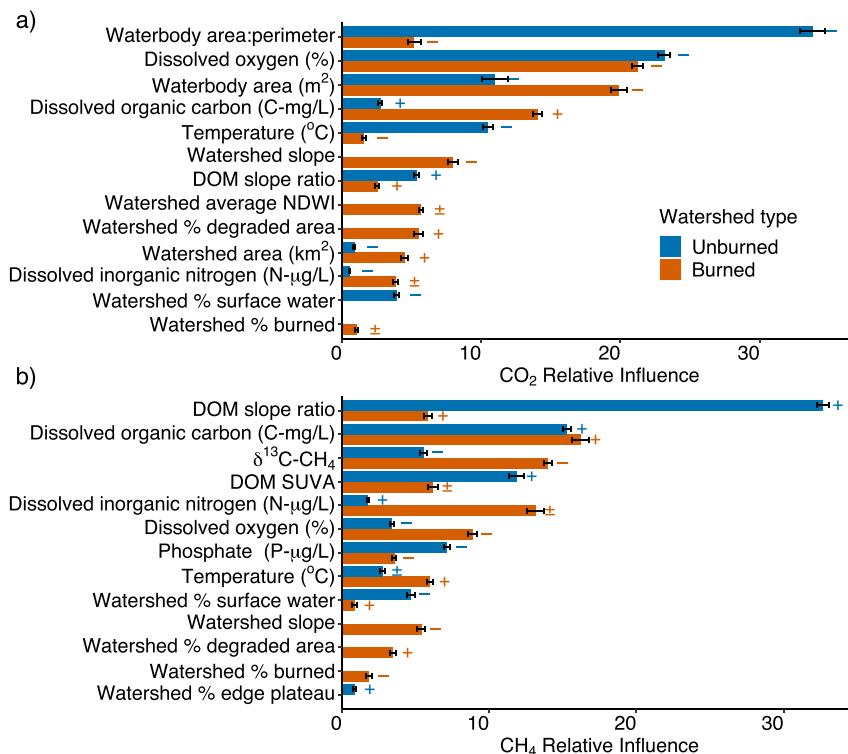


Figure 4. Relative influence of variables in unburned (blue) and burned (orange) watersheds in boosted regression tree models predicting CO₂ (a) and CH₄ (b) concentrations in waterbodies in the YK Delta of Alaska. The symbol labels indicate the overall effect of each predictor on CO₂ or CH₄, whether positive (+), negative (−), or both (±). Error bars indicate standard deviation of relative influence from 10 boosted regression tree models run with different random seeds. Relative influences were scaled to 100%, with low influence predictors not depicted (a: waterbody area, waterbody area:perimeter, watershed area, waterbody pH, watershed NDWI, waterbody conductivity, b: waterbody pH, SUVA, phosphate concentration, conductivity). The full listing of variable relative influences can be found in Table S1 in Supporting Information S1.

decreased, supporting the role of edge effects (Figures 5a and 5c; Figure 4). Compared to the unburned model, the relative importance of waterbody area increased in the burned CO₂ model, whereas the relative importance of the area:perimeter ratio decreased. This would indicate that waterbodies in burned watersheds were less sensitive to near-shore edge effects than waterbodies in unburned watersheds, possibly due to changes in thaw depths, hydrology, or vegetation after fire in terrestrial-aquatic transitions at waterbody edges.

Terrestrial-aquatic transition zones, which are relatively more influential in smaller water bodies, have long been recognized as biogeochemical hot spots, where flowpaths converge to potentially supply substrates and conditions that promote disproportionately high reaction rates (Lin et al., 2012; McClain et al., 2003; Zhang et al., 2020). There are numerous mechanisms by which waterbody edges could support greater dissolved CO₂. For example, complex lake shorelines are exposed to more latent heat than smooth shorelines, and could experience greater slumping and soil organic matter inputs from permafrost thaw. Alternatively, riparian and emergent vegetation at waterbody edges could influence the composition of soil porewater or hyporheic flowpaths. Our results are encouraging for applications scaling waterbody CO₂ concentrations, because, although more research is needed to clarify the role of waterbody edge effects in regulating CO₂ concentrations, waterbody size and shape are easy to measure with remote sensing and use as spatially-resolved drivers.

3.2.2. Effects of Carbon Composition and Quantity

The top three drivers of waterbody dissolved CH₄ in unburned watersheds were all related to carbon composition and together comprised 59% of the relative influence on dissolved CH₄, while the remaining variables contributed ~5% or less each (Figure 4b). The highest relative influence predictor was DOM slope ratio, an indicator of carbon lability, at 32% (Figure 4b). DOC concentration was the next strongest predictor variable at 15%

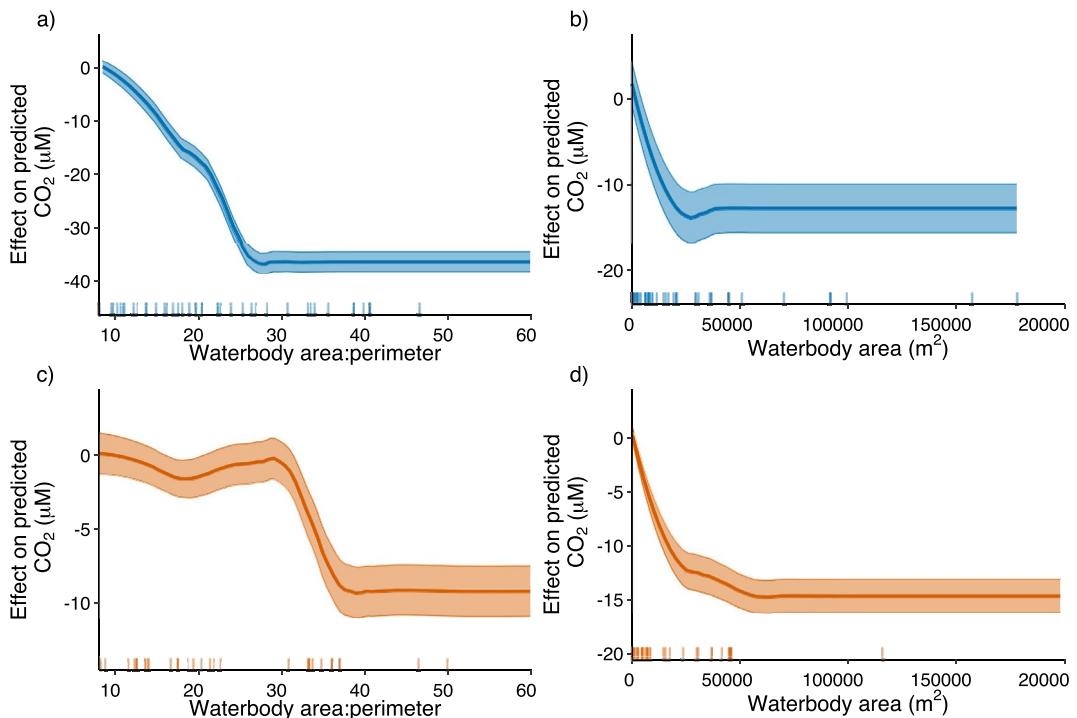


Figure 5. Partial dependence plots of the average effects of waterbody area/perimeter ratio (a and c) and waterbody area (b and d) on predicted carbon dioxide in unburned (blue) and burned (orange) watersheds. Shading indicates the standard deviation of the partial dependence functions from 10 boosted regression tree models run with different random seeds.

relative influence, followed by the SUVA of DOM, an indicator of carbon aromaticity, at 12% relative influence (Figure 4b).

The effects of DOC concentration and composition on waterbody dissolved CH_4 were generally positive, indicating that labile carbon sources might be limiting methanogenesis in unburned waterbodies (Figure 6c). Moreover, there was a strong interaction between DOC concentration and composition. When carbon composition was more unreactive (as derived from low slope ratio and high SUVA values), there was no effect of DOC on CH_4 at low concentrations, and a slight positive effect on CH_4 at high DOC concentrations (Figures 6a and 6b). When carbon composition was labile (as indicated by high slope ratio and low SUVA values) and carbon concentrations were low, there was a negative effect of DOC on CH_4 , likely demonstrating the inability of the energetically unfavorable metabolism of methanogens to compete for carbon (Figures 6a and 6b). When carbon compositions were labile and carbon concentrations were high ($>10 \text{ mg/L}$), CH_4 concentrations increased rapidly with DOC concentration until plateauing at DOC concentrations of $\sim 20 \text{ mg/L}$, where carbon may no longer be limiting (Figures 6a and 6b). Our findings are consistent with radiocarbon tracing studies in boreal fen peatlands that found dissolved CH_4 was mostly derived from labile DOM (Chanton et al., 2008), and with a study of lakes in the Mackenzie River Delta where dissolved CH_4 concentrations were also correlated with DOM slope ratio (Cunada et al., 2018). Our results indicate that in unburned waterbodies in the YK Delta, CH_4 concentrations were primarily controlled by carbon limitation (i.e., CH_4 concentrations were highest when there was abundant labile carbon).

DOM quality and availability were the dominant drivers in methane production in unburned watersheds, but clearly influenced respiration and methanogenesis in all waterbodies. While the effects of DOC and carbon composition were similar for dissolved CH_4 in burned watersheds (Figure 6d), the relative influence of carbon-related drivers was lower at 29% (Figure 4b). We would expect respiration from decomposition more generally, not just methanogenesis, to be driven by carbon substrate availability as well. While dissolved CO_2 in burned and unburned watersheds followed a similar pattern to that of CH_4 (i.e., increasing carbon availability and lability increased CO_2 ; Figures 6e and 6f), the strengths of carbon-related drivers were lower, totaling 19% and 10% relative influence respectively (Figure 4a).

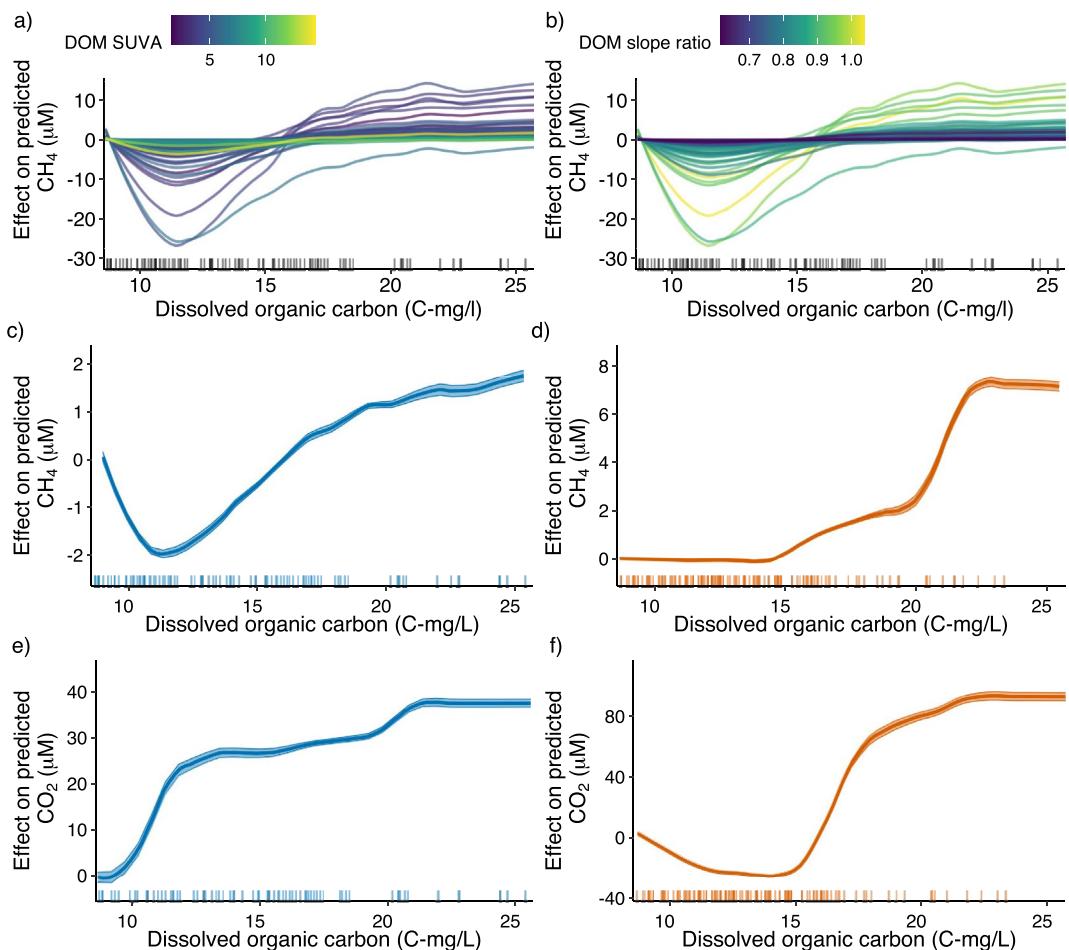


Figure 6. Effects of dissolved organic matter (DOM) quantity and composition on CH₄ and CO₂ concentrations in the Yukon-Kuskokwim Delta of Alaska. Top: individual conditional expectation plots of the effects of dissolved organic carbon concentrations (DOC) on predicted dissolved CH₄ in unburned watersheds. Line color corresponds to dissolved organic matter Specific UV absorbance (SUVA) (a) and slope ratio (b). Partial dependence plots of the average effects of DOC on predicted CH₄ in unburned (c) and burned (d) watersheds, and on predicted CO₂ in unburned (e) and burned (f) watersheds.

3.2.3. Environmental Controls: Dissolved Oxygen, Temperature, and pH

Dissolved oxygen was one of the top drivers of waterbody dissolved CO₂ in both burned and unburned with 21% and 23% relative influence respectively (Figure 4a). As dissolved oxygen increased, waterbody dissolved CO₂ decreased, as expected for increased photosynthetic activity, decreased respiration, or greater exchange of CO₂ with the atmosphere (Figures 7c and 7d). Warmer water temperatures and higher pH also were associated with lower CO₂ concentrations, which is consistent both with primary productivity and respiration regulating CO₂ concentrations (Figure 4, Figure S5g in Supporting Information S1). Chlorophyll-a concentrations and other gross primary productivity measurements have often been used as a proxy for dissolved CO₂ in marine environments and large lakes (Chen et al., 2019; Landschützer et al., 2013). Even though the small lakes and other waterbodies in this study were all relatively high in DOC and likely net heterotrophic, our results indicate that primary productivity was important in regulating waterbody CO₂ concentrations.

Dissolved oxygen and pH had a negative effect on dissolved CH₄ in both burned and unburned watersheds (Figures 4, 7a and 7b, S31 in Supporting Information S1), which is consistent with low oxygen and pH being indicative of redox conditions suitable for methanogenesis and restrictive to methanotrophy (Megonigal et al., 2004; Segers, 1998). Temperature had an overall positive effect on predicted CH₄ concentrations in water-

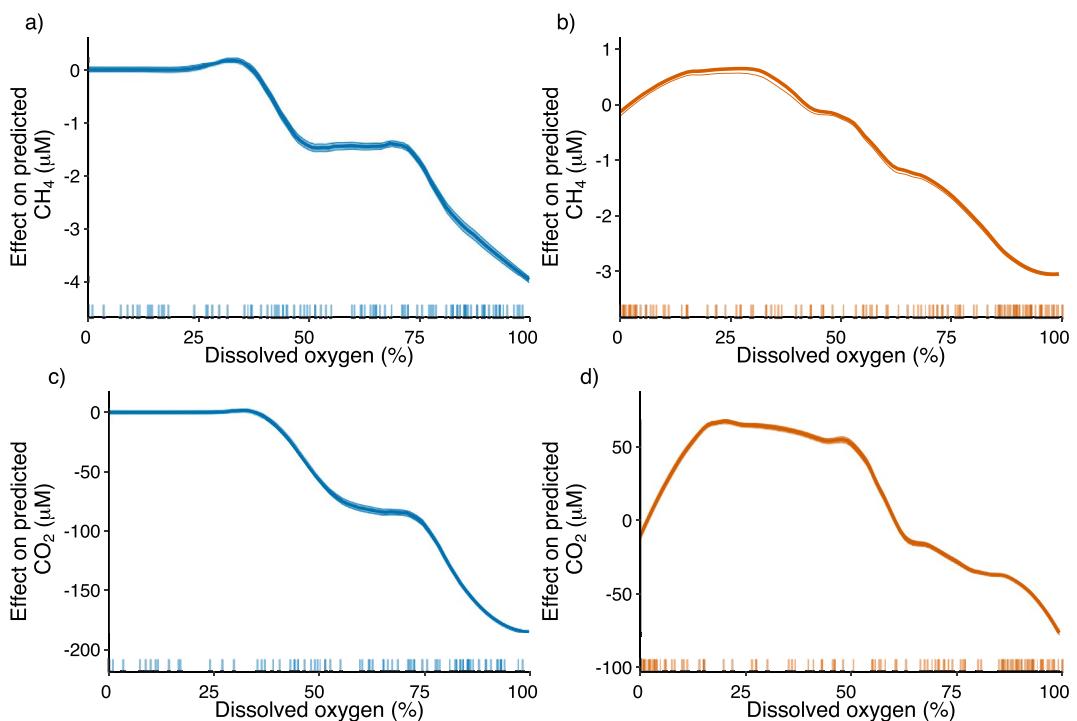


Figure 7. Partial dependence plots of the average effects of dissolved oxygen on predicted CO_2 (c and d) and CH_4 (a and b) in unburned (blue) and burned (orange) watersheds. Shading indicates the standard deviation of the partial dependence functions from 10 boosted regression tree models run with different random seeds.

bodies in burned and unburned watersheds, which is a typical metabolic response (Figure 4). In addition to the direct effects on metabolic rates, these environmental conditions can affect changes in microbial and methanogen community structure and methanogenesis pathways (Chowdhury et al., 2015; Jerman et al., 2009; Turetsky et al., 2008). Empirical relationships among dissolved oxygen and temperature are often used in models to scale up CO_2 and CH_4 emissions (Bridgman et al., 2013; Jiang et al., 2017; Lloyd & Taylor, 1994; Luu & Lin, 2015; Payn et al., 2014; Rinne et al., 2018; Ueyama et al., 2020; Yvon-Durocher et al., 2014; Zheng et al., 2018). However, temperature and dissolved oxygen only contributed 6% and 14% relative influence in the unburned and burned CH_4 model (Figure 4b), indicating that typical scaling strategies for aquatic CH_4 emissions could fall short for the YK Delta.

3.2.4. Effects of Nutrient Availability

Dissolved inorganic nitrogen had a small relative influence in both CH_4 and CO_2 unburned models, but 8-times greater influence in both burned models, while phosphate had a small but significant contribution to all models (Figure 4). The effects of dissolved inorganic nitrogen on dissolved CH_4 and CO_2 in burned watersheds were similar to each other. There was an initial negative relationship spanning the low range of concentrations ($0\text{--}40 \mu\text{g-N L}^{-1}$; Figures 8b and 8d). For nitrogen concentrations greater than median value in unburned watersheds ($\sim 40 \mu\text{g-N L}^{-1}$; Figures 8a and 8c), the relationship reversed and both dissolved CH_4 and CO_2 increased with nitrogen availability until plateauing for nitrogen concentrations higher than $100 \mu\text{g-N L}^{-1}$ (Figures 8b and 8d). Increased nitrogen leaching following wildfires has been observed in other arctic ecosystems, with more severe fires causing greater mobilization of nitrogen to downstream ecosystems (Abbott et al., 2021; Ludwig et al., 2018). The contrasting effects of nitrogen on dissolved CH_4 and CO_2 we observed could depend on the extent and severity of fire in a watershed; the high-N positive effect occurring when there was a large proportion of high severity burns in the watershed, and the low-N negative relationship when low severity burns were more abundant in the watershed.

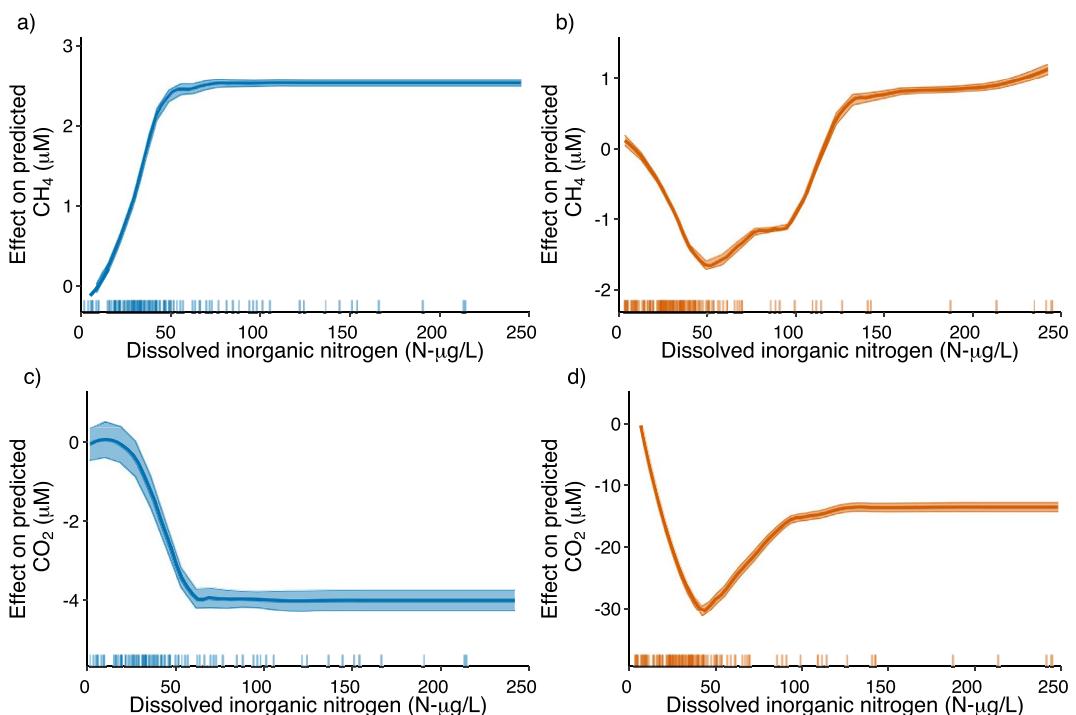


Figure 8. Partial dependence plots of the average effects of dissolved inorganic nitrogen on predicted CH_4 (a and b) and CO_2 concentrations (c and d) in unburned watersheds (blue) and burned watersheds (orange). Shading indicates the standard deviation of the partial dependence functions from 10 boosted regression tree models run with different random seeds.

A shift in the microbial community in burned watersheds could explain the observed changes in the effects of nitrogen. Both methanogenic and methanotrophic activity have been shown to increase in response to nutrient fertilization, with both positive, negative, and neutral net effects on CH_4 emissions (Aerts & Toet, 1997; Juutinen et al., 2018; Keller et al., 2005; Lund et al., 2009; Torn & Chapin, 1993; Veraart et al., 2015). This mechanism is supported by the increase in the relative influence of $\delta^{13}\text{C}-\text{CH}_4$ from 6% in unburned watersheds to 14% in burned watersheds (Figure 4b). For both burned and unburned, CH_4 concentrations declined as the influence of methanotrophy increased, though the correlation in burned observations was stronger (Figure 4). The increased importance of $\delta^{13}\text{C}-\text{CH}_4$ in burned waterbodies could indicate greater control of the microbial community through the balance of methanogenesis and methanotrophy.

3.2.5. Watershed Drivers

Upstream watersheds can directly influence CH_4 and CO_2 concentrations if hydrologic inputs (i.e., upstream waterbodies, sub- and supra-permafrost groundwater) have different concentrations than the water column (Dabrowski et al., 2020) and can indirectly influence CH_4 and CO_2 production in the water column by changing environmental constraints or supplying limiting reactants (McClain et al., 2003). Remotely-sensed watershed drivers (i.e., watershed slope, watershed size, percent area of degraded peat plateau) contributed a large portion of the explained variance in burned models for dissolved CH_4 and CO_2 (total 17% and 27% respectively) but contributed less to the unburned models for dissolved CH_4 and CO_2 (total 10% and 5% respectively; Figure 4). Percent area of surface water and watershed size had a positive effect on waterbody CH_4 and CO_2 concentrations in burned watersheds but a negative effect on downstream waterbody CH_4 and CO_2 concentrations in unburned watersheds (Figure 4). Upstream networks of waterbodies were thus more likely to be a source of dissolved CO_2 and CH_4 in burned watersheds, but dilute CH_4 and CO_2 concentrations in unburned watersheds. Percent area of peat plateau edges had a positive effect on CH_4 in unburned watersheds (Figure 4) and degraded peat plateau had positive effects on dissolved CH_4 in burned watersheds (Figure 9a). Degraded peat plateau had a similar effect on dissolved CO_2 (Figure 9b), but edge plateau area was not retained as a driver in the CO_2 models. These ecosystem margins and disturbed areas could be hot spots of CH_4 and to a lesser extent CO_2 production, leading to greater soil pore and ground water inputs from

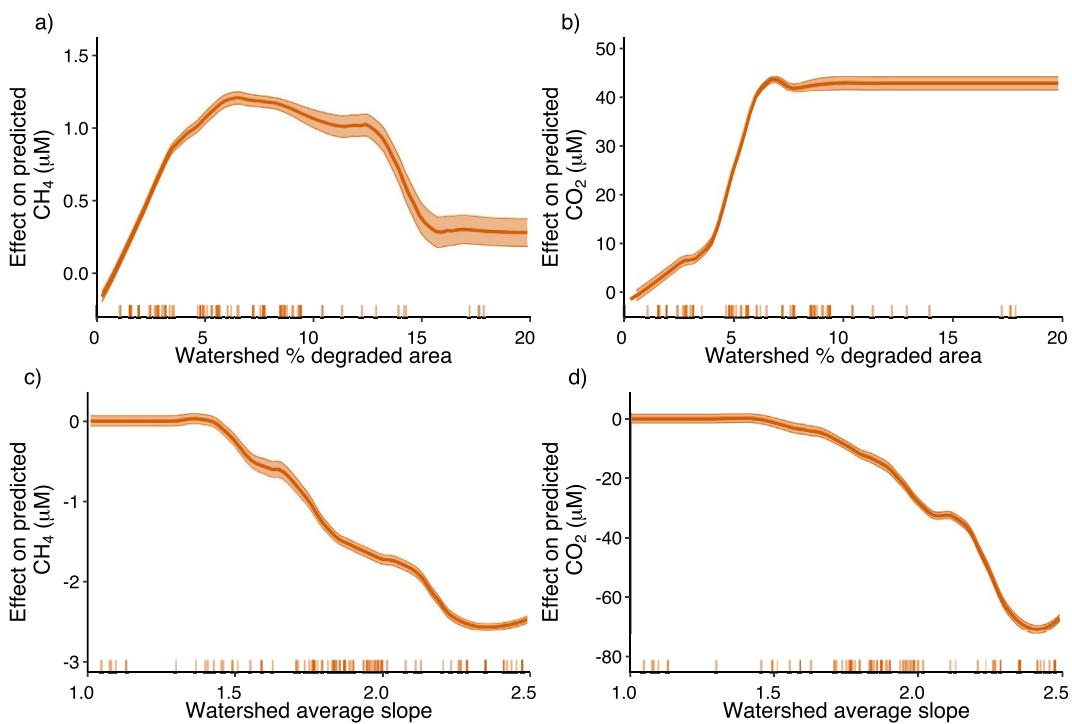


Figure 9. Partial dependence plots of the average effects of the percent of watershed area that is degraded permafrost (a and b) and watershed slope (c and d) on predicted CO_2 (b and d) and CH_4 (a and c) concentrations in burned watersheds. Shading indicates the standard deviation of the partial dependence functions from 10 boosted regression tree models run with different random seeds. Neither “watershed % degraded area” or “watershed average slope” were retained as variables in models for unburned watersheds.

the watershed. The average watershed slope had a negative effect on waterbody CH_4 and CO_2 concentrations, but was only a significant driver in burned watershed models and was not retained as a driver in unburned models (Figures 9c and 9d). Flatter watersheds could have longer water residence times, leading to increased leaching of DOM, more anoxia in pore water, and more reaction time for decomposition and respiration (Harms & Jones, 2012; Harms & Ludwig, 2016; Johnston et al., 2020; Judd & Kling, 2002; Koch et al., 2013; Newman et al., 2015; Olefeldt & Roulet, 2012; Throckmorton et al., 2015; Zarnetske et al., 2011). Our results demonstrate a shift away from waterbody edge effects and towards greater landscape connectivity and watershed level influences driving CO_2 and CH_4 concentrations in burned watersheds.

The percent area of a watershed that actually burned was a relevant driver in both CH_4 and CO_2 burned models. There was a threshold effect; percent watershed area burned did not affect CH_4 and CO_2 concentrations until greater than 65% of the watershed area was burned (Figures S4n and S6o in Supporting Information S1). This could suggest that more thoroughly burned watersheds affect dissolved CH_4 and CO_2 through variables we did not measure in this study. Watershed average NDWI, a metric associated with canopy wetness and soil moisture, was negatively correlated with percent burned area (Pearson correlation = -0.68), indicating wetter conditions in partially burned watersheds than in complete burns. This could be driven by the absence of moss and other vegetation biomass in burned areas or an increased presence of higher severity burns with drier conditions. NDWI was a more important driver in burned than unburned models and had a bimodal effect on waterbody CH_4 and CO_2 concentrations; the highest concentrations occurred in the wettest conditions when NDWI was high and when NDWI values were lower than any of those found in unburned areas, which could be indicative of high severity burns (Figures S4k and S6e in Supporting Information S1). Our results demonstrate that the pattern of a fire, that is, whether watersheds were partially burned or completely burned can regulate the effects of fire on downstream waterbody chemistry, reinforcing the need for a landscape approach to predicting waterbody CH_4 and CO_2 concentrations.

3.3. Consequences of Fire for Waterbody CO₂ and CH₄ Concentrations and Scaling

Averaging across all waterbodies, there was no detectable difference between CH₄ and CO₂ concentrations in burned watersheds. However, the mechanisms driving dissolved CH₄ and CO₂ changed as a consequence of fire. Fire reduced the influence of DOM on dissolved CH₄ but increased the influence of DOM on dissolved CO₂, with potentially balanced impacts on carbon emissions from waterbodies. The spatial extent of watershed burned area directly influenced dissolved CH₄ and CO₂, and while we did not directly account for fire severity, it may have indirectly affected dissolved CH₄ and CO₂ through inorganic nitrogen availability and watershed soil and canopy moisture (NDWI). Fire increased the sensitivity of CH₄ and CO₂ concentrations in waterbodies to watershed landscape drivers (i.e., watershed slope, size, NDWI, percent area degraded permafrost) compared to near-shore effects (i.e., perimeter:area ratio) and internal waterbody mechanisms (i.e., DOM composition). Fire can affect hydrologic regimes in a number of ways, such as increasing thaw depths, deepening flowpaths, increasing the hydrophobicity of soils, increasing small wetland and pond formation through subsidence, or altering the water balance as a result of changes in evapotranspiration from recovering vegetation (Brown et al., 2015; Helbig et al., 2016; Michaelides et al., 2019; Petrone et al., 2007). While we do not have direct measurements of these mechanisms, these results suggest that waterbody CH₄ and CO₂ concentrations were more sensitive to watershed dynamics in burned watersheds. An integrated terrestrial-aquatic approach in fire-affected, wetland-dense, ecosystems could improve scaling of CH₄ and CO₂ emissions and reduce uncertainty in bottom-up estimates of the inland aquatic carbon budget.

4. Conclusions

The boosted regression tree models were able to depict well-documented ecological dynamics, such as temperature sensitivity and carbon limitation of microbial respiration and methanogenesis. The models were consistent with globally-observed patterns, such as the relationship between lake size and dissolved CH₄ and CO₂, and were able to capture non-linear and interactive effects of predictor variables. Given that small waterbodies had the largest concentrations of CH₄ and CO₂, accurately accounting for carbon emissions from these small but abundant sources could greatly reduce the uncertainty in inland aquatic carbon budgets. For example, dissolved CO₂ was largely driven by waterbody size and shape and was saturated with respect to the atmosphere, suggesting that these waterbodies could be a net source of CO₂ emissions, even during the peak growing season. However, these inland water bodies are largely attributed a flux of zero in top-down carbon budgets from atmospheric inversion models for example, Commane et al., 2017. More seasonal observations of inland aquatic CH₄ and CO₂ concentrations are needed to extend predictive models outside of the peak growing season.

Contrary to many empirical studies and process-based models, our results suggest that dissolved CH₄ concentrations were predominantly predicted by carbon availability and quality, as opposed to temperature and dissolved oxygen. However, our sampling regime was not designed to test temperature or oxygen dependence. Remote sensing of chromophoric DOM has been used to predict DOC concentrations in inland waters (Brezonik et al., 2015; Griffin et al., 2018; Kutser et al., 2005), and, though associated with greater uncertainty in complex inland waters with high carbon concentrations, this could be a fruitful avenue for mapping carbon availability and scaling CH₄ emissions in waterbodies in the YK Delta.

Our results suggest wildfires alter lake and wetland ecosystems in the YK Delta to be more sensitive to watershed landscape drivers. After fires, areas of degraded permafrost increased CH₄ and CO₂ concentrations in downstream waterbodies, contributing to a positive feedback to climate as the Arctic continues to warm and permafrost thaws. As wildfires increase in frequency and severity with climate change, it will become more important to use an integrated terrestrial-aquatic approach when scaling inland aquatic carbon fluxes.

Data Availability Statement

The surface water chemistry and environmental data used in the boosted regression tree models in this study are available at the Arctic Data Center repository via <http://doi.org/10.18739/A22804Z8M> and <http://doi.org/10.18739/A23775V7T>.

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