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The Effect of Drying Boreal Lakes on Plants, Soils, and Microbial Communities in Lake Margin Habitats

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Key Points:

- Lake drying in the Yukon Flats National Wildlife Refuge triggers a succession of plant and microbial communities and losses of lake margin soil organic carbon (SOC)
- Lake drying also results in increases in the salinity of lake margin soils, slowing rates of microbial activities
- Although lake drying resulted in losses of SOC, increases in Aboveground Net Primary Production (ANPP) compensated for these losses

Supporting Information:

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

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Abstract Decadal scale lake drying in interior Alaska results in lake margin colonization by willow shrub and graminoid vegetation, but the effects of these changes on plant production, biodiversity, soil properties, and soil microbial communities are not well known. We studied changes in soil organic carbon (SOC) and nitrogen (N) storage, plant and microbial community composition, and soil microbial activities in drying and non-drying lakes in the Yukon Flats National Wildlife Refuge. Historic changes in lake area were determined using Landsat imagery. Results showed that SOC storage in drying lake margins declined by 0.13 kg C m^{-2} yr^{-1} over 30 years of exposure of lake sediments, with no significant change in soil N. Lake drying resulted in an increase in graminoid and shrub aboveground net primary production (ANPP, +3% yr^{-1}) with little change in plant functional composition. Increases in ANPP were similar in magnitude (but opposite in sign) to losses in SOC over a 30-year drying trend. Potential decomposition rates and soil enzyme activities were lower in drying lake margins compared to stable lake margins, possibly due to high salinities in drying lake margin soils. Microbial communities shifted in response to changing plant communities, although they still retained a legacy of the previous plant community. Understanding how changing lake hydrology impacts the ecology and biogeochemistry of lake margin terrestrial ecosystems is an underexamined phenomenon with large impacts to landscape processes.

Plain Language Summary Lake dominated ecosystems in Alaska have experienced periods of widespread lake drying in the past. We understand little of what occurs on these new nearshore habitats following lake drying, especially changes in soil properties and soil microbial communities. Using a combination of remote sensing and field sampling on hundreds of lakes in the Yukon Flats National Wildlife Refuge, we learned that lake margin soils lose significant quantities of soil C in the decades following lake drying, and at the same time soils become increasingly saline and soil microbial activites are reduced. Overall, lake drying has large impacts on the surrounding ecosystems and it is important to understand these changes for management.

1. Introduction

High latitude ecosystems are changing rapidly due to longer growing seasons, increased severity and frequency of wildfire, permafrost thaw, and lake drying (Borner et al., 2008; Euskirchen et al., 2006; Piao et al., 2007). Lake drying is an understudied and important aspect of the changing ecology and biogeochemistry of northern latitude ecosystems (Jones et al., 2022; Riordan et al., 2006). Changes in arctic and boreal lake systems have cascading effects, from changes in wildlife habitat, water quality, climate regulation, and human subsistence (Chapin et al., 2009). In interior Alaska, lake drying has been documented in multiple studies of repeat aerial and satellite imagery over a period of 60 years showing a net decrease in the number and surface area of closed basin lakes (Riordan et al., 2006; Roach et al., 2013; Rover et al., 2012).

The Yukon Flats (YF) is a region in interior Alaska characterized by abundant, highly eutrophic, shallow closed basin lakes (Heglund & Jones, 2003). These lakes were formed during aeolian deposition and fluvial processes since the end of the Pleistocene (Jorgenson et al., 2013). The underlying permafrost is important in forming an aquiclude which perches the water table and supports the mosaic of wetland communities on the floodplain (Roach et al., 2011), despite the arid climate of interior Alaska (Bogard et al., 2019; Ford & Bedford, 1987).

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Climate reconstruction from lake sediments in the YF indicate that many of the lakes may have been larger during the early Holocene (∼5000–1850 BP) but conditions became much drier in the last 1,000 years (Anderson et al., 2013). From 1980 to 2010, there was an overall shrinkage of 3.4% of water bodies in the YF (Rover et al., 2012), and future projections indicate that a decline in lake area of up to 80% is possible in some areas of the YF (Roach et al., 2013). However, these spatially nonuniform decadal-scale drying trends have sometimes been followed by rapid reflooding (Riordan et al., 2006; Roach et al., 2011) such as the local flooding events from 2012 to 2020 along the Yukon river, highlighting the dynamic nature of these water bodies (Anderson et al., 2013; Jepsen et al., 2013, 2016).

The YF lake landscape is responding to multiple factors including precipitation, evaporation, terrestrialization, and permafrost thaw (Briggs et al., 2014; Hinzman et al., 2005; Koch, 2016; Minsley et al., 2012; Roach et al., 2011; Walvoord et al., 2012). This complexity suggests that ecological changes associated with lake drying in the YF could have broad implications for understanding effects of climate change in the circumpolar north (Roach et al., 2011; Walvoord et al., 2012). Lakes provide a number of ecosystem services by maintaining biological diversity and sequestering carbon (C) in sediments and lake margin soils (Hollingsworth et al., 2008; Jorgenson et al., 2013; Roach & Griffith, 2015; Stackpoole et al., 2017; Wilmking et al., 2006). However, how these services will be affected by hydrological disturbances like the drying and flooding of lakes remains unclear. In particular, the effect of lake drying on biogeochemical processes in surrounding terrestrial soils has not been extensively studied (Jones et al., 2022; Marcé et al., 2019). Drying lakes have the potential to expose vast amounts of sediment C to decomposition. Published estimates of the C pool in boreal lake sediments range from ∼20 to 120 Pg of C (Kortelainen et al., 2004; Molot & Dillon, 1996). As lakes continue to shrink, lake margin soils become drier, and exposed sediments undergo aerobic decomposition. Thus, if soil C loss exceeds gains in net primary productivity, drying lake margin soils may become net C sources to the atmosphere (Weise et al., 2016). Furthermore, limnic sediments, defined as high organic lake sediments, are considered to be highly labile and vulnerable to aerobic decomposition (Jorgenson et al., 2013; Schuur et al., 2015; Weise et al., 2016) which could result in even higher net C losses relative to organic soils derived from terrestrial vegetation. On the other hand, exposure of limnic sediments could present new land area and nitrogen (N)-rich soil to newly established plant communities, increasing plant net primary productivity.

In the YF, soil moisture gradients away from lake edges to the surrounding environment creates a progression of ecosystems from near shore graminoid (grass and sedge) communities to willow, mixed deciduous, and finally spruce-dominated forests, creating a series of concentric rings around lake systems (Figure 1). Over time, as lake margin soils dry, graminoid communities quickly establish on newly exposed sediments, willow and tree seedlings gradually begin to emerge in areas occupied by graminoids, with fast-growing willow eventually becoming dominant. Finally, slower growing tree seedlings begin to encroach and overtop willow stands (Figure 2; Berg et al., 2009; Klein et al., 2005). However, spring snowmelt and ice jams frequently cause drained lake basins to reflood, which can abruptly kill established woody communities and reset local successional trajectories.

The composition of plant communities influences the composition and functioning of microbial communities, and thus successional changes in plant communities should result in concomitant changes in soil microbial communities and soil processes (Chapin et al., 2009; De Deyn et al., 2008). Plant communities affect soil microbial communities by altering the resources available to soil microbes either through mutualisms in the root and rhizosphere or indirectly through changes in litter quality, soil pH, and/or soil moisture (Evans & Wallenstein, 2014; Fierer et al., 2012; Waldrop et al., 2017). In a dynamic environment, in which plant communities are shifting, microbial community shifts may precede, parallel, or lag plant community shifts (Hewitt et al., 2017; Inderjit & van der Putten, 2010; Rodrigues et al., 2015; Waldrop & Firestone, 2006; Wolfe & Klironomos, 2005), and may continue to respond to disturbances for decades before they reach a new equilibrium (Mentzer et al., 2006; Terwilliger & Pastor, 1999). However, below-ground processes and microbial community composition are also influenced by a variety of state factors and may not respond to above-ground plant community dynamics in all environments (Porazinska et al., 2003).

Our primary objectives were to test the hypotheses that lake drying drives losses in lake margin soil organic C and N storage at a rate that outpaces changes in plant productivity. Specifically, we hypothesized that lake drying results in significant losses of lake margin soil organic C and N over time due to exposure of limnic sediments to unsaturated aerobic conditions, with increased microbial activities in drying lake soils. Furthermore, we hypothesized that drying lake margin soils would result in more rapid shifts in plant communities than soil microbial communities, resulting in a temporal and spatial separation between plants and their microbial communities.

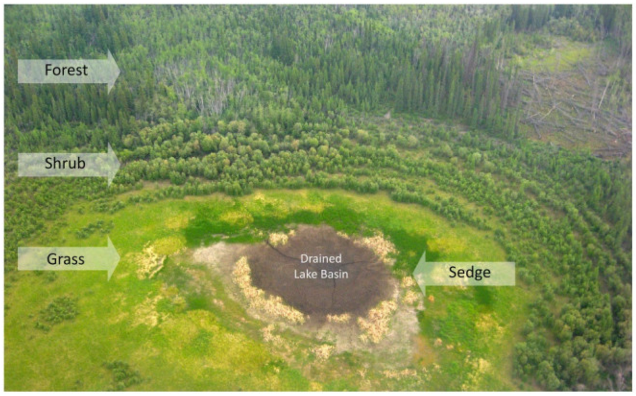

Figure 1. Lakeshore plant communities at a completely dried lake. Grass and sedge-dominant communities co-occur closest to the lakeshore.

2. Methods

2.1. Study Area

Our sites were located in the Yukon Flats National Wildlife Refuge, which is located in a broad unglaciated river floodplain approximately 33,000 km^2 in area, located in north central Alaska (Figure 3; Gallant et al., 1995; Wahrhaftig, 1965; Williams, 1963). It is bounded to the north by foothills of the Brooks range and to the south by a loess plateau rising 300 m above the flats and extends into the White Mountains (Muhs et al., 2003). The underlying substrate of the YF is alluvial sand and gravel (Williams, 1963) due to widespread alluvial fans resulting from the meandering Yukon River and its tributaries (Williams, 1955). Calcareous aeolian sand and silt form a cap over the alluvium (Muhs et al., 2003) which contributes to the regions alkaline lakes and trona deposits (Clautice & Mowatt, 1981; Heglund & Jones, 2003). There are approximately 30,000 shallow closed-basin lakes in the YF that range from 0.5 to 6 m deep, with most averaging around 2 m (Heglund & Jones, 2003), accounting for nearly a quarter of the circumpolar boreal lake area (Bogard et al., 2019). Lakes in the region are primarily formed from fluvial (oxbows and abandoned channels), thermokarst, or aeolian processes (Jorgenson et al., 2013; Roach et al., 2013; Williams, 1963). Vegetation is a mosaic of black spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburg) muskeg, graminoid wetlands, and willow (*Salix* sp. Linnaeus) thickets in the lowlands and swales, and meander scars dominated by upland mixed forest consist mainly of Alaskan birch (*Betula neoalaskana* Sarg.) and white spruce (*Picea glauca* (Moench) Voss) (Heglund & Jones, 2003; Johnson & Vogel, 1966; Williams, 1955). Lowlands of the YF contain discontinuous permafrost (Jorgenson et al., 2008; Pastick et al., 2014) with permafrost free zones occurring beneath lakes and river channels (Jorgenson et al., 2013; Williams, 1955). Annual precipitation averages 170 mm (Gallant et al., 1995), with most precipitation inputs to lakes coming from spring snow melt (Chen et al., 2012). Wildfires are the primary form of disturbance in the YF (Drury & Grissom, 2008) and dried lakes, some with surface layers of trona deposits (gypsum, calcite or $NaCO_3$, that cakes the surfaces of dry lakebeds), are a common feature of the landscape, as are concentric bands of wetland plant communities that establish along the retreating shorelines of drying lakes (Clautice & Mowatt, 1981; Heglund & Jones, 2003; Hopkins, 1955; Jorgenson et al., 2013; Marcus & Wahrhaftig, 1967). This dynamic landscape provides a natural laboratory for understanding how interactions between lakes, lake margin soils, and terrestrial vegetation affect nutrient and C cycling and mediate the effects of long-term warming in boreal landscapes. We focused on lakes bounded by the Yukon River to the north, and the White Mountains to the south (Figure 3), which was the region that showed the strongest drying signal in lakes (Heglund & Jones, 2003; Hopkins, 1955; Jorgenson et al., 2013; Marcus & Wahrhaftig, 1967; Roach et al., 2013).

2.2. Sampling Design, Trends, and Ages

We sampled 135 lakes over three summers (2010–2012) with different subsets of lakes sampled each year depending on the attribute being measured (Table S1 in Supporting Information S1). One hundred and twenty of these lakes were selected using spatially balanced random sampling design (Stevens & Olsen, 2004), and 15 were added due to ease of access. Lakes were analyzed for wetland size trends and plant community characteristics. Different numbers of lakes were sampled for plant productivity, soil, and microbial measurements. These differences were due to differences in lake access by various investigators and the complexity of the analyses. Fewer lakes were sampled for C mineralization and microbial community analysis because fewer people were available to process this number of samples. On the other hand, more lakes were sampled for vegetation composition because more people were involved in those sampling events. For all analyses, sampling was stratified by lake status (see below).

We estimated lake size trends for all lakes using satellite imagery following the methods of Roach et al. (2011, 2013). We classified the lakes as "drying," "stable" or "variable" based on interannual variation in size, using a

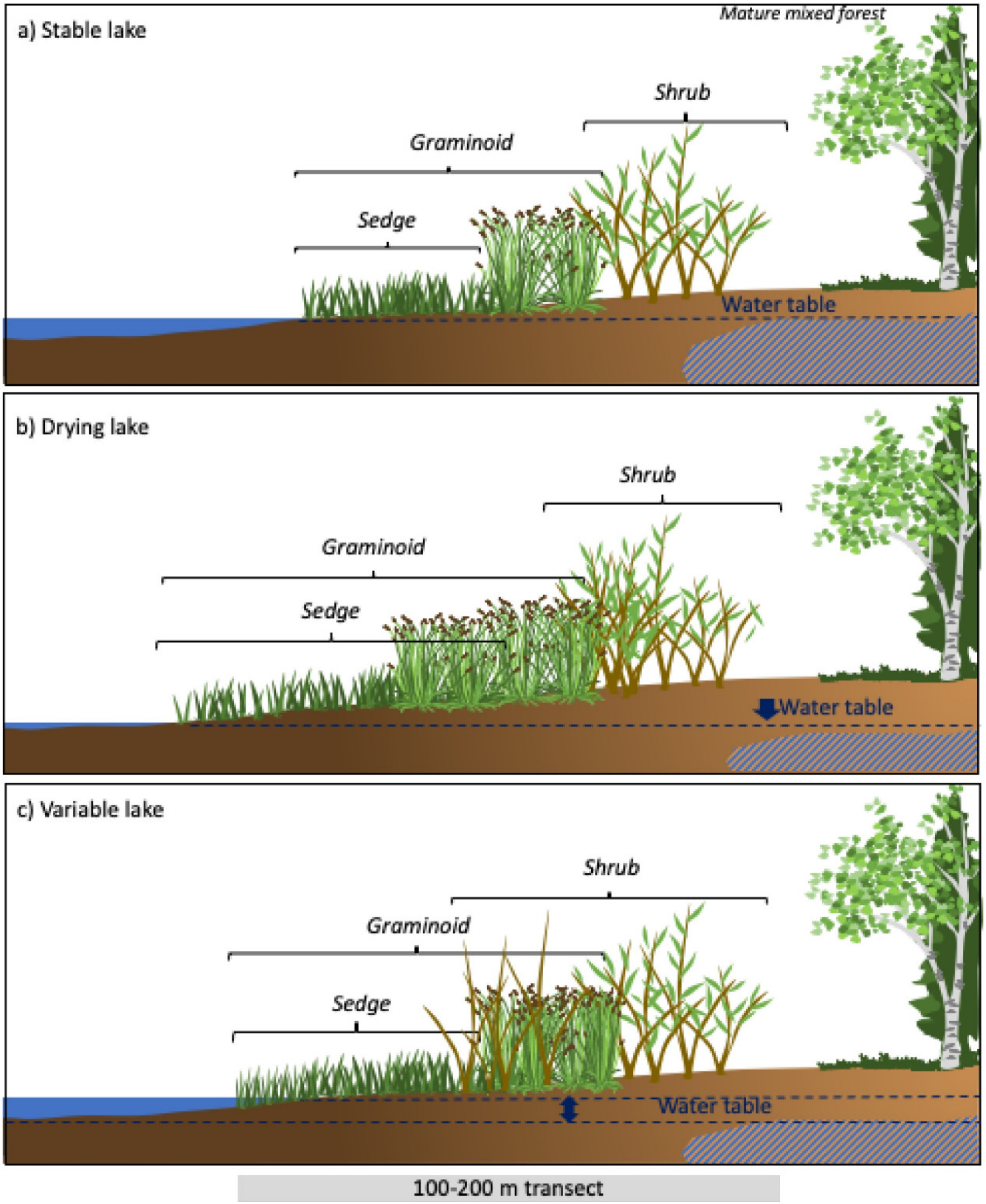

Figure 2. Conceptual figure of lake drying. (a) Stable lakes are characterized by concentric rings of sedge, graminoid, shrub, and deciduous and/or spruce trees. (b) During the process of lake drying, water table level declines and exposed sediment is initially colonized by grasses and sedges, followed by deciduous shrubs and eventually mixed forest trees. (c) Fluctuations in the water table level may kill plants, especially shrubs, due to encroachment and flooding. Discontinuous permafrost may be present around some lakes, although it can be hard to detect. The loss of surrounding permafrost may influence both drying and fluctuating lakes by changing subsurface flow dynamics.

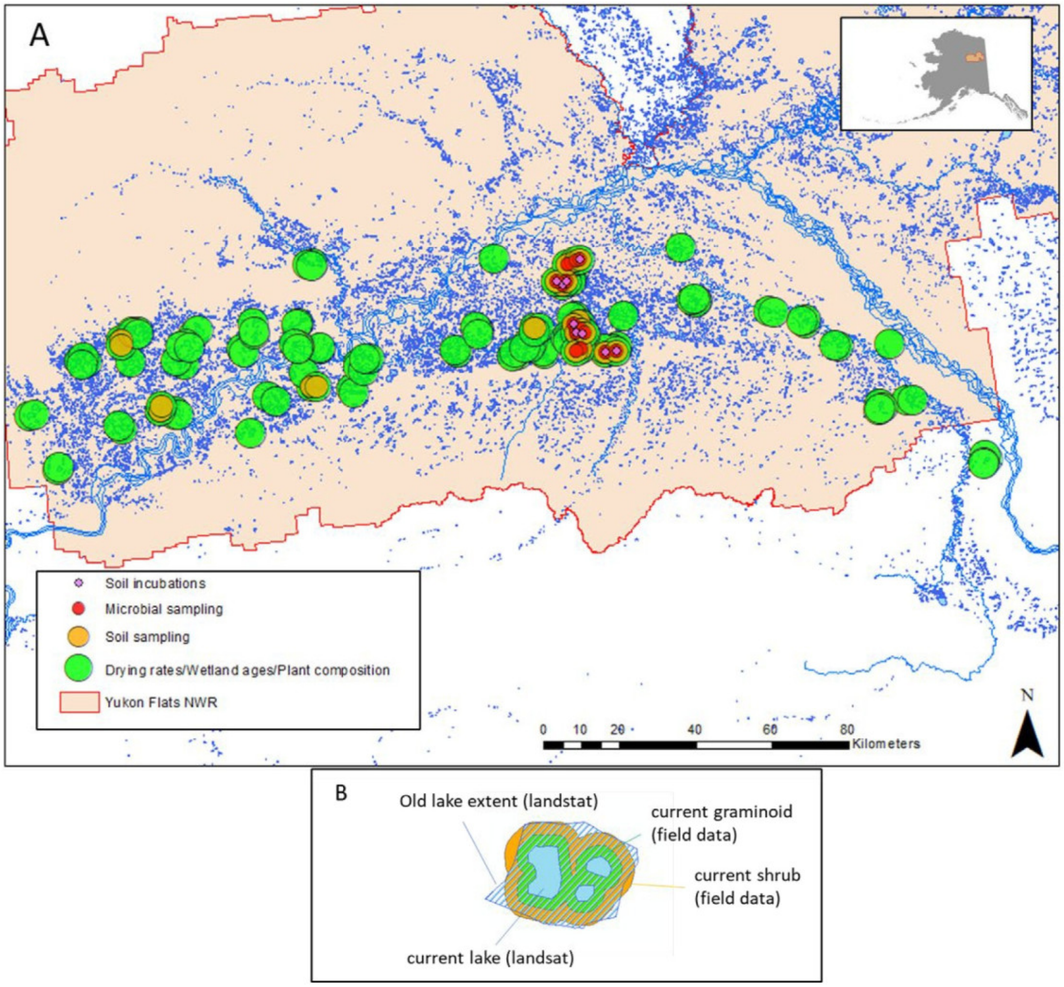

Figure 3. (a) Study lakes in the Yukon Flats National Wildlife Refuge. The refuge boundary is outlined in red, and the location of the refuge within the state of Alaska is shown in the inset map. Lake surface water extent and wetland ages were characterized at 128 lakes. Subsets of those lakes were used to measure soil chemical and microbial attributes (Table S1 in Supporting Information S1). (b) Schematic for estimating the duration of the drying period for a wetland, which represented the number of years that wetland soils had been exposed to aerobic conditions after lakeshore retreat. This involved contrasting Landsat-derived historical lake boundaries with field-derived measurements of current wetland extent.

time series of 22 Landsat satellite images collected between 1979 and 2011 (Rover et al., 2012). We refer to this classification as lake status throughout the paper. We fit linear models using area measurements for each lake in each year between May and September where imagery could be obtained (Equation 1; Roach et al., 2011).

$$\text{Lake Area} = \beta_1 * \text{Year} + \beta_2 * \text{Month} + \beta_3 * \text{Year} * \text{Month} \tag{1}$$

Month was represented as a number (5–9) which was scaled and normalized to a mean of 0 and SD of 1, so that the main effect of year reflected annual trends during the mean month (July). This allowed us to minimize the influence of transient spring floods on our estimates of annual trends in lake size. Lakes with statistically significant negative annual trends >0.05% per year (β_1 with 95% confidence intervals and slope <0) were characterized as drying, while lakes with significant positive annual trends were characterized as increasing. There were so few lakes characterized as increasing (4 of 135) that they were not included in subsequent analyses. Lakes with no significant annual trend were categorized as stable or variable based on the root mean square error coefficient of variation (CV(RMSE)) of the model fit using Equation 1, which reflected variability relative to the predicted trends. Lakes whose CV(RMSE) exceeded the 75 percentile of CV(RMSE) values for all lakes were classified as variable, while lakes with less interannual variability were classified as stable.

2.3. Vegetation Sampling

At each lake, we randomly located 3–4,100-m transects extending from the lake margin toward the surrounding forest. If the forest edge was >100 m from the lake edge, we extended the transect 10–20 m into the mature forest. We first subdivided each transect into 3–4 plant community types, which were forest (F), shrub (SH), and graminoid/sedge (GS). In some cases, we could sample this latter category separately as graminoid or sedge. We distinguished communities based on the tallest plant growth form comprising at least 50% ground cover. Shrub communities were those dominated by multi-stemmed woody shrubs, primarily of mixed willow species (*Salix* L. spp.), while forest communities were characterized by single-stemmed woody trees, primarily white and black spruce (*P. glauca*, *P. mariana* (Mill.) B.S.P.), with some mixed stands containing Alaskan paper birch (*B. neoalaskana*) and aspen (*Populus tremuloides*). Plant communities typically formed distinct bands of vegetation surrounding each lake (Figure 1), but plant species composition varied widely among lakes within each community type. We categorized vascular and nonvascular plants within each community into eight morphology-based functional types (non-vascular, graminoid, forb, evergreen shrub, deciduous woody shrub, tree, dead wood, and bare ground). We visually estimated percent cover for all functional types within 5 m of the transect centerline.

We summarized functional type composition in each community at each lake, and characterized plant functional diversity (Petchey et al., 2004) using a Shannon diversity index (H) with percent cover as a measure of functional type abundance, where $F =$ the total number of functional types, and $p_i =$ the proportional abundance of functional type I (Equation 2).

$$H = -\sum_{i=1}^{F} pi \cdot \ln pi \tag{2}$$

Finally, we estimated the area of GS and SH wetlands at the time of sampling for all lakes, by calculating the average width of each community and the average position of community transitions (GS to SH, SH to Forest) among all transects. We used these average values to create polygons representing GS and SH wetlands surrounding the current shoreline of all lakes using GIS tools in R (Bivand & Rundel, 2019; Bivand et al., 2013).

We used polygons delineating the spatial extent of GS and SH wetlands in 2010–2011 to estimate the number of years since wetland soils were exposed by lakeshore retreat. We refer to this metric as time since drying, although changes in lake size can be driven by many factors other than evaporative water loss, including terrestrialization through vegetation growth and drainage due to permafrost thaw (Roach et al., 2011). Estimating time since drying was central to our analysis because it allowed us to understand how lake margin soil properties and wetland plant communities changed over time at drying and variable lakes. We used vegetation transect data to calculate the mean positions of GS and SH wetland communities around each lake, then created concentric GIS polygons representing both communities. We next overlaid these wetland polygons with Landsat-derived polygons representing the historical extent of surface water of each lake and computed the percentage of current wetland extent that was inundated at the time of each Landsat image acquisition. If a wetland polygon was >50% covered by a lake polygon, we considered it "inundated" on that date. Because we did not have continuous temporal coverage for most lakes, we defined the temporal midpoint between the last inundated date and the next non-inundated date as the date of last inundation and used this date to compute an estimated age in years for all GS and SH wetlands. Because the Landsat timeseries did not extend beyond 1980, we truncated estimates of time since drying at an upper bound of 30 years. We were able to calculate time since drying for 128 lakes (Table S1 in Supporting Information S1, Figure 3).

2.4. Aboveground Net Primary Productivity (ANPP)

We collected aboveground biomass and ANPP measurements at 14 lakes (6 stable lakes, 4 drying, and 4 variable) in GS and SH wetland plant communities. We estimated Aboveground Net Primary Productivity (ANPP; g m^{-2} yr^{-1}) with destructive quadrat harvests (Fahey & Knapp, 2007) collected in a 2-week period corresponding to peak biomass (late July–early August). Ten 20 × 50 cm quadrats were distributed randomly in each plant community type (GS, SH, and F). Due to limited time in the field, samples were kept cool until freezing within 1–2 days of collection. Once in the lab, thawed samples were dried at 60°C for 48 hr and visually separated into previous years' biomass and seasonal new growth. New growth biomass was used to estimate NPP (Shaver &

Chapin, 1991). Because nonvascular functional groups could not be reliably separated into new and old growth, all live (green) non-vascular tissues were included in new growth biomass. C content was estimated as biomass * 0.5 (Pregitzer & Euskirchen, 2004).

2.5. Soil Sampling

Soils in this study were derived from both sediments (depositional origin) as well as soils (weathered in situ), but we will use the term soils throughout because they were sampled above shoreline. Thus, material collected for this study in lake margins is considered "soil," even though it is a mixture of both soil and sediment. We collected soil cores for C and N storage estimation, moisture content, electrical conductivity (EC), and pH from 23 lake margins (14 drying, 7 stable, 2 variable, Figure 3). At each of these lakes, we extracted a single core from a 3 × 3 m plot located at the midpoint of each plant community and centered along one randomly selected vegetation transect. We collected soil cores using a 30-cm long, 4.5-cm diameter stainless steel sharpened core barrel attached to a handheld battery-operated power drill (Nalder & Wein, 1998). We gently extracted the core from the tube to avoid compression. We measured levels of compression on all cores by comparing core length to the depth of hole from which it was retrieved. Cores with >2 cm compression were not used for bulk density analysis. Cores were split in half vertically, visually separated into organic and mineral horizons and measured for length and weight in the field. We used one half of each horizon for soil chemical analysis and the second half for a laboratory incubation (see below). Samples were stored at 4°C until transport and final processing, typically within 2 weeks for soil chemical analysis. We collected one deep core from the center of a completely dried lake (lake 1991) using a 1-m long, 12.7 cm diameter metal serrated core barrel to 1 m depth. This deep core was collected to estimate C storage in the center of a dried lakebed.

We sieved soils to 2.33 mm to remove large roots, litter, and woody debris. No rocks were observed among any samples. We took subsamples for soil moisture, bulk density, % C, % N, soil pH, EC, carbon mineralization, and an archive. We determined gravimetric soil moisture (%) by weighing a subsample, drying the subsample for 48 hr at either 105°C (mineral horizon), or 60°C (organic horizon), then weighing it again. Bulk density was calculated from the dry weight and volume of the horizon. Volumetric water content (VWC) was calculated by multiplying % moisture by bulk density. Total C and N analyses were conducted on dried subsamples that were powdered in a modified roller mill and analyzed using combustion analysis on a LECO 2000 CNS autoanalyzer (LECO, St. Joseph, Michigan, USA). We calculated C density for each soil horizon as bulk density (g soil cm^{-3}) × % C. We then multiplied C density by soil horizon volume within each core (cm^3) and divided by the core surface area (15.9 cm^2) to calculate C storage per cm^2 within the top 30 cm of soil, which we converted to kg m^{-2}. Finally, to estimate organic C (OC) per m^2 we corrected for carbonates using a correction factor. This correction factor was generated by regressing OC (carbonates removed through 24–48 hr acid fumigation) against total carbon using soil data from a subset of six Alaskan lake margins that spanned regions, vegetation types, and soil horizons ($R^2 = 0.96$, $p < 0.0001$; Figure S1 in Supporting Information S1; total organic $\text{C} = 0.84 * \text{total C} - 0.12$). pH was determined from a 1:2 (mass:volume) slurry of soil and deionized water equilibrated at room temperature for 30 min (Fisher Scientific AB15). Soil electrical conductivity was measured at room temperature on the same 1:2 slurry following an additional equilibration time of 2 hr (CDM80, Radiometer Analytical, Lyon, France).

2.6. Carbon Mineralization

Carbon mineralization rates were measured on soils collected from 10 lake margins (6 drying, 4 stable/variable; Table S1 in Supporting Information S1). Because only one variable lake was sampled for C mineralization, we were unable to include variable lakes as a separate treatment group. Instead, we included the variable lake with stable lakes because there was no declining trend in its lake area, which allowed us to contrast C mineralization in soils exposed by drying lakes against a control group comprised of all non-drying lakes. Soils (10–40 g DW) were weighed into 490 mL glass jars and sealed with screw top metal lids containing a stopcock valve fitted into a John Guest (push-to-fit) bulkhead union. Jars were incubated at 15°C in the dark for 16 weeks but opened between sampling events to allow for headspace equilibration. Twenty-four hours prior to weekly measurement, jars were flushed with ambient air and sealed; gas samples were collected with a 10 mL syringe fitted with a three-way stop cock. To mix the headspace, the inserted syringe was pumped 10 times before a final 10 mL sample volume was collected. Between measurements, headspace was flushed with ambient air and sealed with 0.5 mil polyethylene sheeting to permit gas exchange and reduce moisture loss. Soil moisture was adjusted gravimetrically to maintain water content. Samples and blanks (incubation jars without soil) were analyzed for [CO_2] using a micro GC P200 (Agilent Technologies Inc., Santa Clara, CA, USA). Three point calibration curves were developed with certified gas standards balanced with N_2 (Air Liquide America Specialty Gases, Plumsteadville, PA, USA). The decomposition rate constant (k) and available C pool (A_o in mg C/g soil C) were estimated using the equation $C = A_o\,(1 - e^{-kt})$ in which C is cumulative carbon flux and t is time (JMP software, SAS Institute, Cary, NC).

2.7. Soil Microbial Community Characterization

Soil microbial communities were characterized from margins of 14 lakes (10 drying, 4 stable/variable). In the center of each plant community band along a transect, we collected three push cores within a 3 × 3 m area (2.5 cm diameter × 20–25 cm deep), avoiding obvious disturbances and obstacles (e.g., wildlife trails and downed trees). The push core was collected into a sterile plastic sleeve inserted into the core barrel (1″ × 12″ stainless steel soil recovery probe, AMS Inc., Idaho) to minimize cross contamination between cores. We divided the cores into organic and mineral horizons in the field. Using a flame-sterilized steel spatula, we lightly homogenized each mineral or organic core segment on a combusted aluminum sheet (450°C for 4 hr), then subsampled into a sterile 50 mL tube (Falcon centrifuge tube, fisher scientific, Waltham, MA). Falcon tubes were usually frozen in the field on dry ice, and stored at −20°C until lyophilization, but in some cases they were kept cool by burying and storing just above the permafrost for several days until they could be transported to the University of Alaska Fairbanks and frozen. Once returned to the lab, samples were lyophilized and then composited by plot for each horizon, yielding a total of three replicates per lake for each vegetation class (Virtis Freezemobile 12ES, SP Industries, Warminster, PA, USA).

Phospholipid Fatty acids (PLFAs) were extracted from ~1 g (organic) or 5 g (mineral) of freeze-dried soil following the protocols outlined in White and Ringelberg (1997) with some modification. We extracted lipids from soil using a chloroform-methanol extraction with a phosphate buffer in hexane-rinsed 50-ml Oak Ridge PTFE round-bottom tubes (Thermo Scientific Nalgene, Rochester, NY), shaken at 180 rpm for 1 hr and centrifuged at 2,500 rpm for 30 min. The supernatant was allowed to sit overnight to permit separation, after which the aqueous phase was removed with a vacuum aspirator and the remaining chloroform phase was slowly evaporated under N_2. The PLFA fraction was isolated by silica gel chromatography (Grace Discovery Science, Deerfield, IL SPE) and transesterified by a mild alkaline methanolysis.

We analyzed samples for phospholipid fatty acids using a Hewlett Packard 6890 Gas Chromatograph with FID detection after establishing elution times for each analyte using a single quadrupole mass spectrometer detector (MSD 5975). To identify individual PLFA peaks and coordinate elution times between detectors we used several certified FAME standards: a mixture of 19 FAMEs (Grain Fatty Acid Methyl Mixture 47801; Supelco, Inc.), a mixture of 26 bacterial FAMEs (BAME 47080-U; Supleco, Inc.), a 37 FAME mixture (Supelco 37 47885; Supelco, Inc.) and the branched chain, methyl 10-methylhexadecanoate (10me16:0; Catalog # 1792, Matreya, LLC). Nonedecane (19:0) was added as an internal standard. FAMEs were separated on a 60 m DB-1ms column (0.32 mm × 0.25 μm film, Agilent Technologies, Inc.) under the following conditions: 0.1 μL splitless injection with 50 mL min^{-1} purge at 0.5 min, an initial temperature of 40°C ramping to 150°C at 20°C min^{-1}, holding 1 min each step then to 210°C at 1.5°C min^{-1}, then to 280°C at 10°C min^{-1} and holding for 8 min at a constant He flow of 1.5 mL min^{-1}. Individual FAMEs are expressed as mole fraction PLFA and named accordingly to convention (Frostegard et al., 1993; Zelles, 1999).

2.8. Soil Enzyme Activities

Activities for four extracellular hydrolytic enzymes (acid-phosphatase, ß-glucosidase, N-acetyl-ß-glucosaminidase, and cellobiohydrolase) and two oxidative enzymes (polyphenol oxidase and peroxidase) were determined colorimetrically based on the quantity of pNP released (405 nM) or L-DOPA oxidized (450 nM) when soil was incubated with a buffered substrate (Sinsabaugh, 2010). Substrates were 5 mM p-nitrophenol- [pNP-] linked phosphate, 2 mM pNP-acetyl-ß-D-glucosaminide, 2 mM pNP-ß-D-glucoside, and 5 mM L-DOPA (oxidative enzymes), respectively. Two g freeze-dried soil was mixed with 100 mL of 50 mM pH 5 sodium acetate buffer and stirred vigorously in a 250 mL wide-mouth mason jar with a magnetic stir bar for 15 min. Assays were replicated eight-fold in 96-well microplates containing blanks (buffer only), substrate controls (substrate + buffer), homogenate controls (homogenate + buffer) as well as the soil enzyme assay (homogenate + substrate). For the peroxidase assays, we added 10 μL 0.3% H_2O_2 to the substrate control and assay wells.

The extinction coefficient for pNP was determined from standard curves of absorbance versus concentration using known quantities of pNP. Oxidative assays were standardized using horseradish peroxidase (0.2 mg mL^{-1}) to completely oxidize 2mM and 1 mM L-DOPA solutions and a blank, and measuring absorbance of the products generated. Peroxidase activity is the difference in activity between peroxidase and phenol oxidase assays. Enzyme specific activity was normalized to the amount of soil carbon per sample (ug substrate transformed hr^{-1} g^{-1} soil C).

2.9. Statistics

We used linear mixed models with random intercepts for each lake to examine changes in organic layer OC storage, soil N storage, soil EC, soil VWC, plant ANPP, plant functional diversity, and microbial parameters (PLFA, enzyme activities, Ao, *k*) in lake-margin wetlands. Fixed effects included either a categorical effect of lake status (drying, stable, and variable lakes) or a continuous effect of drying period length (years of drying), allowing us to examine how ecological effects of lake drying developed over time (Bolker et al., 2009). Estimates for years of drying had an upper bound of 30 years due to the constraints of the Landsat data set, which may have resulted in conservative estimates for the strength of relationships between lake drying and soil or plant community characteristics, but nevertheless allowed us to quantify these relationships at decadal timescales. For microbial response variables, we included "variable" lakes with stable lakes in models with an effect of lake status because we only had data from 1 to 2 variable lakes for these variables and were primarily interested in drawing contrasts between lakes with and without drying trends. We also included fixed effects of wetland community vegetation type and, where appropriate, soil horizon. Response variables were graphically checked for normality and transformed appropriately. Transformed data are indicated as such in all figures, tables, and text. For each response variable, we fit a nested set of candidate models containing either lake status or years of drying and other fixed effects, including some models with interaction between lake status/drying period length and vegetation type. All models also included a random effect of lake ID on the intercept to account for pseudoreplication and uneven sample sizes among lakes. We fit all models in the program R (R Core Team, 2021) using the LmerTest package (Kuznetsova et al., 2017). We then selected the best model from each candidate set using AIC (Anderson & Burnham, 2004). Except where otherwise noted, model fit metrics (conditional R^2; Bartoń, 2022), predictions and parameter estimates represent the selected model in each candidate set.

We conducted principal components analysis (PCA) to examine changes in plant composition (% cover of plant functional types) and microbial community composition (relative abundance of phospholipid fatty acid) among plant communities and in relation to lake drying. To test for significant effects of lake status, years of drying, and vegetation type on plant and microbial community composition, we conducted PERMANOVA analysis using the vegan package in R (Oksanen et al., 2022). PERMANOVAs did not support random effects (Oksanen et al., 2022), but we included lake as a blocking variable in each analysis. This PERMANOVA analysis replaced the multi-model analysis used for other responsive variables. We summarized the proportion of variance in each PCA that was explained by the first and second axes ($PC1_{plant}$ and $PC2_{plant}$ for plant composition, $PC1_{mic}$ and $PC2_{mic}$ for soil microbial PCA). We then used significant terms from the PERMANOVA analyses as fixed effects in 2-way linear mixed effects models with a random effect of lake, and used these models to conduct post-hoc comparisons among plant and microbial communities in drying and non-drying lake margin environments.

3. Results

3.1. Rate of Lake Change and Length of Drying Period

In a spatially balanced random sample of 120 YF lakes, 18 (15%) were classified as drying, four (3%) were classified as increasing, and 25 (21%) were classified as variable. The remaining 73 lakes (61%) were classified as stable lakes. The 18 drying lakes lost surface area at a median rate of −1.7% yr^{-1} (95% CI: −7% to −1% yr^{-1}). Among all 120 lakes, the median rate of change in lake size was −0.4% per year (−1.6% to +0.1%) (Table S1 in Supporting Information S1).

Years of drying and wetland plant community establishment varied substantially among the random sample of 120 lakes, although those classified as drying lakes tended to feature younger graminoid-dominant wetlands (GS median = 5 years of drying, range 3–28), compared to variable (GS median = 17, range 3–30) and stable lakes (GS median 29, range 29–30). Shrub (SH) wetlands tended to have been established later than adjacent graminoid wetlands. Although SH wetlands ranged from 0 to 30 years of drying, drying time for SH wetlands varied little based on lake status (median = 29 years since inundation for drying, stable, and variable lakes).

3.2. Soil Characteristics

In the organic horizon, a mixed-model analysis with fixed effects of lake status, vegetation type, and status*vegetation interaction showed that water content (VWC) was highest in GS wetlands but did not vary significantly among drying, flooding, and stable lakes in either wetland community (Figure 4). EC varied by lake status, and drying lakes had saltier soils (higher EC) compared to stable lakes for both GS and SH community types (Figure 4). Variable lake EC was not different from stable or drying lakes (Figure 4). Mixed-model analysis indicated that drying lake margin soils in SH communities had lower C:N ratios compared to flooding and stable lakes, but not in GS communities (Figure 4). SH soils were more acidic than GS at variable lakes, but less acidic in drying lakes, while the two plant communities had similar soil pH levels at stable lakes (Figure 4). Mixed models explained 54% of variation in VWC, 62% in EC, 43% in C:N, and 77% in pH, as indicated by mixed model conditional R^2 values. Soil characteristics for all vegetation types, lake status, and soil horizons are summarized in Table S2 of the Supporting Information S1.

The top-ranked model of surface soil organic C (SOC) included years of drying but not vegetation type (Table S3 in Supporting Information S1). SOC was negatively correlated with years of drying ($F_{1,91} = 4.84$, $p = 0.03$, $\beta = -0.13$ kg m^{-2} year^{-1}, 95% CI: −0.26 to −0.01). Predicted SOC from the top model ranged from 12.53 kg m^{-2} (95% CI: 9.18–15.89) at 0 years since drying to 7.83 kg m^{-2} (5.16–10.51) at 35 years (Figure 5a). The top model explained 35% of observed variation in soil organic C stock (conditional R^2).

Total soil N stocks were approximately 10% the size of SOC stocks among all wetland types (Figure 5b). The top model of SON only included vegetation type (Table S3 in Supporting Information S1). SON was lower for SH wetlands compared to GS on average ($F_{1,81} = 16.12$, $p < 0.001$, $\beta_{SH} = -0.33$, CI: −0.5 to −0.17; Figure 5b). The top-ranked model explained 41% of observed variation in SON.

The top-ranked model of EC included fixed effects of years of drying and soil horizon (organic vs. mineral; Table S3 in Supporting Information S1), and explained 80% of observed variation in EC. EC was positively correlated with years of drying ($F_{1,132} = 5.61$, $p = 0.02$, $\beta = 0.03$ mS cm^{-1}, 95% CI: 0–0.05), and lower in mineral soil ($F_{1,121} = 14.24$, $p < 0.001$, $\beta_{\text{mineral}} = -0.62$ mS cm^{-1}, CI: −0.94 to −0.29; Figure 6). Predicted EC in organic soils ranged from 2.50 mS cm^{-1} (95% CI: 1.56–3.45) at 0 years of drying to 3.31 mS cm^{-1} (2.37–4.24) at 32 years. In mineral soils, predicted EC ranged from 1.89 mS cm^{-1} (0.93–2.84) at 0 years of drying to 2.69 mS cm^{-1} (0.93–2.84) at 32 years of drying. GS and SH wetlands had similar average soil EC levels within site, and all wetland soils had higher EC than the surrounding upland forest (Table S2 in Supporting Information S1). Overall, GS and SH wetlands at drying lakes had higher soil conductivity than wetlands at stable lakes, regardless of how long those soils had been drying (Figure 4).

3.3. Aboveground Plant Communities

Because ANPP values spanned several orders of magnitude, we used log-transformed ANPP values in mixed-effects models. The top-ranked model included effects of years of drying and vegetation type (Table S3 in Supporting Information S1; Figure 7) and explained 13% of observed variation in log-transformed ANPP. In the top model, ANPP increased by 3% per year of drying ($F_{1,27} = 5.12$, $p = 0.03$, $\beta = 0.03$, 95% CI: 0–0.05), and was 70% lower in SH wetlands than in GS wetlands of similar age ($\beta = -0.69$, CI: −1.13 to −0.25, Figure 7). Predicted GS ANPP ranged from 115.5 g m^{-2} yr^{-1} (95% CI: 81.5–163.8) after 2 years of drying to 240.5 (132.9–435.2) at 30 years of drying and predicted SH ANPP ranged from 57.9 (38.0–88.3) after 2 years of drying to 120.6 (78.4–185.7) after 30 years of drying.

Plant functional diversity (Shannon index derived from plant function type % cover) was best predicted by vegetation type alone (Figure S2, Table S3 in Supporting Information S1). Years of drying did not have a significant effect on functional diversity in either plant community type, but SH wetlands were significantly more diverse compared to GS ($F_{1,92} = 18.65$, $p < 0.001$, $\beta = 0.20$, 95% CI: 0.11–0.29).

Given the lack of evidence for effects of drying time on plant diversity, we only examined variation in plant community composition as a function of categorical lake status. In a principal components analysis (PCA), the

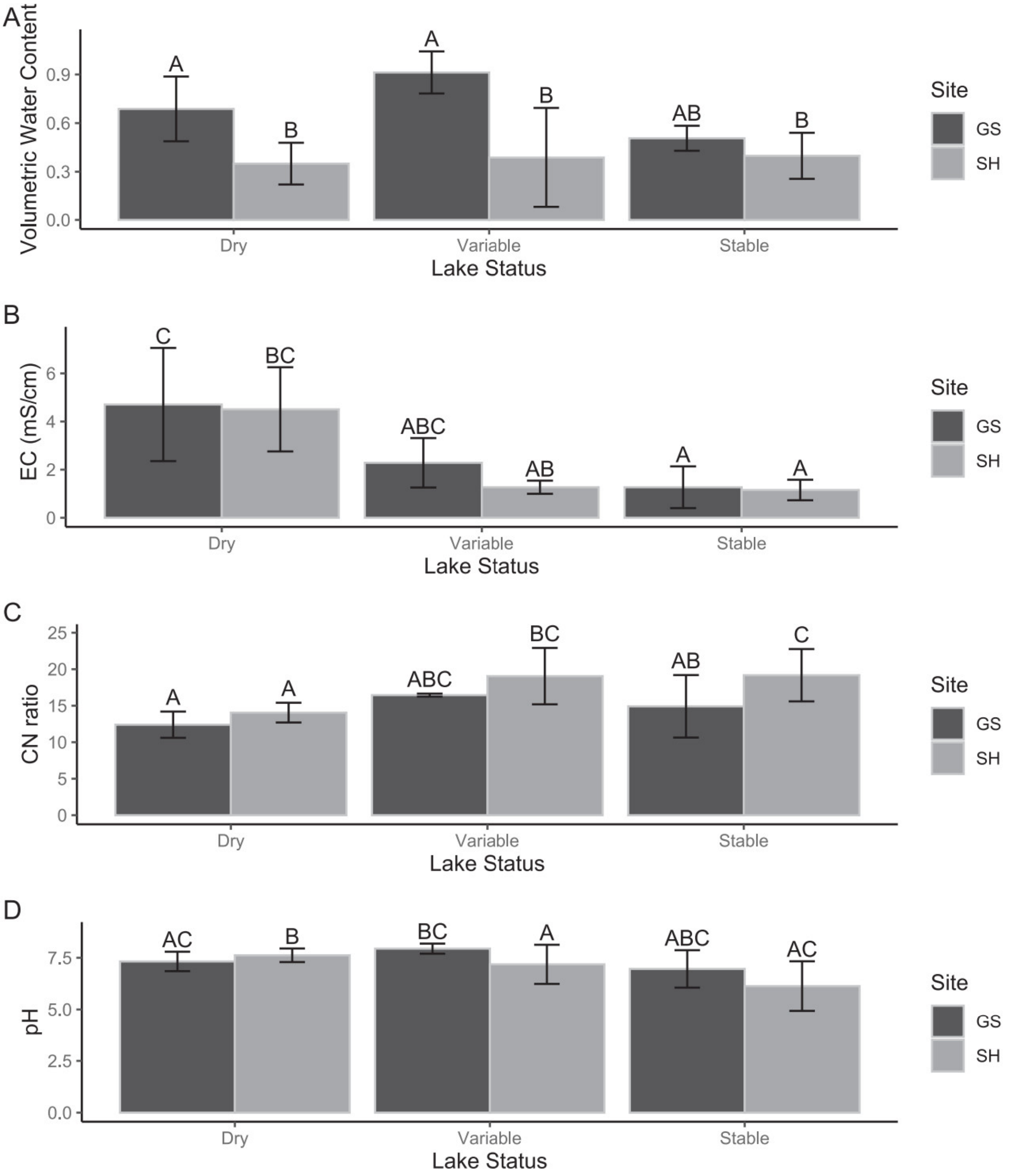

Figure 4. Effects of wetland vegetation type and lake status on soil characteristics in the organic horizon. (a) Volumetric water content (VWC). (b) Electrical conductivity (EC). (c) Soil C:N ratio, and (d) pH. Mixed models included full interaction between vegetation type and lake Status as fixed effects, and a random effect of replication at each lake. Bars represent means, error bars are 1 standard deviation (SD) and different letters indicate significant differences among pairs based on post-hoc Tukey tests.

first principal component ($PC1_{plant}$) explained 29.5% of observed variance, and the second principal component ($PC2_{plant}$) explained 15.7%. PERMANOVA analysis of plant functional type percent cover scores resulted in a significant interaction between vegetation type and lake status ($F_{2,686} = 3.44$, $p = 0.002$). The top mixed-effects model of $PC1_{plant}$ included full interaction between vegetation type and lake status ($F_{2,582} = 4.1$, $p = 0.02$), but

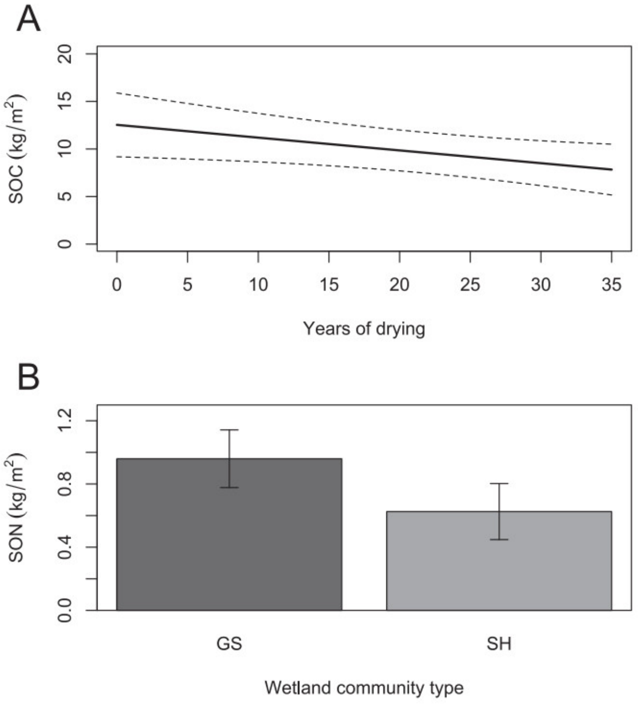

Figure 5. Predicted soil organic carbon stocks (SOC) (a) relative to wetland drying (years since soils were exposed to aerobic conditions by lakeshore retreat), and soil organic nitrogen stocks (SON) as a function of wetland vegetation type (b) for 13 lakes in the Yukon Flats National Wildlife Refuge. In panel (a), thick lines are predictions from mixed effects linear models, and dotted lines are 95% confidence intervals. In panel (b), Son predictions are shown for Grass/Sedge (GS) and Shrub-dominated (SH) wetlands.

only had a conditional R^2 of 7% (Table S3 in Supporting Information S1). In post-hoc Tukey tests, GS and SH wetlands were significantly distinct based at stable lakes based on $PC1_{plant}$ ($p < 0.001$), but not at drying or variable lakes (Figure S3 in Supporting Information S1). The top model for $PC2_{plant}$ included vegetation type, but $PC2_{plant}$ and vegetation type were not significantly correlated (Table S3 in Supporting Information S1).

3.4. Soil Microbial Activities

AICc model selection using mixed effects models revealed that the mineralization rate constant (k) and the available substrate pool (Ao) varied among vegetation types and horizon types (Table S3 in Supporting Information S1). The top model of k included soil horizon*vegetation type interaction ($F_{3,111} = 5.44$, $p = 0.002$). Ao was 14 mg C/g soil C higher in organic horizons on average (95% CI = 0–28, $F_{1,113} = 4.03$, $p = 0.047$), and higher in the forest soil than the graminoid soil and sedge soils (Figure 8; $F_{3,111} = 3.22$, $p = 0.03$).

We tested whether limnic sediments were inherently more decomposable compared to soils presumably derived from terrestrial organic matter. We compared cumulative rates of CO_2 flux from lab incubations on soil horizons categorized as limnic based upon visual inspection (coprogenous earth, presence of shells and fecal pellets, little to no plant detritus) and compared them to organic and mineral soil incubation data. Limnic horizons were only identified within sedge and graminoid communities of three lake systems. Results showed that limnic soils did not have higher rates of CO_2 flux compared to organic or mineral soils under laboratory conditions (Figure S4 in Supporting Information S1).

We observed lower potential rates of enzyme specific activity in drying lake margin soils compared to stable lake margin soils for most enzymes studied in both soil horizons (Figure 9, Table S4 in Supporting Information S1). In organic horizon soils, there was a significant effect of lake status, vegetation, or their interaction on enzyme specific activity (activity normalized to soil % C). Specific enzyme activities were all higher in stable soils compared to drying lake margin soils, and they were generally highest in the forest community and declined in communities nearer to the lake edge (Figure 9, Table S4 in Supporting Information S1). In mineral horizon soils we did not observe significant vegetation or lake status effects (or their interaction) for any enzyme except phenol oxidase and peroxidase (Table S4 in Supporting Information S1). But we did observe a significant lake status effect for phenol oxidase in which activity was higher in stable lakes, and a significant lake status by vegetation interaction for peroxidase in which activity in drying forest and shrub soils was lower than stable forest and shrub soils (Table S4 in Supporting Information S1, Figure 9).

3.5. Soil Microbial Community Composition

$PC1_{mic}$ explained 38% and $PC2_{mic}$ explained 22% of the variance in composition. We then used PC1 and PC2 to examine changes in microbial composition among vegetation types, soil horizons, and lake status. The top-ranked candidate mixed models for $PC1_{mic}$ and $PC2_{mic}$ each included full interaction between soil horizon, vegetation type, and lake status (Table S3 in Supporting Information S1). To facilitate interpretation of the results, we fit an additional mixed effects model for $PC1_{mic}$ and $PC2_{mic}$ in each soil horizon, with full interaction between vegetation type and lake status. For the organic horizon there were significant main effects of vegetation type and lake status effects on $PC1_{mic}$ ($F_{3,163} = 41.18$, $p < 0.0001$ and $F_{1,15.62} = 6.38$, $p = 0.02$, respectively, Figure 10). $PC1_{mic}$ scores differed among plant communities, except between the sedge and graminoid communities. For the $PC2_{mic}$ axis on organic soils, there was a significant lake status by vegetation interaction ($F_{3,105} = 2.79$, $p = 0.04$) which showed that lake status only affected $PC2_{mic}$ scores in the sedge community. In the mineral horizon there was a significant lake status by vegetation interaction for $PC1_{mic}$ ($F_{3,105} = 5.15$, $p = 0.002$) and $PC2_{mic}$ ($F_{3,74} = 3.6$, $p = 0.0165$). Mineral horizon $PC1_{mic}$ varied significantly

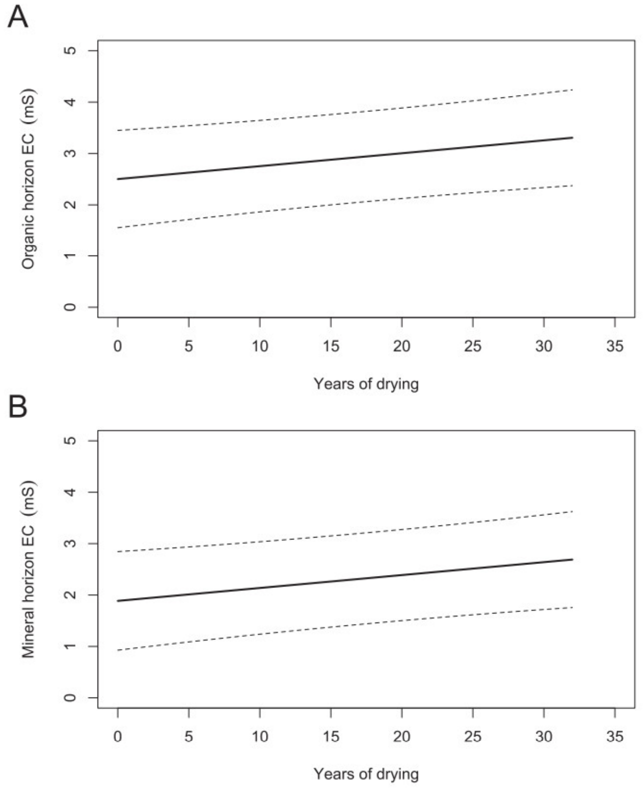

Figure 6. Electrical conductivity as a function of wetland drying, in organic (panel a) and mineral soils (panel b) in lake-margin wetlands from the Yukon Flats National Wildlife Refuge, Alaska. Thick horizontal lines are predictions from mixed effects linear models, and dotted lines represent 95% confidence intervals.

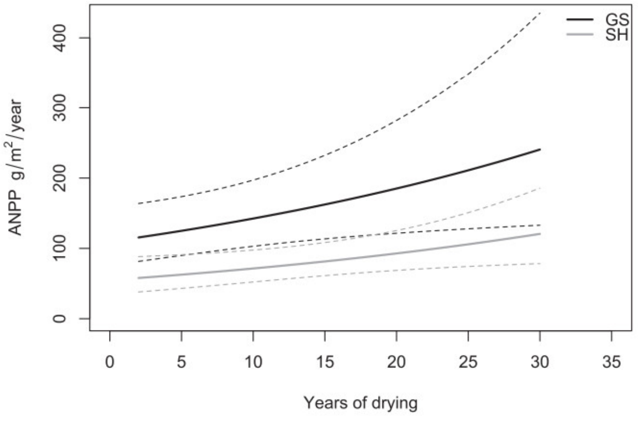

Figure 7. Aboveground net primary production (ANPP, g m^{-2} yr^{-1}) at lake-margin wetlands in the Yukon Flats National Wildlife Refuge, Alaska. GS is ANPP for Grass/Sedge wetlands, SH is ANPP for shrub wetlands. Thick horizontal lines are predictions from mixed effects linear models, and dotted lines represent 95% confidence intervals.

between drying and non-drying lakes in forest and sedge communities. For $PC2_{mic}$ in the mineral horizon, Tukey post hoc tests indicated that microbial communities only differed between drying and non-drying lakes in graminoid wetlands. At drying lakes, though, mineral soil $PC2_{mic}$ scores differed significantly between sedge, graminoid, and shrub plant communities. Overall, microbial communities differed among forest, shrub, and sedge/graminoid communities, but the effect of lake drying was least apparent in shrub wetland communities, which did not differ significantly among stable and drying lakes along either PCA axis in organic or mineral soils (Figure 10). In the mineral horizon, differences in community composition were observed between the extremes, such as the forest versus graminoid and sedge communities. The $PC1_{mic}$ axis was strongly indicative of changes in fungal abundance as the fungal biomarkers 18:2ω6 and 18:3 (which were combined in the analysis) the highest value eigenvector for that axis (−0.88, Table S5 in Supporting Information S1). Along axis $PC1_{mic}$, microbial communities in the forest community differed from the shrub communities which both differed from the grass and sedge communities. The largest eigenvector for the second principal component (PC2) was 18:1 (eigenvector = 0.80), a biomarker that could be indicative of methane oxidizers (Zelles, 1999).

Total microbial biomass (measured as nmol PLFA per gram soil) showed a three-way lake status by vegetation by horizon interaction ($F_{3,275} = 4.27$, $p = 0.006$). Organic horizon soils had higher microbial biomass than mineral soils and there were few differences in PLFA abundance among vegetation types (Table S6 in Supporting Information S1). For example, we only observed that forest soil mineral horizons of drying lakes had higher microbial biomass than shrub or sedge mineral soils in stable lake margins (Table S6 in Supporting Information S1).

4. Discussion

4.1. Are the Yukon Flats Drying?

Drying arctic and boreal lakes have been documented around the world in recent years due to the widespread availability of satellite data products such as Landsat and MODIS (Finger Higgens et al., 2019; Nicol et al., 2013; Pastick et al., 2017; Riordan et al., 2006). Remote sensing and aerial photography have also been used to document changes in plant community structure associated with lake drying, primarily a successional shift from herbaceous wetlands to woody shrub communities (Klein et al., 2005). However, the effects of lake drying on soil characteristics and processes have remained poorly understood, as past research focused mainly on changes within drying lakes themselves, such as increased nutrient loads and salinity caused by evaporation (Johnston et al., 2020; Lewis et al., 2015). In contrast to previous studies of boreal plant communities near drying lakes, lake-margin communities in the YF did not follow a consistent successional trajectory over time. Although both graminoid and shrub communities were able to establish on recently exposed soils within a few years, the graminoid communities were generally associated with wetter soils, suggesting that woody vegetation was constrained by soil moisture regardless of lake dynamics. The fate of C and nutrients stored in the sediments of drying arctic and boreal lakes has received less attention, although high limnic organic C stocks could lead to rapid microbial decomposition if exposed to aerobic conditions (Jorgenson et al., 2013). We used a combination of remote sensing data, field sampling, and laboratory experiments to assess regional lake

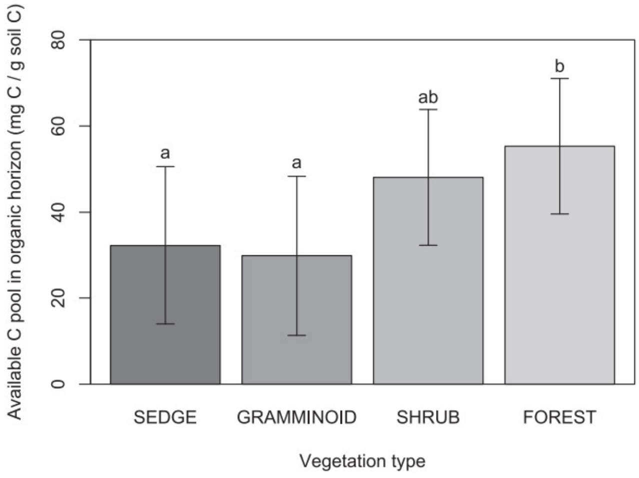

Figure 8. Available substrate pool (Ao) among different lake margin plant communities. Different letters indicate significant differences following Tukey post hoc tests ($p < 0.05$). Vegetation type refers to the type of plant community, based on the dominant growth form. Bars are predictions from a mixed-effects linear model analysis, and error bars are 95% confidence intervals.

drying trends, quantify the effects of lake drying on above- and below-ground ecosystem processes in lake-margin wetlands, and to investigate the mechanisms behind those effects. We found evidence of substantial soil organic C loss in these YF lake margins, even though lake drying also increased the salinity of lake margin soils, which tended to limit potential soil microbial activities.

Based on our analysis the majority of lakes in the YF (~80%) had not shrunk significantly from the beginning of the satellite record to 2010. This trend is consistent with previous analyses of the region (Roach et al., 2013; Rover et al., 2012). Despite the small fraction of drying lakes on the landscape, observed drying rates in the central Yukon Flats could eventually lead to an 80% reduction in lake surface area over 50 years if sustained (Roach et al., 2013). Many non-drying lakes in the YF, however, showed substantial inter-annual variation in size. Lakes in discontinuous permafrost can drain suddenly due to the effects of permafrost thaw, and drained basins can rapidly refill from spring floods caused by ice jams (Rey et al., 2019). Stochastic influences such as these make it difficult to extrapolate drying trends beyond the timespan of our study. Nevertheless, wetlands near drying and non-drying lakes were clearly ecologically and biogeochemically distinct. Space for time analyses indicated that the effects of lake drying on wetland soils developed over multiple years, and the duration of the drying period was a key predictor of soil chemistry and organic matter content.

4.2. The Fate of Carbon Along Drying Lake Margins

Widespread lake drying that has occurred over several decades in the YF resulted in losses of soil C from surrounding lake margin soils. Loss of soil C following drying was hypothesized to occur based upon a regional analysis of soil C stocks and available moisture in various landscapes of Alaska (Jorgenson et al., 2013). Organic horizon C losses observed in this study were similar in magnitude to losses of soil C that Jorgenson et al. (2013) found. Although soil C and N storage in this study were similar to values observed in other ecosystem types (Jorgenson et al., 2013; Wilmking et al., 2006), we have likely underestimated both storage and losses because we limited our analysis to C and N storage in the surface 30 cm organic layer only, while organic soils were often deeper than this 30 cm further into the center of the drying lakebed.

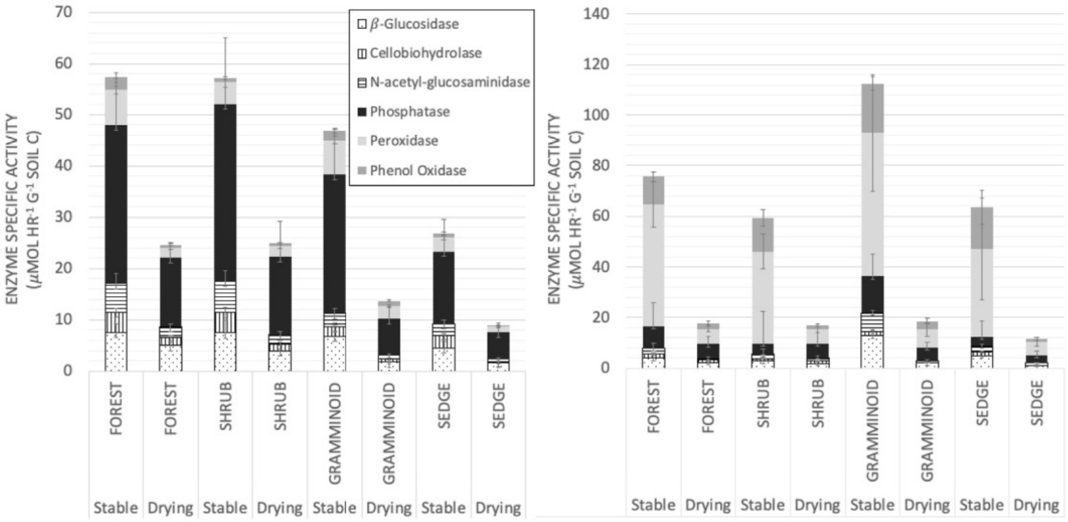

Figure 9. Soil enzyme activities in stable and drying lake margins O horizon soils (a) and mineral horizon soils (b) from different plant communities. Stacked bars represent cumulative enzyme activity (mean ± SE).

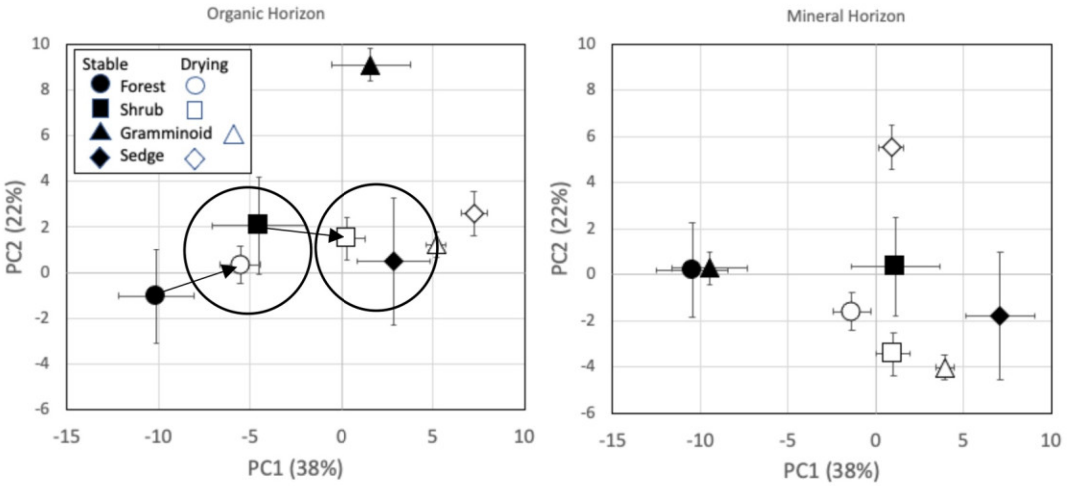

Figure 10. Changes in microbial community composition with lake drying among different plant communities. The legacy effect is shown by circles, in which with microbial communities within drying lake soils with forest vegetation are similar to communities from stable shrub microbial communities because forests from drying lakes have moved into what was previously shrub vegetation. Similarly, microbial communities beneath shrubs zones near drying lakes are more like sedge communities from stable lakes because shrubs have moved into zones previously occupied by sedges. Symbols represent means and 1 s.e. for vegetation types and lake status ($n = 6–36$ depending on vegetation and soil horizon). Eigenvectors are given in Table S5 of the Supporting Information S1.

Lake margin soil C storage declined at sites where lakes continued to dry for a longer period of time, but differences in microbial activity between stable and drying lake margin soils were not as we expected. We expected microbial activity to be higher in lake sediments that were newly exposed to the atmosphere (Weise et al., 2016), because newly exposed sediments may contain the most labile organic matter. Instead, we found lower potential rates of microbial activity in drained lake margin soils compared to stable lake margin soils, and lower rates in lake edge soils compared to soils further away. Furthermore, lab incubations revealed that easily identifiable limnic horizons were not more decomposable than terrestrial organic matter when compared side by side in a laboratory incubation. Some studies have suggested that newly exposed limnic sediments are highly labile (Jorgenson et al., 2013; Schuur et al., 2015; Weise et al., 2016). But our comparison of fluxes from limnic versus terrestrial soil organic matter shows that limnic sediments are not more decomposable in these lake systems. However, limnic sediments are not all the same and thus may have very different decomposition rates. Some limnic sediments may derive from algae and floating vegetation and others derive from fluvial deposits, for example, which can vary considerably in their decomposability. Additionally, our "terrestrial" soil organic matter could have contained some unidentifiable limnic material due to periodic inundation over time, thus biasing our results. We also did not measure methane flux from lake margin soils which could be an additional C loss mechanism of interest in this setting.

Declines in microbial activity in drying lake margin soils were supported by lower potential soil enzyme activities. C and P degrading enzyme activities were often lower in drying lake margin soils compared to stable lake margin soils. C degrading enzyme activities are often the limiting step in decomposition of organic matter and, thus, support the observation that potential rates of decomposition were lower in drying lake margin soils compared to stable lake margin soils. Low phosphatase potential enzyme activity could be indicative of higher P availability, caused by concentrating elements in drying lake margin soils (Lewis et al., 2016). Salinity has a large impact on soil enzyme activities (Adviento-Borbe et al., 2006; Garcia & Hernandez, 1996) and therefore is probably one of the more dominant factors reducing soil enzyme activities in drying lake margin soils in this study.

Higher salinity in drying lake margin soils was not only measured as increased EC, but it was also visually apparent around some lakes as surficial deposits (Clautice & Mowatt, 1981) known as trona. Moreover, shrinking lakes in the YF have elevated Na, Mg, Ca, and Cl, indicating that the increased EC is indicative of salt concentrations that inhibit microbial activity (Adviento-Borbe et al., 2006; Halm & Griffith, 2014; Lewis et al., 2015; Mazumdar et al., 2009; Rietz & Haynes, 2003). As lakes in the YF shrink and dry, salts are often concentrated in the water and surrounding soils (Lewis et al., 2015; Roach et al., 2011), increasing the EC value above 4 mS cm^{-1} which classifies them as saline. Despite the high salinity of drying lake margin soils, however, soil C was still lost from newly exposed sediments through a combination of erosion/export and decomposition/respiration. Field CO_2 fluxes measured at lakes in the YF, including 12 Mile Lake (Wickland et al., 2009) and Canvasback Lake (Figure S5 in Supporting Information S1) show higher rates of ecosystem respiration in the wetter, deeper organic soils at the lake margin compared to drier soils in the shrub and forest communities, which suggests that aerobic respiration was an important driver of soil C losses at the margins of drying lakes. At the same time, it is possible that those losses would have even greater if drying had not led to a gradual increase in soil salinity and microbial inhibition. The effect of salinity on plant and microbial activity in the context of lake drying is an important aspect of the YF due to its water chemistry, shallow lakes, low relief, and aridity (Clautice & Mowatt, 1981; Heglund & Jones, 2003).

4.3. The Relationship Between Above and Below Ground Communities

Microbial communities were strongly associated with aboveground plant communities, as has been seen in much previous research (Cline & Zak, 2015; Van Der Heijden et al., 2008; Waldrop & Firestone, 2006). Microbial PLFAs, strongly controlled by changes in the relative abundance of fungi, differed among all plant communities, with fungal biomarkers being most abundant in the forest and declining toward the lake margin. This pattern was also supported by measures of oxidative enzyme activities: oxidative enzyme activities typically show higher potential activities in forests, in part due to the higher relative abundance of fungi, and also the higher concentration lignocellulose in plant litter (Sinsabaugh, 2010).

Microbial communities also differed between drying and stable lake margin soils, which offered a unique opportunity to test ecological legacies of microbial communities (Hawkes & Keitt, 2015; Martiny et al., 2017). Microbial community composition changed in response to changing plant communities following lake drying. They did not remain compositionally similar to the soil community where they originated. Rather, they reflected an intermediate state—reflective of both the old community and new community. Following lake drying, plant communities shifted toward the drying lake center; spruce where willows had been, willows where graminoids had been, and graminoids on newly exposed sediments (Figure 1). Although GS and SH communities could still be distinguished based on the dominance of graminoid or deciduous shrub growth forms at drying lakes, these rapid successional shifts led to substantial overlap in community composition (Figure S3 in Supporting Information S1). Microbial communities shifted to reflect changing aboveground plant community composition, but they retained a signature, a phospholipid fatty acid pattern, reflective of the soil community from the pre-drying plant community (Figure 10). Thus, microbial communities showed legacies of previous communities following plant community change, which has the potential to impact soil processes (Reed & Martiny, 2012). The shifts in community composition between drying and stable lakes observed along the $PC1_{mic}$ axis indicates that the fungal community declined in response to lake drying. Also, shifts along the $PC2_{mic}$ axis indicates that methane oxidizer communities may have been reduced by lake drying, especially in the lakeshore graminoid community. Reduced fungal and methane oxidizer abundance could be caused by increased salinity in drying lake margin soils (Osudar et al., 2017), which could allow for increased methane emissions and lower rates of fungal decomposition. Furthermore, changing fungal and bacterial communities may help to facilitate plant establishment in new areas (Rodrigues et al., 2015) through mechanisms such as nutrient mineralization, plant symbiosis, or pathogenicity (Schütte et al., 2019).

4.4. Importance to the Regional Carbon Budget

Lake margin soils appear to have been strongly impacted by the legacy of historical lake dynamics. While SOC decreased steadily with wetland age, plant productivity increased, and plant functional diversity remained unchanged. ANPP was 2–3 times higher in GS versus SH wetlands, yet the two plant communities overlapped substantially in terms of soil C storage. Thus, above-ground plant community indicators may not always be useful predictors of soil C change in dynamic landscapes like the YF.

Although lakes cover only 5.5% of the YF, and less than 5% of Alaska overall (Arp & Jones, 2009), C storage within lake basins can be large. Boreal lake sediments store several times more C than forest soils, and estimates of boreal lake sediment C storage range from 20 to 120 Pg globally (Kortelainen et al., 2004; Molot & Dillon, 1996). This amount of C may be 10%–15% of total C storage in the boreal biome (Benoy et al., 2007). Annual soil C loss rates at drying lakes in our study were also comparable to increases in the rate of ANPP in those same wetlands, suggesting that although lake drying results in losses of lakeshore soil C, this loss is compensated for by increases in plant productivity at decadal scales.

We observed substantial C loss from wetland surface soils, but the fate of this C and deeper soil horizons is unclear, complicating our ability to assess the regional implications of lake drying. In the discontinuous soils that dominate the YF, thawed taliks that reach into deeper soil layers could be stabilized by permafrost aggradation as lakes recede and graminoids and then shrubs begin to colonize newly exposed soil (Briggs et al., 2014). Although this can protect deeper soil C temporarily, over decades permafrost will likely thaw at depth and this protection mechanism will no longer operate (Briggs et al., 2014). Second, erosion of surface C to the center of the lake basin or transport into nearby lakes or rivers by spring floods, where it could be buried, respired, or exported complicates estimates of regional C balance. If C lost from drying lake margin soils was washed into adjacent lakes and sequestered in lake sediments instead of being respired, then we are overestimating the influence of drying lake margin soils on atmospheric C flux. However, recent evidence also suggests that the closed basin shallow boreal lakes of the YF receive negligible allochthonous C inputs (Bogard et al., 2019). Additionally, several studies suggest that a majority of allochthonous organic C inputs to inland waters in permafrost peatlands is thought to be respired to the atmosphere as CO_2 rather than accumulating in lake sediments (Hugelius et al., 2020; Stackpoole et al., 2017). In light of previous research, it is likely that much of the organic C loss in this study represented an atmospheric flux.

In addition to their relevance to regional C budgets, organic C losses associated with lake drying have implications for local land management (Patton et al., 2015). The National Wildlife Refuge System provides billions of dollars of value in ecosystem services, and refuge wetlands provide more value per acer than any other land cover type (Ingraham & Foster, 2008). Wetlands are valuable because they provide waterfowl habitat, which is the primary management objective for many Refuges including the YF (Meretsky et al., 2006). As lakes dry, local waterfowl diversity declines, potentially making it harder to meet management objectives and reducing the economic value of refuge lands (Roach & Griffith, 2015). Wetland soils are also valued for their capacity to help regulate atmospheric CO_2 by sequestering C (Ingraham & Foster, 2008). Case studies have produced estimates of C storage value ranging anywhere from \$2800 to \$11400 per wetland ha, depending on the estimated value of the social cost of carbon (Patton et al., 2015), yet protection of organic C stocks is often a secondary management objective if considered at all. Because they are likely driven by processes associated with global climate change, lake drying trends are unlikely to be mitigated through local management actions alone. However, efforts to restore or conserve extant lake and wetland ecosystems could nevertheless provide benefits with both economic and ecological value, including maintenance of stored C on the landscape as well as improved wildlife habitat. Consideration of the value associated with C storage could help inform local decisions about resource extraction and other activities that might disturb extant lakes and wetlands, while contributing to a better accounting of costs associated with climate change.

5. Conclusion

In the YF, lake drying was associated with significant declines in soil C storage in lake margin soils, but were similar in magnitude (but opposite in direction) to increases in plant productivity observed with lake drying. The tradeoff between losses of soil C and increases in plant productivity with lake drying indicates that C is moved from belowground to aboveground pools. Although our results indicate that there is no net change in ecosystem carbon with lake drying, shifting C from soils to plants increases the possibility of C losses from wildfire, drought, and export as allocthonous material during flood events. Closed basin northern lakes in arid regions do not process or store much allocthonous C, and organic C accumulates slowly in boreal lake sediments (Bogard et al., 2019; Stackpoole et al., 2017). However, after thousands of years of accumulation, those sediments collectively contain a substantial fraction of all boreal organic C (Kortelainen et al., 2004), which is vulnerable to microbial respiration when lake sediments are exposed and colonized by terrestrial vegetation. Lake drying in this region is also associated with increasing soil salinity, reduced soil moisture, and reduced rates of microbial activity, which could impact patterns of plant colonization and productivity into the future. Ecohydrological processes associated with lake drying are not well represented in current models of peatland C loss due to warming (Hugelius et al., 2020), and although drying lakes and adjacent wetlands represent a small fraction of all boreal peatlands, lake drying trends are sufficiently widespread to represent a potentially important source of uncertainty in regional C budgets.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data for this research are available in Waldrop and Patil (2023).

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