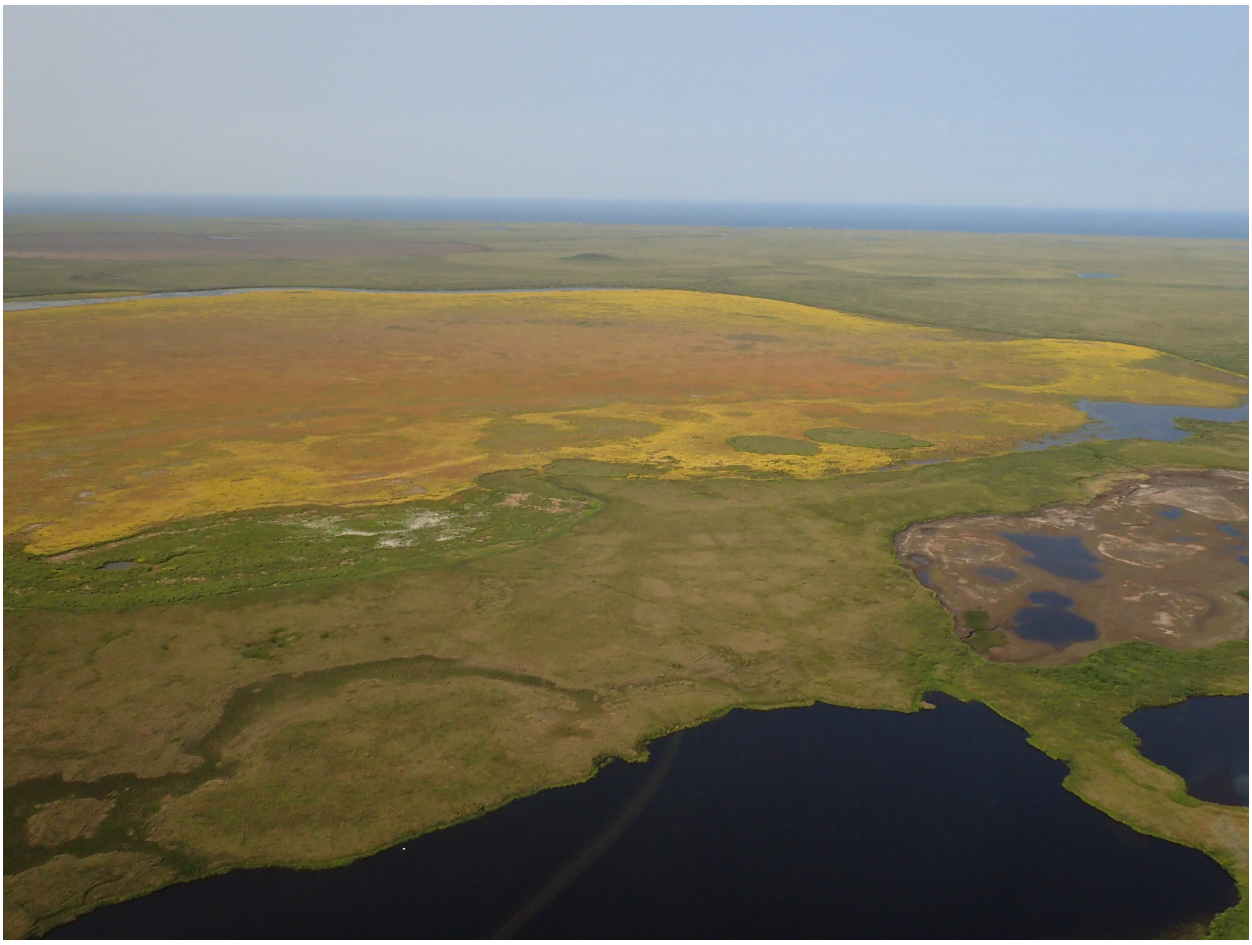
National Park Service
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Natural Resource Stewardship and Science

Drained Lakes in Bering Land Bridge National Preserve

Vegetation Succession and Impacts on Loon Habitat

Natural Resource Report NPS/ARCN/NRR—2023/2492





ON THIS PAGE
Dense stand of cottonsedge (*Eriophorum scheuchzeri*) on 12 July 2021 on Central Lake. This was 3 years after the lake drained (NPS /SWANSON)

ON THE COVER
Aerial view of drained lakes on 10 July 2019. The large “Central” drained lake is visible in the midground. It drained in 2018 and is brightly colored due to blooming mastodon flower (*Tephroseris palustris*, yellow colors, densest near the former shore) and spike rush (*Eleocharis acicularis*, reddish brown, in the center). The blue Chukchi Sea is visible near the skyline, and the brown oval in the upper left is the “North” lake that drained just weeks before the photo date. On the right is a small lake that also drained in the spring of 2019.
(NPS /SWANSON)

Drained Lakes in Bering Land Bridge National Preserve

Vegetation Succession and Impacts on Loon Habitat

Natural Resource Report NPS/ARCN/NRR—2023/2492

David K. Swanson[1] , Celia J. Hampton-Miller[1]

[1]National Park Service
Arctic Inventory and Monitoring Network
4174 Geist Rd
Fairbanks, Alaska 99709

January 2023

U.S. Department of the Interior
National Park Service
Natural Resource Stewardship and Science
Fort Collins, Colorado

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Executive Summary

The northern coastal plain of Bering Land Bridge National Preserve (BELA) lost lakes at an alarming rate over the first two decades of this century, including four lakes over 100 ha in size in 2018-2019 alone. To understand the effects of these lake drainages, we sampled vegetation of these lakes in 2019 (a reconnaissance visit) and 2021 (for the installation of permanent vegetation monitoring plots). We used these data to summarize the changes that occurred in the first three years after drainage, and to create vegetation maps from 3-m resolution satellite images coinciding with the visit dates. We used time series of these satellite images to study the rate of drainage and vegetation colonization on the lakes. We analyzed our existing data from older drained lake basins (estimated to be more than 200 years since drainage) and reviewed the literature on vegetation change in drained lakes to understand the vegetation changes that are likely in the future. Finally, we used a model of lake occupancy by loons developed by Mizel et al. (2021) to predict the effect of the 2018-2019 lake drainages on available loon habitat, using both our detailed maps of the four sampled drained lakes, and also data on all drained lakes over most of northern BELA derived from Landsat satellite images.

Our results show that the four study lakes drained early in the summer, before the end of June, in 2018 (3 lakes) and 2019 (one lake). All four drained by deepening of pre-existing drainage outlet channels. A combination of record warm weather and heavy snowfall made 2018 and 2019 especially favorable for lake drainage: thaw subsidence probably enlarged drainage outlet channels from the lakes, and large amounts of spring snowmelt runoff deepened the outlet channels by thermal erosion (the combination of thaw and erosion).

Drainage exposed moist loamy sediment on the lake bottoms that was rapidly colonized by plants. Substantial vegetation cover developed by late summer in the same year as lake drainage in one lake, in the first post-drainage summer in a second lake, and during the 2nd year after drainage in the remaining two lakes. The first vegetation communities to develop consisted of just one or two dominant species, notably *Eleocharis acicularis* (spike rush), *Equisetum arvense* (horsetail), and/or *Tephroseris palustris* (mastodon flower). Other important early species were *Arctophila fulva* (pendant grass) and *Rorippa palustris* (yellow cress). Some of these plants probably established from seeds dispersed previously from lakeshore communities and stored in lake-bottom muds (*E. acicularis, T. palustris, R. palustris*) or existing clones and seeds (*A. fulva*). *E. arvense* probably grew from spores dispersed from plants surrounding the lake in early summer, immediately after the lakes drained. By year 3, the communities had become more diverse, with significant cover by taller wetland graminoid species, including *A. fulva*, *Eriophorum scheuchzeri*, and *Carex aquatilis*. Frozen soil was observed in most locations on the lakes in July of 2021, suggesting that permafrost was forming on the lake bottoms. Comparison of the three-year trends in vegetation change with data from older lake basins suggest that ultimately most lake basins will develop wet tundra communities dominated by *Carex aquatilis* and mosses, with various low shrub species on acid, peat-dominated soils and permafrost; however, this process should take several centuries. In the interim, some of the early colonists are likely to persist, and a transitional phase with willow shrubs could develop in some drier locations within a few decades. The vegetation and soils of drained lake basins will

probably develop differently if continued climate warming causes the incipient permafrost to be lost from the lake basins.

The loon habitat model suggests that drainage essentially eliminated the potential habitat for Yellow-billed Loons on the four study lakes, because the residuals ponds were too small for Yellow-billed Loons to take flight from. A total of 17 lakes drained in northern BELA in 2018-2019. As a result, the potential Yellow-billed Loon nesting habitat in northern BELA probably decreased by approximately 2%, while habitat for Pacific Loons decreased less, by about 0.6%. Habitat for the more abundant Red-throated Loons probably increased slightly as a result of lake drainage, because of their ability to use the small residual ponds created by lake drainage.

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This study was supported by the NPS Natural Resource Stewardship and Science's "Focused Condition Assessment" program and the NPS Arctic Inventory and Monitoring Network. Special thanks also to the staff at Bering Land Bridge National Preserve for their support with logistics and procuring funding, especially Letty Hughes, Ken Adkisson, and Mike Thompson.

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Introduction

The northern part of Bering Land Bridge National Preserve (BELA, Figure 1) lost lakes at an alarming rate over the past two decades (Swanson 2019, 2020; Nitze et al. 2020). Numerous lakes drained through outlet channels over the course of days to weeks in a single summer. Most of the lakes in this region are of thermokarst origin (Jorgenson 2001), meaning that they owe their existence to subsidence caused by thaw of permafrost. The banks of these lakes contain ice-rich permafrost; new outlets can form or existing outlets can deepen rapidly by a combination of thaw and erosion, providing a pathway for water to drain out. Historically, the formation and expansion of thermokarst lakes by permafrost thaw in this region was probably in approximate dynamic equilibrium with lake loss by rapid drainage (Jones et al. 2011). However, in the past two decades the rate of lake loss has outpaced lake formation; loss was especially rapid in 2018 and 2019, probably as a result of unprecedented warm temperatures that have prevailed in the area since 2014 (Swanson et al. 2021). In 2005 there were 8 lakes larger than 100 ha in the low coastal plain in northeastern BELA (an area of about 400 square kilometers). Today only three of these large lakes remain, and four of the five lost lakes drained in 2018 and 2019. The area of lakes and ponds in this region dropped from over 8% of the landscape in 2000-2005 to less than 7% in 2019 (Swanson 2020).

The lakebeds exposed by drainage are flat expanses of moist mud that are subsequently colonized by new vegetation. In 2019, we made reconnaissance visits to three lakebeds that drained in 2018. In spite of the similarity in lake size, shape, setting, and time since drainage, the vegetation on the three lakes differed greatly: one was dominated by the tiny spike rush *Eleocharis acicularis* and mastodon flower (*Tephroseris palustris;* Figure 2), another by horsetail (*Equisetum arvense*), and another was sparsely vegetated. These species were uncommon in the surrounding landscape of sedge- and moss-dominated wetlands. The initial composition of the colonizing vegetation appeared to depend strongly on local factors such as the initial abundance of propagules (seeds and spores). The successional trajectory of these communities is uncertain due to lack of previous studies and rapid climatic warming in this region. Older drained lake basins in the region are underlain by permafrost (Jones et al. 2012), which strongly influences the vegetation. Given the record warm temperatures in recent years (Swanson et al. 2021), it is not certain that permafrost will re-form in these recently drained lakebeds or that the vegetation will evolve to resemble what is found in older drained lake basins. Recently drained lake basins were not included in the initial sampling round (2011-2014) of vegetation monitoring in the Arctic Inventory and Monitoring Network (ARCN, Figure 1), because at that time they were relatively rare, and they are not accessible by fixed wing aircraft. In response to our lack of data from drained lakes and their increasing importance, we established new monitoring plots in 2021 in several drained lakes, including the lakes from our 2019 reconnaissance visit (Figure 1).

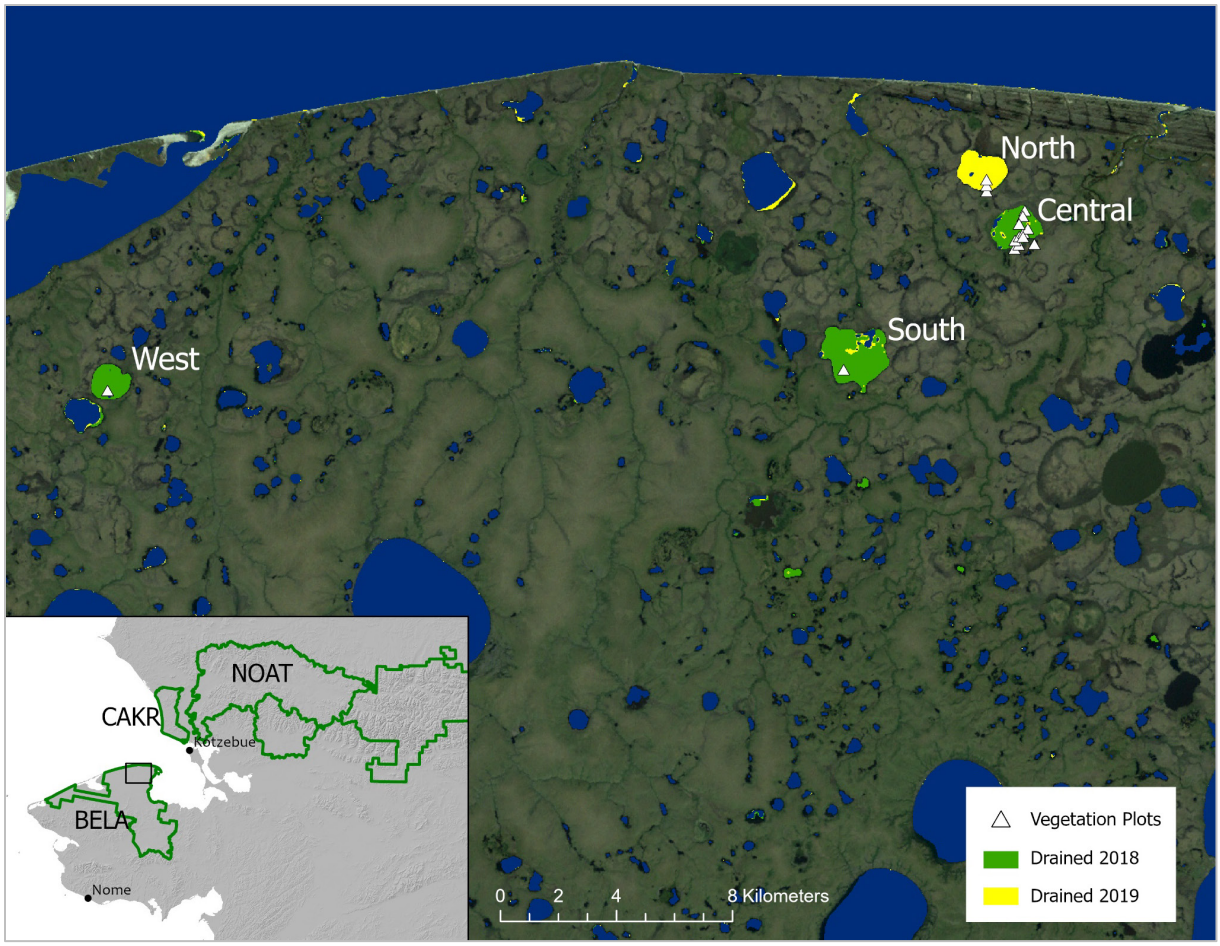


Figure 1. Overview map of the study area, showing lakes that drained in 2018 and 2019, as well as the location of vegetation plots installed in 2021. “North”, “Central”, “South”, and “West” are informal names used in this report of these unnamed lakes. The regions outlined in green on the inset map are National Park Service units of the Arctic Inventory and Monitoring Network (ARCN); BELA (Bering Land Bridge National Preserve), CAKR (Cape Krusenstern National Monument) and NOAT (Noatak National Preserve). Lake extents are from Swanson (2020). The background image is a c. 2002 Landsat mosaic (Macander 2010).



Figure 2. An example of unique vegetation that developed one year after drainage of the "Central" drained lake. Here flowering *Tephroseris plaustris* plants are growing over a dense mat of the spike rush *Eleocharis acicularis*. The hill in the background is a pingo (ice-cored hill). Photo date 7/10/2019, GPS latitude 66.552105, longitude -164.079217.

In addition to our new plot data, several other local data sets were available to help understand successional trends in drained lake basins. As of 2020, ARCN had 471 vegetation monitoring plots, installed in 2011-2014, of which 87 were in BELA and 30 were in drained lake basins in tundra settings (16 in BELA and 14 in the Noatak National Preserve). We also examined data from 763 vegetation sampling plots in ARCN that were collected by Jorgenson et al. (2009) as a part of their ecotype mapping project; 49 of these plots were in drained lake basins in tundra portions of ARCN. Most of the lake basins with existing plots drained prior to 1950 (before the earliest historical or remote-sensing records), with 5 plots from a basin that drained between 1980 and 1985. These plots provide insight into the historical late-successional vegetation of our drained lake basins. ARCN also has vegetation data from the shores of 114 lakes or ponds in BELA, collected in 2008 and 2012 as a part of the Shallow Lakes Vital Sign (Larsen et al. 2011). These data provide valuable information about the shoreline plants that are available to colonize newly drained lakebeds.

The lakes in northern BELA are nesting habitat for multiple loon species, including the Yellow-billed (*Gavia adamsii*), Red-throated (*G. stellata*), Pacific (*G. pacifica*), and Arctic Loon (*G. arctica*). Pacific and Arctic loons are combined in our analysis because they cannot be reliably differentiated from the air during surveys (Mizel et al. 2021). Common Loons (*G. immer*) are also present in this

region, but rarely breed and were excluded from our analysis. The Yellow-billed Loon is the largest bodied member of the loon family, and requires large bodies of water for take-off. Bering Land Bridge National Preserve contains a significant portion of breeding habitat for Yellow-billed Loons in Alaska (Schmidt et al. 2014). The Yellow-billed Loon has been considered for listing as an endangered species, and it was selected as a monitoring Vital Sign for the Arctic Network (Flamme et al. 2018). Red-throated Loon populations are considered to be particularly vulnerable to climate change due to their dependence on marine fish (Dickson 1993). Loon habitat in BELA is believed to be saturated (Mizel et al 2021), and consequently the loss of four large freshwater lakes is likely to represent a direct loss in the breeding population.

Loons are obligate aquatic species that come ashore only to nest. Yellow-billed Loons are most affected by lake drainage events because they require larger lakes than Red-throated Loons and other waterfowl species (e.g., swans, geese, or ducks) that may be able to use the small residual ponds left after lake drainage events. Yellow-billed Loon populations in BELA have been sampled as a part of the ARCN Yellow-billed Loons vital sign in the study area from 2009 to 2018 (odd years only 2009-2017; Flamme et al. 2018). Mizel et al. (2021) analyzed the habitat requirements of all three species of loons.

Water surface area from the 1980s to the present has been estimated as a part of the ARCN Terrestrial Landscape Patterns and Dynamics vital sign (Swanson 2017), based on classification of Landsat satellite data by USGS (2019). These data were analyzed to determine identify lake drainage events in BELA, and to quantify the potential impacts of lake drainage on loon habitat.

The purpose of this report is to summarize our current knowledge of vegetation succession in drained lake basins in northern BELA and estimate the potential impacts of lake drainage on loon habitat. We present a data summary for 16 new permanent vegetation monitoring plots installed in 2021 and vegetation maps of the newly drained lakes. We analyzed vegetation data from both these recently drained lakes (drained in 2018 and 2019) and older drained lakes (most drained prior to the earliest remote sensing records, which were around 1950) to understand vegetation succession on drained lakes in BELA. Finally, we used data on the change in lake area associated with drainage to estimate the resulting changes in potential loon habitat.

Methods

Study Area

Bering Land Bridge National Preserve occupies the northern portion of the Seward Peninsula, bordering the Chukchi Sea (Figure 1). Our study area is the nearly flat, lake-rich lowland in northernmost BELA. Lake basin elevations range from 9 m (North Lake) to 23 m (West Lake) above sea level. The area is underlain by continuous permafrost, and much of the area is occupied by existing thermokarst lakes or wetlands that occupy basins of drained thermokarst lakes (Jorgenson 2001). Vegetation is dominantly wet arctic tundra.

The nearest long-term climate monitoring station at Kotzebue, Alaska (about 80 km to the west-northwest) showed unusually high air temperatures in 2014-2019, culminating in record high mean annual air temperatures of -0.9 and -0.5 °C in 2018 and 2019, respectively (Figure 3; Swanson et al. 2021). Mean annual air temperatures at the Devil Mountain remote automated climate monitoring station (27 km southwest of South Lake and at 221 m elevation) were also exceptionally high in 2018 and 2019: -1.9 °C and -1.6 °C, respectively (Swanson et al. 2021). The mean annual air temperature at Kotzebue for the 12-month period immediately preceding our 2021 fieldwork (July 2020 through June 2021) was -4.7 °C , closer to the long-term average (Figure 3; Devil Mountain is missing data for this period). Modeled long-term average ground temperatures near the top of the permafrost in northern BELA were -3 °C to -4 °C in the 2000 decade, expected to rise to -1 °C to -2 °C in the 2050s decade and then to near or above 0 °C by the end of the century (Panda et al. 2016).

Winter and early spring precipitation (October through May) in 2018 was the second highest on record, and 2019 precipitation was also above average (Figure 4). Precipitation from these months is mostly stored as snow and released during the annual snowmelt event in late May and early June.

The four study drained lakes are in the Bering Straits Lower Coastal Plain subsection, which means that they are surrounded mostly by ice-rich sediments of Holocene age, and the lake basin relief due to thermokarst is several meters (as opposed to tens of meters in nearby subsections in Pleistocene “yedoma” sediments, Jorgenson et al. 2001). The lakes were flat-bottomed and shallow before drainage: synthetic aperture radar data from 1992-2010 showed that all the lakes were shallow enough before drainage to freeze to the bottom at least in some portions in some years, with typical late winter ice thicknesses of 1 to 1.5 m in this region (Engram et al. 2018). However, three of the four study lakes were deep enough to have had a dominantly floating ice regime in 1992-2010, while one (Central Lake) had an intermediate regime that was floating in some years and bedfast in others (Engram et al. 2018). The presence of unfrozen water under the ice in some or most years in the study lakes prevented the formation of permafrost in the lake bottoms prior to drainage. Thus the initial state of the lake basin sediments after drainage was unfrozen, and permafrost formation was probably minimal in 2019 due to the record temperatures mentioned above.

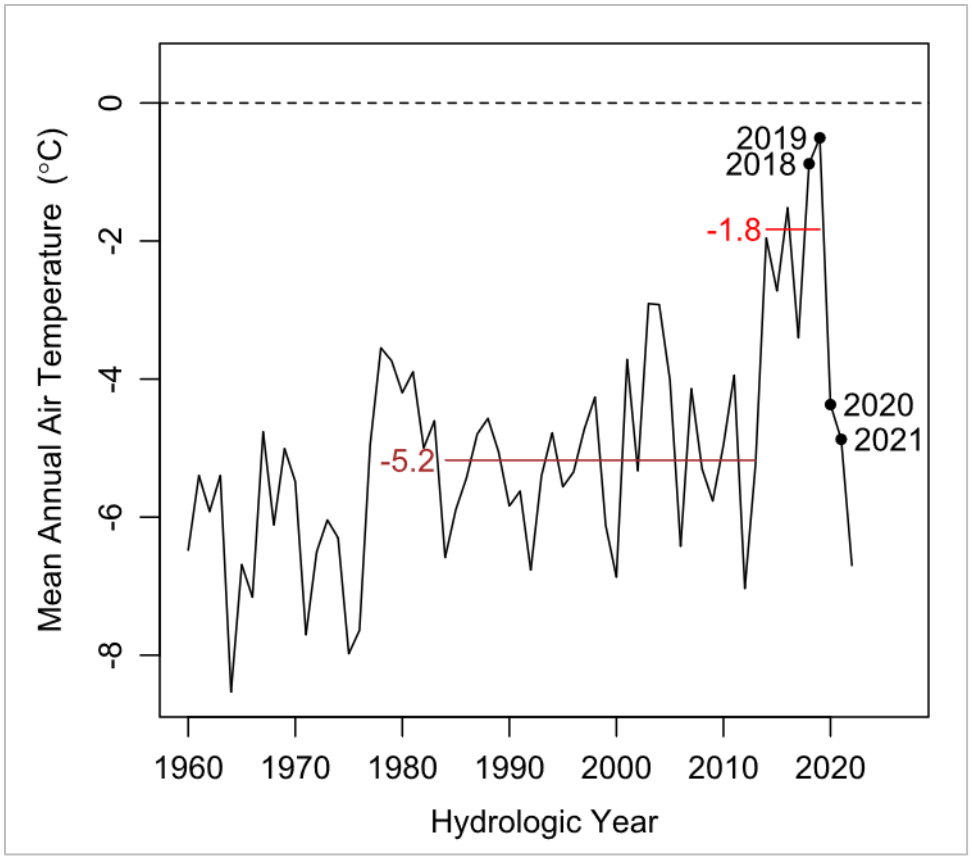


Figure 3. Mean annual air temperatures (MAAT) at Kotzebue, Alaska, 1960-2022. The MAAT was -5.2 °C for the 30-year period 1984-2013, and -1.8 °C for the six-years preceding and including the lake drainage events (2014-2019;). The hydrologic years 2018 and 2019 were the warmest on record (-0.9 and -0.5 °C, respectively). National Weather Service Data (NOAA Regional Climate Centers. 2022). Data are for hydrologic years, Oct-Sept, named for the latter of the two calendar years included in the average. Data for 5/2019-8/2019 were missing and replaced by data from the nearby NPS Mt. Noak station.

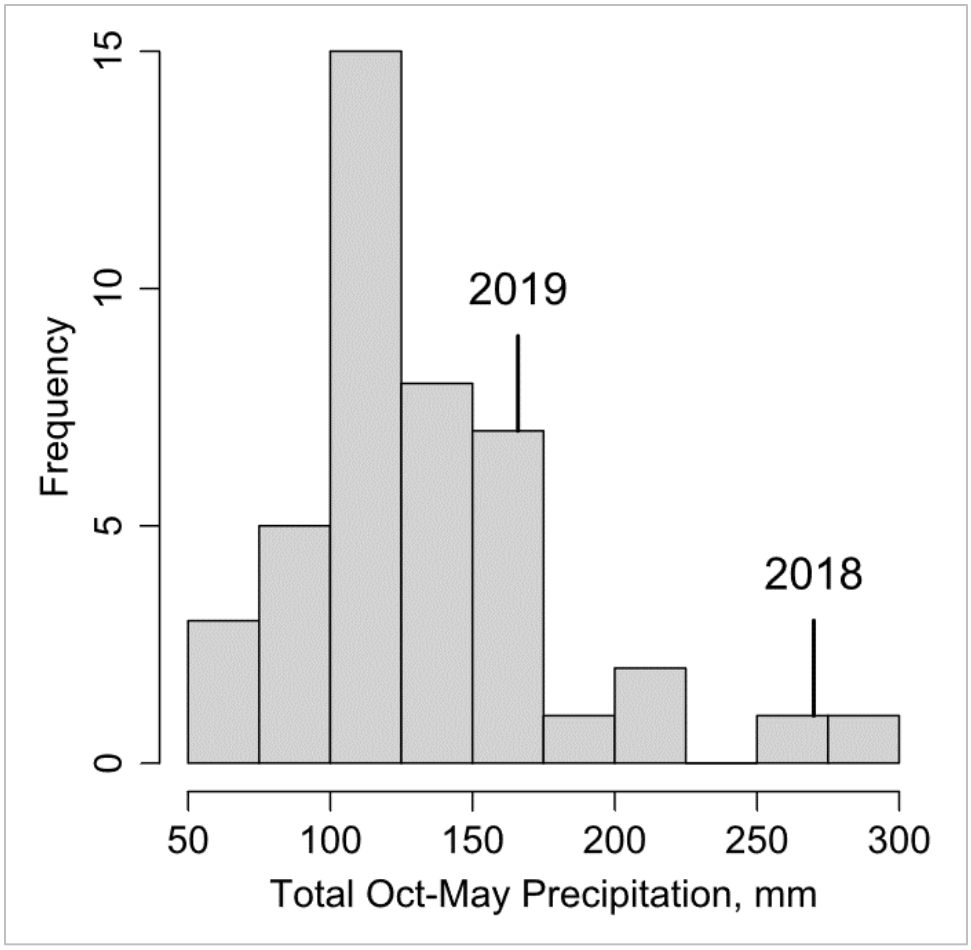


Figure 4. Histogram of the sum of precipitation for the snow season (Oct-May) at Kotzebue, National Weather Service data (NOAA Regional Climate Center 2022; data for 1980-2022). Oct-Dec precipitation is assigned to the following year. The precipitation sums for the two years of lake drainage (2018 and 2019) are indicated.

Vegetation Sampling

This report is based on data from various sources, collected by or for NPS as a part of this study and previous studies (Table 1). In July of 2019, vegetation data were opportunistically collected at one representative point in each of three lakes that had drained in 2018 (the Central, South, and West lakes; ESL in Table 1). Species were identified within an approximately 200 m^2 circular area, and cover was visually estimated in six broad categories (< 1%, 1-5 %, 6-25%, 26-50%, 51-75%, 75-100%).

Table 1. Vegetation plot data sources used in the analyses.

Abbreviation[A]	Reference	Location[B]	Age post-drainage	Date Sampled	No. plots	Method
ESL	This paper	Northern BELA	1 year	2019	3	Visual estimate
	This paper	Northern BELA	2-3 years	2021	16 [C]	Point-intercept transect
ABR	Jorgenson et al. 2009	BELA, CAKR, NOAT	>50 years	2002-2006	43	Visual estimate
	Jorgenson et al. 2009	BELA, CAKR, NOAT	21-25 years	2005	5	Visual estimate
ARCN	Swanson and Neitlich 2016	BELA, NOAT	>50 years	2013	30	Point-intercept transect
Shallow Lakes	Larsen et al. 2011	BELA	Undrained lakeshores	2008-2012	114	Line Intercept on 3 transects

[A]ABR –ABR Inc. the organization that produced Jorgenson et al 2009; ARCN – the NPS Arctic Inventory and Monitoring Network (Figure 1); ESL – the Espenberg-area drained lakes.

[B]BELA – Bering Land Bridge National Preserve, CAKR – Cape Krusenstern National Monument, NOAT – the Noatak National Preserve (Figure 1).

[C]Three of the 16 plots were resamples of the 2019 plots.

In July of 2021, we installed 16 long-term vegetation monitoring plots in basins of lakes that drained in 2018 and 2019 (Figure 5), following ARCN vegetation monitoring protocols (Swanson and Neitlich 2016; the ESL plots in Table 1). Most of the plots were placed systematically along transects with a randomized start and azimuth. Five plots were located deliberately: three at the 2019 photo and data points (plots 1, 14, and 16), one in a small lake that drained in 2019, next to Central Lake (plot 11), and one more in a relatively dry spot within Central Lake (plot 15). These monitoring plots were circular with an 8 m^2 radius (200 m^2 area) and 100 point-intercept points collected at 0.25 m intervals along two intersecting transects. The entire plot was also searched for species not encountered on the transects, with cover estimated by the categories described in the preceding paragraph. Any species not identifiable in the field were collected and identified in the lab. Vegetation data at the one plot on West Lake (plot 16) was collected by the simple plot-wide ocular estimate method as in 2019, due to time constraints in the field.



Figure 5. Locations of permanent vegetation plots installed in 2021. See Figure 1 for lake locations. Imagery is from 2019. Maxar Products. Alaska High Resolution Imagery (RGB). ©2021 Maxar Technologies Inc.

The existing ARCN vegetation monitoring program data set (Swanson and Neitlich 2016) contained 30 plots in older drained lakes (ARCN in Table 1), collected by the same protocol as the ESL plots. These all drained prior to the first aerial photographs, around 1950.

We also analyzed data collected as a part of a vegetation mapping effort by Jorgenson et al. (2009; the ABR plots in Table 1). These data were visual estimates of plant cover by species on plots with approximately 10 m radius, located along transects that were chosen to represent typical vegetation types in the region. These plots were also in basins of lakes that drained prior to the first (c. 1950) aerial photographs, except for one transect of 6 plots in NOAT in the basin of a lake that drained between 1980 and 1984 (based on aerial photographs and Landsat images) and was sampled in 2005, i.e. 21 to 25 years after drainage.

To evaluate lakeshores as potential seed sources for the newly established vegetation, we compared our collected data to the vegetation data collected as part of ARCN's Shallow Lakes Vital Sign (Larsen et al. 2011). The Shallow Lakes program sampled the near-shore vegetation at a total of 114 lakes in BELA in 2008 and 2012, including West Lake of this project. For each sampled lake, three transects, spaced 10 m apart, were collected perpendicular to the shoreline until open water was reached, and species were recorded as linear distance covered within 10 cm of the transect.

Vegetation Plot Data Summary and Ordination

We computed basic summary statistics (mean, minimum, and maximum cover, and frequency) for the ESL and ARCN data sets. We computed richness (total number of species), and the Simpson Diversity Index (McCune and Grace 2002) for the ESL plots. The Simpson diversity index responds to both the number of species present and their evenness (e.g. the dominance of one plant vs. co-dominance of many). It ranges from zero for a monoculture (one species present) to near 1 for a community with many plants of similar abundance. We used the "Shallow Lakes" data set to compute the number of plots where each species we observed as colonists on newly drained lakes had been observed on undrained lakeshores.

Two ordinations were run to visualize vegetation succession. The first consisted of the 16 plots from the ESL data set of recently drained lakes that we sampled in 2019 and 2021, including three that were sampled on both dates. The second ordination combined the data collected in 2019 and 2021 with data from older drained lakes in the tundra portion of ARCN (the ARCN and ABR data sets, Table 1). Scientific names were synonymized to match the existing ARCN botanical inventory (Parker 2006). Some taxa were reduced to genus to cope with plant identification and taxonomic problems.

The ordinations were based on Bray-Curtis dissimilarities (McCune et al. 2002), computed after the removal of plants with solely one occurrence or less than 1% cover. We ran non-metric multidimensional scaling ordinations using the package 'vegan' in R (Oksanen et al. 2022), with the following settings: 3 dimensions (*k*=3), with 250 runs of data ('*try*= 250'), maximum number of random starts 500 ('*trymax*= 500') and maximum iterations 999 ('*maxit* =999'). Previous ordination positions were used as a starting point ('*previous.best* = TRUE'), and data were centered but not otherwise transformed (parameters '*center* = TRUE', '*autotransform* = FALSE').

The community matrix used for the ESL-only ordination consisted of 19 plots (3 in 2019, 16 in 2021) and 14 species. For the combined ordination of newly drained and older lakes, one of the ABR plots

with only sparse aquatic vegetation was removed, and the resulting matrix consisted of 96 plots and 85 species.

Soil and Site Observations

Soils at the 16 plots established in 2021 were sampled using a ¾-inch push-probe and described by standard USDA-NRCS procedures (Soil Survey Division Staff 1993). The maximum depth of observation was 90 cm. The depth to water and frozen soil were also noted. The depth to frozen soil was also recorded at 4 points along the vegetation transects using a push probe with maximum depth of 1 m. Soils at ARCN plots from pre-2021 were described in a small soil pit. Photos, site descriptions, and GPS locations (post-processed to sub-meter accuracy) were also collected using standard ARCN protocols (Swanson and Neitlich 2016).

Vegetation and Water Mapping by Satellite Image Analysis

We used satellite images taken by Planet Labs (2021) to analyze lake drainage and vegetation growth. These images have 3 m resolution and 4 wavelength bands: blue, green, red, and near-infrared, converted to top-of-atmosphere reflectance. The images are taken daily from a fleet of small satellites; we downloaded every image free of ice, snow, and clouds for each lake from 2018 through 2021 (n=36 for North and Central Lakes, 43 for South Lake, and 45 for West Lake). We also downloaded one or more cloud-free images of each lake from late summer 2017 to obtain the original water extent of the lakes that drained in 2018.

We then selected the images with a date nearest to the field visits to create vegetation maps by supervised classification (Table 2). In all cases the image dates were within one week of the field visit. Supervised classification is a remote sensing technique in which areas with known vegetation, called "training areas," are used to identify the vegetation of unknown areas on the images.

Table 2. Dates of images used to create vegetation maps, and the field visits used for training data.

Lake	Pre-drainage Water Extent	2019 Field Visit	2019 Map	2021 Field Visit	2021 Map
North	2018_08_14	NA[A]	NA	2021_07_10	2021_07_13
Central	2017_08_25	2019_07_10	2019_07_10	2021_07_08 to 07_12	2021_07_13
South	2017_08_24	2019_07_10	2019_07_10	2021_07_07	2021_07_12
West map	2017_08_29	2019_07_10	2019_07_16	2021_07_13	2021_07_12

[A]NA – not applicable; North Lake lacks a 2019 visit and map because it drained in 2019 and had no vegetation at the time of our visit.

Images were smoothed and then classified by the k-nearest-neighbor (knn) method. Smoothing was by a two-step process. First, we computed the median for each spectral band for a circular neighborhood around the pixel with 11 pixel diameter; this is a neighborhood of 89 pixels (801 m^2, 0.2 acres). A median filter removes noise with less edge blurring than a mean filter. To provide additional edge preservation, we applied a sliding window operation as follows. The value of each pixel was compared to the median at its location and to the medians of 8 pixels located around it at a

distance of 2 pixels (i.e. to the north, northeast, east, southeast, etc.). It was then assigned the median that it most closely resembled. The effect of this second operation was to better preserve convex features along sharp natural boundaries. All raster operations were made using the R "raster" package (Hijmans 2015).

An informal vegetation classification was developed based on field data and photographs. The units mapped are listed in Appendix A. We digitized training points that we judged to represent the vegetation classes, by manual interpretation of the images. We then extracted the 4-band spectral information from the smoothed image for each digitized training point. These were screened for errors by leave-one-out cross validation and the weighted knn classification method, using the R library "kknn" (Schliep and Hechenbichler 2016), with a Euclidean distance measure, "k" value (number of nearest neighbors evaluated) of 3 to 5, and inverse distance weighting scheme. Then we classified the entire image by weighted knn, using 3 nearest neighbors in the training data. To reduce speckling noise in the resulting classified image, we applied the same sliding 11-pixel filter to the classified result, except that instead of a median operator we used the mode (the most common class in the window).

To investigate the timing of lake drainage and overall vegetation colonization, we estimated the fraction of water cover and computed the mean NDVI, normalized difference vegetation index for every snow- and cloud-free Planet image of the 4 lakes 2018-2021. NDVI is a measure of vegetation greenness that ranges from 0 to 1.0. Bare ground and water have NDVI of less than 0.3, while dense green vegetation has an NDVI of more than 0.6. NDVI is computed with the formula (NIR-R)/(NIR + R), where NIR is near-infrared reflectance and R is red reflectance. These quantities were computed for the footprint of the lake in the summer prior to drainage, taken from the vegetation maps described above. The fraction of water cover on the lakes was estimated by simple thresholding of the near-infrared band. Trial-and-error showed that a near-infrared value of 900 from the original Planet data approximately separated water and land.

Loon Habitat Availability

Since 2011, ARCN has monitored Yellow-billed Loons via aerial surveys in Bering Land Bridge National Preserve and Cape Krusenstern National Monument (Flamme et al. 2018). Surveys were conducted in late June, when most breeders would be expected to have initiated nests, but prior to the onset of hatching. Repeated observations were made on a set of 24 randomly located large (12 km × 12 km) permanent sample blocks. Using tandem seat fixed-wing aircraft, observers searched lakes larger than 7 ha for loon nests. Data were collected for all 5 species of loons.

Three of the four drained lakes (North, Central and South) were within the boundaries of the sample blocks. We summarized loon observations on the studied lakes for 2016-2018, the most reliable years of data collection for the three monitored loon species (Mizel et al. 2021).

Mizel et al. (2021) surveyed loons in northern BELA and developed models for estimating breeding occupancy for Yellow-billed and Pacific Loons, and occupancy with or without breeding (i.e., use) by Red-throated Loons. Here "breeding occupancy" refers to the presence or absence of a nesting pair of loons on a lake, and "occupancy with or without breeding" refers to the presence or absence

of the species irrespective of its breeding state. Covariates included lake area, shoreline complexity (perimeter/(4 × √area)) , distance to the ocean, and connectivity (the presence of ≥1 intersecting stream channel). The minimum lake area assumed for each species was 7 hectares for Yellow-billed Loons, 1 ha for Pacific Loons and 0.02 ha for Red-throated Loons.

To assess changes in potential loon breeding habitat due to drainage of the four intensively studied lakes, we used the models of Mizel et al. (2021) to predict loon occupancy before and after drainage; the covariates were the properties of water bodies as mapped with high-resolution imagery, described in the previous paragraph. We summed the predicted occupancy probabilities over all usable lakes before and after drainage. This sum is referred to as "aggregate occupancy" and is an estimate of the total number of loon pairs that the habitat can support.

We also estimated changes in loon habitat resulting from lake drainage in 2018-2019 for an expanded study area covering the lake-rich coastal plain of northern BELA (Figure 6). This study area is the overlap of Mizel et al.'s (2021) northern Seward Peninsula loon study area and Swanson's (2020) ARCN-wide water body monitoring study. We used Swanson (2020, based on 30 m-resolution Landsat data) to identify all of the lakes (n = 17) that drained in 2018 and 2019 and to compute the properties of these lakes needed to run Mizel et al.'s (2021) loon models. We then computed aggregate occupancy for the three loon species in the 17 lakes before and after drainage. To understand how the changes in loon habitat on these 17 drained lakes relate to loon habitat in the expanded study area, we also summed aggregate occupancy of the three loon species computed by Mizel et al. (2021) for the expanded study area shown in Figure 6; this provided a perspective on how much loon habitat was lost or gained in the Preserve due to lake drainage in 2018-2019, relative to the total available habitat.

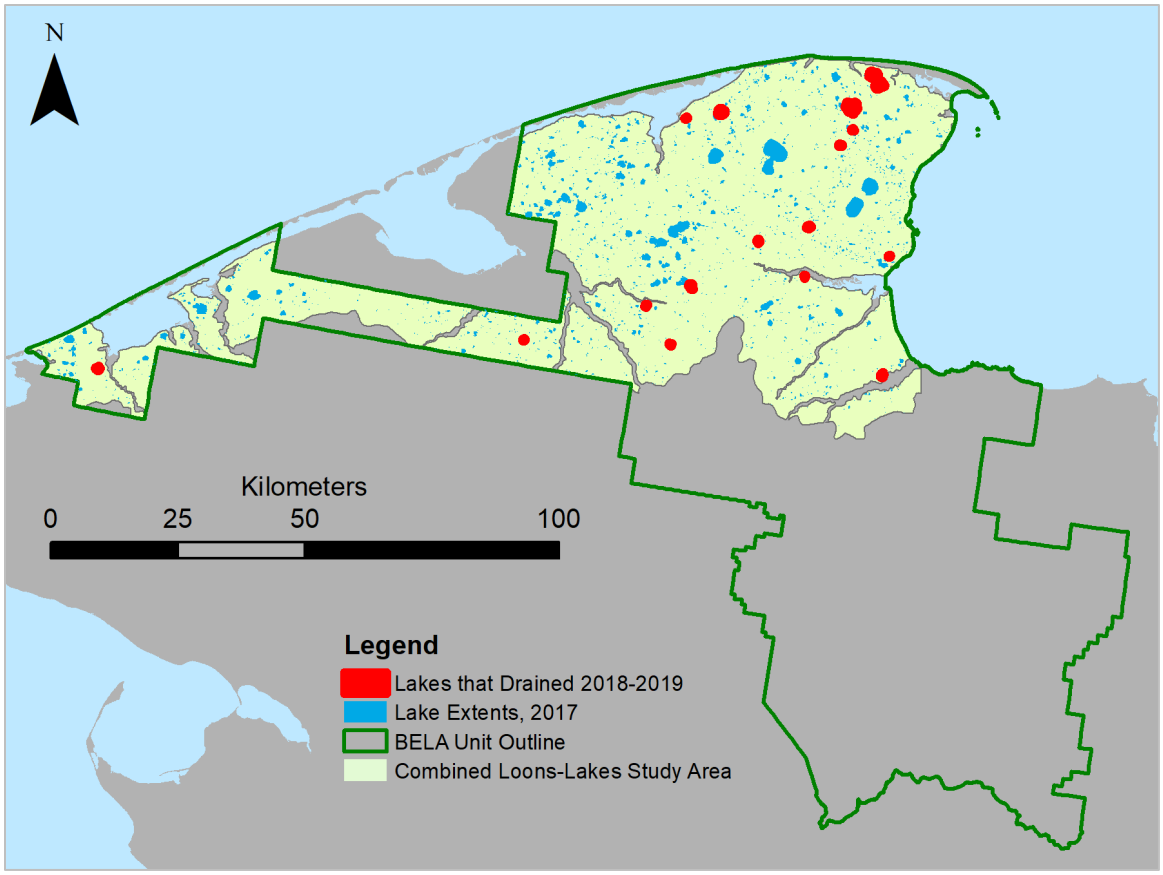


Figure 6. Expanded study area for estimate of lake drainage effect on loon habitat. This is the intersection of the study areas of Mizel et al. (2021, loon occupancy) and Swanson (2020, lake drainage history). The size of small drained lakes has been exaggerated for visibility.

Results

Timing and Route of Drainage

Inspection of high-resolution images showed that all four lakes drained by deepening of pre-existing drainage outlets. The time-series of satellite images show that the lakes drained early in the thaw season (Figure 7). Water cover on North Lake was high for all of 2018 because it drained in 2019; All other lakes drained in 2018. In all four lakes the fraction of water cover fell below 0.2 (i.e., 20% water cover) by the end of June in the year of drainage, and as early as mid-June in the case of North and West Lakes. In the latter two lakes, drainage began before the ice cover was gone, so the water cover was never high in the year of drainage. Due to the persistence of residual ponds, the water cover fraction remained above zero after drainage in all lakes. High water covers were recorded in May of most subsequent years, due to temporary ponding of snowmelt in the lake basins.

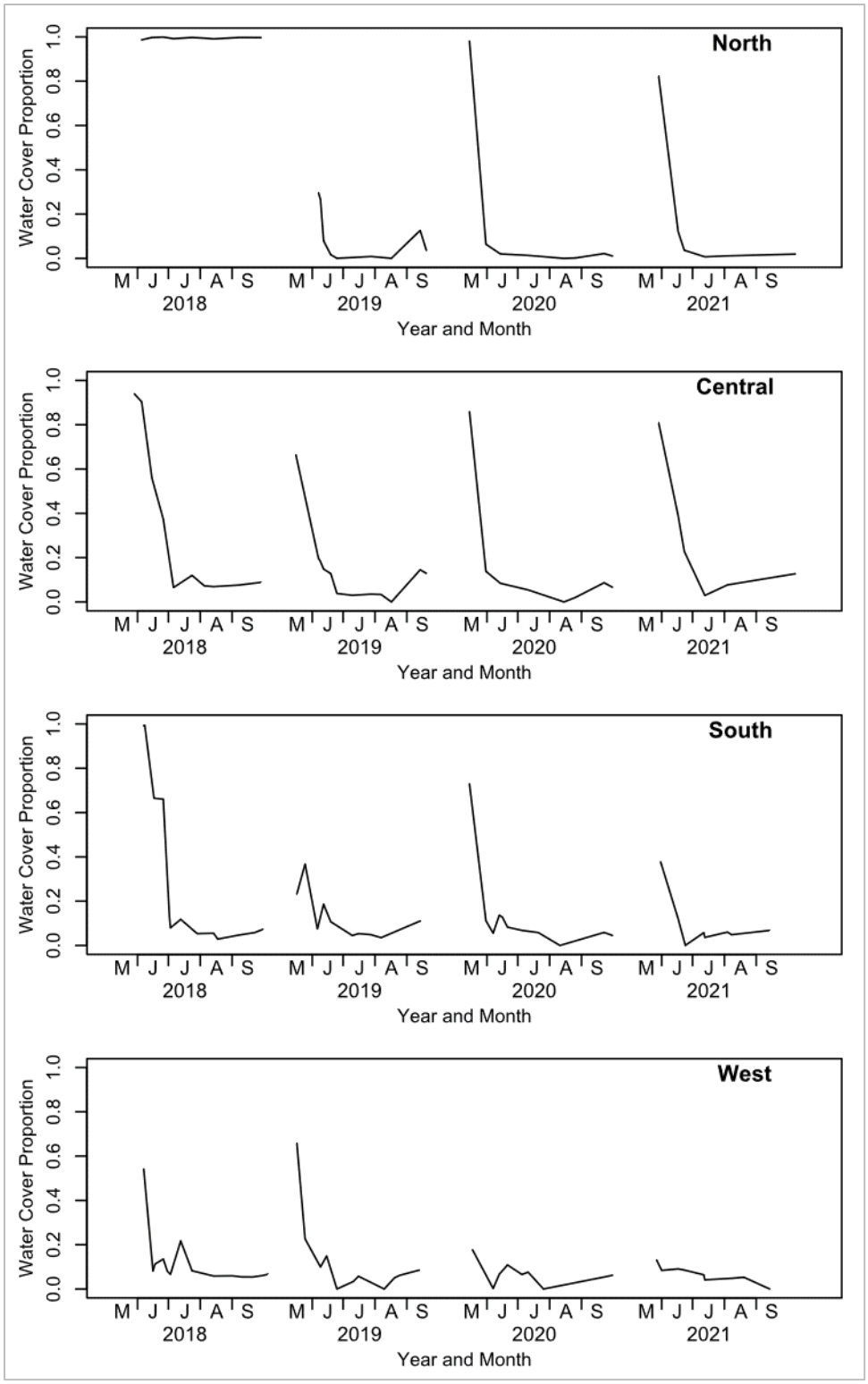


Figure 7. Water cover in the four study lakes as a proportion of the pre-drainage surface area.

Soil and Site

Lakes that drained in 2018-2019

Fine-grained, organic-rich soil was recorded at all 16 plot centers on the recently drained lakes. Most textures were silt loam. Colors were dark (all Munsell® soil color values were 3 or less and chromas 2 or less) due to the presence of organic matter. Plot 1, the only sample from South Lake, had a slightly coarser soil texture (fine sandy loam). Soil pH measurements were all between 6.2 and 6.8 (slightly acid to neutral). Soil electrical conductivity measurements all showed relatively low values: 505 µS cm^{-1} in plot 1 (South drained lake), 433-810 µS cm^{-1} at plots on Central Lake, 135 µS cm^{-1} in plot 11 on the small drained lake by Central Lake, and 1010 µS cm^{-1} in West Lake. All soils were saturated with water throughout the profile, and a water table was present within 20 cm of the surface in all profiles at the time of observation (7 to 13 July 2021).

Buried organic horizons were noted in soil profiles of three plots on Central Lake (plots 4, 5, and 15). These were all located in the southeastern part of the lake, on a relatively high spot as shown by its exposure early in the drainage process. The organic horizons were formed by exposure of the lake bottom to the air long enough for terrestrial plant litter to accumulate. These profiles had two buried organic horizons, suggesting two different episodes of previous exposure of the lake bottom, separated by a period of inundation (Figure 8).

In 2021 (7 to 13 July), frozen soil was observed at every plot center (except one where the depth of investigation was insufficient to determine frozen soil presence), with a mean depth of 71 cm (standard deviation 11 cm). Probing at four points along the transects showed similar results: the median depth was 79 cm, 25^{th} quantile 72 cm, and 75^{th} quantile 88 cm; 8 of 60 measurements were not frozen down to the 1 m depth of observation. These results were deeper than the soil investigations, probably because the observer made an effort to push through soft frozen material to more solidly frozen material before recording the depth.



Figure 8. Example drainage lake basin soil profile (a sample core) containing buried organic horizons. Dimensions in cm give the depth range of the core segment, measured from the surface. The C1, C2, and C3 horizons are silt loam lake sediment, the Oeb1 and Oeb2 horizons are buried mucky peat horizons that represent episodes when this location was not submerged. The C horizons here were typical of all soil profiles in the study area: dark colored and water saturated.

Older drained lakes

Thirty ARCN vegetation plots sampled in 2013 were in well-defined drained lake basins on thermokarst lake plains in BELA and NOAT that are similar to our study drained lakes, except that they drained prior to the first available aerial photographs (c. 1950). All of these plots were frozen at shallow depths (0.2 to 0.3 m for mid-July observations, and 0.4 to 0.5 m for August observations). All had organic (peat) surface layers, many of which extended deeper than the depth of observation, which was limited by frozen soil. The thinnest surface peat layers were about 20 cm thick, and many were thicker than 35 cm. The surface peat layers were much more acidic than the recently drained

lake muds reported above: the surface peat layers at all 30 plots except one had pH values less than 6.0, and they ranged as low as 4.0.

Most of the ABR plots in older drained lakes had soil properties within the ranges noted above for ARCN. All were in basins that drained prior to the 1950 advent of aerial photographs, except transect NOAT_T04, which drained 21 to 25 years before sampling and had unique properties: deeper thaw (median 59 cm in July 2005) and thinner organic layers (median 5 cm).

Vegetation

NDVI and Vegetation Establishment

The time-series of NDVI from satellite images revealed varying rates of vegetation colonization on the 4 lakes (Figure 9). The most rapid colonization occurred on Central Lake, where lake basin-wide average NDVI values exceeded 0.5 by the end of July in the year of drainage, just a month after drainage was complete. The slowest colonization by plants occurred on South Lake, where no increase in NDVI occurred in the year of drainage, a rather weak increase in post-drainage year 1, and NDVI values above 0.5 indicating dense vegetation arrived only in the 2nd year after drainage. Note that this lake also drained relatively late in its year of drainage, and required all of June to reach low water cover values (Figure 7). Colonization by plants was also relatively slow in North Lake, while West Lake showed little response in the year of drainage but dense vegetation in post-drainage year 1.

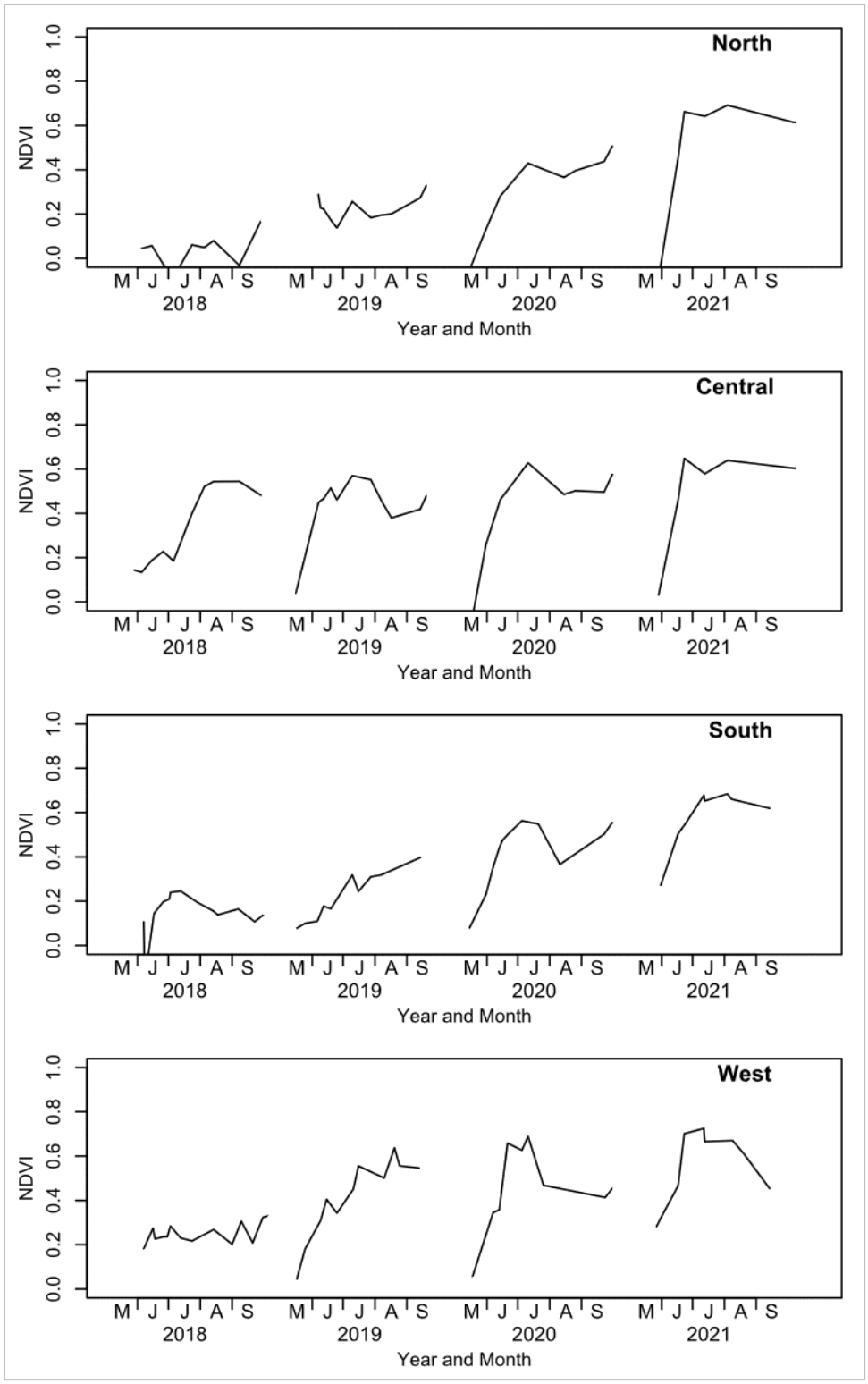


Figure 9. Mean NDVI trend with time in the four drained lake basins. North lake drained in 2019 (thus the low 2018 NDVI values represent water cover), while the other three lakes drained in 2018.

Plant Species Cover Trends

Post-drainage year 1

Vegetation in the year following drainage consisted of a few dominant pioneering species, or, in the case of South Lake, little vegetation (Table 3). Dense mats of spike rush (*Eleocharis acicularis;* on Central lake) and horsetail (*Equisetum arvense*; on West lake) had developed, locally with a conspicuous overstory of mastodon flower (*Tephroseris palustris*; Figures 10-11). The only tall graminoid (grasslike plant) observed in year one was *Arctophila fulva*, a grass that is common as an aquatic emergent in arctic lakes. The forb (flowering, non-woody plant) *Rorippa palustris* was widespread at low cover (Figure 12).

Table 3. Plant cover for the plots sampled one year after drainage.[A]

Lake	Plot	Plant	Life Form	Cover (estimated)
South	1	*Eleocharis acicularis*	Graminoid	5.0
	1	*Tephroseris palustris*	Forb	1.0
	1	*Arctophila fulva*	Graminoid	1.0
	1	*Rorippa palustris*	Forb	0.5
	1	*Equisetum arvense*	Forb	0.5
Central	14	*Eleocharis acicularis*	Graminoid	90.0
	14	*Tephroseris palustris*	Forb	8.0
West	16	*Equisetum arvense*	Forb	75.0
	16	*Arctophila fulva*	Graminoid	2.0
	16	*Tephroseris palustris*	Forb	0.5
	16	*Salix pulchra*	Shrub	0.5
	16	*Rorippa palustris*	Forb	0.5

[A]Lakes drained in 2018 and were sampled in 2019.



Figure 10. Vegetation of plot 14 on Central Lake in 2019, one year after drainage. A dense mat of the small spike rush *Eleocharis acicularis* was present, with scattered plants of flowering *Tephroseris palustris*.



Figure 11. Vegetation of plot 16 on West Lake in 2019, one year after drainage. The ground was covered by a nearly continuous mat of horsetail (*Equisetum arvense*). Young shoots of the aquatic grass *Arctophila fulva* are visible, and a single flowering *Tephroseris palustris* plant.



Figure 12. Vegetation of South Lake in 2019, one year after drainage. Vegetation was sparse and the exposed mud had visible desiccation cracks. The small grass clumps are *Arctophila fulva*. The curving lines are the forb *Rorippa palustris*, arrayed along former water's edge of the lake as its level dropped during drainage.

Post-drainage year 2

The same species that were dominant in year one after drainage were also the most common plants in plots that had been exposed for two years (plots 8, 9, 10, and 11; on lakes that drained in 2019 and were sampled in 2021; Table 4). Significant cover by *A. fulva* on one plot (37% cover on plot 10) foreshadowed future dominance by taller wetland graminoids (Figure 13). Dense stands of *Tephroseris palustris* were present locally (Figure 14). A variety of new species were present in trace amounts. These included both small wetland forbs (*Caltha natans, Stellaria crassifolia, Tripleurospermum phaeocephalum*) and common wet tundra dominants (sedges *Carex aquatilis, Eriophorum angustifolium,* and willows (*Salix* sp.)).

Table 4. Summary statistics for plant cover and frequency for all plots sampled two years after drainage.[A]

	Cover statistics[B]				
Plant	**Life Form**	**Mean**	**Min**	**Max**	**Freq**
Equisetum arvense	Forb	31.75	7.0	56.0	1.00
Tephroseris palustris	Forb	18.25	1.0	62.0	1.00
Rorippa palustris	Forb	12.75	7.0	18.0	1.00
Arctophila fulva	Graminoid	10.75	0.5	37.0	1.00
Eriophorum scheuchzeri	Graminoid	0.63	0.5	1.0	1.00
Moss, other	Moss	6.00	0.0	19.0	0.75
Ranunculus hyperboreus	Forb	0.25	0.0	0.5	0.50
Salix chamissonis	Shrub	0.25	0.0	0.5	0.50
Carex aquatilis	Graminoid	0.25	0.0	1.0	0.25
Eleocharis acicularis	Graminoid	0.25	0.0	1.0	0.25
Equisetum fluviatile	Forb	0.25	0.0	1.0	0.25
Caltha natans	Forb	0.13	0.0	0.5	0.25
Eriophorum angustifolium	Graminoid	0.13	0.0	0.5	0.25
Juncus castaneus	Graminoid	0.13	0.0	0.5	0.25
Salix pulchra	Shrub	0.13	0.0	0.5	0.25
Stellaria crassifolia	Forb	0.13	0.0	0.5	0.25
Tripleurospermum phaeocephalum	Forb	0.13	0.0	0.5	0.25

[A]Lakes that drained in 2019 and sampled in 2021, n = 4; these were in North Lake (plots 8, 9, and 10) and the small lake next to Central Lake (plot 11).

[B]Min - minimum cover, Max – maximum cover, Freq – frequency, the proportion of plots with the plant present.

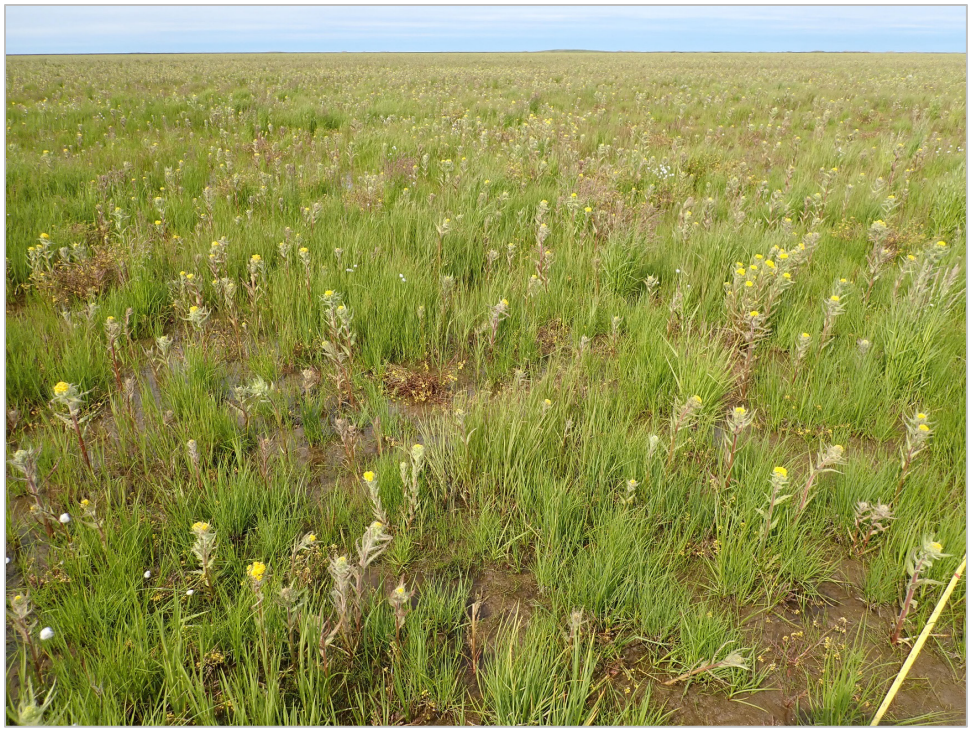


Figure 13. Vegetation of plot 10 on North Lake in 2021, 2 years after drainage. The tall yellow-flowering plant is *Tephroseris palustris*, the low-growing plant with small yellow flowers is *Rorippa palustris*, and the abundant grass is *Arctophila fulva.*



Figure 14. Nearly pure stand of Tephroseris palustris in July, 2021 on Plot 11 in a small drained lake that drained in 2019, just southeast of Central Lake.

Post-drainage year 3

Plots that had been exposed for three years had *Eleocharis acicularis* and *Equisetum arvense* persisting in most places underneath a lush stand of wetland graminoids, dominated by *Arctophila fulva* and *Eriophorum scheuchzeri* (Table 5, Figure 15). The common wetland sedge *Carex aquatilis*, or cottonsedge *Eriophorum angustifolium*, had appeared in most of the plots, at less than 10% cover in most cases. Dense stands of *Tephroseris palustris* persisted locally, though not on any of our plots.

Table 5. Summary statistics for plant cover and frequency for all plots sampled 3 years after drainage.[A]

	Cover statistics[B]				
Plant	**Life Form**	**Mean**	**Min**	**Max**	**Freq**
Eleocharis acicularis	Graminoid	35.5	3	93	1.00
Stellaria crassifolia	Forb	11.7	2	26	1.00
Arctophila fulva	Graminoid	7.8	2	18	1.00
Eriophorum scheuchzeri	Graminoid	14.4	0	40	0.91
Equisetum arvense	Forb	25.3	0	63	0.82
Carex aquatilis	Graminoid	6.9	0	38	0.82
Eriophorum angustifolium	Graminoid	4.1	0	22	0.64
Equisetum fluviatile	Forb	1.9	0	6	0.64
Moss, other	Moss	16.4	0	78	0.55
Rorippa palustris	Forb	2.9	0	14	0.36
Salix pulchra	Shrub	0.5	0	2	0.36
Tephroseris palustris	Forb	0.3	0	1	0.27
Epilobium palustre	Forb	0.3	0	2	0.18
Salix chamissonis	Shrub	0.3	0	2	0.18
Liverwort, other	Liverwort	0.2	0	2	0.09

[A]Lakes that drained in 2018 and were sampled in 2021 (n = 11). These were on South Lake (plot 1), Central Lake (plots 2 through 7 and 12 through 15), and West Lake (plot 16).

[B]Min - minimum cover, Max – maximum cover, Freq – frequency, the proportion of plots with the plant present.



Figure 15. Vegetation of plot 3 on Central Lake in 2021, 3 years after drainage. The white flowers are the cottonsedge *Eriophorum scheuchzeri*, the lacy tall grass is *Arctophila fulva*. A mat of *Equisetum arvense* is visible on the ground.

Older drained lakes

The vegetation of older drained lake basins was quite different from that of recently drained lakes (Table 6). The dominant plant was *Sphagnum* sp. mosses, and a wide variety of low shrubs was present (*Betula, Ledum, Oxycoccus, Andromeda, Vaccinium, Empetrum, Salix*). *Carex aquatilis* was the most abundant sedge, and *Eriophorum chamissonis* was also widespread. (The listing of *Eriophorum chamissonis* in the older lakes vs. *E. scheuchzeri* may be due to taxonomic confusion, and in any case does not represent an important ecological change between these two very similar species.) All of the plant species that we observed in the recently drained lakes described above were absent except *Carex aquatilis* and *E. chamissonis/scheuchzeri*.

Table 6. Summary statistics of plants on older drained lake basins.[A]

Plant	Cover statistics[B]				
	Life Form	**Mean**	**Min**	**Max**	**Freq**
Sphagnum	Moss	60.5	6	97	1.00
Carex aquatilis	Graminoid	8.4	0.5	34	1.00
Betula nana	Shrub	6.9	0	44	0.97
Ledum palustre	Shrub	7.9	0	34	0.87
MOSS	Moss	6.3	0	29	0.87
Oxycoccus microcarpos	Shrub	2.3	0	7	0.87
Eriophorum chamissonis	Graminoid	6.6	0	31	0.83
Andromeda polifolia	Shrub	5.5	0	26	0.83
Vaccinium uliginosum	Shrub	4.7	0	26	0.83
Empetrum hermaphroditum	Shrub	3.1	0	13	0.83
Vaccinium vitis-idaea	Shrub	7.5	0	32	0.80
Polytrichum sp.	Moss	1.8	0	8	0.80
Cladonia sp.	Lichen	1.2	0	6	0.67
Flavocetraria cucullata	Lichen	1.0	0	9	0.60
Cladina arbuscula/mitis	Lichen	0.7	0	4	0.60
Eriophorum vaginatum	Graminoid	5.5	0	22	0.57
Cladina rangiferina/stygia	Lichen	2.4	0	12	0.57
Cladonia amaurocraea/uncialis	Lichen	1.6	0	10	0.57
Cetraria ericetorum/islandica/laevigata	Lichen	1.1	0	8	0.53
Salix fuscescens	Shrub	0.8	0	5	0.50

[A]NPS-ARCN Data from 30 drained lakes in BELA and NOAT. Only species with a frequency of more than 0.5 are included.

[B]Min - minimum cover, Max – maximum cover, Freq – frequency, the fraction of plots with the plant present.

Plants of lakeshores

Almost all species recorded on plots in drained lakes in this study have been recorded on lakeshore transects in BELA by the Shallow Lakes monitoring program (Table 7). Only *Tephroseris palustris* and *Salix chamissonis* were missing; the former was frequently observed on lakeshores outside of plots, and the latter may be missing because of difficulties in its identification (A. Larsen, personal communication). *Rorippa palustris* and *Eleocharis acicularis* were abundant on the drained lakes but rare on lakeshores. These are species for which the current supply of propagules on the shore probably cannot explain their abundance on the drained lakes, and thus some kind of seed banking is required.

Table 7. Comparison of species present on the drained lakes to Shallow Lakes vegetation data.

Plant[A]	Life Form	No. Drained Lakes[B]	No. Lake-shores[C]	Lakeshore Data Note[D]
Arctophila fulva	Graminoid	4	34	–
Carex aquatilis	Graminoid	3	91	–
Eleocharis acicularis	Graminoid	3	1	–
Epilobium palustre	Forb	1	6	–
Equisetum arvense	Forb	4	22	–
Equisetum fluviatile	Forb	3	7	–
Eriophorum angustifolium	Graminoid	1	70	–
Eriophorum scheuchzeri	Graminoid	3	42	*E. scheuchzeri* + *russeolum*
Rorippa palustris	Forb	4	3	*Rorippa* sp.
Salix chamissonis	Shrub	1	0	–
Salix pulchra	Shrub	2	47	–
Stellaria crassifolia	Forb	2	10	*Stellaria* sp.
Tephroseris palustris	Forb	4	0	–

[A]Plant species recorded in drained lakes (post-drainage years 1 through 3) in this study.

[B]Number of drained lakes where the plant was recorded on point-intercept transects, out of 4 lakes sampled.

[C]Number of lakes with the plant in ARCN shallow lakes shoreline line-transect data, out of 114 lakes sampled.

[D]Notes indicate taxonomic differences between the two data sets.

Species Richness, Diversity, and Total Cover

Species richness (number of species on the plot) was low in year 1 after drainage and higher in subsequent years as additional species became established (Table 8). Total cover was highly variable between different plots in year one; it increased over time on the 3 plots that were sampled twice, and exceeded 100% on the majority of plots by year 3 (plant cover can exceed 100% due to overlapping plant canopies). The Simpson diversity index responds to both the number of species present and their evenness (e.g. the dominance of one plant vs. co-dominance of many). It was low (0.25 or less) on two plots after one year as a result of near monoculture conditions there. It was high (0.7 or more) on many of the year-3 plots due to the formation of a relatively diverse community with multiple co-dominant species.

Table 8. Richness, Total Plant Cover and Simpson Diversity Index.

Sample Year	Years since drainage	Plot	Richness[A]	Total Cover[B] (%)	Simpson Diversity[C]
2019	1	1	5	12.5	0.77
2019	1	14	2	103.5	0.25
2019	1	16	4	64.5	0.05
2021	2	8	10	37.0	0.65
2021	2	9	8	72.5	0.57
2021	2	10	12	78.0	0.70
2021	2	11	9	155.0	0.69
2021	3	1	14	163.0	0.79
2021	3	2	11	121.0	0.73
2021	3	3	12	185.5	0.80
2021	3	4	12	141.0	0.78
2021	3	5	12	93.0	0.63
2021	3	6	12	86.5	0.72
2021	3	7	11	137.0	0.54
2021	3	12	11	73.0	0.84
2021	3	13	12	109.0	0.83
2021	3	14	10	132.0	0.48
2021	3	15	9	185.5	0.69
2021	3	16	9	104.5	0.71

[A]Total count of species on the plot.

[B]Sum of cover by individual species; exceeds 100% due to overlapping canopies.

[C]Simpson diversity index (McCune and Grace 2002).

Vegetation Maps

Maps of vegetation on the drained lakes in 2019 and 2021 show an increase in vegetation density and complexity over time (Figures 16-19). In 2019 there were large patches of simple communities (e.g. *Eleocharis acicularis,* or *Equisetum arvense*), sparse vegetation, or bare mud. In 2021 there was a complex mosaic with residual patches of vegetation like 2019, and larger areas of tall wetland graminoids. See Appendix A for more detailed descriptions of the vegetation mapping units.

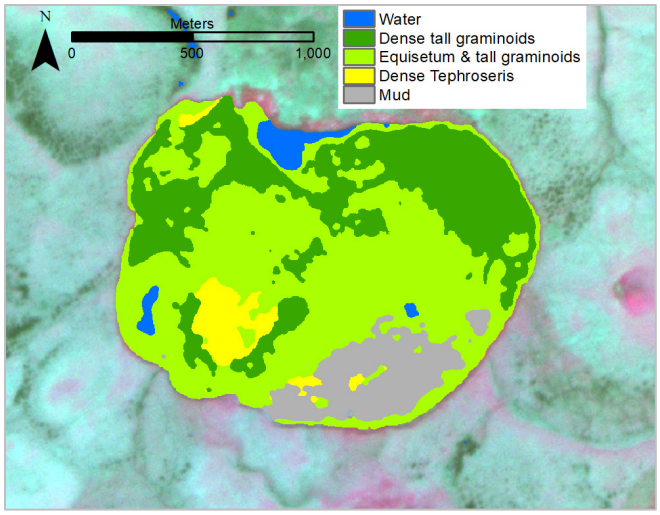


Figure 16. Vegetation map of North Lake in 2021. At the time of our 2019 visit, this lake had just drained and was unvegetated.

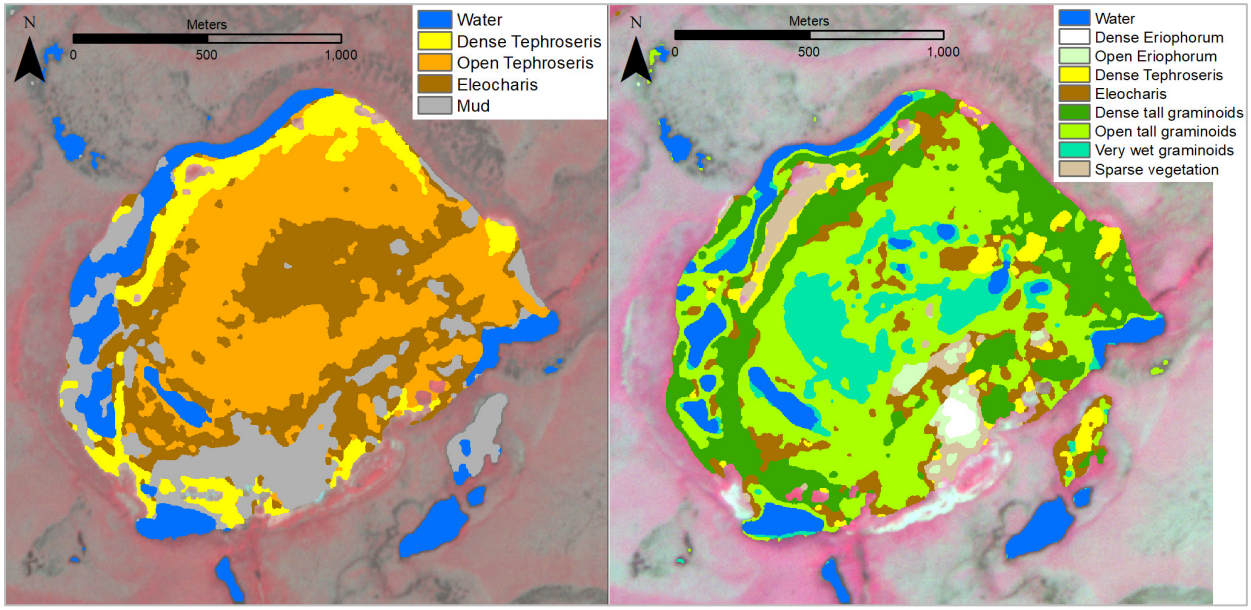


Figure 17. Vegetation map of Central Lake in 2019 (left) and 2021 (right).

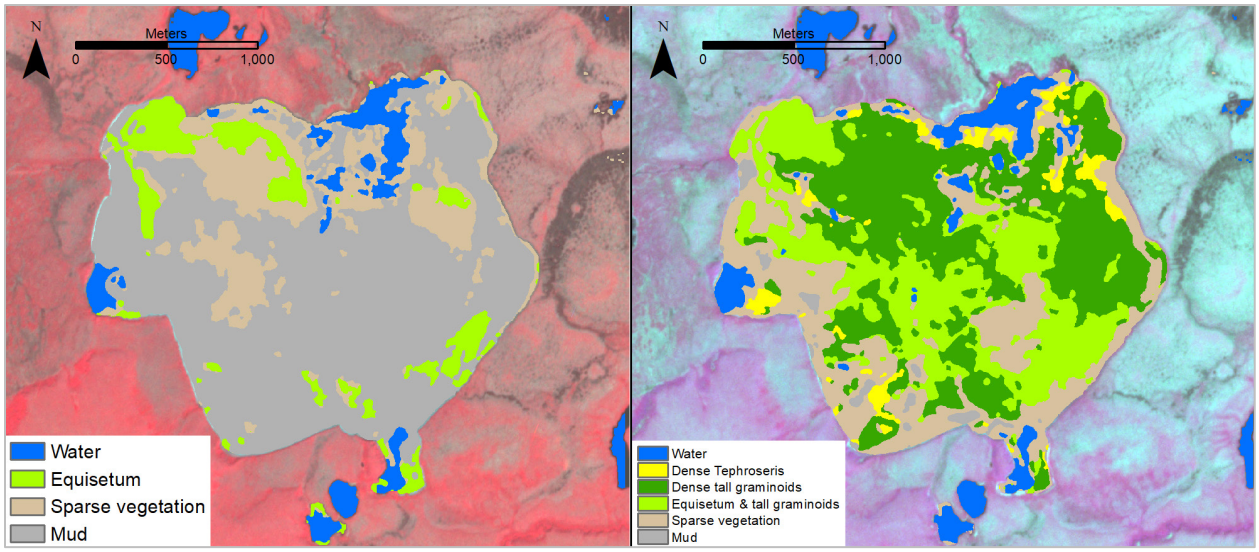


Figure 18. Vegetation map of South Lake in 2019 (left) and 2021 (right).

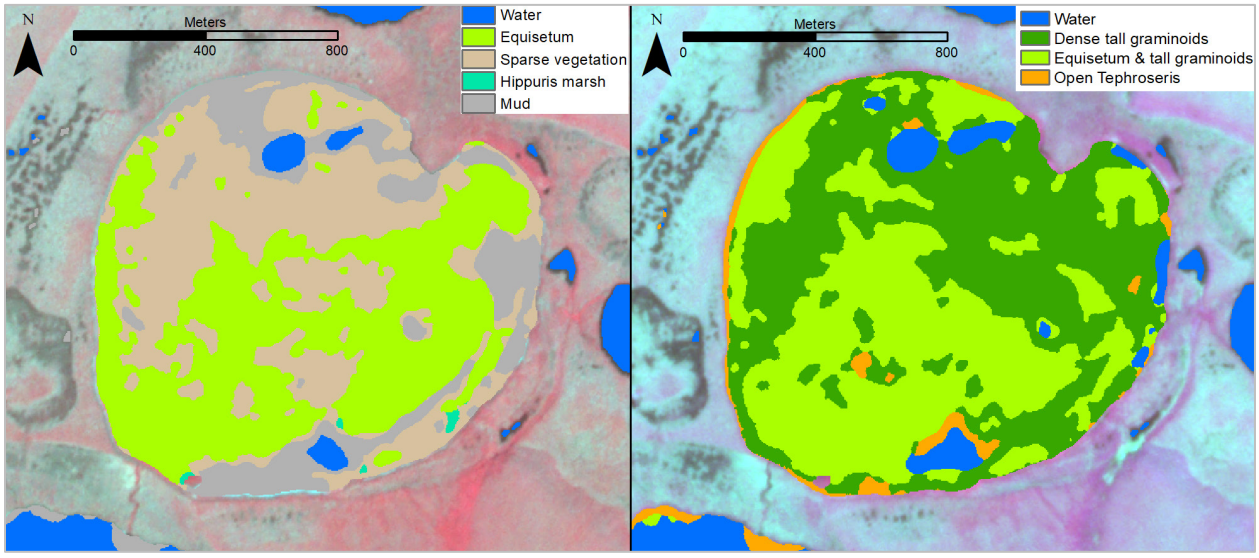


Figure 19. Vegetation map of West Lake in 2019 (left) and 2021 (right).

Vegetation Ordination

Ordinations are used to reduce the complexity of plot data with many species. They show similarity in community structure between different samples: the closer two plots are on the figure, the more similar they are.

In the ordination with only ESL plots from 2019 and 2021 (Figure 20), the extremes in the ordination (upper left, upper right, and bottom center) are represented by the three plots sampled in year 1 after drainage. The upper left corner of the ordination (typified by plot 14, year 1: Figure 10) is plots dominated by *Eleocharis acicularis*. The upper right corner (typified by plot 16, year 1: Figure 11) is plots dominated by *Equisetum arvense*. At the bottom of the plot is plot 1, year 1 with a very sparse stand of *Rorippa palustris*, *Tephroseris palustris*, and *Arctophila fulva* (see Figure 12). The change

trajectories indicated by the three arrows show that the three plots sampled one year after drainage in 2019 were highly dissimilar, but they became more similar by year three. The most dramatic change was on plot 1 on South Lake, which had less than 10% plant cover in 2019, gained 9 species and increased to 88% vegetation cover to become similar to the plots on Central Lake. Based on the trends from years 1 to 3 on the ordination, it appears that the plots are converging to be like those in the upper center of the plot. The location of *Carex aquatilis* on the ordination plot (the weighted average MDS scores for plots where it occurs) marks an approximate point of convergence for the plots as plant succession occurs. *C. aquatilis* was the most abundant vascular plant on older drained lake basins in ARCN's vegetation database (Table 6). The plots near *C. aquatilis*' centerpoint (plots 1 and 2 in year 3) had a relatively diverse and balanced set of plants, including significant cover by moss and *C. aquatilis*.

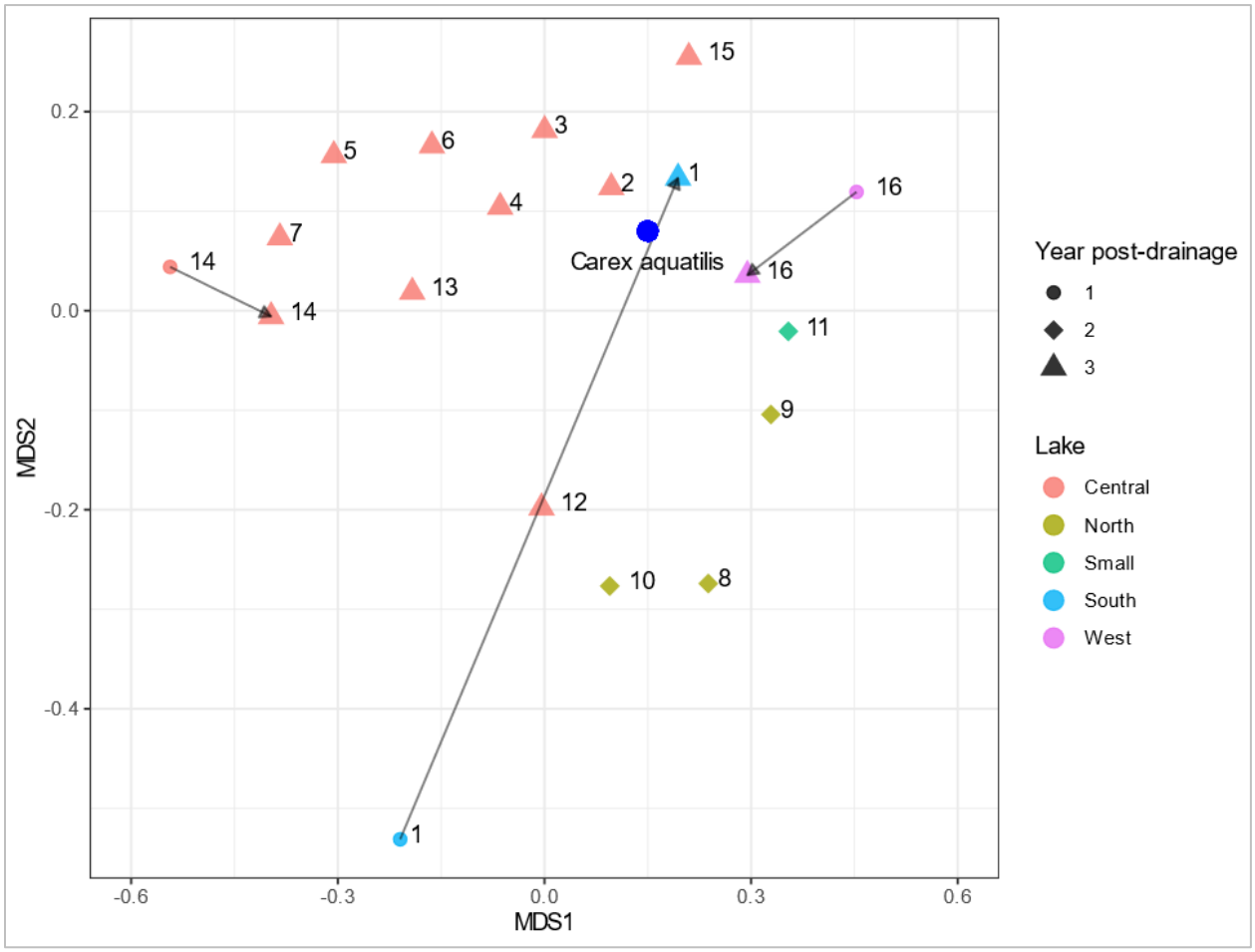


Figure 20. Ordination results for the recently drained lakes sampled in 2019 and 2021 (the ESL data set in Table 1). Re-sampled plots are connected by arrows. The axes (MDS1 and MDS2) are non-metric multidimensional scaling scores.

An ordination combining our data from recently drained lakes (ESL) with data from lakes that drained prior to c. 1950 remote sensing records (ARCN and ABR; Table 1) shows clear differentiation of the older vs. newly drained lakes (Figure 21). Ordination axis 1 separates older (left

side) and newly drained lakes (right side); the species characteristic of older drained lake basins (e.g. *Sphagnum* sp. and various low shrubs; see Table 6) are negatively correlated with axis 1. Ordination axis 2 generally separates very wet (positive MDS2) from more mesic (negative MDS2) sites. Arrows connecting recently drained plots that were sampled twice (in post-drainage years 1 and 3) show them becoming more like the older drained lakes over time. As in the ESL-only plot (Figure 20), plot 1 showed a major change toward typical wet tundra vegetation between 2019 and 2021. Plot 16 become more like the older drained lakes and developed a "wetter" community as the mesic species *Equisetum arvense* was partly replaced by the wetland graminoids *Carex aquatilis* and *Arctophila fulva*. The three older plots at the bottom of the diagram had shallow-water emergent plant communities, including *A. fulva* in its more typical shallow-water habitat. The five ABR plots that drained 21-25 years before sampling fell in between the recent post-drainage plots and the bulk of the older drained lake basins. These plots lacked *Sphagnum* but had abundant other wetland mosses and the grass *Calamagrostis canadensis*, along with some willows and the late-seral wetland graminoids *C. aquatilis* and *E. angustifolium*. As is apparent in the species pools and NDVI trends, the most rapid changes happen in the years immediately post-drainage.

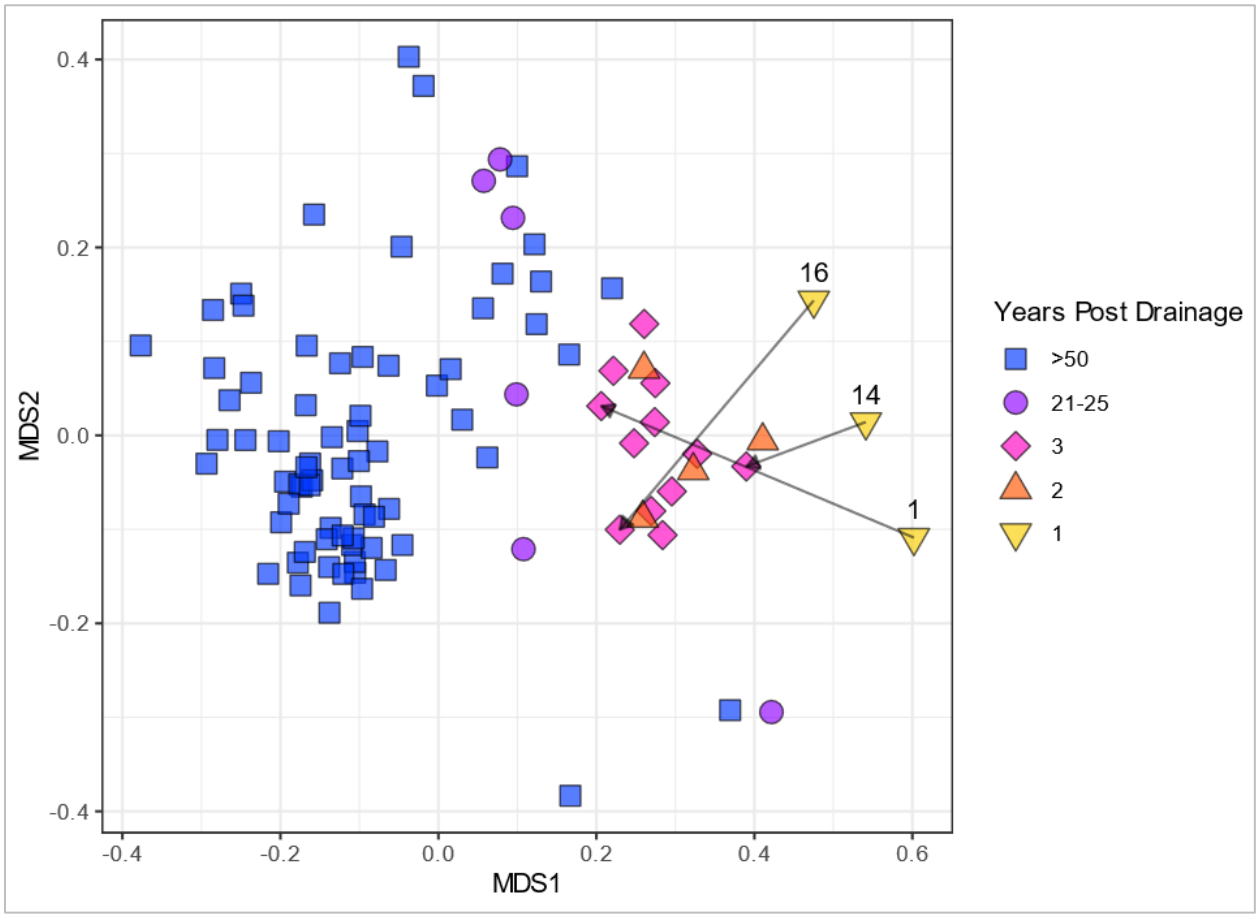


Figure 21. Ordination for combined vegetation data. Resampled plots are connected by arrows, and the number labels are plot numbers. The data sets are described in Table 1.

Loon Habitat

Loons occupied each of the recently drained lakes during surveys conducted in 2016-2018 (Table 9). Central and South lakes had mostly drained at the time of the 2018 survey (20-28 June), and no Yellow-billed Loons were present on them at that time.

Table 9. Loon species recorded via aerial survey for 2016-2018.[A]

	Lake		
Year	**North**	**Central[B]**	**South[B]**
2016	P, Y	P, R	Y
2017	P, Y	P	R, Y
2018	Y	P	R

[A]P - Pacific or Arctic Loon; R - Red-throated Loon; Y - Yellow-billed Loon.

[B] Lake was draining during the 2018 surveys.

The lake drainages had dramatic effects on loon occupancy probabilities, and these effects differed by species (Table 10, Figures. 22-24, and Appendix Tables B1-B4). “Occupancy probability” is the probability that a lake will have a pair of loons nesting on it. Prior to draining, all four lakes had a moderately high probability (0.43 to 0.63) of being occupied by breeding Yellow-billed Loons, with aggregated occupancy of 2.0. In other words, in any given year two loon pairs were expected to nest on the four lakes together. After draining, only South Lake had a remnant pond greater than the Yellow-billed Loon minimum area requirement, and due to its small size this pond had a low probability of breeding occupancy (0.1). Breeding occupancy probabilities for Pacific Loons were between 0.27 and 0.38 for each of the four lakes prior to drainage, with aggregate occupancy of 1.2. Pacific Loon occupancy probability also declined after drainage, though not as dramatically, with a post-drainage aggregate occupancy of 0.67, i.e. approximately half of the pre-drainage level. The probability of being occupied by Red-throated Loons (with or without breeding) was low prior to drainage, less than 0.1 for the individual lakes, with an aggregate occupancy of just 0.2 for all four lakes. However, after drainage most of the residual ponds were above the minimum area requirement for Red-throated Loons and there were many residual ponds, so the aggregate occupancy probability increased to 16. It is unlikely that this many potential nesting ponds would actually be occupied without a significant increase in the Red-throated Loon population size.

Table 10. Change in modeled loon occupancy for lakes in northern BELA due to 2018-2019 lake draining.

	Water area (ha)		Loon occupancy probability[A]					
Lakes	**pre**	**post**	**Yellow-billed pre**	**Yellow-billed post**	**Pacific pre**	**Pacific post**	**Red-throated pre**	**Red-throated post**
Four study drained lakes[B]	922.9	49.2	2.0	0.1	1.2	0.7	0.2	16.2
Loon Study Area, drained lakes[C]	1100.6	83.9	4.1	0.3	3.2	1.2	1.7	21.9

[A]Occupancy probablilities by the model of Mizel (2021). “Pre” and “Post” refer to before and after the lakes drained.

[B]The four drained lakes studied in detail in the present study (Figure 1).

[C]Loon study area is the overlap of Swanson (2020) lake-rich lake monitoring zones with Mizel et al.’s (2021) northern Seward Peninsula loon occupancy modeling study (Figure 6); covers most of the lakes in northern BELA, including the four study drained lakes. Data are for lakes that drained in 2018-2019, a total of 17 lakes.

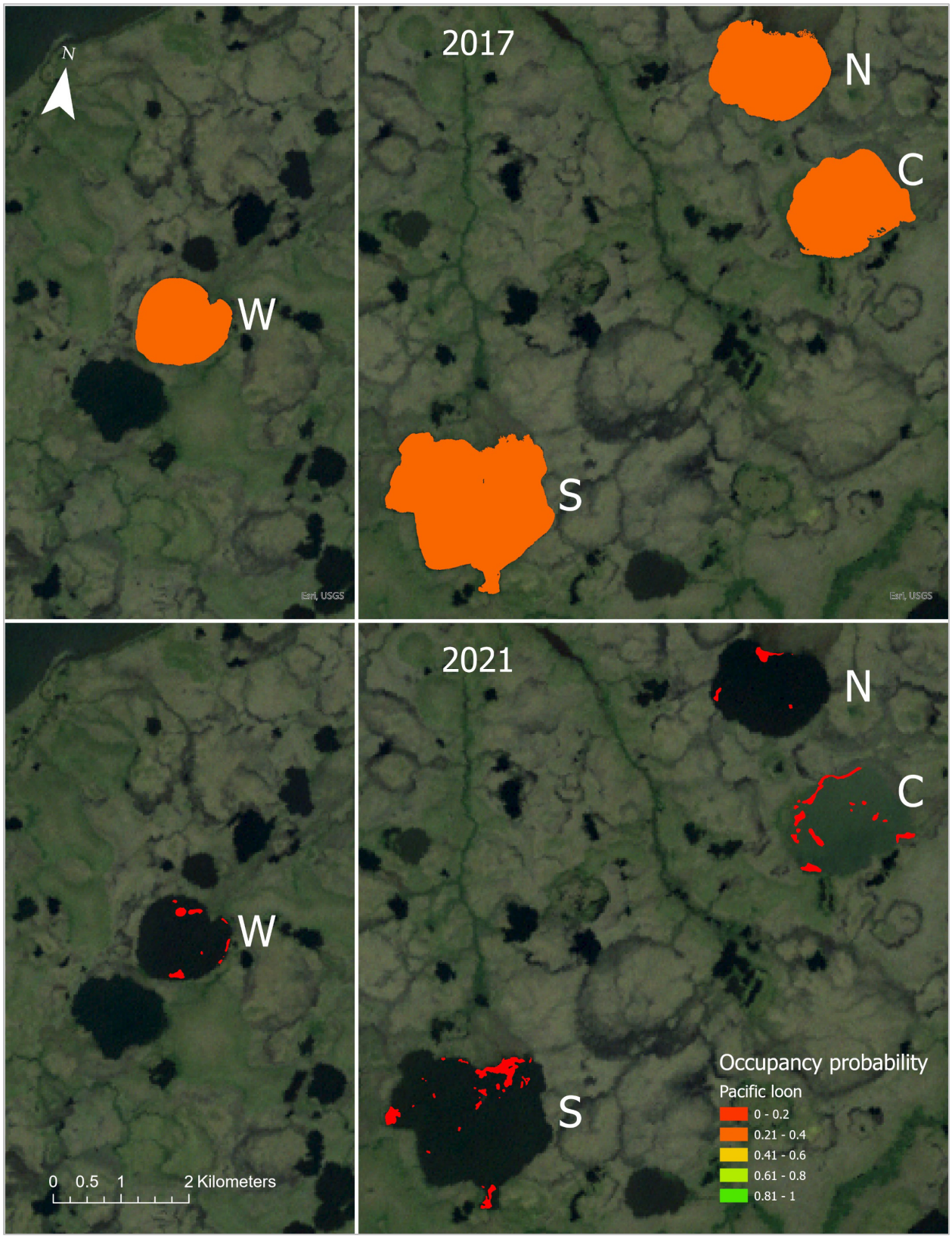


Figure 22. Pacific Loon occupancy probability in the four drained lakes, pre- and post-drainage.

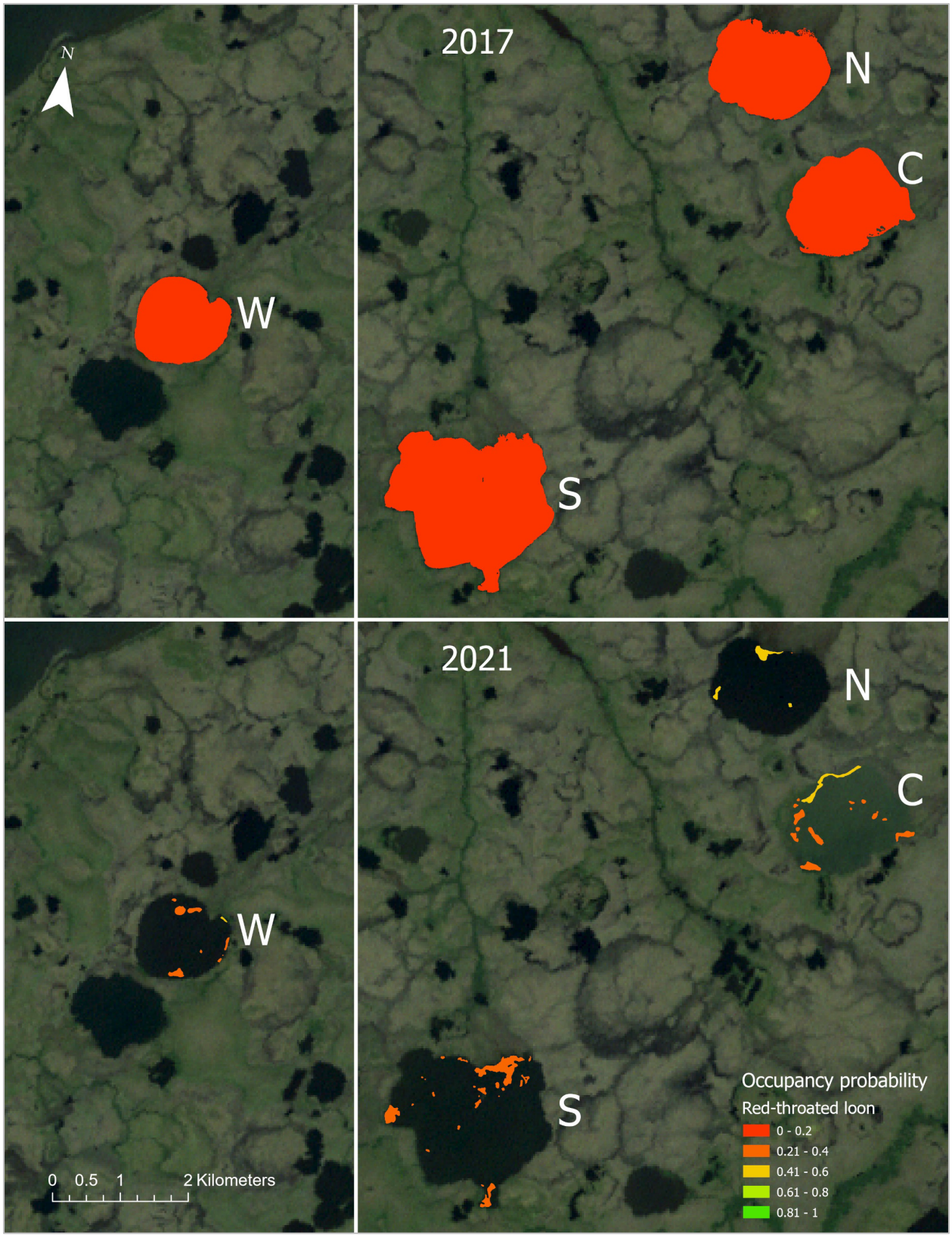


Figure 23. Red-throated Loon occupancy in the four drained lakes, pre- and post-drainage.

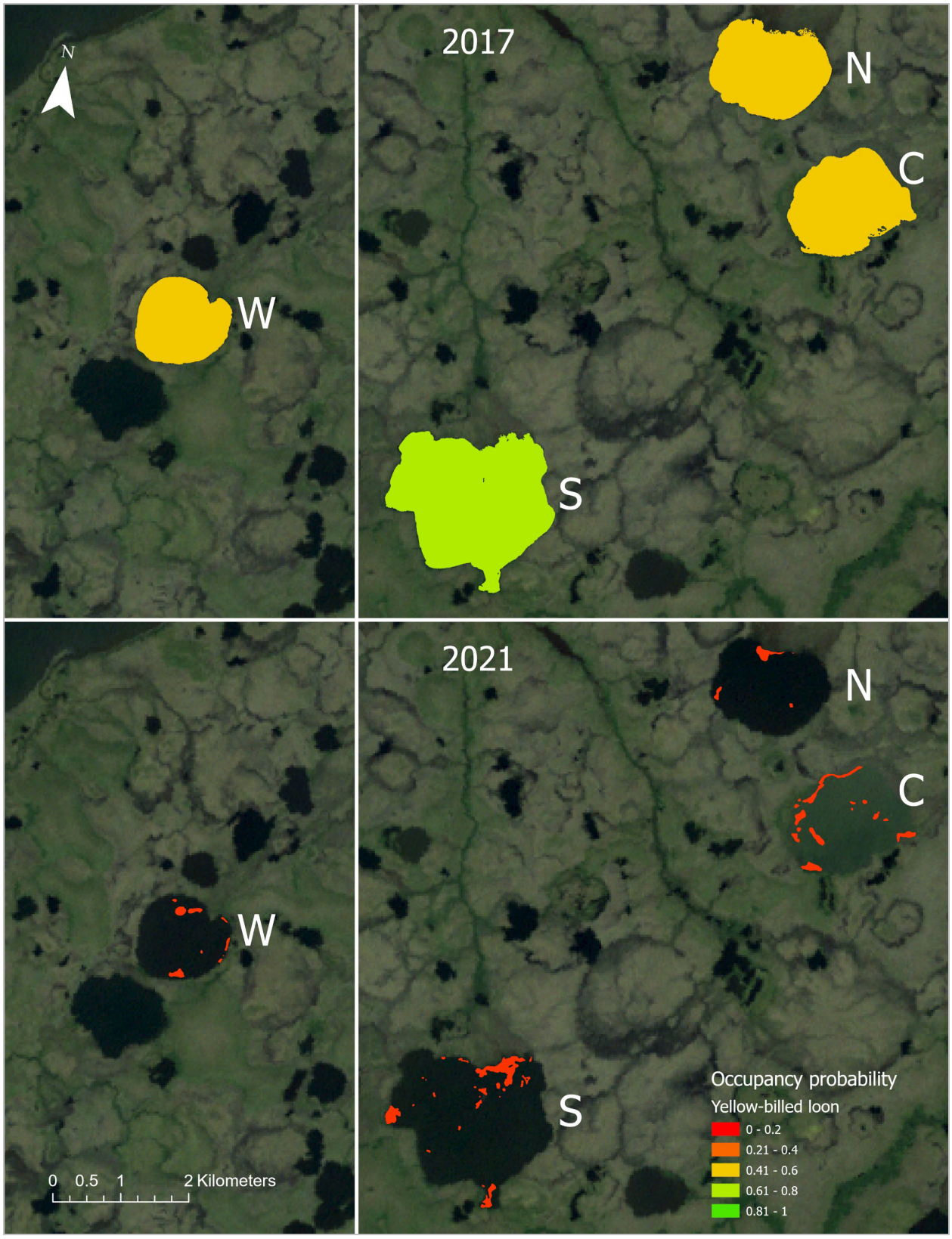


Figure 24. Yellow-billed Loon occupancy probability in the four drained lakes, pre- and post-drainage.

To better understand the effect of the 2018-2019 lake drainages on loons in BELA as a whole, we used the models of Mizel et al. (2021) to estimate loon occupancy before and after drainage of all the lakes that drained in 2018 and 2019 in the lake-rich zones of BELA as identified by Swanson (2020). The area of overlap between the study areas of Swanson (2020) and Mizel et al. (2021) is 5169 km^2 and covers most of the lakes in northern BELA (Figure 6). In 2018-2019, 17 lakes drained in this expanded study area, the four largest of which are our study lakes. The aggregate loon occupancy probability on these 17 drained lakes declined from 4.1 to 0.3 after drainage for Yellow-billed Loons and from 3.2 to 1.2 for Pacific Loons (Table 10). In contrast, the estimated aggregate occupancy probability of Red-throated Loons on the 17 lakes increased from 1.7 to 21.9. When compared to the estimated available loon habitat in the expanded study area covering most of northern BELA (Figure 6), the habitat change due to 2018-2019 lake drainage was -2.1% and -0.6% for Yellow-billed Loons and Pacific Loons, respectively, whereas Red-throated Loon habitat increased by +0.6% (Table 11).

Table 11. Change in modeled loon occupancy for drained lakes compared to occupancy available in all lakes.

Species	Study Area-Wide Occupancy[A] (pairs)	Change in Occupancy Units due to Lake Drainage, 2018-2019[B] (pairs)	Change in Occupancy Units due to Lake Drainage, 2018-2019[B] (percent of study area-wide occupancy)
Yellow-billed Loon	178.9	-3.8	-2.1
Pacific Loon	310.6	-2.0	-0.6
Red-throated Loon	3205.4	+20.2	+0.6

[A]Total loon occupancy units (number of mated pairs) in the overlap of Swanson's (2020) lake monitoring zones with Mizel et al.'s (2021) northern Seward Peninsula loon occupancy modeling study (Figure 6); covers most of the lakes in northern BELA. Estimates are for 2016-2018.

[B]Loss of occupancy units from lakes that drained in 2018-2019, a total of 17 lakes; see Table 10.

Wildlife Observations

During aerial loon surveys in 2018 observers reported caribou (*Rangifer tarandus*) on the barren mudflats of recently drained lakes. During fieldwork in 2019 we observed large waterfowl tracks (tundra swans, *Cygnus columbianus*, possibly Canada geese, *Branta canadensis*) in the mud of South Lake. In 2021 we observed a brown bear (*Ursus arctos*) grazing on herbaceous vegetation in North Lake. On 10 October 2022 during air travel over northern BELA ARCN staff (P. Sousanes) observed caribou grazing in the basins of recently drained lakes in the BELA vicinity, where green vegetation persisted after most vegetation had senesced.

Discussion

Lake Drainage and Permafrost

The drainage of the lakes early in the thaw season suggests that thermal erosion occurs during high water from snowmelt runoff. All lakes drained by deepening of pre-existing outlets, and not creation of entirely new drainageways. These outlets were small and mostly vegetated prior to drainage. The outlets apparently were stable when the water flow was limited, but vulnerable to thermal erosion due to the presence of massive ice bodies (probably mostly wedge ice). Record warm temperatures were observed during 2014-2019, culminating in mean annual temperatures above -2 °C and -1 °C at Devil Mountain and Kotzebue, respectively, in 2018-2019 (Figure 3; Swanson et al. 2021). Deep thaw during this time may have caused subsidence along the existing drainage outlets, so that water could overflow and erode a deeper outlet in the year of drainage. Deep snow and spring rains lead to increased runoff, which can also increase the hazard of thermo-erosion (Jones and Arp 2015). The sum of precipitation at Kotzebue for the period October-May consists almost entirely of snow and is released suddenly during snowmelt in late May and early June. Oct-May precipitation was the second highest on record for 2018 and above average for 2019 (Figure 4). Thus both temperature and precipitation were highly favorable for lake drainage in 2018 and 2019.

We lack frozen soil observations from 2019, but indirect evidence suggests minimal presence of frozen soil immediately after drainage, and thus initial plant colonization probably occurred in a permafrost-free environment. As noted in the "Study Area" section above, the lake bottoms lacked permafrost before drainage. Mean temperatures for the year immediately preceding our 2019 site visit (July 2018 through June 2019) were -1.6 °C and -0.1 °C at Devil Mountain and Kotzebue, respectively; these temperatures are generally too high to create permafrost in our environment (Jorgenson et al. 2008).

The presence of frozen soil at most locations sampled in July 2021 in the drained lake basins suggests that permafrost was re-forming in the drained lake bottoms. This would be expected according to the traditional concept of the thaw lake cycle (Billings and Peterson 1980) and the long-term mean annual air temperatures of the region near -5°C (Figure 3). However, the mean annual air temperature of -1.8 at Kotzebue during 2014-2019 (Figure 3 and Swanson et al. 2021) is in fact typical of the discontinuous permafrost zone, where permafrost is not present under all portions of the landscape, leaving some doubt as to whether permafrost would form in the drained lake basins. Apparently, colder temperatures during the year immediately preceding our sampling (-4.7 °C at Kotzebue for July 2020 through June 2021) were sufficient to allow initial permafrost aggradation in the drained lake basins. This had the important consequence of perching water over frozen soil and thereby making the soils considerably wetter in 2021 than they were at the time of our first visit in 2019.

Soils

The soils of the recently drained lake bottoms were relatively favorable for plant growth. Thaw depths were relatively deep (0.7 to 1.0 m by early July of 2021), thanks to the absence of a surface organic layer. Dark colors suggest high organic matter content and thus likely high availability of

nitrogen and probably other organic-matter associated nutrients such phosphorus. The organic matter was finely disseminated in mineral sediment, producing a weakly acid to neutral pH (6.2 to 6.8) and thus ideal growing conditions for species adapted to wetness and generally cold conditions.

The soils of the older drained lake basins had more severe plant growth limitations: in addition to wetness, these peat-dominated soils were acidic (pH 4.0 to 5.8), and hence had poorer nutrient availability, and were colder with thin active layers (0.5 m or less) over permafrost. The species that dominate drained lakes after centuries of peat accumulation consist of species (e.g. *Sphagnum* mosses and *Carex aquatilis*) are adapted to these specific plant growth limitations.

The thickness of the surface organic layers in the older drained lake basins (from 20 cm to more than 35 cm) suggest centuries have elapsed since drainage. Jones et al. (2012) studied the rate of peat accumulation in drained lake basin of northern BELA using cores and radiocarbon dating. They found rather rapid rates of initial peat accumulation: for lakes that drained in the last 2000 years, the rate of accumulation was roughly linear ($R^2 = 0.68$), $y = 0.0286x + 11.508$, where y is the peat depth and x the age in years. By this formula, about 300 years would typically be required to develop a 20-cm thick surface peat layer; this is probably the point beyond which most plants are forced to root mainly in acid peat rather than the organic-rich mineral soil that composes the post-drainage lake bottom mud. Jones et al.'s (2012) data showed considerable scatter; several sites with 20-cm thick peat layers had radiocarbon dates indicating drainage about 700 years previously, and one lake with a date of 250 years already had 35 cm of peat. Hinkel et al. (2003) studied cores from drained lake basins near Barrow, Alaska and found comparable rates of peat accumulation to Jones et al. (2012). Therefore, it appears that in our area, 200 to 700 years are needed to accumulate the 20+ cm-thick surface peat layer typical of older drained lake basins. Thus several centuries are probably required to create conditions that allow only the more acid-tolerant plants (Table 6: *Sphagnum*, *Betula nana*, *Carex aquatilis*, *Ledum*, etc.) to survive.

The buried peat horizons at 3 out of 10 plots in Central Lake indicate two episodes of lower water levels that exposed only part of the lake bottom. Both the peaty horizons (4 to 10 cm thick) and the overlying lake sediment layers (13-30 cm over the upper peat horizon, 14 to 41 cm between the two peat horizons) suggest substantial time of both subaerial exposure and submergence, but radiocarbon dating would be required to determine the actual dates and durations. Buried peat horizons were not encountered in the other lakes, but the few plots in the other lakes do not rule out the possibility of partial exposure there too. The fact that these episodes were localized and reversible suggest a different process than near-total lake drainage that occurred in 2018-2019. It is possible that minor changes in ground elevation in the outlet stream channel near a lake, due to gain or loss of ground ice, could affect the lake level. Another possibility is that dry climatic conditions caused a drop in water levels, exposing parts of the lake bottom and allowing permafrost formation and frost heave on the exposed areas to raise the surface further. Significant fluctuations in lake level could have implications for seed dispersal and banking, as discussed below.

Greenness and Phenology

A remote sensing study on drained lake basins in the North Slope of Alaska found that peak midsummer vegetation greenness rapidly increased following drainage, and after 5 years it exceeded

that of the surrounding areas (Chen et al. 2021). They also found that the elevated greenness that develops post-drainage vegetation persists for at least 15 years. Satellite imagery from the fall of 2022 shows green vegetation in the study drained lakes persisted after most of the landscape has senesced (Figure 25).

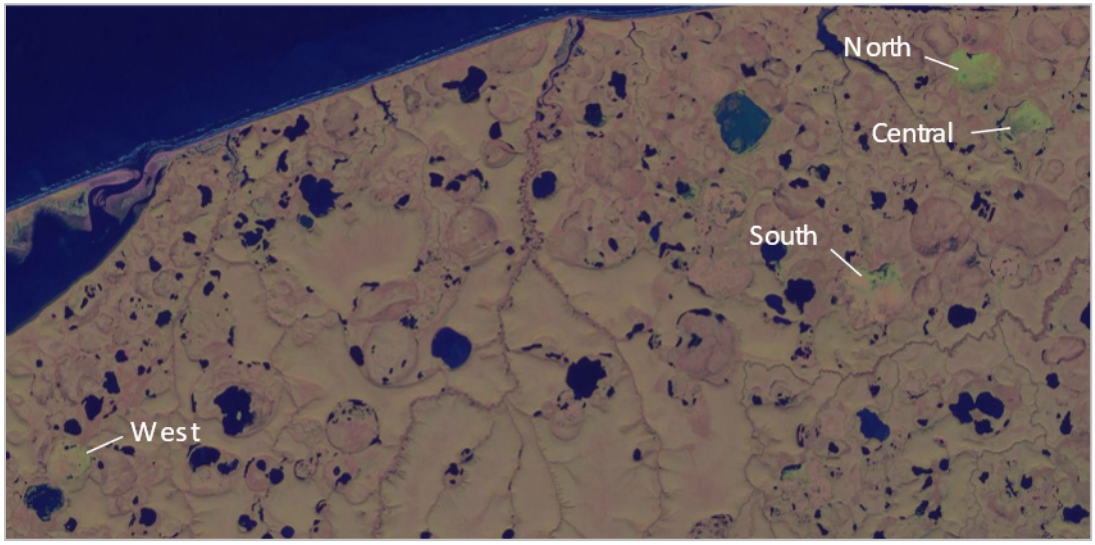


Figure 25. Persistent green vegetation in drained lake basins in the fall. This Sentinel-2 satellite image from 30 September 2022 shows brown senesced vegetation over most of the landscape in northern BELA, with conspicuous patches of persistent green vegetation in the study drained lakes.

Plant Establishment

The very rapid colonization of some of the lake bottoms suggest that plant propagules were present in the lake-bottom mud prior to lake drainage. Central Lake provided especially strong evidence for lake-bottom seed-banking: the lake drained in June 2018 and new vegetation expanded rapidly on the lake bottom in July of 2018 (Figure 9); this was too soon for the release and establishment of seeds from the 2018 crop of the surrounding area. Our visit in 2019 showed that the new vegetation was mostly *Eleocharis acicularis* (Figures. 10 and 26), a small graminoid (spike rush) which is uncommon but occasionally recorded along lakeshores. This suggests that stands of *E. acicularis* on lakeshores supplied seeds that accumulated in lake-bottom muds hundreds of meters from the shore. It is possible that temporary low lake levels (which can occur, as shown by the buried peat layers in the lake sediments) in the past allowed *E. acicularis* to expand along the shore and shed more seeds into the water than would be expected from its current sparse occurrence. While vegetative spread is clearly important for many species, given realistic growth rates in the arctic of any plant of only a few meters per year, vegetative growth can explain densification of stands and gradual growth of clones, but not the sudden appearance of plants such as *E. acicularis* over large areas. *E. acicularis* seed was found to be viable for up to 20 years in a midwestern study of prairie wetland seedbanks (Wienhold and van der Valk 1989).



Figure 26. *Eleocharis acicularis* (“spike rush”), a small wetland graminoid that formed dense stands very quickly after drainage in some lakes.

Equisetum arvense also rapidly colonized the drained lake bottoms to form nearly continuous stands in post-drainage year 1, most notably in West lake (Figures 11 and 19). *E. arvense* is fairly common on lakeshores and in surrounding tundra habitats, especially on disturbed soils, and it produces windborne spores in the spring. *Equisetum* spores are short-lived, germinate quickly on moist mud, and lose viability within weeks (Husby 2013). Lake-bottom banking of propagules for *Equisetum arvense* (spores) is therefore unlikely. After germination, *Equisetum* spores do not immediately form the familiar plants that we observe (the sporophyte generation), but instead must first form small male and female gametophyte plants that form a sporophyte after fertilization, a process that takes about a month and requires a moist substrate (Matzke 1941). This is probably why in the year of drainage (2018) West Lake did not show a discernable rise in NDVI that would indicate a dense plant cover (Figure 9), but then *E. arvense* rapidly colonized it in the following year. Apparently lightweight *Equisetum* spores released from land surrounding the lake in 2018 were able to establish on moist mud across the lake, pass through the gametophyte stage to form small sporophytes later in 2018. Then the sporophytes rapidly spread vegetatively to fill in gaps by the time of our early July 2019 visit.

Tephroseris palustris has windborne seeds that can survive submergence in lake-bottom mud and germinate readily after exposure (ter Heerdt and Drost 1994). *T. palustris* is uncommon in our area except on moist, disturbed soil, and dispersal from a few plants along the shore flowering in the fall

of 2018 to form extensive stands like the one illustrated in Figure 2 in 2019 is unlikely. *T. palustris* is considered to be an annual or biennial, so in principle there could have been scattered plants that sprouted from lake-bottom muds in 2018 and produced seed that resulted in dense flowering stands in 2019. However, the lack of dead stems in 2019 from plants that flowered in the previous year (Figure 2) suggests that the dense stands visible in 2019 came mostly from banked seeds that sprouted in 2018 and flowered in 2019 as biennials. Dense, near-monocultural stands of *Tephroseris* that persisted locally into the second and third years after drainage show how this plant is able to temporarily out-compete perennials and continue to establish from seed.

Rorippa palustris is another plant that is uncommon on lakeshores but common on recently drained lakes. *R. palustris* formed distinctive curvilinear stands on South lake that coincided with linear accumulations of mollusk shells, which we interpret to be temporary shorelines as the water level dropped during drainage. In European studies, *R. palustris* has been found to be primarily water-dispersed, and its seeds remain buoyant for over a month (Bendová 2002 in Klimešová et al. 2004). Multiple studies have found *R. palustris* seeds to be disproportionately abundant in the seedbanks of wetlands and floodplains (Beas et al. 2013; Cho et al. 2018; Neff et al. 2009). Long-term viability of *R. palustris* seeds is not known; one study found seeds were only viable for five years with a sharp decrease in germination after two years (Jonsell 1968). However, colder climates may have longer viability periods. Thus *R. palustris* can be dispersed by floating in water, and seeds produced by relatively rare plants on the shore could accumulate in a lake and colonize newly exposed lake bottoms.

Arctophila fulva is a common emergent grass in arctic lakes. Its colonization of the drained lake bottoms from banked seeds or vegetative expansion from existing plants that were formerly in shallow water is not surprising. Vigorous *A. fulva* plants growing from moist mud illustrate that it does not require standing water, and that its absence from older drained lake basins is probably due to it being out-competed by other species on peaty, acidic soils.

The generally slower colonization of South Lake by plants could be the result of 1) later drainage of this lake in the summer: late drainage may have caused much of the lake bottom to be exposed after *Equisetum* spores of the year had been dispersed or had become non-viable. Or, 2) the sandier substrate of South Lake than in the other lakes, may have been less favorable for spore or seedling establishment due to dryness in the first summer after drainage. The soil electrical conductivity and pH of South Lake sediments were similar to other lakes, suggesting that unfavorable soil chemistry was not an issue. Small patches of *E. acicularis* were brown and appeared desiccated on South Lake in 2019. Dessication cracks in July 2019 also suggest drought limitations on plant establishment (Figure 27), and as discussed above, there was probably no perching of water on frozen soil at this point. By 2021, perhaps due in part to the formation of permafrost and consequent perching of water, the typical drained-lake plants had colonized South Lake like the others.



Figure 27. Desiccation cracks in South Lake on 10 July 2019, one year after drainage. The yellow flowering plants are *Tephroseris palustris*. Latitude 66.498245, longitude -164.196103.

Plant Succession in the Past and Present

The ordinations suggest that in the first few years after drainage, the disparate initial plant communities (often dominated by just one or two pioneering species) converge toward more diverse communities composed of several common wetland-adapted perennials. Dispersal from surrounding areas, or establishment from lake-bottom seed banks, result in few species becoming established and expanding quickly over the resource-rich lake-bottom environment. Most of these species are poor competitors in a more crowded plant environment due to low stature or short lifespan. Taller, more long-lived species such as *Arctophila fulva*, *Eriophorum scheuchzeri*, and *Carex aquatilis* were often already dominant in year 3 after drainage and will presumably remain so in the coming years. There is still an element of chance dominance by early arrival among these plants, as shown by near monocultures of *E. schezuchzeri* on Central Lake in 2021, for example (see the front cover overleaf photo), but the trend appears to be toward a more diverse mixture.

The older drained lakes sampled for ARCN vegetation monitoring differ from our third-year samples: *C. aquatilis* was the dominant rather than a subordinate graminoid species, *Sphagnum* mosses were widespread, a variety of wetland-adapted shrubs were present in low cover, *Arctophila*

fulva was absent, soils were acidic peats rather than circumneutral organic mud. The transition from *Arctophila*-dominated organic mud to *C. aquatilis*-dominated acid peat probably depends on the accumulation of peat, colonization by *Sphagnum*, and the growth of *C. aquatilis* clones. As noted previously, accumulation of about 20 cm of peat in our study area requires 200-700 years (Jones et al. 2012).

Our data show that in just 3 years the drained lakes already appear to be transitioning towards the vegetation established in older drained lake basins. The complete transition could take centuries as acid peat accumulates and *Sphagnum* mosses come to dominate.

Clues about what the vegetation of the thaw lakes will look like a few decades after thaw lake drainage are provided by several other studies of drained lake vegetation in North America. Billings and Peterson (1980) studied an artificially drained lake near Barrow Alaska. They described mosses (other than *Sphagnum*) as the colonists of drained lakes during the first few years. Their main sample was 27 to 28 years after drainage, and then the most common plant was the coastal grass *Dupontia fisheri*, which we did not observe, along with *Arctophila fulva* and *Eriophorum scheuchzeri*. The typical species of older drained lakes, *Carex aquatilis* and *Eriophorum angustifolium*, were still quite rare after 28 years. They suggested a gradual transition from *Dupontia-Eriophorum scheuchzeri-Arctophila* to dominance by *Carex aquatilis* over an unknown length of time.

Hinkel et al. (2003) developed a developmental sequence for vegetation, soils, and permafrost on the North Slope of Alaska near Utqiagvik (Barrow) that was supported by radiocarbon dates. Their data suggest that the transition to a *C. aquatilis* community on peaty soil occurs gradually over several centuries. They described young lake basins (less than 50 years since drainage) as dominated by *A. fulva*, *D. fisheri*, and *E. scheuchzeri* on soils with little accumulated surface peat. Medium-aged basins (50-300 years) showed clones of *Eriophorum angustifolium* and *C. aquatilis* expanding within a matrix of plants like the young phase, on soils with 10-15 cm of surface peat. Old basins (300-2000 years) were dominated by *C. aquatilis* and *Sphagnum* sp. mosses, with 15-30 cm of surface peat. Ancient basins (2000-5500 years old) were still dominated by *C. aquatilis* but had a variety of drier microsites, with other plants, that formed as ice-wedge polygons developed, along with new ponds formed by thaw of the ice wedges.

Wilson (2018) summarized vegetation change in a lake in the Mackenzie River delta of Canada that was experimentally drained in 1978 and vegetation sampled 7, 15, 23, and 38 years later. Over half of the lake basin was still sparsely vegetated after 7 years and portions remained sparsely vegetated throughout the study, perhaps due to fluctuations in the size of residual ponds. Year 7 was still dominated by pioneering species, including many that we observed (*Equisetum arvense*, *Tephroseris palustris*, *Arctophila fulva*) and some that we did not (*Puccinellia* sp., *Descuriana sophioides*). In year 15 grasses and *Equisetum arvense* dominated, and a variety of willows had become established. Notably, the grasses were not the aquatic *Arctophila fulva* but instead more mesic species, especially *Arctagrostis latifolia*. By year 23 the willows had become common, *A. latifolia* and *E. arvense* persisted, and *Carex aquatilis* had expanded. By year 38 the plants with greatest cover were mosses, an assortment of low to tall willows (*Salix alaxensis, arbusculoides, glauca, pulchra, richardsonii*), and *Carex aquatilis*. *Betula glandulosa* was widespread, and ericaceous shrubs had become

established (*Ledum, Vaccinium*), while *Equisetum arvense* and *Arctagrostis latifolia* had declined. By year 38, soils had a pH of about 6 and the active layer was 0.6 to 1.1 m, depending on vegetation; soils were loamy.

Wilson's (2018) data are interesting because they show both a transition to *Carex aquatilis* (which our data also suggests) and to dominance of low- to tall willows over much of the lake bottom. Willows were not significant components of either the recent or the older drained lakes in ARCN that we sampled. Wet, acid, peat soils are not ideal for willow growth (Swanson 2015), so willows are not likely to dominate in wet lake basins several centuries after drainage when peat soils have accumulated. But a transitory willow phase in the drained lake basins beginning in a decade or two and lasting a few centuries until acid peat soils develop is possible and would be a significant development.

We have observed willow thickets in drained lakes in ARCN (Figure 28). It is likely that locations with better drainage favor the success of willows over dense stands of wetland graminoids. In contrast, our four study lakes had very poor drainage conditions, such that they became covered with water each spring due to snowmelt (Figure 7). The lake in Figure 28 has a slightly incised channel across its length that clearly has favored the growth of willows. Headward erosion of the drainage channel across the lakebed that results in an incised channel could be a path to willow dominance. Locally better drainage on a drained lakebed can also be present on topographic highs surrounded by thermokarst depressions.

Jorgenson et al. (2009) recognized a variety of ecotypes (vegetation types) associated with drained lake basins in ARCN. The most widespread drained lake ecotype is Lacustrine Wet Sedge Meadow, which is dominated by *Carex aquatilis*, mosses, and a variety of forbs, especially *Comarum palustre*. Willow thickets were also identified in lake basins as ecotype Lacustrine Willow Shrub, dominated by *Salix pulchra* and *S. richardsonii*, with a sedge and moss understory. Lacustrine Willow Shrub had distinctly deeper average water tables (31 cm) than Lacustrine Wet Sedge Meadow (7 cm), confirming that drier lakebeds are indeed more likely to be colonized by willows. Other ecotypes of drained lakes include Lacustrine Barrens (in recently drained lakes) and several very wet types found in or around residual ponds (Lacustrine Buckbean Fen, Lacustrine Horsetail Marsh, Lacustrine Marestail Marsh, and Lacustrine Pendent Grass Marsh). This variety of types demonstrates the diverse mosaic of vegetation types that develops in drained lakes.

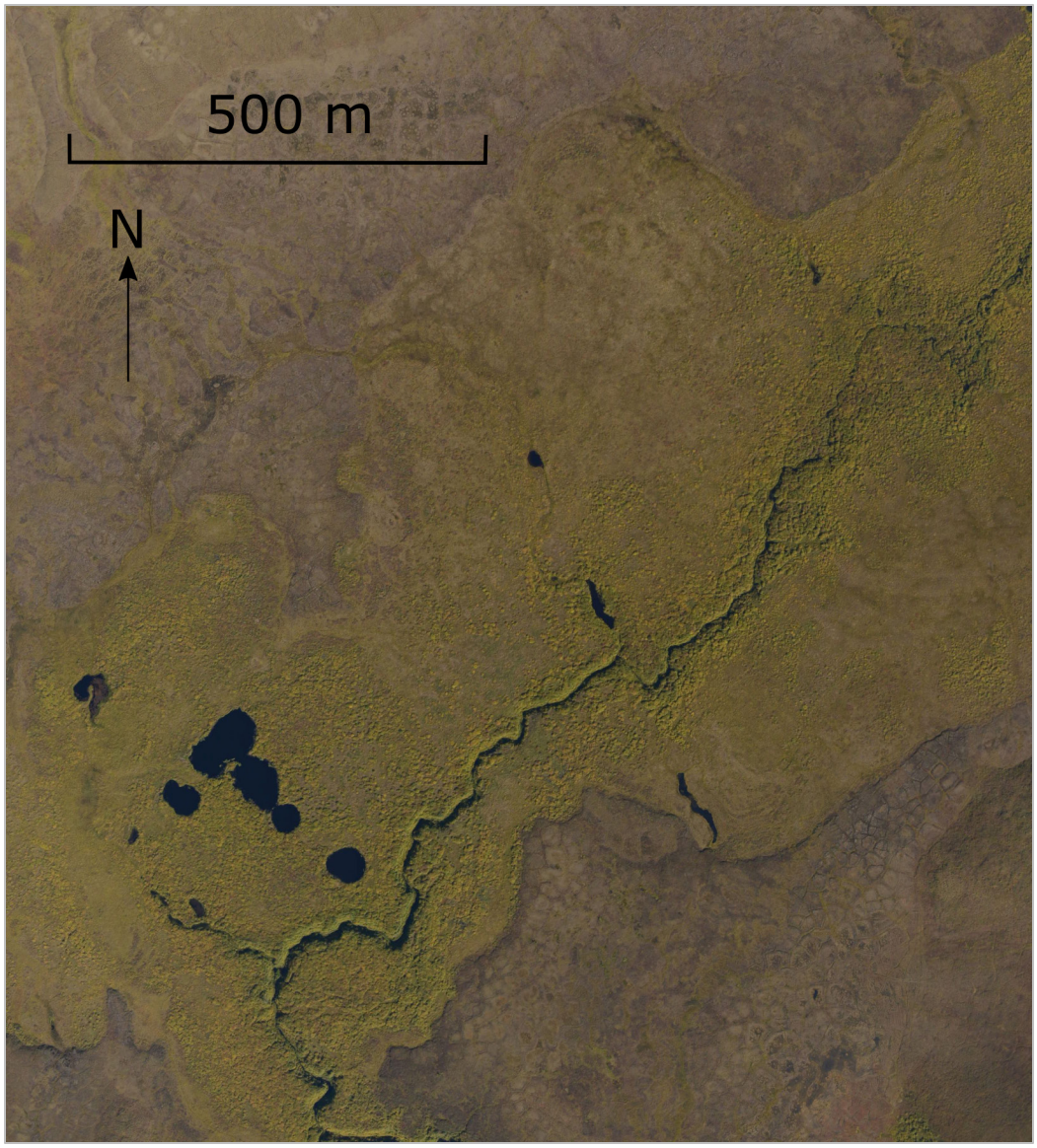


Figure 28. Aerial photograph of a drained lake in BELA with abundant shrubs, most likely willows. Shrubs cover the bright green areas with mottled texture (due to shadows cast by the shrubs). This drained lake is centered near latitude 66.25°, longitude -164.65°. NPS photo by Matt Nolan, 1 Sept 2013. This lake drained before the earliest available aerial photographs (8 Sept 1949).

Plant Succession in the Future with Climate Warming

One important question is whether new communities that form in the long term under the warming climate regime will be different from those of older drained lakes that we see today. Whether the incipient permafrost that we observed will persist and aggrade further in the future is especially significant. If permafrost fails to form, or if conditions are not cold enough for new ice-wedge formation, then the communities of the future will be different from what we see on older drained lakes today. As a result of their flat topography and low-permeability substrate, wetlands are likely to dominate these lake basins in the future even if permafrost fails to form; indeed *Sphagnum*-dominated peatlands are common on flat, fine-grained lake sediments in moist, modern non-

permafrost climates (Heinselman 1963). The spring saturation and inundation due to snowmelt that we observed are likely to continue in the future, and the type of wetlands that develop will depend on how long saturation persists through the summer.

We suggest two likely scenarios in a warmer climate: 1) Peat-dominated, permanent wetlands. Permafrost re-establishes, or at least seasonal frozen soil persists through much of the growing season; this frozen soil in combination with the moderately low permeability of the silt-loam lake basin sediments and adequate summer precipitation maintain soil saturation near the surface. *Carex aquatilis-Sphagnum* wetlands develop similar to those present in older drained lake basins today, though without development of new ice-wedge polygons and related microtopography. 2) Seasonal wetlands. Permafrost fails to develop and seasonal frozen layers thaw by mid-summer. Soil permeability is adequate to allow the water table to drop below plant rooting zones by late summer. A peat layer fails to develop. Vegetation is dominated by more mesic vegetation such as willow shrubs and grasses such as *Calamagrostis canadensis*. This scenario is most likely in places with more permeable sandy lake sediments such as on South Lake. Continued long-term monitoring of these lake basins will provide information about long-term trends.

Loon Habitat

The diverse mosaic of highly productive vegetation and residual small ponds that develops after lake drainage is probably good habitat for a variety of wildlife species. We predicted that habitat for the most abundant loon species, the Red-throated Loon, could actually increase as lakes drain and split into multiple residual ponds. This is because loons tend to defend a lake as a nesting territory, and a lake drainage typically results in the creation of several residual ponds, some of which are still large enough for a pair of Red-throated Loons. However, these ponds are typically too small for Yellow-billed and Pacific Loons, which require a larger body of water as a runway for flight take-offs. The Yellow-bill Loon in particular requires rather large water bodies, and it showed the largest modeled decline in potential habitat as a result of lake drainage. Our estimate of a 2% loss in Yellow-billed Loon nesting habitat as a result of lake drainages in 2018-2019 alone appears small in isolation, but could be significant if lakes continue to drain or decline in size.

Future work

The projected re-visit interval for ARCN vegetation monitoring plots is 10 to 15 years. Assuming that funding and personnel are available, the 16 permanent monitoring plots established as a part of this study will be re-visited in the 2030 decade. In view of the rapid change that we observed, a visit approximately 5 years after the one reported here (i.e. around 2026) could be justified if funding is available. If a helicopter large enough to accomplish transport of the crew and gear in one trip from Nome is available, the whole project requires about 5.5 hours of flight time and about a week of staff time for two people.

Additional low-cost monitoring of major trends in vegetation greenness could be accomplished by satellite remote sensing. Analysis of trends in greenness (NDVI), similar to what was performed here for the first three years after drainage, could be continued in the future. To provide additional perspective on long-term changes, this analysis could also be performed using archived satellite images on other lakes that drained earlier. See Swanson (2020) Figure 8 for potential study lakes that

drained in the 2000 decade. NDVI analysis could be performed on images from a variety of sources, including Planet images as in this report, Landsat as in Swanson (2020), Sentinel-2 (European Space Agency 2022), or MODIS/VIIRS as in Swanson (2021). Planet images for BELA became available starting in 2016 and provide almost daily coverage at 3 m resolution. Sentinel-2 has 10 m resolution, with coverage every few days beginning in 2017. Landsat has 30 m resolution and the oldest record, beginning with sporadic images in the 1980s and approximately weekly images starting around the year 2000. MODIS and VIIRS provide daily images at coarse resolution (250 and 375 m, respectively) starting in the year 2000. We recommend investigating both the peak greenness, which is related to the biomass and plant community present, and the persistence of greenness into the fall, which is of interest for wildlife forage. A convenient way to access MODIS and VIIRS data is through the AppEEARS tool (AppEEARS 2020), which would allow one to extract long time series for a point or small area in a drained lake. Using these data, one could construct annual NDVI curves similar to those in Figure 9, using the methods described in Swanson (2021), and extract information about the height of peak greenness and timing of fall senescence.

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Appendix A: Vegetation Mapping Units

Table A1. Vegetation mapping unit descriptions.

Sort	Maps[A]	Name	Description	Examples[B]
1	All	Water	Water with little or no emergent or submerged vegetation	–
2	C19, N21, S19, S21, W19	Mud	Mud with vegetation cover of less than 10%	Plot 1 (S 2019), P7100968_A_2019.JPG (S 2019)
3	W19	Hippuris marsh	Formerly emergent stands of *Hippuris* sp. that are now growing out of wet mud.	P7100987_A_2019.JPG (W 2019, far right), P7101001_A_2019.JPG (W 2019, far right)
3	C21, S19, S21, W19	Sparse vegetation	Ground cover of *Equisetum arvense* is not continuous, patches of bare mud are visible; scattered plants of *Arctophila* and *Rorippa* present	P7100986_A_2019.JPG (W 2019), P7100978_A_2019.JPG (S 2019)
4	C19, C21	Eleocharis	Dense mat of *Eleocharis acicularis*, sparse to no cover by taller plants	Plot 14 (C 2019), P7100954_A_2019.JPG (C 2019)
5	S19, W19	Equisetum	Dense mat of *Equisetum arvense*, sparse to no cover by taller plants	Plot 16 (W 2019), P7100997_A_2019.JPG (W 2019), P7100998_A_2019.JPG (W 2019)
6	N21, S21, W21,	Equisetum with tall graminoids	Ground covered by *Equisetum arvense* with open tall graminoids (*Arctophila fulva*, *Eriophorum scheuchzeri*, occasionally *Carex aquatilis*)	Plot 1(S 2021), P7070069.JPG (S 2021), P7130521.JPG (W 2021),
7	C21	Very wet graminoids	Ponded shallow water with *Eleocharis acicularis* and sparse tall graminoids	Plot 7 (C 2021)
8	C19, W21	Open Tephroseris	*Tephroseris palustris* cover less than 50%, often over *Eleocharis acicularis*	P7100960_A_2019.JPG (C 2019)

[A]C – Central, N – North, S – South, W – West Lakes; 19 and 21 refer to the years 2019 and 2021.

[B]Plots numbers are from the ARCN Espenberg monitoring plots; photos are from the ARCN Vegetation Vital Sign Monitoring collection.

Table A1 (continued). Vegetation mapping unit descriptions.

Sort	Maps[A]	Name	Description	Examples[B]
9	S21, C19, C21, N21	Dense Tephroseris	*Tephroseris palustris* cover over 50%	P7070076.JPG (C 2021), P7130519.JPG (W 2021), Plot 11 (C 2021)
10	C21	Open Eriophorum	*Eriophorum scheuchzeri* conspicuous but less than 50% cover.	Plot 15 (C 2021)
11	C21	Dense Eriophorum	*Eriophorum scheuchzeri* dominates	P7120370.JPG (C 2021)
12	C21	Open tall graminoids	*Arctophila fulva, Eriophorum scheuchzeri*, occasionally *Carex aquatilis* with over 50% cover	Plots 12 and 14 (C 2021), P7070069.JPG (S 2021)
13	C21, N21, S21, W21	Dense tall graminoids	*Arctophila fulva, Eriophorum scheuchzeri*, occasionally *Carex aquatilis* with over 50% cover	P7070071.JPG (S 2021)

[A]C – Central, N – North, S – South, W – West Lakes; 19 and 21 refer to the years 2019 and 2021.

[B]Plots numbers are from the ARCN Espenberg monitoring plots; photos are from the ARCN Vegetation Vital Sign Monitoring collection.

Appendix B: Estimated Loon Occupancy of Lakes

Table B1. Water area and loon occupancy of the four study lakes before drainage.[A]

Lake	Water area (ha)	Loon occupancy		
		Yellow-billed	Pacific	Red-throated
Central	203.88	0.50	0.30	0.06
North	193.50	0.48	0.29	0.07
South	384.95	0.63	0.38	0.03
West	140.56	0.43	0.27	0.07
All	922.89	2.04	1.24	0.23

[A]Lake areas taken from detailed (3-m resolution) maps for the four lakes in the current study, produced from Planet Lab satellite images.

Table B2. Water area and aggregated loon occupancy of post-drainage residual ponds in the four study lakes.[A]

Lake	Water area (ha)	Loon occupancy		
		Yellow-billed	Pacific	Red-throated
Central	16.43	0.00	0.26	5.23
North	4.57	0.00	0.06	1.52
South	22.06	0.10	0.23	6.12
West	6.14	0.00	0.13	3.28
All	49.20	0.10	0.67	16.15

[A]Values in the table are sums for all residual ponds that originated from drainage of the listed lake. Lake areas taken from detailed (3-m resolution) maps for the four lakes in the current study, produced from Planet Lab satellite images.

Table B3. Water area and loon occupancy before drainage of BELA lakes that drained in 2018-2019.[A]

Lake ID	Water area (ha)	Loon occupancy		
		Yellow-billed	Pacific	Red-throated
221	362.54	0.63	0.39	0.02
236	130.10	0.44	0.28	0.06
317	7.35	0.09	0.09	0.24
524	9.55	0.11	0.11	0.16
811	16.70	0.17	0.14	0.11
1499	30.90	0.21	0.16	0.13

[A]Lake areas taken from 30-m resolution maps of surface water covering most of northern BELA, produced using Landsat satellite images by USGS (2019) and Swanson (2020).

Table B3 (continued). Water area and loon occupancy before drainage of BELA Lakes that drained in 2018-2019.[A]

Lake ID	Water area (ha)	Loon occupancy		
		Yellow-billed	Pacific	Red-throated
1988	180.01	0.48	0.30	0.06
2219	182.20	0.49	0.30	0.06
2337	30.07	0.23	0.17	0.09
2661	20.67	0.21	0.17	0.06
3210	5.49	0.00	0.07	0.33
4271	6.46	0.00	0.09	0.18
4717	57.19	0.42	0.28	0.01
5233	11.23	0.18	0.16	0.02
5920	6.95	0.00	0.13	0.03
5993	9.93	0.17	0.16	0.02
6441	33.18	0.22	0.17	0.14
All	1100.55	4.06	3.17	1.73

[A]Lake areas taken from 30-m resolution maps of surface water covering most of northern BELA, produced using Landsat satellite images by USGS (2019) and Swanson (2020).

Table B4. Water area and aggregated loon occupancy of post-drainage residual ponds of lakes that drained in BELA, 2018-2019.[A]

Lake ID	Water area (ha)	Loon occupancy		
		Yellow-billed	Pacific	Red-throated
221	28.00	0.13	0.34	6.11
236	2.08	0.00	0.04	1.16
317	2.14	0.00	0.05	1.19
524	0.63	0.00	0.00	0.48
811	1.20	0.00	0.00	0.42
1499	1.18	0.00	0.00	0.85
1988	5.31	0.00	0.10	3.08
2219	14.28	0.09	0.18	4.15
2337	10.81	0.12	0.12	0.46
2661	0.21	0.00	0.00	0.13
3210	0.27	0.00	0.00	0.74
4271	0.32	0.00	0.00	0.25
4717	3.84	0.00	0.14	0.23

[A]Values in the table are sums for all residual ponds that originated from drainage of the listed lake. Lake IDs are arbitrary numbers assigned by the GIS. Lake areas taken from 30-m resolution maps of surface water covering most of northern BELA, produced using Landsat satellite images by USGS (2019) and Swanson (2020).

Table B4 (continued). Water area and aggregated loon occupancy of post-drainage residual ponds of lakes that drained in BELA, 2018-2019.[A]

Lake ID	Water area (ha)	Loon occupancy		
		Yellow-billed	Pacific	Red-throated
5233	0.49	0.00	0.00	0.11
5920	0.49	0.00	0.00	0.17
5993	4.86	0.00	0.16	0.18
6441	7.82	0.00	0.09	2.15
All	83.92	0.35	1.21	21.85

[A]Values in the table are sums for all residual ponds that originated from drainage of the listed lake. Lake IDs are arbitrary numbers assigned by the GIS. Lake areas taken from 30-m resolution maps of surface water covering most of northern BELA, produced using Landsat satellite images by USGS (2019) and Swanson (2020).

The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

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Natural Resource Stewardship and Science
1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525