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# Patterns of Terrestrial and Limnologic Development in the Northern Greater Yellowstone Ecosystem (USA) during the Late-Glacial/Early-Holocene Transition

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# Patterns of Terrestrial and Limnologic Development in the Northern Greater Yellowstone Ecosystem (USA) during the Late-Glacial/Early-Holocene Transition

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## Abstract

A high-resolution record of pollen, charcoal, diatom, and lithologic data from Dailey Lake in southwestern Montana describes postglacial terrestrial and limnologic development from ice retreat ca. 16,000 cal yr BP through the early Holocene. Following deglaciation, the landscape surrounding Dailey Lake was sparsely vegetated, and erosional input into the lake was high. As summer insolation increased and ice recessional processes subsided, *Picea* parkland developed and diatoms established in the lake at 13,300 cal yr BP. Closed subalpine forests of *Picea*, *Abies*, and *Pinus* established at 12,300 cal yr BP followed by the development of open *Pinus* and *Pseudotsuga* forests at 10,200 cal yr BP. Increased planktic diatom abundance indicates a step-like warming at 13,100 cal yr BP, and alternations between planktic and tychoplanktic taxa suggest changes in lake thermal structure between

12,400 and 11,400 cal yr BP. An increasingly open forest, in combination with increased benthic diatoms, indicates warm dry summers during the early Holocene after 11,400 cal yr BP, in contrast to nearby records in northern Yellowstone that register prolonged summer-wet conditions until ca. 8000 cal yr BP. Because of its low elevation, Dailey Lake was apparently sensitive to the direct effects of increased summer insolation on temperature and effective moisture, registering dry summers. In contrast, higher elevations in northern Yellowstone responded to the indirect effects of an amplified seasonal insolation cycle on atmospheric circulation, including elevated winter snowpack and/or increased summer convective storms as a result of enhanced monsoonal circulation.

**Keywords:** late-glacial, early Holocene, pollen, diatoms, Yellowstone

## 1. Introduction

The period from 20,000 to 8000 cal yr BP was a time of rapid environmental change in the western US as the region shifted from full glacial conditions to the summer insolation maximum of the early Holocene. In the northern Rocky Mountains, glaciers receded from their maximum position by ca. 17,000 cal yr BP and were largely gone by 14,000 cal yr BP (Licciardi et al., 2004; Pierce, 2004; Licciardi and Pierce, 2008; Thackray, 2008). The freshly exposed landscapes created by ice recession afforded new habitats for plants and animals to colonize and set in motion a series of time-dependent changes in local-scale processes, including soil, vegetation, and limnologic development.

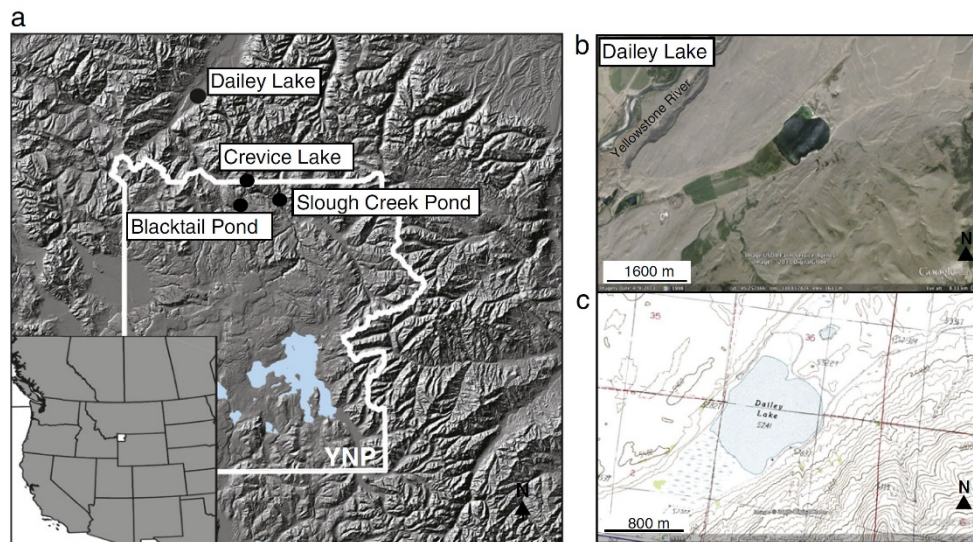
Although the record of postglacial colonization is clear from paleoecological data throughout the northern Rocky Mountains (e.g., Whitlock, 1993; Brunelle et al., 2005; Power et al., 2011), the relative trade-off between climate and local-scale controls in shaping the sequence of biotic development during the late-glacial/early-Holocene transition is poorly understood. Large-scale climatic variability is clearly the primary driver of postglacial ecosystem change at broad temporal and spatial scales; however, substrate, local topography, and species life-history traits become increasingly important at finer scales (e.g., Brubaker, 1975; Millspaugh et al., 2000; Oswald et al., 2003; Briles et al., 2011). Furthermore, modern studies have highlighted strong linkages between limnologic development and trajectories of soil and vegetation development in newly deglaciated catchments (Engstrom et al., 2000; Engstrom and Fritz, 2006), but few paleoecological sites compare terrestrial and aquatic responses in the past to understand how well these linkages were expressed in the early stages of postglacial landscape development (but see Birks et al., 2000).

This paper examines early postglacial ecosystem development in the Greater Yellowstone region during the period from ca. 16,000 to ca. 7000 cal yr BP based on pollen, charcoal, diatom, and lithologic data from Dailey Lake, Montana (45.262°N, 110.815°W; 1598 m elev, 82 ha). Dailey Lake is a low-elevation site located 23 km up-valley of the terminal moraine of the northern Yellowstone outlet glacier and thus provides one of the earliest records of postglacial environmental change in the region. Our objectives in this paper are to: (1) describe the sequence of terrestrial and limnologic changes that occurred between the time of ice retreat to the early Holocene insolation maximum; (2) identify linkages be-

tween vegetation and limnobiotic development to assess the dominant climatic and non-climatic drivers of ecosystem development; and (3) compare the Dailey Lake reconstruction with other paleoecological records to better understand postglacial vegetation and climate dynamics in the northern Yellowstone region.

### 1.1. Modern setting

Dailey Lake occupies a shallow trench on a low bench carved by the late-Pleistocene northern Yellowstone outlet glacier. The semi-closed basin lies on a bench 85 m above the Yellowstone River in the Paradise Valley of southwestern Montana, and the lake discharges periodically through a low gradient outlet (0.3 m/500 m) into a 500 m<sup>2</sup> wetland to the north (fig. 1). Present-day vegetation patterns in northern Yellowstone are strongly influenced by elevation (Despain, 1990). Dailey Lake is located 100 m below lower treeline (1700 m elevation), and the surrounding vegetation is primarily grassland and steppe dominated by *Artemisia tridentata* (big sagebrush), *Ericameria nauseosa* (rabbitbrush), *Festuca idahoensis* (Idaho fescue), and *Leymus cinereus* (Great Basin wild rye), with isolated populations of *Juniperus scopulorum* (Rocky Mountain juniper). *Salix* (willow spp.), *Carex* (sedge), and *Typha latifolia* (cattail) are present along the lake margin and in the adjacent wetland. Montane and subalpine forests grow on nearby mountain slopes: *Pinus flexilis* (limber pine) is most abundant between 1700 and 1900 m elevation; *Pseudotsuga menziesii* (Douglas-fir) and *Pinus contorta* (lodgepole pine) grow between 1900 to 2400 m elevation and are replaced by *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and *Pinus albicaulis* (whitebark pine) above 2400 m elevation. Alpine tundra occurs above 2900 m elevation.



**Figure 1.** Location of Dailey Lake. (a) Location of northern Yellowstone sites discussed in text. (b) Aerial image of Dailey Lake. (c) Topographic map of Dailey Lake. Contour interval 20 feet.

At present, northern Yellowstone receives the majority of its precipitation during the summer months from convective storms produced by monsoonal circulation from the Gulf of Mexico and the subtropical Pacific Ocean (Mock, 1996). Winter precipitation in the region is the result of westerly stormtracks from the Pacific Ocean. Available climate information for Dailey Lake comes from NOAA coop station Livingston 12S, located 31 km northeast of Dailey Lake in northern Paradise Valley. During the period from 1951 through 2012, January temperatures averaged  $-2.7^{\circ}\text{C}$ , and July temperatures averaged  $19.1^{\circ}\text{C}$ . Mean annual precipitation was 41 cm, and May and June were the wettest months, 6.7 and 6.9 cm, respectively (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt5080>). The high summer/winter precipitation ratio (JJA/DJF = 3.29) classifies the lake as a summer-wet site (*sensu* Whitlock and Bartlein, 1993), as a result of low winter precipitation (January average = 1.6 cm) and frequent summer convective storms (July average = 3.9 cm).

Dailey Lake is presently warmer and effectively drier than other parts of the northern Yellowstone region because of its low elevation and location in precipitation shadows of the Gallatin Range and Yellowstone Plateau. This orographic effect particularly impacts westerly storm tracks during the winter months, and Dailey Lake receives approximately 165 cm of winter snowfall (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt5080>) compared with similar lower forest settings at higher elevations in northern Yellowstone that receive between 190–250 cm (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy9905>; <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy9025>).

## 2. Methods

### 2.1. Field

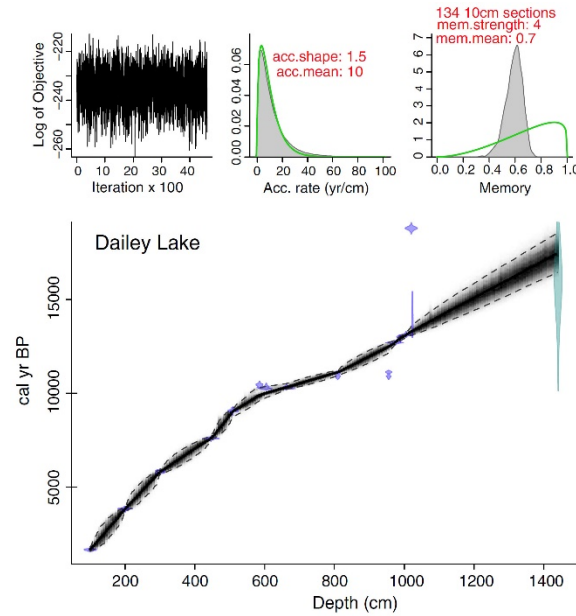
A 14.40-m long sediment core was collected from the ice surface at Dailey Lake in February 2009 using a Livingstone square-rod piston sampler (Wright et al., 1983). Core segments were extruded in the field and wrapped in plastic and aluminum foil and transported back to the Montana State University Paleoecology Lab and refrigerated.

### 2.2. Chronology

Plant macrofossils, charcoal, and pollen concentrates were submitted for AMS radiocarbon dating. Pollen concentrates for dating were obtained from the pollen residue remaining after standard pollen preparation procedures (Bennett and Willis, 2001), except no alcohols were used in processing and a Schulze procedure was substituted for acetolysis to oxidize organics (Doher, 1980). When possible, dates were obtained from organic material near critical lithologic transitions to accurately estimate changes in sedimentation rates.

The  $^{14}\text{C}$  dates were converted to calendar ages using the IntCal13 calibration curve (Reimer et al., 2013), and the age-depth model was constructed using Bayesian accumulation histories for deposits (Bacon) software for modeling in R (Blaauw and Christen, 2011). Bacon repeatedly samples from the probability density function of each calibrated age, fits many possible splines to the age-depth data, and rejects fitted splines that result in age reversals. At each sediment core depth, a probability density function is generated from the population of retained splines. The software requires an a priori assignment of the mean accumulation rate throughout the sediment core, which we estimated as 10 years

cm<sup>-1</sup> based on core length and the age of local ice recession (~16,100 cal yr BP; Licciardi and Pierce, 2008). Splines were calculated piece-wise based on a user-defined section length of 10 cm. All dates were included in the model, including a suspected outlier at 1020.0 cm depth (table 2; fig. 2), inasmuch as outlier dates only affect model uncertainty and do not affect the best age estimates.



**Figure 2.** Age-depth model for Dailey Lake. Solid black line indicates weighted averages of all possible chronologies. Grayscale cloud represents age model probability and is bounded by dotted-line confidence interval (95%). *Left inset* shows the iteration history, the *middle inset* shows the prior (lines) and posterior densities (area fill) for the mean accumulation rate, and the *right inset* shows the prior (line) and posterior (fill) of the memory (1-cm autocorrelation strength).

### 2.3. Lithology

Initial core descriptions were performed at the LacCore facility, University of Minnesota–Twin Cities. Cores were split, imaged, and magnetic susceptibility was measured at contiguous 0.5-cm intervals using a Geotek XYZ MSCL logger to record changes in mineral clastic sedimentation (Gedye et al., 2000). Measurements were reported in SI units. The magnetic susceptibility record serves as a proxy of landscape stability. In this paper, landscape stability refers to the degree of erosion occurring in the Dailey Lake catchment as a result of ice-recessional processes, such as solifluction and surface run-off, poor soil development, and eolian activity. High magnetic susceptibility values are hypothesized to reflect elevated sediment input into the lake system both from increased slopewash and possible wind-derived sources. Landscape stabilization occurs when erosional activity subsides and soils develop, as indicated by decreased magnetic susceptibility.

#### 2.4. Pollen analysis

Samples of 1 cm<sup>3</sup> were taken at 2 to 8 cm intervals and prepared using pollen methods described by Bennett and Willis (2001), except a brief Schulze treatment was substituted for acetolysis to oxidize organics (Doher, 1980). A *Lycopodium* tracer was added to the samples to calculate pollen concentration (grains cm<sup>-3</sup>) and pollen accumulation rates (PAR; grains cm<sup>-2</sup> yr<sup>-1</sup>). Pollen grains were identified at magnifications of 400× and 1000×, and 200 to 400 terrestrial pollen grains were counted per sample. Identifications were made to the lowest taxonomic level possible using reference collections and atlases (e.g., Moore and Webb, 1978; Kapp et al., 2000). *Pinus* grains with intact distal membranes were distinguished between diploxylon-type and haploxylon-type. Based on phytogeography, diploxylon-type *Pinus* pollen is attributed to *P. contorta* and haploxylon-type *Pinus* pollen as either *P. albicaulis* or *P. flexilis*. *Pinus* grains missing a distal membrane were identified as “undifferentiated *Pinus*.” Pollen grains that could not be identified using available reference material were classified as “unknown,” while degraded or hidden pollen grains were classified as “indeterminate.”

Pollen percentages, ratios, concentrations, and accumulation rates were used to reconstruct the vegetation history. Reconstructions were aided by comparisons to modern pollen assemblages from surface samples in the Greater Yellowstone region (Baker, 1976; Whitlock, 1993; Fall, 1994) and from surface samples collected from Dailey Lake (table 1). Percentages were calculated based on the total pollen sum of terrestrial taxa, including pteridophytes, unknown, and indeterminate grains. The pollen-percentage record was divided into zones based on constrained cluster analysis (CONISS; Grimm, 1988) and visual inspection.

Table 1. Modern pollen rain from Dailey Lake	
Pollen Taxa	Relative Abundance
Trees	
Total <i>Pinus</i>	59%
<i>Pinus albicaulis/flexilis</i> -type	5%
<i>Pinus contorta</i> -type	7%
<i>Picea</i>	3%
<i>Abies</i>	2%
<i>Juniperus</i> -type	4%
<i>Pseudotsuga</i>	1%
Shrubs and Herbs	
<i>Alnus</i>	2%
<i>Salix</i>	2%
<i>Sarcobatus</i>	1%
<i>Betula</i>	1%
Rosaceae-type	1%
<i>Artemisia</i>	12%
Poaceae	7%
<i>Ambrosia</i> -type	1%
Amaranthaceae	2%
Other Asteraceae	1%
AP/NAP	2.23

Dailey Lake's position below present-day lower treeline enabled us to examine lower treeline dynamics relative to present-day. Comparison of the modern pollen rain at Dailey Lake, specifically the arboreal to nonarboreal pollen ratios (AP/NAP), to its fossil assemblages was used to infer the relative position of lower treeline and/or changes in forest density. At present, the AP/NAP ratio is 2.23, which lies within the range of modern surface samples from below treeline at other sites in the region (1.23–2.79; Whitlock, 1993; Millspaugh et al., 2000; Mumma et al., 2012). In general, the lower forest/steppe boundary in the Rocky Mountains is controlled by effective moisture (precipitation – evaporation) (Thompson et al., 1999). Higher AP/NAP values compared to modern values are evidence of a downward shift in lower treeline and/or of increased forest density in its existing position. In either case, the data imply an increase in effective moisture. Lower AP/NAP values than at present suggest an upward expansion of steppe and grassland and/or an opening of the forest and thus effectively drier conditions. Alternatively, variations in AP/NAP values could reflect changes in forest structure due to disturbance events such as fire (Baker, 2009), with increased fire activity associated with forest opening and decreased AP/NAP values.

### 2.5. *Charcoal analysis*

Charcoal particles  $>125\ \mu\text{m}$  were extracted at 2-cm intervals,  $2\ \text{cm}^3$  volume samples at Dailey Lake using standard sieving methods (Whitlock and Larsen, 2001). Large charcoal particles  $>125\ \mu\text{m}$  provide a record of high-severity fires within a few kilometers of the site (Higuera et al., 2010). Analysis focused on long-term trends in charcoal concentration (particles  $\text{cm}^{-3}$ ) and accumulation rates (CHAR; particles  $\text{cm}^{-2}\ \text{yr}^{-1}$ ) rather than the frequency of fire episodes, inasmuch the charcoal sampling interval was not contiguous and individual fire events may not have been detected. CHAR was calculated using CharAnalysis software (Higuera et al., 2008). Charcoal concentrations and deposition times were interpolated into contiguous bins based on the median resolution of the record (19 years), and CHAR was calculated by dividing resampled concentrations (particles  $\text{cm}^{-3}$ ) by resampled deposition times ( $\text{yr cm}^{-1}$ ). The long-term trends (background CHAR = BCHAR) were calculated by smoothing the CHAR time series with a 500-year lowess smoother, robust to outliers. BCHAR reflects levels of arboreal fuel biomass, which is related to the amount of forest cover as well as the size and severity of fires that produce charcoal (Marlon et al., 2006). BCHAR was compared to trends in charcoal concentration to identify depths where changes in sediment accumulation may have strongly affected charcoal accumulation rates.

### 2.6. *Diatoms*

Diatom samples were taken at 0.5 to 5 cm intervals and treated with cold hydrochloric acid and hydrogen peroxide to digest the carbonate and organic material, respectively. Samples were then rinsed four times and dried onto coverslips and mounted onto slides with a permanent mounting media (Battarbee, 1986). At least 300 diatom valves were counted on each slide, and diatom data are shown as relative abundance. Diatom zones were identified using constrained cluster analysis (CONISS; Grimm, 1988), using all species identified at any point in the record.



### 3. Results

#### 3.1. Chronology

The Dailey Lake age model is based on fourteen AMS  $^{14}\text{C}$  dates and the accepted age of the Mazama Ash (table 2, fig. 2). Due to the lack of dateable material near the base of the sediment core, the age of the Chico recessional moraines ( $16.1 \pm 1.7$   $^{10}\text{Be}$  ka, assumed  $16,100 \pm 1700$  cal yr BP; Licciardi and Pierce, 2008) located 10 km down-valley from Dailey Lake was used as the core's basal maximum age. No substantial moraines or outwash are noted between Dailey Lake and the Chico moraines, implying rapid ice recession. Above 500 cm depth, the age model is primarily linear with moderate associated uncertainties. Accumulation rates decreased after 500 cm depth, and uncertainties increased rapidly after 1025 cm depth. The model yields a core basal date between 16,450 and 18,570 cal yr BP (2 sigma error).

**Table 2.** Uncalibrated and calibrated  $^{14}\text{C}$  ages for Dailey Lake

Depth (cm) <sup>a</sup>	$^{14}\text{C}$ age ( $^{14}\text{C}$ yr BP)	Calibrated age range <sup>b</sup> (cal yr BP)	Material dated	Lab number/reference <sup>c</sup>
100.00	$1740 \pm 25$	1570–1709	pollen	OS-98610
200.00	$3550 \pm 25$	3724–3906	pollen	OS-98617
300.00	$5080 \pm 35$	5746–5909	pollen	OS-98618
446.00	$6730 \pm 40$	7514–7665	Mazama ash	Zdanowicz et al., 1999
509.25	$8140 \pm 35$	9005–9242	pollen	OS-88594
585.00	$9260 \pm 40$	10292–10559	pollen	OS-95045
604.50	$9120 \pm 50$	10199–10412	pollen	Beta-330381
663.00	$9130 \pm 35$	10226–10395	pollen	OS-88481
809.25	$9630 \pm 40$	10786–11178	pollen	OS-88480
955.25	$9660 \pm 45$	10791–11200	<i>Carex</i> leaf	OS-76183
972.50	$10750 \pm 50$	12602–12743	pollen	OS-95044
988.50	$11100 \pm 45$	12827–13074	pollen	OS-95077
1005.00	$11250 \pm 40$	13050–13192	pollen	OS-90974
1020.00	$15550 \pm 75$	18643–18951	pollen	OS-91010
1023.25	$12000 \pm 510$	13001–15618	charcoal	OS-87766
1441.0	na	14440–17800	Chico Recessional Moraine	Licciardi and Pierce, 2008

a. Depth below mud surface.

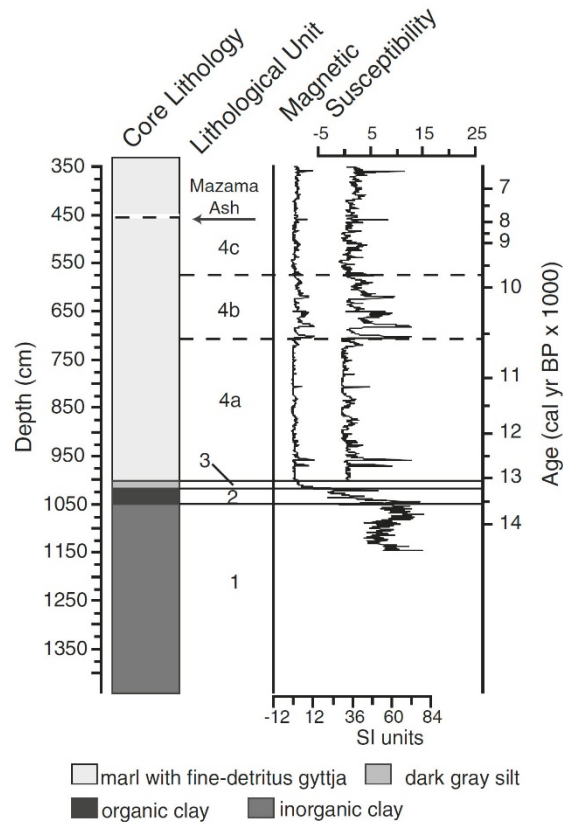
b. 95% calibrated age ranges determined using CLAM program and the IntCal13 curve calibration curve (Blaauw, 2010a,b).

c. OS-National Ocean Sciences AMS Facility; Beta-Beta Analytic.

#### 3.2. Lithology

The core lithology for the period of interest consisted of four units between 14.40 and 3.50 m depth (17,470–6430 cal yr BP; fig. 3). Unit 1 (14.40–10.48 m depth; 17,730–13,580 cal yr BP) was glacial inorganic clay and featured the highest magnetic susceptibility (13.4–79.6 SI units; average = 57.0), indicating considerable mineral clastic input. Unit 2 (10.48–10.18 m depth; 13,580–13,270 cal yr BP) was composed of organic clay with decreasing magnetic

susceptibility (12.9–76.8 SI units; average = 37.2). Unit 3 (10.18–10.06 m depth; 13,370–13,130 cal yr BP) was a relatively thin layer of dark gray silt, and magnetic susceptibility continued to decrease through this unit (2.5–23.0 SI units; average = 7.2). Unit 4 (10.06–3.50 m depth; 13,130–6430) was marl with fine-detritus gyttja and was divided into three sub-units based on changes in magnetic susceptibility. Unit 4a (10.06–7.00 m depth; 13,130–10,530 cal yr BP) had low magnetic susceptibility (–0.6–12.9 SI units; average = 0.8), which subsequently increased (–0.1–12.7 SI units; average = 3.6) in Unit 4b (7.00–5.70 m depth; 10,530–9730 cal yr BP), and then returned to low values (–1.1–11.4 SI units; average = 1.5) in Unit 4c (5.70–3.50 m depth; 9730–6430 cal yr BP).

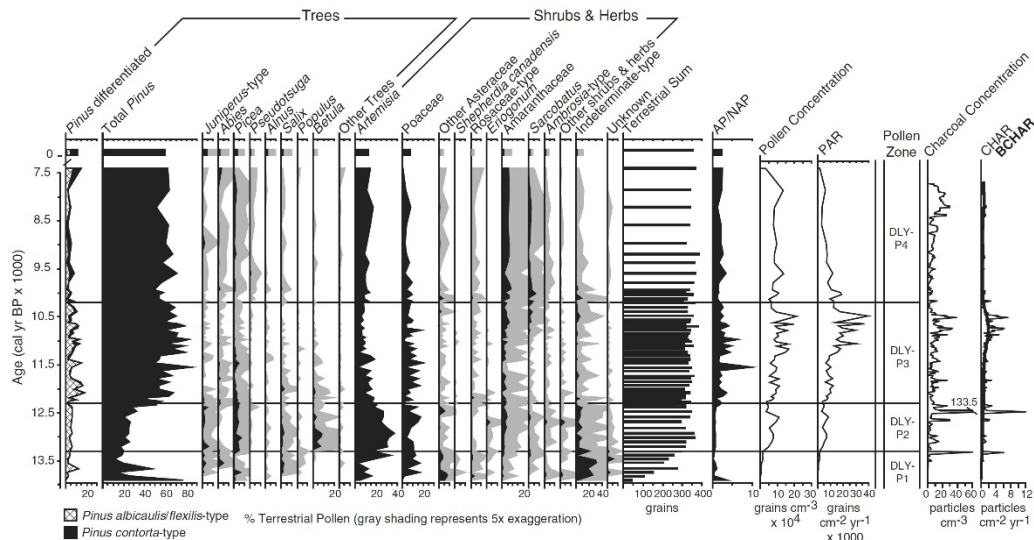


**Figure 3.** Lithologic data from Dailey Lake.

### 3.3. Pollen and charcoal record

The pollen record at Dailey Lake was divided into four zones between 13,900 and 7500 cal yr BP (fig. 4). Zone DLY-P1 (10.82–10.22 m depth; 13,900–13,300 cal yr BP) was characterized by very low pollen concentration (1000–16,200 grains cm<sup>-3</sup>) and accumulation rates (PAR; 100–1600 grains cm<sup>-2</sup> yr<sup>-1</sup>), and high levels of indeterminate pollen grains (8–34%) suggest subaerial exposure prior to deposition. Taxa included early successional shrubs and forbs, including *Shepherdia canadensis* (<2%), *Juniperus*-type (<5%), Rosaceae-type (<6%), and Asteraceae (<10%). *Pinus* (12–77%) levels were high but likely originated from

distant source populations and were artificially elevated due to low pollen counts early in the record. Significant levels of *Abies* (<7%) were present at 13,600 cal yr BP. Charcoal concentration (average = 1.63 particles cm<sup>-3</sup>) and background CHAR values (BCHAR; average = 0.02 particles cm<sup>-2</sup> yr<sup>-1</sup>) were extremely low.



**Figure 4.** Charcoal and pollen data for selected taxa from Dailey Lake.

Pollen zone DLY-P2 (10.22–9.40 m depth; 13,300–12,300 cal yr BP) featured high levels of *Artemisia* (14–37%) and *Picea* (3–9%). In addition, levels of *Betula* (<10%), *Juniperus*-type (1–8%), *Salix* (<4%), and *Poaceae* (1–17%) were high, while *Pinus* (17–51%), *Abies* (<3%), *Shepherdia canadensis* (<1%), and forbs such as *Asteraceae* (<8%) were moderate. Indeterminate-type grains (4–28%) decreased over DLY-P1, and average AP/NAP (0.81) was much lower than at present (2.23). Pollen concentrations (17,200–111,000 grains cm<sup>-3</sup>) and PAR (1700–8500 grains cm<sup>-2</sup> yr<sup>-1</sup>) increased during this period, as did charcoal concentration (average = 10.60 particles cm<sup>-3</sup>) and BCHAR (average = 0.35 particles cm<sup>-2</sup> yr<sup>-1</sup>).

*Pinus* levels (41–85%) were at their highest of the record in pollen zone DLY-P3 (9.40–6.36 m depth; 12,300–10,200 cal yr BP). The majority of *Pinus* grains were attributed to *P. albicaulis/flexilis*-type (1–18%) versus *P. contorta*-type (<6%). *Abies* (<4%) increased while *Picea* (<1–8%) and *Juniperus*-type (<3%) levels decreased. The majority of shrub and herb taxa decreased, including *Artemisia* (2–19%), *Betula* (<4%), *Asteraceae* (<3%), and *Ambrosia*-type (<3%). *Alnus* (<1%), *Salix* (<4%), and *Poaceae* (1–20%) remained relatively unchanged, while *Rosaceae*-type (<6%) was elevated over the previous period, and *Sarcobatus* levels (<5%) increased toward the end of the zone. Average AP/NAP was slightly higher (2.74) than today (2.23). Indeterminate-type grains (1–8%) continued to decrease, and pollen concentrations (36,700–213,800 grains cm<sup>-3</sup>) and PAR (4000–39,600 grains cm<sup>-2</sup> yr<sup>-1</sup>) were at their highest of the record, as was BCHAR (average = 1.09 particles cm<sup>-2</sup> yr<sup>-1</sup>). Charcoal

concentrations were elevated (average = 9.12 particles  $\text{cm}^{-3}$ ), but not as high as in the previous zone.

*Pinus* pollen (49–70%) slightly decreased in pollen zone DLY-P4 (6.36–4.40 m depth; 10,200–7500 cal yr BP), while *Pseudotsuga* levels (<2%) increased. Other conifers such as *Picea* (<4%), *Abies* (<3%), *Juniperus*-type (<3%), and *P. contorta*-type (<4%) were unchanged in the record, while *P. albicaulis/flexilis*-type decreased (1–5%). Riparian obligates like *Salix* (<2%), *Betula* (<1%), and *Alnus* (<1%) decreased, while levels of xerophytic shrub taxa, such as *Artemisia* (8–18%) and *Sarcobatus* (1–8%), were elevated. Average AP/NAP was lower (1.90) than at present (2.23). Pollen concentrations (50,600–138,200 grains  $\text{cm}^{-3}$ ) and PAR (3200–218,700 grains  $\text{cm}^{-2} \text{yr}^{-1}$ ) decreased during this period, as did BCHAR (average = 0.47 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) and charcoal concentrations (average = 8.78 particles  $\text{cm}^{-3}$ ).

### 3.4. Diatoms

The diatom record at Dailey Lake was divided into four zones between 13,270 and 10,470 cal yr BP (fig. 5). Diatoms were absent in older and younger sediments. Diatom zone DLY-D1 (10.18–10.03 m depth; 13,270–13,090 cal yr BP) was characterized by the dominance of pioneering benthic taxa, including *Achnanthes rosenstockii* (1–5%), *Achnanthes zieglerei* (<5%), *Amphora pediculus* (6–22%), *Amphora thumensis* (5–12%), and *Navicula diluviana* (17–29%), as well as by relatively high percentages of the planktic species *Aulacoseira ambigua* (<1–16%). Colonial *Fragilaria* species (*F. brevistriata*, *F. pinnata*, *F. construens* var. *venter*, and *F. cf. tenera*) were also present in relatively high abundance (20–40%) within the zone.

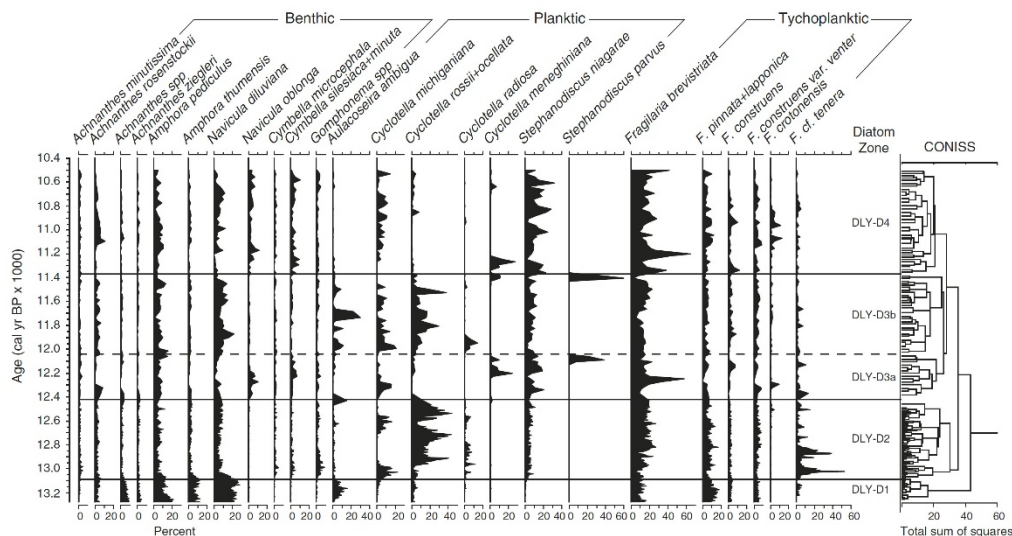


Figure 5. Percentages of selected diatom taxa from Dailey Lake.

An increase in the abundance of planktic taxa, such as *Cyclotella michiganiana*, *C. rossii*, *C. ocellata*, *C. radiosa*, (combined abundance of 5–46%) and *Stephanodiscus niagarae* (1–11%), marked the transition to diatom zone DLY-D2 (10.03 m–9.48 m depth; 13,090–12,420 cal yr

BP). This increase coincided with a decline in the abundances of pioneering benthic species, including *Achnanthes* (1–13%), *Amphora* (2–23%) and *Navicula* (4–25%).

Diatom zone DLY-D3 was divided into two subzones. Zone DLY-D3a (9.48–9.08 m depth; 12,420–12,040 cal yr BP) was marked by lower abundances of the common *Cyclotella* species found in the previous zone (1–16%) and increased percentages of colonial *Fragilaria* species (15–64%) in the lower part of the subzone and *Cyclotella meneghiniana* (1–24%) and *Stephanodiscus parvus* (7–40%) in the upper part of the subzone. The transition to zone DLY-D3b (9.08–8.36 m depth; 12,040–11,370 cal yr BP) was characterized by the return of the *Cyclotella* species common in zone DLY-D2 (*C. michiganiana*, *C. rossii*, *C. ocellata*, *C. radiosa*—combined abundance of 1–38%) and an increase in *Aulacoseira ambigua* (1–30%).

Diatom zone DLY-D4 (8.36–6.89 m depth; 11,370–10,470 cal yr BP) included the youngest samples analyzed in the diatom record and was marked by decreasing percentages of *Cyclotella* (<19%) and *Aulacoseira* (<2%) species and increased abundance of all benthic species (17–55%) and *Stephanodiscus niagarae* (1–22%). Diatoms were not present above 6.89 m in the sediment core.

## 4. Discussion

### 4.1. Postglacial terrestrial and limnologic development at Dailey Lake

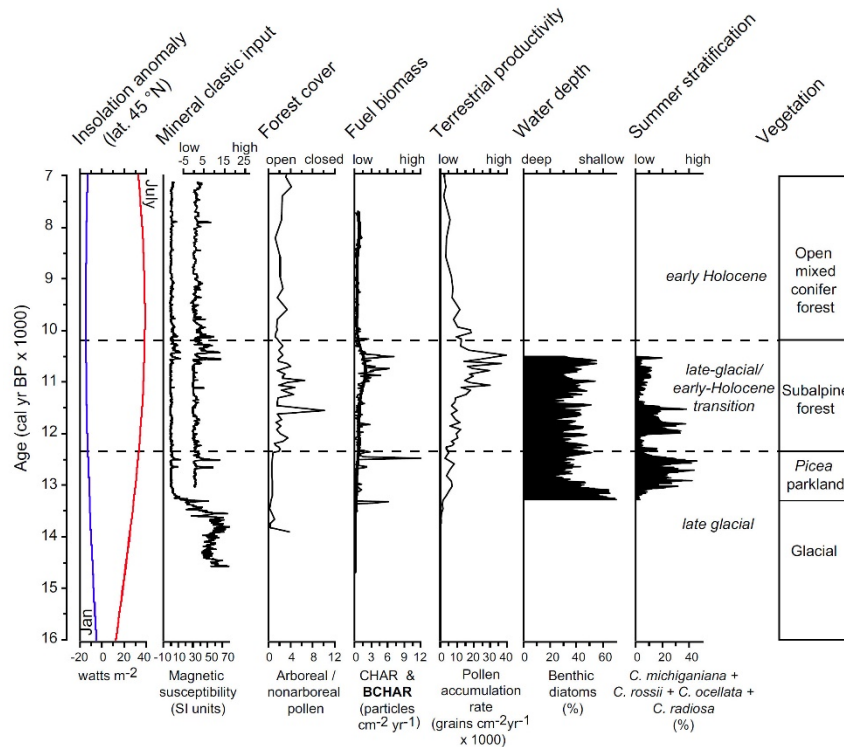
The Dailey Lake datasets document postglacial terrestrial and limnologic development in the Greater Yellowstone region. During the late-glacial/early-Holocene transition, the record features significant changes in catchment processes, vegetation, fire activity, hydrology, and limnobiota (fig. 6).

#### 4.1.1. Late-glacial period (>12,300 cal yr BP)

Paleoclimate model simulations for western North America during the late-glacial period highlight the direct and indirect effects of increasing summer insolation on regional climate (Bartlein et al., 1998). Direct effects included rising summer temperatures and decreasing effective moisture relative to full-glacial conditions, whereas the indirect effects were a strengthening of the northeast Pacific subtropical high-pressure system in summer and a northward shift of the jet stream from its full-glacial position. As a result, summers were warmer and drier than before, and winter precipitation increased (Bartlein et al., 1998).

Driven by increasing summer insolation and temperatures, the northern Yellowstone outlet glacier retreated from its maximum extent at ca. 16,500 cal yr BP ( $16.5 \pm 1.4$   $^{10}\text{Be}$  ka,  $16.6 \pm 1.3$   $^3\text{He}$  ka; Licciardi and Pierce, 2008) in Paradise Valley, and for the next 3000 years, ice recessional processes shaped the Dailey Lake area. Prior to 13,300 cal yr BP, lake sediments were characterized by high magnetic susceptibility and low pollen concentration and accumulation rates (PAR), indicating a sparsely vegetated unstable landscape with considerable clastic mineral input into the lake, either as eroded sediment from the freshly deglaciated landscape, meltwater, or wind-blown material. The pollen record implies discontinuous shrub-herb cover, and early successional species, such as *Shepherdia canadensis*, *Salix*, *Alnus*, *Juniperus*, and Asteraceae species, likely established on stagnant outwash bars and rocky glacial till. Trees were rare; however, low persistent levels of *Abies* in the pollen

record after 13,600 cal yr BP suggest local occurrence of *Abies lasiocarpa*. Low charcoal concentration and BCHAR values indicate limited fire activity, probably as a result of discontinuous fuels and cool conditions. Diatoms were absent from the lake during this time, likely as a result of high turbidity from the input of fine minerogenic sediment (Bradshaw et al., 2000) and suggests low lake productivity.



**Figure 6.** Summary of environmental proxy at Dailey Lake during the late-glacial/early-Holocene transition plotted against January and July insolation anomalies.

Beginning at 13,300 cal yr BP, a number of environmental changes occurred in the vicinity of Dailey Lake. Magnetic susceptibility reached sustained low values, indicating landscape stabilization as a result of decreased landscape erosion. It is possible that early pioneering shrub species, such as *Shepherdia canadensis*, *Salix*, and *Alnus* present in the pollen record prior to 13,300 cal yr BP, helped stabilize the landscape. Overall pollen concentration and PAR subsequently increased, and an abrupt rise in *Picea* pollen percentages marked the expansion of *P. engelmannii* populations. Increasing summer temperatures, in combination with more stable soils, likely favored its establishment. At present, *P. engelmannii* prefers moderately deep, well-drained soils compared to other subalpine tree species, such as *Abies lasiocarpa* which can establish on minerogenic substrates and rocky glacial till (Franklin and Mitchell, 1967; Alexander et al., 1984).

Within 100 years of landscape stabilization and *Picea* expansion, diatom populations developed in Dailey Lake beginning at 13,270 cal yr BP. As slopes became increasingly

stabilized, clastic mineral input into the lake decreased and pioneering benthic diatoms, including *Navicula*, *Amphora*, and *Achnanthes* species, established in the lake. Shortly afterward, populations of *Aulacoseira ambigua* expanded, reflecting increased nutrient availability for planktic diatom production and likely an unstratified water column because of cool temperatures. Euplanktic diatoms, particularly *Cyclotella* spp., colonized and expanded at 13,100 cal yr BP, and it is likely that the lake became thermally stratified during the summer months (Interlandi et al., 1999; Battarbee et al., 2002; Sorvari et al., 2002; Ruhland et al., 2003).

#### 4.1.2. Late-glacial to early-Holocene transition (12,300–10,200 cal yr BP)

Summers became increasingly warmer and drier during the late-glacial/early-Holocene transition as summer insolation peaked in the region between 11,000 and 10,000 cal yr BP (Berger, 1978). Furthermore, increasing summer insolation indirectly strengthened the subtropical high-pressure system and summer monsoonal circulation, creating drier summers than at present in some areas of western North America and wetter conditions in others (Whitlock and Bartlein, 1993; Bartlein et al., 1998). Winter precipitation was also likely higher in the early Holocene as a result of diverted storm tracks by the lingering ice sheet (Williams et al., 2010) and lower-than-present winter insolation at that time (Bartlein et al., 1998).

Warmer drier summers than before facilitated the expansion of *Abies lasiocarpa* and *Pinus* (likely *P. albicaulis*) into *Picea* parkland beginning at 12,300 cal yr BP at Dailey Lake. The *Picea*, *Abies*, and *P. albicaulis/flexilis*-type percentages during this period are consistent with those from modern *Picea-Abies-Pinus* forest in the Yellowstone region (Whitlock, 1993). Higher-than-present AP/NAP values suggest the upslope forest was either denser than it is presently, or forests grew at lower elevations where *Artemisia*-steppe and grassland grow today. Nonetheless, moderate levels of *Artemisia* and Poaceae pollen during this period indicate the presence of *Artemisia*-steppe/grassland but possibly only on the valley floor. Although conditions were likely warmer and drier than before, growing season moisture was apparently high enough to support a closed forest and/or forests at lower elevations than today.

At the end of the late-glacial period, the diatom record indicates a period of fluctuating conditions between 12,400 and 11,400 cal yr BP that is not evident in the pollen data. Starting approximately 12,400 cal yr BP, the dominant *Cyclotella* species decline in abundance and are replaced by a sequence of taxa, including tychoplanktic *Fragilaria* species, *Cyclotella meneghiniana*, and *Stephanodiscus parvus*. These taxa share a common life-history trait of blooming in unstratified waters, which suggests that lakewater temperatures cooled or the lake became shallower or both. At least for the period between 12,400 and 12,000 cal yr BP, the dominance of *C. meneghiniana* suggests a moderately shallow unstratified lake during summer months, consistent with the inference of summer warming evident in the vegetation data. At 12,000 cal yr BP, the resurgence of *Cyclotella* species characteristic of stratified summer conditions (e.g., *C. rossii*, *C. ocellata*, *C. michiganiana*, *C. radiosa*) indicates that the lake became deeper and thermally stratified again, suggesting both warm summer conditions and increased water balance. A possible scenario for this interval is one of enhanced



winter precipitation and snowpack coupled with early spring warming. The spring conditions, in particular, caused early ice off and longer periods of isothermal mixing. The moderate increase of *Aulacoseira ambigua*, a species characteristic of intervals of water-column mixing, is consistent with this hypothesis. Despite the high-frequency variation in the diatom assemblages, apparently the magnitude of the climate variability in this interval was not sufficient to alter the course of vegetation development.

Beginning 11,400 cal yr BP, lake level at Dailey Lake decreased, as indicated by increased percentages of benthic diatoms. Planktic taxa, such as *Cyclotella* and *Aulacoseira*, became less abundant, and percentages of benthic taxa, including *Achnanthes*, *Cymbella*, and *Navicula*, increased. In addition, colonial *Fragilaria* species (tychoplanktons) were also more abundant than in the previous period. Shallow lake conditions could explain the increased percentages of benthic and tychoplanktic species and the decrease in planktic taxa, and it is likely that Dailey Lake transitioned from an open/semi-closed lake system to a closed system at this time. Water levels likely continued to decrease after 10,500 cal yr BP, reducing recharge to the lake and increasing water alkalinity; these conditions caused diatom dissolution and the end of the diatom record.

Fire activity also increased between 11,000 and 10,000 cal yr BP with rising summer temperatures, effectively drier summer conditions, and possibly more convective storms. High fuel availability is evidenced by high BCHAR, high terrestrial productivity (inferred from high PAR and pollen concentration), and forest cover (based on the high AP/NAP ratios). Increased magnetic susceptibility between 10,500 and 9700 cal yr BP may be a result of fire-related erosional events at this time, as BCHAR peaked just prior to elevated magnetic susceptibility.

#### **4.1.3. Early Holocene (10,200–7500 cal yr BP)**

At 10,200 cal yr BP, warm dry summer conditions produced a more open landscape at Dailey Lake than immediately before or at present. *Artemisia*-steppe was more extensive based on higher pollen percentages of *Artemisia*, *Sarcobatus*, and Poaceae. *Pseudotsuga* and *P. contorta* expanded into the lower forests above the site based on increases in their pollen abundances, and AP/NAP decreased from the previous period, indicating an upward displacement and/or opening of the lower forest. It is also possible that increased fire activity between 11,000 and 10,000 cal yr BP created a more open landscape. *Abies* and *Picea* were still present at moderate levels and likely moved to cooler higher elevations. The development of a lower forest composed of *Pseudotsuga* and *P. contorta* and the upslope expansion of *Artemisia*-steppe suggests that the period from 10,200 to 7500 cal yr BP was the warmest and effectively driest interval of the record. As the landscape became more open, fire activity decreased, indicated by low BCHAR after 10,000 cal yr BP, suggesting a shift to a fuel-limited system.

#### **4.2. Linkages between vegetation and limnobiologic development**

Because high-resolution terrestrial and limnologic data are available from the same cores at Dailey Lake, it is possible to compare the timing of biotic development in the watershed with that of the lake as well as the sensitivity of the two systems to climate change. Early



in landscape development at Dailey Lake, large-scale changes in catchment processes elicited synchronous responses in the vegetation and limnobiota. In the initial period of deglaciation, the geomorphic instability created by stagnant ice, wind, and meltwater inhibited vegetation and limnobiotic development. After 13,300 cal yr BP, dramatic changes in lithology (decreased MS) indicate stabilization of the terrestrial environment. This shift was accompanied by an expansion of *Picea* populations in the upland vegetation and the colonization of pioneering benthic diatoms in the lake. Not only did warmer summers in combination with stabilizing substrates allow for the germination and establishment of *Picea*, but also increasing slope stability decreased minerogenic input into the lake, that until this time had limited the growth of diatoms. It appears that erosional processes associated with ice recession mediated the effects of climate change on early biotic development at Dailey Lake.

Other studies show similar linkages between catchment processes and limnobiotic development in glaciated regions (Fritz and Anderson, 2013). At Krakenes Lake in western Norway, postglacial limnobiotic colonization was initiated once deglacial silt settled, and during the Younger Dryas Cold Interval, there was very little aquatic life due to high silt inwash into the lake (Birks et al., 2000). In northwestern Montana, Foy Lake shows a similar progression of postglacial vegetation and limnobiotic development as at Dailey Lake (Stone and Fritz, 2006; Power et al., 2011). At that site, *Picea* parkland establishment at 13,150 cal yr BP coincided with the colonization of *Navicula diluviana* within the lake system, and it is probable that landscape-scale processes of slope stabilization facilitated a synchronous shift in the terrestrial and aquatic system there as well. Like recently deglaciated lakes (Engstrom et al., 2000; Engstrom and Fritz, 2006), tight coupling between terrestrial succession and lake trophic change at Dailey Lake may have been facilitated by the establishment of nitrogen-fixing plants (e.g., *Shepherdia canadensis* and *Alnus*) that increased lake nitrogen loads and diatom productivity. However, synchrony between decreased minerogenic input and diatom establishment points to the importance of decreased landscape erosion in driving early limnobiotic development at Dailey Lake.

After 13,300 cal yr BP, vegetation and limnobiotic changes at Dailey Lake became asynchronous, reflecting different sensitivities to climate change. Vegetation development once initiated was unidirectional through time and tracked slowly increasing summer insolation and temperatures. The sparsely vegetated landscape became increasingly forested as *Picea* parkland developed, followed by the establishment of closed subalpine forest, and eventually open mixed conifer forest in the early Holocene. In contrast, the abrupt shifts in diatom assemblages between planktic and tychoplanktic taxa between 12,400 and 11,400 cal yr BP suggest a response to climate-driven changes in spring and summer lake thermal structure and lake depth.

In general, the limnobiota at Dailey Lake were sensitive to short-term variations in climate during the late-glacial/early-Holocene transition, whereas the vegetation was more strongly directed by orbital-scale changes in the seasonal cycle of insolation and its effect on temperature and effective moisture. This difference in sensitivity is also evident at Crevice Lake in northern Yellowstone, where the diatom assemblages show dramatic excursions attributed to summer water-column mixing and spring duration that are not matched in the pollen data. The charcoal record, on the other hand, shows fluctuations in the fire

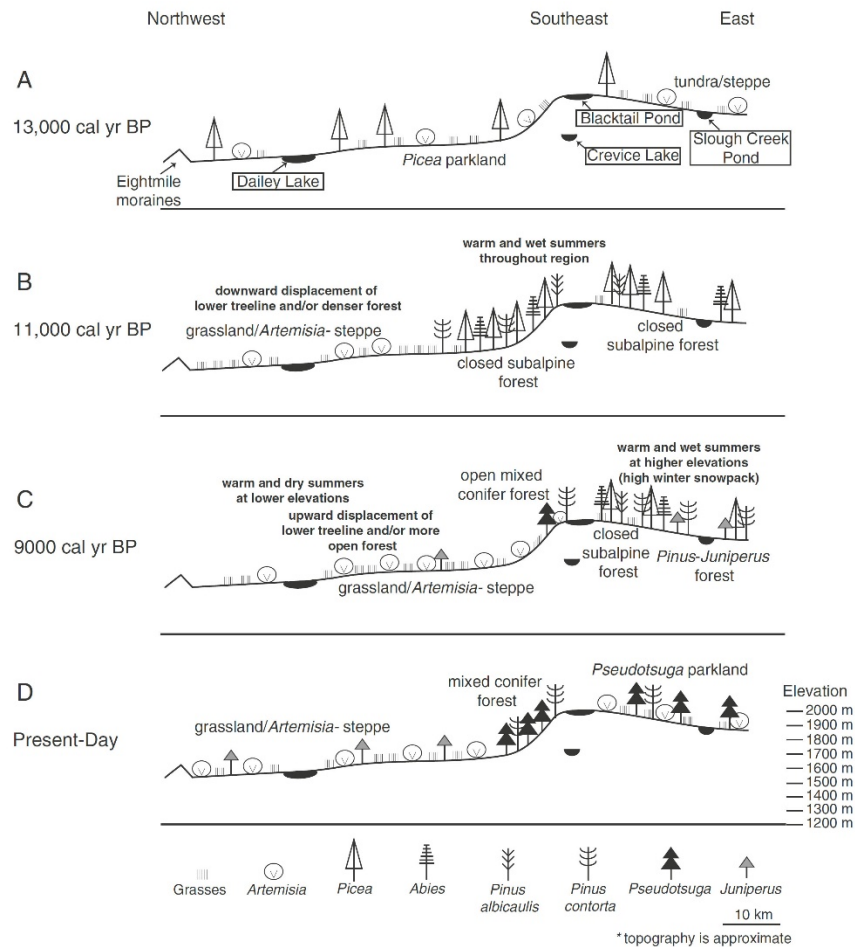
activity that match some of the diatom events and suggest shared responses to summer conditions (Whitlock et al., 2012). At Foy Lake, diatom data indicate low water levels between 12,500 and 11,000 cal yr BP (Stone and Fritz, 2006) as a result of cool dry conditions (Shuman et al., 2009) at a time when the pollen data indicate little change in the prevailing mesophytic vegetation (Power et al., 2011). Similarly, at Krakenes Lake in Norway, changes in terrestrial and aquatic assemblages occurred asynchronously during the Holocene, highlighting their independent responses and sensitivity to environmental drivers (Birks et al., 2000).

#### 4.3. Comparison with other northern Yellowstone paleoecological records

To gain better insight on local vegetation and climate dynamics during the late-glacial/early-Holocene transition, the Dailey Lake record was compared with other sites in the northern Yellowstone region (fig. 7; see fig. 1 for site locations). These include: Blacktail Pond (44.95°N, 110.60°W, elev. 2012 m; Huerta et al., 2009; Krause and Whitlock, 2013); Crevice Lake (45.00°N, 110.58°W, elev. 1684 m; Whitlock et al., 2012); and Slough Creek Pond (44.92°N, 110.35°W, elev. 1884 m; Whitlock and Bartlein, 1993; Millspaugh et al., 2004; Krause, unpublished data). All sites are classified as summer-wet (*sensu* Whitlock and Bartlein, 1993), however, Blacktail Pond, Crevice Lake, and Slough Creek Pond are located 200 to 500 m in elevation above Dailey Lake and receive more winter snowfall. Blacktail and Slough Creek Ponds are situated on broad plateaus, and Crevice Lake lies in the Black Canyon of the Yellowstone River and has an analyzed record that begins 9800 cal yr BP. Dailey Lake's lower elevation in Paradise Valley and position in a precipitation shadow distinguish it from the other sites in northern Yellowstone; its climate is both warmer and drier.

Following deglaciation, sparsely vegetated landscapes transitioned to *Picea* parkland at 13,300 cal yr BP near Dailey Lake, 12,900 cal yr BP near Blacktail Pond (Krause and Whitlock, 2013), and later at Slough Creek Pond beginning 12,500 cal yr BP (Millspaugh et al., 2004; Krause, unpublished data). As growing season temperatures increased, closed subalpine forests developed on the upper slopes near Dailey Lake at 12,300 cal yr BP and then later near Blacktail and Slough Creek ponds at 11,300 cal yr BP. Although summers were gradually becoming warmer and drier than before, soil moisture was high enough to support closed forests at this time.

In the early Holocene, Crevice Lake, Blacktail Pond, and Slough Creek Pond, located above 1700 m in elevation, experienced relatively wet summer conditions. For example, mesophytic closed subalpine forests grew at Crevice Lake and Blacktail Pond until 8200 cal yr BP (Whitlock et al., 2012; Krause and Whitlock, 2013), and *Pinus-Juniperus* forest was present at Slough Creek Pond prior to 8000 cal yr BP (Millspaugh et al., 2004). In addition, charcoal data from the three sites indicate low fire-episode frequency during the early Holocene. Wet summers are attributed to a combination of high winter snowpack and/or summer precipitation from convectional storms. Low carbonate  $\delta^{18}\text{O}$  values from Crevice Lake between 9800 and 8200 cal yr BP suggest that carryover of winter precipitation into the summer season was as important or more important than increased summer convectional storms in producing wet summers in northern Yellowstone (Whitlock et al., 2012).



**Figure 7.** Schematic vegetation reconstruction of northern Yellowstone based on data presented in this paper and other published records.

In contrast, Dailey Lake received less winter precipitation in the early Holocene than the other sites in northern Yellowstone due to its lower elevation and orographic setting. As a result, the site was more influenced by the direct effects of the summer insolation maximum, namely changes in summer temperature and effective moisture. As a result, alkaline lake conditions led to the dissolution of the diatoms after 10,500 cal yr BP, closed subalpine forests were replaced by open mixed conifer forest as early as 10,200 cal yr BP, and fire activity, as indicated by BCHAR, peaked between 11,000 and 10,000 cal yr BP.

## 5. Conclusions

Our multi-proxy paleoecological reconstruction from Dailey Lake contributes new information on early postglacial development of the Greater Yellowstone Ecosystem. Following deglaciation, the Dailey Lake record describes an initial period of landscape instability

driven by ice recessional processes from the northern Yellowstone outlet glacier. Once climate warmed and these processes attenuated, *Picea* population expansion occurred and *Picea* parkland grew on the slopes above the lake. As slopes stabilized and minerogenic input into the lake decreased, limnobiotic communities within the lake established. The nearly synchronous terrestrial and aquatic responses to landscape stabilization suggest erosional processes in the catchment inhibited early vegetation and limnobiotic development.

Once established, the plant and limnobiotic assemblages at Dailey Lake responded independently to climate change. Vegetation development following deglaciation to the early Holocene was largely a response to increasing summer insolation and temperatures and their influence on effective moisture. Concurrently, the diatom assemblage registered short-duration variations in climate seasonality. The differing response to past climatic variations may be explained by the fast generation times of the limnobiota as compared with the slow rate of population change among the dominant tree species.

The sequence of vegetation changes at Dailey Lake following ice retreat is comparable to other sites in northern Yellowstone during the late-glacial period: sparsely vegetated landscapes to *Picea* parkland to closed subalpine forest. However, as the seasonal cycle of insolation amplified during the early Holocene, the high elevation sites were more strongly influenced by the indirect effects of insolation, namely changes in atmospheric circulation, whereas Dailey Lake at a low elevation was more strongly affected by the direct effects of greater-than-present summer insolation, higher summer temperature, and decreased effective moisture. As a result, Dailey Lake shows drier-than-present summers when higher elevation sites in northern Yellowstone register prolonged summer-wet conditions.

Although climate was the primary driver of postglacial ecosystem development in the greater Yellowstone region, this study shows that non-climatic factors, such as catchment stabilization, species life-history traits, and local topography, mediated the impacts of climate change. Once established, the terrestrial and limnologic systems responded independently to climate change, reflecting their unique sensitivities and response times. In spatially complex mountainous regions like Yellowstone, the combination of climate and non-climatic factors produced heterogeneous environmental histories at different elevations and among different proxy. These historical legacies need to be considered in interpreting the modern landscape and in projecting future trajectories of change.

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