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Climate and vegetation change during the late-glacial/early-Holocene transition inferred from multiple proxy records from Blacktail Pond, Yellowstone National Park, USA

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ABSTRACT

A series of environmental changes from late-glacial ice recession through the early Holocene are revealed in a 7000-yr-long record of pollen, charcoal, geochemistry, and stable isotopes from Blacktail Pond, a closed-basin lake in Yellowstone National Park. Prior to 11,500 cal yr BP, cool conditions dominated, fire activity was low, and alpine tundra and *Picea* parkland grew on the landscape. A step-like climate change to warm summer conditions occurred at 11,500 cal yr BP. In response, fire activity increased facilitating a transition from *Picea* parkland to closed *Pinus* forest. From 11,500 to 8280 cal yr BP, warm summers and abundant moisture mostly likely from high winter snowfall supported closed *Pinus contorta* forests. Cooler drier summer conditions prevailed beginning 8280 cal yr BP due to decreased summer insolation and winter snowpack, and lower parkland developed. The timing of vegetation change in the Blacktail Pond record is similar to other low- and middle-elevation sites in the northern Rocky Mountains during the late-glacial period, suggesting local plant communities responded to regional-scale climate change; however, the timing of vegetation changes was spatially variable during the early and middle Holocene due to the varying influences of strengthened summer monsoons and subtropical high on regional precipitation patterns.

Introduction

The late-glacial/early-Holocene transition, 20 to 8 ka, was a period of rapid environmental change around the world (Alley and Clark, 1999; Shakun and Carlson, 2010), and the magnitude of warming that occurred over thousands of years is similar to that projected under future climate scenarios in the coming century (IPCC, 2007; USCCSP, 2009). Superimposed on the late-glacial warming trend were a series of step-like changes and reversals in climate, most notably during the Younger Dryas chronozone (12,900 to 11,500 cal yr BP; Alley et al., 2002). In the northern Rocky Mountains, valley glaciers and large ice fields extensively covered the landscape at the beginning of the late-glacial period (Pierce, 2004). Beginning ca. 17 ka, widespread rapid deglaciation occurred as a result of increasing summer insolation and greenhouse gases, and shifts in the positions of winter storms (Clark and Bartlein, 1995; Licciardi et al., 2004). Minor still stands or readvances of some northern Rocky Mountain glaciers occurred during the Younger Dryas chronozone (Pierce et al., 2003), but then ice recession resumed as conditions warmed during the summer insolation maximum at ca. 9 ka (Bartlein et al., 1998). The range of climate variations in the northern Rocky Mountains makes the late-glacial/early-Holocene transition an ideal case study for understanding ecological responses to past climate change. Most pollen records describe shifts in vegetation from barren deglaciated landscapes to closed forests from 20 to 8 ka. However, these records are primarily from high-elevation sites located in montane and subalpine forests (Whitlock and Brunelle, 2006), and little is known about how climate changes during this transition affected low- and middle-elevation landscapes at lower treeline in the region. These areas were deglaciated prior to high-elevation sites and likely served as corridors for postglacial plant dispersal and colonization (e.g., Lyford et al., 2003).

This paper examines the late-glacial/early-Holocene transition in the northern Greater Yellowstone area based on pollen, charcoal, geochemical properties, and carbonate $\delta^{18}O$ isotope data from Blacktail Pond (44.954°N, 110.604°W; 2012 m elev). This middle-elevation site has been studied previously. Gennett and Baker (1986) developed a postglacial pollen record; however, the sediment core was poorly dated as the chronology was based primarily on bulk sediment ^{14}C- dating that suffered errors related to the highly calcareous nature of the sediments. Huerta et al. (2009) developed a postglacial vegetation history and a high-resolution fire history from a new sediment core. The Huerta et al. (2009) chronology was based on tephrochronology and AMS ^{14}C-dated macrofossils and charcoal. We build upon this work by focusing on the late-glacial/early-Holocene transition at multidecadal temporal resolution and by using multiple proxy, particularly the inclusion of $\delta^{18}O$ analysis of authigenic carbonates and geochemical data, to better understand the physical environment during this transition. Our

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objectives in this study are to: (1) describe the sequence of landscape changes that occurred following the glacial retreat and leading up to the early-Holocene insolation maximum at Blacktail Pond; and (2) compare the Blacktail Pond results with paleoclimate simulations and other paleoecological records in Yellowstone and the northern Rocky Mountains to assess regional patterns of vegetation change during this critical period of ecological development.

Modern setting

Blacktail Pond is situated in a remnant late-Pleistocene meltwater channel that formed when Blacktail Deer Creek abandoned its course during ice retreat and flowed north to the Yellowstone River, creating a marshy environment and a small closed-basin lake (Fig. 1; Pierce, 1979). Cosmogenic exposure dating of glacial boulders indicates an age of 14.3 ± 1.2 ^{10}Be ka for moraines up valley of the lake and 15.3 ± 1.4 ^{10}Be ka for moraines downvalley (Licciardi and Pierce, 2008). These ages imply that ice recession at Blacktail Pond occurred between about 15,000 and 14,000 cal yr BP.

Climate information is available from Mammoth, Yellowstone National Park, located 8 km west of Blacktail Pond. During the period from 1894 to 2011, the average January temperature at Mammoth was −6.7°C, July temperatures averaged 17.4°C, and mean annual precipitation was 39 cm (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy9905). Blacktail Pond is located within the area of high July/January precipitation ratios classified as summer-wet, due to the penetration of summer convectional storms into northern Yellowstone (Whitlock and Bartlein, 1993).

Present-day vegetation patterns in northern Yellowstone are influenced by elevation, aspect, and geology (Despain, 1990). Grassland and steppe communities dominated by *Artemisia tridentata* (big sagebrush), *Festuca idahoensis* (Idaho fescue), and *Ericameria nauseosa* (rabbitbrush) are present below 1700 m elevation. Montane and subalpine conifer forests grow between 1700 and 2900 m elevation and are replaced by alpine tundra at elevations above 2900 m. Within the forest zone, *Pinus flexilis* (limber pine) and *Juniperus scopulorum* (Rocky Mountain juniper) occur at lower elevations (1700 to 1900 m elevation), *Pseudotsuga menziesii* (Douglas-fir) (1900 to 2000 m elevation) and *Pinus contorta* (lodgepole pine) (2000 to 2400 m elevation) at middle to high elevations, and *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and *Pinus albicaulis* (whitebark pine) dominate at the highest elevations (2400 to 2900 m elevation). With regards to substrate, calcareous fine-grained glacial outwash and till support grassland and sagebrush steppe communities due to the substrate's high water-holding capacity, nutrient-poor rhyolite supports *P. contorta*, and Tertiary outcrops of andesite and basalt favor mixed conifer forests of *P. engelmannii*, *A. lasiocarpa*, *P. albicaulis*, and *P. menziesii*. Whitlock (1993) showed that climate and edaphic controls influenced vegetation patterns in the past as well.

Blacktail Pond lies within calcareous glacial outwash and is surrounded by *Artemisia tridentata* steppe. *Pseudotsuga* forest grows on adjacent rocky slopes of basalt and andesite, while *P. contorta* forest grows on rhyolite areas, which dominate in the central part of Yellowstone National Park. Small populations of *Abies* and *Picea* are found in nearby cold air drainages, and stands of *Populus tremuloides* (quaking aspen) grow on the lower slopes in areas of seepage. *Salix* spp. (willow), *Scirpus americanus* (three-square bulrush), *Carex* spp., and *Typha latifolia* (broadleaf cattail) are present along the lake margin, and submerged aquatics include *Chara*, *Uticularia* (bladderwort), and *Myriophyllum* (water milfoil).

Methods

Field

A modified Livingstone square-rod sampler (Wright et al., 1983) was used to obtain a 2.85-m-long sediment core from 5.25 m to 8.10 m depth below the fen surface at Blacktail Pond in October

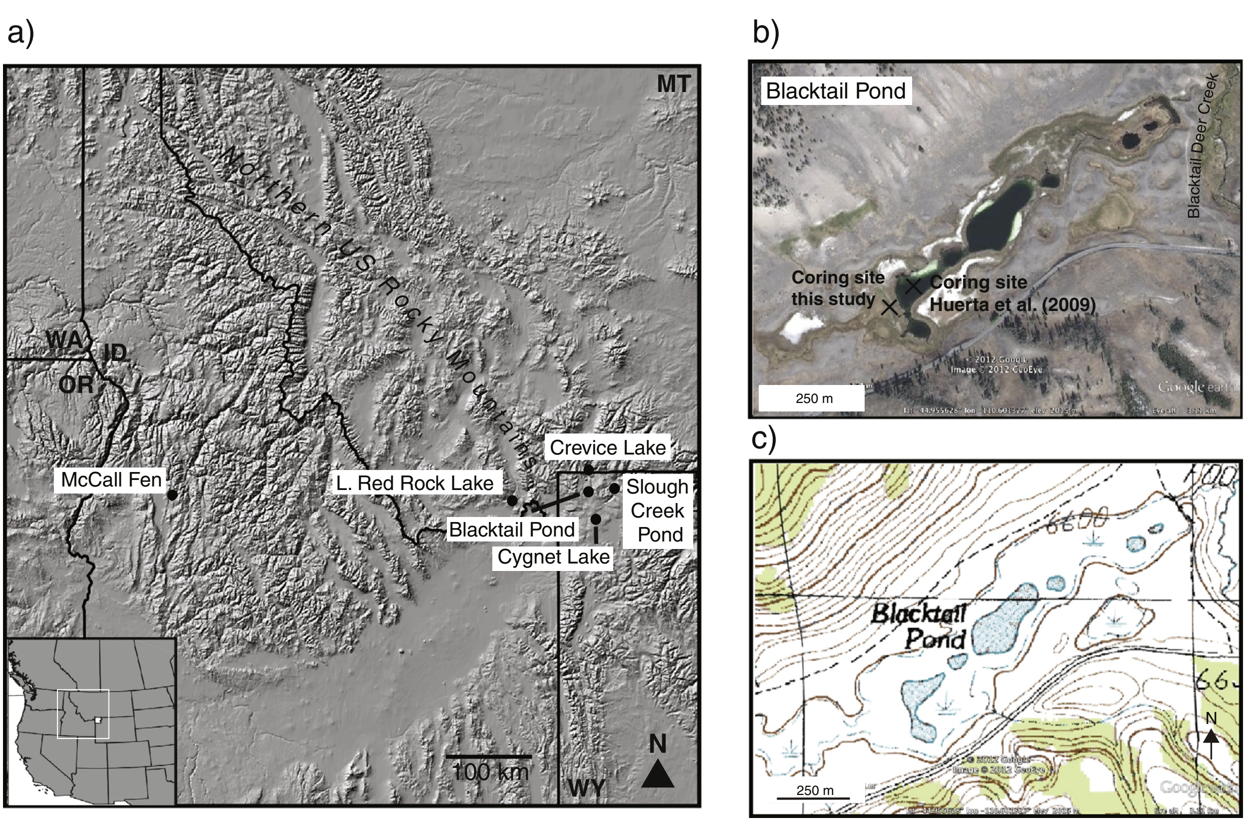

Figure 1. Location of Blacktail Pond. a) Location of sites discussed in text. b) Aerial image of Blacktail Pond. c) Topographic map of Blacktail Pond. Contour interval 20 feet.

2008. Core segments were extruded in the field and wrapped in plastic and aluminum foil and transported back to the MSU Paleoecology Lab where they were refrigerated.

Chronology and correlation

Plant macrofossils, charcoal, and pollen concentrates were submitted for AMS radiocarbon dating. Pollen concentrates for dating consisted of 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). In addition, ash layers identified in the sediment core were utilized in the chronology. To include AMS ^{14}C age determinations from Huerta et al. (2009) in this study, the cores used in both studies were correlated based on lithologic and pollen stratigraphy.

Lithology and geochemical analysis

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 inorganic allochthonous sediment (Gedye et al., 2000). Measurements were reported in SI units. Geochemical elemental analysis of the cores was conducted at the Large Lakes Observatory, University of Minnesota-Duluth. Split cores were run through an ITRAX XRF scanner at contiguous 0.5-cm intervals, and the final analysis focused on the ratio of calcium (Ca) and titanium (Ti). The Ca:Ti record is interpreted as a measure of calcite production in the lake system through time. Ti is a detrital sediment indicator in our record because it is only produced allogenically through the physical erosion of Ti-bearing rocks (Cohen, 2003), and minerals containing Ti are not sensitive to dissolution (Demory et al., 2005). The Ca:Ti ratio corrects the influence of detrital Ca on the Ca geochemical record, which varies with detrital Ti in the lake sediments.

Calcite production is a proxy of lake productivity, inasmuch as calcite precipitation is triggered when algal photosynthesis during the summer months consumes CO_2, increasing water pH, and CO_3^{2-} subsequently binds with available Ca^{2+} (Dean and Megard, 1993). Calcite production is thus related to more sunlight and higher summer temperatures (Meyers and Ishiwatari, 1993).

Oxygen isotopes from authigenic carbonates

The $\delta^{18}O$ values on authigenic carbonates were measured from 5.26 to 7.21 m depth at 1.5-cm intervals at the Environmental Isotope Laboratory, University of Arizona, using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252). The carbonate content of sediment below 7.21 m depth was too low for accurate $\delta^{18}O$ measurements. Powdered samples were treated with dehydrated phosphoric acid under vacuum at 70°C. Measurements are reported as ppm relative to Vienna PeeDee *Belemnitella* (VPDB).

Many factors, including temperature, hydrology, and timing of carbonate precipitation, can influence the $\delta^{18}O$ values of authigenic carbonates (Shapley et al., 2008). Because Blacktail Pond is a closed system, with no surficial inflow or outflow, we infer that the $\delta^{18}O$ record from Blacktail Pond tracks changes in summer evaporation; but we cannot rule out the possible amplifying effects of groundwater on $\delta^{18}O$ values or changes in moisture source area through time. In our simple model, increases in (less negative) $\delta^{18}O$ correspond with increased evaporation of lake water and higher summer temperatures and vice versa (Benson, 2003). Alternatively, it is also possible that $\delta^{18}O$ values reflect changes in seasonal precipitation balance, with high $\delta^{18}O$ values reflecting some combination of increased rainfall and reduced snowfall (Anderson, 2011). In this case, lower (more negative) $\delta^{18}O$ values would be associated with periods of high snow accumulation. However, the lack of significant inflowing streams and long lake-water residence time likely limited the influence of seasonal precipitation on the $\delta^{18}O$ record, and summer evaporative effects were more important. Therefore, we interpret the $\delta^{18}O$ record at Blacktail Pond as an evaporation proxy driven primarily by summer temperatures.

Pollen analysis

Samples of 1 cm^3 were taken at 2- to 8-cm intervals from the core and prepared using pollen methods described by Bennett and Willis (2001), except a Schulze procedure was substituted for acetolysis to oxidize organics (Doher, 1980). A *Lycopodium* tracer was added to the samples to calculate pollen concentration (grains cm^{-3}) and pollen accumulation rates (PAR; grains cm^{-2} yr^{-1}). 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 were separated into haploxylon and diploxylon-types, and those missing a distal membrane were identified as "Undifferentiated *Pinus*". Based on modern phytogeography, haploxylon-type *Pinus* was attributed to *P. albicaulis* and diploxylon-type to *P. contorta*. A ratio of diploxylon-type *Pinus* to haploxylon-type *Pinus* (D_p/H_p) was calculated based on the relative proportion of grains with intact membranes.

Pollen percentages, ratios, and accumulation rates were used to reconstruct vegetation history. Reconstructions were aided by comparisons to modern pollen from surface samples in the Greater Yellowstone region (Baker, 1976; Whitlock, 1993; Fall, 1994). Percentages were calculated based on total pollen sum of terrestrial trees, shrubs, herbs, and pteridophytes. The pollen-percentage record was divided into zones using constrained cluster analysis (CONISS; Grimm, 1988) and visual inspection. Pollen accumulation rates (PARs) were determined by dividing pollen concentrations (grains cm^{-3}) by deposition time (yr cm^{-1}).

Charcoal analysis

Huerta et al. (2009) analyzed macroscopic charcoal particles (>125 μm) from Blacktail Pond to reconstruct high-severity fires occurring within a few kilometers of the site (Whitlock and Larsen, 2002; Higuera et al., 2010). Charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) were calculated using CharAnalysis (Higuera et al., 2008). Using this software, long-term trends in accumulation rates (background CHAR) were separated from positive deviations representing peak charcoal events. Charcoal concentrations and deposition times were interpolated into contiguous 25-yr bins (the median resolution of the record) and CHAR was determined by dividing the time-interpolated concentrations (particles cm^{-3}) by new deposition times (yr cm^{-1}). Background CHAR was calculated by smoothing the CHAR time series (with a 500-yr lowess smoother, robust to outliers) to infer levels of arboreal fuel biomass (Marlon et al., 2006). Charcoal peaks are the positive residuals remaining after background CHAR is removed from the CHAR time series and identified above a 95th percentile of the noise distribution (Whitlock et al., 2004; Higuera et al., 2010). A noise component of the charcoal peak values within 250 yr of every sample was modeled using a Gaussian mixture model. The time span between peaks is the fire-episode return interval, and fire-episode frequencies (number 1000 yr^{-1}) were determined by smoothing the time series using a 2000-yr moving window (Huerta et al., 2009).

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Results

Chronology

The Blacktail Pond chronology is based on four AMS ^{14}C dates, two known tephra ages, and three AMS ^{14}C dates from the previously collected core (N76636, AA0024, AA70025; Huerta et al., 2009) (Table 1; Fig. 2). A 0.5-cm-thick ash layer from Mount Mazama was identified at 543.5 cm depth and assigned an age of 6730 ± 40 ^{14}C yr BP (Zdanowicz et al., 1999). Additionally, two 0.5-cm-thick ash layers presumably from Glacier Peak (B or G) were identified at 697.5 and 699.5 cm depth, and the former depth was assigned an age of 11,600 ± 50 ^{14}C yr BP (Kuehn et al., 2009). Two AMS ^{14}C age determinations at 604.75 and 721.25 cm depth were out of chronological order and left out of the age model.

The ^{14}C dates were converted to calendar ages using CALIB 6.0 (Reimer et al., 2009; Stuiver et al., 2010). The age-depth model was constructed using MCAgeDepth (Higuera et al., 2008). This modeling software employs a cubic smoothing spline and a Monte Carlo approach that allowed each date to influence the age model through the probability density function of the calibrated age (two sigma error; Higuera et al., 2008; Stuiver et al., 2010). The chronology suggests Blacktail Pond formed ca. 14,650 cal yr BP, an age that is consistent with recessional moraines (Licciardi and Pierce, 2008).

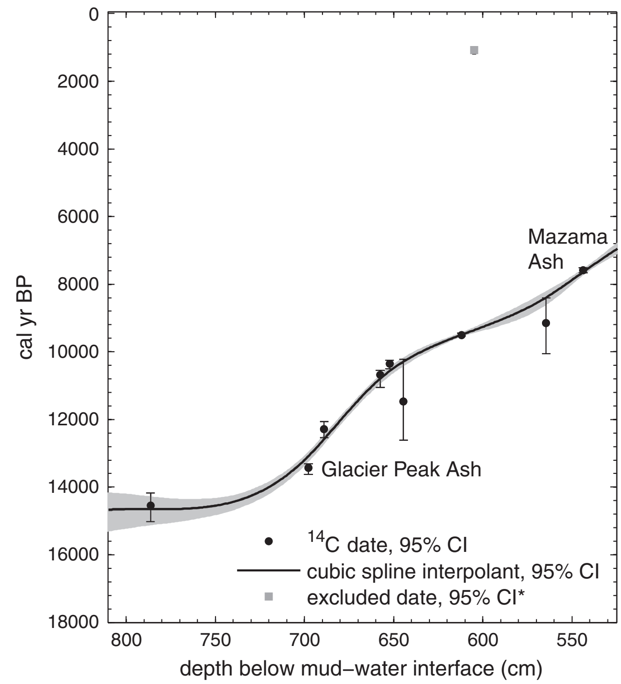

Figure 2. Age–depth model for Blacktail Pond based on radiocarbon determinations and tephrochronology. Gray shading represents range of dates and black lines indicate the 50th (i.e., median age) percentile of all runs. The 50th (circle), 2.5th and 97.5th (bars) percentiles of the probability distribution function of calibrated dates are shown. See Table 1 for age determinations.

Lithology and geochemical data

Core BTP08B was divided into six lithologic units from 8.10 to 5.25 m depth (Fig. 3). From 8.10 to 7.57 m depth, Unit 1 consisted of interbedded silt and inorganic clay. This unit had the highest magnetic susceptibility values (124.6–463.7 SI units) and the lowest Ca:Ti ratios (average = 4) of the record, implying considerable detrital mineral input and very little calcite production in the lake. Unit 2 (7.57–7.18 m depth) consisted of gray inorganic clay. Magnetic susceptibility remained high (12.3–293.6 SI units), but was slightly reduced from the previous unit. Ca:Ti ratios (average = 29) increased slightly. Sediments from Unit 3 (7.18–6.89 m depth) were organic clay. Ca:Ti ratios (average = 195) continued to increase, while magnetic susceptibility was markedly lower (−0.1–16.5 SI units), with the exception of the Glacier Peak tephra couplet at 6.975 and 6.995 m depth (40.1 and 22.1 SI units, respectively), suggesting increased lake productivity and decreased mineral clastic input. Unit 4 (6.89–6.70 m depth) consisted of green fine-detritus gyttja. Magnetic susceptibility remained low (0–5.8 SI units), while Ca:Ti ratios (average = 39) decreased. Unit 5 (6.70–6.45 m) was a transitional unit consisting of interbedded light-brown marl and green gyttja. Magnetic susceptibility was low (−1.3–5.0 SI units), and Ca:Ti ratios (average = 429) increased. The topmost unit, 6.45 to 5.25 m, consisted of light-brown marl. Ca:Ti ratios (average = 689) were at their highest for the entire record, while magnetic susceptibility values (−1.5–2.8 SI units) were at their lowest.

Oxygen isotopes from authigenic carbonates

The carbonate $\delta^{18}O$ record for Blacktail Pond from 14,040 to ca. 7000 cal yr BP (7.21–5.26 m depth) ranged from −7.87 to −17.77 ppm (Fig. 3). $\delta^{18}O$ values were lowest from 14,040 to 11,500 cal yr BP, averaging −16.27 ppm. Values gradually increased during this period and then sharply increased at 11,500 cal yr BP. High values extended to 9000 cal yr BP, averaging −11.08 ppm. There is a brief excursion to low $\delta^{18}O$ values (averaging −13.25 ppm)

Table 1
Uncalibrated and calibrated ^{14}C ages for Blacktail Pond.

Depth (cm)[a]	Uncalibrated ^{14}C age (^{14}C yr BP)	Calibrated age (cal yr BP) with 2-sigma range[b]	Material dated	Lab number/reference[c]
Core BTP08B				
543.75	6730 ± 40	7597 (7513–7539)	Mazama ash	Zdanowicz et al., 1999
564.50	8220 ± 340	9146 (8379–9940)	Pollen	OS-84445
604.75	1160 ± 40	rejected	*Carex* leaf	OS-76344
644.50	9920 ± 460	11,439 (9701–12,967)	Pollen	OS-84446
652.25	9180 ± 55	10,348 (10,235–10,444)	*Carex* seed	OS-76229
697.75	11,600 ± 50	13,434 (13,300–13,616)	Glacier Peak ash	Kuehn et al., 2009
721.25	16,450 ± 70	Rejected	*Carex* leaf	OS-76184
786.25	12,450 ± 50	14,549 (14,158–15,000)	*Artemisia* wood	OS-86819
Core BTP06A[d]				
612.00	8485 ± 40	9501 (9450–9537)	Charcoal	N76636
657.50	9444 ± 57	10,683 (10,515–10,799)	Charcoal	AA0024
689.00	10,414 ± 71	12,291 (12,064–12,546)	Twig	AA70025

[a] Depth below mud surface.
[b] Calibrated ages derived from CALIB 6.0. Two-sigma range is given in parentheses.
[c] OS—National Ocean Sciences AMS Facility; N—Lawrence Livermore AMS Facility; AA—University of Arizona AMS Facility.
[d] Huerta et al., 2009.

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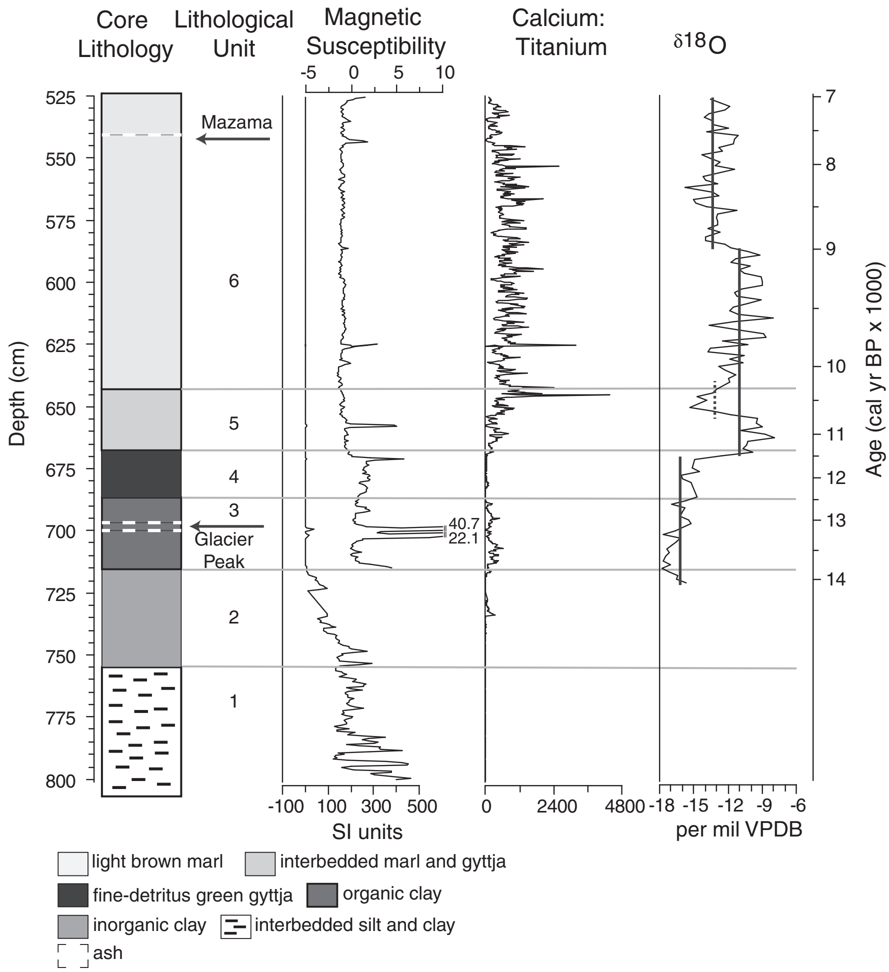

Figure 3. Lithologic, geochemical, and $\delta^{18}O$ isotope data for Blacktail Pond. Solid vertical lines on $\delta^{18}O$ isotope graph indicate mean values of phases; dotted vertical line indicates $\delta^{18}O$ excursion mean.

between 10,600 and 10,100 cal yr BP. After 9000 cal yr BP, values decreased and averaged −13.10 ppm until 7000 cal yr BP.

Pollen record

The pollen record from 14,500 to 7000 cal yr BP was divided into four zones (Fig. 4). Zone BP-1 (7.39–6.68 m depth; ca. 14,400–11,350 cal yr BP) featured high percentages of *Artemisia* (18–58%) and low to moderate percentages of *Pinus* (6–47%), *Abies* (<1%), and *Juniperus*-type (<3%) pollen. Percentages of *Salix* (1–6%), Rosaceae (<10%), and *Shepherdia canadensis* (<2%) were their highest of the record, as were nonarboreal taxa, such as Poaceae (<3%) and Asteraceae Tubuliflorae (1–7%). Amaranthaceae (2–9%) and *Betula* (<3%) occurred at moderate levels. *Picea* pollen was low at the beginning of the period (<2%) and reached high levels (8%) by the end of the zone. PAR values were low (37–475 grains cm^{-2} yr^{-1}), however they may be inaccurate before 13,400 cal yr BP (Glacier Peak tephras) due to unreliable calculations of sedimentation rates. High percentages of indeterminate grains (2–24%) suggest subaerial exposure prior to deposition. High percentages of *Artemisia* and low values of arboreal taxa, in combination with *Salix*, *Betula*, and a diverse herb assemblage suggest a period of alpine tundra similar to present-day alpine environments in the Rocky Mountains (Whitlock, 1993; Fall, 1994; Minckley et al., 2008). Increasing *Picea* pollen at the end of the zone marks a gradual transition to a parkland dominated by *P. engelmannii* species (Whitlock, 1993).

Zone BP-2a (6.68–6.30 m depth; 11,350–9900 cal yr BP) had dramatically increased levels of arboreal taxa (71–96%) and decreased levels of nonarboreal taxa (9–29%). *Pinus* (56–89%) and *Abies* (<5%) percentages increased, while those of *Picea* (2–5%) decreased slightly. Identifiable *Pinus* grains were attributed equally to *P. albicaulis*- and *P. contorta*-type (P_D/P_H~0.75). *Artemisia* (3–16%) and Amaranthaceae (<4%) pollen decreased, as did most other nonarboreal taxa. Overall PAR values increased (60–317 grains cm^{-2} yr^{-1}). This zone resembles modern pollen rain studies from *Picea–Abies–Pinus* forests in the Yellowstone region (Baker, 1976; Whitlock, 1993). Due to edaphic controls on the vegetation, it is likely these forests grew on basaltic or andesitic slopes near the site, while *Artemisia* steppe or grassland grew on the calcareous glacial till of the valley. Although percentages of *Artemisia* and Poaceae were low during this period, it is likely that the dominance of *Pinus* in the pollen record diminished the relative contributions of *Artemisia* and Poaceae.

Zone BP-2b (6.30–5.60 m depth; 9900–8275 cal yr BP) is similar to zone BP-2a, but featured higher *Pinus* (44–95%) and *Pseudotsuga* (<4%) pollen percentages and increased overall PAR (97–1288 grains cm^{-2} yr^{-1}). Consequently, *Picea* (<3%) and *Abies* (<2%) pollen decreased. P_D/P_H ratios (~1.04) increased, suggesting increased presence of *P. contorta* on the landscape. The overall dominance of *Pinus* pollen in the record, particularly of *P. contorta*, in combination with low frequencies of shrub and herbaceous pollen, suggests a dense closed *P. contorta* forest growing on rhyolite outcrops near the site, and possibly on andesite and/or basalt areas. The high overall PAR values likely correspond with increased vegetation cover and/or more intense pollination season.

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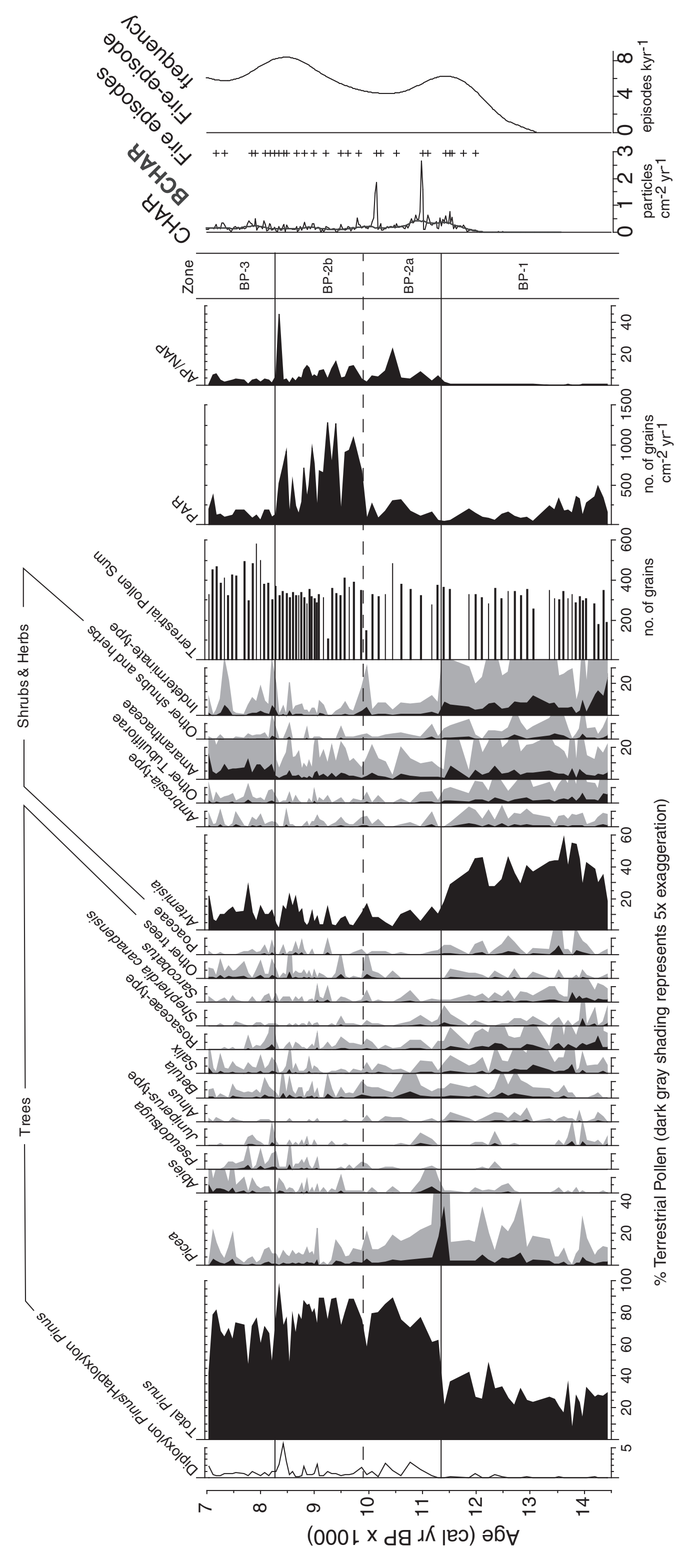

Figure 4. Charcoal and pollen data for selected taxa from Blacktail Pond.

Zone BP-3 (5.60–5.25 m depth; 8275–7000 cal yr BP) was characterized by decreased levels of *Pinus* (42–81%) and increased *Artemisia* (5–28%), *Juniperus*-type (<3%), and Amaranthaceae (4–17%) frequencies. Levels of *Picea* (<4%), *Abies* (<6%), and *Pseudotsuga*-type (<3%) pollen remained relatively unchanged. Overall PAR decreased (56–367 grains cm^{-2} yr^{-1}), suggesting sparser vegetation cover compared with the previous period. Increased levels of *Artemisia* and Amaranthaceae, and moderate levels of conifer taxa suggest a mixture of *Artemisia* steppe and conifer forest. Again, edaphic controls likely created a mosaic of plant communities on the landscape, with *Artemisia* steppe near the lake, *Pseudotsuga* on adjacent slopes of basalt and/or andesite, and *P. contorta* populations on rhyolite outcrops.

Charcoal

Background CHAR values were initially low and increased to 0.04 particles cm^{-2} yr^{-1} at 12,000 cal yr BP (Fig. 4). Levels increased further at 11,000 cal yr BP to 0.43 particles cm^{-2} yr^{-1} and subsequently decreased and remained relatively constant for the rest of the record, averaging 0.18 cm^{-2} yr^{-1}. Charcoal peaks were not detected before 12,000 cal yr BP, implying few or very small fires. After that time, the fire frequency fluctuated between 4 and 8 episodes 1000 yr^{-1}, and charcoal peaks ranged from 0.04 to 8.15 particles cm^{-2} yr^{-1} for the record, with the exception of large peaks at 10,975 and 10,125 cal yr BP. Between 12,000 and 10,500 cal yr BP, fire frequency was moderate (~6 episodes 1000 yr^{-1}), and the lowest fire activity occurred between 10,500 and 9000 cal yr BP (~5 episodes 1000 yr^{-1}). Fire activity increased between 9000 and 7500 cal yr BP (~8 episodes 1000 yr^{-1}), and fire frequency was moderate (~6 episodes 1000 yr^{-1}) after 7500 cal yr BP.

Discussion

The Blacktail Pond data register changes in the local climate, watershed characteristics, and vegetation during the late-glacial period and early Holocene (Fig. 5) and provide a point of comparison with other records from low- and middle-elevation forests in the northern Rocky Mountains (see Fig. 1). In addition, paleoclimate model simulations from 16, 11, and 6 ka provide a framework for understanding the regional climate history of western North America (Bartlein et al., 1998). In northern Yellowstone, comparison sites include Crevice Lake (45.000° N, 110.578° W, elev. 1684 m; 6 km E of Blacktail Pond; Whitlock et al., 2012), Slough Creek Pond (44.924°N, 110.353°W, elev. 1884 m; 20 km E; Whitlock and Bartlein, 1993; Millspaugh et al., 2004), and Cygnet Lake (44.660°N, 110.615°W, elev. 2350 m; 32 km S; Millspaugh et al., 2000). The Crevice Lake record began 9800 cal yr BP and thus provides only a Holocene comparison. The other comparison sites are Lower Red Rock Lakes in the Centennial Valley of southwest Montana (44.630° N, 111.837° W, elev 2015 m; 95 km E; Mumma et al., 2012), and McCall Fen in the Long Valley of Central Idaho (44.933°N, 116.033°W, elev. 1615 m; 425 km E; Doerner and Carrara, 2001). All but Slough Creek Pond and Crevice Lake are located in summer-dry regions as described by Whitlock and Bartlein (1993) based on the fact that they receive the majority of precipitation during the winter months from westerly storm tracks (climate data: http://www.wrcc.dri.edu). Slough Creek Pond and Crevice Lake are located in summer-wet regions influenced by summer monsoonal circulation.

Environmental reconstruction

Late-glacial period (>11,500 cal yr BP)

Paleoclimate simulations for 16 and 11 ka show the direct and indirect effects of variations in the seasonal cycle of insolation on

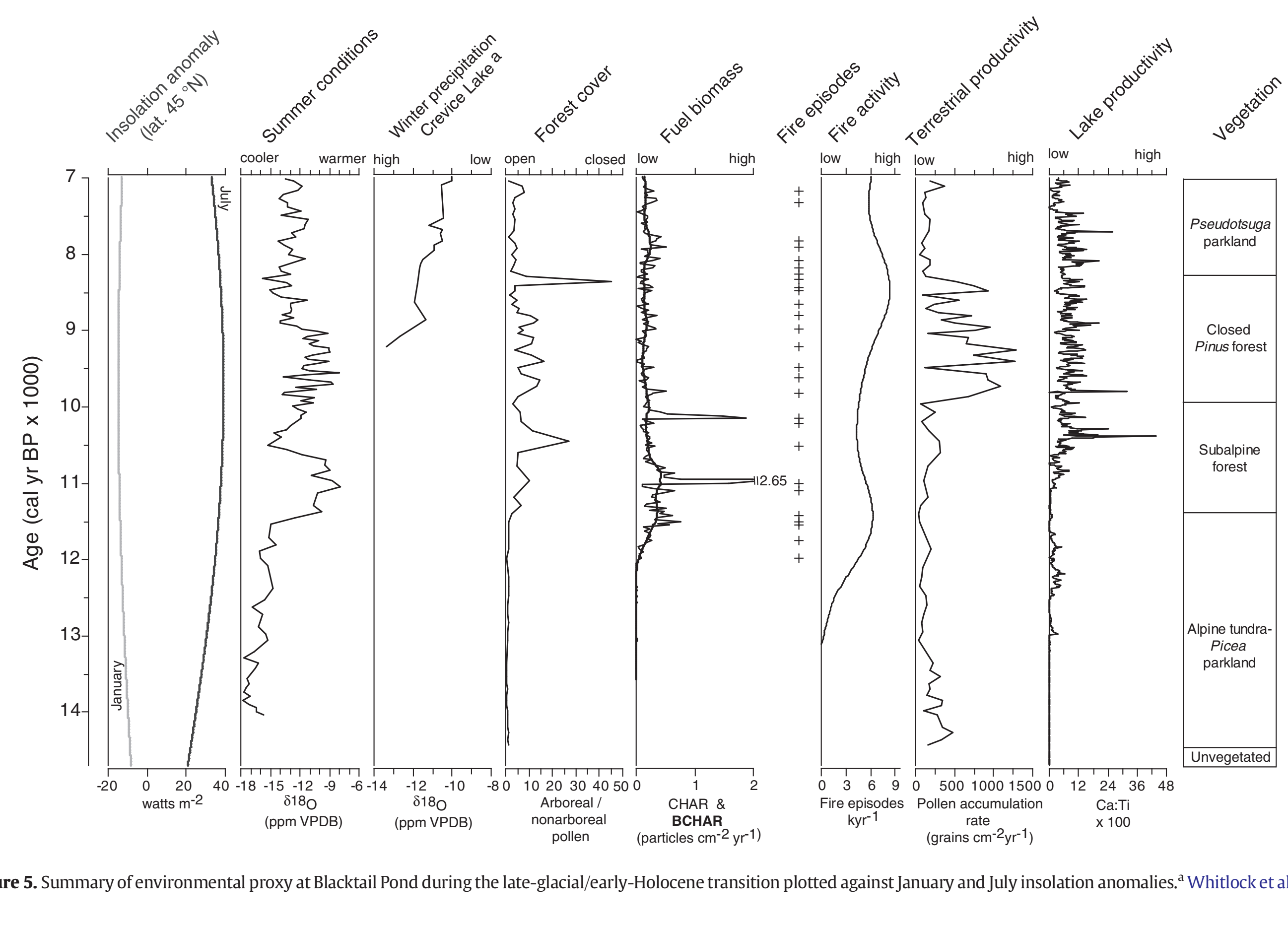

Figure 5. Summary of environmental proxy at Blacktail Pond during the late-glacial/early-Holocene transition plotted against January and July insolation anomalies.[a] Whitlock et al., 2012.

western North American climate (Bartlein et al., 1998). Direct effects include increasing temperatures and decreasing effective moisture relative to full-glacial conditions, while indirect effects include a strengthening of the northeast Pacific subtropical high-pressure system, resulting in warmer drier summers than before, and a northward shift of the jet stream. The northward shift of the jet stream in the late-glacial period was also aided by the retreat of North American ice sheets and likely resulted in increased winter precipitation in the region (Bartlein et al., 1998).

The environmental history of Blacktail Pond supports this climatic reconstruction. The period from 14,000 to 11,500 cal yr BP featured low carbonate $\delta^{18}O$ values, suggesting low evaporation, consistent with cool summer conditions and possibly higher-than-present snowfall. In addition, the $\delta^{18}O$ data show a slightly increasing trend over this period, suggesting increasing summer temperatures during the late-glacial period. Blacktail Pond initially occupied a sparsely vegetated landscape with little soil cover located just down valley of the wasting Yellowstone glacier complex (Pierce, 1979; Licciardi and Pierce, 2008). Lake sediments from this period are primarily inorganic silt and clay with high values of magnetic susceptibility and low Ca:Ti ratios, characteristic of poorly developed soils and unstable slopes.

Decreasing magnetic susceptibility and slightly increased Ca:Ti ratios after 14,600 cal yr BP are associated with low AP/NAP ratios and PARs that indicate sparse open vegetation with low biological productivity. *Artemisia*, Rosaceae, *Salix*, and herbs as well as early successional species, such as *S. canadensis*, were present. Discontinuous fuels and cool conditions likely limited fire activity during this period.

After 12,900 cal yr BP, *P. engelmannii* formed parkland vegetation at Blacktail Pond and nearby Slough Creek Pond, and after 12,500 cal yr BP, *Picea*, *Abies*, and *Pinus* were present in open forest communities at both sites. Elsewhere in Yellowstone, the vegetation at Cygnet Lake shifted from alpine communities to closed *P. contorta* forest at 12,200 cal yr BP without an intervening mixed conifer parkland period (Whitlock, 1993). At Lower Red Rock Lakes, full-glacial tundra changed to *Picea–Pinus* parkland after 17,000 cal yr BP (Mumma et al., 2012), and the pollen record from McCall Fen indicates a transition from *Artemisia* steppe to closed *Picea–Pinus* forest at 14,300 cal yr BP (Doerner and Carrara, 2001). Thus, steadily increasing summer temperatures in the northern Rocky Mountains at the end of the late-glacial period supported the development of first alpine tundra, then spruce parkland and open mixed-conifer forest throughout the region.

Climate and vegetation proxies from Blacktail Pond do not show a climate reversal associated with the Younger Dryas chronozone (12,900 to 11,500 cal yr BP; Alley et al., 2002). In the northern Rocky Mountains, Younger Dryas cooling is primarily inferred from minor glacial advances in the Wind River Range (Gosse et al., 1995a, b) and the Canadian Rockies (Reasoner et al., 1994). In contrast, most fossil pollen records in the region, including Blacktail Pond, do not register a cool event. The one exception may be McCall Fen (Doerner and Carrara, 2001) where decreases in *Pinus*/*Artemisia* ratios and organic sedimentation from 12,700 to 12,200 cal yr BP imply a more open landscape than before or immediately after. The absence of a Younger Dryas signal in most paleoecologic records may be explained by: (1) the coarse sampling resolution of many late-glacial pollen records; (2) the presence of alpine and subalpine forest communities that were insensitive to an abrupt cold interval; and/or (3) the possibility that Younger Dryas cooling did not occur in this part of the northern Rocky Mountains. The climate and vegetation history and carbonate $\delta^{18}O$ data at Blacktail Pond indicate gradual warming and support the latter explanation.

Early Holocene (11,500–8200 cal yr BP)

Greater summer insolation in the early Holocene directly increased summer temperatures and indirectly strengthened the subtropical high-pressure system and summer monsoonal circulation, creating drier summers than at present in some areas of the northern Rocky Mountains and wetter conditions in others (Whitlock and Bartlein, 1993; Bartlein et al., 1998). Beginning at 11,500 cal yr BP, Blacktail Pond carbonate $\delta^{18}O$ values sharply increased, indicating a dramatic rise in evaporation that was likely caused by increased summer temperatures. Fire activity also increased, as indicated by high CHAR values and increased fire frequency from 4 to 8 episodes ka^{-1} (Fig. 5). It is likely that increased summer temperatures during the early Holocene dried fuels and promoted fire spread just as they have at present (Westerling et al., 2011).

Closed subalpine forest developed at Blacktail Pond after 11,350 cal yr BP, based on increasing AP/NAP pollen ratios dominated by *Pinus* (mostly *P. contorta*). This shift lagged the rise in summer temperature and fire activity, inferred from isotopic and charcoal data, by approximately 150 yr (Fig. 6). Mesophytic *Picea* populations were uncommon in the Blacktail Pond area by 9900 cal yr BP, and *Pinus* (presumably *P. contorta*) was the forest dominant. A similar lagged response in ecosystem changes is seen in other Yellowstone records where high-resolution charcoal and pollen data are available (Fig. 6). At Slough Creek Pond, fire activity (inferred from high CHAR) increased at ca. 12,250 cal yr BP, whereas forest closure (inferred from high AP/NAP) was delayed until 11,000 cal yr BP. The tradeoff between *Picea* and *Pinus* dominance occurred at 10,750 cal yr BP. Thus, the development of closed *Pinus* forest lagged the change in the fire regime by approximately 1500 yr. At Cygnet Lake, fire activity increased at 13,000 cal yr BP but did not substantially rise until 11,000 cal yr BP. Forests increased at 11,000 and the *Picea* to *Pinus* tradeoff occurred at 10,750 cal yr BP, such that closed *Pinus* forest lagged the change in fire activity by less than 250 yr.

The data thus suggest that climate changes first drove a shift in fire activity, which in turn favored the expansion and dominance of *P. contorta* over *P. engelmannii*. At present, *P. engelmannii* is a “fire avoider”, as it slowly reinvades burned areas and has essentially no adaptation to fire (Agee, 1993). Slow regeneration of *P. engelmannii* likely set the stage for *P. contorta*, a fire-adapted and early seral species tolerant of warm summer conditions, to colonize burned areas. Although climate change was the primary control of postglacial vegetation change in Yellowstone, increased fire activity facilitated the transition from *Picea* parkland to eventually *P. contorta* forest during a sequence of events that took place over several centuries in the early-Holocene period.

Carbonate $\delta^{18}O$ values in the early Holocene were the highest of the record, averaging -11.08 ppm from 11,500 to 9000 cal yr BP, suggesting high rates of evaporation in association with warm summer conditions. Within this period, an excursion to cool conditions is inferred from a decrease in $\delta^{18}O$ values between 10,600 and 10,100 cal yr BP. This event is not registered in the pollen, charcoal, nor the Ca:Ti data which shows a peak in values. Once again, the terrestrial records of the region seem rather insensitive to short cooling events than other paleoclimate proxy. Furthermore, it appears vegetation was the primary driver of lake productivity during this time versus climate. Like the Younger Dryas chronozone, this isotopic event recorded at Blacktail Pond for the first time bears further study.

PARs at Blacktail Pond were high during the early Holocene and peaked at 9900 cal yr BP, suggesting elevated forest productivity and intense pollination season consistent with increased spring temperatures and longer as well as warmer summers than at present. *P. contorta* forest likely expanded on nearby rhyolite outcrops at this time, where edaphic factors favor their growth. *Picea* and *Abies* populations were greatly reduced at Blacktail Pond, suggesting that populations probably moved to higher elevations where temperatures and/or fire activity was lower or were confined to areas of cold-air drainage near the site. Calcareous substrates surrounding the lake likely supported *Artemisia* steppe or grassland, as they do today. *Pseudotsuga* became more abundant during this time, probably on rocky slopes of andesite and/or basalt. *Pseudotsuga* may have been present on

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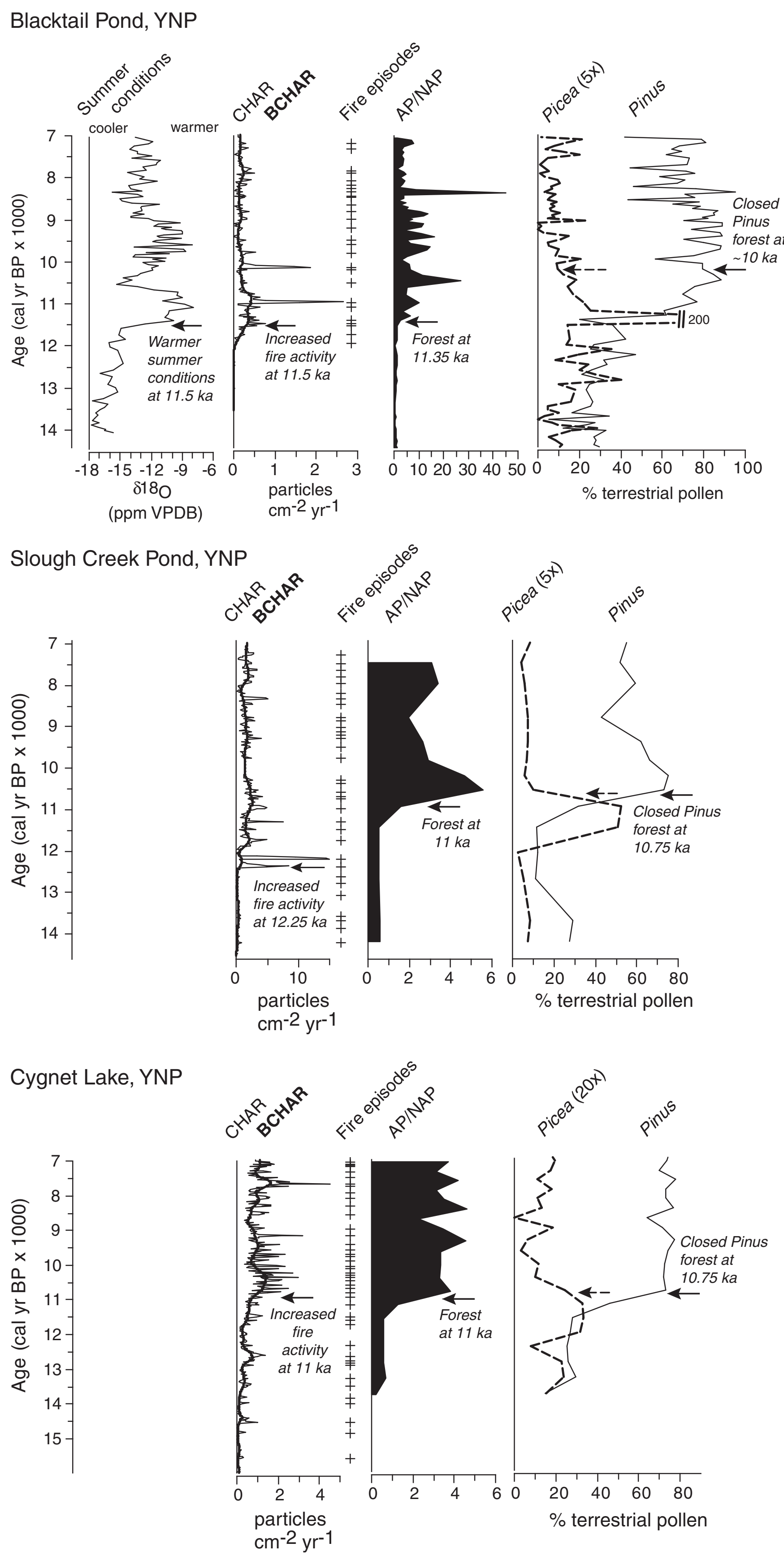

Figure 6. Comparison of fire and vegetation history at Blacktail Pond with other Yellowstone sites, Slough Creek Pond and Cygnet Lake. CHAR—charcoal accumulation rate; BCHAR—background charcoal accumulation rates; AP—arboreal pollen; NAP—nonarboreal pollen.

these rocky slopes since 12,300 cal yr BP, given the fact that trace amounts of *Pseudotsuga* pollen are found throughout the record, but it was not until conditions warmed sufficiently that these populations were able to expand.

At nearby Crevice Lake, a multi-proxy (carbonate, fossil pollen, diatoms, organic carbon, charcoal, and geochemical data) study of seasonal variability suggests that the early Holocene was characterized by cool winters, protracted springs, and warm but effectively wet summers that supported a closed forest. The Blacktail Pond data are consistent with this reconstruction. Increased PAR at Blacktail Pond between 9900 and 8280 cal yr BP are consistent with a long or more intense pollination season due to protracted springs and summers, while closed *P. contorta* forest during this time may reflect some combination of warm summer conditions and adequate soil moisture. Concurrently, *Pinus–Juniperus* forest at Slough Creek Pond suggest effectively wet summers, and all three sites in northern Yellowstone indicate low fire-episode frequency and high fuel biomass despite initial increases in fire activity at the beginning of the early Holocene. Large standing-replacing events occurred at widely spaced intervals at this time typical of *Pinus* and *Picea* forests in Yellowstone at present (Baker, 2009).

The Crevice Lake $\delta^{18}O$ record suggests that summer-wet conditions in the early Holocene arose from the carryover of moisture from high winter snowpack, rather than from increased summer precipitation (Whitlock et al., 2008, 2012). In low $\delta^{18}O$ values there is evidence of a high winter snowpack between 9800 and 8200 cal yr BP (Fig. 5), given its groundwater connection with the Yellowstone River. High carbonate $\delta^{18}O$ values between 11,500 and 9000 cal yr BP at Blacktail Pond, in contrast, suggest warmer-than-present summers, because this closed lake is most sensitive to evaporation. Although high carbonate $\delta^{18}O$ values can also occur due to more rainfall than snow due to increased spring, summer, or fall temperatures, or an enhanced monsoon (e.g., Anderson, 2011), the combination of $\delta^{18}O$ records from the two very different lake systems suggests that early-Holocene winters in northern Yellowstone were wetter than present while summer conditions were warmer and effectively wetter than today.

Other paleoecological records in the northern Rocky Mountains suggest warmer-than-present summer conditions during the early Holocene; however, many indicate that summer conditions were effectively drier than in northern Yellowstone. In central Yellowstone, *P. contorta* forest grew at Cygnet Lake and fire frequency was high, providing evidence of warm dry conditions. Lower Red Rock Lakes supported *Artemisia* steppe from 10,500 to 7100 cal yr BP (Mumma et al., 2012), and McCall Fen indicates open *Pinus* forest from 11,000 to 3500 cal yr BP (Doerner and Carrara, 2001), suggesting warmer and drier conditions at each site during the early Holocene than at present. At Jones Lake in the Ovando Valley of northwest Montana, maximum $\delta^{18}O$ values occurred between 10,000 and 8000 cal yr BP, indicating summer drought with little groundwater recharge (Shapley et al., 2009).

Thus, all paleoecological sites register higher-than-present summer temperatures in the early Holocene, but effective moisture varied. Sites in northern Yellowstone (Blacktail Pond, Crevice Lake, and Slough Creek Pond) were warmer and effectively wetter than at present, whereas those in central Yellowstone (Cygnet Lake) and farther west (Lower Red Rock Lakes and McCall Fen) were warmer and effectively drier. The influence of possible strengthened monsoonal circulation, creating summer-wet conditions in northern Yellowstone, and a stronger subtropical high, resulting in summer-dry responses further south and west in the northern Rocky Mountains may have created the spatial variability in moisture patterns (Whitlock and Bartlein, 1993; Bartlein et al., 1998). However, the carryover of winter moisture into the growing season, evident at Blacktail Pond and Crevice Lake, may also account for some of the summer-wet signal.

Middle Holocene (8200–7000 cal yr BP)

The middle Holocene was characterized by declining summer insolation and rising winter insolation. Furthermore, paleoclimate model simulations for western North America at 6 ka suggest a weakening of the subtropical high-pressure system and summer monsoon, as well as slightly warmer winters (Bartlein et al., 1998). In northern Yellowstone, low carbonate $\delta^{18}O$ values from Blacktail Pond indicate reduced summer evaporation from 9000 to 7000 cal yr BP implying cooler summers than before. However, high carbonate $\delta^{18}O$ values from Crevice Lake suggest decreased winter precipitation after 8000 cal yr BP. Forests became sparser as indicated by decreasing AP/NAP pollen ratios and PARs after 8200 cal yr BP at Blacktail Pond and Crevice Lake, and after 7500 cal yr BP at Slough Creek Pond. Summers were effectively drier than before during the middle Holocene at these sites, based on high fire activity centered at 8000 cal yr BP at all three sites. At Cygnet Lake in central Yellowstone, fire frequency decreased at 8000 cal yr BP, and conditions were likely wetter there than in northern Yellowstone.

Other paleoecological records from the northern Rocky Mountains also indicate warm dry conditions in the middle Holocene. For example, at Lower Red Rock Lakes, *Artemisia* steppe was replaced at 7100 cal yr BP by closed mixed conifer forest (Mumma et al., 2012), and at McCall Fen, open *Pinus* forest was followed by closed mixed conifer forest after 3500 cal yr BP (Doerner and Carrara, 2001). Both records suggest the establishment of cooler and/or wetter conditions in the early late Holocene. The late development at McCall Fen may be due to its lower elevation (100–600 m lower) than other sites or a combination of climatic and nonclimatic feedbacks.

Conclusions

The Blacktail Pond study contributes new information to our understanding of the ecological history of northern Yellowstone and middle elevations in the northern Rocky Mountains during the late-glacial period and early Holocene in several ways. First, the $\delta^{18}O$ record indicates gradual warming during the late-glacial period followed by a step-like transition to warmer summer temperatures at 11,500 cal yr BP, marking the beginning of the early Holocene at Blacktail Pond. There was no evidence of a climate reversal during the Younger Dryas chronozone, in contrast with records from the Wind River Range, Canadian Rockies, and possibly central Idaho. Most late-glacial pollen records from the northern Rocky Mountains indicate unidirectional vegetation change, as the landscapes shifted from alpine tundra to parkland to forest, that implies progressive warming.

Second, increasing summer temperatures were the primary control of vegetation change in northern Yellowstone during the late-glacial period and early Holocene; however, increased fire activity facilitated and preceded the development of closed *Pinus* forest in available paleoecological records from Yellowstone. In Yellowstone during the late-glacial/early-Holocene transition, climate change served as a distal control of vegetation change, whereas fire was the likely the proximal control catalyzing that change.

Third, the Blacktail Pond record supports the findings at nearby Crevice Lake in that the carryover of winter moisture was as or more important as moisture contributions from enhanced summer monsoons at effectively wet sites during the early Holocene. Blacktail Pond data imply warmer-than-present summers, and the Crevice Lake $\delta^{18}O$ record indicates that moisture carryover from high winter snowpack supported closed forest. Our comparison with other paleoecological records in the region suggest the northern Rocky Mountains featured warm summer conditions in the early Holocene, while the patterns of precipitation were more variable due to the competing influences of strengthened summer monsoons and a stronger subtropical high.

Fourth, climatic conditions in northern Yellowstone became cooler and drier following the early Holocene. *Artemisia* and Amaranthaceae became increasingly abundant, as did populations of *Pseudotsuga* after 8200 cal yr BP. Summers were cooler than before, as indicated by low $\delta^{18}O$ values at Blacktail Pond and drier due to decreased winter snowfall, as indicated by high $\delta^{18}O$ values at Crevice Lake. Other paleoecological records in the northern Rocky Mountains indicate prolonged warm dry conditions as late as 3500 cal yr BP, suggesting that the transition to middle Holocene conditions did not occur synchronously throughout the region due to climatic and nonclimatic feedbacks.

Finally, paleoecological records in Yellowstone provide evidence for past fire-facilitated vegetation change following warming conditions during the late-glacial/early-Holocene transition, and additional work examining the fire histories of low- and middle-elevation areas of the northern Rocky Mountains is needed to adequately assess the sensitivity of the region's forests to future climate change. Nonetheless, the combination of proximal and distal drivers of vegetation change in the past suggests fire has the ability to amplify the effects of future warming on vegetation change in the northern Rocky Mountains.

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