Title: Organic layers preserved in ice patches: A new record of Holocene environmental change on the Beartooth Plateau, USA.

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Abstract

Growing season temperatures play a crucial role in controlling treeline elevation at regional to global scales. However, understanding of treeline dynamics in response to long-term changes in temperature is limited. In this study, we analyze pollen, plant macrofossils, and charcoal preserved in organic layers within a 10,400-year-old ice patch and in sediment from a 6,000-year-old wetland located above present-day treeline in the Beartooth Mountains, Wyoming, to explore the relationship between Holocene climate variability and shifts in treeline elevation. Pollen data indicate a lower-than-present treeline between 9000-6200 cal yr BP during the warm, dry summer and cold winter conditions of the early Holocene. Increases in arboreal pollen at 6200 cal yr BP suggest an upslope treeline expansion when summers became cooler and wetter. A possible hiatus in the wetland record at ca. 4200-3000 cal yr BP suggests increased snow and ice cover at high elevations and a lowering of treeline. Treeline position continued to fluctuate with growing season warming and cooling during the late Holocene. Periods of high fire activity correspond with times of increased woody cover at high elevations. The two records indicate that climate was an important driver of vegetation and treeline change during the Holocene. Early Holocene treeline was governed by moisture limitations, whereas late-Holocene treeline was sensitive to increases in growing season temperatures. Climate projections for the region suggest warmer temperatures could decrease effective growing season moisture at high elevations resulting in a reduction of treeline elevation.

Key Words: alpine treeline, pollen analysis, ice patches, vegetation change, Rocky Mountains, Holocene

Introduction

Ecosystems throughout the western U.S. are responding to rapid warming, and evidence suggests some alpine environments are warming at greater rates than lowland environments (Pepin et al., 2015). Ecosystem models predict latitudinal and altitudinal shifts in treeline with warming temperatures (Lenoir et al., 2008), although local site conditions potentially complicate the specific trajectories of change (Quadri et al., 2021). For example, subalpine forests that

become moisture-limited could decline rather than exhibit an expected positive growth and recruitment response to warming temperatures (Andrus et al., 2018). The current rate of climatic changes driving high-elevation ecosystems towards possible extinction events related to mountaintop bioclimatic envelope 'traps' (Rehm and Feeley, 2016) highlights a need to better understand the magnitude of paleoclimatic and paleoecological changes, as well as their effect on subalpine treeline. Additionally, records focusing on how subalpine treeline position has fluctuated across multiple timescales may clarify whether temperature or moisture acts as the primary drivers of change.

Warming temperatures are causing rapid melting of perennial ice patches in alpine environments worldwide, exposing organic debris and cultural materials that have been preserved in ice for millennia. Ice Patch Archaeology has grown in response, shedding new light on the human use of high-elevation landscapes (Lee, 2012; Lee and Puseman, 2017). Though the interest in ice patches primarily has been archaeological, work has been done to understand how the development of ice patches relates to climate conditions (Meulendyk et al., 2012). Recent efforts also have sought to uncover paleoclimatic information from within the ice, aided by the presence of organic sediment layers which allow for radiocarbon-based age-depth estimates (Chellman et al., 2021).

Across the northern Rocky Mountains, numerous ice patches are situated near and above modern treeline. Although some of these patches have persisted for millennia, under current climatic conditions, many are shrinking in volume or disappearing altogether. In concert with their location at high elevations, the information they contain provides us with a unique but at-risk opportunity to examine high-elevation paleoenvironments typically not captured by traditional paleoecological methods. Chellman et al. (2021) reconstructed cool-season temperature and moisture for the last 10,400 years from an ice patch (named TL1) on the Beartooth Plateau of northwestern Wyoming, within the Greater Yellowstone Ecosystem (GYE). Unlike other records from alpine glaciers, the Beartooth TL1 Ice Patch record was not impacted by ice thinning, and the chronology was well-constrained by 29 radiocarbon dates obtained from organic layers relatively evenly distributed throughout the ice profile. These layers not only provide unparalleled opportunities to develop age-depth chronologies, but also to examine macrofossils, pollen, and charcoal to reconstruct the environmental conditions associated with the time intervals when the organic layers formed.

The postglacial vegetation history of the GYE has been described through the analysis of pollen, charcoal, and diatoms from lakes and wetlands (Huerta et al., 2009; Iglesias et al., 2018; Krause et al., 2015; Krause and Whitlock, 2013; Millspaugh et al., 2000; Whitlock, 1993; Whitlock et al., 2012), yet records obtained from alpine settings exploring the subalpine forest to alpine tundra ecotone are more scarce (Fall et al., 1995; Lynch, 1996; Rust and Minckley, 2020). Ice patches above treeline offer an opportunity to investigate elevation shifts and fluctuations in the composition and density of subalpine forests (Benedict, 2011; Benedict et al., 2008). Present-day treeline is a harsh environmental setting where upslope/downslope shifts are likely governed by variations in climate and local site conditions. At large spatial scales (subregional to continental), the location of subalpine treeline is associated most strongly with growing season temperature (Harsch and Bader, 2011; Hoch and Körner, 2009; Körner and Paulsen, 2004). Although growing season temperature is a dominant factor, local treeline position also is mediated by moisture availability, wind, avalanches, slope, aspect, topography, and disturbance (Andrus et al., 2018; Schwörer et al., 2017).

Here, we set out to develop an understanding of subalpine climate and treeline dynamics (e.g., changes in elevation, species composition, and structure) during the Holocene (i.e., the last 12,000 years) by: 1) analyzing pollen, charcoal, and macrofossils from organic layers in ice cores from the Beartooth TL1 Ice Patch and in sediment cores from an adjacent wetland, Meltwater Pond, on the Beartooth Plateau, WY, 2) comparing the information contained within the two records, 3) discussing the similarities and differences between these proxies and what processes drive the accumulation of organic layers, 4) evaluating these new paleoenvironmental records in the context of published $\delta^{18}O$ and ice accumulation records from the same ice patch (Chellman et al., 2021), as well as with other records across the Greater Yellowstone Ecosystem and northern Rocky Mountains.

Study site

The Beartooth Plateau is an expansive high-elevation peneplain in the Beartooth Mountain Range, located in south-central Montana and northwest Wyoming, reaching elevations up to 3900 masl. The two sites in this study, Beartooth TL1 Ice Patch (hereafter referred to as TL1; 3145 masl) and Meltwater Pond (MP; 3090 masl) are located in a glacially carved basin on

the Beartooth Plateau (Fig. 1). TL1 is situated on the southwest wall of the basin and was a 215 x 120 m ellipsoidal patch at the time of coring (Chellman et al., 2021). At the time of coring, MP was .07 ha and had a maximum water depth of 1 m. The water in MP largely originates from melting upland snow, the amount of which can alter the size and depth of the pond. The west side of the pond has a wetland margin.

Vegetation in the Beartooth Mountain Range is arrayed by elevation. *Pinus flexilis* (limber pine) and *Pseudotsuga menziesii* (Douglas-fir) forests are prevalent at elevations between 1700-2500 masl, *Pinus contorta* (limber pine) forests are found at 2000-2800 masl, and *Abies lasiocarpa* (subalpine fir) subalpine forests dominate elevations between 2500-3000 masl, although *Picea engelmanii* (Engelman spruce) forests are found in cold and wet sites (Pfister et al., 1977; Williams, 2012). *Pinus albicaulis* (whitebark pine) forests are found at the highest elevations between 2500-3000 masl, and stunted *Pinus albicaulis, Abies lasiocarpa,* and *Picea engelmannii* occur in krummholz patches above upper forest treeline between 3000-3200 masl (Williams, 2012). Above treeline (approximately 3000 masl), alpine tundra includes species of Poaceae (e.g., *Poa alpina* and *Festuca brachyphylla*), *Carex* (e.g., *C. rupestris*, *C. phaeochephala, C. scopulorum,* and *C. nigricans,*) *Salix* (e.g., *S. reticulata* and *S. glauca*), and *Artemisia* (*A. scopulorum and A. tridentata*), as well as other small shrubs and herbaceous vegetation (e.g., *Dryas octopetala, Geum rossii, Phlox ceaspitosa, Polygonum bistortoides, Potentilla diversifolia, Gentiana algida,* and *Phyllodoce empetriforims*; Heidel et al., 2017; Williams, 2012)

The alpine-parkland ecotone in the TL1 and MP basin is diffuse with an approximate upper elevation of ~3050 m asl, about 0.6 km away from TL1 and MP. The closest subalpine forest stand is located ~1 km away from the two sites at ~3000 m asl. Vegetation immediately surrounding the sites include grasses, sedges, shrubs, and herbs typical of alpine tundra (as listed above).

Interpolated climate normals for 1991-2020 indicate temperatures are highest in July (average of 12ºC) and lowest in December (average of -9.5ºC), with an average annual temperature of -0.1ºC (PRISM Climate Group, 2022). The high-elevation parts of the basin receive an average of ~800 mm of annual precipitation, most of which is received as snow in the winter and spring months (DJF=175 mm, MAM=275 mm), and least in the summer months (JJA=165 mm; PRISM Climate Group, 2022). Cool season precipitation comes from westerly

storm tracks originating over the Pacific Ocean. A secondary spring precipitation pulse also delivers substantial amounts of moisture to the region from regional recycling of winter moisture and upsloping easterlies laden with moisture advected from the Gulf of Mexico (Wise et al., 2018). Spring precipitation events occur in the form of convectional storms or snowfall at high elevations. Late summer is typically dry due to the influence of the Pacific subtropical high-pressure system, which suppresses precipitation in the northern Rocky Mountains (Whitlock and Bartlein, 1993).

[Insert Figure 1]

Methods

Field

Three ice cores were recovered from the TL1 Ice Patch in 2016, using a 4" diameter "PrairieDog" two-barreled ice coring device (Kyne and McConnell, 2007; for more information on ice core methods see Chellman et al., 2021). The longest ice core was 5.61 m in length and contained 29 layers of organic sediment (henceforth termed "organic layers"), ranging in thickness from 0.5-4 cm. The organic layers were isolated by a hand saw, bagged in the field, and refrigerated until analysis. In 2022, a sample of the organic matter deposited on the surface of the TL1 was collected and refrigerated until analysis.

In 2018, two 100-cm sediment cores were retrieved using a Russian Peat coring device from the wetland margin of Meltwater Pond, where sediments were the deepest. In 2022, surface samples from the wetland were collected. Cores and the surface samples were wrapped in plastic wrap and aluminum foil and stored in the cold storage room at Montana State University until analysis.

Lithology and chronology

The 29 organic layers from the longest TL1 core were inspected, and material from each layer was sent to the AMS Radiocarbon Preparation and Research facility in Boulder, CO for

accelerated mass spectrometry (AMS) radiocarbon dating (for more information see Chellman et al., 2021). The lithology of the MP core was described, and because no macrofossils were found in the core, six bulk sediment samples were submitted to the NOSAMS Woods Hole Oceanographic Institute for AMS radiocarbon dating. The AMS radiocarbon ages were converted to calibrated ages using CALIB Radiocarbon Calibration Program 8.2 (Stuiver and Reimer, 1993). Age-depth models for both the TL1 and MP were created using the BACON software, which utilizes a Bayesian statistical approach to reconstruct accumulation rates (Blaauw and Christen, 2011). While the processes driving the deposition of layers of ice in the ice patch differ from those responsible for sediment accumulation in the wetland, the approach for developing the well-dated chronology associated with the ice patch age-depth model is supported by multiple lines of evidence indicating that thin layers of ice and organic material accumulated chronologically as discussed in detail in Chellman et al. 2021.

TL1 Ice Patch macrofossil analysis

The organic samples from the ice core were rinsed through chiffon fabric, dried, and weighed. They were screened using a series of graduated screens (US Standard Sieves with 4-mm, 2-mm, 1-mm, 0.5-mm, and 0.25-mm openings), and the contents of each screen were examined under a Stereozoom microscope at magnifications of 10-70x. Some charcoal specimens also were examined using magnifications of 100-600x. Macrofloral remains were recorded as charred and/or uncharred, whole and/or fragments using counts, weights, and/or frequencies. Macrofloral remains and charcoal fragments were identified to the lowest taxonomic level possible using standard identification manuals (Cappers and Bekker, 2013; Carlquist, 1988; Core et al., 1976; Delorit, 1970; Hoadley, 1990; Knobel, 1980; Martin and Barkley, 2000; Panshin and deZeeuw, 1980), databases (InsideWood, 2004; Schweingruber and Landolt, 2005) and a modern comparative collection.

Pollen analysis

The TL1 surface sample, sediment from 15 of the organic layers, and sediment from 25 sections of the MP core were processed for pollen following standard procedures (Bennett and

Willis, 2001). A *Lycopodium* tracer was added to each sample to calculate pollen concentration (grains/cm^3) and accumulation rates (grains/cm^2/yr). A minimum of 300 pollen grains was counted at 400-1000x magnification and identified to the lowest possible taxonomic level using reference collections at Montana State University and pollen manuals (McAndrews et al, 1973; Faegri and Iverson, 1989; Kapp et al., 2000). Pollen results were separated into stratigraphic zones designated through cluster analysis performed by the CONISS program (Grimm, 1987). Tree species (*Populus sp., Tsuga heterophylla, Juniperus sp.,* and *Pseudotsuga menziesii)* and several upland herb species that were present in small percentages (<1%) were grouped into "other trees" and "other shrubs and herbs" categories. Arboreal pollen (AP) represents all trees and shrubs other than *Artemisia*, and non-arboreal pollen (NAP) includes *Artemisia*, all herbs, and grasses. The AP:NAP ratio was calculated as (AP-NAP/AP+NAP).

Charcoal analysis

For the TL1 organic layers, microscopic charcoal was counted on the pollen slides and converted to concentration, and macroscopic charcoal particles were counted as described above in the TL1 macrofossil analysis section. For the MP core, contiguous sediment samples of 2 cm^3 at 1-cm intervals were processed following the procedures outlined by Whitlock and Larsen (2001), and particles (> 125 μm) were counted under a stereomicroscope. Charcoal counts were converted to charcoal accumulation rates (CHAR), and fire events and changes in fire frequency over time were identified using the CharAnalysis software for MatLab (Higuera et al., 2009). Background charcoal accumulation rates (BCHAR) were calculated using a 900-year lowess smoother, which optimized the signal-to-noise ratio (Kelly et al., 2011).

Results

TL1 Ice Patch

Lithology

The 29 organic layers consisted of organic detritus, small gravel, degraded plant macrofossils, and herbivore digesta (plant material digested by herbivores). The thickness of the

deposits varied from 0.5-4 cm, and weights varied between 0.015 g and 317.6 g (Table 1). The heaviest layers (>2 g) were numbers 1, 3, and 4 (deposited between ca. 940-2436 cal yr BP), 17 (ca. 5800 cal yr BP), 21 (ca. 7800 cal yr BP), and 27-29 (ca. 9600-10400 cal yr BP). The lightest layers (<1 g) were layers 15 and 16 (ca. 5488-5993 cal yr BP), 22 and 23 (ca. 8994-9020 cal yr BP), 25 and 26 (ca. 8994-9180 cal yr BP), and a long sequence between layers 5 and 13 (ca. 2800-5100 cal yr BP). The heaviest sample (layer 29 at the base of the ice core), consisted of numerous small pieces of gravel.

Chronology

The age-depth model for the TL1 core was based on 29 AMS radiocarbon dates from organic material (e.g., seeds, leaves, twigs) from each of the organic layers (Table 1; SM Fig. 1). See Chellman et al., 2021 for more information on the age-depth chronology. The deepest organic layer dated to 10,333-10,415 cal yr BP (1σ uncertainty), and the most recent layer at a depth of 166 cm dated to 945-955 cal yr BP (1σ uncertainty).

Table 1. TL1 Ice Patch sediment depths, ages, and weights.

Lag Number	Depth (cm)	Uncalibrated Age (^{14}C yr BP)	Calibrated Age Range (Cal yr BP)(Probability)	Sample Weight (g)
1	166	1,025 ± 15	945-955(.56)	11.888
2	216	1,790 ± 15	1633-1658(.64)	1.416
3	255	2,060 ± 15	2022-2044(.47)	3.444
4	272	2,465 ± 15	2636-2698(.60)	3.474
5	298	2,715 ± 20	2816-2847(.55)	0.694
6	314	2,850 ± 20	2930-2997(.90)	0.967
7	321	3,540 ± 20	3827-2873(.66)	0.147
8	325	3,005 ± 20	3162-3229(1.0)	0.594
9	371	3,220 ± 20	3401-3429(.70)	0.548
10	381	3,680 ± 20	4033-4082(.69)	0.047
11	392	4,030 ± 20	4440-4487(.76)	0.714
12	396	4,175 ± 20	4700-4739(.42)	0.015
13	410	4,500 ± 20	5053-5142(.60)	0.385
14	415	5,340 ± 20	6114-6147(.36)	1.488
15	422	4,825 ± 20	5488-5504(.51)	0.104
16	431	5,220 ± 20	5959-5993(.69)	0.155
17	433	5,185 ± 20	5917-5938(.64)	16.413
18	442	5,460 ± 20	6276-6292(.55)	0.278
19	449	5,980 ± 25	6810-6853(.55)	1.511
20	472	6,095 ± 25	6933-6994(.81)	0.495
21	484	7,165 ± 25	7964-8009(1.0)	19.699
22	512	8,085 ± 25	8994-9023(1.0)	0.444
23	529	8,065 ± 25	8987-9020(1.0)	0.168
24	537	8,045 ± 25	8982-9012(.62)	1.689
25	539	8,080 ± 25	8994-9020(1.0)	0.582
26	542	8,255 ± 25	9137-9180(.36)	0.556
27	555	8,725 ± 25	9598-9710(.88)	2.754
28	557	8,765 ± 25	9688-9784(.74)	2.299
29	560	9,215 ± 25	10333-10415(.64)	317.601

Pollen, charcoal, and macrofossils

The TL1 record was divided into 5 zones based on a constrained cluster analysis of the pollen percentages (Grimm, 1987; Fig. 2). Zone IP1 (layers 29-24; ca. 10,400-8500 cal yr BP) had the highest levels of *Pinus* pollen of the record at the very base (48%), as well as moderate amounts of *Picea* (5%), although both pollen species declined towards the top of the zone (to 21% and 2%, respectively). Poaceae levels were low in the deepest sample (5%), but quickly rose (to 50%). *Artemisia* pollen levels were moderate (15%), and *Selaginella* levels increased (from 5% to 10%) towards the top of the zone. The arboreal pollen to nonarboreal pollen ratio (AP:NAP) declined from the highest of the record at the very base to the lowest of the record near the top of the zone. Numerous Poaceae parts (stems, leaves, florets, and caryopses), *Potentilla* seeds, and unidentified leaf fragments were found in each layer, as well as seeds and perigynia of *Carex* species favoring both wetlands (*C. capitata, C. illota, C. scirpoidea),* and high-elevation rocky outcrops (*C. albonigram, C. elynoides, and C. haydeniana). Picea* needles were found in layers 27-29, as well as a Pinaceae seed wing in layer 29 (SM Fig. 2). Microcharcoal concentrations were high at the base, and decreased to the top of the zone, suggesting a decrease in fire activity.

Zone IP2 (layers 21-19; 8500-6500 cal yr BP) was characterized by low AP:NAP levels, including low amounts of *Pinus* pollen (25-35%), as well as the least amount of *Picea* pollen of the record (2-4%). *Artemisia* values increased through the zone (26-29%), and Poaceae levels declined (21-11%), suggesting an open sagebrush steppe or tundra landscape. A few *Picea, Abies,* and *Pinus* needle fragments were found in layer 21. Poaceae parts (stems, leaves, florets, and caryopses) and *Carex* seeds and perigynia were still present, as well as *Potentilla* seeds. Microscopic charcoal concentrations decreased in this zone, indicating low fire activity.

Zone IP3 (layers 18-14; 6500-4900 cal yr BP) was characterized by lower levels of Artemisia (10-15%) than before, and high levels of Poaceae (35-45%), except for layer 16, which had a low percentage of Poaceae (11%). *Pinus* and *Picea* levels increased from Zone IP2 (25-42% and 4-7% respectively), as did Rosaceae (2-10%). AP:NAP was high in layer 16, and although layers 18 and 14 were below average, they were higher than the AP:NAP in Zone IP2, indicating that forest density increased. Microscopic charcoal concentrations also increased in this zone, indicating more fire activity than in Zone IP2.

Zone IP4 (layers 11-6; 4900-2800 cal yr BP) was characterized by an increase of *Pinus* (37-39%) and *Picea* (4-8%), an increase in *Artemisia* (11-27%), and a decrease in Poaceae pollen (27-11%). Caryophyllaceae values increased, as did those of other shrubs and herbs. Poaceae macrofossils (stems, leaves, and florets), *Potentilla* seeds, and Cyperaceae seeds and perigynia continued to be present throughout the zone, and there was one *Pinus* needle found in layer 6. Brassicaceae seeds also were abundant. AP:NAP increased in this zone, and microscopic charcoal concentration decreased in layer 10 before increasing again at the top of the zone.

Zone IP5 (layers 4-1; 2800-1000 cal yr BP) had elevated levels of *Pinus* (36-46%), and *Picea* values that were comparable to Zone IP4 (4-7%). *Artemisia* levels were moderate (19%), and Poaceae levels dropped to the lowest of the record (7-13%). Asteroideae, Rosaceae, and Fabaceae levels increased (5-8%, 4-6%, and 1-7% respectively), as did those of other shrubs and herbs, such as *Eriogonum*. AP:NAP increased in this zone to the second highest level of the record (highest at the very base of the core), and microscopic charcoal increased as well. *Picea, Pinus,* and *Abies* needle fragments, Poaceae parts (stems, leaves, florets, and caryopses), *Polygonum* sp., *Plagiobothrys* sp., and Caryophyllaceae seeds, and *Juniperus* sp. leaves were all present in this zone.

Surface organic matter on TL1 had high amounts of *Pinus* pollen (58%) and *Picea* pollen (8%). *Artemisia* levels were slightly less than in the deeper samples (10%), and Poaceae increased from Zone IP5 but was lower than in previous zones (14%). AP:NAP increased from Zone IP5, and charcoal decreased slightly.

[Insert Figure 2]

Meltwater Pond

Lithology

Meltwater Pond sediment cores totaled 93 cm in length. The top 13 cm consisted of dark brown watery peat, which transitioned to dark brown large detritus peat from 20-36 cm depth. At 36 cm depth, there was a transition to medium-brown fine detritus gyttja until 60 cm depth. At 60 cm depth, there was a lithological change from gyttja to medium-brown-to-gray clay, which persisted to the bottom of the core (Fig. 3).

[Insert Figure 3]

Chronology

The Meltwater Pond age-depth model was based on six AMS radiocarbon ages (Table 2; Fig. 4). The change in sediment deposition rate and lithology at 60 cm depth suggests a hiatus from ca. 4200-3000 cal yr BP.

Table 2. Meltwater Pond radiocarbon information.

Core	Depth (cm)	Lab Number/ Reference	Material Dated	Uncalibrated Age (^{14}C yr BP)	Calibrated Age Range (Cal yr BP) (Probability)
MP1	30	155578	Bulk sediment	405 ± 20	448-508 (.93)
MP1	45	175596	Bulk sediment	1790 ± 20	1621-1670 (.62)
MP1	57	175597	Bulk sediment	2760 ± 20	2780-2884 (.92)
MP1	61	155579	Bulk sediment	4010 ± 25	4418-4524(1.0)
MP1	80	175598	Bulk sediment	5540 ± 25	6291-6357 (.65)
MP1	95	155580	Bulk sediment	5060 ± 25	5741-5900 (1.0)

[Insert Figure 4]

Pollen and charcoal

The Meltwater Pond pollen record was divided into four zones based on a constrained cluster analysis (Grimm, 1987). *Pinus, Picea Artemisia*, Poaceae, Asteroideae, and Cyperaceae dominated most pollen spectra (Fig. 5).

Zone MP1 (100-75 cm depth; >6000-5100 cal yr BP,) had high amounts of *Pinus* (37%-47%) and *Picea* (7-8%), and moderate amounts of shrubs, herbs, and grasses including *Artemisia* (13-20%), Poaceae (16-24%), and Asteroideae (3-7%). This assemblage is consistent with an open *Pinus*/*Picea Artemisia*/Poaceae parkland. AP:NAP was higher than average during this zone, suggesting a period when subalpine forests were dense. There was a fire episode at the base of the core, therefore CHAR and BCHAR were high (relative to the rest of the core) at the base and decreased towards the top of the zone (0.28-.04 and 0.14-.04 grains/cm^2/yr, respectively).

Zone MP2 (75-52 cm depth; ca. 5100-2300 cal yr BP) pollen data were similar to Zone MP1 representing subalpine parkland, with high amounts of *Pinus* (42-47%), and slightly higher amounts of *Picea* (6-10%), which declined throughout the zone. Poaceae and *Artemisia* decreased slightly (12-22%; 12-17%, respectively), and Asteroideae increased (5-9%).

Cyperaceae values increased from the base to the top of the zone (0.4-9%). AP:NAP was above average at the base of the zone and then declined. Two small fire episodes were identified, but CHAR and BCHAR remained low throughout the zone (<0.06 and <0.05 grains/cm^2/yr, respectively).

Zone MP3 (52-36 cm depth; ca. 2300-990 cal yr BP) had the highest abundance of grasses and the lowest amount of arboreal pollen. *Pinus* levels decreased (50-23%), and Poaceae levels increased to the highest of the record (27-48%). Pollen percentages of *Picea, Artemisia,* and Asteroideae also decreased (5-2%, 16-10%, and 7-0%, respectively). These data suggest expanded grassland at the expense of forest. CHAR and BCHAR increased from the previous zone (0.01-0.09 grains/cm^2/yr), but were still minimal, with two fire episodes during this period.

Zone MP4 (36-7 cm depth; ca. 990 cal yr BP-present day) had the highest amounts of *Pinus* pollen of the record (28-59%), which generally increased through the zone with the exception of a decrease from 22-9 cm (ca. 350-150 cal yr BP). *Artemisia* increased in this zone (9-24%), Poaceae decreased (34-18%), and Cyperaceae abundance increased until the top three samples when it dropped (3-17%). AP:NAP increased through the zone (other than with the decrease in *Pinus* at ca. 350-150 cal yr BP), suggesting an increase in the density of subalpine forests through the late Holocene. The surface sample AP:NAP (-0.02) is slightly higher than the long-term average (-0.05). Fluctuations from the long-term average likely represent increases and decreases in subalpine forest density compared to present day. CHAR and BCHAR increased in this zone (.01-0.6 and 0.01-0.24 grains/cm^2/yr, respectively), and one fire episode was recorded. The CHAR record only goes until 300 cal yr BP, and the most recent fire episode occurred at ca. 344 cal yr BP.

[Insert Figure 5]

Discussion

Paleoenvironmental reconstructions from the TL1 Ice Patch and Meltwater Pond

Paleoenvironmental records derived from organic layers preserved within an approximately 10,400-year-old ice patch and a 6200-year-old wetland provide new information

on past environmental conditions on the Beartooth Plateau. These records highlight dynamic shifts in forest position and changes in the alpine environment in response to climate variations throughout the Holocene. Here, we compare the TL1 Ice Patch and Meltwater Pond sediment records with other regional proxy records to gain a broader picture of past environmental change in the Greater Yellowstone Ecosystem and northern Rocky Mountains. We discuss the conditions that led to the formation of organic layers, and how the information contained within them underscores the potential for ice patches to provide novel records of past climate and environmental change at high elevations.

Late-glacial to early Holocene transition (>10,200 cal yr BP): Ice patch formation and subalpine parkland development

Deglaciation of the Beartooth Plateau occurred in the region between ca. 16,000 and 13,000 cal yr BP (Licciardi and Pierce, 2018). A moraine at Emerald Lake (2790 m asl; Fig. 1) has been dated to ~12,500 cal yr BP, which suggests that high-elevation glaciers (possibly a resurgence during the Younger Dryas) still persisted on the Beartooth Plateau in the vicinity of the study site at that time (Barth et al., 2022). Although there was late Pleistocene ice in the TL1 location during the Last Glacial Maximum, lack of evidence for ice deformation or movement in the cores suggests the TL1 was not a remnant of a larger glacier (Chellman et al., 2021). The age of the oldest organic layer in the TL1 core suggests ice-patch formation at ca. 10,400 cal yr BP, several centuries after glacial retreat.

Pollen and macrofossil evidence from the oldest organic layer dating to ca. 10,400 cal yr BP suggests that TL1 formed during a time when the area supported parkland with *Pinus* and *Picea* (Fig. 2). Pollen data from nearby Beauty Lake (Spaulding et al., 2020) and Rainbow Lake (Rust and Minckley, 2020) indicate tundra vegetation was the dominant cover type before the formation of the TL1, depicting a cold, dry, and newly exposed postglacial environment. These records then track the development of *Pinus* and *Picea* parkland at higher elevations, at 2874 m (Beauty Lake) at ca. 11,500 cal yr BP, and then at 2963 m (Rainbow Lake) at ca. 11,000 cal yr BP. Conifers migrated upslope during the late-glacial to early-Holocene transition, in response to warmer and possibly wetter climatic conditions after the Last Glacial Maximum (Alder and Hostetler, 2015; Bartlein et al., 1998; Krause and Whitlock, 2017).

Lake-level reconstructions in the region indicate a dry, late-glacial period and an increase in moisture into the early Holocene (Shuman et al., 2010; Shuman and Serravezza, 2017). Rainbow Lake and Lake of the Woods, WY (150 km to the south) both deepened at ca. 11,300 cal yr BP (Shuman et al., 2010; Shuman and Serravezza, 2017). This is likely the result of increased moisture brought to the region by changes in mid-continent atmospheric circulation, such as the northerly shift of the westerly mid-latitude jet stream in response to the retreating Laurentide ice sheet (Alder and Hostetler, 2015; Bartlein et al., 1998). Other sites at lower elevations in the GYE also recorded effectively wetter summers during the early Holocene, implying increased winter snowpack or increased convection summer storms (Krause and Whitlock, 2013). Many pollen records in the GYE indicate an increase in forest density at this time as well (Benes et al., 2019; Iglesias et al., 2018; Krause et al., 2015; Whitlock, 1993; Whitlock et al., 2012). Increasing moisture in addition to warming summer temperatures after the late-glacial period allowed infilling of forests and an upslope expansion of conifers to higher elevations.

The formation of TL1 during early-Holocene warming is likely a result of the increased precipitation in the region and/or cooler winter temperatures. TL1 $\delta^{18}O$ evidence indicates this time was a period of relatively cooler winter temperatures and/or enhanced snowfall (Chellman et al., 2021). During the early Holocene, paleoclimate model simulations (Alder and Hostetler, 2015; Bartlein et al., 1998) suggest that increasing summer insolation and decreasing winter insolation (Berger, 1978) brought about warmer summers and cooler winters than today in this region. Ice accumulation could have increased with the development of permafrost on exposed ground during the cooler winters.

Early Holocene (~10,200-6200 cal yr BP): Steppe formation

By 9000 cal yr BP, the high-elevation *Pinus* and *Picea* parkland was replaced by steppe vegetation, which persisted for approximately 3000 years. This shift is indicated by the decrease in *Pinus* pollen and increase in *Artemisia* and Poaceae pollen in the TL1 organic layers (Fig. 2). Low elevation sites in the GYE also record an expansion of steppe and xerophytic conifers from ca. 10,200-7500 cal yr BP (Iglesias et al., 2018; Krause and Whitlock, 2013; Krause et al., 2015; Schiller et al., 2022; Whitlock, 1993; Whitlock et al., 2012), suggesting regional warm and dry

conditions. The Rainbow Lake record showed little change in vegetation after the initial increase of *Pinus* at 11,000 cal yr BP (Rust and Minckley, 2020), and the pollen record from Beauty Lake indicates only a small increase in Poaceae and *Artemisia* at 10,000 cal yr BP (Spaulding et al., 2020). These lakes are located at elevations currently below modern treeline. Therefore, it is possible parklands persisted near those sites, or due to their larger size, they recorded a more regional signal from forests at lower elevations.

Although a lowering of treeline could signify cooler conditions (Harsch and Bader, 2011; Morgan et al., 2014), higher summer insolation levels (Berger, 1978) and paleoclimate model simulations suggest this region experienced greater summer drought in the early Holocene than at present due to an expansion of the Pacific high-pressure system (Alder and Hostetler, 2015; Bartlein et al, 1998; Thompson et al., 1997). Conifer tree establishment is often temperature dependent but moisture limitation impacts tree success as well, so the continued summer warming during the early Holocene could have decreased effective moisture and prevented tree growth. Significant shallowing of Rainbow Lake (Fig. 6) is consistent with hot summers leading to greater evaporative demand (Shuman and Serravezza, 2017), and MP had not yet formed, likely because summers were too dry. The TL1 $\delta^{18}O$ record shows colder-than-present winter temperatures throughout this period (Chellman et al., 2021; Fig. 6), though this may be evidence of strong seasonality and does not preclude warm dry summers. Severe winter temperatures could have additionally caused tree damage and dieback on the Beartooth Plateau.

[Insert Figure 6]

Middle Holocene (6200-4200 cal yr BP): Parkland development

Drought conditions lessened after ca. 6200 cal yr BP, as evidenced by the initiation of sediment accumulation in MP, as well as increased levels of conifer pollen in both the TL1 and MP records (Figs. 2 and 5). MP sediment accumulation suggests effective precipitation increased (or warm season evapotranspiration decreased) enough to allow surplus runoff to collect in the topographic depression. The increase in effective moisture supported an upslope shift in treeline. Both records suggest the presence of *Pinus* and *Picea* parkland with areas of tundra dominated by *Artemisia* and Poaceae.

The onset of wetter conditions at ca. 6000 cal yr BP is also evident in other records of the GYE and northern Rocky Mountains. Many lake pollen records show an increase in forest density at ca. 6000-5000 cal yr BP (Alt et al., 2018; Brunelle et al., 2005; Mack et al., 1978; McWethy et al., 2020; Mehringer et al., 1977). In addition to the formation of the MP, other lakes in Montana and Wyoming (including Rainbow Lake) deepened around ca. 5500 cal yr BP (Minckley et al., 2012; Shuman and Serravezza, 2017), and the synchronous increase of TL1 $\delta^{18}O$ values suggests that winters warmed during this period (Fig. 6; Chellman et al., 2021). The enhanced seasonality of the early Holocene lessened as orbital changes caused a progression toward modern seasonal insolation levels. This potentially resulted in an increase in winter precipitation and a decrease in summer evaporative demand, enabling conifer expansion and lake level rise (Marsicek et al., 2018; Shuman et al., 2009; Whitlock et al., 2012).

The MP record suggests the presence of trees at higher elevations until ca. 4500 cal yr BP when arboreal pollen decreased until ca. 4200 cal yr BP (Fig. 6). Arboreal pollen in the TL1 record declined at ca. 5000 cal yr BP, although macrofossil evidence suggests that *Picea* was still locally present (Figs. 2 and 6). Although the TL1 arboreal pollen rose slightly after 5000 cal yr BP, the downward trend from ca. 6000 cal yr BP to ca. 4200 cal yr BP in both records suggests that treeline once again shifted downslope. With no evidence for a decrease in regional moisture, the downslope shift in treeline elevation at this time was likely in response to cooling temperatures.

Late Holocene (4200 cal yr BP-present day): Shifts between parkland and steppe

After ca. 4200 cal yr BP, there is evidence for another shift in the environment and climate of the Beartooth Plateau. The MP age-depth model suggests extremely slow deposition and/or a hiatus between ca. 4200-3000 cal yr BP (Fig. 4), and a lithological change from fine detritus/clay at ca. 4200 cal yr BP to more organic-rich sediment by ca. 2900 cal yr BP within 3 cm of the core supports a hiatus occurred (Fig. 3). Hiatuses are commonly caused by drought, although the pollen in the sample immediately below the hiatus shows no evidence of degradation to suggest post-deposition subaerial exposure. We suggest that the hiatus resulted from colder conditions that covered MP with snow and/or ice for a long portion of the year, with the extended ice cover preserving the pollen but preventing sediment accumulation. The pollen

accumulation rate in the sample below the hiatus was extremely high, supporting this scenario of pollen influx despite little sediment accumulation – which would be unlikely in a desiccated pond. The sample below the hiatus additionally shows a decrease in forest density, indicating treeline decline coincided with increased snow accumulation and colder temperatures. At TL1, the decrease of *Pinus* at ca. 3200 cal yr BP and increase in *Artemisia* and Poaceae at the end of the hiatus are also consistent with lowering of treeline elevation and colder summer conditions (Fig. 2 and 6).

Evidence from other sites also suggests that cool and relatively wet conditions prevailed during this hiatus interval. Beginning around ca. 3900 cal yr BP, the TL1 $\delta^{18}O$ record declined and ice accretion rates more than doubled likely indicating cool, wet winters and cool summers (Fig 6; Chellman et al., 2021). Similarly, at ca. 6300 cal yr BP, the Teton Glacier in the Teton Range, WY (~160 km to the southwest of the Beartooth Plateau) advanced slowly (coinciding with the decrease in summer temperatures and increase in effective moisture seen in the TL1 record), and then advanced dramatically between 3900-2800 cal yr BP, after which it retreated (Larsen et al., 2020). Fairy Lake, a high-elevation site in the northern part of the GYE, recorded an increase in snow avalanches at ca. 4500-2000 cal yr BP, signifying higher snowpack and unstable late-season snow conditions (Benes et al., 2019). Other mid-elevation forests in the northern Rocky Mountains region also experienced an increase in mesophytic trees such as *Picea* and *Abies* during this time period, which may have been in response to increases in moisture and cool conditions (Alt et al., 2018; Mack et al., 1978, 1978, 1983; Mehringer et al., 1985; McWethy et al., 2020). The Rainbow Lake record, while rather stable after the dramatic rise at ca. 5900 cal yr BP, indicates a slight additional deepening at ca. 4100 cal yr BP (Fig. 6; Shuman and Serravezza, 2017). Although the timing is asynchronous among records, it is probable that the Beartooth Plateau and other nearby mountainous regions experienced the coldest wettest conditions of the postglacial period from ca. 4000-3000 cal yr BP.

Although evidence supports a cold and wet period, other regional records indicate the possibility of drought conditions during the MP hiatus. The timing of the hiatus is not definitive (after ca. 4400 until before ca. 2900 cal yr BP based on the two surrounding radiocarbon dates), but 4200-3800 cal yr BP corresponds to a period in the TL1 $\delta^{18}O$ record that suggests warm dry winter conditions (Chellman et al., 2021). Diatom records from lakes on the Beartooth Plateau (Emerald Lake and Beauty Lake) similarly suggest the lake thermal structures from ca. 4500-

3200 cal yr BP were similar to today, and cold harsh winters (represented by deeper lake mixing), did not exist until one thousand years later at ca. 3200-2300 cal yr BP (Stone et al., 2016). Therefore, it is possible the MP hiatus was the result of desiccation during a warm dry period that also affected the plains and the midcontinent (Diffenbaugh et al., 2006; Liefert and Shuman, 2020, 2022). Yellowstone Lake and Lake of the Woods, WY additionally had low water periods until ca. 3000 cal yr BP (Pierce et al., 2002; Shuman et al., 2010). However, the presence of abundant pollen with few signs of degradation (i.e., from exposure) in the MP core, and the possibility that the difference in timing could be the result of age-depth uncertainty suggests the MP drying scenario is less plausible.

Following this cool, wet period, there is evidence that trees returned to higher elevations between ca. 3000-2000 cal yr BP. Both TL1 and MP records show high amounts of *Pinus* and moderate levels of Poaceae and *Artemisia*, suggesting an open parkland (Figs. 2 and 5). The Rainbow Lake record features a slight increase in *Pinus* during this period (Rust and Minckley, 2020; Fig. 7), and many records in the northern Rocky Mountains indicate the establishment of modern forest composition after ca. 3000 cal yr BP (Alt et al., 2018; McWethy et al., 2020; Whitlock et al., 2012). Though this suggests relatively stable climate conditions during recent millennia, the MP record indicates more variability in forest dynamics at high elevations on the Beartooth Plateau.

At ca. 2000 cal yr BP, Poaceae pollen increases in the MP record and reaches a maximum at ca. 1000 cal yr BP. This increase marks a transition to alpine tundra and a downslope shift in treeline (Figs. 5 and 7). In contrast, the TL1 record has moderate amounts of Poaceae pollen and *Pinus* and *Picea* percentages equivalent to those at the base of the record at ca. 10,400 cal yr BP, which are interpreted as parkland. The abundance of Poaceae macrofossils declined at 2000 cal yr BP (SM Fig. 2), and leaf and stem macrofossils (SM Fig. 2) and Asteroideae and Rosaceae pollen increased (Fig. 2). Thus, the TL1 record suggests an open landscape with shrubs and possibly scattered trees. The TL1 record ends with a similar, although less sharp, downward trend in the AP:NAP ratio, also implying a transition towards open conditions (Fig. 6).

Few other records in the region suggest a change in vegetation at ca. 2000 cal yr BP similar to those recorded in the Beartooth sites but several records show evidence of drought at this time. For example, diatom data from low-elevation Crevice Lake in the GYE, register shortened springs and longer summers (Whitlock et al., 2012), and charcoal data at several sites

in the northern Rocky Mountains indicate increased fires at ca. 2000 cal yr BP, possibly signifying warm and dry conditions (Alt et al., 2018; Brunelle et al., 2005). A 2000-year-long streamflow reconstruction for the Upper Colorado River, to the south of the Beartooth Plateau, indicates a severe 2nd century drought unmatched in terms of magnitude and duration (Gangopadhyay et al., 2022). While the grassland period seen in the MP record precedes the Medieval Climate Anomaly (MCA), the decrease in treeline indicates either the onset of drier conditions leading into the MCA or intensified cooling (Shuman and Marsicek, 2016).

Our records indicate that vegetation on the Beartooth Plateau responded to both the MCA (1000-750 cal yr BP; Cook et al., 2004) and the Little Ice Age (LIA; 500-250 cal yr BP; Cook et al., 2010; Mann et al., 1999). The TL1 record ends during the MCA with evidence of *Pinus* presence, and the MP record displays an increase in arboreal pollen throughout the MCA. Other GYE high-elevation sites also show denser forests at ca. 1500 cal yr BP (Iglesias et al., 2018), and stumps above present-day treeline that date to between 1500-800 cal yr BP in central Yellowstone National Park (Meyer et al., 1995) and in the Wind Rivers Range, WY (Morgan et al., 2014) suggest that trees migrated upslope during the prolonged warm conditions of the MCA.

Following the MCA, MP *Pinus* and *Picea* pollen decreased between ca. 500-300 cal yr BP, coincident with the LIA. *Artemisia* expanded around Beauty Lake (Spaulding et al., 2020), and other high-elevation sites in the GYE recorded a decrease in conifer pollen (Iglesias et al., 2018). This suggests that high-elevation trees shifted downslope in response to the colder conditions of the LIA. After the LIA cooling, arboreal pollen in the MP record increased to present day, which reflects the treeline migration upslope to its current position in response to warming conditions.

[Insert Figure 7]

Holocene fire history

During the early Holocene, TL1 microcharcoal concentrations started high, but decreased between ca. 9500-6000 cal yr BP, paralleling the decrease in conifer tree pollen (Figs 5 and 6). Both the TL1 and MP records show elevated charcoal accumulation at ca. 6000 cal yr BP when

there is evidence of a return of trees to higher elevations. Charcoal in the MP record decreased after ca. 5700 cal yr BP, while TL1 charcoal concentrations remained high until ca. 4000 cal yr BP. Since the TL1 charcoal is microscopic and that at MP is macroscopic, this difference could be explained by grass fires or long-distance transport of microscopic charcoal versus the local forest and shrub fires registered in the macroscopic (predominantly woody) charcoal records (Leys et al., 2017). The records from Rainbow and Beauty Lakes also showed minimal charcoal throughout their records, although an increase in fire activity at ca. 6000-5500 cal yr BP (Rust and Minckley, 2020; Spaulding et al., 2020) supports an increase in fire activity on the Beartooth Plateau consistent with the pollen interpretation of forest expansion during this time period.

The TL1 charcoal declined during the period when the MP record shows a hiatus. If the hiatus was in response to drought, we would expect more evidence of fire in the TL1 record, so the lack of charcoal supports our hypothesis that the hiatus was due to cold temperatures and greater ice cover. The MP record in the late Holocene shows one more increase in charcoal after ca. 1000 cal yr BP, again paralleling an increase in conifer pollen, suggesting fire activity returned to high elevations when there was fuel to burn.

Organic layers from ice patches as a novel paleoenvironmental proxy

Our analysis of pollen, charcoal, and macrofossils from organic layers deposited in ice cores is the first record of this type for North America. Previous efforts to analyze pollen from sediment within perennial ice deposits in high-elevation caves in the Pyrenees succeeded in creating a record of altitudinal treeline fluctuation over the mid-to-late Holocene (Leunda et al., 2019). While the Pyrenees ice cave deposits are formed through processes that are different than those that result in the development of high-elevation ice patches, the organic layers in both ice deposits are thought to be related to acute periods of ablation (Leunda et al., 2019; Chellman et al., 2021). Chellman et al. (2021) propose that the organic layers in the ice patch formed as windblown or animal-deposited material collected on the summer snowpack, which then concentrated into one organic-rich layer during periods of surface melt and ablation. The most recent TL1 organic layer dates to ca. 1000 cal yr BP, which corresponds to the MCA, supporting the hypothesis that the organic layers form during periods of warm and possibly dry conditions (Chellman et al., 2021).

In contrast with continuous wetland records, the ice patch organic layers record represents discontinuous snapshots in time. If the layers represent severe, multi-decadal drought events, their duration is likely within the range of multi-decadal droughts documented in tree-ring records from the western US (Ault et al., 2013, 2018; Cook et al., 2010). The absence of major discontinuities in the TL1 ice accumulation chronology suggests the droughts were not sufficiently long or intense enough to melt the ice patch enough to result in significant mass loss or chronological discontinuities. Droughts severe enough to generate an organic layer occurred on average every few hundred years throughout the Holocene, which matches the approximate frequency of megadroughts deduced from fire-related sediment runoff in Yellowstone National Park (Meyer et al., 1995) and recorded in tree-ring records over the last millennium (Ault et al 2013).

Another depositional feature of the ice patch record that is not well understood is the amount and volume of organic sediment deposited in an organic layer. The magnitude of deposition could be related to the duration or severity of a drought, or to the duration of animal activity depositing feces and vegetative matter. It also could be related to periods when strong winds transported and deposited large amounts of organic material onto the ice. If the latter, mass and volume of the organic layers could potentially be used as another paleoclimate proxy. The mass of organic material did increase during times when conifers were more abundant at higher elevations (Table 2; the most recent layers over the past ~2500 years, one at ca. 5800 cal yr BP, and at the very base of the ice core from ca. 10,400-9800 cal yr BP). Thus, increased deposition and preservation of organic material in the ice occurred when subalpine parklands or forests were located at higher elevations. This association suggests that the thicker layers were formed when decadal-scale droughts and anomalous summer warmth resulted in periods of negative mass balance during an overall wetter and cooler time conducive to high-elevation tree growth.

Counter to this general pattern, one heavy organic layer formed when treeline elevations were lower (ca. 7800 cal yr BP) during the early Holocene period. This layer contained increased levels of animal digesta and may have formed during a time of high animal occupation of the ice patch, possibly as a water source during summer drought. The longest consecutive sequence of light organic layer masses (<1g) occurred between ca. 5100-2800 cal yr BP, which is a period of increased ice accumulation and cooler summers with more effective cool-season precipitation

(Fig 6). This time may have been characterized by shorter and less severe droughts as well as less intense use of ice patches by ungulates.

Conclusions

The Beartooth TL1 Ice Patch and Meltwater Pond records provide new insight into high-elevation treeline dynamics and climate change during the Holocene. During the late-glacial to early Holocene transition, treeline elevation rose with warmer temperatures and increased moisture (Fig. 7). As summer insolation levels continued to increase and winter insolation levels decreased after ca. 10,000 cal yr BP, cold harsh winters and dry summers led to increased tree mortality and a lowering of treeline elevation despite warmer growing season temperatures. After ca. 6200 cal yr BP, relatively cooler summers and warmer, wetter winters than before led to the formation of the Meltwater Pond and an increase in Rainbow Lake water levels (Fig 6). Subalpine conifers established at higher elevations, and fire activity increased due to more fuel availability. By 5000 cal yr BP, treeline elevation decreased again, possibly caused by a return of cooler winter and summer conditions. An increase in ice accumulation and an apparent hiatus in the MP core suggests the high-elevation basin had more perennial snow and ice coverage during a possible neoglacial period spanning from ca. 4000 to 3000 cal yr BP (Fig. 6 and 7). After the MP hiatus, treeline rose in elevation from ca. 3000 to ca. 2000 cal yr BP, in response to warming temperatures after the neoglacial period and then decreased until the onset of the MCA, perhaps in response to persistent drought or cooler summer temperatures. Treeline advanced in response to warming conditions during the MCA, lowered with cold summer temperatures during the LIA, and then gradually rose to its present location.

Although climate projections suggest that temperatures will rise 4 to 6°F higher in the coming decades (Hostetler et al. 2021), this warming may not lead to an expansion of forest cover on the Beartooth Plateau. The paleoecological evidence from TL1 and MP show a nonlinear response to warming temperatures in the past. Conifer forests on the Beartooth Plateau declined during a time of increased summer drought in the early Holocene despite warmer temperatures. During the late Holocene, relatively warmer winters and cooler summers were the primary limitations of treeline elevation, allowing treeline to move upslope. Recent and projected climate conditions suggest a shift in the seasonality of precipitation will reduce growing season

moisture availability (Hostetler et al. 2021), and it is likely that high-elevation forests will again become moisture limited, decreasing density and ultimately lowering treeline as occurred during the early Holocene.

While the exact processes behind the deposition and preservation of organic material in the ice patch are uncertain, it is likely that they occur during extended periods of drought. It is possible that these organic layers represent landscape vegetation during a drought spanning multiple decades but the continuity of ice accumulation precludes the droughts from lasting much longer. Therefore, even though one TL1 organic layer sample could represent decades, the layers are thought to be capturing snapshots of more gradual long-term vegetation changes, and not a decades-long vegetation change within the timespan of the drought period. If our understanding of the organic layer formation and accretion of material in the ice is accurate, the TL1 record suggests that extended and severe droughts were common throughout the Holocene, occurring at least 29 times over the last 10,400 years – or on average once every ~300 years.

Although questions remain about the formation and persistence of ice patches and the layers within, recent investigations show that they can serve as a paleoenvironmental record, providing new climate and ecosystem insights that complement information derived from traditional paleoenvironmental records. In order to better interpret these records, future research could seek to better understand the specific processes and mechanisms that underly their formation. Additionally, the human artifacts and biological information frozen within ice patches (pollen, macrofossils, etc.) combined with their physical record of ice accumulation rates, water isotopes, as well as frequency and timing of organic layer development make them unique recorders of the combined human-climate-ecosystem response. Paleoenvironmental records from ice patches present a unique opportunity to generate a greater understanding of the effects of seasonal climate changes on high-elevation ecosystems, and the organic layers can augment traditional analyses of proxies from wetland sediments by highlighting extreme climatic events as well as documenting the more gradual ecological change in areas with few paleoenvironmental proxies.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figures

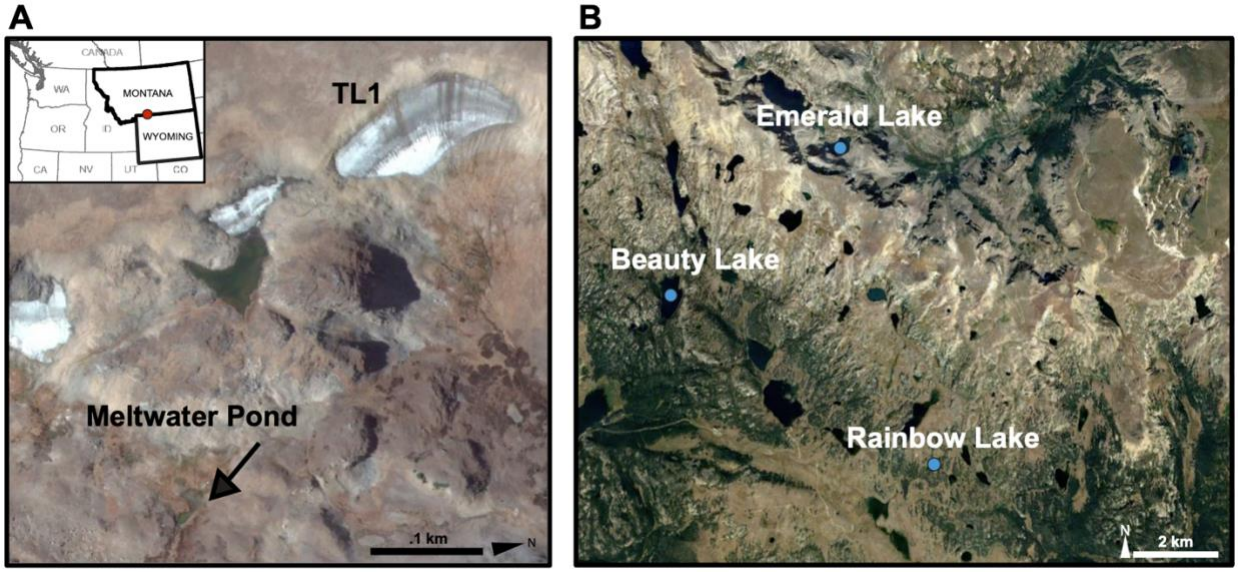


Figure 1A) TL1 Ice Patch and Meltwater Pond. B) Referenced Beartooth Plateau study sites used in comparative analyses, within 20 km of TL1: Emerald Lake (Barth et al., 2022), Rainbow Lake (Shuman and Serrevezza, 2017, Rust and Minckley, 2020); Beauty Lake (Spaulding et al., 2020). Images from Google Earth.

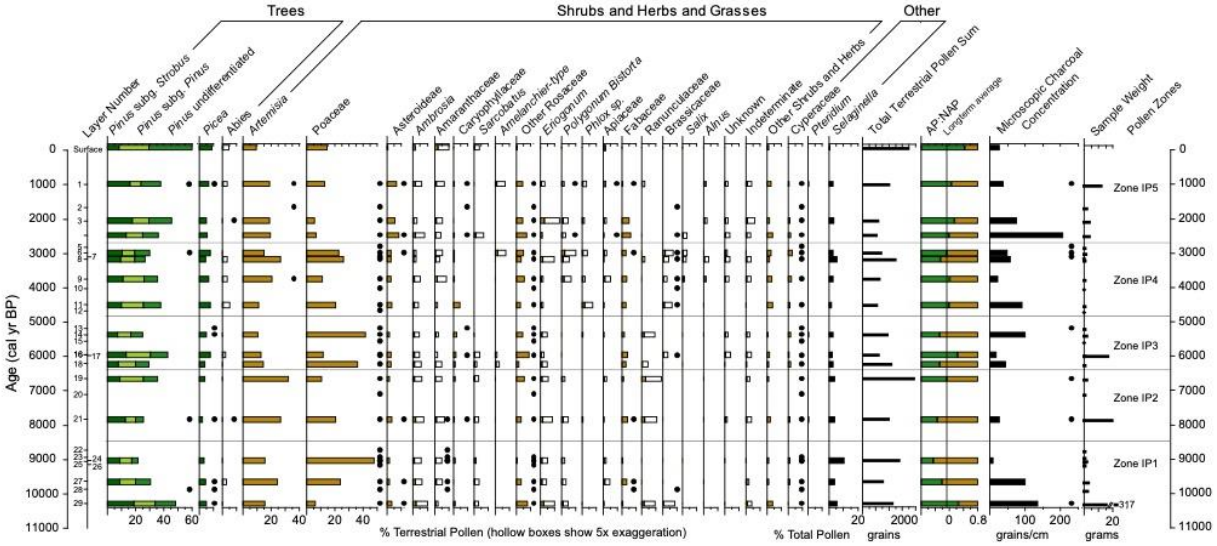


Figure 2. Pollen, macrofossils, and charcoal concentration data from the TL1 Ice Patch. Hollow boxes are 5x exaggeration of the pollen percentages for species that never exceed 3%, and circles denote the presence of at least one macrofossil. Surface sample is not an organic layer.

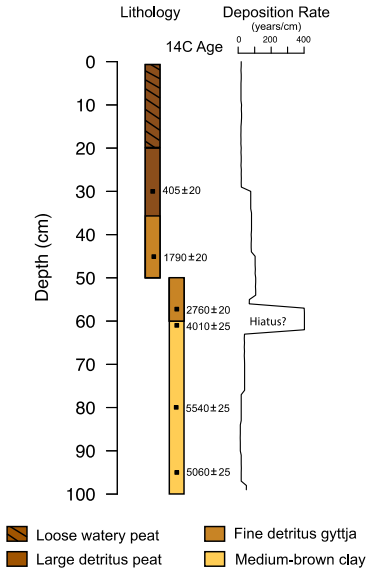


Figure 3. Lithology of the Meltwater Pond sediment, location of samples submitted for radiocarbon dating, and deposition rate of sedimentation.

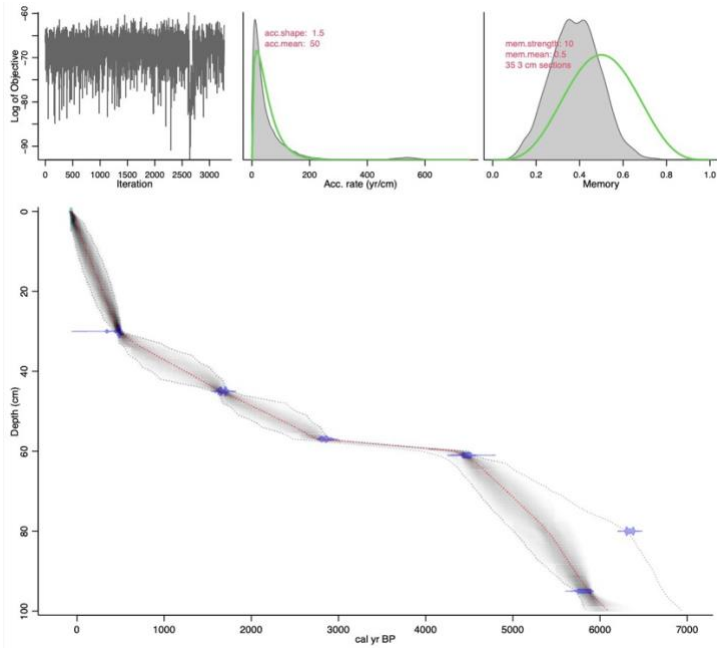


Figure 4. Age-depth model for Meltwater Pond based on six radiocarbon dates.

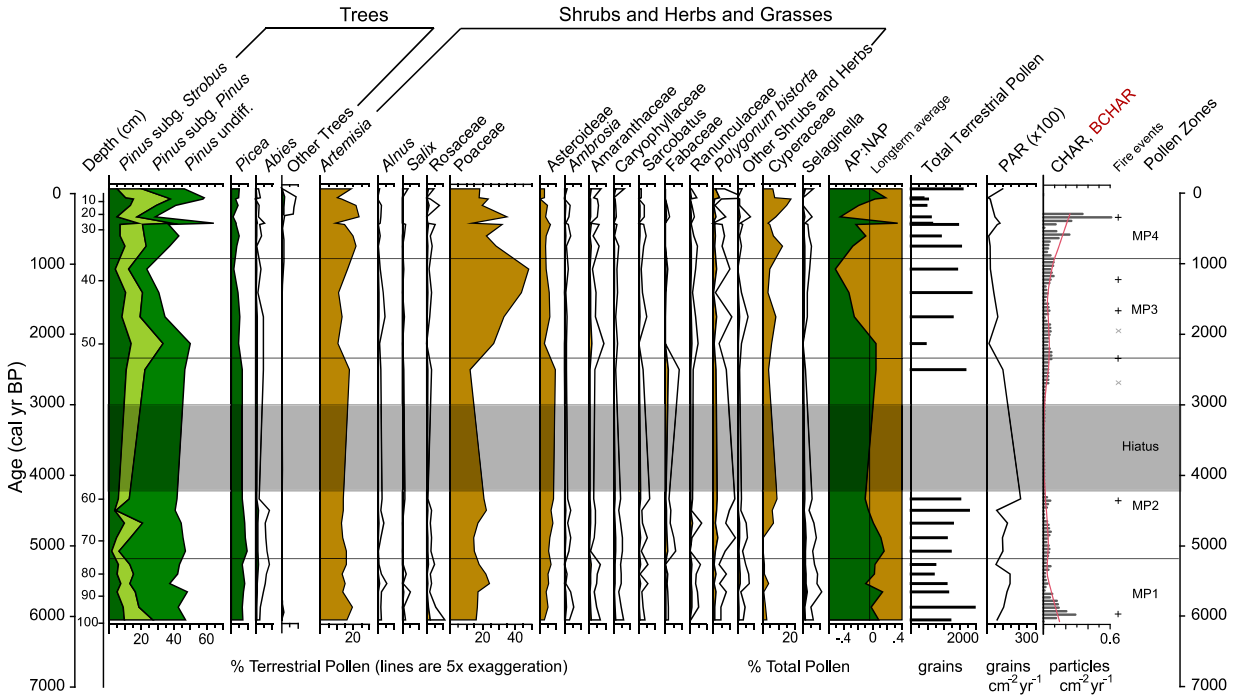


Figure 5. Pollen and charcoal data from Meltwater Pond, WY. Black lines are 5x exaggeration of the pollen time series, and (+) symbols denote significant fire events, and (x) symbols indicate insignificant fire events.

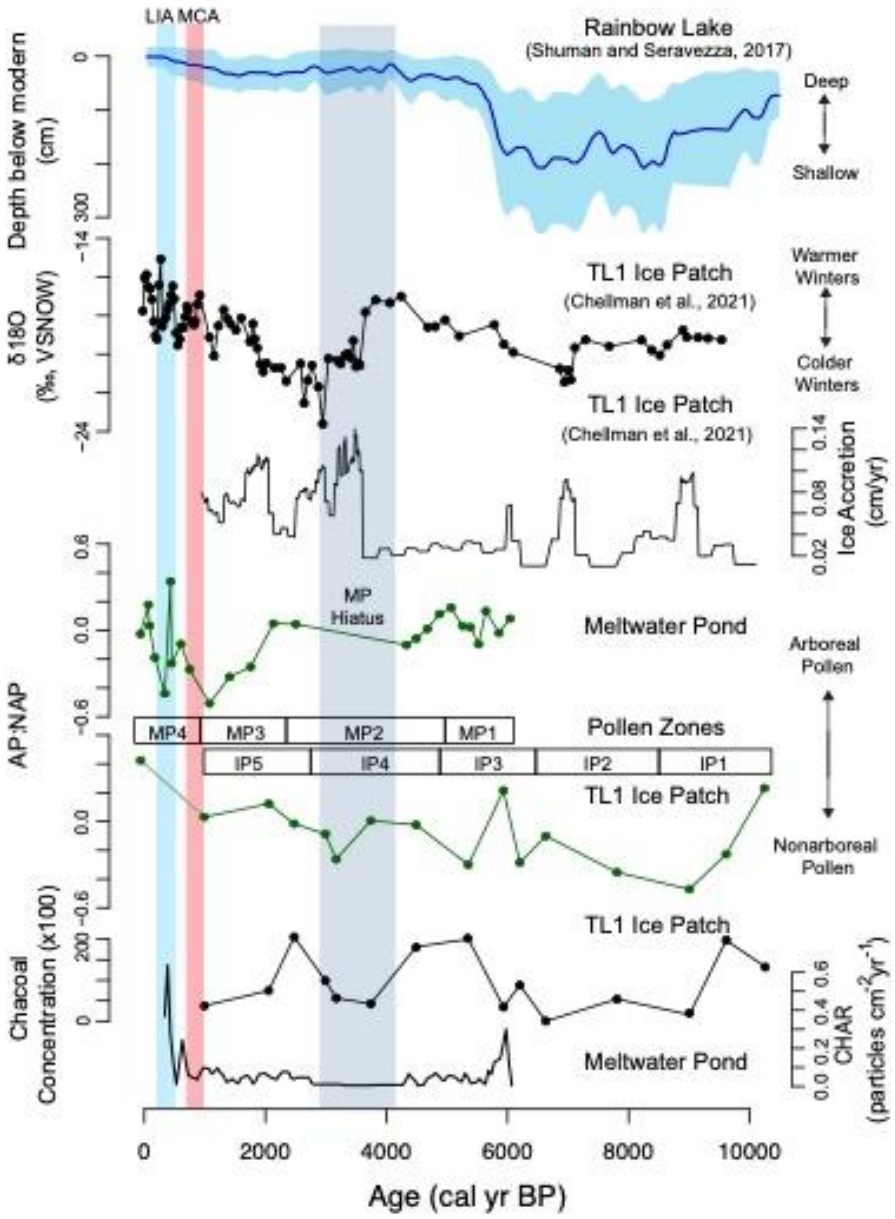


Figure 6. Multiproxy comparison of lake level data from Rainbow Lake (Shuman and Serravezza, 2017), isotope and ice accumulation data from the TL1 Ice Patch (Chellman et al., 2021), the ratio of arboreal to non-arboreal pollen from the TL1 Ice Patch and Meltwater Pond, and charcoal data from the TL1 Ice Patch and Meltwater Pond (this study). Pollen zones are noted in boxes and TL1 surface arboreal pollen ratio is not from an organic layer.

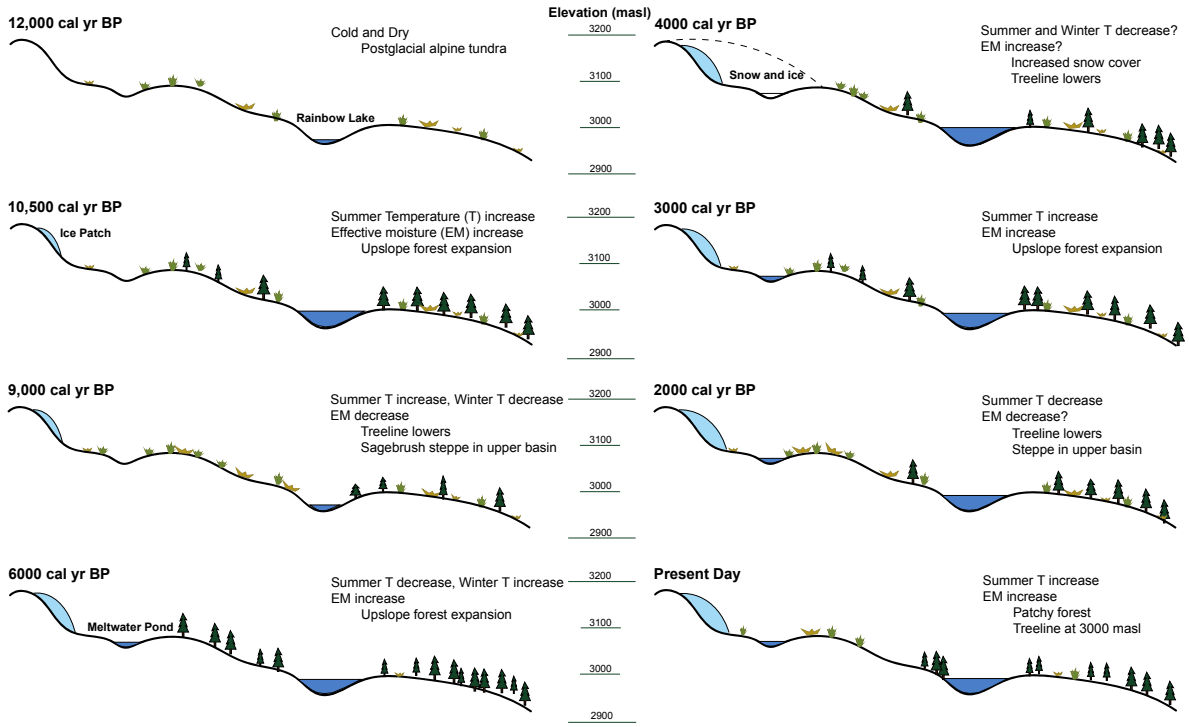
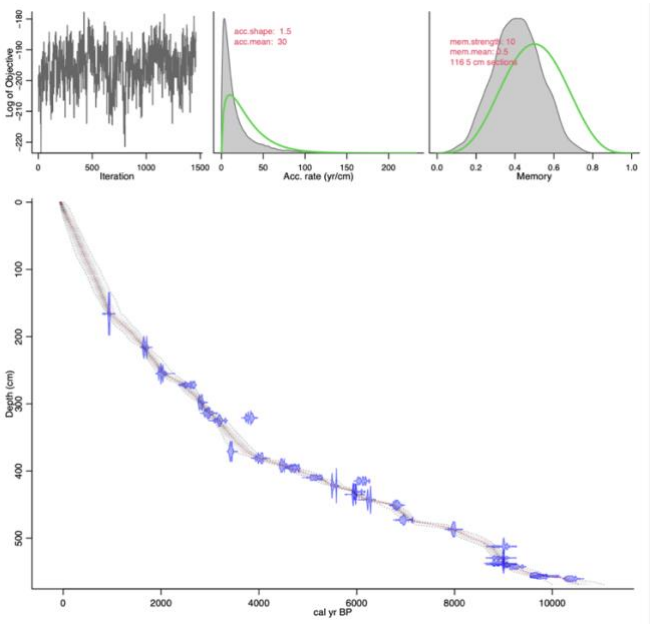
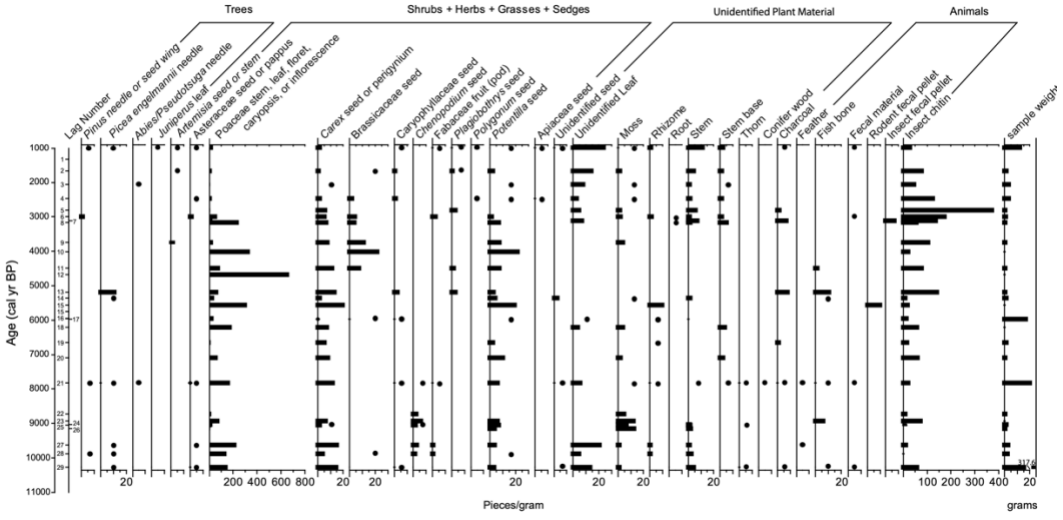


Figure 7. Sequence of major paleoenvironmental changes through time on the Beartooth Plateau based on records from this study and Rainbow Lake studies (Rust and Minckley, 2020; Shuman and Serravezza, 2017). Changes in temperature and precipitation are relative to the time period before. Each panel illustrates prominent shifts in vegetation recorded by pollen samples corresponding to the time period indicated.

Supplementary Materials



SM Fig 1. Age-depth diagram of the TL1 Ice Patch, based on 29 radiocarbon dates.



SM Fig 2. Macrofossils from TL1 Ice Patch organic layers. Dots indicate an amount under 1 piece/gram.