POSTGLACIAL CLIMATE, VEGETATION, AND FIRE DYNAMICS OF WESTERN MONTANA

by

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of

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DEDICATION

To Jita and Ka.

ACKNOWLEDGEMENTS

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GLOSSARY or NOMENCLATURE

GYE	Greater Yellowstone Ecosystem
NRM	Northern Rocky Mountains
YNP	Yellowstone National Park
AP	Arboreal pollen
NAP	Non-arboreal pollen
MASL	Meters above sea level
Cal yr BP	Calendar years before present (1950)

ABSTRACT

In recent decades, fires in the western U.S. have grown in size and severity, a trend expected to continue, raising concerns about future forest ecosystems. Fire is a primary disturbance in northern Rocky Mountain forests, but human activities—like logging, fire suppression, igniting fires, and ecosystem fragmentation—combined with anthropogenic contributions to climate change, have altered the natural fire regime. To contextualize these changes, it is essential to understand the co-evolution of forests and fire and to examine past shifts in fire regimes to better grasp the consequences of increased fire activity for forest ecosystems today. This study provides pollen and charcoal data from twelve locations across western Montana and presents vegetation and fire histories from forest types and regions that are underrepresented in the existing paleorecord. Chapter 2 investigates high-elevation records from an ice patch and pond on the Beartooth Plateau, offering insights into ecosystem changes at upper treeline. Chapter 3 examines a middle-elevation site in a mesic mixed conifer forest, exploring the stability of these ecosystems. Lastly, Chapter 4 discusses a network of sites from low to high elevation, revealing regional shifts in vegetation and fire activity in response to climate. Climate has been the primary driver of ecosystem change over the past 14,000 years, and fire activity has responded to both climate and site-specific conditions. As summer insolation levels rose at the end of the late-glacial period, forests were established, fuel biomass increased, and wildfires became more frequent. Open Douglas-fir parkland prevailed at low elevations during the warm, dry early Holocene, lower treeline moved upslope, and upper treeline shifted downslope in some areas. The openness of the vegetation was controlled by summer drought, and an attendant decline in fire activity reflected a lack of fuel connectivity. Forest density increased after 6000 cal yr BP and closed forests persisted throughout the cold, wet late Holocene. This period experienced the highest fire activity as a result of ample biofuel and increased short-term climate variability.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Temperate forest ecosystems are a key component of the Earth's system, influencing the hydrological cycle, atmospheric chemistry, and the carbon cycle while also being essential for biodiversity and providing numerous economic and social benefits for humankind (Bonan, 2008). Forest fires are a primary natural disturbance process in temperate forests, shaping biodiversity, vegetation distribution, and forest structure (Bowman et al., 2009).
Although wildfires are a natural aspect of forest ecosystems and essential for their survival, in the Northern Rocky Mountains (NRM), they have become larger and more severe in recent decades due to longer, drier summers (Abatzoglou and Williams, 2016; Westerling et al., 2006) and, in many xeric forests, due to fuel accumulation after decades of fire suppression (Schoennagel et al., 2017). Forest disturbances in the NRM are expected to increase in the future as a result of longer, drier summer conditions, with coniferous forests being especially vulnerable (Seidl et al., 2017). With projected increases in fire frequency and size (Westerling et al., 2011), forest ecosystems risk crossing a tipping point and becoming significantly altered (Reyer et al., 2015; Turner et al., 2019). Increased fire size and severity threaten post-fire regeneration by increasing the distance to the seed source, and projected warm and dry conditions are not conducive to post-fire tree establishment (Davis et al., 2019). The increased frequency of disturbances will likely reshape the structure and distribution of forests into the future.

Paleoenvironmental studies are essential for contextualizing present-day forest structure and fire regimes, and they provide valuable insights into how vegetation and fire activity have responded to climate change across varying temporal scales. Sediments from lakes and wetlands

preserve pollen, charcoal, and macrofossils from the surrounding landscape, with each stratigraphic sample reflecting the environmental conditions at the time of deposition. Paleoecologists take sediment cores, and by analyzing pollen and charcoal throughout these cores, they create detailed reconstructions of vegetation and fire in the landscape surrounding the lake over time, revealing periods of ecosystem change. These natural archives are the key to understanding the long-term relationship between climate, vegetation, and fire (Schiller et al., 2023).

The NRM forests of western Montana (MT) have long been of interest to paleoecologists, although most studies focus on the Greater Yellowstone Ecosystem (GYE) in southwestern MT and northwestern WY (Benes et al., 2019; Huerta et al., 2009; Iglesias et al., 2018, 2015; Krause et al., 2015; Krause and Whitlock, 2017, 2013; Lynch, 1998; Millspaugh et al., 2000; Mumma et al., 2012; Schiller et al., 2022; Whitlock, 1993; Whitlock et al., 2012, 1995). Meanwhile, pollen studies throughout the rest of western Montana in the NRM are more scarce (Alt et al., 2018; Brunelle et al., 2005; Mack et al., 1983, 1978; McWethy et al., 2020; Mehringer et al., 1977; Power et al., 2011, 2006; Whitlock et al., 2011). Combined, these studies indicate that forest structure primarily responded to changes in summer and annual insolation levels. Forests developed after ca. 13,000 cal yr BP in northern Montana and between 12,000 and 11,000 cal yr BP in the GYE, coinciding with the rise in summer insolation following a cold, dry tundra-steppe and parkland phase during the late glacial period. Forest structure evolved throughout the Holocene epoch, although the changes were not always spatially and temporally synchronous.

Although there is a general understanding of vegetation patterns across the region, the spatial and temporal variability among sites has not been thoroughly investigated, and many

studies from northwestern MT lack fire-history reconstructions. Advances in radiocarbon dating since the 1980s enable more accurate dating of pollen and charcoal records, offering new insights into the region's vegetation and fire history. Additionally, the topography of the NRM disrupts large-scale atmospheric circulation, resulting in localized climate conditions that may differ from regional trends (Williams et al., 1996). Variability stems from factors such as wind channels, rain shadows, aspect, and elevation, leading to temperature and moisture differences that create a mosaic of microclimates (Barnard et al., 2017; Dobrowski, 2011). Therefore, single-site paleorecords may not provide a reliable account of past climates, making it essential to synthesize data from multiple sites for a clearer understanding of regional climate variability (Bracht-Flyr and Fritz, 2012).

By investigating periods of past ecological change, paleoecological studies provide insights into how vegetation and fire activity may adapt to current and future climate changes of similar magnitude. The last 3000 years of the late Holocene is of particular interest in this dissertation because the annual/summer temperatures are more comparable to those of today than those of the early Holocene and late-glacial periods (Alder and Hostetler, 2015; Bartlein et al., 1998; Kutzbach et al., 1998). Closely examining conditions in the late Holocene, when orbital parameters and ice-sheet size are more comparable to today, provides a context for understanding how vegetation and fire might respond to current and future climate conditions.

Northern Rocky Forests and Fire Regimes

The forests of the NRM in western Montana consist of a variety of conifer species, and forest types are arranged by elevation. Specific elevations vary between mountain ranges, but the lower elevation foothills typically consist of parklands featuring *Pseudotsuga menziesii, Pinus flexilis,* and *Juniperus communis* (common names found in Table 1.1), and forest density increases with elevation. This is followed by *Pinus contorta* forests and/or mixed conifer forests of *Pseudotsuga menziesii, Pinus contorta, Picea engelmannii,* and *Abies lasiocarpa* at middle elevations. Upper-elevation subalpine forests consist of *Picea engelmannii* and *Abies lasiocarpa,* and the highest elevations are characterized by forests and parklands with *Pinus albicaulis.* In northwest Montana, forest structure follows a similar pattern, although lower elevations also support *Pinus ponderosa,* and due to a more maritime climate regime, low and middle elevations also contain *Tsuga heterophylla, Thuja plicata,* and *Larix occidentalis*. *Abies grandis* co-occurs at middle elevations, and *Larix lyallii* is also found at the highest elevations with *Pinus albicaulis* (Pfister et al., 1977).

Fire regimes are typically defined by characteristics of fire, such as the fire frequency (the rate at which fires occur) and fire severity (ecosystem impacts of a fire). They are shaped by vegetation structure and climate, and in the NRM, forests are typically classified according to low, mixed, or high-severity fire regimes. Low-severity fires are non-lethal, consuming grass, litter, and undergrowth, and occur frequently, approximately every 25 to 35 years (Jain et al., 2012). These fires are typically found in low-elevation xeric forest types, such as *Pseudotsuga menziesii, Larix occidentallis,* and/or *Pinus ponderosa* forests, which are highly fire-adapted, with attributes such as thick bark and deep roots (Fischer and Bradley, 1987). High-severity fire

regimes consist of stand-replacing fires that result in tree mortality and occur infrequently, typically at intervals of 70 to 500 years (CSKT, 2021; Baker, 2009). These fires occur in mesic subalpine forests, such as those dominated by *Picea engelmannii* and *Abies lasiocarpa*, which are not adapted to fire due to their thin bark and shallow roots (Fischer and Bradley, 1987). Mixed-conifer forests typical of mid-elevations experience both nonlethal and stand-replacing fires of varying sizes every 30 to 100 years, which is considered a mixed-severity fire regime (Arno et al., 2000; CSKT; 2021). These forests are typically mesic forests with very fire-adapted (e.g., *Pseudotsuga menziesii*), moderately adapted (*Pinus contorta,*), and fire-susceptible (e.g., *Abies lasiocarpa)* trees (CSKT, 2021; Fischer and Bradley, 1987).

Table 1.1 Scientific and common names of species mentioned in this dissertation

Scientific Name	**Common Name**
Abies lasiocarpa	Subalpine fir
Artemisia tridentata	Big sagebrush
Betulaceae (*Betula* spp.)	Birch family
Cyperaceae	Sedge family
Juniperus communis	Common juniper
Larix occidentalis	Western larch
Picea engelmannii	Engelmann spruce
Pinus albicaulis	Whitebark pine
Pinus contorta	Lodgepole pine
Pinus flexilis	Limber pine
Pinus ponderosa	Ponderosa pine
Poaceae	Grass family
Populus tremuloides	Quaking aspen
Pseudotsuga menziesii	Douglas-fir
Rosaceae	Rose family
Salicaceae *(Salix* spp.*)*	Willow family

Objectives

This dissertation investigates changes in vegetation and fire activity since the Last Glacial Maximum (ca. 23,000-15,000 cal yr BP) in the forests of western Montana (Fig. 1.1) to better understand the factors driving shifts in montane and subalpine ecosystems. In addition to providing vegetation and fire histories of forests at different elevations, the specific objectives for each chapter are as follows: determine how forest structure and timberline have changed at high elevations in response to climatic events over the last 10,000 years and explore whether organic material found in a permanent ice patch can be used to reconstruct past environmental change (Chapter 2); examine the potential of mid-elevation mesic sites as areas of climate refugia (Chapter 3); and compare the vegetation response and changes in fire activity across an elevational gradient in the NRM to better understand local and regional drivers of environmental change (Chapter 4).

To address these objectives, I utilized new and published fossil pollen, charcoal, and macrofossils from sediment cores from two wetlands, one small pond, eight lakes, and one high-elevation ice patch in western Montana (Fig. 1.1). The sites investigated in this dissertation are listed below from south to north (sites marked with (*) have been published in the past, but new data has been added since then):

1) TL1 Ice Patch (exact location redacted to preserve archaeological integrity, 3145 masl): A 10,000-year-old ice patch on the Beartooth Plateau that provides a record from above timberline. Present-day vegetation is primarily grasses (e.g., *Poa alpina*) and small shrubs (e.g. *Salix reticulata*), and herbs (e.g., *Potentilla diversifolia* and *Geum rossii*). Current upper treeline lies approximately 0.6 km from the ice patch at 3050 masl.

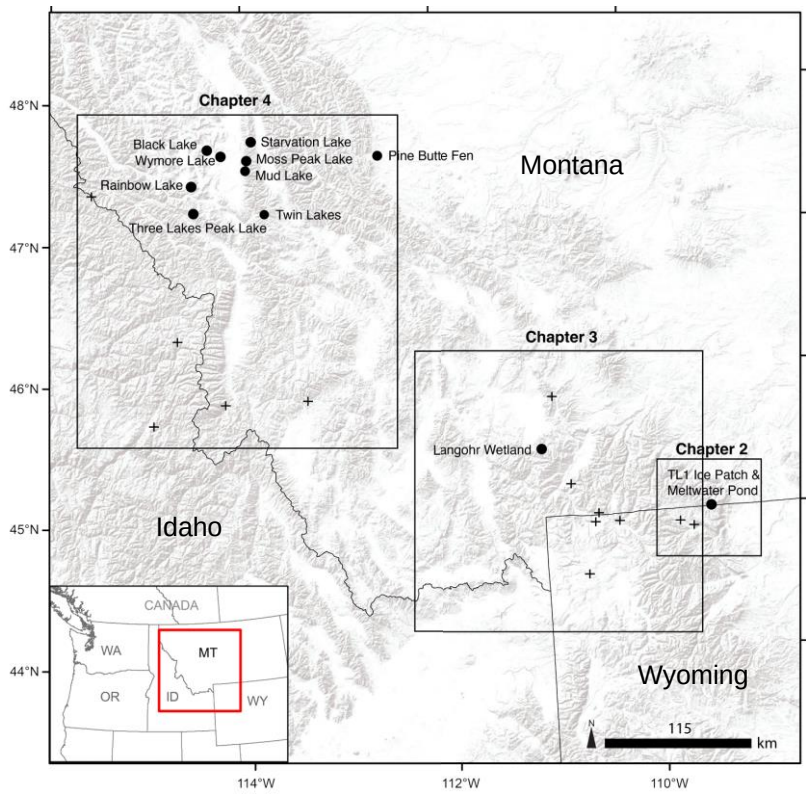


Fig. 1.1 Map of western Montana and location of sites investigated in this dissertation. Boxes designate regions discussed in each chapter, and locations marked with (+) are previously published sites used in the regional comparisons. Should come sooner.

2) Meltwater Pond (exact location redacted to preserve archaeological integrity, 3090 masl): A small pond adjacent to the TL1 ice patch that provides a point of comparison for the ice patch to help assess the validity of the ice patch as a paleoenvironmental archive. It also provides a ca. 6000-year-long record of high-elevation vegetation and fire activity. Present-day vegetation is primarily alpine grasses, small shrubs, and herbs (same as TL1), and upper treeline is located 0.6 km from the pond at 3050 masl.

3) Langohr Wetland (45.52425°N, 111.01807°W, 1898 m asl, ~2 ha): A middle-elevation wetland of late-glacial origin located in the northern Gallatin Range. This site provides an approximately 14,000-year-long sediment record. Present-day vegetation is a mesic

mixed conifer forest with *Picea engelmannii, Pinus contorta, Abies lasiocarpa,* and *Pseudotsuga menziesii* on the southerly slopes.

4) *Twin Lakes (47.241491°N, 113.91093°W, 1236 masl): A low-to-mid-elevation lake of late-glacial origin located in the Mission Range (Alt et al., 2018). This site provides a 14,000-year-long record, and present-day vegetation is a mixed conifer mesic montane forest dominated by *Pseudotsuga menziesii, Pinus ponderosa,* and *Picea engelmannii.*
5) Three Lakes Peak Lake (47.254727°N, 114.55861°W, 2072 masl): A high-elevation cirque lake close to upper timberline in the Reservation Divide Mountains. This lake provides a 5000-year-long record, and present-day vegetation surrounding the lake is a *Picea engelmannii* and *Abies lasiocarpa* forest. This study was a part of Shelby Sly's master's thesis project (Sly, 2020).
6) Rainbow Lake (47.525469°N, 114.76135°W, 1093 masl): A low-elevation lake in the Mission Valley that provides a 10,000-year-long sediment record. It is situated within a xeric mixed conifer forest of *Pseudotsuga menziesii, Pinus ponderosa, Pinus contorta,* and *Larix occidentalis.* This study was a part of Matthew Weingart's master's thesis project (Lapierre, 2021).
7) Mud Lake (47.616691°N, 113.99786°W, 1765 masl): A high-elevation cirque lake in the Mission Range, which provides a 5500-year-long record. It is surrounded by subalpine forest of *Picea engelmannii, Abies lasiocarpa, Pinus contorta,* and *Pseudotsuga menziesii.* This study was a part of Shelby Sly's masters thesis project (Sly, 2020).
8) Moss Peak Lake (47.684638°N, 113.99952°W, 1500 masl): A mid-to-high elevation lake in the Mission Range that provides a 1500-year-long record. It is situated within a mesic

mixed-conifer forest with *Picea engelmannii, Abies lasiocarpa, Pinus contorta, Larix occidentalis,* and *Pseudotsuga menziesii.*

9) Wymore Lake (47.786741°N, 114.17115°W, 884): The lowest elevation site in this study, located in the Mission Valley. Wymore Lake is a kettle lake that formed during the retreat of the Cordilleran Ice Sheet. It provides a ca. 14,500-year-long record, and is surrounded by open montane forest with *Pseudotsuga menziesii, Pinus ponderosa, Pinus contorta,* and *Larix occidentalis.* This site was a part of Kari Lapierre's master's thesis project (Lapierre, 2021).
10) Pine Butte Fen (47.840256°N, 112.56413°W, 1390 masl): A low-elevation wetland that sits at the ecotone of the northern Rocky Mountains and the northern Great Plains. It provides a 7500-year-long record and the wetland currently supports grasses (e.g., *Pseudoroegneria spicata* and *Festuca campestris*), shrubs (e.g., *Salix* spp. and *Betula glandulosa*), and herbs (e.g., species of Asteraceae). The upland vegetation is an open parkland dominated by *Pinus flexilis* and *Populus tremuloides.*
11) *Black Lake (47.863622°N, 114.32341°W, 985 masl): A low-elevation lake in the Mission Valley that provides a 7500-year-long record (McWethy et al., 2020). It is situated in montane forest of *Pseudotsuga menziesii* and *Pinus ponderosa.*
12) Starvation Lake (47.865251°N, 113.97042°W, 1710 masl): A high-elevation lake in the Mission Range with basal clay that dates to 1500 cal yr BP. It is situated within a *Picea engelmannii* and *Abies lasiocarpa* subalpine forest.

Overview of Dissertation

The objective of this dissertation research is to increase our understanding of climate-vegetation-fire dynamics in western Montana since the Last Glacial Maximum by specifically examining these questions: 1) How does forest structure change in response to changing solar insolation levels? 2) How does fire activity differ with varying vegetation structure and climate conditions? To address these questions, I focus on forests at different elevations and regions in each chapter and examine the patterns of vegetation change and fire activity over time. I utilize fossil pollen and charcoal to reconstruct vegetation and fire histories, comparing this data with additional published pollen and charcoal data from the respective regions of each chapter (Fig. 1.1). Vegetation and fire trends are then compared with independent paleoclimate information, including records of past changes in lake level, ice cover, limnobiota, geochemistry and paleoclimate models that describe the large-scale changes in the climate system.

Chapter Two explores the development of high-elevation alpine tundra and upper treeline through the Holocene on the Beartooth Plateau in the Greater Yellowstone Ecosystem. The data source for this chapter is unique because, in addition to sediment from a small pond, I use sediment from within an ice core from a high-elevation ice patch on the Beartooth Plateau, the first North American record of its kind. Additionally, vegetation records from above treeline are scarce in the NRM; there are only two in the southern portion of the GYE (Fall et al., 1995; Lynch, 1998). Therefore, this chapter serves as proof of concept for the utilization of high-elevation ice patches and also provides a Holocene-length record of upper treeline fluctuations and forest development. We compare these records with other paleoenvironmental proxy data

from the ice patch and the Beartooth Plateau to understand the climate parameters that led to upslope and downslope movement of treeline.

This chapter has been published in *The Holocene* (Alt et al., 2024) and was a collaboration among scientists with diverse specialties. Kathryn Puseman carried out a detailed macrofossil analysis on the sediment, complementing the pollen record. Drs. Nathan Chellman and Joseph McConnell conducted an oxygen isotope analysis on the ice core, producing a proxy record for winter temperatures, which was published in 2021 (Chellman et al., 2021) and used for comparison with the pollen record. Dr. Craig Lee recovered artifacts that have been melting out of high-elevation ice patches, underscoring the need for scientific work on these vanishing ice patches and providing evidence of human use of high-elevation landscapes (Lee, 2012). Drs. Gregory Pederson and David McWethy were crucial in assisting with the development of this study, writing, reviewing, and editing the manuscript. This study was supported by funding acquired from multiple sources by Drs. Craig Lee, Joseph McConnell, Gregory Pederson, and David McWethy, which are acknowledged at the end of Chapter Two.

Chapter Three examines a middle-elevation wetland and investigates its role as a potential climate refugium in Southwestern Montana. This chapter is in press and will be published in 2025 in the *Quaternary Research* journal. It presents a post-glacial vegetation and fire record from Langohr Wetland, which is unique for two reasons: 1) the sediment from this wetland is believed to capture highly localized high-severity fire events (unlike lake sediments that can collect charcoal transported over great distances) and therefore, this record enables us to isolate periods when large fires occurred directly around the wetland; and 2) this is the only middle-elevation record from a mesic montane forest in the northern GYE region. We compared

this wetland record with several other pollen and charcoal records from the region (Benes et al., 2019; Huerta et al., 2009; Krause et al., 2015; Krause and Whitlock, 2013; Millspaugh et al., 2000; Rust and Minckley, 2020; Whitlock, 1993; Whitlock et al., 2012) to enhance our understanding of postglacial conifer migration from the Gallatin Valley to Yellowstone National Park following the retreat of the Yellowstone Ice Cap, as well as Holocene vegetation and fire trends. Existing records are primarily derived from low- and high-elevation forests, and reconstructing the history from a mid-elevation mesic mixed conifer forest demonstrates the vital role these areas play in maintaining forest ecosystems during overall adverse conditions.

This study builds on research previously done in Yellowstone National Park and showcases the substantial work done in the Paleoecology Laboratory at Montana State University. It uses data from studies done by former lab members under the guidance of Dr. Cathy Whitlock, who contributed her expertise on the GYE to this chapter and helped with the writing and editing. Dr. David McWethy helped design the study, selected Langohr Wetland as a study site, assisted in the fieldwork, and also helped write and revise the manuscript. This study was supported by National Science Foundation grants acquired by Drs. Cathy Whitlock and David McWethy (EAR-2149482 and BCS-1832486).

Chapter Four synthesizes a network of records from the Mission Range in northwestern Montana. This chapter brings together multiple sites within a small geographic area to examine vegetation responses to climate and changes in fire activity. Considering site-to-site differences in fire activity or vegetation structure could be the result of local conditions, analyzing multiple sites within a small geographic area minimizes differences. It focuses on the changes in fire activity at low-elevation and high-elevation sites over time, though it has a slight focus on low-

elevation sites, due to the fact that low-elevation sites had longer records. This chapter produces a composite charcoal and pollen record for the Mission Range, and showcases the importance of fuel structure and density as well as short-scale climate oscillations to increases in fire activity. It also investigates how low-elevation forests are particularly sensitive to changes in moisture.

Chapter Four also builds on previous work conducted in the Paleoecology Laboratory and represents the culmination of efforts over the past decade. MSU Master's students Kari Lapierre, Matthew Weingart, and Shelby Sly, as well as David McWethy and I, contributed pollen and charcoal data from various lakes. David McWethy and I designed the study, and Gregory Pederson, David McWethy, and Cathy Whitlock assisted in fieldwork, as well as reviewing and editing the chapter. This study was supported by National Science Foundation grants acquired by Drs. David McWethy and Gregory Pederson (NSF EAR 2149482 and BCS1539820).

References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113, 11770–11775. https://doi.org/10.1073/pnas.1607171113

Alder, J.R., Hostetler, S.W., 2015. Global climate simulations at 3000-year intervals for the last 21 000 years with the GENMOM coupled atmosphere–ocean model. Climate of the Past 11, 449–471. https://doi.org/10.5194/cp-11-449-2015

Alt, M., McWethy, D., Everett, R., Whitlock, C., 2018. Millennial scale climate-fire-vegetation interactions in a mid-elevation mixed coniferous forest, Mission Range, northwestern Montana, USA. Quaternary Research 90, 1–17. https://doi.org/10.1017/qua.2018.25

Alt, M., Puseman, K., Lee, C.M., Pederson, G.T., McConnell, J.R., Chellman, N.J., McWethy, D.B., 2024. Organic layers preserved in ice patches: A new record of Holocene environmental change on the Beartooth Plateau, USA. The Holocene 34, 338–352. https://doi.org/10.1177/09596836231211877

Arno, S.F., Parsons, D.J., Keane, R.E., 2000. Mixed-severity fire regimes in the Northern Rocky Mountains: consequences of fire exclusion and options for the future. United States Department of Agriculture Forest Service Proceedings RMRS-P-15 5, 225–233.

Baker, W.L., 2009. Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington, DC

Barnard, D.M., Barnard, H.R., Molotch, N.P., 2017. Topoclimate effects on growing season length and montane conifer growth in complex terrain. Environ. Res. Lett. 12, 064003. https://doi.org/10.1088/1748-9326/aa6da8

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quaternary Science Reviews 17, 549–585. https://doi.org/10.1016/S0277-3791(98)00012-2

Benes, J., Iglesias, V., Whitlock, C., 2019. Postglacial vegetation dynamics at high elevation from Fairy Lake in the northern Greater Yellowstone Ecosystem, Montana, USA. Quaternary Research 92, 1–16. https://doi.org/10.1017/qua.2019.9

Bonan, G.B., 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science 320, 1444–1449. https://doi.org/10.1126/science.1155121

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E.,

Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., Van Der Werf, G.R., Pyne, S.J., 2009. Fire in the Earth System. Science 324, 481–484. https://doi.org/10.1126/science.1163886

Bracht-Flyr, B., Fritz, S.C., 2012. Synchronous climatic change inferred from diatom records in four western Montana lakes in the U.S. Rocky Mountains. Quat. res. 77, 456–467. https://doi.org/10.1016/j.yqres.2011.12.005

Brunelle, A., Whitlock, C., Bartlein, P., Kipfmueller, K., 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. Quaternary Science Reviews 24, 2281–2300. https://doi.org/10.1016/j.quascirev.2004.11.010

Chellman, N.J., Pederson, G.T., Lee, C.M., McWethy, D.B., Puseman, K., Stone, J.R., Brown, S.R., McConnell, J.R., 2021. High elevation ice patch documents Holocene climate variability in the northern Rocky Mountains. Quaternary Science Advances 3, 100021. https://doi.org/10.1016/j.qsa.2020.100021

Confederated Salish and Kootenai Tribes (CKST), Division of Fish, Wildlife, Recreation, and Conservation, 2021. Fire on the Land. https://fwrconline.csktnrd.org/Fire/index.html.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences 116, 6193–6198. https://doi.org/10.1073/pnas.1815107116

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Fall, P.L., Davis, P.T., Zielinski, G.A., 1995. Late Quaternary Vegetation and Climate of the Wind River Range, Wyoming. Quaternary Research 43, 393.

Fischer, W.C., Bradley, A.F., 1987. Fire ecology of western Montana forest habitat types (No. INT-GTR-223). U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT. https://doi.org/10.2737/INT-GTR-223

Huerta, M.A., Whitlock, C., Yale, J., 2009. Holocene vegetation–fire–climate linkages in northern Yellowstone National Park, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 170–181. https://doi.org/10.1016/j.palaeo.2008.10.015

Iglesias, V., Krause, T.R., Whitlock, C., 2015. Complex Response of White Pines to Past Environmental Variability Increases Understanding of Future Vulnerability. PLoS ONE 10, e0124439. https://doi.org/10.1371/journal.pone.0124439

Iglesias, V., Whitlock, C., Krause, T.R., Baker, R.G., 2018. Past vegetation dynamics in the Yellowstone region highlight the vulnerability of mountain systems to climate change. Journal of Biogeography 45, 1768–1780. https://doi.org/10.1111/jbi.13364

Jain, T.B., Battaglia, M.A., Han, H.-S., Graham, R.T., Keyes, C.R., Fried, J.S., Sandquist, J.E., 2012. A comprehensive guide to fuel management practices for dry mixed conifer forests in the northwestern United States (No. RMRS-GTR-292). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO. https://doi.org/10.2737/RMRS-GTR-292

Krause, T.R., Lu, Y., Whitlock, C., Fritz, S.C., Pierce, K.L., 2015. Patterns of terrestrial and limnologic development in the northern Greater Yellowstone Ecosystem (USA) during the late-glacial/early-Holocene transition. Palaeogeography, Palaeoclimatology, Palaeoecology 422, 46–56. https://doi.org/10.1016/j.palaeo.2014.12.018

Krause, T.R., Whitlock, C., 2017. Climatic and non-climatic controls shaping early postglacial conifer history in the northern Greater Yellowstone Ecosystem, USA. J. Quaternary Sci. 32, 1022–1036. https://doi.org/10.1002/jqs.2973

Krause, T.R., Whitlock, C., 2013. Climate and vegetation change during the late-glacial/early-Holocene transition inferred from multiple proxy records from Blacktail Pond, Yellowstone National Park, USA. Quat. res. 79, 391–402. https://doi.org/10.1016/j.yqres.2013.01.005

Kutzbach, J., Gallimore, R., Harrison, S., Behling, P., Selin, R., Laarif, F., 1998. Climate and biome simulations for the past 21,000 years. Quaternary Science Reviews 17, 473–506. https://doi.org/10.1016/S0277-3791(98)00009-2

Lapierre, K., 2021 Long-term environmental history of two low-elevation mixed-conifer forests, Mission Valley, Montana. Master's Thesis, Montana State University.

Lee, C.M., 2012. Withering Snow and Ice in the Mid-latitudes: A New Archaeological and Paleobiological Record for the Rocky Mountain Region. ARCTIC 65, 165-177-165–177. https://doi.org/10.14430/arctic4191

Lynch, E.A., 1998. Origin of a park-forest vegetation mosaic in the Wind River Range, Wyoming. Ecology 79, 1320–1338. https://doi.org/10.1890/0012-9658(1998)079[1320:OOAPFV]2.0.CO;2

Mack, R.N., Rutter, N.W., Bryant, V.M., Valastro, S., 1978. Reexamination of postglacial vegetation history in northern Idaho: Hager Pond, Bonner Co. Quaternary Research 10, 241–255. https://doi.org/10.1016/0033-5894(78)90104-7

Mack, R.N., Rutter, N.W., Valastro, S., 1983. Holocene Vegetational History of the Kootenai River Valley, Montana. Quat. res. 20, 177–193. https://doi.org/10.1016/0033-5894(83)90076-5

McWethy, D., Alt, M., Argiriadis, E., Battistel, D., Everett, R., Pederson, G., 2020. Millennial-Scale Climate and Human Drivers of Environmental Change and Fire Activity in a Dry, Mixed-Conifer Forest of Northwestern Montana. Frontiers in Forests and Global Change 3. https://doi.org/10.3389/ffgc.2020.00044

Mehringer, P., Arno, S., Petersen, K., 1977. Postglacial History of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arctic and Alpine Research 9, 345. https://doi.org/10.2307/1550528

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park 4.

Mumma, S.A., Whitlock, C., Pierce, K., 2012. A 28,000year history of vegetation and climate from Lower Red Rock Lake, Centennial Valley, Southwestern Montana, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 326–328, 30–41. https://doi.org/10.1016/j.palaeo.2012.01.036

Pfister, R., Kovalchik, B., Arno, S., Presby, R., 1977. Forest habitat types of Montana (General Technical Report No. INT-34). USDA Forest Service.

Power, M.J., Whitlock, C., Bartlein, P., Stevens, L.R., 2006. Fire and vegetation history during the last 3800 years in northwestern Montana. Geomorphology, Quaternary landscape change and modern process in western North America 75, 420–436. https://doi.org/10.1016/j.geomorph.2005.07.025

Power, M.J., Whitlock, C., Bartlein, P.J., 2011. Postglacial fire, vegetation, and climate history across an elevational gradient in the Northern Rocky Mountains, USA and Canada. Quaternary Science Reviews 30, 2520–2533. https://doi.org/10.1016/j.quascirev.2011.04.012

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J., Vanderwel, M.C., Verbeeck, H., Villela, D.M., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. Journal of Ecology 103, 5–15. https://doi.org/10.1111/1365-2745.12337

Rust, R.A., Minckley, T.A., 2020. Fire and hydrologically mediated diversity change in subalpine forests through the Holocene. Journal of Vegetation Science 31, 380–391. https://doi.org/10.1111/jvs.12853

Schiller, C.M., Alt, M., Nanavati, W.P., Wendt, J.A.F., Stahle, L.N., 2023. Getting Information from the Past: Palaeoecological Studies of Terrestrial Ecosystems. In: Clifford, N., Cope, M., Gillespie, T., French, S. (Eds), *Key Methods in Geography, 4th ed*. Sage Publications, pp. 393-418.

Schiller, C.M., Whitlock, C., Brown, S.R., 2022. Holocene geo-ecological evolution of Lower Geyser Basin, Yellowstone National Park (USA). Quat. res. 105, 201–217. https://doi.org/10.1017/qua.2021.42

Schoennagel, T., Balch, J.K., Brenkert-Smith, H., Dennison, P.E., Harvey, B.J., Krawchuk, M.A., Mietkiewicz, N., Morgan, P., Moritz, M.A., Rasker, R., Turner, M.G., Whitlock, C., 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences of the United States of America 114, 4582–4590. https://doi.org/10.2307/26481841

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nature Clim Change 7, 395–402. https://doi.org/10.1038/nclimate3303

Sly, S., 2020. Late holocene vegetation and fire history in subalpine forests of southwestern montana. Master's Thesis, Montana State University.

Turner, M.G., Braziunas, K.H., Hansen, W.D., Harvey, B.J., 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc. Natl. Acad. Sci. U.S.A. 116, 11319–11328. https://doi.org/10.1073/pnas.1902841116

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834

Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H., Ryan, M.G., 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. PNAS 108, 13165–13170. https://doi.org/10.1073/pnas.1110199108

Whitlock, C., 1993. Postglacial Vegetation and Climate of Grand Teton and Southern Yellowstone National Parks. Ecological Monographs 63, 173–198. https://doi.org/10.2307/2937179

Whitlock, C., Bartlein, P.J., Van Norman, K.J., 1995. Stability of Holocene Climate Regimes in the Yellowstone Region. Quaternary Research 43, 433–436. https://doi.org/10.1006/qres.1995.1049

Whitlock, C., Briles, C.E., Fernandez, M.C., Gage, J., 2011. Holocene vegetation, fire and climate history of the Sawtooth Range, central Idaho, USA. Quaternary Research 75, 114–124. https://doi.org/10.1016/j.yqres.2010.08.013

Whitlock, C., Dean, W.E., Fritz, S.C., Stevens, L.R., Stone, J.R., Power, M.J., Rosenbaum, J.R., Pierce, K.L., Bracht-Flyr, B.B., 2012. Holocene seasonal variability inferred from multiple proxy records from Crevice Lake, Yellowstone National Park, USA.

Palaeogeography, Palaeoclimatology, Palaeoecology 331–332, 90–103. https://doi.org/10.1016/j.palaeo.2012.03.001

Williams, M.W., Losleben, M., Caine, N., Greenland, D., 1996. Changes in climate and hydrochemical responses in a high-elevation catchment in the Rocky Mountains, USA. Limnology and Oceanography 41, 939–946. https://doi.org/10.4319/lo.1996.41.5.0939

CHAPTER TWO

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.

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. 2.1). 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).

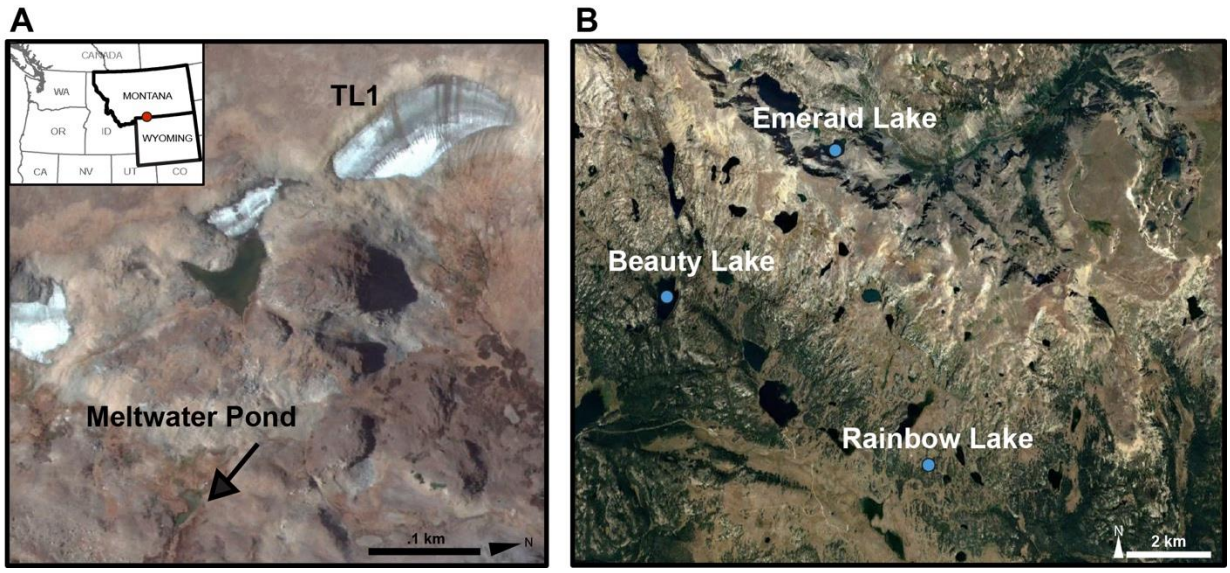


Figure 2.1(A) TL1 Ice Patch and Meltwater Pond. (B) Referenced Beartooth Plateau study sites used in comparative analyses, within 20 km of TL1: Emerald Lake (Barth et al., 2022; Stone et al., 2016), Rainbow Lake (Rust and Minckley, 2020; Shuman and Serravezza, 2017); Beauty Lake (Spaulding et al., 2020; Stone et al., 2016).

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 2.1; Fig. SM2.1). 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).

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. 2.2). 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 (Fig. SM2.2). Microcharcoal concentrations were high at the base, and decreased to the top of the zone, suggesting a decrease in fire activity.

Table 2.1 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

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.

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. 2.3).

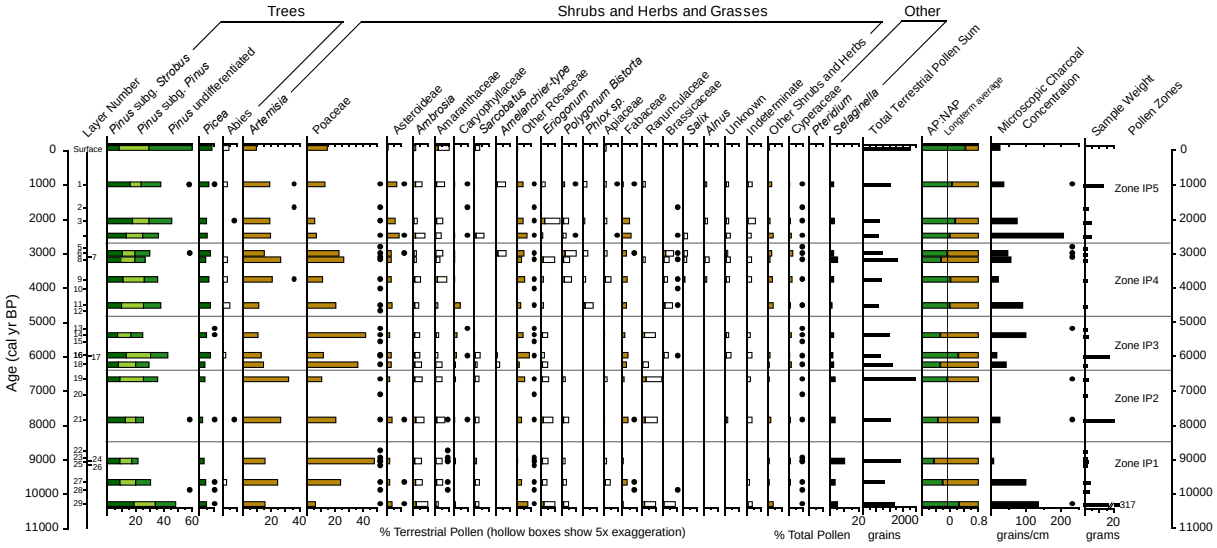


Figure 2.2 Pollen, macrofossil, and charcoal concentration data from the TL1 Ice Patch. Hollow boxes are 5x exaggeration of the pollen percentages for species that never exceed 3%, and circles denote the presence of at least one macrofossil. Surface sample is not an organic layer.

Chronology. The Meltwater Pond age-depth model was based on six AMS radiocarbon ages (Table 2.2; Fig. 2.4). The change in sediment deposition rate and lithology at 60 cm depth suggests a hiatus from ca. 4200-3000 cal yr BP.

Table 2.2 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)

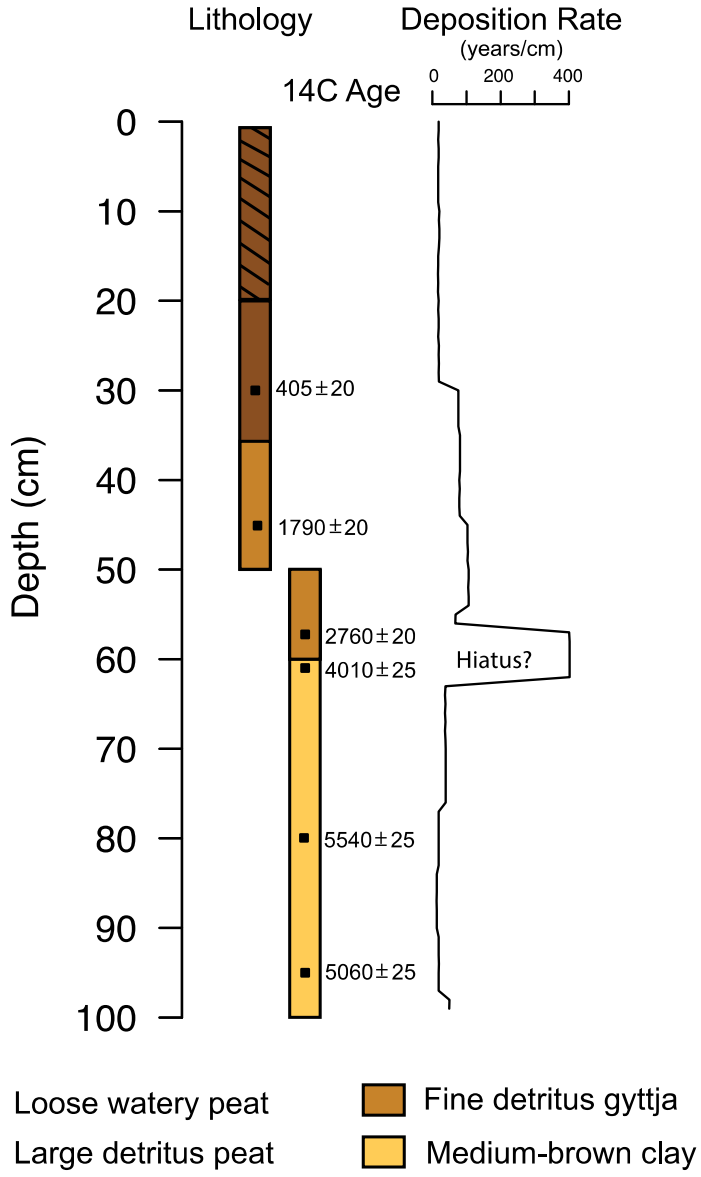


Figure 2.3 Lithology of the Meltwater Pond sediment, location of samples submitted for radiocarbon dating, and the deposition rate of the sedimentation.

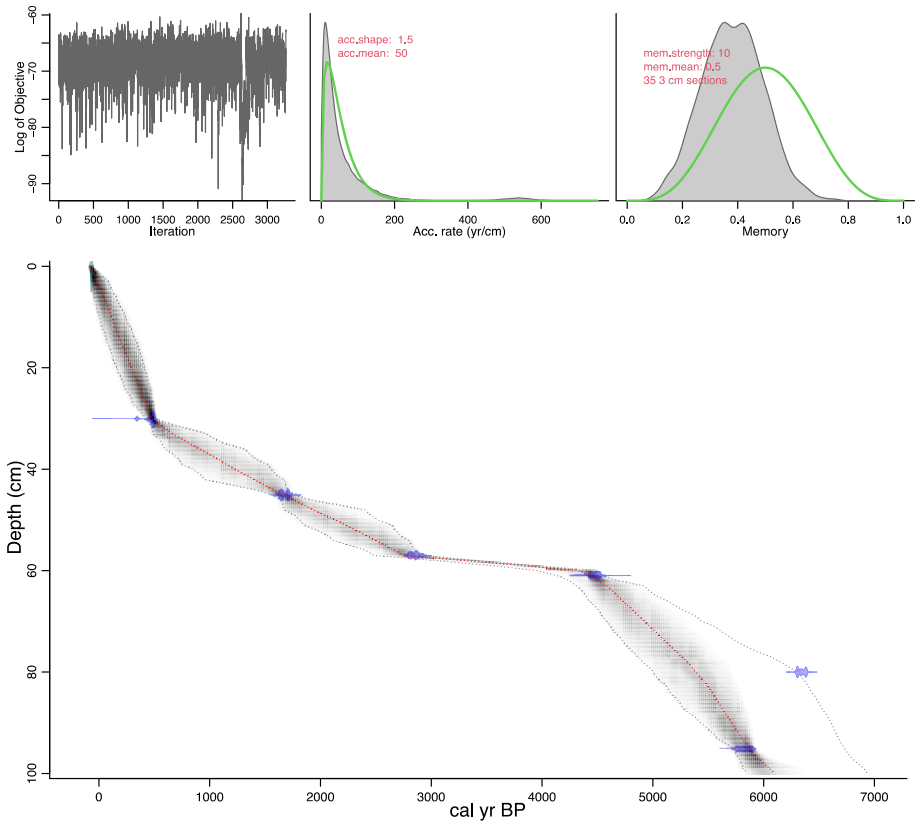


Figure 2.4. Age-depth model for Meltwater Pond based on six radiocarbon dates.

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. 2.5).

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.

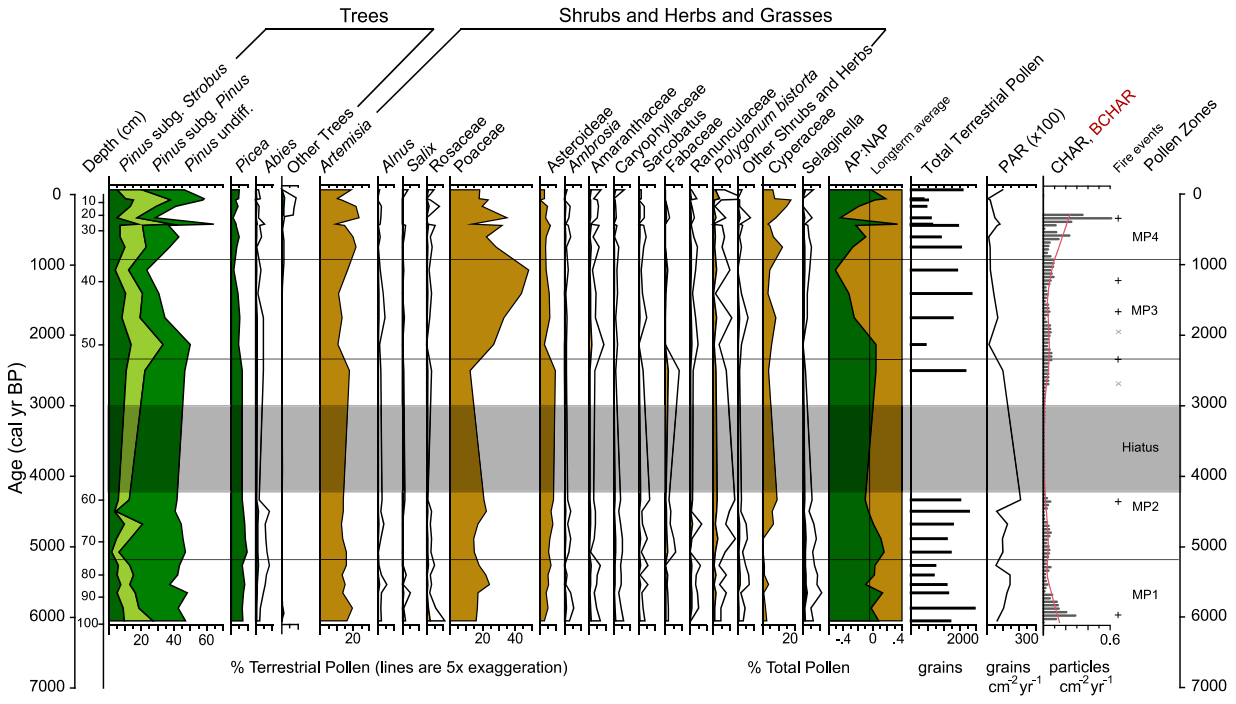


Figure 2.5 Pollen and charcoal data from Meltwater Pond, WY. Black lines are 5x exaggeration of the pollen time series, (+) symbols denote significant fire events, and (x) symbols indicate insignificant fire events. Grey bar represents a hiatus in the core.

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 masl; Fig. 2.1) 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. 2.2). 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. 2.2). 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. 2.6) 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. 2.6), 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.

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. 2.2 and 2.5). 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. 2.6; 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. 2.6). Arboreal pollen in the TL1 record declined at ca. 5000 cal yr BP, although macrofossil evidence suggests that *Picea* was still locally present (Figs. 2.2 and 2.6). 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.

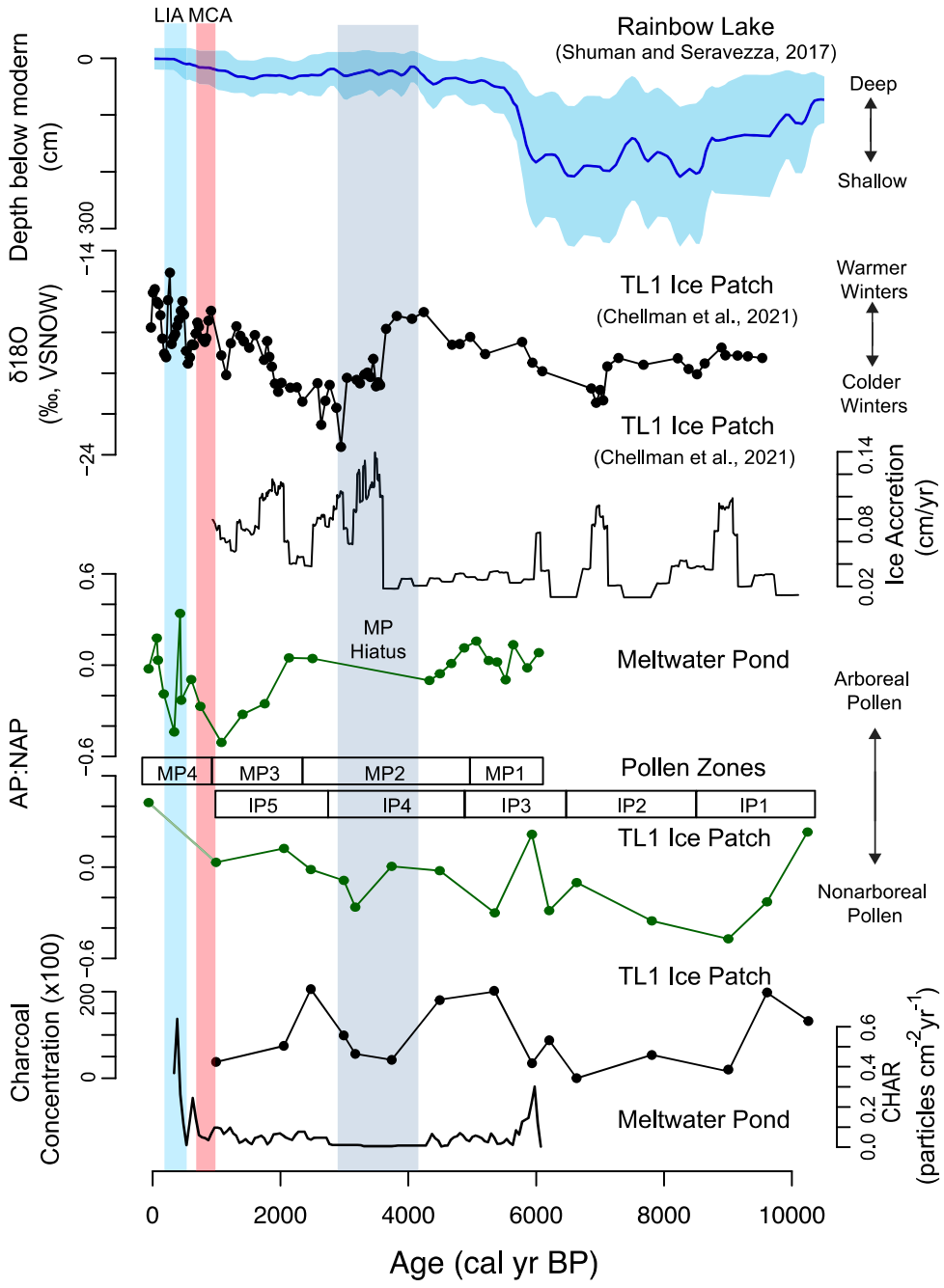


Figure 2.6 Multiproxy comparison of lake level data from Rainbow Lake (Shuman and Serravezza, 2017), isotope and ice accumulation data from the TL1 Ice Patch (Chellman et al., 2021), the ratio of arboreal to non-arboreal pollen from the TL1 Ice Patch and Meltwater Pond, and charcoal data from the TL1 Ice Patch and Meltwater Pond (this study). Pollen zones are noted in boxes and TL1 surface AP:NAP ratio is not from an organic layer.

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. 2.4), 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. 2.3). 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. 2.2 and 2.6).

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 2.6; 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. 2.6; 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. 2.2 and 2.5). The Rainbow Lake record features a slight increase in *Pinus* during this period (Rust and Minckley, 2020; Fig. 2.7), 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. 2.5 and 2.7). 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. 2.2), and leaf and stem macrofossils (SM Fig. 2.2) and Asteroideae and Rosaceae pollen increased (Fig. 2.2). 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. 2.6).

There are not many records that 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.

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 2.5 and 2.6). 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.

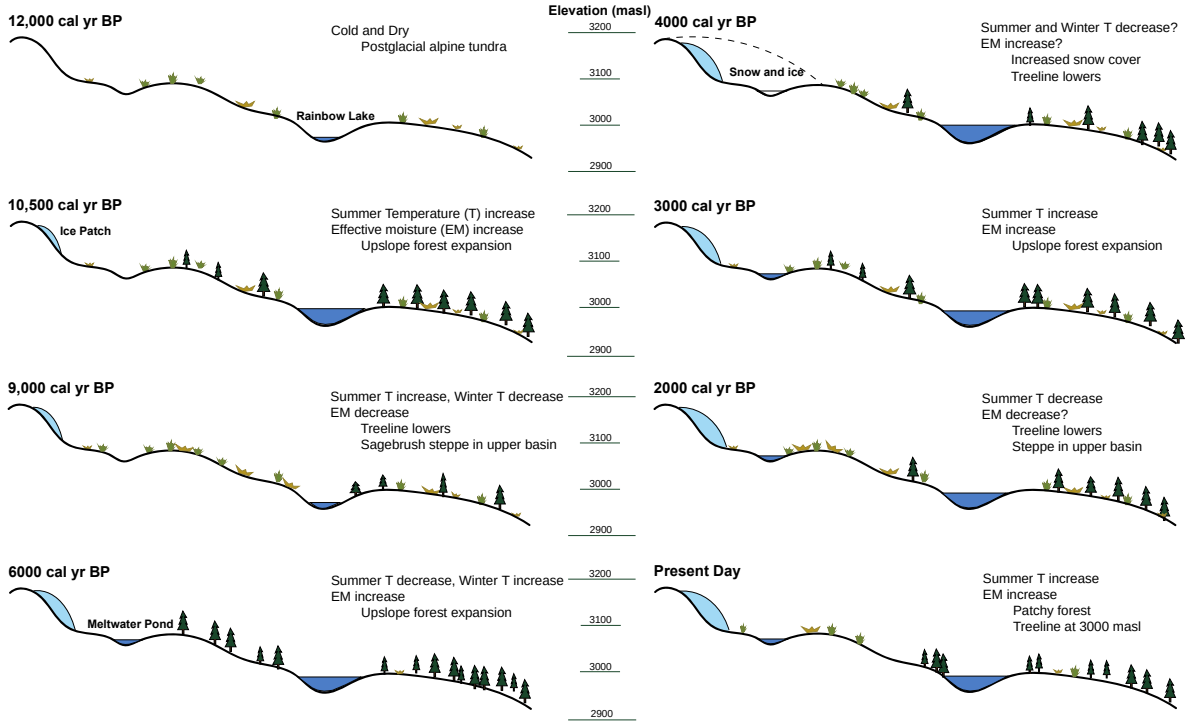


Figure. 2.7 Sequence of major paleoenvironmental changes through time on the Beartooth Plateau based on records from this study and Rainbow Lake studies (Rust and Minckley, 2020; Shuman and Serravezza, 2017). Changes in temperature and precipitation are relative to the time period before. Each panel illustrates prominent shifts in vegetation recorded by pollen samples corresponding to the time period indicated.

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 2.6). 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. 2.7). 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 2.6). 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. 2.6 and 2.7). 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.

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References

Alder, J.R., Hostetler, S.W., 2015. Global climate simulations at 3000-year intervals for the last 21 000 years with the GENMOM coupled atmosphere–ocean model. Clim. Past 11, 449–471. https://doi.org/10.5194/cp-11-449-2015

Alt, M., McWethy, D., Everett, R., Whitlock, C., 2018. Millennial scale climate-fire-vegetation interactions in a mid-elevation mixed coniferous forest, Mission Range, northwestern Montana, USA. Quat. Res. 90, 1–17. https://doi.org/10.1017/qua.2018.25

Andrus, R.A., Harvey, B.J., Rodman, K.C., Hart, S.J., Veblen, T.T., 2018. Moisture availability limits subalpine tree establishment. Ecology 99, 567–575. https://doi.org/10.1002/ecy.2134

Ault, T.R., Cole, J.E., Overpeck, J.T., Pederson, G.T., St. George, S., Otto-Bliesner, B., Woodhouse, C.A., Deser, C., 2013. The Continuum of Hydroclimate Variability in Western North America during the Last Millennium. J. Clim. 26, 5863–5878. https://doi.org/10.1175/JCLI-D-11-00732.1

Ault, T.R., St. George, S., Smerdon, J.E., Coats, S., Mankin, J.S., Carrillo, C.M., Cook, B.I., Stevenson, S., 2018. A Robust Null Hypothesis for the Potential Causes of Megadrought in Western North America. J. Clim. 31, 3–24. https://doi.org/10.1175/JCLI-D-17-0154.1

Barth, A.M., Ceperley, E.G., Vavrus, C., Marcott, S.A., Shakun, J.D., Caffee, M.W., 2022. ^{10}Be age control of glaciation in the Beartooth Mountains, USA from the latest Pleistocene through the Holocene. Geochronol. Discuss. 1–18. https://doi.org/10.5194/gchron-2022-17

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quat. Sci. Rev. 17, 549–585. https://doi.org/10.1016/S0277-3791(98)00012-2

Benedict, J.B., 2011. Sclerotia as indicators of mid-Holocene tree-limit altitude, Colorado Front Range, USA. The Holocene 21, 1021–1023. https://doi.org/10.1177/0959683610395078

Benedict, J.B., Benedict, R.J., Lee, C.M., Staley, D.M., 2008. Spruce trees from a melting ice patch: evidence for Holocene climatic change in the Colorado Rocky Mountains, USA. The Holocene 18, 1067–1076. https://doi.org/10.1177/0959683608095578

Benes, J., Iglesias, V., Whitlock, C., 2019. Postglacial vegetation dynamics at high elevation from Fairy Lake in the northern Greater Yellowstone Ecosystem, Montana, USA. Quat. Res. 92, 1–16. https://doi.org/10.1017/qua.2019.9

Bennett, K.D., Willis, K.J., 2001. Pollen. In: Smol JP, Birks HJB and Last WM (eds) *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, 3.* Dordrecht: Kluwer Academic Publishers, pp. 5–32.

Berger, A., 1978. Long-term variations of caloric insolation resulting from the earth's orbital elements. Quaternary Research 9: 139–167.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. https://doi.org/10.1214/11-BA618

Brunelle, A., Whitlock, C., Bartlein, P., Kipfmueller, K., 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. Quat. Sci. Rev. 24, 2281–2300. https://doi.org/10.1016/j.quascirev.2004.11.010

Cappers, R.T.J., Bekker, R.M., 2013. *A Manual for the Identification of Plant Seeds and Fruits. Groningen Archaeological Studies, Vol. 23.* Barkuis Publishing, Eelde.

Carlquist, S., 1988. *Comparative Wood Anatomy*. Springer-Verlag, Berlin.

Chellman, N.J., Pederson, G.T., Lee, C.M., McWethy, D.B., Puseman, K., Stone, J.R., Brown, S.R., McConnell, J.R., 2021. High elevation ice patch documents Holocene climate variability in the northern Rocky Mountains. Quat. Sci. Adv. 3, 100021. https://doi.org/10.1016/j.qsa.2020.100021

Cook, E.R., Seager, R., Heim, R.R., Vose, R.S., Herweijer, C., Woodhouse, C., 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context: MEGADROUGHTS IN NORTH AMERICA. J. Quat. Sci. 25, 48–61. https://doi.org/10.1002/jqs.1303

Cook, E.R., Woodhouse, C.A., Eakin, M.C., Meko, D.M., Stahle, D.W., 2004. Long-term aridity changes in the western United States. Science 306, 1015–1018.

Core, H.A., Côté, W.A., Day, A.C., 1976. *Wood Structure and Identification.* Syracuse University Press*,* New York.

Delorit, R.J., 1970. *An Illustrated Taxonomy Manual of Weed Seeds.* Wisconsin State University Agronomy Publications, River Falls.

Diffenbaugh, N.S., Ashfaq, M., Shuman, B., Williams, J.W., Bartlein, P.J., 2006. Summer aridity in the United States: Response to mid-Holocene changes in insolation and sea surface temperature. Geophys. Res. Lett. 33. https://doi.org/10.1029/2006GL028012

Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analysis 4th ed.* New Jersey: The Blackburn Press.

Fall, P.L., Davis, P.T., Zielinski, G.A., 1995. Late Quaternary Vegetation and Climate of the Wind River Range, Wyoming. Quat. Res. 43, 393.

Gangopadhyay, S., Woodhouse, C.A., McCabe, G.J., Routson, C.C., Meko, D.M., 2022. Tree Rings Reveal Unmatched 2nd Century Drought in the Colorado River Basin. Geophys. Res. Lett. 49, e2022GL098781. https://doi.org/10.1029/2022GL098781

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35. https://doi.org/10.1016/0098-3004(87)90022-7

Harsch, M.A., Bader, M.Y., 2011. Treeline form - a potential key to understanding treeline dynamics: The causes of treeline form. Glob. Ecol. Biogeogr. 20, 582–596. https://doi.org/10.1111/j.1466-8238.2010.00622.x

Heidel, B., Fertig, W., Mellmann-Brown, S., Houston, K.E., Dwire, K.A., 2017. Fens and their rare plants in the Beartooth Mountains, Shoshone National Forest, Wyoming (No. RMRS-GTR-369). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO. https://doi.org/10.2737/RMRS-GTR-369

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol. Monogr. 79, 201–219. https://doi.org/10.1890/07-2019.1

Hoadley, R.B., 1990. *Identifying Wood: Accurate Results with Simple Tools*. The Taunton Press, Newtown, CT.

Hoch, G., Körner, C., 2009. Growth and carbon relations of tree line forming conifers at constant vs. variable low temperatures. J. Ecol. 97, 57–66. https://doi.org/10.1111/j.1365-2745.2008.01447.x

Hostetler, S., Whitlock, C., Shuman, B., et al., 2021. *Greater Yellowstone climate assessment: past, present, and future climate change in greater Yellowstone watersheds.* Montana State University, Institute on Ecosystems, Montana. https://doi.org/10.15788/GYCA2021.

Huerta, M.A., Whitlock, C., Yale, J., 2009. Holocene vegetation–fire–climate linkages in northern Yellowstone National Park, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 271, 170–181. https://doi.org/10.1016/j.palaeo.2008.10.015

Iglesias, V., Whitlock, C., Krause, T.R., Baker, R.G., 2018. Past vegetation dynamics in the Yellowstone region highlight the vulnerability of mountain systems to climate change. J. Biogeogr. 45, 1768–1780. https://doi.org/10.1111/jbi.13364

InsideWood, 2004. InsideWood Database. Available at: http://insidewood.lib.ncsu.edu/search (accessed 2013-2017).

Kapp, R.O., Davis, O.K., King, J.E., 2000. *Pollen and Spores. 2nd ed.* American Association of Stratigraphic Palynologists Foundation, Dallas, TX.

Kelly, R.F., Higuera, P.E., Barrett, C.M., Hu, F.S., 2011. Short Paper: A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quat. Res. 75, 11–17. https://doi.org/10.1016/j.yqres.2010.07.011

Knobel, E., 1980. *Field Guide to the Grasses, Sedges and Rushes of the United States.* Dover Publications, New York.

Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures: Study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x

Krause, T.R., Lu, Y., Whitlock, C., Fritz, S.C., Pierce, K.L., 2015. Patterns of terrestrial and limnologic development in the northern Greater Yellowstone Ecosystem (USA) during the late-glacial/early-Holocene transition. Palaeogeogr. Palaeoclimatol. Palaeoecol. 422, 46–56. https://doi.org/10.1016/j.palaeo.2014.12.018

Krause, T.R., Whitlock, C., 2017. Climatic and non-climatic controls shaping early postglacial conifer history in the northern Greater Yellowstone Ecosystem, USA. J. Quat. Sci. 32, 1022–1036. https://doi.org/10.1002/jqs.2973

Krause, T.R., Whitlock, C., 2013. Climate and vegetation change during the late-glacial/early-Holocene transition inferred from multiple proxy records from Blacktail Pond, Yellowstone National Park, USA. Quat. Res. 79, 391–402. https://doi.org/10.1016/j.yqres.2013.01.005

Kyne, J., McConnell, J., 2007. The PrairieDog: a double-barrel coring drill for ‘hand’ augering. Ann. Glaciol. 47, 99–100. https://doi.org/10.3189/172756407786857703

Larsen, D.J., Crump, S.E., Blumm, A., 2020. Alpine glacier resilience and Neoglacial fluctuations linked to Holocene snowfall trends in the western United States. Sci. Adv. 6, eabc7661. https://doi.org/10.1126/sciadv.abc7661

Lee, C.M., 2012. Withering Snow and Ice in the Mid-latitudes: A New Archaeological and Paleobiological Record for the Rocky Mountain Region. Arctic 65, 165–177.

Lee, C.M., Puseman, K., 2017. ICE PATCH HUNTING IN THE GREATER YELLOWSTONE AREA, ROCKY MOUNTAINS, USA: WOOD SHAFTS, CHIPPED STONE PROJECTILE POINTS, AND BIGHORN SHEEP (*OVIS CANADENSIS*). Am. Antiq. 82, 223–243. https://doi.org/10.1017/aaq.2016.32

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. Science 320, 1768–1771. https://doi.org/10.1126/science.1156831

Leunda, M., González-Sampériz, P., Gil-Romera, G., Bartolomé, M., Belmonte-Ribas, Á., Gómez-García, D., Kaltenrieder, P., Rubiales, J.M., Schwörer, C., Tinner, W., Morales-Molino, C., Sancho, C., 2019. Ice cave reveals environmental forcing of long-term Pyrenean tree line dynamics. J. Ecol. 107, 814–828. https://doi.org/10.1111/1365-2745.13077

Leys, B.A., Commerford, J.L., McLauchlan, K.K., 2017. Reconstructing grassland fire history using sedimentary charcoal: Considering count, size and shape. PLOS ONE 12, e0176445. https://doi.org/10.1371/journal.pone.0176445

Licciardi, J.M., Pierce, K.L., 2018. History and dynamics of the Greater Yellowstone Glacial System during the last two glaciations. Quat. Sci. Rev. 200, 1–33. https://doi.org/10.1016/j.quascirev.2018.08.027

Liefert, D.T., Shuman, B.N., 2022. Expression of the "4.2 ka event" in the southern Rocky Mountains, USA. Clim. Past 18, 1109–1124. https://doi.org/10.5194/cp-18-1109-2022

Liefert, D.T., Shuman, B.N., 2020. Pervasive Desiccation of North American Lakes During the Late Quaternary. Geophys. Res. Lett. 47. https://doi.org/10.1029/2019GL086412

Lynch, E.A., 1996. The ability of pollen from small lakes and ponds to sense fine-scale vegetation patterns in the Central Rocky Mountains, USA. Rev. Palaeobot. Palynol. 94, 197–210. https://doi.org/10.1016/S0034-6667(96)00040-1

Mack, R.N., Rutter, N.W., Bryant, V.M., Valastro, S., 1978. Reexamination of postglacial vegetation history in northern Idaho: Hager Pond, Bonner Co. Quat. Res. 10, 241–255. https://doi.org/10.1016/0033-5894(78)90104-7

Mack, R.N., Rutter, N.W., Valastro, S., 1983. Holocene Vegetational History of the Kootenai River Valley, Montana. Quat. Res. 20, 177–193. https://doi.org/10.1016/0033-5894(83)90076-5

Mann, M.E., Bradley, R.S., Hughes, M.K., 1999. Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. Geophys. Res. Lett. 26, 759–762. https://doi.org/10.1029/1999GL900070

Marsicek, J., Shuman, B.N., Bartlein, P.J., Shafer, S.L., Brewer, S., 2018. Reconciling divergent trends and millennial variations in Holocene temperatures. Nature 554, 92–96. https://doi.org/10.1038/nature25464

Martin, A.C., Barkley, W.D., 2000. *Seed Identification Manual*. The Blackburn Press, Caldwell.

McAndrews, J.H., Berti, A.A., Norris, G.N., 1973. *Key to Quaternary Pollen and Spores of the Great Lakes Region.* Royal Ontario Museum Life Sciences Miscellaneous Publication, Toronto.

McWethy, D., Alt, M., Argiriadis, E., Battistel, D., Everett, R., Pederson, G., 2020. Millennial-Scale Climate and Human Drivers of Environmental Change and Fire Activity in a Dry, Mixed-Conifer Forest of Northwestern Montana. Front. For. Glob. Change 3. https://doi.org/10.3389/ffgc.2020.00044

Mehringer, P., 1985. Late-quaternary pollen records from the interior Pacific northwest and northern great basin of the United States. In: Bryant Jr. V and Holloway WG (eds.) *Pollen Records of the Late Quaternary North American Sediments.* American Association of Stratigraphic Palynologists foundation, Dallas. pp. 167–189.

Mehringer, P., Arno, S., Petersen, K., 1977. Postglacial History of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arct. Alp. Res. 9, 345. https://doi.org/10.2307/1550528

Meulendyk, T., Moorman, B.J., Andrews, T.D., MacKAY, G., 2012. Morphology and Development of Ice Patches in Northwest Territories, Canada. Arctic 65, 43–58.

Meyer, G.A., Wells, S.G., Timothy Jull, A.J., 1995. Fire and alluvial chronology in Yellowstone National Park: Climatic and intrinsic controls on Holocene geomorphic processes. Geol. Soc. Am. Bull. 107, 1211–1230. https://doi.org/10.1130/0016-7606(1995)107<1211:FAACIY>2.3.CO;2

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park 4.

Minckley, T.A., Shriver, R.K., Shuman, B., 2012. Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17 000 years. Ecol. Monogr. 82, 49–68. https://doi.org/10.1890/11-0283.1

Morgan, C., Losey, A., Trout, L., 2014. Late-Holocene paleoclimate and treeline fluctuation in Wyoming's Wind River Range, USA. The Holocene 24, 209–219. https://doi.org/10.1177/0959683613516817

Panshin, A.J., de Zeeuw, C., 1980. *Textbook of Wood Technology*. McGraw-Hill Book Co, New York.

Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Change 5, 424–430. https://doi.org/10.1038/nclimate2563

Pfister, R., Kovalchik, B., Arno, S., Presby, R., 1977. Forest habitat types of Montana (General Technical Report No. INT-34). USDA Forest Service.

Pierce, K., Cannon, K., Meyer, G., Trebesch, M., Watts, R., 2002. Post-glacial inflation-deflation cycles, tilting, and faulting in the Yellowstone Caldera based on Yellowstone Lake shorelines (Open-File Report No. 02–0142), Open-File Report. US Geological Survey.

PRISM Climate Group, 2014. Oregon State University. Available at: https://prism.oregonstate.edu (accessed 20 Feb 2021).

Quadri, P., Silva, L.C.R., Zavaleta, E.S., 2021. Climate-induced reversal of tree growth patterns at a tropical treeline. Sci. Adv. 7, eabb7572. https://doi.org/10.1126/sciadv.abb7572

Rehm, E., Feeley, K.J., 2016. Many species risk mountain top extinction long before they reach the top. Front. Biogeogr. 8. https://doi.org/10.21425/F5FBG27788

Rust, R.A., Minckley, T.A., 2020. Fire and hydrologically mediated diversity change in subalpine forests through the Holocene. J. Veg. Sci. 31, 380–391. https://doi.org/10.1111/jvs.12853

Schiller, C.M., Whitlock, C., Brown, S.R., 2022. Holocene geo-ecological evolution of Lower Geyser Basin, Yellowstone National Park (USA). Quat. Res. 105, 201–217. https://doi.org/10.1017/qua.2021.42

Schweingruber, F.H., Landolt, W., 2005. The Xylem Database. Available at http://www.wsl.ch/dendropro/xylemdb/index.php?BNAM=Bilder (accessed 2013-2017).

Schwörer, C., Gavin, D.G., Walker, I.R., Hu, F.S., 2017. Holocene tree line changes in the Canadian Cordillera are controlled by climate and topography. J. Biogeogr. 44, 1148–1159. https://doi.org/10.1111/jbi.12904

Shuman, B., Henderson, A.K., Colman, S.M., Stone, J.R., Fritz, S.C., Stevens, L.R., Power, M.J., Whitlock, C., 2009. Holocene lake-level trends in the Rocky Mountains, U.S.A. Quat. Sci. Rev. 28, 1861–1879. https://doi.org/10.1016/j.quascirev.2009.03.003

Shuman, B., Pribyl, P., Minckley, T.A., Shinker, J.J., 2010. Rapid hydrologic shifts and prolonged droughts in Rocky Mountain headwaters during the Holocene: HOLOCENE DROUGHTS IN THE ROCKY MOUNTAINS. Geophys. Res. Lett. 37, n/a-n/a. https://doi.org/10.1029/2009GL042196

Shuman, B.N., Marsicek, J., 2016. The structure of Holocene climate change in mid-latitude North America. Quat. Sci. Rev. 141, 38–51. https://doi.org/10.1016/j.quascirev.2016.03.009

Shuman, B.N., Serravezza, M., 2017. Patterns of hydroclimatic change in the Rocky Mountains and surrounding regions since the last glacial maximum. Quat. Sci. Rev. 173, 58–77. https://doi.org/10.1016/j.quascirev.2017.08.012

Spaulding, S.A., Stone, J.R., Norton, S.A., Nurse, A., Saros, J.E., 2020. Paleoenvironmental context for the Late Pleistocene appearance of Didymosphenia in a North American alpine lake. Aquat. Sci. 82, 10. https://doi.org/10.1007/s00027-019-0681-9

Stone, J.R., Saros, J.E., Pederson, G.T., 2016. Coherent late-Holocene climate-driven shifts in the structure of three Rocky Mountain lakes. The Holocene 26, 1103–1111. https://doi.org/10.1177/0959683616632886

Stuiver, M., Reimer, P.J., 1993. Extended 14C data base and revised CALIB 3.0 14C age calibration program *Radiocarbon* 35: 215-230

Thompson, R.S., Whitlock, C., Bartlein, P.J., et al., 1993. Climatic changes in Western United States since 18,000 yr BP. In: Wright HE, Kutzbach JE, Web III T, et al. (eds.) *Global Climates Since the Last Glacial Maximum.* University of Minnesota Press, Minneapolis, pp. 468–513.

Whitlock, C., 1993. Postglacial Vegetation and Climate of Grand Teton and Southern Yellowstone National Parks. Ecol. Monogr. 63, 173–198. https://doi.org/10.2307/2937179

Whitlock, C., Bartlein, P.J., 1993. Spatial Variations of Holocene Climatic Change in the Yellowstone Region. Quat. Res. 39, 231–238. https://doi.org/10.1006/qres.1993.1026

Whitlock, C., Dean, W.E., Fritz, S.C., Stevens, L.R., Stone, J.R., Power, M.J., Rosenbaum, J.R., Pierce, K.L., Bracht-Flyr, B.B., 2012. Holocene seasonal variability inferred from multiple proxy records from Crevice Lake, Yellowstone National Park, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 331–332, 90–103. https://doi.org/10.1016/j.palaeo.2012.03.001

Whitlock, C., Larsen, C., 2001. Charcoal as fire proxy. In: Smol JP, Birks HJB and Last WM (eds) *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, 3.* Kluwer Academic Publishers, Dordrecht, pp. 75–97.

Williams, K.L., 2012. Classification of the grasslands, shrublands, woodlands, forests and alpine vegetation associations of the Beartooth mountains in southcentral Montana. Masters thesis, Montana State University, Montana.

Wise, E.K., Woodhouse, C.A., McCabe, G.J., Pederson, G.T., St-Jacques, J.-M., 2018. Hydroclimatology of the Missouri River Basin. J. Hydrometeorol. 19, 161–182. https://doi.org/10.1175/JHM-D-17-0155.1

CHAPTER THREE

POSTGLACIAL FIRE AND VEGETATION HISTORY OF A MID-ELEVATION MIXED CONIFER FOREST IN THE GALLATIN RANGE, MT, USA

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Abstract

A 13,500-year-old record from Langohr Wetland in the Gallatin Range of southwestern Montana offers new insights into the vegetation and fire history at middle elevations within the Greater Yellowstone Ecosystem. Pollen data suggest that following deglaciation, a tundra-steppe established until warmer and wetter conditions than before could support *Picea* parkland. The development of an open, predominantly *Pinus* mixed conifer forest from ca. 9300-7000 cal yr BP suggests warming summer temperatures led to an increase in forest cover and fire activity; the increase in tree abundance supported infrequent, stand-replacing fires every ~600 years. *Picea* and *Pseudotsuga* increased their presence at ca. 7000 cal yr BP, and the mixed conifer forest became denser during the middle and late Holocene, suggesting summers became cooler and wetter. The additional fuel load led to increased fire activity, with stand-replacing fires occurring every ~350 years in the late Holocene. The forest surrounding Langohr Wetland experienced less change in vegetation composition and structure than other low and high-elevation sites in the Greater Yellowstone Ecosystem and fewer fire episodes. The stability of this forested ecosystem over thousands of years is likely a result of its cool mesic mid-elevation setting, limiting the frequency of intense fire episodes.

Introduction

In recent decades, warming temperatures and a lengthened fire season have led to increased fire activity in the western US (Westerling et al., 2006), and annual area burned and fire size are expected to increase with continued warming (Westerling et al., 2011). Higher elevations have disproportionately felt the effects of warming temperatures (Pepin et al., 2015,

2022), and fires have increasingly advanced upslope in recent decades (Alizadeh et al., 2021, 2023). Subalpine forests of the Rocky Mountains have been burning more than ever in recent history (Higuera et al., 2021), particularly due to factors such as earlier spring snowmelt (Westerling, 2016, Alizadeh et al., 2023). To contextualize recent fire trends, fire records from subalpine forests are necessary to understand how fire activity responded to past periods of warm temperatures.

Within the Rocky Mountains, the Greater Yellowstone Ecosystem (GYE) measures approximately 22 million acres and is one of the world's largest, nearly intact temperate ecosystems (Marcus et al., 2022). The environmental history of the GYE is among the best studied in the U.S., with records from all elevations (Whitlock, 1993; Whitlock et al., 1995; Fall et al., 1995; Millspaugh et al., 2000; Huerta et al., 2009; Mumma et al., 2012; Whitlock et al., 2012; Krause and Whitlock, 2013; Iglesias et al., 2015; Krause and Whitlock, 2017; Iglesias et al., 2018; Rust and Minckley, 2020). Pollen and charcoal analyses from these sites indicate that the vegetation and fire history generally track millennial-scale climate variations. Most of these studies have focused on the subalpine forest history in the central and southern GYE, while sites in the northern GYE are located in low-elevation steppe and xeric forests (Huerta et al., 2009; Mumma et al., 2012; Krause and Whitlock, 2013; Krause et al., 2015), other than one site in a high-elevation subalpine forest in the Bridger Range (Benes et al., 2019).

The vegetation and fire history of mixed conifer forests in the northern GYE is not well known in the absence of paleoecological records from middle elevations. This study provides a 13,500-year-long record from Langohr Wetland (45.52425°N, 111.01807°W, 1898 m asl, ~2 ha), located in a mixed conifer forest in the northern Gallatin Range adjacent to the Gallatin Valley

and the city of Bozeman. The primary objective of this study was to reconstruct the long-term climate-fire-vegetation interactions at Langohr Wetland and compare its vegetation and fire history with sites in other ecological settings in the region.

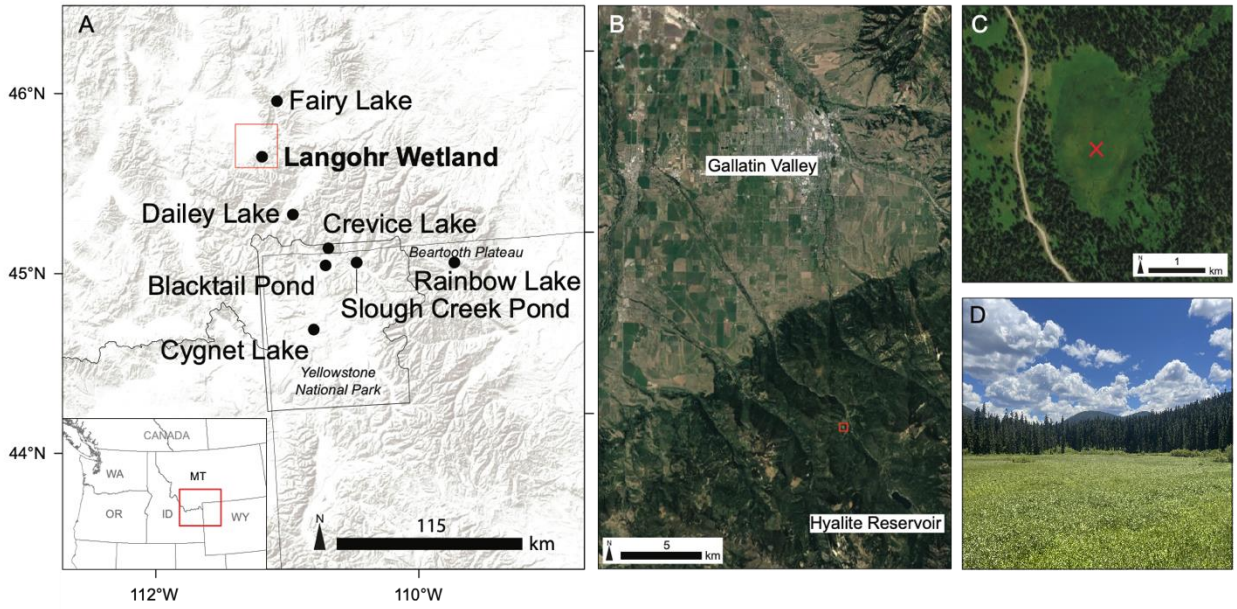


Figure 3.1. (A) Regional map showing Langohr Wetland and other study sites discussed in the text. (B) Location of Langohr Wetland in relation to the Gallatin Valley. (C) coring location in Langohr Wetland. (D) Langohr Wetland.

Study Site

The Gallatin Range spans ~120 km north to south and averages 32 km in width, hosting several peaks above 3000 masl, the highest of which is Electric Peak (3433 m) in Yellowstone National Park (YNP). Present-day vegetation in the region varies with elevation and aspect. *Artemisia* (sagebrush) steppe and grassland (mainly *Festuca idahoensis,* Poaceae spp.) cover valley floors, and in the northern Gallatin Range (closest to Langohr Wetland), lower treeline is at approximately 1650 masl. *Juniperus scopulorum* (Rocky Mountain juniper), *Pinus flexilis*

(limber pine), and *Pseudotsuga menziesii* (Douglas-fir) constitute low-elevation dry forests from ~1650 to 1800 masl, and forest density increases with elevation. Subalpine conifer forests of *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and *Pinus contorta* (lodgepole pine) occur between 1800-2100 masl, with *A. lasiocarpa* increasing in abundance with elevation. Forests dominated by *Picea engelmannii* and *A. lasiocarpa* are generally above ~2100 masl, and *Pinus albicaulis* (whitebark pine) forests are found at the highest elevations above 2400 masl. Alpine tundra is found on the highest peaks, above ~3000 masl (Arno, 1979; Whitlock, 1993; Iglesias et al., 2018).

Langohr Wetland is located in the Custer Gallatin National Forest in a glacially-formed depression (Weber, 1965) within the Hyalite Creek watershed. It has a small inlet spring entering from the south and flowing to the northeast (Fig. 3.1). The wetland supports *Carex* spp., *Eleocharis* spp. (sedges), and Poaceae spp. (grasses), and *Salix* spp. (willow) *Betula* spp. (birch) shrubs grow along the margins. A closed mixed conifer forest of *Picea engelmannii, Pinus contorta*, and lesser amounts of *A. lasiocarpa* surrounds the wetland. *Pseudotsuga menziessii* and *J. scopulorum* grow on nearby south-facing slopes, and *Pinus albicaulis* dominates at higher elevations in the watershed. *Juniperus communis* (common Juniper) is found in the forest understory along with other shrubs, including species of Rosaceae (i.e., *Rosa woodsi* (wood's rose), *Physocarpus malvaceus* (ninebark), *Potentilla gracilis* (cinquefoil), *Amelanchier alnifolia* (serviceberry), and *Spiraea betulifolia* (birch leaf spirea)), *Symphoricarpos albus* (snowberry), *Berberis repens* (creeping mahonia), *Shepherdia canadensis* (buffaloberry), and *Arctostaphylos uva-ursi* (bearberry). The adjacent grassy west-facing hillslope supports *Juniperus horizontalis* (creeping juniper) and a diverse array of herbs from the Asteraceae, Rosaceae, Amaranthaceae,

Brassicaceae, Ranunculaceae, and Caryophyllaceae families. *Artemisia tridentata* shrubs are present in a meadow ~0.25 km NW of the wetland, and *Alnus viridis* (green alder)*, Populus tremuloides* (quaking aspen)*,* and *Populus balsamifera* (black cottonwood) grow on the wet banks of Hyalite Creek ~0.5 km NW of the wetland.

Extensive logging in the Hyalite Creek watershed started in the late 1800s and primarily targeted large merchantable *Pseudotsuga menziesii* trees. Post-logging forest openings have since been colonized by *Pinus contorta* and *Pseudotsuga menziesii.* Secondary forests tend to be dense and have a homogeneous structure, similar to other logged forests in Montana (Naficy et al., 2010).

Large fires (>400 ha) have occurred historically throughout the Custer Gallatin National Forest between the mid-1500s and early 1900s (Barrett et al., 1997). Large fires were infrequent between 1940 and 1980 due to a combination of cooler temperatures (Littell et al., 2009) and intensified fire suppression efforts (Agee, 1993; Barrett, 1997; Erickson, 2022). In recent decades, fire activity in the western U.S. has increased due to rising temperatures and drought (Abatzoglou and Williams, 2016). Contrary to this trend, the total acreage burned in the Custer Gallatin National Forest has decreased since the large Yellowstone fires of 1988, and xeric forests that historically experienced high- (0-35 yr fire return interval) and moderate-frequency (35-100+ yr fire return interval) fire regimes are assumed to have a fire deficit at present (Erickson, 2022).

Wet *Picea-Pinus* forests, like those surrounding Langohr Wetland, currently experience a high-severity fire regime with a 35-200+ year return interval. The south-facing *Pseudotsuga* forests experience a higher frequency mixed/low-severity fire regime (every 35-100+ years)

(Erickson, 2022; LANDFIRE, 2014). No major fires have occurred in the Hyalite Creek watershed in the last 100 years (Erickson, 2010), although small, lightning-caused fires were immediately suppressed in 2013 (Horsetail fire) and 2014 (Sleeping Giant and Lick Creek fires). In the Gallatin Range as a whole, large fires last occurred in 2001 (Fridley and Purdy fires) and 2012 (Millie Creek fire; MTBS, 2021). Because *Picea-Pinus* forests have a relatively long natural fire return interval, fire suppression efforts of the last 100 years have likely had minimal effect on the forest around Langohr Wetland (Schoennagel et al., 2004).

Interpolated climate data based on 30-year mean monthly temperature and precipitation data (PRISM Climate Group, 2022) indicate that mean summer (July-August) temperature at Langohr Wetland is 14°C, with a maximum of 25.6°C, and mean winter temperature (December-February) is -5.6°C, with a minimum of -12°C. Langohr Wetland receives an average of 720 mm annual precipitation, most of which is received in late spring to early summer (April-June = 280 mm of precipitation on average). Late summer and early fall months are driest (July-September = 120 mm on average), and ~35% of total precipitation falls as snow (November- March = 250 mm on average). The ratio of summer (June to August) precipitation to winter (December to February) precipitation is ~1.20, suggesting the high amount of June precipitation causes it to receive slightly more precipitation in the early summer than in the winter.

Methods

Field and Laboratory

A 250-cm-long sediment core was collected from Langohr Wetland using a Russian D-section Peat Borer. Cores were taken at continuous 50-cm-long intervals until the borer hit bedrock. Sediment cores were wrapped in plastic and aluminum foil in the field and stored in the

cold room at Montana State University until they were analyzed. In the laboratory, core lithology was described by sediment type (Schnurrenberger et al., 2003) and subsampled. Nine bulk sediment samples were taken throughout the core and submitted to the National Ocean Sciences Accelerator Mass Spectrometry facility at Woods Hole for accelerator mass spectrometry (AMS) radiocarbon dating (Table 1). AMS C^{14} dates were calibrated with the IntCal20 calibration curve (Reimer et al., 2020), and an age-depth model was created with BACON age-depth modeling software, which uses a Bayesian statistical approach (Blaauw and Christen, 2011).

Charcoal Analysis

To reconstruct the local fire history, 2 cm^3 samples were taken from contiguous 1 cm intervals of the entire core for charcoal analysis. Samples were processed following standard methods and gently washed through a 125-μm sieve (Whitlock and Larsen, 2001). The residue was examined under a stereomicroscope, and charcoal particles were counted at 50-100x magnification. Charcoal counts were analyzed with CharAnalysis software (Higuera et al., 2009). Charcoal concentrations (particles cm^{-3}) were binned into 47-yr time intervals (median sampling interval) to minimize differences in charcoal accumulation due to changes in sedimentation rate, and charcoal accumulation rates (CHAR, particles cm^{-2} yr^{-1}) were calculated by dividing the charcoal concentration by the sediment accumulation rate (yr cm^{-1}). The charcoal record was separated into a background component (background CHAR=BCHAR) and a higher frequency peaks component. BCHAR was calculated using a 600-yr LOWESS smoother robust to outliers, which optimized the signal-to-noise ratio (SNI>3; Kelly et al., 2011). A Poisson minimum count test identified charcoal peaks that exceeded a 90% threshold as significant fire episodes. Charcoal data register local fire episodes, one or more fires within 3 km of the site that

occurred during the time span of the peak (Whitlock and Larsen, 2001; Higuera et al., 2009). Charcoal peaks are usually a record of stand-replacement fires rather than surface fires, which do not produce much charcoal and carry lesser amounts aloft. BCHAR is considered either (1) a representation of regional biomass burned, (2) a result of secondary charcoal deposition and sediment mixing (Whitlock and Larsen, 2001), and/or (3) a measure of arboreal fuel biomass on the landscape (Marlon et al., 2006). Peak magnitude measures the total charcoal deposition per fire event (particles cm^{-2} $peak^{-1}$) and can potentially measure changes in fuel consumption or fire size (Higuera et al., 2009). Fire-episode frequency was determined using a smoothed 1000-year moving window, and the mean fire-episode return interval is the years between significant fire episodes.

To analyze regional charcoal trends, a composite charcoal record was created with records from nearby sites in the GYE that extended through the late-glacial period. Published age-depth models and counts were first analyzed in CharAnalysis with the same parameters as the Langohr record analysis, except that charcoal peaks that crossed a 95% threshold were considered significant fire episodes. To standardize the data for the composite record, CHAR results were subjected to statistical minmax-, Box-Cox, and finally Z-score- transformations as described in Power et al., (2008).

Pollen Analysis

Samples of 1 cm^3 volume were processed for pollen following the procedures of Bennett and Willis (2001). A *Lycopodium* table of known concentration was added to each sample to calculate pollen concentration (grains cm^{-3}) and pollen accumulation rates (PAR; grains cm^{-2} yr^{-1}). A minimum of 300 terrestrial pollen grains were counted per sample at 400 and 1000x

magnification. Pollen reference slides at Montana State University and pollen keys (McAndrews et al., 1973; Faegri and Iversen, 1975; Kapp et al., 2000) were used to identify the grains. Terrestrial pollen counts were converted to percentages based on the terrestrial pollen sum, and aquatic pollen counts were converted to percentages with the combined terrestrial and aquatic pollen sum. *Carex* spp. is a dominant Langohr Wetland plant; accordingly, Cyperaceae is considered an aquatic taxon in this study.

Based on the conifer species present in our study region, *Pinus* subg. *Strobus* pollen was attributed to *Pinus flexilis* or *Pinus albicaulis* and *Pinus* subg. *Pinus* pollen was ascribed to *Pinus contorta*. Damaged *Pinus* grains that were missing distal membranes were classified as *Pinus* undifferentiated. *Abies* grains were attributed to *A. lasiocarpa, Picea* grains to *Picea engelmannii,* and *Juniperus*-type pollen to *J. communis* or *J. scopulorum*. Species in the "Total Rosaceae" category include undifferentiated Rosaceae and *Spiraea, Potentilla,* and *Amelanchier*-type pollen grains. Shrubs and herbs under 1% were grouped in an "other shrubs and herbs" category. Non-arboreal pollen amounts are higher in non-forested landscapes and increase with distance from forest boundaries (Whitlock, 1993; Fall, 1994; Iglesias et al., 2018), and the ratio between arboreal pollen (AP) and non-arboreal pollen (NAP) was used as an indicator of forest cover. Arboreal pollen is the sum of all tree and shrub species, excluding *Artemisia,* since *Artemisia* is predominantly found in open landscapes and forest meadows. Non-arboreal pollen is the sum of *Artemisia,* herbs, and grasses. The AP:NAP ratio was calculated by [(AP-NAP)/(AP+NAP)]. CONISS was used to identify pollen zones through stratigraphically constrained cluster analysis (Grimm, 1987).

Results

Lithology

The Langohr core consisted of four lithological units (Fig. 3.2). Unit 1 (250-240 cm depth) was inorganic gray clay and sand. Unit 2 (240-175 cm depth) was dark brown fragmental granular peat. Unit 3 (175-105 cm) was primarily fine-detritus sapropel and contained two layers with increased levels of inorganic silt and clay (silty-clayey sapropel), one at 150-138 cm and one at 120-115 cm depth. Unit 4 (105 cm depth- surface) consisted of fragmental sedge herbaceous peat that increased in coarseness towards the top.

Chronology

The Langohr age-depth chronology was based on nine AMS ^{14}C dates from bulk sediment (Table 1, Fig. 3.2). Extrapolated ages from the bottom two dates suggest sediment accumulation began between ca. 14,000 and 13,000 cal yr BP. One age reversal was noted at the base of the core. The age of 14,168-13,976 cal yr BP at 216 cm depth may be anomalously old due to incorporating ancient carbon in the sediments. However, the date at 242 cm depth could be anomalously young, therefore, the basal age primarily influenced by the 13,300-13,100 cal yr BP date at 242 cm depth is considered a minimum age. An anomalously young age at 175 cm depth was rejected in the age-depth model. The sedimentation rate in units 1 and 2 averaged 0.02 cm/yr. Unit 3 had the slowest sedimentation rate of 0.01 cm/yr average. The low sedimentation rate in unit 3 may suggest undetected hiatuses in deposition, but we assume unit 3 had uninterrupted sedimentation. It is also possible that the two silty-clay layers in unit 3 represent rapid depositional events, but without distinct boundaries, they were not conclusively identified

as such and retained in the age-depth model as continuous deposition. Unit 4 had the fastest accumulation rate of the core, with an average of 0.07 cm/yr.

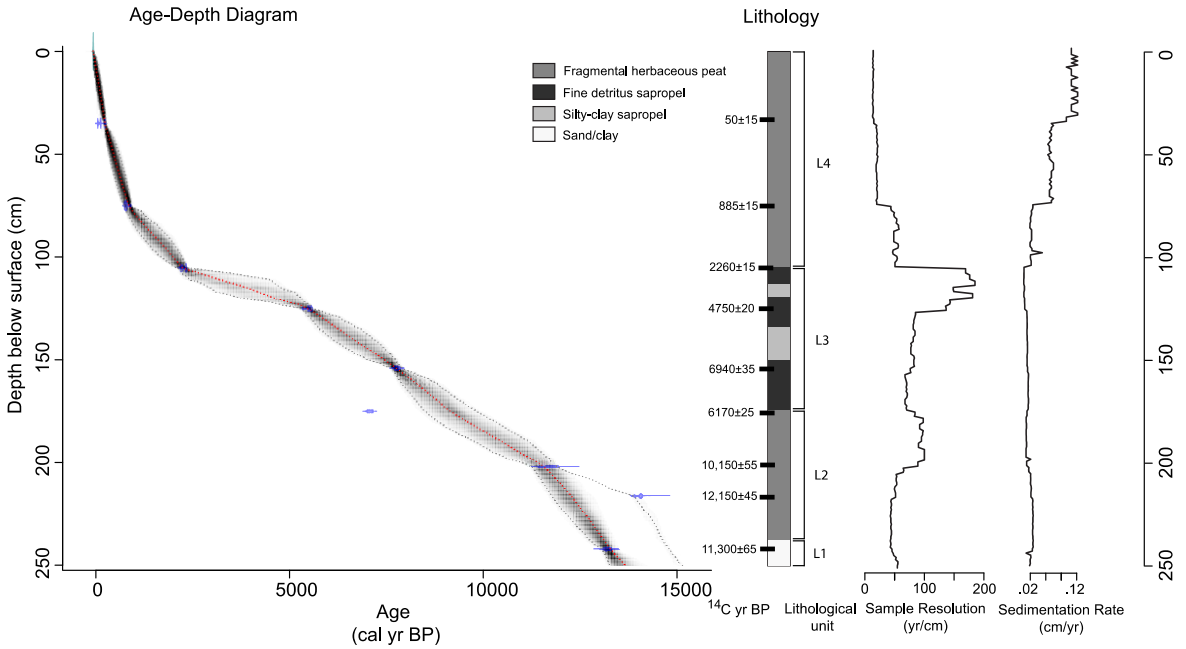


Figure 3.2. Age-depth diagram and lithology of Langohr Wetland core. The age-depth diagram is based on nine radiocarbon dates. The red dotted line is the median probability age for each depth, and the black dotted lines indicate the 95% probability range. The lithology includes sediment types, sample depths for radiocarbon dates, and lithologic units discussed in the text.

Table 3.1. Radiocarbon information for Langohr Wetland. The "*" symbol denotes a rejected date.

Depth (cm)	Lab Number/ Reference	Material Dated	Uncalibrated Age (^{14}C yr BP)	2σ Calibrated Age Range (cal yr BP)(Probability)
35	145880	Bulk sediment	50 ± 5	347-609
75	145881	Bulk sediment	885 ± 15	732-794(.96)
105	175601	Bulk sediment	2260 ± 15	2302-2340(.5)
125	177831	Bulk sediment	4750 ± 20	5498-5581 (.75)
154	175602	Bulk sediment	6940 ± 35	7679-7846 (.99)
175	145882	Bulk sediment	*6170 ± 25	6985-7161 (1)
202	175599	Bulk sediment	10,150 ± 55	11,601-11,948(.91)
216	145883	Bulk sediment	12,150 ± 45	13,976-14,168(.82)
242	175600	Bulk sediment	11,300 ± 65	13,100-13,303(1)

Pollen and Charcoal

The pollen record was divided into four pollen zones and three subzones based on constrained cluster analysis (Grimm, 1987; Fig. 3.3). Pollen percentages are reported as zone ranges, and the PAR, AP:NAP, and *Pinus* subg. *Strobus* to *Pinus* subg. *Pinus* ratios are reported as entire zone averages unless otherwise noted.

Zone L1 (250-238 cm depth; 14,000-13,000 cal yr BP) consists of two pollen samples at the base of the core that were characterized by high levels of nonarboreal pollen taxa. Both samples had high *Artemisia* and Poaceae percentages (30-33% and 32-34%, respectively), and a diverse assemblage of shrubs and upland herbs, including *Salix* (3-4%), *Thalictrum* (3-5%), Asteraceae subfam. Asteroideae (2-3%), Amaranthaceae (2%), Caryophyllaceae (<1%), Ranunculaceae (<1%), Fabaceae (<1%), and *Polygonum bistortoides*-type (<1%). Values of *Pinus* pollen (16-18%) were low, and the *Pinus* subg. *Strobus* to *Pinus* subg. *Pinus* ratio (1.38) was high. *Picea* values (2-3%) were low, and other conifer percentages were negligible (0-1%). The low total pollen accumulation rate (PAR; 314 grains $cm^{-2}yr^{-1}$) suggests a sparsely vegetated environment (Davis et al., 1973), and the lowest AP:NAP value of the record (-.49 vs. long-term average = .43) indicates an open landscape (Fall, 1994). Cyperaceae pollen was abundant (34-37%) in the zone and may have been a part of the upland vegetation; no other aquatic species were present. Charcoal was absent in this zone, suggesting minimal to no fires (Fig. 3.4). Overall, the assemblage suggests a cold tundra-steppe environment dominated by *Artemisia* and Poaceae with alpine herbs and scattered *Pinus albicaulis/flexilis* and *Picea*.

Zone L2 was characterized by increased arboreal pollen taxa and separated into two subzones. Subzone L2a (238-200 cm depth; 13,000-11,500 cal yr BP) had increased *Pinus* (40-61%) and *Picea* (to 7%), and a low appearance of *Pseudotsuga* (0.2-2%), *Juniperus*-type (1%),

and *Populus* (1-4%) pollen. The *Pinus* subg. *Strobus* to *Pinus* subg. *Pinus* ratio decreased (0.53) suggesting an increase in *Pinus contorta*, although moderate levels of *Pinus* subg. *Strobus* pollen (avg=8.5%) indicate *Pinus albicaulis/flexilis* was still present (Fall, 1994). *Artemisia* and Poaceae declined (9-17% and 5-24%, respectively), as did *Salix* (<3%) and *Thalictrum* (<1%). Other shrubs and herbs (such as Asteraceae subfam. Asteroideae, Amaranthaceae, and Caryophyllaceae) remained at similar levels as in Zone L1, and *Betula*, *Ambrosia*-type, Rosaceae, and Brassicaceae pollen appeared in this subzone in low amounts (< 2%). Cyperaceae percentages were high at the base of the zone (high of 57%) but declined towards the top (low of 17%), and *Typha* pollen was present in moderate amounts (1-5%). CHAR remained negligible at the bottom of the subzone until 201 cm depth (ca. 11,500 cal yr BP) when values increased (to 0.06 particles $cm^{-2}yr^{-1}$) with the first small significant fire peak (peak magnitude = 1.9 particles cm^{-2} $peak^{-1}$).

Subzone L2b (200-177 cm depth; 11,500-9300 cal yr BP) was distinguished from Subzone 2a by a slight decline in *Pinus* pollen (37-54%) and an increase in *Picea* (3-11%) and *Pseudotsuga* (1-4%). *Artemisia* and Poaceae pollen percentages remained unchanged (7-19% and 11-22%, respectively), and *Juniperus* and *Populus* percentages were low (<2%). *Betula* and Amaranthaceae percentages increased at the top of the subzone (up to 4%), but other shrubs and herbs were the same as in Subzone L2a. *Selaginella densa*-type spore percentages increased during this subzone (1-2%), and after an initial decline from Subzone L2a, Cyperaceae and *Typha* increased towards the top of the subzone (from 13 to 32% and 0 to 5%, respectively). CHAR and BCHAR remained low at the base of the zone (<0.1 particles $cm^{-2}yr^{-1}$), although one fire episode with a small peak magnitude (8.3 particles cm^{-2} $peak^{-1}$) was recorded at 196 cm

depth (ca. 11,000 cal yr BP). After a ~1200-year period of minimal CHAR, values increased to 2 particles cm^{-2} yr^{-1} at the top of the subzone, and two fire episodes were recorded: one with a peak magnitude of 158.7 particles $cm^{-2}peak^{-1}$ (ca. 9800 cal yr BP) and the other with 13.2 particles cm^{-2} $peak^{-1}$ (ca. 9400 cal yr BP). Other than a ~1200-year gap with no fire, the mean return interval for fire episodes was ~380 years. Increases in PAR (1850 grains $cm^{-2}yr^{-1}$) and AP:NAP (0.28) during Zone L2 suggest a parkland (Davis et al., 1973; (Fall, 1994, 1992), and the pollen and charcoal data suggest *Picea* was the dominant conifer with some *Pinus albicaulis/flexilis* surrounding the wetland at a time when stand-replacing fires started to occur.

Zone L3 was characterized by another increase in arboreal pollen taxa and decrease in nonarboreal pollen taxa. Subzone L3a (177-147 cm depth; 9300-7200 cal yr BP) registered an increase in *Pinus* pollen (55-71%) and decreases in *Picea* (1-4%) and *Pseudotsuga* (0-1%) pollen. The *Pinus* subg. *Strobus* to *Pinus* subg. *Pinus* ratio decreased (to 0.32), suggesting the increased presence of *Pinus contorta.* All shrubs, herbs, and grasses (such as *Artemisia* (11-16%), Poaceae (4-10%), and *Betula* (<1%)) decreased, other than Amaranthaceae, which increased (3-5%). Cyperaceae decreased (8-22%), and *Typha latifolia* increased to the highest values of the record (up to 7%). CHAR increased during this subzone to 2.4 particles cm^{-2} yr^{-1}, and three significant charcoal peaks with magnitudes of 29.1, 128.1, and 74.5 particles cm^{-2} $peak^{-1}$ (ca. 9000, 8200, and 7700 cal yr BP, respectively). The mean return interval between fire episodes averaged ~570 years, or 1-2 episodes per 1000 years.

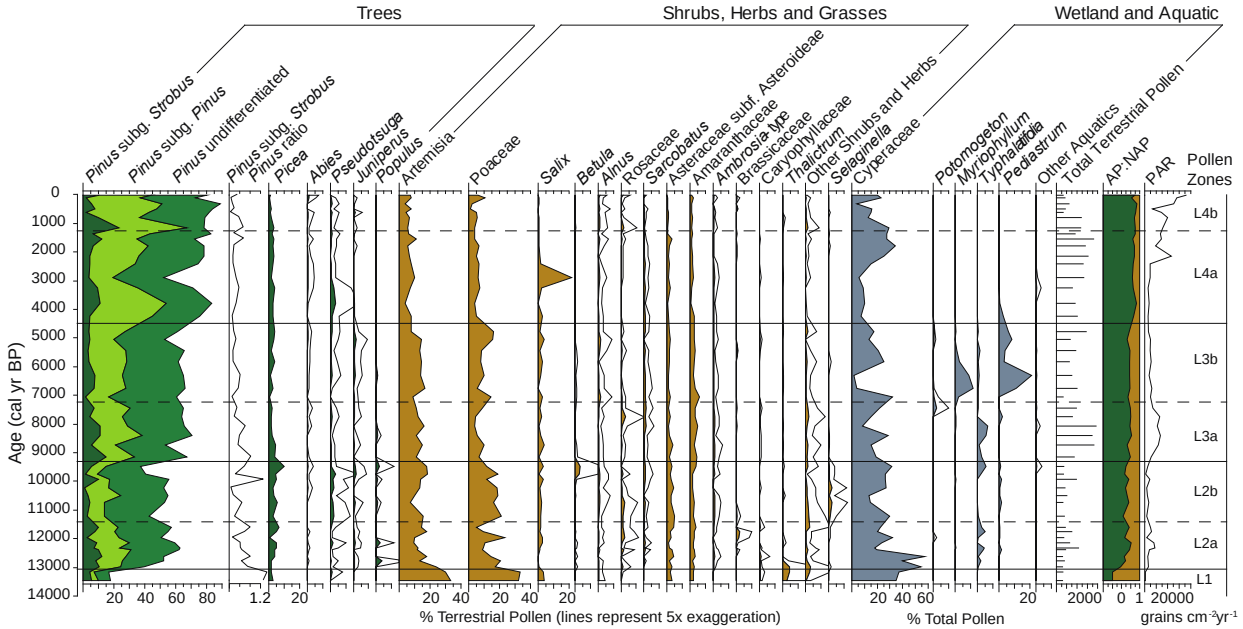


Figure 3.3. Pollen percentage diagram of selected taxa for Langohr Wetland, MT. Terrestrial pollen percentages are based on the terrestrial pollen sum, and wetland and aquatic pollen percentages are based on the total pollen sum.

Subzone L3b (147-118 cm depth; 7200-4400 cal yr BP) was distinguished from Subzone L3a primarily by the increase in aquatic taxa. Cyperaceae pollen percentages reached the lowest values of the record (2%), *Typha latifolia* declined (<1%), and *Pediastrum* (0-21%) and *Myriophyllum* (1-11%) increased. CHAR levels decreased from the previous subzone (up to 1.7 particles cm^{-2} yr^{-1}), although four fire episodes were recorded with peak magnitudes of 1.4, 17. 8, 74.9, and 6.5 particles cm^{-2} $peak^{-1}$ (ca. 6600, 5835, 5690, 5300 cal yr BP, respectively). The mean fire-episode return interval averaged ~900 years between ca. 8000 and 6000 cal yr BP and decreased to ~260 years between 6000 and 5000 cal yr BP. BCHAR increased for the first time in the record during this same period (to 0.5 particles cm^{-2} yr^{-1}), suggesting more fires in the region. The increase in AP:NAP (0.44) and PAR (3704 grains $cm^{-2}yr^{-1}$) in Zone L3 provides evidence of forest closure (Davis et al., 1973; Fall 1992). A forest with *Pinus, Picea,* and

Pseudotsuga surrounded Langohr Wetland, and fires were likely stand-replacement events. The Subzone L3b aquatic pollen percentages suggest that the wetland may have deepened into a shallow pond.

Zone 4 was characterized by the highest levels of arboreal pollen in the record and split into two subzones. Subzone L4a (118-84 cm depth; 4400-1200 cal yr BP) had an overall increase in *Pinus* pollen (70-82%), although one sample showed a decrease to 52% at 109 cm depth (ca. 3000 cal yr BP). This decrease in *Pinus* values may be an artifact of percentage calculations since a large increase in *Salix* percentages (to 27%) occurs at this level. *Pinus* PAR, in fact, increased from 1083 grains $cm^{-2}yr^{-1}$ at 111 cm depth to 1266 grains $cm^{-2}yr^{-1}$ at 109 cm depth, and 1720 grains $cm^{-2}yr^{-1}$ at 106 cm depth (data not shown). Continued decrease in the *Pinus* subg. *Strobus* to *Pinus* subg. *Pinus* ratio (0.23) suggests the dominance of *Pinus contorta* over *Pinus albicaulis/flexilis. Picea* values were the same as in the previous zone (1-3%), while those of *Pseudotsuga* declined to the top of the zone following an initial increase (up to 4%), and those of *Juniperus* were negligible (<1%). *Artemisia* and Poaceae levels decreased (4-12% and 3-8% respectively). Cyperaceae percentages increased towards the top of the subzone (from 5 to 34%), and *Myriophyllum, Potamogeton, Typha,* and *Pediastrum* values dropped to 0%. CHAR was low at the base of the subzone (~0 particles cm^{-2} yr^{-1} until 102 cm depth, ca. 2000 cal yr BP) and increased at the top of the subzone (to 0.5 particles cm^{-2} yr^{-1}), recording seven charcoal peaks with magnitudes of 1.2, 0.1, 0.3, 43.4, 11.1, 2.8 and 65.1 particles cm^{-2} $peak^{-1}$ (at ca. 3150, 2600, 2475, 2140, 1900, 1470, 1275 cal yr BP, respectively). Following a period of 1700 years with no fire episodes (from ca. 4700-3000 cal yr BP), fire-episode frequency increased to ~2-3 episodes per 1000 years, with a mean return interval of ~312 years.

Subzone L4b (84-0 cm depth; 1200 cal yr BP-present day) was distinguished from Subzone L4a by the highest levels of *Pinus* pollen in the record (73-90%), whereas *Picea* (1-3%), *Pseudotsuga* (<1%), and *Juniperus* (<1%) pollen remained low. *Abies* reached the highest levels of the record at the top of the zone, although still minimal (1.5%). *Artemisia* and Poaceae values were the same as in the previous subzone, although Poaceae percentages increased at the top of the subzone (to 10%). Other shrubs and herbs were in low abundance throughout the subzone. Cyperaceae was the only aquatic pollen type present in this subzone and its percentages increased at the top (from 4 to 23%). CHAR levels increased (high of 0.8 particles cm^{-2} yr^{-1}), and three significant peaks had magnitudes of 16.4, 71.9, and 0.02 particles cm^{-2} $peak^{-1}$ (ca. 800, 600, 270 cal yr BP, respectively). Mean return interval of fire episodes remained similar to before, at 336 years, which equals 2-3 episodes per 1000 years. BCHAR also increased towards the top of this subzone (to 0.26 particles cm^{-2} yr^{-1}). The highest AP:NAP (0.70) ratio and PAR (7070 grains $cm^{-2}yr^{-1}$) suggest Zone L4 (and particularly Subzone L4b) was a period of dense forest (Davis et al., 1973, Fall, 1994). A closed mixed conifer forest of predominantly *Pinus contorta* with *Picea* and *Pseudotsuga* surrounded the Cyperaceae-covered Langohr Wetland, and episodes of stand-replacing fires were approximately 300 years apart with the most recent fire episode occurring ~330 years ago. Elevated levels of CHAR and BCHAR at the very top of the core suggest that fire activity in the region increased between 600 years ago and present day.

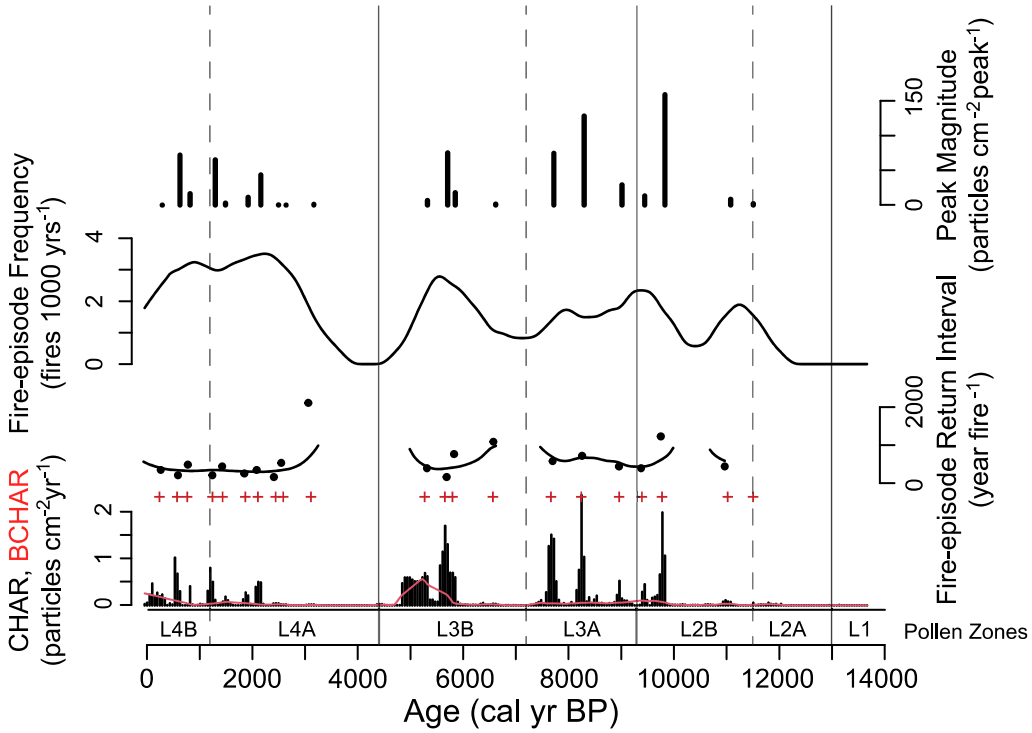


Figure 3.4. Charcoal accumulation rates (CHAR) from Langohr Wetland with background CHAR (BCHAR in red). Significant fire peaks (+ signs) likely represent stand-replacing fire episodes. Fire-episode return interval is the years between significant peaks, fire-episode frequency is the number of peaks smoothed over a 1000-yr moving window, and peak magnitude is the number of charcoal pieces per cm^2 from all samples in a peak.

Discussion

The Langohr Wetland record provides a postglacial vegetation and fire history of a mixed conifer subalpine forest in the northern Greater Yellowstone Ecosystem and highlights the relative stability of these wet forests throughout time. Vegetation structure and fire activity generally followed millennial-scale climate trends driven by changes in the seasonal cycle of insolation (Berger, 1978).

Here, we describe the Langohr Wetland record and compare it with other pollen and charcoal records from sites across the northern GYE (Table 2, Fig. 3.1). Background charcoal levels were minimal throughout the Langohr record, and it is likely that fine charcoal particles (<120microns) were not preserved in wetland sediments (due to degradation, or other factors). As a result, charcoal peaks are likely limited to representing very local fires within the Langohr watershed (<1km). Hence, we assume that the fire record likely focuses on fire events immediately adjacent to Langohr Wetland, and does not include fire events that lacustrine records would capture from a larger landscape**.**

The nearest study sites to Langohr Wetland are high-elevation Fairy Lake (~40 km NE from Langohr), a subalpine lake surrounded by mixed-conifer forest in the Bridger Mountain Range (Benes et al., 2019), and low-elevation Dailey Lake (~30 km SE from Langohr) in the Yellowstone River Valley surrounded by steppe (Krause et al., 2015). These three sites allow for comparison across an elevational gradient, although Dailey Lake's published vegetation and charcoal record only covers ca. 13,900-7500 cal yr BP. Other sites located farther south are Slough Creek Pond (Millspaugh et al., 2004), Blacktail Pond (Huerta et al., 2009; Krause and Whitlock, 2013), and Crevice Lake (record spans 9400-present day; Whitlock et al., 2012) located in steppe/*Pseudotsuga* parkland in northern YNP. We also considered data from Cygnet Lake (Whitlock, 1993; Millspaugh et al., 2000), which lies in the *Pinus contorta* forest on the rhyolite plateau of central YNP. The highest elevation record for comparison is Rainbow Lake, (Rust and Minckley, 2020) located in *Picea*, *Abies*, and *Pinus albicaulis* parkland on the Beartooth Plateau in the northeastern GYE.

Four of the sites (Dailey Lake, Crevice Lake, Slough Creek Pond, and Blacktail Pond) receive less than 500 mm annual precipitation and are considered summer-wet sites, meaning they receive more precipitation during summer than winter months (Whitlock and Bartlein, 1993). The other three sites receive over 500 mm of annual precipitation and are located in the summer-dry region, which receives more precipitation in winter. It has been proposed that during the early Holocene, summer-wet areas became wetter as a result of strengthened monsoonal circulation, whereas summer-dry regions became drier as a result of a stronger-than-present subtropical high (Whitlock and Bartlein, 1993). A comparison of these records offers insight into how different forest ecosystems responded to late-glacial and Holocene climate variations and provides new information to compare with a regional study by Iglesias et al. (2018).

Table 3.2. Sites in the Greater Yellowstone Ecosystem used for pollen and charcoal comparison. JJA/DJF is the summer to winter precipitation ratio.

Lake Name	Lat/Long	Elevation	Modern Vegetation	JJA/DJF	Reference
Dailey Lake	45.262N, 110.815W	1601 m	Steppe/parkland	2.23	Krause et al., 2015
Crevice Lake	45.000N, 110.578W	1695 m	Open *Pseudotsuga* forest	1.24	Whitlock et al., 2012
Slough Creek Pond	44.937N, 110.337W	1884 m	Steppe/parkland	1.27	Millspaugh et al., 2004
Langohr Wetland	45.524N, 111.018W	1898 m	Mixed-conifer forest	1.20	This study
Blacktail Pond	44.953N, 110.604W	2017 m	Steppe/parkland	1.34	Krause et al., 2013 Huerta et al., 2009
Fairy Lake	45.904N, 110.958W	2308 m	Mixed-conifer forest	.67	Benes et al., 2019
Cygnet Lake	44.663N, 110.613W	2550 m	*Pinus contorta* forest	.54	Millspaugh et al., 2000 Whitlock, 1993
Rainbow Lake	44.935N, 109.500W	2963 m	Open mixed-conifer parkland	.52	Rust and Minckley, 2000

Late Glacial (>14,000-11,500 cal yr BP): Transition from Tundra-Steppe to *Picea* Parkland

During the Last Glacial Maximum (LGM), a large glacial complex covered the Greater Yellowstone Ecosystem, and alpine glaciers covered adjacent mountain ranges (Weber, 1965; Pierce et al., 1979; Licciardi and Pierce, 2018). Terminal moraines approximately 20 km to the east of Langohr Wetland retreated from their maximum position after ca. 17,900 ka (Licciardi and Pierce, 2018). Recessional moraines ~40 km to the southeast in the Yellowstone Valley that date to ca. 15,100 ka (Licciardi and Pierce, 2018) suggest that the basal inorganic clay at Langohr Wetland dating to a minimum of ca. 13,500 cal yr BP accumulated in an ice-free depression as part of deglaciation.

An *Artemisia* tundra-steppe vegetation developed initially at Langohr Wetland and was replaced by *Picea*-dominated parkland with lesser amounts of *Pinus* at ca. 13,000 cal yr BP. *Picea* percentages above 6% suggest that *Picea* trees were abundant (Iglesias et al., 2018), and though the rapid increase in *Pinus* at ca. 13,000 cal yr BP likely marks its arrival in the Hyalite Creek watershed, the fact that percentages were below 60% suggests that *Pinus* trees were not abundant locally (Iglesias et al., 2018). The high *Pinus subg. Strobus* to *Pinus subg. Pinus* ratio indicates *Pinus albicaulis/flexilis* dominance initially, consistent with a colder-than-present climate. The transition from steppe to parkland, along with the appearance of *Typha latifolia* and the formation of organic peat sediment (lithological unit L2), implies the development of a productive wetland and warmer conditions than before by 13,000 cal yr BP.

In addition to *Picea* and *Pinus,* the pollen record indicates that *Pseudotsuga* trees were also present at Langohr Wetland as early as 13,000 cal yr BP. *Pseudotsuga* pollen fluctuated between 0-1% until 11,500 cal yr BP before increasing in abundance during the Holocene.

Pseudotsuga is often underrepresented in pollen records due to its poor production, dispersal, and preservation, and pollen levels as low as 0.5% can suggest its presence on the landscape (Gugger and Sugita, 2010). Thus, it seems likely that *Pseudotsuga* was present in low numbers, probably on south-facing slopes where it grows today. *Abies* pollen percentages were low throughout the entire record until the very top of the core, and *Abies* was probably not well-represented in the local vegetation until recently.

The late-glacial transition from tundra-steppe to parkland is recorded in sites across the region (Iglesias et al., 2018) and supports paleoclimate model simulations, which show that following a cold, dry late-glacial period, rising summer insolation and a northward shift of the jet stream from its full-glacial position, increased summer temperatures and brought increased moisture to the region (Bartlein et al., 1998; Alder and Hostetler, 2015). Landscapes dominated by *Artemisia*, Poaceae, and herbs were replaced primarily by *Picea* parkland at all but the highest elevations by the end of the late-glacial period. Dailey Lake and Fairy Lake differed in the timing of conifer arrival as a consequence of their elevations. Similar to Langohr Wetland, *Picea* parkland established at low-elevation Dailey Lake at ca. 13,300 cal yr BP (Krause et al., 2015), whereas high-elevation Fairy Lake supported tundra-steppe until 11,000 cal yr BP (Benes et al., 2019). *Picea* parkland was established at Blacktail and Slough Creek ponds in northern YNP by 12,500 cal yr BP (Millspaugh et al., 2004; Krause and Whitlock, 2013), and similar to Fairy Lake, higher-elevation Rainbow and Cygnet Lakes in central YNP supported tundra-steppe throughout the late-glacial period until ca. 10,500 and 11,500 cal yr BP, respectively (Millspaugh et al., 2000; Rust and Minckley, 2020). Thus, the development of early parkland was influenced by glacial recession, distance to refugial conifer populations, and the rate of warming and soil

development (Iglesias et al., 2018). Tree establishment occurred first at low elevations and last at high elevations and in central YNP (Krause and Whitlock, 2017).

No fire episodes were recorded at Langohr Wetland in the late-glacial period, suggesting patchy woody fuel cover and low temperatures at this time likely limited fire spread. Fire activity remained low throughout the parkland period between ca. 13,000-11,500 cal yr BP, when conditions were still cool. It is possible that low-severity surface fires, which do not produce much charcoal, occurred but were not detected in the charcoal record.

Fire activity was generally low across the region during the late-glacial period (Fig. 3.5). Unlike Langohr Wetland, however, fire activity did increase with the appearance of *Picea* parkland at Dailey Lake, Slough Creek, and Blacktail Pond at ca. 13,200, 12,250, and 12,000 cal yr BP, respectively (Millspaugh et al., 2004; Krause et al., 2015). These records suggest biomass burning increased in the late-glacial period as *Picea* established and expanded, but generally low charcoal influx from regional records indicates biomass burning was limited.

Early Holocene (ca. 11,500-7000 cal yr BP):
Transition from Parkland to Open Mixed Conifer Forest

The *Picea*-dominated parkland persisted at Langohr Wetland at the start of the early Holocene, indicated by the high percentages of Poaceae and *Selaginella densa*-type (Iglesias et al., 2018). The increase and consistent presence of *Pseudotsuga* pollen after ca. 11,500 cal yr BP indicates *Pseudotsuga* trees became more established on the landscape, suggesting the continued warming conditions of the early Holocene. *Populus* spp. and patches of *Salix* likely grew in the riparian areas along the stream and wetland.

The parkland became more forested at ca. 9300 cal yr BP, indicated by an increase in arboreal pollen percentages and decreases in Poaceae and *Selaginella densa*-type values. *Picea*

and *Pseudotsuga* were still present but less abundant, and *Pinus* dominated the forest. A low *Pinus subg. Strobus* to *Pinus subg. Pinus* ratio suggests the presence of both *Pinus flexilis/albicaulis* and *Pinus contorta,* with *Pinus contorta* dominating, also suggesting warming conditions. The presence of *Artemisia* in moderate amounts implies areas of steppe at lower and/or upper elevations and in dry forest openings.

Open and closed forests replaced parkland across the region in response to the continued warming and increased effective moisture during the late-glacial and Holocene transition (Bartlein et al., 1998; Alder and Hostetler, 2015). The timings of forestation varied (Iglesies et al., 2018), with most sites becoming forested before Langohr Wetland. At Dailey Lake, it occurred at ca. 12,300 cal yr BP, with increases in *Abies, Picea,* and *Pinus albicaulis/flexilis* (Krause et al., 2015), and Fairy Lake became more closed with conifer forest development at ca. 11,000 cal yr BP (Benes et al., 2019). Upper treeline and subalpine parkland moved upslope while lower and middle-elevation forests became denser and *Pinus*-dominated in the other areas of the GYE as well. *Pinus* forest was established at Blacktail Pond and Cygnet Lake by 11,500 cal yr BP, and *Pinus* and *Juniperus* trees were present at Slough Creek Pond at ca. 11,000 cal yr BP (Millspaugh et al., 2000; Millspaugh et al., 2004; Krause and Whitlock, 2013). High-elevation Rainbow Lake transitioned from tundra-steppe to open *Pinus* forest by ca. 10,000 cal yr BP (Rust and Minckley, 2020).

Summer (winter) insolation levels continued to increase (decrease) into the early Holocene, reaching a maximum (minimum) at 11,000-10,000 cal yr BP (Berger, 1978). Higher summer insolation increased summer temperature and transpiration (reducing effective moisture), and indirectly strengthened the northeastern Pacific subtropical high-pressure system.

These conditions increased summer drought in the region (Bartlein et al., 1998; Alder and Hostetler, 2015); and at some sites, this led to more open forests. Dailey Lake recorded an open *Pseudotsuga* and *Pinus* forest at ca. 10,200 cal yr BP (Krause et al., 2015), and Fairy Lake supported a similar forest after ca. 9000 cal yr BP (Benes et al., 2019). A record from an ice patch on the Beartooth Plateau also suggests more open vegetation at high elevations at ca. 10,000 cal yr BP (Alt et al., 2024). Evidence of drier conditions also comes from declining lake levels in the GYE at Moran Bay in Grand Teton National Park in the southern GYE at ca. 10,400 cal yr BP (Dilworth et al., 2024), Rainbow Lake on the Beartooth Plateau at ca. 10,000 cal yr BP (Shuman and Serravezza, 2017), and Lake of the Woods, WY, just south of YNP, at ca. 9000 cal yr BP (Shuman et al., 2009). These vegetation and hydrological changes seem explained by climate conditions created by the summer insolation maximum.

Other sites, like Langohr Wetland, remained forested during the early Holocene, despite warmer and drier conditions, but probably for different reasons. The wet setting of Langohr Wetland may have provided a refugium for mesophytic taxa and thus was not as responsive to intensified summer drought as other locations. Cygnet Lake was surrounded by a closed *Pinus contorta* forest because of its location on the infertile rhyolitic Central Plateau, which is most conducive to *Pinus contorta* growth (Whitlock, 1993). High-elevation Rainbow Lake showed an increase in forest cover as a result of an upslope shift in treeline under warming conditions. Parkland surrounding Fairy Lake and alpine tundra at the ice patch suggests some high-elevation areas did not support closed forests despite an overall upward shift in treeline, which could be attributed to local topographical features (such as locations in large open basins and high plateaus) causing them to be more susceptible to summer drought.

Slough Creek Pond, Blacktail Pond, and Crevice Lake show evidence of more forest cover in the early Holocene followed by a shift to more open forest and steppe after ca. 8000 cal yr BP. This later timing for forest opening has been attributed to their location in a summer-wet precipitation regime that may have been wetter during the early-Holocene insolation maximum and subsequently became more open as summer insolation decreased (Whitlock and Bartlein, 1993). At the other summer-wet site, Dailey Lake, the transition toward open vegetation occurred at ca. 10,000 cal yr BP (2000 years earlier), with the increase in summer insolation levels, suggesting it was not wetter during the early Holocene, despite its location in a summer-wet region.

The earliest evidence of *Pseudotsuga* occurred at Langohr Wetland (pollen percentage of 1.5% at ca. 13,100 cal yr BP), and its sustained presence after 11,500 cal yr BP (continuous percentages between 1-5%) also pre-dates other sites. Dailey Lake first registered *Pseudotsuga* pollen at ca. 12,500 cal yr BP with a sustained presence after ca. 10,200 cal yr BP, and Slough Creek Pond, Blacktail Pond, and Fairy Lake do not have pollen evidence of *Pseudotsuga* until ca. 9000 cal yr BP. Both Dailey Lake and Langohr Wetland provide support for the hypothesis of a glacial-age refugial population of *Pseudotsuga* in the unglaciated parts of the Gallatin or upper Yellowstone Valleys close to the Yellowstone Ice Cap. As conditions warmed, *Pseudotsuga* populations at low and middle elevations were able to colonize higher deglaciated elevations (Krause & Whitlock, 2017).

Fire activity at Langohr Wetland was low until ca. 10,000 cal yr BP, when an increase in charcoal peaks marks a shift towards more stand-replacing fires. After a large fire episode in the record (ca. 9800 cal yr BP), *Pinus* percentages decreased, and those of *Juniperus, Artemisia,* and

Betula increased for ~500 years. The timing of the first large fires during the summer insolation maximum (ca. 10,000 cal yr BP) suggests that warm, dry conditions led to increased fire activity and prevented forest regeneration for hundreds of years. The slight increase in *Juniperus* and *Pseudotsuga* at this time suggests more drought-tolerant species after the fire episode.

As the forest around Langohr Wetland became more *Pinus*-dominated after ca. 9300 cal yr BP, stand-replacing fire episodes occurred regularly until ca. 7500 cal yr BP. The mean fire-episode return interval of 570 years between fire episodes suggests a long time between stand-replacing fire episodes, characteristic of a high-intensity fire regime, although the fire return interval was longer than the 150-300-year fire return interval based on tree ring studies in northern Rocky Mountain subalpine forests (Baker, 2009). The coincidence of the first large fire episodes and a shift from *Picea*-dominated parkland to *Pinus*-dominated mixed-conifer forest suggests that an increase in fire activity may have fostered the transition from open to closed forest by favoring more fire-tolerant *Pinus* over *Picea* (Krause and Whitlock, 2013).

Fire activity similarly increased across the GYE during the late-glacial to early-Holocene transition, likely in response to warming and increased woody fuel (Iglesias et al., 2018). Many sites register an increase in fire activity earlier than at Langohr Wetland, as part of their vegetation transition to more conifers on the landscape during the late-glacial (Fig. 3.5). Dailey Lake, for example, experienced increased fire activity during the shift from parkland to forest at ca. 12,000 cal yr BP, and Fairy Lake registered increased fire activity with the establishment of open *Picea* forest at ca. 11,000 cal yr BP. Rainbow Lake supported more fires when steppe-tundra transitioned to open forest at ca. 10,000 cal yr BP (Rust and Minckley, 2020). Similar to Langohr Wetland, Cygnet Lake recorded an increase in fire frequency at ca. 10,000 cal yr BP in

response to the summer insolation maximum. Mean fire return intervals for all sites were shorter than at Langohr Wetland, which may reflect its uniquely mesic setting, or be reflective of Langohr only registering fires immediately surrounding the wetland.

Similar to Langohr Wetland, a rise in fire activity at many sites also accompanied the subsequent transition from *Picea* parkland to closed *Pinus* forest (Fig. 3.5; Krause & Whitlock, 2013). Stand-replacing fire activity increased at Blacktail Pond at 11,500 cal yr BP, and forest cover increased soon thereafter and became a closed *Pinus* forest at 10,000 cal yr BP. At Slough Creek Pond, fires increased at 12,250 cal yr BP, followed by forest development at 11,000 cal yr BP, and then closed *Pinus* forest at 10,750 cal yr BP. Fire activity increased at Cygnet Lake at 11,000 cal yr BP coincident with the development of *Pinus contorta* establishment, and closed *Pinus* forest was present at 10,750 cal yr BP. The synchronous rise in fire activity was initiated by a warming climate, and then *Pinus albicaulis, Pinus flexilis., and Pinus contorta* colonized burned areas at the expense of *Picea engelmannii* (Iglesias et al., 2015; Krause and Whitlock, 2017, 2013), which has little adaptation to fire (Agee, 1993). The predominantly *Pinus* forests were then maintained by more frequent fires than before (Krause and Whitlock, 2013; Iglesias et al., 2015; Krause and Whitlock, 2017).

After ca. 10,000 cal yr BP, many forests that became more open experienced a decrease in stand-replacing fires. Fire activity decreased at Dailey and Fairy lakes when the vegetation transitioned to parkland at ca. 10,000 cal yr BP. However, at Blacktail Pond, Cygnet Lake, Rainbow Lake, and Langohr Wetland, fire activity increased at 10,000 cal yr BP with the increase in summer drought and forest cover (Millspaugh et al., 2004; Rust and Minckley 2018). Fire activity at the forested sites likely increased due to a combination of abundant fuel and

warm, dry conditions. Only open sites at upper and lower treeline had a decline in fire episodes, probably because of lack of fuel connectivity; however, we cannot rule out the possibility that these ecotones experienced low-severity fires not detected in the charcoal record. At Blacktail Pond and Crevice Lake, fires were less frequent after the forest transitioned to *Pseudotsuga-Pinus* parkland at ca. 8000 cal yr BP. This suggests that while vegetation at some of the "summer-wet" sites seems to suggest a wetter early Holocene (forests at Blacktail Pond, Slough Creek Pond, and Crevice Lake), regional fire activity generally corresponds to the availability of woody biomass, increasing with early Holocene warmth, and decreasing with the transition to parkland.

Middle Holocene (ca. 7000-4500 cal yr BP):
Establishment of Mixed Conifer Forest

The mixed-conifer forest surrounding Langohr Wetland became less *Pinus*-dominated at ca. 7000 cal yr BP with the increased presence of *Pseudotsuga* and *Picea,* and changes in lithology and aquatic taxa suggest variations in wetland hydrology. At ca. 7000 cal yr BP, a lithological change from peat to fine-detritus sapropel (lithological unit 2 to 3), followed by a decline in emergent wetland taxa (Cyperaceae and *Typha*) and an increase in aquatic taxa (*Myriophyllum* and green algae *Pediastrum)* from ca. 7000-4500 cal yr BP imply areas of open water in the wetland. *Myriophyllum*, in particular, is a submerged aquatic plant (Lesica, 2012), and the increased abundance of both taxa suggests a deeper wetland and increased effective moisture.

As summer insolation declined into the middle Holocene, the high seasonality of the early Holocene attenuated and the strength of the subtropical high-pressure system weakened, decreasing summer drought (Alder and Hostetler, 2015). Vegetation conditions across the region

responded to these changing climate conditions, although again the timing varied from site to site. Langohr Wetland maintained a mixed-conifer forest, but the increase in aquatic taxa suggests greater effective moisture at ca. 7000 cal yr BP, and Fairy Lake transitioned from *Pseudotsuga* parkland to a mixed-conifer parkland at ca. 5000 cal yr BP. There was an increase in *Pseudotsuga* abundance around Dailey Lake (Benes et al., 2019), and tree density increased on the Beartooth Plateau at ca. 6000 cal yr BP (Alt et al., 2024). Low and middle-elevation sites in other regions of the northern Rocky Mountains also transitioned to closed forests between ca. 6000 and 5500 cal yr BP (Alt et al., 2018; McWethy et al., 2020). Lake levels in sites from the GYE and across the northern Rocky Mountains rose to present levels between ca. 6600-5500 cal yr BP, also indicating wetter conditions than before (Shuman et al., 2009; Shuman and Marsicek, 2016; Shuman and Serravezza, 2017; Dilworth et al., 2024).

Other sites in this study did not experience a vegetation change reflective of cooler wetter conditions at this time. For some of them, it may be attributed to their summer-wet precipitation regime (Whitlock and Bartlein, 1993). After the transition to parkland at ca. 8000 cal yr BP, summer-wet sites Slough Creek Pond, Blacktail Pond, and Crevice Lake experienced conditions that became drier towards the present day (Whitlock and Bartlein, 1993), and forest structure remained open (Huerta et al., 2009, Whitlock et al., 2012). The summer-dry sites that did not record a vegetation change were Cygnet Lake which was surrounded by closed *Pinus contorta* forest due to edaphic controls (Whitlock 1993), and high-elevation Rainbow Lake, which maintained open forest/parkland throughout the entire Holocene, similar to other high-elevation sites in the GYE (Iglesias et al., 2018). Although there was no vegetation shift at these sites, a decrease in fire-episode frequency after ca. 6000 cal yr BP at Rainbow and Cygnet Lakes is

consistent with decreased summer temperatures and increased effective moisture (Alder and Hostetler, 2015).

Fire activity at Langohr Wetland decreased between 7200-6000 cal yr BP, during the same time period with the increase in aquatic taxa and lacustrine-derived sediment. Also, within the lacustrine sediment (lithological unit 3) was an interval of high inorganic silt/clay content (150-138 cm depth), suggesting the introduction of allochthonous material during flood events or periods of rapid snowmelt. These wet events could have contributed to the absence of fire during this time. An increase in CHAR and BCHAR at 6000 cal yr BP after ~1000 years without large fires indicates a return of stand-replacing fires, as well as an increase in fires regionally.

Fairy Lake and Langohr Wetland registered increased fire-episode frequency after 6000 cal yr BP, coincident with forest closure (Fig. 3.5). Higher fire activity may have been a result of greater fuel availability at those sites, but the increase is also noted throughout the GYE (Iglesias et al., 2018), including at summer-dry site Crevice Lake (Whitlock et al., 2012) and coincides with an increase in fire-related sedimentation events at 5500 cal yr BP in northern YNP (Meyer et al., 1995). The overall vegetation changes of the early and middle Holocene generally support the summer-wet and summer-dry hypothesis of the precipitation amplification in the early Holocene (Whitlock and Bartlein, 1993), but the fire histories seem to reflect more site-to-site variations in local vegetation and climate.

Late Holocene (ca. 4500-present day):
Increase in Forest Cover

After ca. 4500 cal yr BP, the present-day dense mixed-conifer forest of *Pinus, Picea,* and *Pseudotsuga* was established at Langohr Wetland, with *Abies* becoming more prevalent in the last 100 years. AP:NAP and PAR reached a maximum, and *Artemisia,* Poaceae, and other shrubs

and herbs declined to their lowest levels of the record. Aquatic taxa also declined, and at ca. 2500 cal yr BP, the lithology shifted from limnic back to sedge-dominated peat (lithological unit 4), suggesting an infilling of the basin and marking the establishment of the modern wetland. A slight increase in *Pinus flexilis/albicaulis* at ca. 1100 cal yr BP occurred at the onset of the Medieval Climate Anomaly (MCA; ca. 1050-650 cal yr BP; Cook et al., 2004). It may be evidence of an upslope shift in the range of low-elevation *Pinus flexilis* during warmer and drier conditions, but this hypothesis bears further investigation.

The late-Holocene climate was characterized by continued cool and wet conditions but superimposed on this trend were warmer and cooler centuries, including during the MCA and the Little Ice Age (LIA; 550-200 cal yr BP; Mann et al., 2009). Forest composition around Langohr Wetland and Fairy Lake changed little during the late Holocene, but forest cover increased after ca. 3000 cal yr BP. At this same time, Crevice Lake registered a transition from open *Juniperus-Pinus* forest to open *Pseudotsuga-Pinus* forest, and pollen data at Blacktail Pond and Slough Creek Pond indicate the establishment of the present-day steppe and forest ecotone. Generally, summer-wet sites maintained an open xerophytic vegetation structure, also reflective of their minimal annual precipitation amounts. No change in vegetation was noted during the MCA or LIA, other than an increase in *Pinus flexilis/albicaulis* at Langohr Wetland during the MCA.

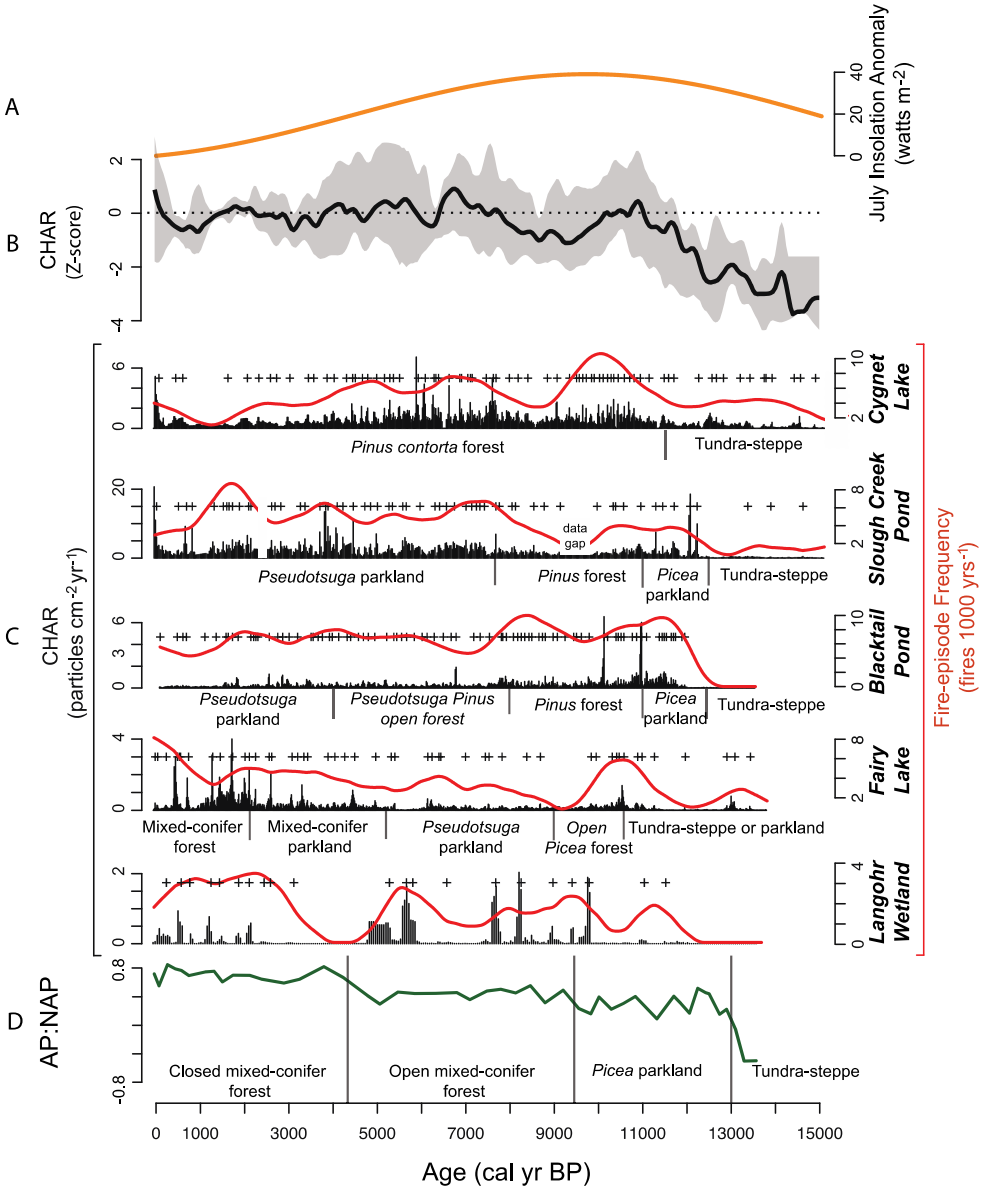


Figure 3.5 Select regional charcoal accumulation (CHAR) records and a CHAR composite from sites in the GYE that extend into the late-glacial period (13,500-15,000 cal yr BP), arranged by their proximity to Langohr Wetland: Fairy Lake (Benes et al., 2019), Blacktail Pond (Millspaugh et al., 2004), Slough Creek Pond (Huerta et al., 2009), and Cygnet Lake (Millspaugh et al., 2000). (A) July insolation anomaly at 45°N (Berger, 1978). (B) Regional fire history based on z-score anomalies of composited CHAR data from the five sites. Gray shading represents 95% confidence interval. (C) CHAR (black bars), fire-episode frequency reconstruction (red lines), and pollen-inferred vegetation for each site. Small black bars denote vegetation changes, and (+) signifies significant fire episodes. (D) The arboreal-to-non-arboreal pollen ratio, which indicates the abundance of forest vs. open vegetation at Langohr Wetland, and the inferred vegetation. Black bars between text denote the timing of vegetation changes.

A decrease in fire activity at Langohr Wetland from ca. 4700 to 3000 cal yr BP occurred during the deposition of silty-clay sediment (120-115 cm depth, unit L3), which could again suggest wetter conditions or a hiatus. Episodes of stand-replacing fires increased in frequency between ca. 2500 cal yr BP and the present day, and the shortest mean return interval of fire episodes was approximately 330 years. This interval is consistent with fire return intervals from dendrochronological studies in subalpine forests in western Montana (Baker, 2009), although it is longer than the 35-200+ year fire return interval reported for the Custer-Gallatin National Forest (Erickson et al., 2022). Charcoal peak magnitudes during this period were lower than earlier in the record, but the long 330-year interval between fire episodes suggests that they were likely stand-replacing events. The most recent significant fire episode in the Langohr Wetland record occurred approximately 330 years ago (ca. 270 cal yr BP), and a general increase in BCHAR in the last century (Fig. 3.4) indicates increased fire activity in the region during Euro-American settlement.

Fire trends diverged across the region during the late Holocene. From 3000 cal yr BP to present day, Fairy Lake and Langohr Wetland had the highest level of fire activity in their records, while other sites had a decrease. The frequency of stand-replacing fire episodes increased for both sites at a time when surrounding forests were becoming denser and woody fuel load was increasing. Although the fire-episode frequency at Fairy Lake was within the expected range for stand-replacing fires in subalpine forests (~6 episodes/1000 yr), that at Langohr (2-3 episodes/1000 years) was longer than the expected range (Baker, 2009).

Charcoal records from Blacktail Pond, Slough Creek Pond, Cygnet Lake, and Rainbow Lake all registered a decrease in fire frequency over the last 3000 years, likely reflecting a

decline in stand-replacing fires (Huerta et al., 2009). At Slough Creek Pond and Blacktail Pond, a decrease in fire frequency was likely due to more surface fires in expanded steppe vegetation. Fire episodes at Cygnet Lake and Rainbow Lake continued to decrease in frequency from the middle Holocene, and over the last ca. 2000 years, the frequency was similar to that of Langohr Wetland (2-3 episodes/1000 yr), within current estimates of stand-replacing fires in subalpine forests (Baker, 2009). Fire activity at Crevice Lake fluctuated throughout the late Holocene, but remained at about 8 episodes/1000 yr, until the last 300 years when large fires became more frequent (Whitlock et al., 2012). Regional CHAR also suggests an increase in fire activity over the last ca. 300 years (Fig. 3.5), mainly influenced by CHAR inputs from the 1988 fires in YNP. Despite increases in regional fire activity over the last ca. 300 years, the Langohr shows little increase in charcoal influx in the most recent decades, suggesting local site conditions may limit fire activity as conditions warm.

At ca. 2000 cal yr BP, a synchronous rise in fire-episode frequency and/or CHAR occurred at many sites regardless of overall trends in fire activity. In the northern GYE, Slough Creek Pond, Crevice Lake, Fairy Lake, Dailey Lake, and Langohr Wetland had increased CHAR and/or fire episode frequency, coincident with increased fire-related debris flows in northern YNP (Meyer et al., 1995). Sites in northwestern Montana also had an increase in fire-episode frequency at this time (Brunelle et al., 2005; Alt et al., 2018; McWethy et al., 2020). The increase in fires occurs at the same time as increased marl production in Blacktail Pond between ca. 2900 and 1300 cal yr BP (Huerta et al., 2009), diatom assemblages at Crevice Lake that suggest shorter springs and drier conditions between ca. 2100 and 850 cal yr BP (Whitlock et al., 2012), and tree-ring evidence of pronounced drought in the Upper Colorado River Basin at ca. 2000 cal

yr BP (Gangopadhyay et al., 2022). This suggests a regional shift in climate to warm, dry conditions.

Indigenous peoples may have contributed to the increase in fire recorded at ca. 2000 cal yr BP as well. Archaeological evidence from Montana and the northern Rocky Mountains suggests an increase in human population in the late Holocene (MacDonald, 2012), and analysis of radiocarbon-dated cultural materials suggests a peak in population at ca. 2000 cal yr BP (Kelly et al., 2013, 2022). The drier conditions would have facilitated fire spread for both human and natural ignitions.

Across the northern GYE region, fire-episode frequencies vary during the MCA and LIA, although there is little evidence for vegetation change associated with changes in fire activity (Fig. 3.5). Slough Creek Pond featured more stand-replacing fires during the MCA at ca. 1000-700 cal yr BP (Millspaugh et al., 2004), and fire-related sedimentation events in northern YNP increased between 1300-750 cal yr BP as well (Meyer et al., 1995). In contrast, charcoal data from Langohr Wetland showed a decrease in fire episodes during the MCA between ca. 1200-800 cal yr BP, which is also noted at Blacktail Pond, Cygnet Lake, and Fairy Lake (Fig. 3.5). However, Slough Creek, Cygnet Lake, and Fairy Lake also saw slightly decreased levels of CHAR during the LIA, when cold conditions may have inhibited fires.

One period of interest in the Langohr fire record is the long ~1500-year period from ca. 4500-3000 cal yr BP with little to no fire activity. Fairy Lake also shows evidence of fewer fires during this time period (Fig. 3.5). Cooler, wetter winter conditions are inferred independently from ^{18}O isotope and ice accumulation records from the Beartooth Plateau (Chellman et al., 2021), an increase in avalanches or landslides at Fairy Lake (Benes et al., 2019), and glacial

readvances in western Canada and the Canadian Rockies (Menounos, 2009). Beyond the GYE, fire activity also decreased in northwestern Montana (Alt et al., 2018; McWethy et al., 2020). It is possible that the more northern and higher elevation locations of Langohr Wetland and Fairy Lakes were more susceptible to the late-Holocene cooling conditions that were seen in northwestern Montana and the Canadian Rockies, whereas more southern and lower elevation sites in the GYE were not.

Conclusions

The pollen and charcoal data from Langohr Wetland document changes in vegetation and fire activity at middle elevations in the northern GYE in response to millennial-scale changes in climate variability over the last 13,500 years. The record highlights the relative stability of vegetation composition and structure across the late-glacial and Holocene despite variability in fire activity. The sequence of vegetation changes starts with the early establishment of tundra-steppe following deglaciation and the development of predominantly *Picea* parkland after 13,000 cal yr BP. Open mixed-conifer forest of *Pinus* with some *Picea* and *Pseudotsuga* was established in the early Holocene at ca. 9300 cal yr BP, when conditions were warmer and drier than today. This period was followed by the establishment of a closed mixed conifer forest of *Pinus, Picea,* and *Pseudotsuga* during the mid-Holocene, when conditions were cooler and wetter than before. The forest became most dense during the late Holocene.

Following the establishment of mixed conifer forest at ca. 9300 cal yr BP, episodes of high-severity fire occurred 1-2 times per millennium, and the frequency increased during the late Holocene when dense mixed conifer forest was present. The mixed conifer forest experienced infrequent stand-replacing fires throughout the entire record (one fire episode every ~600 years

in the early Holocene and every ~350 years in the late Holocene). The Langohr fire return interval is longer than expected for most mixed-conifer forests in the northern Rocky Mountains (Baker, 2009), although the charcoal record likely only recorded stand-replacing fires adjacent to the wetland and not broader fire trends.

The sequence of environmental change that occurred at Langohr Wetland in response to long-term climate trends generally corresponds to other sites in the region, and the Langohr record provides insights into the location of glacial refugia and fire-facilitated vegetation transitions (Krause et al., 2017). The early appearance of *Pinus, Picea,* and *Pseudotsuga* during late-glacial warming suggests lower elevations near Langohr Wetland, such as the Gallatin Valley, served as refugia during the full-glacial period. As the climate warmed, these conifers were able to quickly colonize the foothills and mountains surrounding the valley. Additionally, increased fire activity during the late-glacial period facilitated a transition from *Picea* parkland to an open *Pinus*-dominated forest (mixed-conifer at Langohr), a pattern also observed at Dailey Lake, Blacktail Pond, Slough Creek Pond, and Cygnet Lake.

The Langohr Wetland vegetation history also has notable differences from reconstructions at other sites. Persistent high percentages of conifer pollen from the early Holocene to the present contrasts with other sites, which show more dynamic forest responses through time, particularly from ca. 10,000-6000 cal yr BP. The complacency of the forests near Langohr Wetland suggests that the site was less affected by early-Holocene summer drought conditions than other locations. The Langohr record also indicates a shift towards wet conditions earlier than other sites during the mid-Holocene between ca. 7000 and 4500 cal yr BP, consistent with its generally mesic setting.

Comparisons of a network of paleofire records across the region, while generally varying over smaller temporal scales, show some synchronous trends and times of high fire activity, such as an increase in fires at the start of the early Holocene (ca. 11,000-10,000 cal yr BP), and in the middle Holocene (7000-5000 cal yr BP). They also recorded decreases in fire activity with the transition from forest to open forest/parkland (though at differing times). The variation in the timing of the changes in vegetation and fire activity was likely influenced by atmospheric patterns and the associated spatial heterogeneity in the delivery of moisture, as well as site-to-site differences in local conditions (topography, substrate, elevation, and microclimates). The Langohr record shares most similarities in fire trends with nearby Fairy Lake, including an increase in fire activity as forests became more dense during the middle Holocene (after ca. 6000 cal yr BP), and an increase in fire activity when present-day closed mixed-conifer forest established (after ca. 3000 cal yr BP).

The fire record from Langohr Wetland is unique in that it generally records infrequent fire episodes compared to other sites in the region. The relatively low fire occurrence suggests that the forest surrounding this wetland may have been less impacted by droughts that affected the region more broadly. These mesic settings will likely serve as important fire refugia for fire-sensitive conifers, like *Picea* and *Abies*, as temperatures increasingly warm into the future.

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References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113, 11770–11775. https://doi.org/10.1073/pnas.1607171113

Agee, J.K., 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.

Alder, J.R., Hostetler, S.W., 2015. Global climate simulations at 3000-year intervals for the last 21 000 years with the GENMOM coupled atmosphere–ocean model. Clim. Past 11, 449–471. https://doi.org/10.5194/cp-11-449-2015

Alizadeh, M.R., Abatzoglou, J.T., Adamowski, J., Modaresi Rad, A., AghaKouchak, A., Pausata, F.S.R., Sadegh, M., 2023. Elevation-dependent intensification of fire danger in the western United States. Nat. Commun. 14, 1773. https://doi.org/10.1038/s41467-023-37311-4

Alizadeh, M.R., Abatzoglou, J.T., Luce, C.H., Adamowski, J.F., Farid, A., Sadegh, M., 2021. Warming enabled upslope advance in western US forest fires. Proc. Natl. Acad. Sci. U. S. A. 118, e2009717118. https://doi.org/10.1073/pnas.2009717118

Alt, M., McWethy, D., Everett, R., Whitlock, C., 2018. Millennial scale climate-fire-vegetation interactions in a mid-elevation mixed coniferous forest, Mission Range, northwestern Montana, USA. Quat. Res. 90, 1–17. https://doi.org/10.1017/qua.2018.25

Alt, M., Puseman, K., Lee, C.M., Pederson, G.T., McConnell, J.R., Chellman, N.J., McWethy, D.B., 2024. Organic layers preserved in ice patches: A new record of Holocene environmental change on the Beartooth Plateau, USA. The Holocene 34, 338–352. https://doi.org/10.1177/09596836231211877

Arno, S.F., 1979. Forest Regions of Montana. United States Department of Agriculture, Forest Service Research Paper, INT-218, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Baker, W.L., 2009. *Fire Ecology in Rocky Mountain Landscapes*. Island Press, Washington, DC.

Barrett, S.W., 1993. Fire history of Tenderfoot Creek Experimental Forest, Lewis and Clark National Forest. Final Report INT-92679-RJVA. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory. 23 p.

Barrett, S.W., Arno, S.F., Menakis, J.P., 1997. Fire episodes in the Inland Northwest (1540–1940) based on fire history data. Gen. Tech. Rep. INT–370. Ogden, UT: USDA Forest Service

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quat. Sci. Rev. 17, 549–585. https://doi.org/10.1016/S0277-3791(98)00012-2

Benes, J., Iglesias, V., Whitlock, C., 2019. Postglacial vegetation dynamics at high elevation from Fairy Lake in the northern Greater Yellowstone Ecosystem, Montana, USA. Quat. Res. 92, 1–16. https://doi.org/10.1017/qua.2019.9

Berger, A., 1978. Long-term variations of caloric insolation resulting from the Earth's orbital elements. Quaternary Research 9, 139–167.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. https://doi.org/10.1214/11-BA618

Brunelle, A., Whitlock, C., Bartlein, P., Kipfmueller, K., 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. Quat. Sci. Rev. 24, 2281–2300. https://doi.org/10.1016/j.quascirev.2004.11.010

Chellman, N.J., Pederson, G.T., Lee, C.M., McWethy, D.B., Puseman, K., Stone, J.R., Brown, S.R., McConnell, J.R., 2021. High elevation ice patch documents Holocene climate variability in the northern Rocky Mountains. Quat. Sci. Adv. 3, 100021. https://doi.org/10.1016/j.qsa.2020.100021

Cook, E.R., Woodhouse, C.A., Eakin, M.C., Meko, D.M., Stahle, D.W., 2004. Long-term aridity changes in the western United States. Science 306, 1015–1018.

Davis, M.B., Brubaker, L.B., Webb, T., (1973). Calibration of pollen influx. In: *Quaternary Plant Ecology* (eds: H.J.B. Birks and R.G. West). Blackwell.

Dilworth, J.R., McGlue, M.M., Thigpen, R.J., Brown, S.J., Yeager, K.M., Woolery, E.W., Johnson, S.E., Whitehead, S.J., Cortese, C.J., Matocha, C., 2024. Holocene paleoenvironmental history of Jackson Lake (Grand Teton National Park, USA) deduced from CHIRP seismic reflection and radiocarbon-dated sediment cores. Quat. Sci. Rev. 336, 108748. https://doi.org/10.1016/j.quascirev.2024.108748

Erickson, 2010. Bozeman Municipal Watershed Final Environmental Impact Statement. USDA, Forest Service, Custer Gallatin Forest Service, Bozeman, MT.

Erickson, 2022. Final Environmental Impact Statement. USDA, Forest Service Publication no. R1-22-03a, Custer Gallatin Forest Service, Bozeman, MT

Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analysis 4th ed*. The Blackburn Press, New Jersey.

Fall, P.L., 1994. Modern Pollen Spectra and Vegetation in the Wind River Range, Wyoming, U.S.A. Arct. Alp. Res. 26, 383–392. https://doi.org/10.2307/1551800

Fall, P.L., 1992. Pollen accumulation in a montane region of Colorado, USA: a comparison of moss polsters, atmospheric traps, and natural basins. Rev. Palaeobot. Palynol. 72, 169–197. https://doi.org/10.1016/0034-6667(92)90026-D

Fall, P.L., Davis, P.T., Zielinski, G.A., 1995. Late Quaternary Vegetation and Climate of the Wind River Range, Wyoming. Quat. Res. 43, 393.

Gangopadhyay, S., Woodhouse, C.A., McCabe, G.J., Routson, C.C., Meko, D.M., 2022. Tree Rings Reveal Unmatched 2nd Century Drought in the Colorado River Basin. Geophys. Res. Lett. 49, e2022GL098781. https://doi.org/10.1029/2022GL098781

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35. https://doi.org/10.1016/0098-3004(87)90022-7

Gugger, P.F., Sugita, S., 2010. Glacial populations and postglacial migration of Douglas-fir based on fossil pollen and macrofossil evidence. Quat. Sci. Rev. 29, 2052–2070. https://doi.org/10.1016/j.quascirev.2010.04.022

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol. Monogr. 79, 201–219. https://doi.org/10.1890/07-2019.1

Higuera, P.E., Shuman, B.N., Wolf, K.D., 2021. Rocky Mountain subalpine forests now burning more than any time in recent millennia. Proc. Natl. Acad. Sci. 118, e2103135118. https://doi.org/10.1073/pnas.2103135118

Huerta, M.A., Whitlock, C., Yale, J., 2009. Holocene vegetation–fire–climate linkages in northern Yellowstone National Park, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 271, 170–181. https://doi.org/10.1016/j.palaeo.2008.10.015

Iglesias, V., Krause, T.R., Whitlock, C., 2015. Complex Response of White Pines to Past Environmental Variability Increases Understanding of Future Vulnerability. PLOS ONE 10, e0124439. https://doi.org/10.1371/journal.pone.0124439

Iglesias, V., Whitlock, C., Krause, T.R., Baker, R.G., 2018. Past vegetation dynamics in the Yellowstone region highlight the vulnerability of mountain systems to climate change. J. Biogeogr. 45, 1768–1780. https://doi.org/10.1111/jbi.13364

Kapp, R.O., Davis, O.K., King, J.E., 2000. *Pollen and Spores 2nd ed*. The American Association of Stratigraphic Palynologists, College Station.

Kelly, R.F., Higuera, P.E., Barrett, C.M., Hu, F.S., 2011. Short Paper: A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quat. Res. 75, 11–17. https://doi.org/10.1016/j.yqres.2010.07.011

Kelly, R.L., Mackie, M.E., Robinson, E., Meyer, J., Berry, M., Boulanger, M., Codding, B.F., Freeman, J., Garland, C.J., Gingerich, J., Hard, R., Haug, J., Martindale, A., Meeks, S., Miller, M., Miller, S., Perttula, T., Railey, J.A., Reid, K., Scharlotta, I., Spangler, J., Thomas, D.H., Thompson, V., White, A., 2022. A New Radiocarbon Database for the Lower 48 States. Am. Antiq. 87, 581–590. https://doi.org/10.1017/aaq.2021.157

Kelly, R.L., Surovell, T.A., Shuman, B.N., Smith, G.M., 2013. A continuous climatic impact on Holocene human population in the Rocky Mountains. Proc. Natl. Acad. Sci. 110, 443–447. https://doi.org/10.1073/pnas.1201341110

Krause, T.R., Lu, Y., Whitlock, C., Fritz, S.C., Pierce, K.L., 2015. Patterns of terrestrial and limnologic development in the northern Greater Yellowstone Ecosystem (USA) during the late-glacial/early-Holocene transition. Palaeogeogr. Palaeoclimatol. Palaeoecol. 422, 46–56. https://doi.org/10.1016/j.palaeo.2014.12.018

Krause, T.R., Whitlock, C., 2017. Climatic and non-climatic controls shaping early postglacial conifer history in the northern Greater Yellowstone Ecosystem, USA. J. Quat. Sci. 32, 1022–1036. https://doi.org/10.1002/jqs.2973

Krause, T.R., Whitlock, C., 2013. Climate and vegetation change during the late-glacial/early-Holocene transition inferred from multiple proxy records from Blacktail Pond, Yellowstone National Park, USA. Quat. Res. 79, 391–402. https://doi.org/10.1016/j.yqres.2013.01.005

LANDFIRE, 2014. LANDFIRE Mean Fire Return Interval, 2014 – last update. U.S. Department of Interior, Geological Survey, and U.S. Department of Agriculture.[Online]. Available: https://landfire.gov/viewer/ [2024, March 27].

Lesica, P., 2012. *Manual of Montana Vascular Plants.* Brit Press, Fort Worth, TX.

Licciardi, J.M., Pierce, K.L., 2018. History and dynamics of the Greater Yellowstone Glacial System during the last two glaciations. Quat. Sci. Rev. 200, 1–33. https://doi.org/10.1016/j.quascirev.2018.08.027

Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021. https://doi.org/10.1890/07-1183.1

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G., Ni, F., 2009. Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. Science 326, 1256–1260. https://doi.org/10.1126/science.1177303

Marcus, W. A., Meacham, J. E., Rodman, A. W., Steingisser, A. Y., Menke, J. T., & West, R., 2022. *Atlas of Yellowstone.* Second edition. University of California Press, Oakland, Ca.

Marlon, J., Bartlein, P.J., Whitlock, C., 2006. Fire-fuel-climate linkages in the northwestern USA during the Holocene. The Holocene 16, 1059–1071. https://doi.org/10.1177/0959683606069396

McAndrews, J.H., Berti, A.A., Norris, G., 1973. *Key to the Quaternary Pollen and Spores of the Great Lakes Region*. Life Sciences Miscellaneous Publication, Royal Ontario Museum, Toronto.

McWethy, D., Alt, M., Argiriadis, E., Battistel, D., Everett, R., Pederson, G., 2020. Millennial-Scale Climate and Human Drivers of Environmental Change and Fire Activity in a Dry, Mixed-Conifer Forest of Northwestern Montana. Front. For. Glob. Change 3. https://doi.org/10.3389/ffgc.2020.00044

Meyer, G.A., Wells, S.G., Timothy Jull, A.J., 1995. Fire and alluvial chronology in Yellowstone National Park: Climatic and intrinsic controls on Holocene geomorphic processes. Geol. Soc. Am. Bull. 107, 1211–1230. https://doi.org/10.1130/0016-7606(1995)107<1211:FAACIY>2.3.CO;2

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2004. Postglacial Fire, Vegetation, and Climate History of the Yellowstone- Lamar and Central Plateau Provinces, Yellowstone National Park, in: After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press, pp. 10–28.

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park 4.

MTBS Data Access: Fire Level Geospatial Data, 2021-last revised. MTBS Project. USDA Forest Service/U.S. Geological Survey). Available online: http://mtbs.gov/direct-download [2025, April 24].

Mumma, S.A., Whitlock, C., Pierce, K., 2012. A 28,000year history of vegetation and climate from Lower Red Rock Lake, Centennial Valley, Southwestern Montana, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 326–328, 30–41. https://doi.org/10.1016/j.palaeo.2012.01.036

Naficy, C., Sala, A., Keeling, E.G., Graham, J., Deluca, T.H., 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecol. Appl. 20.

Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., Mountain Research Initiative EDW Working Group, 2015. Elevation-

dependent warming in mountain regions of the world. Nat. Clim. Change 5, 424–430. https://doi.org/10.1038/nclimate2563

Pepin, N.C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., Terzago, S., Thornton, J.M., Vuille, M., Adler, C., 2022. Climate Changes and Their Elevational Patterns in the Mountains of the World. Rev. Geophys. 60, e2020RG000730. https://doi.org/10.1029/2020RG000730

Pierce, K.L., 1979, History and Dynamics of Glaciation in the Northern Yellowstone National Park Area: U.S. Geological Survey Professional Paper 729-F, 91 p.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H.W., Carcaillet, C., Cordova, et al., 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. Clim. Dyn. 30, 887–907. https://doi.org/10.1007/s00382-007-0334-x

PRISM Climate Group, 2014. Oregon State University, https://prism.oregonstate.edu, data created 4 Feb 2014, accessed 16 Dec 2023

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., et al., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). Radiocarbon 62, 725–757. https://doi.org/10.1017/RDC.2020.41

Rust, R.A., Minckley, T.A., 2020. Fire and hydrologically mediated diversity change in subalpine forests through the Holocene. J. Veg. Sci. 31, 380–391. https://doi.org/10.1111/jvs.12853

Schnurrenberger, D., Russell, J., Kelts, K., 2003. Classification of lacustrine sediments based on sedimentary components. J. Paleolimnol. 29, 141–154.

Schoennagel, T., Veblen, T.T., Romme, W.H., 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. BioScience 54, 661–676. https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2

Shuman, B., Henderson, A.K., Colman, S.M., Stone, J.R., Fritz, S.C., Stevens, L.R., Power, M.J., Whitlock, C., 2009. Holocene lake-level trends in the Rocky Mountains, U.S.A. Quat. Sci. Rev. 28, 1861–1879. https://doi.org/10.1016/j.quascirev.2009.03.003

Shuman, B.N., Marsicek, J., 2016. The structure of Holocene climate change in mid-latitude North America. Quat. Sci. Rev. 141, 38–51. https://doi.org/10.1016/j.quascirev.2016.03.009

Shuman, B.N., Serravezza, M., 2017. Patterns of hydroclimatic change in the Rocky Mountains and surrounding regions since the last glacial maximum. Quat. Sci. Rev. 173, 58–77. https://doi.org/10.1016/j.quascirev.2017.08.012

Weber, M., 1965. General geology and geomorphology of the Middle Creek area, Gallatin County. Thesis, Montana State College, MT.

Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150178. https://doi.org/10.1098/rstb.2015.0178

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834

Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H., Ryan, M.G., 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proc. Natl. Acad. Sci. 108, 13165–13170. https://doi.org/10.1073/pnas.1110199108

Whitlock, C., 1993. Postglacial Vegetation and Climate of Grand Teton and Southern Yellowstone National Parks. Ecol. Monogr. 63, 173–198. https://doi.org/10.2307/2937179

Whitlock, C., Bartlein, P.J., 1993. Spatial Variations of Holocene Climatic Change in the Yellowstone Region. Quat. Res. 39, 231–238. https://doi.org/10.1006/qres.1993.1026

Whitlock, C., Bartlein, P.J., Van Norman, K.J., 1995. Stability of Holocene Climate Regimes in the Yellowstone Region. Quat. Res. 43, 433–436. https://doi.org/10.1006/qres.1995.1049

Whitlock, C., Dean, W.E., Fritz, S.C., Stevens, L.R., Stone, J.R., Power, M.J., Rosenbaum, J.R., Pierce, K.L., Bracht-Flyr, B.B., 2012. Holocene seasonal variability inferred from multiple proxy records from Crevice Lake, Yellowstone National Park, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 331–332, 90–103. https://doi.org/10.1016/j.palaeo.2012.03.001

Whitlock, C., Larsen, C., 2001. Charcoal as a Fire Proxy, in: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, Developments in Paleoenvironmental Research. Springer Netherlands, Dordrecht, pp. 75–97. https://doi.org/10.1007/0-306-47668-1_5

CHAPTER FOUR

MULTI-SCALE DRIVERS OF HOLOCENE FOREST DYNAMICS AND FIRE ACTIVITY ACROSS AN ELEVATIONAL GRADIENT IN THE U.S. NORTHERN ROCKY MOUNTAINS

Contribution of Authors and Co-Authors

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Contributions: Analyzed pollen and charcoal for Wymore Lake.

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Manuscript Information

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Abstract

Projected warming summers, decreasing mountain snowpack, and longer fire seasons in the northern Rocky Mountains underscore the necessity for long-term vegetation and fire reconstructions across various forest types. Pollen and charcoal records from a network of sites surrounding the Mission Valley, MT, are presented here to explore the long-term relationship between climate, vegetation, and fire over time. The sites span an elevational gradient from low-elevation xeric and mesic montane Douglas-fir and pine forests to high-elevation subalpine spruce and fir forests. Postglacial open parkland dominated much of the landscape prior to ca. 13,500 cal yr BP, when sparse vegetation and cold, dry conditions limited fire occurrence. After ca. 13,500 cal yr BP, warming temperatures facilitated forest expansion and densification, primarily of spruce and fir at higher elevations and pine at middle and low elevations. Forest fire activity subsequently increased with forest closure and the increase in woody biofuel. Lower treeline moved upslope during the warm, dry conditions of the early Holocene (ca. 10,500-6000 cal yr BP) and open Douglas-fir parkland covered lower elevations. During this period, low-intensity surface fires became more frequent. Denser forests were reestablished and fire activity increased after ca. 6000 cal yr BP as conditions became cooler and wetter. Fire activity was highest at all elevations between ca. 2500 and 2000 cal yr BP. This prolonged period of increased fire activity during the generally cool and wet late Holocene suggests years or decades of warm, dry summers and perhaps increased burning by Indigenous communities. This synchronous rise in fire activity across elevations indicates that all northern Rocky Mountain forest types are susceptible to elevated fire activity in a warming climate.

Introduction

In recent decades, the United States (U.S.) northern Rocky Mountains (NRM) have experienced the effects of climate, including rising temperatures, a reduction of snowpack, and altered disturbance regimes, threatening the loss of ecosystem services (Hostetler et al., 2021). In general, snowpack in the Rocky Mountains contributes 70% of spring and summer runoff (Li et al., 2017), but over recent decades, increasingly warm spring conditions have led to earlier runoff, reduced summer baseflows, and decreased summer soil moisture (Mote et al., 2018; Pederson et al., 2013). Earlier spring runoff and decreased summer soil moisture have been linked to increases in fire activity (Heyerdahl et al., 2008), which is projected to increase into the future in response to longer fire seasons (Westerling et al., 2011). The NRM region has warmed faster than the global average, with greatest rates of warming expected at higher elevations (Pederson et al., 2010). The median elevation of wildfire activity has also shifted upslope (Alizadeh et al., 2021) and high-elevation forest fires contribute to even earlier snowmelt in burned areas (Reis et al., 2024) and threaten postfire regeneration for trees that need adequate soil moisture (Davis et al., 2019).

Examining long-term fire-climate linkages is important for anticipating how changing climate may alter the vegetation structure and fire activity across different forest types and elevations in the NRM. Mountain ranges alter large-scale atmospheric circulation patterns by creating rain shadows and wind channels, and topography-influenced temperature and moisture differences (i.e., from aspect and elevation) create a mosaic of microclimates and forest types (Barnard et al., 2017; Dobrowski, 2011). Therefore, multiple-site networks are important to discern local influences and separate them from broader patterns. Previous paleoecological

studies suggest that the NRM is home to forests that reflect long-term fluctuations in vegetation structure and fire activity from the late-glacial period to the present (Alt et al., 2018, 2018; Brunelle et al., 2005; Mack et al., 1983, 1978; Mehringer et al., 1977; Power et al., 2011). Comparisons of mid-elevation (Alt et al. 2018) and high-elevation pollen and charcoal records (Brunelle et al., 2005), and regional comparisons of records across elevation gradients (Carter et al., 2018; Power et al., 2011) in the NRM have been undertaken in previous studies.

Here, we build upon these studies by describing new records from five low-elevation and four high-elevation sites in and around the Mission Valley of northwestern Montana (Fig. 4.1). Our objective is to expand understanding of Holocene climate-vegetation-fire interactions along an elevational gradient, and in particular, the synchronicity of past fires and vegetation change across the region. Information on past climatic conditions comes from published paleoclimate model simulations, while vegetation composition and structure are inferred from pollen data, and fire activity is reconstructed from particulate charcoal.

Site description

Eight sites are located surrounding the Mission Valley in Northwestern Montana, and the ninth site is directly east, at the ecotone of the Rocky Mountain Front and the northern Great Plains (Fig. 4.1). The Mission Valley (elevation of approximately 880-1000 masl) is bordered by the Mission Range to the east, the Salish and Cabinet Mountains to the west, and the Reservation Divide to the southwest. The highest point of all surrounding mountain ranges is McDonald Peak in the Mission Range at 2990 masl. During the last glaciation (23,000-16,000 cal yr BP), the region was inundated by ice and water. The Flathead lobe of the Cordilleran ice sheet terminated at the Polson moraine just north of the Mission Valley, alpine glaciers covered the mountain

ranges, and Glacial Lake Missoula formed between the Polson moraine and Missoula, MT until ca. 14,500 cal yr BP (Smith, 2017). The timing of glacial retreat in the Flathead Valley is not well-constrained. However, radiocarbon-dated sediments from lakes in the region suggest the area was ice-free, and Glacial Lake Missoula drained by ca. 14,000 cal yr BP (Carrara, 1995; Hofmann and Hendrix, 2010).

The present-day climate of the region is predominantly continental, with dry summers and cold winters influenced by air masses from the Pacific Ocean and the continental polar region. Precipitation originates from Pacific storm systems in the winter, and local convective storms in the spring and summer. The 30-year climate average indicates precipitation amounts vary from ~350 mm per year at the Mission Valley floor to ~1500 mm per year at the highest elevations (1991-2020, PRISM, 2024). The valley floor receives more precipitation during spring and summer months, and the upper elevations receive the majority of precipitation as snow in the winter. Mean annual temperatures vary from an average of 7.5°C in the valley floors to 2.2°C at the highest elevations (PRISM, 2024).

Situated at the intersection of the Pacific Northwest maritime climate and the continental polar climate, the region hosts a diversity of conifer species, including species not found in the interior Rocky Mountains (e.g., western redcedar *(Thuja plicata),* western hemlock *(Tsuga heterophylla),* white pine (*Pinus monticola*)*,* grand fir (*Abies grandis)*, western larch *(Larix occidentalis*)*,* and alpine larch (*Larix lyallii*); Pfister et al. 1977). Additionally, conifers from the interior Rocky Mountains are present (e.g., lodgepole pine (*Pinus contorta),* ponderosa pine (*Pinus ponderosa),* limber pine *(Pinus flexilis),* whitebark pine (*Pinus albicaulis*)*,* Douglas-fir *(Pseudotsuga menziesii),* Engelmann spruce *(Picea engelmannii*)*,* subalpine fir (*Abies*

lasiocarpa), and Rocky Mountain juniper (*Juniperus scopulorum).* Forests of ponderosa pine and Douglas-fir surround the valley floors and lower mountain slopes (1,060-1,500 masl)*,* with lodgepole pine, western larch, Engelmann spruce, western redcedar, grand fir, and white pine in more mesic environments. At higher elevations (1,500- 2,400 masl), subalpine forests of subalpine fir, grand fir, Engelmann spruce, and whitebark pine are found. Subalpine parklands featuring whitebark pine and alpine larch grow at upper treeline (2,400-2,700 masl). Alpine tundra is present at the highest mountain elevations (above 2,700 masl; Pfister et al., 1977).

Located below lower treeline, Pine Butte Fen is a ~450 ha peatland fen approximately 9km east of the Rocky Mountains. The fen has areas of open fen, dwarf-carr, carr (wooded terrain), and aspen groves (Lesica, 1986). It consists of graminoids (e.g., grasses (Poaceae spp.), sedges (*Carex* spp.), and rushes (*Juncus* spp.)), forbs (e.g., northern bedstraw (*Galium boreale)* and asters (e.g., *Aster junciformis*), and small shrubs (e.g., species of birch (*Betula spp. (e.g. B. glandulosa* and *B. nana)),* willow *(Salix spp. (*e.g. *S. candida* and *S. monticola),* and cinquefoil *(Potentilla fruticosa*; Lesica, 1986). Upland vegetation is predominantly open limber pine parkland.

Low-elevation Wymore, Black, Rainbow, and Twin lakes are situated in the foothills of the Mission Valley, surrounded by closed Douglas-fir and ponderosa pine forest, with smaller amounts of lodgepole pine and western larch. Twin Lakes also features Engelmann spruce, grand fir, and western redcedar along its margins and in wet settings. High-elevation Moss Peak, Starvation, and Mud lakes are located in the Mission Range, and the highest-elevation site, Three Lakes Peak Lake, is located in the Reservation Divide mountains. Moss Peak and Mud lakes are surrounded by mixed conifer forest and subalpine forest taxa, including Douglas-fir, western

larch, lodgepole pine, subalpine fir, and Engelmann spruce, whereas forests at Starvation and Three Lakes Peak lakes include subalpine fir and Engelmann spruce.

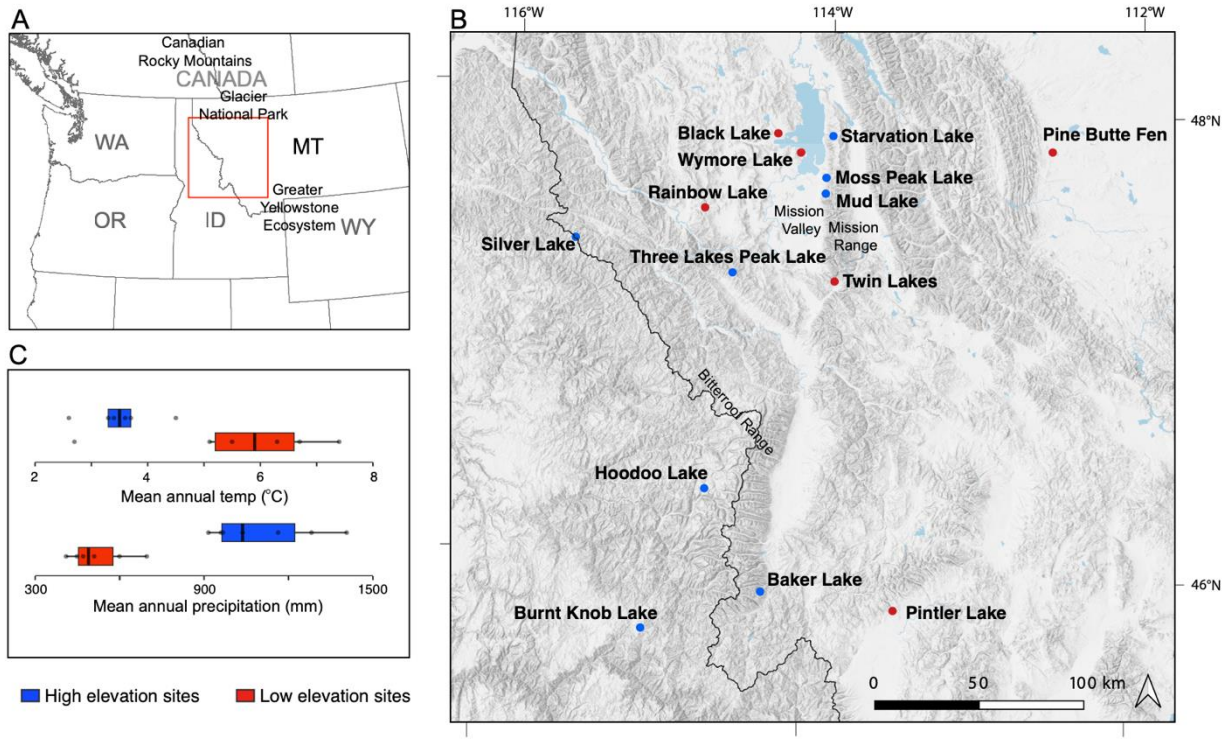


Figure 4.1. (A) Northwest United States and southwest Canada with locations mentioned in the text and a box around the study region. (B) Location of the study sites and areas mentioned in text. (C) 30-year (1991-2020) average temperature and precipitation data from 4 km grid cells focused around each site location.

Methods

Field

The eight lakes and one wetland were cored between 2012 and 2020. The deepest area of each lake was identified with a depth finder, and a modified Livingstone corer was used to retrieve lake sediments in one-meter increments until the corer could not penetrate any farther.

The deepest part of Pine Butte Fen was identified using maps of the wetland basin (Nimick, 1983) and a soil probe, and a Russian peat coring device was used to extract sediment in 50 cm increments until an impenetrable surface was reached. All cores were wrapped in plastic wrap and aluminum foil in the field and stored in the cold room at Montana State University until analysis.

Chronology and Lithology

Cores were split lengthwise, and sediments were analyzed for lithological changes. Sediments were described and inspected for macrofossils, and macrofossils (when found) and bulk sediment samples were sent to the National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) facility for Accelerator Mass Spectrometry (AMS) radiocarbon dating. Radiocarbon dates were converted to calendar years using IntCal 2020, and age-depth models were created using BACON modeling software with the *rbacon* package (Blaauw and Christen, 2011) with R software (R Core Team, 2024).

Charcoal Analysis

Entire cores were subsampled at 0.5 or 1-cm contiguous intervals for charcoal analysis. Samples of 2-5cm^3 were taken from each interval for charcoal processing following standard procedures (Whitlock and Larsen, 2001). Samples were soaked in a mixture of bleach and sodium hexametaphosphate for 24 hours to deflocculate the sediment and sieved through 125-micron sieves since charcoal particles greater than 125 microns provide a record of local fires occurring within a few kilometers of the study site (Higuera et al., 2011). Charcoal particles were counted under a stereomicroscope and identified as woody or grass wherever possible.

A fire history for each site was created in CharAnalysis (Higuera, 2009). Charcoal counts were converted to charcoal accumulation rates (CHAR; particles $cm^{-2}yr^{-1}$), and time series were interpolated to equal time steps to minimize differences in charcoal accumulation due to changes in deposition rate. A 600-yr lowess smoother was applied to distinguish long-term background trends (bCHAR) and a peaks component. A Poisson-minimum counts test identified peaks that exceeded a 95% threshold as fire episodes (one or more fires in the time span of the peak). The time between fire episodes was calculated to determine the fire-episode return interval (FRI), and the number of fire episodes was smoothed with a 1000-year window to estimate the fire-episode frequency per 1000 years.

Pollen Analysis

Pollen analysis provided a reconstruction of the vegetation history near each site. Samples of 0.5-1 cm^3 volume were taken at approximate 100 to 200-year intervals for pollen processing. Standard pollen processing procedures outlined by Bennett and Willis (2001) were followed, and a *Lycopodium* tracer of known concentration was added to each sample to calculate pollen concentrations (grains cm^{-3}) and pollen accumulation rates (PAR; grains $cm^{-2}yr^{-1}$). Pollen was counted at 400x magnification to a minimum of 300 grains per slide, and grains were identified using published keys (McAndrews et al., 1973; Faegri and Iversen, 1975; Kapp et al., 2000) and reference material housed at Montana State University. Terrestrial pollen counts were converted to percentages based on the terrestrial pollen sum, and aquatic pollen percentages were based on the sum of aquatic and terrestrial grains. *Carex* spp. is a common wetland species at many of the lake sites, therefore Cyperaceae was considered aquatic taxa and not included in the terrestrial sum.

The Mission Range is home to several conifer species, and many pollen types were ascribed to more than one species. *Pinus* subg. *Strobus* pollen was attributed to *P. flexilis, P. albicaulis,* and/or *P. monticola,* and *Pinus* subg. *Pinus* pollen to *P. contorta* and/or *P. ponderosa*. Damaged *Pinus* grains that were missing distal membranes were classified as *Pinus* undifferentiated. *Abies* grains were attributed to *A. lasiocarpa* and/or *A. grandis,* and Cupressaceae pollen was attributed to *Juniper communis, J. scopulorum, J. horizontalis,* and/or *Thuja plicata*. *Pseudotsuga menziesii* pollen is indistinguishable from *Larix spp.* pollen, and therefore attributed to *Pseudotsuga menziesii, L. occidentalis,* and/or *L. lyallii.* However, in the regional vegetation descriptions, we refer to the more dominant species *(Pseudotsuga menziesii)* while recognizing *Larix* is also be represented. Non-arboreal pollen amounts are higher in non-forested landscapes and increase with distance from forest boundaries (Fall, 1994; Iglesias et al., 2018; Whitlock, 1993); thus, the AP:NAP ratio was used as an indicator of forest cover. Arboreal pollen (AP) is the sum of all tree and shrub species, excluding *Artemisia,* since *Artemisia* is found primarily in steppe and open meadows, and non-arboreal pollen (NAP) is the sum of *Artemisia,* herbs, and grasses. The AP:NAP ratio was calculated by [(AP-NAP)/(AP+NAP)] for all sites.

Regional Analysis

The sites in this study were designated as high or low elevations based on their elevation and forest type. Sites below 1500 masl located in grasslands, xeric, or mesic montane forest were classified as low elevation, and sites above 1500 m asl in mesic mixed-conifer or subalpine forest were classified as high elevation. The age of the three low-elevation records extended into the early Holocene and late glacial periods (up to 14,000 cal yr BP), but none of the high-elevation

records were older than 5500 cal yr BP. Therefore, additional published charcoal and pollen records from lake sites in the nearby Bitterroot, Clearwater, and Anaconda Ranges were accessed from the Global Paleofire Database, Neotoma Explorer, and the Dryad Digital Repository and included in the study (Table 4.1).

Two of the additional high-elevation sites (Baker and Burnt Knob Lakes) are surrounded by a subalpine mixed conifer forest of subalpine fir, Engelmann spruce, lodgepole pine, and whitebark pine (Brunelle et al., 2005), and the other (Silver Lake) lies within a subalpine forest of subalpine fir and Engelmann spruce (Clark-Wolf et al., 2023). One site (Pintler Lake) lies within a forest of lodgepole pine, Douglas-fir, and Engelmann spruce, and although situated above 1500 masl, is classified as a low-elevation site due to its primarily montane vegetation and proximity to the lower treeline.

To create a regional fire history, charcoal records for high and low elevations were compiled, interpolated to equal time steps, min-max, and box-cox transformed to standardize for site-to-site differences in charcoal abundance (Power et al., 2008). For the regional pollen history, all pollen data was compiled, and key taxa and pollen ratios were plotted with a loess smoother in r package *ggplot2* using a span =.3 (span is the fraction of points used to fit each local regression). Additionally, the squared-chord distance (SCD) between each sample and the youngest sample of the record was calculated to assess changes in pollen assemblages through time (Gavin et al., 2003), and a loess smoother was applied to the time series to visualize the trends in vegetation changes. A regime shift index (RSI) algorithm (Rodionov, 2004) was applied to the charcoal z-score composite and SCD time series to indicate shifts in the fire regime and vegetation assemblage over time.

Table 4.1 Site data for the records utilized in this study. (*) indicates a location surrounding the Mission Valley, and elevations in bold denote low-elevation sites.

Site	Elevation (m)	Lat long	Precip. (mm)	Annual temp	Vegetation	Record age (cal yr BP)	Reference
Baker Lake	2300	45.891944, -114.26194	916	3.7	Subalpine	14300	Brunelle et al., 2005
Burnt Knob Lake	2250	45.704444, -114.98667	1038	2.6	Subalpine	15000	Brunelle et al., 2005
Three Lakes Peak Lake*	2072	47.254727, -114.55861	975	3.4	Subalpine	4800	Sly, 2020; this study
Pintler Lake	**1921**	45.840556, -113.44028	600	2.7	Dry mixed conifer	14700	Brunelle et al., 2005
Hoodoo Lake	1770	46.320556, -114.650267	1282	3.3	Subalpine	12000	Brunelle et al., 2005
Mud Lake*	1765	47.616691, -113.99786	1160	3.7	Mesic mixed conifer	5500	Sly, 2020; this study
Starvation Lake*	1710	47.865251, -113.97042	1400	3.6	Mesic mixed conifer	1000	This study
Silver Lake	1623	47.35916, -115.56685	1300	3.3	Subalpine	4800	Parish et al., 2022
Moss Peak Lake*	1500	47.684638, -113.99952	960	4.5	Mesic mixed conifer	1500	This study
Pine Butte Fen	**1390**	47.840256, -112.56413	470	5.1	Grassland	7000	This study
Twin Lakes*	**1236**	47.241491, -113.91093	695	5.5	Dry mixed conifer	15000	Alt et al, 2018
Rainbow Lake*	**1093**	47.525469, -114.76135	510	6.3	Dry mixed conifer	9800	Lapierre 2021; his study
Black Lake*	**985**	47.863622, -114.32341	450	6.7	Dry mixed conifer	7300	McWethy et al., 2020
Wymore Lake*	**884**	47.786741, -114.17115	410	7.4	Dry mixed conifer	14000	Lapierre 2021; This study

Results

Chronology and Lithology

Detailed pollen results for the Mission Valley sites are described in Appendix S1. Here, we present the main results for all sites used in the study.

All elevations recorded moderate levels of *Artemisia,* Poaceae, and herbs, and high elevations additionally had moderate levels of *Picea*, while low elevations had moderate levels of *Pinus* subg. *Strobus, Picea,* and Cupressaceae prior to ca. 13,900 and 13,500 cal yr BP,

respectively (Fig.4. 2, Fig. SM4.2). This suggests the presence of spruce parkland at high elevations in the Bitterroot Range, and juniper, whitepark pine, and spruce parkland at lower elevations in the Mission Range. High elevations recorded an increase in *Picea, Pinus* subg. *Strobus,* and *Abies* after ca. 13,900*,* indicating the development of subalpine forests in the Bitterroot Range at that time. An increase in *Pinus.* subg. *Pinus* at low elevations after ca. 13,500 cal yr BP, along with elevated percentages of *Pinus* subg. *Strobus* resulted in an increase in AP:NAP suggests the presence of dense pine forest between ca. 13,500 and 10,500 cal yr BP (Fig. 4.2).

From 10,500-5500 cal yr BP, upper elevation sites featured moderate pollen percentages of *Artemisia,* Poaceae, and *Alnus*, slight increases in *Pseudotsuga*-type pollen, and a slight decrease in AP:NAP (Fig. 4.2). The pollen percentages from low-elevation sites changed dramatically during this time period, when percentages of *Pinus* pollen decreased and those of *Pseudotsuga*-type*, Artemisia,* and Poaceae pollen increased. Low-elevation sites also registered an increase in pollen from riparian shrubs (e.g., *Alnus*) and a variety of herbs (Figs. 4.2, SM4.2). The pollen data indicate slightly more open montane and subalpine forests at upper elevations and open Douglas-fir parkland at low elevations.

AP:NAP began to gradually increase at low elevations at ca. 7500 cal yr BP, correlating with a decrease in *Artemisia* and increases in *Pinus* (Figs. 4.2, SM4.2). Both low and high-elevation sites experienced increases in AP:NAP between ca. 6000 and 4200 cal yr BP as *Artemisia* percentages declined, and those of *Pinus, Picea,* and *Abies* increased (Figs. 4.2, SM4.2, SM4.3). Although the exact timings varied between 7500 and 5000 cal yr BP, subalpine spruce, fir, and pine forests established at high elevations, and montane forests composed of

predominantly pine and Douglas-fir, with spruce and fir established at low elevations (Figs. SM4.2, SM4.3). *Pseudotsuga*-type pollen decreased at all elevations between 5500 and 4000 cal yr BP, while that of *Picea* and *Abies* increased. Pollen percentages of *Picea* and *Abies* reached their highest values between ca. 4000 and 2000 cal yr BP. *Alnus* (alder) pollen was abundant at upper elevation sites with notable increases between ca. 4800 and 3800 cal yr BP and between ca. 2500 and 1900 cal yr BP. *Pseudotsuga*-type pollen increased significantly at upper elevations between ca. 1300 and 800 cal yr BP, although the pollen data at high elevations suggest that *Pinus, Picea,* and *Abies* remained the dominant conifer species, reflecting the composition of today's subalpine forests (Figs. 4.2, SM4.3). *Pseudotsuga*-type percentages gradually increased at lower elevations from 3000 cal yr BP, and paired with high values of *Pinus* pollen*,* mark the formation of present-day montane forest of Douglas-fir, ponderosa, and lodgepole pine over the last 3000 years (Figs. 4.2, SM4.2).

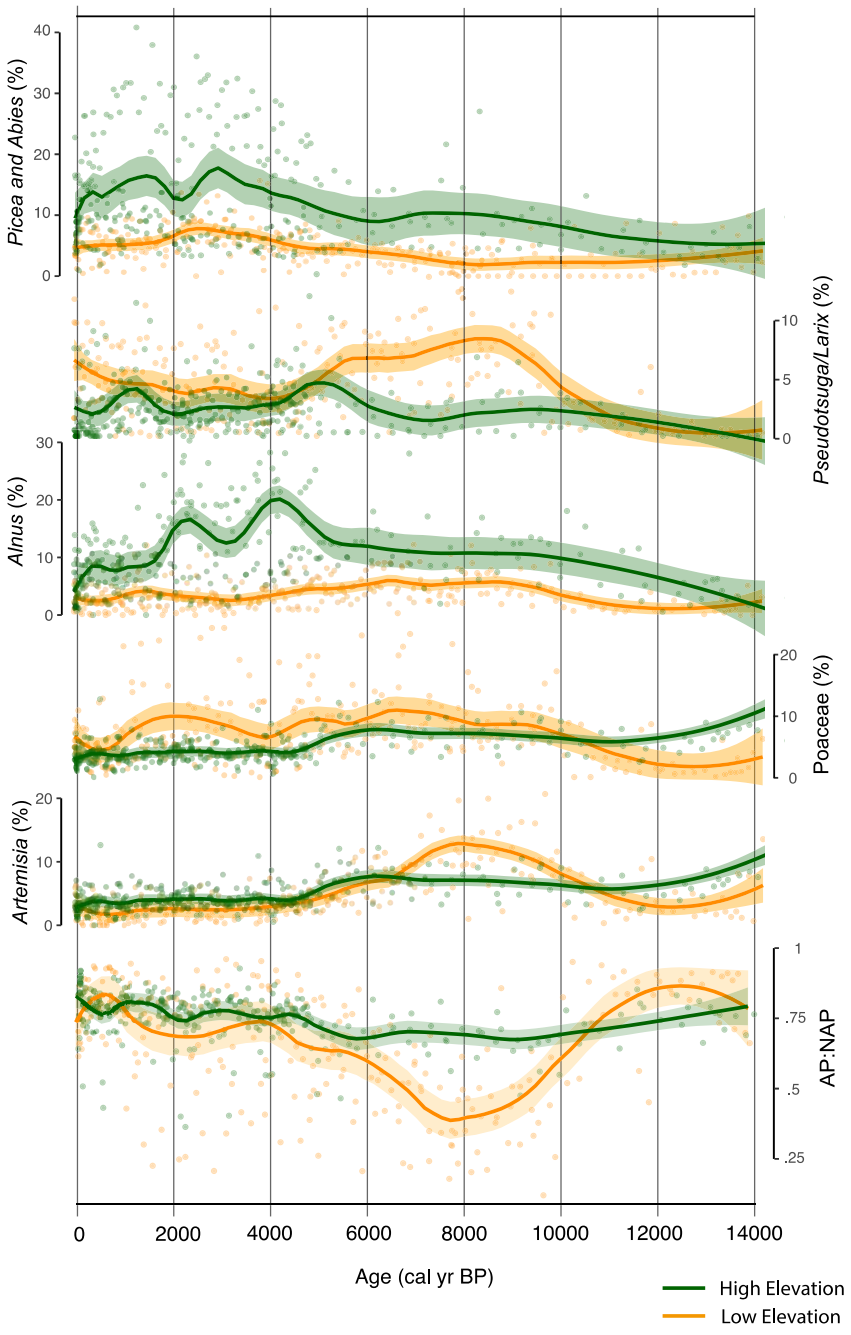


Figure 4.2. Select pollen percentages from all regional sites, separated by elevation. The data is fitted with a loess smoother with a 30% smoothing span, and shading represents the 95% confidence interval.

Fire History

Detailed charcoal results for the Mission Valley sites are described in Appendix S1. Here, we present the main results for all sites used in the study.

Fire activity and regime shift index (RSI) values were the lowest during the late-glacial period from 14,000 to 13,500 cal yr BP (Fig.4.3). Fire activity increased across high and low elevations at ca. 13,500 cal yr BP, although only high-elevation charcoal influx z-scores increased to a positive anomaly at ca. 12,000 cal yr BP. However, this is based on two charcoal records (Burnt Knob and Baker lakes), which have very low amounts of CHAR (increases to 0.4 and 0.25 particles $cm^{-2}yr^{-2}$; Brunelle et al., 2005). Fire activity and RSI values remained low with negative charcoal influx anomalies until ca. 8000 cal yr BP for high elevations and 6000 cal yr BP for low elevations, when charcoal influx z-scores increased to positive charcoal anomalies. High-elevation charcoal influx decreased but remained elevated until ca. 3000 cal yr BP, whereas low-elevation charcoal influx remained anomalously low until ca 3000 cal yr BP. Charcoal influx and RSI values from high- and low-elevation sites became synchronized at ca. 3000 cal yr BP, increasing to the highest levels of the record from 2500 to 1500 cal yr BP, before decreasing to the present day.

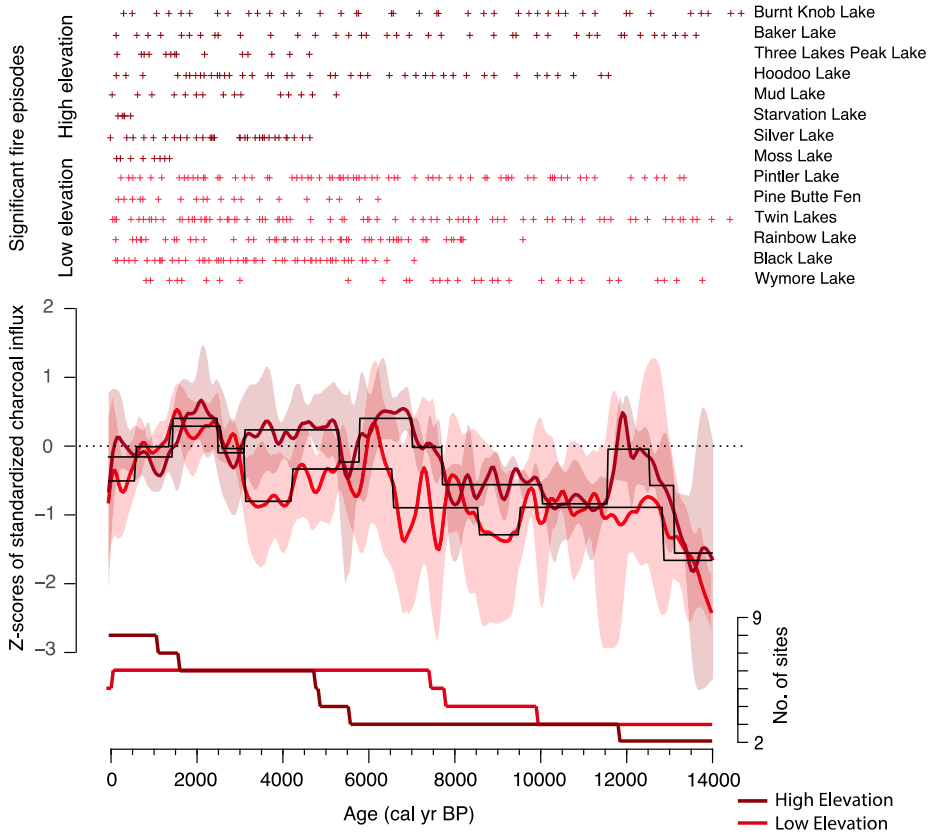


Figure 4.3. Composite charcoal data for all regional sites. Significant fire events denoted by (+) signs, arranged by elevation within each elevational group. Z-scores of standardized charcoal influx, the shading indicates the 95% confidence interval and black lines indicate regime shifts (Rodionov, 2004).

Discussion

The vegetation and fire records from western Montana show periods of uniform vegetation change alongside both synchronous and asynchronous fire activity. These patterns likely reflect variations in effective moisture and differences in fuel type and abundance across elevations. Fire activity, as inferred from overall CHAR levels, peaked across all elevations during the cooler and wetter late Holocene. Here, we present regional trends in fire and

vegetation history, comparing both elevational variations and site-specific differences. We also compare our findings with other vegetation and climate proxy records and paleoclimate models to enhance our understanding of the prevailing climate conditions of that period.

Late-glacial Period (>14,000-11,000 cal yr BP)

Following the retreat of the Cordilleran Ice Sheet and alpine glaciers at the end of the Pleistocene, tundra and parkland vegetation were established across the region, reflective of cold, dry postglacial conditions (Bartlein et al., 1998). Sagebrush and grasses dominated the low-lying vegetation, while spruce was present at high elevations (Brunelle et al., 2005), and juniper and whitebark pine grew at low elevations. High-elevation sites in the Bitterroot Range transitioned from spruce parkland to subalpine forests of spruce, whitebark pine, and fir at ca. 13,900 cal yr BP, while low-elevation forests in the Mission Range transitioned to forests of whitebark pine and lodgepole and/or ponderosa pine at ca. 13,500 cal yr BP. Forest closure was likely a response to warming temperatures, increasing summer insolation (Berger, 1978), and the northward shift of the jet stream after ca. 14,000 cal yr BP, which brought increased moisture to the region (Alder and Hostetler, 2015; Bartlein et al., 1998). The earlier forest transition in the Bitterroot Range may be due to the Mission Range's more northerly location near the Cordilleran Ice Sheet.

Fire activity (CHAR) was minimal during the late-glacial period, reflecting cold, dry conditions and limited fuel (low-lying steppe). Fire activity and episode frequency increased at all elevations with the transition to a more forested landscape, indicating warmer conditions than before after ca. 13,500 cal yr BP. Fire activity was higher in the upper-elevation spruce and fir forest compared to the low-elevation pine forests, likely reflecting the prevalence of less-fire-

adapted subalpine forests at high elevations. Although there was an increase at all elevations, fire activity remained low, likely due to still cooler conditions than today (Alder and Hostetler, 2015).

Early Holocene (11,000-8000 cal yr BP)

Low-elevation vegetation underwent significant changes during the early Holocene. *Pseudotsuga*-type pollen levels increased at low elevations by ca. 10,000 cal yr BP and were accompanied by rises in *Artemisia* and Poaceae, suggesting that low-elevation forests transitioned from closed pine forests to open Douglas-fir parkland and steppe. The SCD between present-day and past pollen assemblages indicates that the vegetation was most different from today between 11,000 and 10,000 cal yr BP, attributed to the open xeric vegetation structure (Fig. 4.4). Additional low-elevation records from sites just north of the Flathead Valley (Kintla Bog, Johns Lake, and Foy Lake) also register xeric conditions with grasslands and Douglas-fir parkland after ca. 11,000 cal yr BP (Power et al., 2011).

Slightly higher elevation Pintler Lake shifted to a pine and Douglas-fir forest, and other high-elevation sites in the Bitterroot Range had small increases in *Pseudotsuga*-type pollen, indicating that Douglas-fir expanded upslope as low-elevation sites opened up. All high-elevation sites remained forested throughout the early Holocene, as indicated by high percentages of *Pinus, Picea,* and *Abies* pollen (Brunelle et al., 2005). However, increases in shrubs, such as *Alnus* and *Artemisia,* along with decreases in the AP:NAP ratio, suggest slightly more open forests than before.

The regional vegetation indicates that the early Holocene was the warmest and driest period of the last 14,000 years, a response to the direct and indirect effects of increased summer-

insolation levels on regional climate (Berger, 1978, Bartlein et al., 1998). The increased summer insolation levels resulted in warm summer conditions and strengthened the subtropical high-pressure system, suppressing summer precipitation in the region (Bartlein et al., 1998). This is supported by evidence of minimum glacier extents in the western U.S. and Canada (Jones et al., 2023; Menounos et al., 2009; Solomina et al., 2015), as well as minimum lake depths (Shuman et al., 2009; Shuman and Serravezza, 2017). The forests at low elevations responded to the lack of moisture by shifting from closed pine forests to more drought-tolerant Douglas-fir parkland as the lower-elevation treeline moved upslope. Higher-elevation forests were less affected by the warm, dry conditions and remained forested, but became more open during this period.

Fire activity remained anomalously low at all elevations for most of the early Holocene. Low-elevation sites experienced less stand-replacing fire than high-elevation sites, reflecting the widespread Douglas-fir parkland. The open landscape minimized fuel connectivity, and the fires that occurred were likely low-severity grass fires that did not produce abundant charcoal and were not recorded in the sediment record. Douglas-fir can persist without fire, and while fire resistant, it is more fire-sensitive than other low-elevation trees in the region (such as Ponderosa pine), suggesting that mainly low-severity fires were occurring (Hanberry et al., 2020). Foy Lake, located to the north in the Flathead Valley, also had low levels of charcoal influx, yet showed an increase in grass charcoal during this time period, providing further evidence of surface fires (Power et al., 2011).

Unlike low-elevation sites that lacked fuel connectivity, high-elevation sites were more forested during the early Holocene, thus, it is noteworthy that there was not an increase in stand-replacing fires during this period of higher summer insolation. This could be the result of the

slight decline in conifer trees and increase in shrubs, resulting in less fuel connectivity, as well as the upslope migration of fire-resistant Douglas-fir and ponderosa pine trees. However, it may also be the result of subtle changes in monthly insolation levels (Berger, 1978). Power et al. (2011) hypothesized that high-elevation sites may have burned less frequently despite being forested due to the changes in the month of peak summer insolation. The peak of summer insolation shifted from June in the late-glacial period to July in the early Holocene. Consequently, high-elevation forests experienced more burning during the late-glacial, but as the height of summer warmth shifted toward the end of the summer, wetter spring and early summer conditions may have shortened the fire season at that time (Power et al., 2011). Additionally, lower winter insolation led to cooler winters that may have prolonged snowpack into the summer, suppressing fire activity. Furthermore, the persistence of the subtropical high-pressure system likely prevented summer storms, and along with a shorter fire season, may have led to fewer ignitions and, consequently, less fire activity.

Middle Holocene (8000-5000 cal yr BP)

After 8000 cal yr BP, low-elevation Douglas-fir parkland transitioned to closed forests predominantly composed of lodgepole and/or ponderosa pine. This shift occurred earliest at Wymore and Pintler lakes, which saw a decrease in *Pseudotsuga*-type pollen at ca. 7800 cal yr BP. While *Pseudotsuga*-type percentages decreased near Wymore Lake, *Artemisia* levels remained high, slowly declining until about 6500 cal yr BP. The pollen data suggest a shift to pine forest between 7800 and 6500 cal yr BP, and the decline in Douglas-fir at Pintler Lake indicates a lowering of its elevational range. In Glacier National Park to the north, the forests surrounding Kintla Bog also became increasingly forested by 7500 cal yr BP (Power et al.,

2011). The decline in SCD during this period reflects the gradual establishment of low-elevation pine forest, although Douglas-fir parkland remained at other low-elevation sites (Figs. 4.4, SM4.2).

The Black Lake record began with the deposition of clay sediment at ca. 7500 cal yr BP, at the same time that closed pine forests developed at Wymore and Pintler Lakes, suggesting a shift in hydrology toward wetter conditions. However, similar to Twin and Rainbow lakes, the pollen at Black Lake suggests Douglas-fir parkland was present at 7500 cal yr BP, implying that conditions were still relatively warm and dry. Pollen data at Black, Rainbow, and Twin lakes indicate a shift from parkland to forest around 6000 and 5500 cal yr BP, coincident with the development of denser forests near Foy and Johns lakes (Power et al., 2011) and in the Canadian Rockies (Hebda, 1995). The basal clays at both Black Lake and Pine Butte Fen changed from clay sediment to organic sapropel and peat at ca. 6000 and 5500 cal yr BP, respectively, also suggesting an increase in moisture and a more productive landscape at the end of the middle Holocene.

High-elevation sites experienced a slight decrease in the AP:NAP ratio and a decline in *Pseudotsuga*-type pollen, but otherwise maintained their forests during the middle Holocene (Figs. 4.2, 4.4). Similar to Black Lake and Pine Butte Fen, Mud Lake had clay sediment at ca. 6000 cal yr BP, which transitioned to organic sapropel at ca. 5500 cal yr BP, indicating an increase in moisture. The earliest pollen assemblages at Mud Lake indicate a forest of pine and Douglas-fir/larch with high amounts of alder and other shrubs, followed by an increase in arboreal pollen and a shift to subalpine spruce and fir forest at ca. 5000 cal yr BP. Other high-

elevation records, located approximately 170 km south of the Mission Range in the Pioneer and southern Bitterroot Ranges, also suggest an increase in forest density with the shift to subalpine

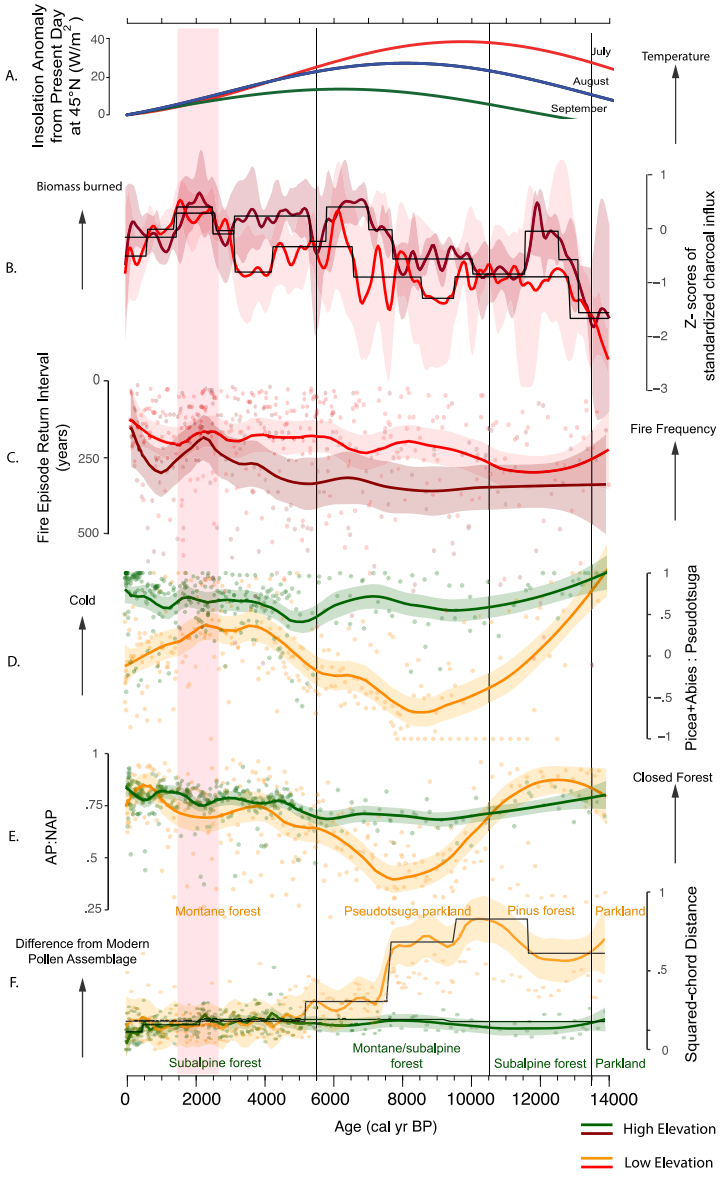


Figure 4.4. Regional pollen and charcoal data. (A) insolation anomaly at 45 N (Berger, 1978). (B) Z-scores of standardized charcoal influx, shading represents 95% confidence interval. (C) The fire-episode return interval (note the reversed y-axis). (D) The ratio of *Picea* + *Abies:Pseudotsuga/Larix* pollen. (E) The ratio of arboreal pollen to nonarboreal pollen. (F) Squared-chord distances between each sample and youngest sample of the record and the inferred vegetation type. FRI, pollen, and SCD data are plotted with a loess smoother (span =.3),

and shading represents the 95% confidence interval. Black lines on charcoal z-scores and SCD are the regime shift index (Rodiodev et al., 2004). Vertical black lines denote the approximate timings of vegetation changes, and the red bar denotes the time of synchronized high-fire activity.

spruce and fir forests at ca. 6000-5800 cal yr BP (Mehringer et al., 1977; Watt et al., 2022). The data support that some high-elevation forests were susceptible to early Holocene drought and an increase in moisture in the mid-Holocene led to forest closure and increased organic deposition into lakes.

Increased moisture is indicated by models that show a decrease in summer insolation levels during the middle Holocene, which lessened the extreme seasonality of the early Holocene (Berger, 1978). This resulted in cooler (warmer)-than-before summers (winters) and increased effective moisture (Alder and Hostetler, 2015). It is possible that there were multiple phases of precipitation increase in the region. Following the warm, dry conditions of the early Holocene, a shift in the hydrology of NW Montana at ca. 8000-7500 cal yr BP, led to forest closure and a lowering of lower treeline at Wymore and Pintler lakes, as well as the onset of sediment collection in the Black Lake basin. Moisture levels increased again at ca. 6000 cal yr BP, which caused the shift to organic sediment deposition at Black Lake, Pine Butte Fen, and Mud Lake, an increase in forest density at Rainbow, Black, and Twin lakes, and the development of mixed conifer subalpine forests at Mud Lake and other high-elevation sites.

Other climate proxies indicate increases in moisture during these two periods, although the rise between 6500 and 5500 cal yr BP is more pronounced. A comprehensive study of lake-level history in North America found that effective moisture increased in western Canada and at high elevations of the Rocky Mountains after 8000 cal yr BP, peaking at 6000 cal yr BP (Liefert and Shuman, 2020). The water level of lakes in northern Wyoming rose after 6600 cal yr BP

(Dilworth et al., 2024) and 5700 cal yr BP (Lynch, 1998; Shuman and Serravezza, 2017), coinciding with vegetation shifts toward denser forest in the Mission Range. Glacial advances also occurred in the Canadian Rocky Mountains after ca. 8500 cal yr BP (Menounos, 2009), in northern Wyoming at ca. 6300 cal yr BP (Larsen et al., 2020), and in Glacier National Park between 6500 and 5500 cal yr BP, indicating increased winter precipitation and cooler summers (Munroe et al., 2012).

Multiproxy compilations of temperature and hydroclimate records in the western U.S. further support climate changes during these periods. Routson et al. (2021) observed decreases in summer temperatures, increases in winter temperatures, and rising moisture both at ca. 8000 cal yr BP and ca. 6000 cal yr BP. Shuman and Marsicek (2016) reported a temperature decrease and significant rise in moisture at ca. 5700 cal yr BP, while Wanner et al. (2011) identified cold periods at ca. 8200 cal yr BP and between 6500 and 5900 cal yr BP. These cooling events may have resulted from changes in ocean and atmospheric circulation due to the final meltwater pulse of the Laurentide ice sheet at ca. 8200 cal yr BP and a decrease in solar irradiance at ca. 6500 cal yr BP (Wanner et al., 2011).

Some lake-level records indicate a mid-Holocene dry period beginning at ca. 7500 cal yr BP, during the same period that the pollen data in the Mission Range indicate an increase in moisture. Foy Lake in the Flathead Valley and Silver Lake in the Bitterroot Range had shallow stands between ca. 7500 and 2000 cal yr BP (Parish et al., 2022; Shuman et al., 2009). Diatom data from Jones Lake, located just south of the Mission Range, suggest shallow lake levels between 7610 and 6180 cal yr BP (Shapley et al., 2009), and seismic reflection data suggest Flathead Lake experienced a low stand between ca. 7600 and 7000 cal yr BP (Hofmann et al.,

2006). This evidence of lower lake levels corresponds with a decrease in sedimentation rates at Wymore Lake at ca. 7200 cal yr BP, potentially representing dry conditions and minimal sediment input. The temporal differences among sites could relate to local site conditions, indicating that some areas were more protected from drought than others or simply that the proxy data did not record changes in moisture in every instance.

Fire activity increased at high elevations at ca. 8000 cal yr BP, coinciding with the initial vegetation turnover at some low-elevation sites (Fig. 4.4). Low-elevation fire activity also increased at ca. 7600 cal yr BP but immediately declined until a larger increase occurred at ca. 6000 cal yr BP. The rise in fire activity observed in both high- and low-elevation records at ca. 7600 cal yr BP corresponds with the Flathead Lake and Jones Lake lowstands (Hofmann et al., 2006; Shapley et al., 2009), suggesting this may have been a response to both increases in forest density and dry conditions. These fires would have produced more charcoal than low-severity surface fires.

The significant increase in fire at ca. 6000 cal yr BP corresponds with the transition to mixed conifer and pine forests at most low-elevation sites, which increased woody fuel biomass. Increased moisture in the region not only supported forest growth but likely also resulted in more storm activity, which may have increased ignition events. Additionally, summer insolation anomalies in August and September remained high at ca. 6000 cal yr BP; thus, as winters became warmer and summers cooler, extending summer drought into September may have prolonged the fire season.

Late Holocene (5000 cal yr BP – present day)

All upper and lower elevation sites were forested by ca. 5000 cal yr BP (except for Pine Butte Fen, which remained below the forest-prairie ecotone). Despite slight shifts in species composition, forests were generally closed from ca. 5000 cal yr BP to the present day. *Pseudotsuga*-type pollen decreased at low-elevation sites, while that of *Pinus* subg. *Pinus, Picea,* and *Abies* increased, indicating the presence of mixed conifer forests from ca. 5000 to 2000 cal yr BP. Some low-elevation sites (Twin and Black lakes) exhibited an increase in *Picea* and *Abies* pollen between ca. 4000-3000 cal yr BP (Figs. 4.2, 4.4, SM4.2), suggesting cooler and wetter conditions than before. From 3000 cal yr BP to the present, the rise in *Pseudotsuga*-type pollen marks the establishment of the current forest composition of Douglas-fir and pine forests at Wymore, Black, and Rainbow lakes, and mixed-conifer Douglas-fir, pine, and spruce forests at Twin and Pintler lakes.

High-elevation sites maintained subalpine spruce, fir, and pine forests, and forest density increased towards the present. There is one increase in *Pseudotsuga*-type pollen at ca. 5000 cal yr BP (Fig. 4.2), but rather than a short-term spike, the Mud Lake record begins at that time with high levels of *Pseudotsuga*, and this likely reflects the end of early and middle Holocene Douglas-fir presence at some middle-to-high elevation areas. Two significant increases in *Alnus* pollen occurred between ca. 5000-4000 and 3000-2000 cal yr BP (Fig. 4.2). The overall high percentage of *Alnus* present at these high elevation sites are consistent with cool and moist conditions in the late Holocene, but they may also be a response to increased fire activity or other disturbances since green alder is often the first species to colonize post-disturbance (Lantz et al., 2010). Mesic taxa also increased after ca. 5000 cal yr BP in the Canadian Rocky Mountains

(Hallett and Hills, 2006), and modern forests established in northern Idaho and Montana after ca. 3000 cal yr BP (Mack et al., 1983; Power et al., 2011).

The closed forest vegetation structure after ca. 5000 cal yr BP indicates a continuation of cooling temperatures and increased moisture throughout the late-Holocene. As summer (winter) insolation levels decreased (increased) towards the present day, and the contrast in seasonal insolation lessened (Berger, 1978), modern climate and forest composition were established. Despite this general cooling trend, short-term periods of even cooler and wetter conditions, as well as warm and dry conditions occurred. Notable examples include warm conditions during the Medieval Climate Anomaly (MCA) at ca. 1050 to 650 cal yr BP (Cook et al., 2004), and cool conditions during the Little Ice Age (LIA) at ca. 550 to 250 cal yr BP (Mann et al., 1999). These periods are documented through various climate proxies and supported by vegetation changes at some of our sites.

One cold wet period between 4000 and 3000 cal yr BP is suggested by increases in *Picea* and *Abies* relative to *Pseudotsuga* at high and low-elevation sites, which indicates an expansion of subalpine forests (Fig. 4.4). Other sites in northern Montana and Idaho record similar increases in mesic taxa, indicating the vegetation response was widespread (Mack et al., 1983, 1978; Mehringer et al., 1977). Glacial advances occurred between ca. 4000 and 2500 cal yr BP to the north in the Canadian Rockies (Luckman et al., 2017; Menounos et al., 2009, 2008; Solomina et al., 2015) and Glacier National Park (Munroe et al., 2012), as well as to the south in Grand Teton National Park, WY (Larsen et al., 2020). It has been suggested that these late-Holocene glacier expansions may have correlated with periods of lower solar irradiance (Denton and Karlen 1973; Koch et al., 2007), and tree-ring reconstructions have linked LIA glacial advances

in Glacier National Park with extended periods of cooler summers and wetter winters (Pederson et al., 2004). Assuming these same conditions controlled glacial advances at ca. 4000 cal yr BP, the cold wet climate would have been conducive to spruce and fir expansion.

Vegetation structure during the MCA and LIA underwent slight changes in response to short-term climate events. *Pseudotsuga*-type pollen percentages increased at higher elevations at ca. 1000 cal yr BP, suggesting an upward movement of treeline during the MCA, similar to the early Holocene. Likewise, during the LIA, arboreal pollen decreased at upper elevations while increasing at lower elevations (Fig. 4.4). The pollen data indicate that the treeline moved down in elevation after the MCA. The basal clay at Starvation Lake dates to ca. 1000 cal yr BP (during the MCA) and transitioned to organic sediment at ca. 500 cal yr BP, further supporting the idea that higher elevations were dry during the MCA and wetter during the LIA.

Lake-level data from Foy Lake (Shuman et al., 2009), Flathead Lake (Hofmann et al., 2006), and Silver Lake (Parish et al., 2022), and isotope data from Jones Lake (Shapley et al., 2009) indicate high lake levels after ca. 3000 cal yr BP. Although this increase in lake levels occurred 2000 years after the initial vegetation change that suggested an increase in moisture in the Mission Range, it supports a climate shift at ca. 3000 cal yr BP when many modern forests were established. Diatom data from Kintla Lake in Glacier National Park and Emerald and Beauty lakes in the Greater Yellowstone Ecosystem also indicate increased winter precipitation between approximately 3200 and 1400 cal yr BP, attributed to the weakening of the Aleutian low-pressure center, which influences storm patterns in the Northwestern US (Stone et al., 2016). Additionally, NRM glaciers surged during the most recent millennia (Menounos et al., 2009;

Munroe et al., 2012). Together, these findings suggest that the last 3000 years were the coolest and wettest of the Holocene.

Fire activity was highly variable during the late-Holocene period. Following the transition from parkland to forest and the increase in fire activity at ca. 6000 cal yr BP, low-elevation fire activity decreased from 5000 to 3000 cal yr BP, coinciding with the cool and wet period that facilitated the expansion of spruce and fir to lower elevations. In contrast, high-elevation sites experienced slightly higher fire activity during this time despite the cool and wet conditions (Figs. 4.3, 4.4). A comparison of charcoal influx anomalies and fire-episode frequency at the six high- and six low-elevation sites that span the last 5000 years shows that low-elevation sites had more frequent fire episodes, even though they produced less charcoal (Fig. 4.5). Despite the increase of spruce and fir, low-elevation forests were still primarily composed of more fire-tolerant Douglas-fir and ponderosa pine, and the combination of cool and wet conditions may have limited the severity of fires at low elevations. However, when fires occurred in the high-elevation spruce and fir forests, the high amounts of charcoal indicate that they were high-severity events. The concurrent increase in *Alnus* pollen in high-elevation sites also may suggest post-fire regeneration of alder following severe fire episodes.

The highest level of fire activity recorded across both high and low-elevation sites occurred at ca. 2500-1500 cal yr BP when there was an increase in charcoal influx and more frequent fire episodes (Figs. 4.4,4.5). The Pine Butte Fen record indicates minimal fire activity throughout its duration, likely reflecting low charcoal output from grass fires, except at ca. 2200 cal yr BP, when evidence suggests that the fen caught on fire. A study across a network of additional sites in the Bitterroot Range found the highest rate of burning between ca. 2500-2300

cal yr BP (Clark-Wolf et al., 2023), and other sites in the western U.S. and Canada also show heightened fire activity at this time (Hallett and Walker, 2000; Lepofsky et al., 2005; Power et al., 2006). Vegetation changes between ca. 2500 and 2000 were minor, but include a slight decrease in AP:NAP, reflecting an increase in Poaceae at lower elevations and a reduction of *Picea* and *Abies* pollen at higher elevations (Figs. 4.2, 4.4), which may indicate warm, dry conditions and more open forest. This period also follows the time of expanded spruce and fir forests, suggesting that as conditions warmed, charcoal influx into lakes increased due to the ignition of these fire-sensitive forests, which also led to their decrease across the landscape. The increase in high-elevation *Alnus* pollen in this study, along with erosion-associated fire events at Silver Lake (Wolf-Clarke, 2023), further supports the occurrence of high-severity fire episodes during this period. Evidence for warm, dry conditions is indicated by low lake level stands in the Bitterroot Range centered around ca. 2300 cal yr BP (Bracht-Flyr and Fritz, 2012; Parish et al., 2022), as well as diatom evidence for abbreviated springs and extended summers at ca. 2000 cal yr BP (Whitlock et al., 2012), and significant glacier retreat from 2400-1000 cal yr BP in the Teton Range (Larsen et al., 2020).

Fire activity and fire-episode frequency show an overall decline from the Holocene maximum at ca. 2000 cal yr BP to the present day. Charcoal influx increased slightly between ca. 1000 and 700 cal yr BP during the MCA, followed by a decline at lower elevations from 700 to 300 cal yr BP during the LIA. This pattern suggests that fire occurrence rose during the warm, dry conditions of the MCA and decreased during the cold conditions of the LIA. However, when compared to other periods in the record, these changes in fire activity are not particularly notable, and other studies also report conflicting results. The pattern of high fire occurrence in

the MCA and less in the LIA was evident at high-elevation sites and less distinct at low-elevation sites in a more geographically extensive regional fire study of the northern Rocky Mountains (from Montana to northern Wyoming and Idaho) (Carter et al., 2018). However, fire activity did not increase during the MCA in the Bitterroot Range (Clark-Wolf et al., 2023). The study that noted an increase in fire during the MCA included sites to the south, where the effects of the MCA may have been more evident than in northern Montana, where the cold and wet effects of La Niña years (discussed below) may have lessened the impacts of the MCA (Clark-Wolf et al., 2023).

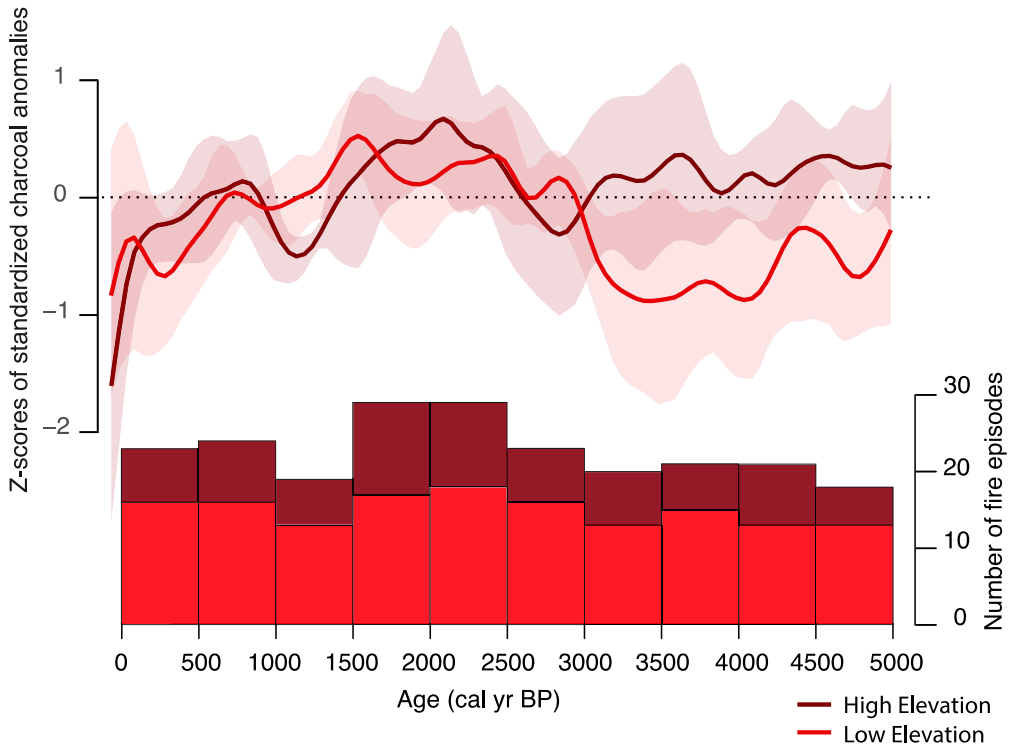


Figure 4.5. Composite charcoal data based on charcoal accumulation rates and fire episodes per 500 years based on significant charcoal peaks for the twelve sites that span the last ~5000 cal yrs. Low-elevation sites are Twin Lakes, Black Lake, Pine Butte Fen, Pintler Lake, Rainbow Lake, Wymore Lake. High elevation sites are Baker Lake, Burnt Knob Lake, Mud Lake, Three Lakes Peak Lake, Hoodoo Lake, and Silver Lake.

High- and low-elevation sites exhibited a slight increase in fire activity at ca. 300 cal yr BP before declining towards present day. This final synchronous decline was recorded at other sites in the northern Rocky Mountains (Carter et al., 2018; Clark-Wolf et al., 2023; Power et al., 2006) and could be attributed to cooler and wetter climate conditions in the mid 20th century, which suppressed large fires (Higuera et al., 2015; Littell et al., 2009). Additionally, it could be related to the arrival of Euro-American settlers in the mid-19th century, who, through grazing and logging, may have eliminated fire for several decades (Carter et al., 2018; Power et al., 2006).

In addition to the influence that Euro-American settlers exerted on fire activity, humans may have contributed to variations in fire throughout the Holocene epoch. Humans have inhabited this region throughout the Holocene (Gajewski et al., 2011), utilizing fire for various purposes at all elevations (e.g., promoting the growth of plant resources, hunting, and clearing travelways (Barrett and Arno, 1999; Boyd et al., 2009)), and studies suggest that their influence on fire activity was not negligible (Alt et al., 2018; Lepofsky et al., 2005; Walsh et al., 2018). Studies indicate the human population in northwest MT rose between ca. 3000 and 1000 cal yr BP, including a biomarker study at Black Lake (McWethy et al., 2020) and population estimates based on radiocarbon-dated archaeological material (Jones et al., 2009). This timeframe overlaps with the peak period of composite fire activity around ca. 2000 yr BP, and while there is no definitive way to identify which fires were set by humans, it is likely they contributed to some of the fires during this time period.

Contemporary fire studies suggest that years with deep winter and spring snowpack suppress fires in the following summer (Heyerdahl et al., 2008). Therefore, the increase in

Holocene fire activity while the climate was getting cooler and wetter is of interest. While humans may have had an influence, increases in climate variability may have also played a role. Oscillations between wet and dry years would have allowed for fuel growth during wet periods, which would then burn during warm, dry years. Isotopic and diatom data from Foy Lake indicate increases in multidecadal dry and wet periods during the late Holocene (Stevens et al., 2006; Stone and Fritz, 2006), and interannual variations, such as ENSO, increased in frequency after approximately 6000 cal yr BP (Barr et al., 2019; Conroy et al., 2008; Moy et al., 2002). While El Niño strength has not been shown to affect fire years in Montana, La Niña years reduce fire activity by bringing deep winter and spring snowpack (Heyerdahl et al., 2008).

Increased climate variability, woody fuel from expanding forests in the mid-to-late Holocene, and human-set fires may have all contributed to the high levels of fire activity prior to 2000 cal yr BP. Additionally, while fire activity increased overall throughout the Holocene, some sites exhibited a decline over the last 2000 years (Black Lake and Silver Lake). These most recent two millennia are associated with the deepest lake level stands of many lakes in the region (Parish et al., 2022; Shapley et al., 2009; Shuman et al., 2009), and the most extensive glacial advances of the late Holocene (Munroe et al., 2012). Decreased fire activity after 2000 cal yr BP is likely attributed to the generally cooler and wetter conditions that prevailed during this time interval.

Conclusions

Data from a network of sites in the northern Rocky Mountains reveal how vegetation and fire responded to climate variability on millennial to centennial time scales. Although vegetation primarily responded to the top-down effects of changing summer insolation levels, changes in

Holocene fire activity at individual sites were influenced by both regional and local factors. Regional fire activity tracked slowly varying trends in summer insolation levels and the establishment of forest in the late glacial period, but differed between high and low elevations throughout most of the Holocene. A widespread increase in biomass burned during the cool, wet late Holocene suggests that vegetation structure and shorter-term climate variability contributed to the heightened fire activity across the region.

The most significant vegetation change occurred during the early Holocene, when open forests and parkland were present at low elevations and slightly open forests at high elevations. Warmer and effectively drier summers led to the most pronounced contrast in vegetation between low- and high-elevation sites, as well as between past and present day. Despite the variations in vegetation, all elevations had low levels of biomass burned. Dry conditions fostered open Douglas-fir parklands and low-severity surface fires on the lower mountain slopes, while warmer conditions increased the numbers of Douglas-fir and lodgepole and/or ponderosa pine trees at higher elevations. High-elevation forests experienced limited fire activity despite being forested, likely due to residual snowpack persisting from cold winters into spring, fewer ignition events, or a somewhat more open forest structure featuring a higher number of fire-resistant trees.

The only period of asynchronous fire activity occurred between ca. 5500 and 3500 cal yr BP, when high-elevation sites experienced high levels of biomass burning, while low-elevation sites had lower levels. This disparity likely resulted from differences in fire severity across elevations. Lower elevation sites experienced low-severity fire episodes that produced minimal charcoal, while higher elevations experienced infrequent high-severity fires that produced more

charcoal. During this period, forest types supported fire regimes similar to those we recognize today.

Fire activity increased simultaneously at all elevations three times during the record. Two involved transitions from open parkland to closed forests (during the late-glacial transition at ca. 13,000 cal yr BP and in the middle Holocene at between ca. 7000 and 6000 cal yr BP) and resulted from an increase in fuel biomass across the landscape. The third instance of high fire activity was the only occurrence of anomalously high fire activity at all elevations, and occurred between ca. 2500 and 2000 cal yr BP. Additional climate proxy data suggest that this rise in fire activity during the cold, wet late Holocene likely stemmed from an extended warm, dry period during the overall wetter period (which allowed for fuel growth) of the last 3000 years.

The vegetation history of western Montana indicates that forests have retained their composition and structure over the last 3,000 years despite increased fire activity. The rise in fire activity at ca. 2000 cal yr BP suggests that projections for warmer and drier conditions in the NRM will result in simultaneous increases in fire activity at all elevations, a finding consistent with future model projections of fire (Westerling et al., 2011). Successful regeneration of forests after 2000 cal yr BP was likely due to the return of cool and wet climate conditions following the warm and dry period. The rapid warming and aridification of NRM landscapes in the future could cause a synchronous increase in fire activity until woody fuel becomes limited, resulting in a more open vegetation structure reminiscent of the early Holocene. This transition to a more open vegetation structure would then create cascading effects on the mountain ecosystems and hydrology of the region.

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References

Alder, J.R., Hostetler, S.W., 2015. Global climate simulations at 3000-year intervals for the last 21 000 years with the GENMOM coupled atmosphere–ocean model. Clim. Past 11, 449–471. https://doi.org/10.5194/cp-11-449-2015

Alizadeh, M.R., Abatzoglou, J.T., Luce, C.H., Adamowski, J.F., Farid, A., Sadegh, M., 2021. Warming enabled upslope advance in western US forest fires. Proc. Natl. Acad. Sci. U. S. A. 118, e2009717118. https://doi.org/10.1073/pnas.2009717118

Alt, M., McWethy, D., Everett, R., Whitlock, C., 2018. Millennial scale climate-fire-vegetation interactions in a mid-elevation mixed coniferous forest, Mission Range, northwestern Montana, USA. Quat. Res. 90, 1–17. https://doi.org/10.1017/qua.2018.25

Barnard, D.M., Barnard, H.R., Molotch, N.P., 2017. Topoclimate effects on growing season length and montane conifer growth in complex terrain. Environ. Res. Lett. 12, 064003. https://doi.org/10.1088/1748-9326/aa6da8

Barr, C., Tibby, J., Leng, M.J., Tyler, J.J., Henderson, A.C.G., Overpeck, J.T., Simpson, G.L., Cole, J.E., Phipps, S.J., Marshall, J.C., McGregor, G.B., Hua, Q., McRobie, F.H., 2019. Holocene El Niño–Southern Oscillation variability reflected in subtropical Australian precipitation. Sci. Rep. 9, 1627. https://doi.org/10.1038/s41598-019-38626-3

Barrett, S.W., Arno, S.F., Menakis, J.P., 1997. Fire episodes in the Inland Northwest (1540–1940) based on fire history data. Gen. Tech. Rep. INT–370. Ogden, UT: USDA Forest Service

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quat. Sci. Rev. 17, 549–585. https://doi.org/10.1016/S0277-3791(98)00012-2

Bennett KD and Willis KJ (2001) Pollen. In: Smol JP, Birks HJB and Last WM (eds) *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, 3.* Dordrecht: Kluwer Academic Publishers, pp. 5–32.

Berger, A., 1978. Long-term variations of caloric insolation resulting from the Earth's orbital elements. Quaternary Research 9, 139–167.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. https://doi.org/10.1214/11-BA618

Boyd, R. (1999). Indians, fire and the Land in the Pacific Northwest. Corvallis: Oregon State University Press.

Bracht-Flyr, B., Fritz, S.C., 2012. Synchronous climatic change inferred from diatom records in four western Montana lakes in the U.S. Rocky Mountains. Quat. Res. 77, 456–467. https://doi.org/10.1016/j.yqres.2011.12.005

Brunelle, A., Whitlock, C., Bartlein, P., Kipfmueller, K., 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. Quat. Sci. Rev. 24, 2281–2300. https://doi.org/10.1016/j.quascirev.2004.11.010

Carrara, P.E., 1995. A 12 000 year radiocarbon date of deglaciation from the Continental Divide of northwestern Montana. Can. J. Earth Sci. 32, 1303–1307. https://doi.org/10.1139/e95-106

Carter, V.A., Power, M.J., Lundeen, Z.J., Morris, J.L., Petersen, K.L., Brunelle, A., Anderson, R.S., Shinker, J.J., Turney, L., Koll, R., Bartlein, P.J., 2018. A 1,500-year synthesis of wildfire activity stratified by elevation from the U.S. Rocky Mountains. Quat. Int. 488, 107–119. https://doi.org/10.1016/j.quaint.2017.06.051

Clark-Wolf, K., Higuera, P.E., Shuman, B.N., McLauchlan, K.K., 2023. Wildfire activity in northern Rocky Mountain subalpine forests still within millennial-scale range of variability. Environ. Res. Lett. 18, 094029. https://doi.org/10.1088/1748-9326/acee16

Clark-Wolf, K.D., Higuera, P.E., McLauchlan, K.K., Shuman, B.N., Parish, M.C., 2023. Fire-regime variability and ecosystem resilience over four millennia in a Rocky Mountain subalpine watershed. J. Ecol. 1365-2745.14201. https://doi.org/10.1111/1365-2745.14201

Conroy, J.L., Overpeck, J.T., Cole, J.E., Shanahan, T.M., Steinitz-Kannan, M., 2008. Holocene changes in eastern tropical Pacific climate inferred from a Galápagos lake sediment record. Quat. Sci. Rev. 27, 1166–1180. https://doi.org/10.1016/j.quascirev.2008.02.015

Cook, E.R., Woodhouse, C.A., Eakin, M.C., Meko, D.M., Stahle, D.W., 2004. Long-term aridity changes in the western United States. Science 306, 1015–1018.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc. Natl. Acad. Sci. 116, 6193–6198. https://doi.org/10.1073/pnas.1815107116

Denton, G.H., Karlén, W., 1973. Holocene climatic variations; their pattern and possible cause. Quat. Res. 3, 155-205.

Dilworth, J.R., McGlue, M.M., Thigpen, R.J., Brown, S.J., Yeager, K.M., Woolery, E.W., Johnson, S.E., Whitehead, S.J., Cortese, C.J., Matocha, C., 2024. Holocene paleoenvironmental history of Jackson Lake (Grand Teton National Park, USA) deduced from CHIRP seismic reflection and radiocarbon-dated sediment cores. Quat. Sci. Rev. 336, 108748. https://doi.org/10.1016/j.quascirev.2024.108748

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Change Biol. 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analysis 4th ed*. The Blackburn Press, New Jersey.

Fall, P.L., 1994. Modern Pollen Spectra and Vegetation in the Wind River Range, Wyoming, U.S.A. Arct. Alp. Res. 26, 383–392. https://doi.org/10.2307/1551800

Gajewski, K., Munoz, S., Peros, M., Viau, A., Morlan, R., and Betts, M. (2011). The Canadian Archaeological Radiocarbon Database (Card): archaeological 14C Dates in North America and their paleoenvironmental context. Radiocarbon 53, 371–394. doi: 10.1017/S0033822200056630

Gavin, D.G., Oswald, W.W., Wahl, E.R., Williams, J.W., 2003. A statistical approach to evaluating distance metrics and analog assignments for pollen records. Quat. Res. 60, 356–367. https://doi.org/10.1016/S0033-5894(03)00088-7

Hallett, D., Walker, R., 2000. Paleoecology and its application to fire and vegetation management in Kootenay National Park, British Columbia. J. Paleolimnol. 24, 401–414. https://doi.org/10.1023/A:1008110804909

Hallett, D.J., Hills, L.V., 2006. Holocene Vegetation Dynamics, Fire History, Lake Level and Climate Change in the Kootenay Valley, Southeastern British Columbia, Canada. J. Paleolimnol. 35, 351–371. https://doi.org/10.1007/s10933-005-1335-6

Hanberry, B.B., Justice, D.C., Powell, D.C., 2020. Discovering Douglas-Fir Woodlands in the Historical Forests of Umatilla National Forest, Eastern Oregon and Washington. Forests 11, 1122. https://doi.org/10.3390/f11101122

Hebda, R., 1995. British Columbia Vegetation and Climate History with Focus on 6 ka BP. Géographie Phys. Quat. 49. https://doi.org/10.7202/033030ar

Heyerdahl, E.K., Morgan, P., Riser, J.P., 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), northern Rockies, USA. Ecology 89, 705–716. https://doi.org/10.1890/06-2047.1

Higuera, P., 2009. CharAnalysis 0.9: Diagnostic and analytical tools for sediment-charcoal analysis.

Higuera, P.E., Abatzoglou, J.T., Littell, J.S., Morgan, P., 2015. The Changing Strength and Nature of Fire-Climate Relationships in the Northern Rocky Mountains, U.S.A., 1902-2008. PLOS ONE 10, e0127563. https://doi.org/10.1371/journal.pone.0127563

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol. Monogr. 79, 201–219. https://doi.org/10.1890/07-2019.1

Higuera, P.E., Whitlock, C., Gage, J.A., 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. The Holocene 21, 327–341. https://doi.org/10.1177/0959683610374882

Hofmann, M.H., Hendrix, M.S., 2010. Depositional processes and the inferred history of ice-margin retreat associated with the deglaciation of the Cordilleran Ice Sheet: The sedimentary record from Flathead Lake, northwest Montana, USA. Sediment. Geol. 223, 61–74. https://doi.org/10.1016/j.sedgeo.2009.10.004

Hofmann, M.H., Hendrix, M.S., Moore, J.N., Sperazza, M., 2006. Late Pleistocene and Holocene depositional history of sediments in Flathead Lake, Montana: Evidence from high-resolution seismic reflection interpretation. Sediment. Geol. 184, 111–131. https://doi.org/10.1016/j.sedgeo.2005.09.019

Hostetler, S., Whitlock, C., Shuman, B., et al., 2021. *Greater Yellowstone climate assessment: past, present, and future climate change in greater Yellowstone watersheds.* Montana State University, Institute on Ecosystems, Montana. https://doi.org/10.15788/GYCA2021.

Iglesias, V., Whitlock, C., Krause, T.R., Baker, R.G., 2018. Past vegetation dynamics in the Yellowstone region highlight the vulnerability of mountain systems to climate change. J. Biogeogr. 45, 1768–1780. https://doi.org/10.1111/jbi.13364

Jones, A.G., Marcott, S.A., Gorin, A.L., Kennedy, T.M., Shakun, J.D., Goehring, B.M., Menounos, B., Clark, D.H., Romero, M., Caffee, M.W., 2023. Four North American glaciers advanced past their modern positions thousands of years apart in the Holocene. The Cryosphere 17, 5459–5475. https://doi.org/10.5194/tc-17-5459-2023

Jones, Megan, 2019. Migration or mortality: a study of summed probability distributions and population decline in the bighorn basin of Wyoming. Master's Thesis, University of Wyoming.

Kapp, R.O., Davis, O.K., King, J.E., 2000. *Pollen and Spores 2nd ed*. The American Association of Stratigraphic Palynologists, College Station.

Koch, J., Osborn, G.D., Clague, J.J., 2007. Pre-'Little Ice Age' glacier fluctuations in Garibaldi Provincial Park, Coast Mountains, British Columbia, Canada. Holocene 17, 1069-1078.

Lantz, T.C., Gergel, S.E., Henry, G.H.R., 2010. Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional

temperature in north-western Canada. J. Biogeogr. 37, 1597–1610. https://doi.org/10.1111/j.1365-2699.2010.02317.x

Lapierre, K., 2021 Long-term environmental history of two low-elevation mixed-conifer forests, Mission Valley, Montana. Master's Thesis, Montana State University.

Larsen, D.J., Crump, S.E., Blumm, A., 2020. Alpine glacier resilience and Neoglacial fluctuations linked to Holocene snowfall trends in the western United States. Sci. Adv. 6, eabc7661. https://doi.org/10.1126/sciadv.abc7661

Lepofsky, D., Lertzman, K., Hallett, D., Mathewes, R., 2005. Climate Change and Culture Change on the Southern Coast of British Columbia 2400-1200 Cal. B.P.: An Hypothesis. amnat 70, 267. https://doi.org/10.2307/40035704

Lesica, Peter, 1986. Vegetation and flora of Pine Butte Fen, Teton County, Montana, Great Basin Naturalist: 46, 22-32. https://scholarsarchive.byu.edu/gbn/vol46/iss1/2

Li, D., Wrzesien, M.L., Durand, M., Adam, J., Lettenmaier, D.P., 2017. How much runoff originates as snow in the western United States, and how will that change in the future? Geophys. Res. Lett. 44, 6163–6172. https://doi.org/10.1002/2017GL073551

Liefert, D.T., Shuman, B.N., 2020. Pervasive Desiccation of North American Lakes During the Late Quaternary. Geophys. Res. Lett. 47. https://doi.org/10.1029/2019GL086412

Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021. https://doi.org/10.1890/07-1183.1

Luckman, B.H., Masiokas, M.H., Nicolussi, K., 2017. Neoglacial history of Robson Glacier, British Columbia. Can. J. Earth Sci. 54, 1153–1164. https://doi.org/10.1139/cjes-2016-0187

Lynch, E.A., 1998. Origin of a park-forest vegetation mosaic in the Wind River Range, Wyoming. Ecology 79, 1320–1338. https://doi.org/10.1890/0012-9658(1998)079[1320:OOAPFV]2.0.CO;2

Mack, R.N., Rutter, N.W., Bryant, V.M., Valastro, S., 1978. Reexamination of postglacial vegetation history in northern Idaho: Hager Pond, Bonner Co. Quat. Res. 10, 241–255. https://doi.org/10.1016/0033-5894(78)90104-7

Mack, R.N., Rutter, N.W., Valastro, S., 1983. Holocene Vegetational History of the Kootenai River Valley, Montana. Quat. Res. 20, 177–193. https://doi.org/10.1016/0033-5894(83)90076-5

Mann, M.E., Bradley, R.S., Hughes, M.K., 1999. Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. Geophys. Res. Lett. 26, 759–762. https://doi.org/10.1029/1999GL900070

McAndrews, J.H., Berti, A.A., Norris, G., 1973. *Key to the Quaternary Pollen and Spores of the Great Lakes Region*. Life Sciences Miscellaneous Publication, Royal Ontario Museum, Toronto.

Mehringer, P., Arno, S., Petersen, K., 1977. Postglacial History of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arct. Alp. Res. 9, 345. https://doi.org/10.2307/1550528

Menounos, B., Clague, J.J., Osborn, G., Luckman, B.H., Lakeman, T.R., Minkus, R., 2008. Western Canadian glaciers advance in concert with climate change circa 4.2 ka. Geophys. Res. Lett. 35. https://doi.org/10.1029/2008GL033172

Menounos, B., Osborn, G., Clague, J., Luckman, B., 2009. Latest Pleistocene and Holocene glacier fluctuations in western Canada. Quat. Sci. Rev. 1877, 71–1. https://doi.org/10.1016/j.quascirev.2008.10.018

Mote, P.W., Li, S., Lettenmaier, D.P., Xiao, M., Engel, R., 2018. Dramatic declines in snowpack in the western US. Npj Clim. Atmospheric Sci. 1, 2. https://doi.org/10.1038/s41612-018-0012-1

Moy, C.M., Seltzer, G.O., Rodbell, D.T., Anderson, D.M., 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. Nature 420, 162–165. https://doi.org/10.1038/nature01194

Munroe, J.S., Crocker, T.A., Giesche, A.M., Rahlson, L.E., Duran, L.T., Bigl, M.F., Laabs, B.J.C., 2012. A lacustrine-based Neoglacial record for Glacier National Park, Montana, USA. Quat. Sci. Rev. 53, 39–54. https://doi.org/10.1016/j.quascirev.2012.08.005

Nimick, D.A., Rasmussen, R.S., Woessner, W.W, Schmidt, J.C., 1983. Geologic and hydrologic investigations at Pine Butte and Mcdonald swamps, Teton county, Montana. Scientific Report. The Nature Conservancy, Helena, MT.

Parish, M.C., Wolf, K.D., Higuera, P.E., Shuman, B.N., 2022. Holocene water levels of Silver Lake, Montana, and the hydroclimate history of the Inland Northwest. Quat. Res. 1–13. https://doi.org/10.1017/qua.2022.17

Pederson, G.T., Betancourt, J.L., McCabe, G.J., 2013. Regional patterns and proximal causes of the recent snowpack decline in the Rocky Mountains, U.S. Geophys. Res. Lett. 40, 1811–1816. https://doi.org/10.1002/grl.50424

Pederson, G.T., Fagre, D.B., Gray, S.T., Graumlich, L.J., 2004. Decadal-scale climate drivers for glacial dynamics in Glacier National Park, Montana, USA. Geophys. Res. Lett. 31. https://doi.org/10.1029/2004GL019770

Pederson, G.T., Graumlich, L.J., Fagre, D.B., Kipfer, T., Muhlfeld, C.C., 2010. A century of climate and ecosystem change in Western Montana: what do temperature trends portend? Clim. Change 98, 133–154. https://doi.org/10.1007/s10584-009-9642-y

Pfister, R., Kovalchik, B., Arno, S., Presby, R., 1977. Forest habitat types of Montana (General Technical Report No. INT-34). USDA Forest Service.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H.W., Carcaillet, C., Cordova, et al., 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. Clim. Dyn. 30, 887–907. https://doi.org/10.1007/s00382-007-0334-x

Power, M.J., Whitlock, C., Bartlein, P., Stevens, L.R., 2006. Fire and vegetation history during the last 3800 years in northwestern Montana. Geomorphology, Quaternary landscape change and modern process in western North America 75, 420–436. https://doi.org/10.1016/j.geomorph.2005.07.025

Power, M.J., Whitlock, C., Bartlein, P.J., 2011. Postglacial fire, vegetation, and climate history across an elevational gradient in the Northern Rocky Mountains, USA and Canada. Quat. Sci. Rev. 30, 2520–2533. https://doi.org/10.1016/j.quascirev.2011.04.012

PRISM Climate Group, 2014. Oregon State University, https://prism.oregonstate.edu, data created 4 Feb 2014, accessed 16 Dec 2023

R core team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reis, W., McGrath, D., Elder, K., Kampf, S., Rey, D., 2024. Quantifying Aspect-Dependent Snowpack Response to High-Elevation Wildfire in the Southern Rocky Mountains. Water Resour. Res. 60, e2023WR036539. https://doi.org/10.1029/2023WR036539

Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31, L09204.

Routson, C.C., Kaufman, D.S., McKay, N.P., Erb, M.P., Arcusa, S.H., Brown, K.J., Kirby, M.E., Marsicek, J.P., Anderson, R.S., Jiménez-Moreno, G., Rodysill, J.R., Lachniet, M.S., Fritz, S.C., Bennett, J.R., Goman, M.F., Metcalfe, S.E., Galloway, J.M., Schoups, G., Wahl, D.B., Morris, J.L., Staines-Urías, F., Dawson, A., Shuman, B.N., Gavin, D.G., Munroe, J.S., Cumming, B.F., 2021. A multiproxy database of western North American Holocene paleoclimate records. Earth Syst. Sci. Data 13, 1613–1632. https://doi.org/10.5194/essd-13-1613-2021

Shapley, M.D., Ito, E., Donovan, J.J., 2009. Lateglacial and Holocene hydroclimate inferred from a groundwater flow-through lake, Northern Rocky Mountains, USA. The Holocene 19, 523–535. http://dx.doi.org.proxybz.lib.montana.edu/10.1177/0959683609104029

Shuman, B., Henderson, A.K., Colman, S.M., Stone, J.R., Fritz, S.C., Stevens, L.R., Power, M.J., Whitlock, C., 2009. Holocene lake-level trends in the Rocky Mountains, U.S.A. Quat. Sci. Rev. 28, 1861–1879. https://doi.org/10.1016/j.quascirev.2009.03.003

Shuman, B.N., Marsicek, J., 2016. The structure of Holocene climate change in mid-latitude North America. Quat. Sci. Rev. 141, 38–51. https://doi.org/10.1016/j.quascirev.2016.03.009

Shuman, B.N., Serravezza, M., 2017. Patterns of hydroclimatic change in the Rocky Mountains and surrounding regions since the last glacial maximum. Quat. Sci. Rev. 173, 58–77. https://doi.org/10.1016/j.quascirev.2017.08.012

Sly, S., 2020. Late holocene vegetation and fire history in subalpine forests of southwestern montana. Master's Thesis, Montana State University.

Smith, L.N., 2017. Repeated sedimentation and exposure of glacial Lake Missoula sediments: A lake-level history at Garden Gulch, Montana, USA. Quat. Sci. Rev. 155, 114–126. https://doi.org/10.1016/j.quascirev.2016.11.018

Solomina, O., Bradley, R., Hodgson, D., Ivy-Ochs, S., Jomelli, V., Mackintosh, A., Nesje, A., Owen, L., Wanner, H., Wiles, G., 2015. Holocene glacier fluctuations. Quat. Sci. Rev. 111. https://doi.org/10.1016/j.quascirev.2014.11.018

Stevens LR, Stone JR, Campbell J et al., 2006. A 2200-yr record of hydrologic variability from Foy Lake, Montana, USA, inferred from diatom and geochemical data. Quaternary Research 65(2): 264–274.

Stone, J., Fritz, S., 2006. Multidecadal Drought and Holocene Climate Instability in the Rocky Mountains. Geology. https://doi.org/10.1130/G22225.1

Stone, J.R., Saros, J.E., Pederson, G.T., 2016. Coherent late-Holocene climate-driven shifts in the structure of three Rocky Mountain lakes. The Holocene 26, 1103–1111. https://doi.org/10.1177/0959683616632886

Walsh, M.K., Duke, H.J., Haydon, K.C., 2018. Toward a better understanding of climate and human impacts on late Holocene fire regimes in the Pacific Northwest, USA. Prog. Phys. Geogr. Earth Environ. 42, 478–512. https://doi.org/10.1177/0309133318783144

Wanner, H., Solomina, O., Grosjean, M., Ritz, S.P., Jetel, M., 2011. Structure and origin of Holocene cold events. Quat. Sci. Rev. 30, 3109–3123. https://doi.org/10.1016/j.quascirev.2011.07.010

Watt, J.H., Brunelle, A., Brewer, S., Bentz, B., Morris, J., DeRose, R.J., 2022. A Holocene Record of Vegetation Change and Mountain Pine Beetle Outbreaks at Lake of the Woods, Montana, USA. West. North Am. Nat. 82. https://doi.org/10.3398/064.082.0308

Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H., Ryan, M.G., 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proc. Natl. Acad. Sci. 108, 13165–13170. https://doi.org/10.1073/pnas.1110199108

Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

Whitlock, C., 1993. Postglacial Vegetation and Climate of Grand Teton and Southern Yellowstone National Parks. Ecol. Monogr. 63, 173–198. https://doi.org/10.2307/2937179

Whitlock, C., Larsen, C., 2001. Charcoal as a Fire Proxy, in: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, Developments in Paleoenvironmental Research. Springer Netherlands, Dordrecht, pp. 75–97. https://doi.org/10.1007/0-306-47668-1_5

CHAPTER FIVE

CONCLUSIONS

This dissertation increases our understanding of temperate forest dynamics in western Montana by providing new pollen and charcoal records from underrepresented regions and forest types. The three studies compare new records with existing paleoenvironmental analyses to develop a regional reconstruction of postglacial climate, vegetation, and fire history. The primary objectives were to address these questions: 1) How did vegetation structure across all elevations respond to late-glacial and Holocene climate changes? And 2) How did fire activity vary with changes in climate and forest structure? These studies present the history of forest development and fire activity across biophysical gradients and examine how climate influenced vegetation structure and fire activity. The paleoenvironmental analyses presented in this dissertation provide new findings, support previous research, and highlight time periods that warrant further investigation.

The evolution of forests in western Montana since the Last Glacial Maximum has involved both periods of stability and change. The most significant variations were driven by the millennial-scale changes in the seasonal cycle of insolation, but there were also shorter, centennial-scale shifts superimposed on the larger insolation-driven climate patterns. Fire was prevalent across the landscape throughout the last 13,000 years, with few instances of high fire activity across elevations. Despite periods of synchronous changes in fire activity, most instances were not associated with major shifts in vegetation. The lack of a clear relationship between fire activity and vegetation change through time indicates that forest structure and fire respond to

different aspects of the climate system. Forest structure is more aligned with millennial-scale climate changes, and fire activity responds to both forest structure, as well as decadal-to-centennial scale climate variability.

Vegetation History of Western Montana

A postglacial tundra-steppe and parkland period was followed by the establishment of subalpine forests at higher elevations (above 1500 m asl) and pine forests at lower elevations at ca. 13,500 cal yr BP in northwestern Montana (Ch. 4), and between 12,000 and 11,000 cal yr BP in the Greater Yellowstone Ecosystem (Ch. 2, 3). From approximately 10,000 to 6,000 cal yr BP, Douglas-fir dominated the region, particularly at lower elevations, creating an open Douglas-fir parkland (Ch. 3, 4). The timing of the transition into and out of Douglas-fir parkland occurred later for some sites in the GYE (ca. 8000 cal yr BP) due to the summer-wet climate patterns (discussed in Ch. 3) that caused these sites to experience arid conditions later than the sites in the north (Millspaugh et al., 2004; Whitlock and Bartlein, 1993). Lower treeline migrated upslope, and Ponderosa pine and Douglas-fir were found at elevations higher than they are currently located (Ch. 3, 4). In some high-elevation areas (>3000 masl on the Beartooth Plateau), upper treeline moved downslope due to moisture limitations (Ch. 2), while forests were most dense at mid-to-high elevations (1500-2500 masl) due to topographic factors that retained moisture despite warmer-than-present summer temperatures (Ch. 3). Pine gradually began to populate the parklands at lower elevations (<1500 masl) at ca. 8,000 cal yr BP, and most sites had a change in forest structure to resemble present-day forest types between 6,000 and 5,000 cal yr BP (Ch. 3, 4). Forest composition remained relatively constant during the late Holocene, although there were subtle changes between ca. 4000-3000 cal yr BP. At this time, treeline was lowered on the

Beartooth Plateau, and spruce and fir increased in northern Montana (Ch. 2, 4). All the sites show a slight reorganization in density and/or composition at ca. 3,000 cal yr BP (Ch. 2,3,4).

Fire History of Western Montana

Following the expansion of woody vegetation across Montana's postglacial environment, fire activity generally increased from the late-glacial period to the late Holocene. Changes in vegetation structure were often associated with shifts in fire activity; however, fluctuations in fire activity did not always result in changes in vegetation.

Fire activity increased with rising summer insolation levels during the late-glacial to early Holocene and catalyzed a shift in vegetation from spruce parkland to pine forest (Ch. 3; Krause and Whitlock, 2017). The vegetation change from pine forest to open parkland in the early Holocene led to decreased fire activity despite warm and dry conditions. Less severe, surface fires may explain the open parkland vegetation structure (Ch. 2, 3, 4). Fire activity increased between ca. 6000 and 5000 cal yr BP with the development of denser forests at all elevations (Ch. 2, 3, 4). Once low-elevation closed forests were established at ca. 5000 cal yr BP, fire activity decreased, although fire-episode frequency was high. In contrast, fire activity increased at high elevations, although fire-episode frequency was low. This indicates more frequent low-severity fires at low elevations and less frequent high-severity fires at upper elevations (Ch. 4)**.** The synchronous increase in fire activity at all elevations at ca. 2500-2000 cal yr BP was likely a response to a prolonged period of warm and dry conditions that was not of sufficient duration to evoke a change in vegetation structure or composition (Ch. 2, 3, 4). This pattern suggests that

periods of high fire activity can maintain vegetation structure as long as environmental conditions permit post-fire regeneration, such as a return to generally cooler and wetter climate conditions. Fire activity generally increased during the late Holocene, likely due to a combination of dense forests and increased climate variability, which allowed for the growth, desiccation, and burning of vegetation. This period also coincided with high human populations.

Key findings

This research has led to several key findings as described in this dissertation and the multi-authored publications. Chapter 2 (Alt et al. 2024) is a study of environmental change on the Beartooth Plateau that highlights the significance of growing-season temperature and moisture on forest development and treeline position at high elevations. Upper treeline shifted upslope and downslope several times since the late-glacial period, most notably when it moved downslope during the early Holocene, likely due to a decrease in effective moisture. The relation between past treeline and climate indicates that treeline position may not move upslope in the future in response to warming growing-season temperatures if moisture is insufficient.

Chapter 3 (Alt et al. 2025; in press) investigates long-term environmental change at Langohr Wetland, a site surrounded by a dense, mid-elevation mixed-conifer forest, and highlights the significance of groundwater-fed wetlands and their surrounding forests as settings that provide relatively stable conditions over millennia. Langohr Wetland sustained a spruce and pine forest throughout most of the Holocene, even during warm and dry periods when forests at higher and lower elevations changed their structure. Forested areas in locations that may be wetter than their surroundings due to topographic influences (e.g., wind channels that bring in cold air and moisture, springs, etc.) can act as refuges for species during adverse conditions,

helping to preserve biodiversity. The mesic conditions supplied sufficient moisture to maintain forests and reduce fire activity.

Chapter 4 (Alt et al., in prep) explores a suite of paleoenvironmental records across a broad biophysical gradient in western Montana and reveals that low-elevation forests are particularly vulnerable to warm, dry conditions. It also demonstrates how periods of fire activity are linked to both vegetation structure and decadal-to-centennial-scale climate variability. Fire activity was lowest during the early Holocene despite warm and dry conditions, when fire-resistant trees were more abundant, and open vegetation covered the lower elevations. Dense forests that developed during cool and wet conditions, together with extended warm and dry periods, contributed to the most significant fire activity across all elevations.

Future Investigations

This research highlights several examples where multiple proxy records indicate a potential widespread shift in past climate that warrants further study. One of these periods is the potential late Holocene cold reversal between ca. 4000-3000 cal yr BP. The Meltwater Pond hiatus and the increase in ice accumulation at the TL1 ice patch during this time coincide with increased pollen from cold and wet-adapted trees, such as spruce and fir, in the Mission Range. Although there was no change in vegetation at Langohr Wetland during this same time, a decrease in overall charcoal levels suggests that fire activity was suppressed, possibly as a response to cold and wet conditions. While independent paleoclimate proxy data both support (Benes et al., 2019; Chellman et al., 2021; Larsen et al., 2020) and contradict (Liefert and Shuman, 2022, 2020; Stone et al., 2016) a phase of cold and wet conditions, the records in this dissertation predominantly indicate a cold and wet period. Future investigations would help us

better understand the spatial and temporal boundaries and identify the potential climate mechanisms responsible for a return to cold conditions in the late Holocene.

A period of high fire activity between ca. 2500 and 2000 cal yr BP is particularly noteworthy, as it is recorded at several sites in the NRM and the GYE. This period is evident at locations from the Canadian Rockies to the Mission Range, as well as at Langohr Wetland, various locations in Yellowstone National Park, and on the Beartooth Plateau, indicating a widespread warm and dry period. Future research should aim to better define this period through well-dated, high-resolution pollen and charcoal studies from various locations in the NRM and beyond, and explore other proxies and climate models to enhance understanding of the climate controls and the spatial and temporal extent of this drought.

Finally, understanding the rate of vegetation change during significant ecosystem transitions is important for assessing the resilience of ecosystem to environmental change. For example, the shift from forest to parkland in the early Holocene and from parkland to forest in the middle Holocene are examples of vegetation shifts that could be better constrained. More precisely dated, high-resolution pollen sequences surrounding these transitions can help define the timeframe for the dynamics of ecosystem changes, enhancing our ability to evaluate future ecosystem rates rates due to fluctuations in temperature and moisture.

Final Remarks

Forest ecosystems have endured variations in climate and disturbance since their formation at the end of the last ice age. Although no species became locally extinct, forest structure is sensitive to climate and can shift dramatically, especially during warm, dry conditions. Trees can shift their biogeographic range (both in elevation and latitude) in response

to changing climate conditions, and this change can occur in a non-linear fashion with temperature, depending on moisture availability. During warm and dry periods, naturally mesic areas can act as climate and fire refugia for species to survive.

Projected increases in temperature and aridity threaten our forests in several ways. Fire activity may intensify in both severity and frequency across all forest types, similar to what has been inferred between ca. 2500 and 2000 cal yr BP. An increase in fire frequency can hinder sufficient fuel growth between fire events, while heightened severity in a warming climate will impede post-fire regeneration, potentially leading to a shift toward a more open vegetation structure, reminiscent of the early Holocene when large-scale transitions to parkland occurred for thousands of years. At some point, limited fuel could lead to fire decline, establishing a new equilibrium between open vegetation and climate (Parks et al., 2016). Changes in the seasonality of moisture could prevent upslope tree expansion, limiting forests to climate and fire refugia that retain cool and wet conditions. Although the forests of the northern Rocky Mountains have shown resilience in the past, projected changes in moisture seasonality, along with warmer and drier conditions (Hostetler et al., 2021), could usher in an era characterized by significantly more open forest structures. This shift would have significant impacts on the hydrological cycle and the various ecosystem services provided by forests, to which humanity would need to adapt.

References

Alt, M., Puseman, K., Lee, C.M., Pederson, G.T., McConnell, J.R., Chellman, N.J., McWethy, D.B., 2024. Organic layers preserved in ice patches: A new record of Holocene environmental change on the Beartooth Plateau, USA. The Holocene 34, 338–352. https://doi.org/10.1177/09596836231211877

Benes, J., Iglesias, V., Whitlock, C., 2019. Postglacial vegetation dynamics at high elevation Benes, J., Iglesias, V., Whitlock, C., 2019. Postglacial vegetation dynamics at high elevation from Fairy Lake in the northern Greater Yellowstone Ecosystem, Montana, USA. Quaternary Research 92, 1–16. https://doi.org/10.1017/qua.2019.9

Chellman, N.J., Pederson, G.T., Lee, C.M., McWethy, D.B., Puseman, K., Stone, J.R., Brown, S.R., McConnell, J.R., 2021. High elevation ice patch documents Holocene climate variability in the northern Rocky Mountains. Quaternary Science Advances 3, 100021. https://doi.org/10.1016/j.qsa.2020.100021

Hostetler, S., Whitlock, C., Shuman, B., et al., 2021. *Greater Yellowstone climate assessment: past, present, and future climate change in greater Yellowstone watersheds.* Montana State University, Institute on Ecosystems, Montana. https://doi.org/10.15788/GYCA2021.

Krause, T.R., Whitlock, C., 2017. Climatic and non-climatic controls shaping early postglacial conifer history in the northern Greater Yellowstone Ecosystem, USA. J. Quaternary Sci. 32, 1022–1036. https://doi.org/10.1002/jqs.2973

Larsen, D.J., Crump, S.E., Blumm, A., 2020. Alpine glacier resilience and Neoglacial fluctuations linked to Holocene snowfall trends in the western United States. Sci. Adv. 6, eabc7661. https://doi.org/10.1126/sciadv.abc7661

Liefert, D.T., Shuman, B.N., 2022. Expression of the “4.2 ka event” in the southern Rocky Mountains, USA. Clim. Past 18, 1109–1124. https://doi.org/10.5194/cp-18-1109-2022

Liefert, D.T., Shuman, B.N., 2020. Pervasive Desiccation of North American Lakes During the Late Quaternary. Geophys. Res. Lett. 47. https://doi.org/10.1029/2019GL086412

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2004. Postglacial Fire, Vegetation, and Climate History of the Yellowstone- Lamar and Central Plateau Provinces, Yellowstone National Park, in: After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press, pp. 10–28.

Parks, S.A., Miller, C., Abatzoglou, J.T., Holsinger, L.M., Parisien, M.-A., Dobrowski, S.Z., 2016. How will climate change affect wildland fire severity in the western US? Environ. Res. Lett. 11, 035002. https://doi.org/10.1088/1748-9326/11/3/035002

Stone, J.R., Saros, J.E., Pederson, G.T., 2016. Coherent late-Holocene climate-driven shifts in the structure of three Rocky Mountain lakes. The Holocene 26, 1103–1111. https://doi.org/10.1177/0959683616632886

Whitlock, C., Bartlein, P.J., 1993. Spatial Variations of Holocene Climatic Change in the Yellowstone Region. Quaternary Research 39, 231–238. https://doi.org/10.1006/qres.1993.1026

CUMULATIVE REFERENCES CITED

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113, 11770–11775. https://doi.org/10.1073/pnas.1607171113

Agee, J.K., 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.

Alder, J.R., Hostetler, S.W., 2015. Global climate simulations at 3000-year intervals for the last 21 000 years with the GENMOM coupled atmosphere–ocean model. Climate of the Past 11, 449–471. https://doi.org/10.5194/cp-11-449-2015

Alizadeh, M.R., Abatzoglou, J.T., Adamowski, J., Modaresi Rad, A., AghaKouchak, A., Pausata, F.S.R., Sadegh, M., 2023. Elevation-dependent intensification of fire danger in the western United States. Nat. Commun. 14, 1773. https://doi.org/10.1038/s41467-023-37311-4

Alizadeh, M.R., Abatzoglou, J.T., Luce, C.H., Adamowski, J.F., Farid, A., Sadegh, M., 2021. Warming enabled upslope advance in western US forest fires. Proc. Natl. Acad. Sci. U. S. A. 118, e2009717118. https://doi.org/10.1073/pnas.2009717118

Alt, M., McWethy, D., Everett, R., Whitlock, C., 2018. Millennial scale climate-fire-vegetation interactions in a mid-elevation mixed coniferous forest, Mission Range, northwestern Montana, USA. Quaternary Research 90, 1–17. https://doi.org/10.1017/qua.2018.25

Alt, M., Puseman, K., Lee, C.M., Pederson, G.T., McConnell, J.R., Chellman, N.J., McWethy, D.B., 2024. Organic layers preserved in ice patches: A new record of Holocene environmental change on the Beartooth Plateau, USA. The Holocene 34, 338–352. https://doi.org/10.1177/09596836231211877

Andrus, R.A., Harvey, B.J., Rodman, K.C., Hart, S.J., Veblen, T.T., 2018. Moisture availability limits subalpine tree establishment. Ecology 99, 567–575. https://doi.org/10.1002/ecy.2134

Arno, S.F., 1979. Forest Regions of Montana. United States Department of Agriculture, Forest Service Research Paper, INT-218, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Arno, S.F., Parsons, D.J., Keane, R.E., 2000. Mixed-severity fire regimes in the Northern Rocky Mountains: consequences of fire exclusion and options for the future. United States Department of Agriculture Forest Service Proceedings RMRS-P-15 5, 225–233.

Ault, T.R., Cole, J.E., Overpeck, J.T., Pederson, G.T., St. George, S., Otto-Bliesner, B., Woodhouse, C.A., Deser, C., 2013. The Continuum of Hydroclimate Variability in Western North America during the Last Millennium. J. Clim. 26, 5863–5878. https://doi.org/10.1175/JCLI-D-11-00732.1

Ault, T.R., St. George, S., Smerdon, J.E., Coats, S., Mankin, J.S., Carrillo, C.M., Cook, B.I., Stevenson, S., 2018. A Robust Null Hypothesis for the Potential Causes of Megadrought in Western North America. J. Clim. 31, 3–24. https://doi.org/10.1175/JCLI-D-17-0154.1

Baker, W.L., 2009. Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington, DC

Barnard, D.M., Barnard, H.R., Molotch, N.P., 2017. Topoclimate effects on growing season length and montane conifer growth in complex terrain. Environ. Res. Lett. 12, 064003. https://doi.org/10.1088/1748-9326/aa6da8

Barr, C., Tibby, J., Leng, M.J., Tyler, J.J., Henderson, A.C.G., Overpeck, J.T., Simpson, G.L., Cole, J.E., Phipps, S.J., Marshall, J.C., McGregor, G.B., Hua, Q., McRobie, F.H., 2019. Holocene El Niño–Southern Oscillation variability reflected in subtropical Australian precipitation. Sci. Rep. 9, 1627. https://doi.org/10.1038/s41598-019-38626-3

Barrett, S.W., 1993. Fire history of Tenderfoot Creek Experimental Forest, Lewis and Clark National Forest. Final Report INT-92679-RJVA. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory. 23 p.

Barrett, S.W., Arno, S.F., Menakis, J.P., 1997. Fire episodes in the Inland Northwest (1540–1940) based on fire history data. Gen. Tech. Rep. INT–370. Ogden, UT: USDA Forest Service

Barth, A.M., Ceperley, E.G., Vavrus, C., Marcott, S.A., Shakun, J.D., Caffee, M.W., 2022. ^{10}Be age control of glaciation in the Beartooth Mountains, USA from the latest Pleistocene through the Holocene. Geochronol. Discuss. 1–18. https://doi.org/10.5194/gchron-2022-17

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quaternary Science Reviews 17, 549–585. https://doi.org/10.1016/S0277-3791(98)00012-2

Benedict, J.B., 2011. Sclerotia as indicators of mid-Holocene tree-limit altitude, Colorado Front Range, USA. The Holocene 21, 1021–1023. https://doi.org/10.1177/0959683610395078

Benedict, J.B., Benedict, R.J., Lee, C.M., Staley, D.M., 2008. Spruce trees from a melting ice patch: evidence for Holocene climatic change in the Colorado Rocky Mountains, USA. The Holocene 18, 1067–1076. https://doi.org/10.1177/0959683608095578

Benes, J., Iglesias, V., Whitlock, C., 2019. Postglacial vegetation dynamics at high elevation from Fairy Lake in the northern Greater Yellowstone Ecosystem, Montana, USA. Quaternary Research 92, 1–16. https://doi.org/10.1017/qua.2019.9

Bennett, K.D., Willis, K.J., 2001. Pollen. In: Smol JP, Birks HJB and Last WM (eds) *Tracking*

Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, 3. Dordrecht: Kluwer Academic Publishers, pp. 5–32.

Berger, A., 1978. Long-term variations of caloric insolation resulting from the earth's orbital elements. Quaternary Research 9: 139–167.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. https://doi.org/10.1214/11-BA618

Bonan, G.B., 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science 320, 1444–1449. https://doi.org/10.1126/science.1155121

Boyd, R. (1999). Indians, fire and the Land in the Pacific Northwest. Corvallis: Oregon State University Press.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., Van Der Werf, G.R., Pyne, S.J., 2009. Fire in the Earth System. Science 324, 481–484. https://doi.org/10.1126/science.1163886

Bracht-Flyr, B., Fritz, S.C., 2012. Synchronous climatic change inferred from diatom records in four western Montana lakes in the U.S. Rocky Mountains. Quat. res. 77, 456–467. https://doi.org/10.1016/j.yqres.2011.12.005

Brunelle, A., Whitlock, C., Bartlein, P., Kipfmueller, K., 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. Quaternary Science Reviews 24, 2281–2300. https://doi.org/10.1016/j.quascirev.2004.11.010

Cappers, R.T.J., Bekker, R.M., 2013. *A Manual for the Identification of Plant Seeds and Fruits. Groningen Archaeological Studies, Vol. 23.* Barkuis Publishing, Eelde.

Carlquist, S., 1988. *Comparative Wood Anatomy*. Springer-Verlag, Berlin.

Carrara, P.E., 1995. A 12 000 year radiocarbon date of deglaciation from the Continental Divide of northwestern Montana. Can. J. Earth Sci. 32, 1303–1307. https://doi.org/10.1139/e95-106

Carter, V.A., Power, M.J., Lundeen, Z.J., Morris, J.L., Petersen, K.L., Brunelle, A., Anderson, R.S., Shinker, J.J., Turney, L., Koll, R., Bartlein, P.J., 2018. A 1,500-year synthesis of wildfire activity stratified by elevation from the U.S. Rocky Mountains. Quat. Int. 488, 107–119. https://doi.org/10.1016/j.quaint.2017.06.051

Chellman, N.J., Pederson, G.T., Lee, C.M., McWethy, D.B., Puseman, K., Stone, J.R., Brown, S.R., McConnell, J.R., 2021. High elevation ice patch documents Holocene climate

variability in the northern Rocky Mountains. Quaternary Science Advances 3, 100021. https://doi.org/10.1016/j.qsa.2020.100021

Clark-Wolf, K., Higuera, P.E., Shuman, B.N., McLauchlan, K.K., 2023. Wildfire activity in northern Rocky Mountain subalpine forests still within millennial-scale range of variability. Environ. Res. Lett. 18, 094029. https://doi.org/10.1088/1748-9326/acee16

Clark-Wolf, K.D., Higuera, P.E., McLauchlan, K.K., Shuman, B.N., Parish, M.C., 2023. Fire-regime variability and ecosystem resilience over four millennia in a Rocky Mountain subalpine watershed. J. Ecol. 1365-2745.14201. https://doi.org/10.1111/1365-2745.14201

Confederated Salish and Kootenai Tribes (CKST), Division of Fish, Wildlife, Recreation, and Conservation, 2021. Fire on the Land. https://fwrconline.csktnrd.org/Fire/index.html.

Conroy, J.L., Overpeck, J.T., Cole, J.E., Shanahan, T.M., Steinitz-Kannan, M., 2008. Holocene changes in eastern tropical Pacific climate inferred from a Galápagos lake sediment record. Quat. Sci. Rev. 27, 1166–1180. https://doi.org/10.1016/j.quascirev.2008.02.015

Cook, E.R., Seager, R., Heim, R.R., Vose, R.S., Herweijer, C., Woodhouse, C., 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context: MEGADROUGHTS IN NORTH AMERICA. J. Quat. Sci. 25, 48–61. https://doi.org/10.1002/jqs.1303

Cook, E.R., Woodhouse, C.A., Eakin, M.C., Meko, D.M., Stahle, D.W., 2004. Long-term aridity changes in the western United States. Science 306, 1015–1018.

Core, H.A., Côté, W.A., Day, A.C., 1976. *Wood Structure and Identification.* Syracuse University Press*,* New York.

Davis, M.B., Brubaker, L.B., Webb, T., (1973). Calibration of pollen influx. In: *Quaternary Plant Ecology* (eds: H.J.B. Birks and R.G. West). Blackwell.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences 116, 6193–6198. https://doi.org/10.1073/pnas.1815107116

Delorit, R.J., 1970. *An Illustrated Taxonomy Manual of Weed Seeds.* Wisconsin State University Agronomy Publications, River Falls.

Denton, G.H., Karlén, W., 1973. Holocene climatic variations; their pattern and possible cause. Quat. Res. 3, 155-205.

Diffenbaugh, N.S., Ashfaq, M., Shuman, B., Williams, J.W., Bartlein, P.J., 2006. Summer aridity in the United States: Response to mid-Holocene changes in insolation and sea surface temperature. Geophys. Res. Lett. 33. https://doi.org/10.1029/2006GL028012

Dilworth, J.R., McGlue, M.M., Thigpen, R.J., Brown, S.J., Yeager, K.M., Woolery, E.W., Johnson, S.E., Whitehead, S.J., Cortese, C.J., Matocha, C., 2024. Holocene paleoenvironmental history of Jackson Lake (Grand Teton National Park, USA) deduced from CHIRP seismic reflection and radiocarbon-dated sediment cores. Quat. Sci. Rev. 336, 108748. https://doi.org/10.1016/j.quascirev.2024.108748

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Erickson, 2010. Bozeman Municipal Watershed Final Environmental Impact Statement. USDA, Forest Service, Custer Gallatin Forest Service, Bozeman, MT.

Erickson, 2022. Final Environmental Impact Statement. USDA, Forest Service Publication no. R1-22-03a, Custer Gallatin Forest Service, Bozeman, MT

Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analysis 4th ed.* New Jersey: The Blackburn Press.

Fall, P.L., 1994. Modern Pollen Spectra and Vegetation in the Wind River Range, Wyoming, U.S.A. Arct. Alp. Res. 26, 383–392. https://doi.org/10.2307/1551800

Fall, P.L., 1992. Pollen accumulation in a montane region of Colorado, USA: a comparison of moss polsters, atmospheric traps, and natural basins. Rev. Palaeobot. Palynol. 72, 169–197. https://doi.org/10.1016/0034-6667(92)90026-D

Fall, P.L., Davis, P.T., Zielinski, G.A., 1995. Late Quaternary Vegetation and Climate of the Wind River Range, Wyoming. Quaternary Research 43, 393.

Fischer, W.C., Bradley, A.F., 1987. Fire ecology of western Montana forest habitat types (No. INT-GTR-223). U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT. https://doi.org/10.2737/INT-GTR-223

Gajewski, K., Munoz, S., Peros, M., Viau, A., Morlan, R., and Betts, M. (2011). The Canadian Archaeological Radiocarbon Database (Card): archaeological 14C Dates in North America and their paleoenvironmental context. Radiocarbon 53, 371–394. doi: 10.1017/S0033822200056630

Gangopadhyay, S., Woodhouse, C.A., McCabe, G.J., Routson, C.C., Meko, D.M., 2022. Tree Rings Reveal Unmatched 2nd Century Drought in the Colorado River Basin. Geophys. Res. Lett. 49, e2022GL098781. https://doi.org/10.1029/2022GL098781

Gavin, D.G., Oswald, W.W., Wahl, E.R., Williams, J.W., 2003. A statistical approach to evaluating distance metrics and analog assignments for pollen records. Quat. Res. 60, 356–367. https://doi.org/10.1016/S0033-5894(03)00088-7

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35. https://doi.org/10.1016/0098-3004(87)90022-7

Gugger, P.F., Sugita, S., 2010. Glacial populations and postglacial migration of Douglas-fir based on fossil pollen and macrofossil evidence. Quat. Sci. Rev. 29, 2052–2070. https://doi.org/10.1016/j.quascirev.2010.04.022

Hallett, D., Walker, R., 2000. Paleoecology and its application to fire and vegetation management in Kootenay National Park, British Columbia. J. Paleolimnol. 24, 401–414. https://doi.org/10.1023/A:1008110804909

Hallett, D.J., Hills, L.V., 2006. Holocene Vegetation Dynamics, Fire History, Lake Level and Climate Change in the Kootenay Valley, Southeastern British Columbia, Canada. J. Paleolimnol. 35, 351–371. https://doi.org/10.1007/s10933-005-1335-6

Hanberry, B.B., Justice, D.C., Powell, D.C., 2020. Discovering Douglas-Fir Woodlands in the Historical Forests of Umatilla National Forest, Eastern Oregon and Washington. Forests 11, 1122. https://doi.org/10.3390/f11101122

Harsch, M.A., Bader, M.Y., 2011. Treeline form - a potential key to understanding treeline dynamics: The causes of treeline form. Glob. Ecol. Biogeogr. 20, 582–596. https://doi.org/10.1111/j.1466-8238.2010.00622.x

Hebda, R., 1995. British Columbia Vegetation and Climate History with Focus on 6 ka BP. Géographie Phys. Quat. 49. https://doi.org/10.7202/033030ar

Heidel, B., Fertig, W., Mellmann-Brown, S., Houston, K.E., Dwire, K.A., 2017. Fens and their rare plants in the Beartooth Mountains, Shoshone National Forest, Wyoming (No. RMRS-GTR-369). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO. https://doi.org/10.2737/RMRS-GTR-369

Heyerdahl, E.K., Morgan, P., Riser, J.P., 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), northern Rockies, USA. Ecology 89, 705–716. https://doi.org/10.1890/06-2047.1

Higuera, P., 2009. CharAnalysis 0.9: Diagnostic and analytical tools for sediment-charcoal analysis.

Higuera, P.E., Abatzoglou, J.T., Littell, J.S., Morgan, P., 2015. The Changing Strength and Nature of Fire-Climate Relationships in the Northern Rocky Mountains, U.S.A., 1902-2008. PLOS ONE 10, e0127563. https://doi.org/10.1371/journal.pone.0127563

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol. Monogr. 79, 201–219. https://doi.org/10.1890/07-2019.1

Higuera, P.E., Whitlock, C., Gage, J.A., 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. The Holocene 21, 327–341. https://doi.org/10.1177/0959683610374882

Higuera, P.E., Shuman, B.N., Wolf, K.D., 2021. Rocky Mountain subalpine forests now burning more than any time in recent millennia. Proc. Natl. Acad. Sci. 118, e2103135118. https://doi.org/10.1073/pnas.2103135118

Hoadley, R.B., 1990. *Identifying Wood: Accurate Results with Simple Tools*. The Taunton Press, Newtown, CT.

Hoch, G., Körner, C., 2009. Growth and carbon relations of tree line forming conifers at constant vs. variable low temperatures. J. Ecol. 97, 57–66. https://doi.org/10.1111/j.1365-2745.2008.01447.x

Hofmann, M.H., Hendrix, M.S., 2010. Depositional processes and the inferred history of ice-margin retreat associated with the deglaciation of the Cordilleran Ice Sheet: The sedimentary record from Flathead Lake, northwest Montana, USA. Sediment. Geol. 223, 61–74. https://doi.org/10.1016/j.sedgeo.2009.10.004

Hofmann, M.H., Hendrix, M.S., Moore, J.N., Sperazza, M., 2006. Late Pleistocene and Holocene depositional history of sediments in Flathead Lake, Montana: Evidence from high-resolution seismic reflection interpretation. Sediment. Geol. 184, 111–131. https://doi.org/10.1016/j.sedgeo.2005.09.019

Hostetler, S., Whitlock, C., Shuman, B., et al., 2021. *Greater Yellowstone climate assessment: past, present, and future climate change in greater Yellowstone watersheds.* Montana State University, Institute on Ecosystems, Montana. https://doi.org/10.15788/GYCA2021.

Huerta, M.A., Whitlock, C., Yale, J., 2009. Holocene vegetation–fire–climate linkages in northern Yellowstone National Park, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 170–181. https://doi.org/10.1016/j.palaeo.2008.10.015

Iglesias, V., Krause, T.R., Whitlock, C., 2015. Complex Response of White Pines to Past Environmental Variability Increases Understanding of Future Vulnerability. PLoS ONE 10, e0124439. https://doi.org/10.1371/journal.pone.0124439

Iglesias, V., Whitlock, C., Krause, T.R., Baker, R.G., 2018. Past vegetation dynamics in the Yellowstone region highlight the vulnerability of mountain systems to climate change. Journal of Biogeography 45, 1768–1780. https://doi.org/10.1111/jbi.13364

InsideWood, 2004. InsideWood Database. Available at: http://insidewood.lib.ncsu.edu/search (accessed 2013-2017).

Jain, T.B., Battaglia, M.A., Han, H.-S., Graham, R.T., Keyes, C.R., Fried, J.S., Sandquist, J.E., 2012. A comprehensive guide to fuel management practices for dry mixed conifer forests in the northwestern United States (No. RMRS-GTR-292). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO. https://doi.org/10.2737/RMRS-GTR-292

Jones, A.G., Marcott, S.A., Gorin, A.L., Kennedy, T.M., Shakun, J.D., Goehring, B.M., Menounos, B., Clark, D.H., Romero, M., Caffee, M.W., 2023. Four North American glaciers advanced past their modern positions thousands of years apart in the Holocene. The Cryosphere 17, 5459–5475. https://doi.org/10.5194/tc-17-5459-2023

Jones, Megan, 2019. Migration or mortality: a study of summed probability distributions and population decline in the bighorn basin of Wyoming. Master's Thesis, University of Wyoming.

Kapp, R.O., Davis, O.K., King, J.E., 2000. *Pollen and Spores. 2nd ed.* American Association of Stratigraphic Palynologists Foundation, Dallas, TX.

Kelly, R.F., Higuera, P.E., Barrett, C.M., Hu, F.S., 2011. Short Paper: A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quat. Res. 75, 11–17. https://doi.org/10.1016/j.yqres.2010.07.011

Kelly, R.L., Mackie, M.E., Robinson, E., Meyer, J., Berry, M., Boulanger, M., Codding, B.F., Freeman, J., Garland, C.J., Gingerich, J., Hard, R., Haug, J., Martindale, A., Meeks, S., Miller, M., Miller, S., Perttula, T., Railey, J.A., Reid, K., Scharlotta, I., Spangler, J., Thomas, D.H., Thompson, V., White, A., 2022. A New Radiocarbon Database for the Lower 48 States. Am. Antiq. 87, 581–590. https://doi.org/10.1017/aaq.2021.157

Kelly, R.L., Surovell, T.A., Shuman, B.N., Smith, G.M., 2013. A continuous climatic impact on Holocene human population in the Rocky Mountains. Proc. Natl. Acad. Sci. 110, 443–447. https://doi.org/10.1073/pnas.1201341110

Knobel, E., 1980. *Field Guide to the Grasses, Sedges and Rushes of the United States.* Dover Publications, New York.

Koch, J., Osborn, G.D., Clague, J.J., 2007. Pre-'Little Ice Age' glacier fluctuations in Garibaldi Provincial Park, Coast Mountains, British Columbia, Canada. Holocene 17, 1069-1078.

Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures: Study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x

Krause, T.R., Lu, Y., Whitlock, C., Fritz, S.C., Pierce, K.L., 2015. Patterns of terrestrial and limnologic development in the northern Greater Yellowstone Ecosystem (USA) during the late-glacial/early-Holocene transition. Palaeogeography, Palaeoclimatology, Palaeoecology 422, 46–56. https://doi.org/10.1016/j.palaeo.2014.12.018

Krause, T.R., Whitlock, C., 2017. Climatic and non-climatic controls shaping early postglacial conifer history in the northern Greater Yellowstone Ecosystem, USA. J. Quaternary Sci. 32, 1022–1036. https://doi.org/10.1002/jqs.2973

Krause, T.R., Whitlock, C., 2013. Climate and vegetation change during the late-glacial/early-Holocene transition inferred from multiple proxy records from Blacktail Pond, Yellowstone National Park, USA. Quat. res. 79, 391–402. https://doi.org/10.1016/j.yqres.2013.01.005

Kutzbach, J., Gallimore, R., Harrison, S., Behling, P., Selin, R., Laarif, F., 1998. Climate and biome simulations for the past 21,000 years. Quaternary Science Reviews 17, 473–506. https://doi.org/10.1016/S0277-3791(98)00009-2

Kyne, J., McConnell, J., 2007. The PrairieDog: a double-barrel coring drill for ‘hand’ augering. Ann. Glaciol. 47, 99–100. https://doi.org/10.3189/172756407786857703

LANDFIRE, 2014. LANDFIRE Mean Fire Return Interval, 2014 – last update. U.S. Department of Interior, Geological Survey, and U.S. Department of Agriculture.[Online]. Available: https://landfire.gov/viewer/ [2024, March 27].

Lantz, T.C., Gergel, S.E., Henry, G.H.R., 2010. Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. J. Biogeogr. 37, 1597–1610. https://doi.org/10.1111/j.1365-2699.2010.02317.x

Lapierre, K., 2021 Long-term environmental history of two low-elevation mixed-conifer forests, Mission Valley, Montana. Master's Thesis, Montana State University.

Larsen, D.J., Crump, S.E., Blumm, A., 2020. Alpine glacier resilience and Neoglacial fluctuations linked to Holocene snowfall trends in the western United States. Sci. Adv. 6, eabc7661. https://doi.org/10.1126/sciadv.abc7661

Lee, C.M., 2012. Withering Snow and Ice in the Mid-latitudes: A New Archaeological and Paleobiological Record for the Rocky Mountain Region. ARCTIC 65, 165-177-165–177. https://doi.org/10.14430/arctic4191

Lee, C.M., Puseman, K., 2017. Ice patch hunting in the Greater Yellowstone Area, Rocky Mountains, USA: wood shafts, chipped stone projectile points, and bighorn sheep (Ovis canadensis). Am. Antiq. 82, 223–243. https://doi.org/10.1017/aaq.2016.32

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. Science 320, 1768–1771. https://doi.org/10.1126/science.1156831

Lepofsky, D., Lertzman, K., Hallett, D., Mathewes, R., 2005. Climate Change and Culture Change on the Southern Coast of British Columbia 2400-1200 Cal. B.P.: An Hypothesis. amnat 70, 267. https://doi.org/10.2307/40035704

Lesica, P., 1986. Vegetation and flora of Pine Butte Fen, Teton County, Montana, Great Basin Naturalist: 46, 22-32. https://scholarsarchive.byu.edu/gbn/vol46/iss1/2

Lesica, P., 2012. *Manual of Montana Vascular Plants.* Brit Press, Fort Worth, TX.

Leunda, M., González-Sampériz, P., Gil-Romera, G., Bartolomé, M., Belmonte-Ribas, Á., Gómez-García, D., Kaltenrieder, P., Rubiales, J.M., Schwörer, C., Tinner, W., Morales-Molino, C., Sancho, C., 2019. Ice cave reveals environmental forcing of long-term Pyrenean tree line dynamics. J. Ecol. 107, 814–828. https://doi.org/10.1111/1365-2745.13077

Leys, B.A., Commerford, J.L., McLauchlan, K.K., 2017. Reconstructing grassland fire history using sedimentary charcoal: Considering count, size and shape. PLOS ONE 12, e0176445. https://doi.org/10.1371/journal.pone.0176445

Li, D., Wrzesien, M.L., Durand, M., Adam, J., Lettenmaier, D.P., 2017. How much runoff originates as snow in the western United States, and how will that change in the future? Geophys. Res. Lett. 44, 6163–6172. https://doi.org/10.1002/2017GL073551

Licciardi, J.M., Pierce, K.L., 2018. History and dynamics of the Greater Yellowstone Glacial System during the last two glaciations. Quat. Sci. Rev. 200, 1–33. https://doi.org/10.1016/j.quascirev.2018.08.027

Liefert, D.T., Shuman, B.N., 2022. Expression of the “4.2 ka event” in the southern Rocky Mountains, USA. Clim. Past 18, 1109–1124. https://doi.org/10.5194/cp-18-1109-2022

Liefert, D.T., Shuman, B.N., 2020. Pervasive Desiccation of North American Lakes During the Late Quaternary. Geophys. Res. Lett. 47. https://doi.org/10.1029/2019GL086412

Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021. https://doi.org/10.1890/07-1183.1

Luckman, B.H., Masiokas, M.H., Nicolussi, K., 2017. Neoglacial history of Robson Glacier, British Columbia. Can. J. Earth Sci. 54, 1153–1164. https://doi.org/10.1139/cjes-2016-0187

Lynch, E.A., 1998. Origin of a park-forest vegetation mosaic in the Wind River Range, Wyoming. Ecology 79, 1320–1338. https://doi.org/10.1890/0012-9658(1998)079[1320:OOAPFV]2.0.CO;2

Mack, R.N., Rutter, N.W., Bryant, V.M., Valastro, S., 1978. Reexamination of postglacial vegetation history in northern Idaho: Hager Pond, Bonner Co. Quaternary Research 10, 241–255. https://doi.org/10.1016/0033-5894(78)90104-7

Mack, R.N., Rutter, N.W., Valastro, S., 1983. Holocene Vegetational History of the Kootenai River Valley, Montana. Quat. res. 20, 177–193. https://doi.org/10.1016/0033-5894(83)90076-5

Mann, M.E., Bradley, R.S., Hughes, M.K., 1999. Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. Geophys. Res. Lett. 26, 759–762. https://doi.org/10.1029/1999GL900070

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G., Ni, F., 2009. Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. Science 326, 1256–1260. https://doi.org/10.1126/science.1177303

Marcus, W. A., Meacham, J. E., Rodman, A. W., Steingisser, A. Y., Menke, J. T., & West, R., 2022. *Atlas of Yellowstone.* Second edition. University of California Press, Oakland, Ca.

Marlon, J., Bartlein, P.J., Whitlock, C., 2006. Fire-fuel-climate linkages in the northwestern USA during the Holocene. The Holocene 16, 1059–1071. https://doi.org/10.1177/0959683606069396

Marsicek, J., Shuman, B.N., Bartlein, P.J., Shafer, S.L., Brewer, S., 2018. Reconciling divergent trends and millennial variations in Holocene temperatures. Nature 554, 92–96. https://doi.org/10.1038/nature25464

Martin, A.C., Barkley, W.D., 2000. *Seed Identification Manual*. The Blackburn Press, Caldwell.

McAndrews, J.H., Berti, A.A., Norris, G.N., 1973. *Key to Quaternary Pollen and Spores of the Great Lakes Region.* Royal Ontario Museum Life Sciences Miscellaneous Publication, Toronto.

McWethy, D., Alt, M., Argiriadis, E., Battistel, D., Everett, R., Pederson, G., 2020. Millennial-Scale Climate and Human Drivers of Environmental Change and Fire Activity in a Dry, Mixed-Conifer Forest of Northwestern Montana. Frontiers in Forests and Global Change 3. https://doi.org/10.3389/ffgc.2020.00044

Mehringer, P., 1985. Late-quaternary pollen records from the interior Pacific northwest and

northern great basin of the United States. In: Bryant Jr. V and Holloway WG (eds.) *Pollen Records of the Late Quaternary North American Sediments.* American Association of Stratigraphic Palynologists foundation, Dallas. pp. 167–189.

Mehringer, P., Arno, S., Petersen, K., 1977. Postglacial History of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arctic and Alpine Research 9, 345. https://doi.org/10.2307/1550528

Menounos, B., Clague, J.J., Osborn, G., Luckman, B.H., Lakeman, T.R., Minkus, R., 2008. Western Canadian glaciers advance in concert with climate change circa 4.2 ka. Geophys. Res. Lett. 35. https://doi.org/10.1029/2008GL033172

Menounos, B., Osborn, G., Clague, J., Luckman, B., 2009. Latest Pleistocene and Holocene glacier fluctuations in western Canada. Quat. Sci. Rev. 1877, 71–1. https://doi.org/10.1016/j.quascirev.2008.10.018

Meulendyk, T., Moorman, B.J., Andrews, T.D., MacKAY, G., 2012. Morphology and Development of Ice Patches in Northwest Territories, Canada. Arctic 65, 43–58.

Meyer, G.A., Wells, S.G., Timothy Jull, A.J., 1995. Fire and alluvial chronology in Yellowstone National Park: Climatic and intrinsic controls on Holocene geomorphic processes. Geol. Soc. Am. Bull. 107, 1211–1230. https://doi.org/10.1130/0016-7606(1995)107<1211:FAACIY>2.3.CO;2

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park 4.

Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2004. Postglacial Fire, Vegetation, and Climate History of the Yellowstone- Lamar and Central Plateau Provinces, Yellowstone National Park, in: After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press, pp. 10–28.

Minckley, T.A., Shriver, R.K., Shuman, B., 2012. Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17 000 years. Ecol. Monogr. 82, 49–68. https://doi.org/10.1890/11-0283.1

Morgan, C., Losey, A., Trout, L., 2014. Late-Holocene paleoclimate and treeline fluctuation in Wyoming's Wind River Range, USA. The Holocene 24, 209–219. https://doi.org/10.1177/0959683613516817

Mote, P.W., Li, S., Lettenmaier, D.P., Xiao, M., Engel, R., 2018. Dramatic declines in snowpack in the western US. Npj Clim. Atmospheric Sci. 1, 2. https://doi.org/10.1038/s41612-018-0012-1

Moy, C.M., Seltzer, G.O., Rodbell, D.T., Anderson, D.M., 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. Nature 420, 162–165. https://doi.org/10.1038/nature01194

MTBS Data Access: Fire Level Geospatial Data, 2021-last revised. MTBS Project. USDA Forest Service/U.S. Geological Survey). Available online: http://mtbs.gov/direct-download [2025, April 24].

Mumma, S.A., Whitlock, C., Pierce, K., 2012. A 28,000year history of vegetation and climate from Lower Red Rock Lake, Centennial Valley, Southwestern Montana, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 326–328, 30–41. https://doi.org/10.1016/j.palaeo.2012.01.036

Munroe, J.S., Crocker, T.A., Giesche, A.M., Rahlson, L.E., Duran, L.T., Bigl, M.F., Laabs, B.J.C., 2012. A lacustrine-based Neoglacial record for Glacier National Park, Montana, USA. Quat. Sci. Rev. 53, 39–54. https://doi.org/10.1016/j.quascirev.2012.08.005

Naficy, C., Sala, A., Keeling, E.G., Graham, J., Deluca, T.H., 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecol. Appl. 20.

Nimick, D.A., Rasmussen, R.S., Woessner, W.W, Schmidt, J.C., 1983. Geologic and hydrologic investigations at Pine Butte and Mcdonald swamps, Teton county, Montana. Scientific Report. The Nature Conservancy, Helena, MT.

Panshin, A.J., de Zeeuw, C., 1980. *Textbook of Wood Technology*. McGraw-Hill Book Co, New York.

Parish, M.C., Wolf, K.D., Higuera, P.E., Shuman, B.N., 2022. Holocene water levels of Silver Lake, Montana, and the hydroclimate history of the Inland Northwest. Quat. Res. 1–13. https://doi.org/10.1017/qua.2022.17

Parks, S.A., Miller, C., Abatzoglou, J.T., Holsinger, L.M., Parisien, M.-A., Dobrowski, S.Z., 2016. How will climate change affect wildland fire severity in the western US? Environ. Res. Lett. 11, 035002. https://doi.org/10.1088/1748-9326/11/3/035002

Pederson, G.T., Betancourt, J.L., McCabe, G.J., 2013. Regional patterns and proximal causes of the recent snowpack decline in the Rocky Mountains, U.S. Geophys. Res. Lett. 40, 1811–1816. https://doi.org/10.1002/grl.50424

Pederson, G.T., Fagre, D.B., Gray, S.T., Graumlich, L.J., 2004. Decadal-scale climate drivers for glacial dynamics in Glacier National Park, Montana, USA. Geophys. Res. Lett. 31. https://doi.org/10.1029/2004GL019770

Pederson, G.T., Graumlich, L.J., Fagre, D.B., Kipfer, T., Muhlfeld, C.C., 2010. A century of climate and ecosystem change in Western Montana: what do temperature trends portend? Clim. Change 98, 133–154. https://doi.org/10.1007/s10584-009-9642-y

Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Change 5, 424–430. https://doi.org/10.1038/nclimate2563

Pfister, R., Kovalchik, B., Arno, S., Presby, R., 1977. Forest habitat types of Montana (General Technical Report No. INT-34). USDA Forest Service.

Pierce, K.L., 1979, History and Dynamics of Glaciation in the Northern Yellowstone National Park Area: U.S. Geological Survey Professional Paper 729-F, 91 p.

Pierce, K., Cannon, K., Meyer, G., Trebesch, M., Watts, R., 2002. Post-glacial inflation-deflation cycles, tilting, and faulting in the Yellowstone Caldera based on Yellowstone Lake shorelines (Open-File Report No. 02–0142), Open-File Report. US Geological Survey.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H.W., Carcaillet, C., Cordova, et al., 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. Clim. Dyn. 30, 887–907. https://doi.org/10.1007/s00382-007-0334-x

Power, M.J., Whitlock, C., Bartlein, P., Stevens, L.R., 2006. Fire and vegetation history during the last 3800 years in northwestern Montana. Geomorphology, Quaternary landscape change and modern process in western North America 75, 420–436. https://doi.org/10.1016/j.geomorph.2005.07.025

Power, M.J., Whitlock, C., Bartlein, P.J., 2011. Postglacial fire, vegetation, and climate history across an elevational gradient in the Northern Rocky Mountains, USA and Canada. Quaternary Science Reviews 30, 2520–2533. https://doi.org/10.1016/j.quascirev.2011.04.012

PRISM Climate Group, 2014. Oregon State University. Available at: https://prism.oregonstate.edu (accessed 20 Feb 2021).

Quadri, P., Silva, L.C.R., Zavaleta, E.S., 2021. Climate-induced reversal of tree growth patterns at a tropical treeline. Sci. Adv. 7, eabb7572. https://doi.org/10.1126/sciadv.abb7572

R core team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rehm, E., Feeley, K.J., 2016. Many species risk mountain top extinction long before they reach the top. Front. Biogeogr. 8. https://doi.org/10.21425/F5FBG27788

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., et al., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). Radiocarbon 62, 725–757. https://doi.org/10.1017/RDC.2020.41

Reis, W., McGrath, D., Elder, K., Kampf, S., Rey, D., 2024. Quantifying Aspect-Dependent Snowpack Response to High-Elevation Wildfire in the Southern Rocky Mountains. Water Resour. Res. 60, e2023WR036539. https://doi.org/10.1029/2023WR036539

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J., Vanderwel, M.C., Verbeeck, H., Villela, D.M., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. Journal of Ecology 103, 5–15. https://doi.org/10.1111/1365-2745.12337

Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31, L09204.

Routson, C.C., Kaufman, D.S., McKay, N.P., Erb, M.P., Arcusa, S.H., Brown, K.J., Kirby, M.E., Marsicek, J.P., Anderson, R.S., Jiménez-Moreno, G., Rodysill, J.R., Lachniet, M.S., Fritz, S.C., Bennett, J.R., Goman, M.F., Metcalfe, S.E., Galloway, J.M., Schoups, G., Wahl, D.B., Morris, J.L., Staines-Urías, F., Dawson, A., Shuman, B.N., Gavin, D.G., Munroe, J.S., Cumming, B.F., 2021. A multiproxy database of western North American Holocene paleoclimate records. Earth Syst. Sci. Data 13, 1613–1632. https://doi.org/10.5194/essd-13-1613-2021

Rust, R.A., Minckley, T.A., 2020. Fire and hydrologically mediated diversity change in subalpine forests through the Holocene. Journal of Vegetation Science 31, 380–391. https://doi.org/10.1111/jvs.12853

Schiller, C.M., Alt, M., Nanavati, W.P., Wendt, J.A.F., Stahle, L.N., 2023. Getting Information from the Past: Palaeoecological Studies of Terrestrial Ecosystems. In: Clifford, N., Cope, M., Gillespie, T., French, S. (Eds), *Key Methods in Geography, 4th ed*. Sage Publications, pp. 393-418.

Schiller, C.M., Whitlock, C., Brown, S.R., 2022. Holocene geo-ecological evolution of Lower Geyser Basin, Yellowstone National Park (USA). Quat. res. 105, 201–217. https://doi.org/10.1017/qua.2021.42

Schnurrenberger, D., Russell, J., Kelts, K., 2003. Classification of lacustrine sediments based on sedimentary components. J. Paleolimnol. 29, 141–154.

Schoennagel, T., Balch, J.K., Brenkert-Smith, H., Dennison, P.E., Harvey, B.J., Krawchuk, M.A., Mietkiewicz, N., Morgan, P., Moritz, M.A., Rasker, R., Turner, M.G., Whitlock, C., 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences of the United States of America 114, 4582–4590. https://doi.org/10.2307/26481841

Schoennagel, T., Veblen, T.T., Romme, W.H., 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. BioScience 54, 661–676. https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2

Schweingruber, F.H., Landolt, W., 2005. The Xylem Database. Available at http://www.wsl.ch/dendropro/xylemdb/index.php?BNAM=Bilder (accessed 2013-2017).

Schwörer, C., Gavin, D.G., Walker, I.R., Hu, F.S., 2017. Holocene tree line changes in the Canadian Cordillera are controlled by climate and topography. J. Biogeogr. 44, 1148–1159. https://doi.org/10.1111/jbi.12904

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nature Clim Change 7, 395–402. https://doi.org/10.1038/nclimate3303

Shapley, M.D., Ito, E., Donovan, J.J., 2009. Lateglacial and Holocene hydroclimate inferred from a groundwater flow-through lake, Northern Rocky Mountains, USA. The Holocene 19, 523–535. http://dx.doi.org.proxybz.lib.montana.edu/10.1177/0959683609104029

Shuman, B., Henderson, A.K., Colman, S.M., Stone, J.R., Fritz, S.C., Stevens, L.R., Power, M.J., Whitlock, C., 2009. Holocene lake-level trends in the Rocky Mountains, U.S.A. Quat. Sci. Rev. 28, 1861–1879. https://doi.org/10.1016/j.quascirev.2009.03.003

Shuman, B., Pribyl, P., Minckley, T.A., Shinker, J.J., 2010. Rapid hydrologic shifts and prolonged droughts in Rocky Mountain headwaters during the Holocene: HOLOCENE DROUGHTS IN THE ROCKY MOUNTAINS. Geophys. Res. Lett. 37, n/a-n/a. https://doi.org/10.1029/2009GL042196

Shuman, B.N., Marsicek, J., 2016. The structure of Holocene climate change in mid-latitude North America. Quat. Sci. Rev. 141, 38–51. https://doi.org/10.1016/j.quascirev.2016.03.009

Shuman, B.N., Serravezza, M., 2017. Patterns of hydroclimatic change in the Rocky Mountains and surrounding regions since the last glacial maximum. Quat. Sci. Rev. 173, 58–77. https://doi.org/10.1016/j.quascirev.2017.08.012

Sly, S., 2020. Late holocene vegetation and fire history in subalpine forests of southwestern montana. Master's Thesis, Montana State University.

Smith, L.N., 2017. Repeated sedimentation and exposure of glacial Lake Missoula sediments: A lake-level history at Garden Gulch, Montana, USA. Quat. Sci. Rev. 155, 114–126. https://doi.org/10.1016/j.quascirev.2016.11.018

Solomina, O., Bradley, R., Hodgson, D., Ivy-Ochs, S., Jomelli, V., Mackintosh, A., Nesje, A., Owen, L., Wanner, H., Wiles, G., 2015. Holocene glacier fluctuations. Quat. Sci. Rev. 111. https://doi.org/10.1016/j.quascirev.2014.11.018

Spaulding, S.A., Stone, J.R., Norton, S.A., Nurse, A., Saros, J.E., 2020. Paleoenvironmental context for the Late Pleistocene appearance of Didymosphenia in a North American alpine lake. Aquat. Sci. 82, 10. https://doi.org/10.1007/s00027-019-0681-9

Stevens LR, Stone JR, Campbell J et al., 2006. A 2200-yr record of hydrologic variability from Foy Lake, Montana, USA, inferred from diatom and geochemical data. Quaternary Research 65(2): 264–274.

Stone, J., Fritz, S., 2006. Multidecadal Drought and Holocene Climate Instability in the Rocky Mountains. Geology. https://doi.org/10.1130/G22225.1

Stone, J.R., Saros, J.E., Pederson, G.T., 2016. Coherent late-Holocene climate-driven shifts in the structure of three Rocky Mountain lakes. The Holocene 26, 1103–1111. https://doi.org/10.1177/0959683616632886

Stuiver, M., Reimer, P.J., 1993. Extended 14C data base and revised CALIB 3.0 14C age calibration program *Radiocarbon* 35: 215-230

Thompson, R.S., Whitlock, C., Bartlein, P.J., et al., 1993. Climatic changes in Western United States since 18,000 yr BP. In: Wright HE, Kutzbach JE, Web III T, et al. (eds.) *Global Climates Since the Last Glacial Maximum.* University of Minnesota Press, Minneapolis, pp. 468–513.

Turner, M.G., Braziunas, K.H., Hansen, W.D., Harvey, B.J., 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc. Natl. Acad. Sci. U.S.A. 116, 11319–11328. https://doi.org/10.1073/pnas.1902841116

Walsh, M.K., Duke, H.J., Haydon, K.C., 2018. Toward a better understanding of climate and human impacts on late Holocene fire regimes in the Pacific Northwest, USA. Prog. Phys. Geogr. Earth Environ. 42, 478–512. https://doi.org/10.1177/0309133318783144

Wanner, H., Solomina, O., Grosjean, M., Ritz, S.P., Jetel, M., 2011. Structure and origin of Holocene cold events. Quat. Sci. Rev. 30, 3109–3123. https://doi.org/10.1016/j.quascirev.2011.07.010

Watt, J.H., Brunelle, A., Brewer, S., Bentz, B., Morris, J., DeRose, R.J., 2022. A Holocene Record of Vegetation Change and Mountain Pine Beetle Outbreaks at Lake of the Woods, Montana, USA. West. North Am. Nat. 82. https://doi.org/10.3398/064.082.0308

Weber, M., 1965. General geology and geomorphology of the Middle Creek area, Gallatin County. Thesis, Montana State College, MT.

Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150178. https://doi.org/10.1098/rstb.2015.0178

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834

Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H., Ryan, M.G., 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. PNAS 108, 13165–13170. https://doi.org/10.1073/pnas.1110199108

Whitlock, C., 1993. Postglacial Vegetation and Climate of Grand Teton and Southern Yellowstone National Parks. Ecological Monographs 63, 173–198. https://doi.org/10.2307/2937179

Whitlock, C., Bartlein, P.J., 1993. Spatial Variations of Holocene Climatic Change in the Yellowstone Region. Quat. Res. 39, 231–238. https://doi.org/10.1006/qres.1993.1026

Whitlock, C., Bartlein, P.J., Van Norman, K.J., 1995. Stability of Holocene Climate Regimes in the Yellowstone Region. Quaternary Research 43, 433–436. https://doi.org/10.1006/qres.1995.1049

Whitlock, C., Briles, C.E., Fernandez, M.C., Gage, J., 2011. Holocene vegetation, fire and climate history of the Sawtooth Range, central Idaho, USA. Quaternary Research 75, 114–124. https://doi.org/10.1016/j.yqres.2010.08.013

Whitlock, C., Dean, W.E., Fritz, S.C., Stevens, L.R., Stone, J.R., Power, M.J., Rosenbaum, J.R., Pierce, K.L., Bracht-Flyr, B.B., 2012. Holocene seasonal variability inferred from multiple proxy records from Crevice Lake, Yellowstone National Park, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 331–332, 90–103. https://doi.org/10.1016/j.palaeo.2012.03.001

Whitlock, C., Larsen, C., 2001. Charcoal as fire proxy. In: Smol JP, Birks HJB and Last WM (eds) *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, 3.* Kluwer Academic Publishers, Dordrecht, pp. 75–97.

Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

Williams, K.L., 2012. Classification of the grasslands, shrublands, woodlands, forests and alpine vegetation associations of the Beartooth mountains in southcentral Montana. Masters thesis, Montana State University, Montana.

Williams, M.W., Losleben, M., Caine, N., Greenland, D., 1996. Changes in climate and hydrochemical responses in a high-elevation catchment in the Rocky Mountains, USA. Limnology and Oceanography 41, 939–946. https://doi.org/10.4319/lo.1996.41.5.0939

Wise, E.K., Woodhouse, C.A., McCabe, G.J., Pederson, G.T., St-Jacques, J.-M., 2018. Hydroclimatology of the Missouri River Basin. J. Hydrometeorol. 19, 161–182. https://doi.org/10.1175/JHM-D-17-0155.1

APPENDICES

APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER 2

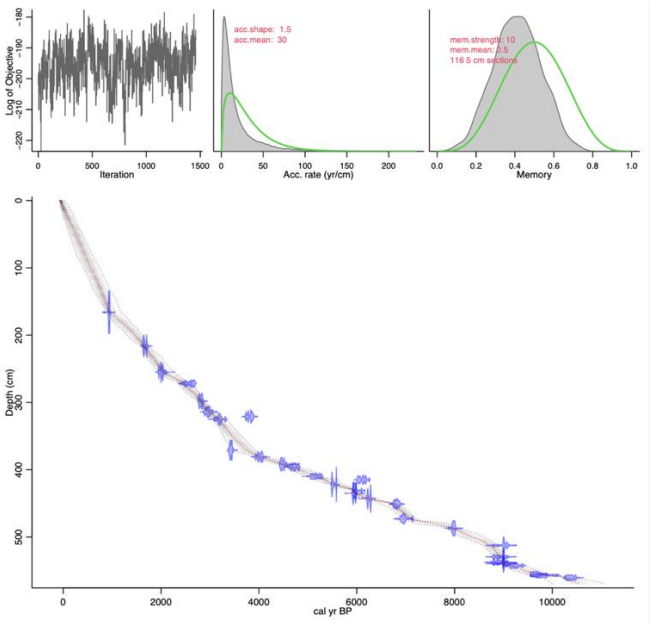


Fig SM2.1 Age-depth diagram for the TL1 Ice Patch, based on 29 radiocarbon dates.

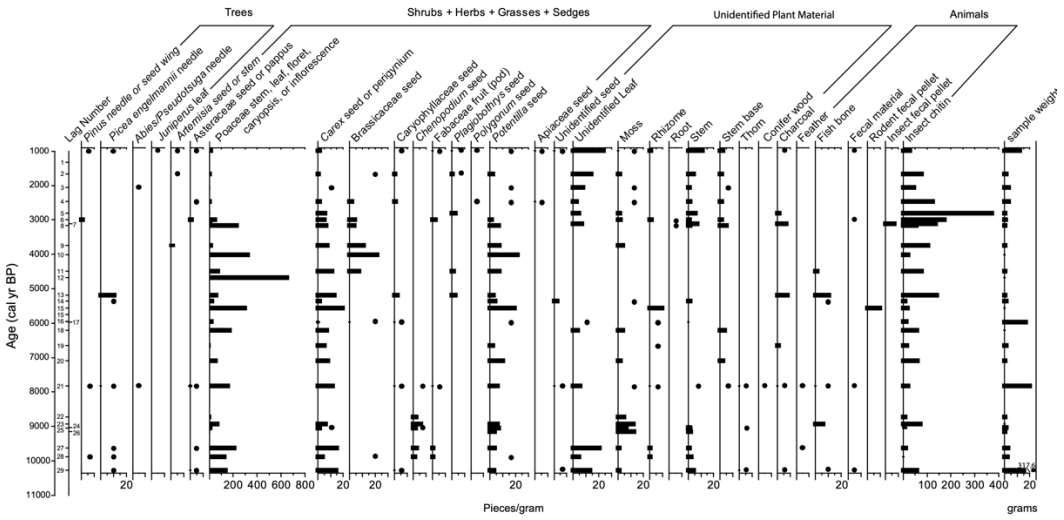


Fig SM2.2. Macrofossils from TL1 Ice Patch organic layers. Dots indicate an amount under 1 piece/gram.

APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Low Elevation Vegetation

Two low-elevation sites extended into the late-glacial period (14,000 cal yr BP): Wymore and Twin Lake. Twin Lake exhibited high levels of *Picea* (5-10%%), *Pinus* subg. *strobus* (25-30%%), Cupressaceae (3-5%), and *Artemisia* (5-10%) pollen, while Wymore Lake showed moderate levels of Cupressaceae (3%) and Poaceae pollen (5%), alongside high levels of undifferentiated *Pinus* (80%) and unknown herb pollen (8%) at the base of their cores (Fig. SM4.2). The lower AP:NAP ratios, between 0.45 and 0.68 (Fig. 4.3), indicate landscape openings and suggest a *Juniperus, Picea,* and *Pinus* subg. *strobus* parkland from >14,000 cal yr BP until ca. 13,500 cal yr BP.

From ca. 13500-10,500 cal yr BP, *Pinus* pollen increased (to 90-95%) and *Artemisia* pollen decreased (0-2%), suggesting a dense *Pinus* forest at Wymore and Twin Lakes. The AP:NAP ratio increased with the increase in *Pinus* pollen to an average of ~.90 from ca. 13,500-11,000 cal yr BP, other than one decrease to .50 at Wymore Lake from ca. 12,000-11500 cal yr BP. *Pseudotsuga menziessii* arrived first at Wymore Lake at ca. 13,000 cal yr BP, but in very small numbers (0.1-0.4%). *Pseudotsuga* values increased at Wymore and Twin Lakes at ca. 9500 cal yr BP (to 10%), and the Rainbow Lake record began at this time with high *Pseudotsuga* values as well (10%). *Pseudotsuga* values remained high at Wymore Lake (5-10%) until ca. 7800 cal yr BP, but remained high at Twin and Rainbow Lakes (10-20%) until ca. 5500 cal yr BP. The Black Lake record began at ca. 7200 cal yr BP with high levels of *Pseudotsuga* pollen (2-7%), which also remained high until ca. 5500 cal yr BP. In addition to high levels of *Pseudotsuga* pollen, there were high levels of *Artemisia* (up to 40%) and Poaceae (up to 20%) at all of the sites, suggesting an open *Pseudotsuga* parkland from ca. 10,000-5500 cal yr BP, although some areas (such as near Wymore Lake), had a gradual increase in *Pinus* beginning at ca. 7800 cal yr BP.

After 5500 cal yr BP, increases in *Pinus* (to 80%) and decreases in *Pseudotsuga* (5-10%) and *Artemisia* (5-10%) suggest all low-elevation sites were forested with montane forests of *Pinus* and *Pseudotsuga.* The Pine Butte Fen pollen record began at ca. 5000 cal yr BP, with moderate amounts of *Pinus* (60%), Poaceae (20%), and herbs (8%), The Pine Butte Fen record remained fairly constant throughout its record, suggesting an open grassland environment below

treeline. There was minimal change after ca. 5500 cal yr BP in the other low-elevation pollen assemblages as well, other than a slight increase in *Picea* and *Abies* (to 10%) and a decrease in *Pseudotsuga* (0-10%) at ca. 4000-2000 cal yr BP at Twin, Rainbow, and Black Lakes. *Pseudotsuga* increased at Black and Wymore Lakes at ca. 3000 cal yr BP, indicating the formation of current-day forest composition.

High Elevation Vegetation

The Mud Lake record began at ca. 5500 cal yr BP with high amounts of *Pseudotsuga* pollen (5-15%) at the base of the core until ca. 4500 cal yr BP, when they declined (1-5%; Fig. SM4.3). During this same time period, the Mud Lake record had high amounts of herbs (3- 5%) and *Artemisia* (5-10%) alongside low amounts of *Pinus* (44-60%), *Picea* (0-2%), and *Abies* (2-4%). This indicates a forest of predominantly *Pseudotsuga,* with minor amounts of *Pinus, Picea,* and *Abies.* At ca. 4800 cal yr BP, there was an increase of *Pinus, Picea,* and *Abies* at Mud Lake (to 56%, 4%, and 7%, respectively), suggesting an increase in forest density with the establishment of subalpine forest. Meanwhile, the Three Lakes Peak Lake record started with high levels of *Pinus* (55%), *Picea* (8%), and *Abies* (5%), also indicating a subalpine forest. *Alnus* was a dominant shrub at both sites, with an average of 10% at Mud Lake and 17% at Three Lakes Peak Lake throughout their entire records. There were two large increases in *Alnus* at Three Lakes Peak Lake between ca. 4500 and 3500 cal yr BP (when it increased to 31%) and ca. 2500 and 2100 cal yr BP (when it increased to 30%), which were seen at Mud Lake to a smaller degree (increases to 17% at ca. 4200 and 2300 cal yr BP).

Mud Lake had an increase in *Picea, Abies,* and *Pinus* subg. *Strobus* (to 8%, 12%, and 16% respectively) at ca. 4200-3200 cal yr BP, and other than one sample at ca. 1500 cal yr BP, the Mud Lake pollen assemblage remained relatively consistent from 3200 cal yr BP to present day, with high levels of *Pinus, Picea,* and *Abies* (averages of 70%,4%, and 4%, respectively). Similarly, the Three Lakes Peak Lake record remained relatively consistent from ca. 3500 cal yr BP to present day, with high levels of *Pinus, Picea* and *Abies* (averages of 67%, 4%, and 5%, respectively).

The Moss Peak record began at ca. 1500 cal yr BP with high levels of *Picea* (7%) and *Abies* (13%) pollen, but they decreased (both to averages of 4%) and *Pinus* subg. *Strobus* pollen increased (20-30%) at ca. 1350 cal yr BP until present day. The Starvation Lake record began at ca. 500 cal yr BP, and maintained high levels of *Pinus, Picea, and Abies* (averages of 62%, 10%, and 6%, respectively) throughout the record. Pollen assemblages from both sites indicate subalpine forests throughout their records.

Fire Record

Twin and Wymore Lakes had very minimal amounts of CHAR from ca. 14,000 until ca. 8000 cal yr BP, although there were minor fluctuations (Fig. SM4.2), such as an increase in CHAR (ranging from .1-.7 particles cm^{-2} yr^{-2}) from ca. 13,000 to 12,000 at Wymore Lake, and an increase (ranging from .2-1.5 particles cm^{-2} yr^{-2}) from ca. 12,000 until 10,000 cal yr BP at Twin Lake. The Rainbow Lake record began with moderate levels of CHAR (.3-1.8 particles cm^{-2} yr^{-2}) from ca. 10,000 until 9300 cal yr BP, then remained negligible until ca. 8200 cal yr BP. The Black Lake record began at ca. 7500 cal yr BP with minimal amounts of CHAR until ca. 6000 cal yr BP.

CHAR increased at all sites other than Pine Butte Fen after ca. 8000 cal yr BP. Wymore had an increase (1.4-2.9 particles cm^{-2} yr^{-2}) between ca. 8000 to 6000 cal yr BP, Rainbow had an increase (1.5-5.6 particles cm^{-2} yr^{-2}) from ca. 7000 to 6000 cal yr BP, Twin had an increase (.5-6.2 particles cm^{-2} yr^{-2}) from ca. 6500 to 5000 cal yr BP, and Black Lake had an increase (.6-5.3 particles cm^{-2} yr^{-2}) from ca. 6500 to 4500 cal yr BP.

CHAR decreased at Wymore and Black Lakes after ca. 5000 cal yr BP until ca. 3000 cal yr BP, when it increased again until 1000 cal yr BP, before decreasing until present day. The increase in CHAR between 3000 and 1000 cal yr BP was minimal at Wymore Lake (high of .5 particles cm^{-2} yr^{-2}), but was significant at Black Lake (high of 5.8 particles cm^{-2} yr^{-2}). The highest CHAR value at Pine Butte Fen (.8 particles cm^{-2} yr^{-2}) also occurred during this interval at ca. 2800 cal yr BP.

CHAR also decreased slightly at Twin Lakes after ca. 5000 cal yr BP, but CHAR at both Twin and Rainbow Lakes remained elevated from 5000 to 2000 cal yr BP (.5-2 and .7-4.8

particles cm^{-2} yr^{-2}), respectively. CHAR then increased at both sites (high of 2.7 and 5.56 particles cm^{-2} yr^{-2}, respectively) towards present day.

CHAR at Mud Lake began at ca. 5500 cal yr BP, and was minimal throughout the whole record, with increases between ca. 4600 and 4200 cal yr BP (to .7 particles cm^{-2} yr^{-2}) and ca. 1200 and 500 cal yr BP (to .17 particles cm^{-2} yr^{-2}; Fig. SM4.3). CHAR was minimal at Three Lakes Peak Lake until ca. 2500 cal yr BP when there was a big increase in CHAR (high of 7.2 particles cm^{-2} yr^{-2}) until ca. 2000 cal yr BP. CHAR then slowly declined towards present day. Moss Peak and Starvation Lakes had low amounts of CHAR until ca. 400 cal yr BP, when they reached the maximum of their records (highest of .8 and 19.1 particles cm^{-2} yr^{-2}, respectively) until ca. 100 cal yr BP.

Table SM4.1. Radiocarbon dating information for sediment cores from Mission Range. Depth is cm below the mud-water interface.

Site Name	Depth (cm)	Uncalibrated ^{14}C age	Material	Lab/Reference
Mud Lake	4.5	425±20	Bulk sediment	161672
Mud Lake	10	922±36	Bulk sediment	16919
Mud Lake	27	1000±27	Bulk sediment	16922
Mud Lake	30	4836±43	Bulk sediment	16923
Mud Lake	47	3408±28	Bulk sediment	14421
Mud Lake	54	3627±30	Bulk sediment	14422
Mud Lake	70	3968±25	Bulk sediment	16924
Mud Lake	89	4499±25	Bulk sediment	14420
Mud Lake	90	6635±33	Bulk sediment	16925
3 Lakes Peak Lake	20	793±32	Bulk sediment	16926
3 Lakes Peak Lake	30	287±23	Bulk sediment	16927
3 Lakes Peak Lake	40	1413±25	Bulk sediment	16920
3 Lakes Peak Lake	48	2562±27	Bulk sediment	14423
3 Lakes Peak Lake	57	1726±31	Bulk sediment	14424
3 Lakes Peak Lake	75	2153±35	Bulk sediment	16921
3 Lakes Peak Lake	68	1840±20	Bulk sediment	155572
3 Lakes Peak Lake	116	2130±50	Bulk sediment	155573
3 Lakes Peak Lake	124	2830±20	Bulk sediment	155574
3 Lakes Peak Lake	151	3440±30	Bulk sediment	155575
3Lakes Peak Lake	169	3450±20	Bulk sediment	155576
3 Lakes Peak Lake	204	4140±20	Bulk sediment	155577

Table SM4.1. Continued

Rainbow Lake	25	425±20	Bulk sediment	25
Rainbow Lake	59	545±15	Bulk sediment	59
Rainbow Lake	76	736±32	Bulk sediment	76
Rainbow Lake	100	1240±20	Bulk sediment	100
Rainbow Lake	130	1340±20	Bulk sediment	130
Rainbow Lake	158	1514±28	Bulk sediment	158
Rainbow Lake	190	2170±15	Plant/wood	190
Rainbow Lake	249	3070±20	Plant/wood	249
Rainbow Lake	255	3267±31	Bulk sediment	255
Rainbow Lake	260	3340±20	Plant/wood	260
Rainbow Lake	293	3690±20	Plant/wood	293
Rainbow Lake	364	4530±20	Plant/wood	364
Rainbow Lake	494	4800±28	Plant/wood	494
Rainbow Lake	499	6150±25	Bulk sediment	499
Rainbow Lake	522	7633±49 cal yr BP	Mazama tephra	Egan et al., 2015
Rainbow Lake	599	7390±30	Bulk sediment	599
Rainbow Lake	653	8360±35	Bulk sediment	653
Rainbow Lake	728	8750±35	Bulk sediment	728
Wymore Lake	12	785±15	Bulk sediment	145873
Wymore Lake	101	4790±20	Bulk sediment	142361
Wymore Lake	123	5790±20	Bulk sediment	145874
Wymore Lake	178	7170±30	Bulk sediment	145875
Wymore Lake	196	7633±49 cal yr BP	Mazama tephra	Egan et al., 2015
Wymore Lake	203	7910±40	Bulk sediment	169642
Wymore Lake	208	7780±30	Bulk sediment	169643
Wymore Lake	298	9560±40	Bulk sediment	169644
Wymore Lake	306	9740±40	Bulk sediment	169645
Wymore Lake	396	11300±50	Bulk sediment	169646
Wymore Lake	405	7920±30	Bulk sediment	169647
Wymore Lake	489	12900±65	Bulk sediment	169648
Wymore Lake	498	13200±75	Bulk sediment	145890
Wymore Lake	524	13600±25 cal yr BP	Glacier peak tephra	Keuhn et al., 2009
Starvation Lake	45	180±15	Bulk sediment	128404a
Starvation Lake	55	260±20	Bulk sediment	128405a
Starvation Lake	71	315±15	Bulk sediment	128402b
Starvation Lake	92	1140±15	Bulk sediment	128406b
Pine Butte Fen	69	1130±15	Wood	E69

Table SM4.1 Continued

Pine Butte Fen	126	2130±20	Menyanthes seeds	E126
Pine Butte Fen	157	2430±15	Wood	E157
Pine Butte Fen	206	2850±25	Seeds	E206
Pine Butte Fen	256	4470±25	Bulk sediment	E256
Pine Butte Fen	298	13650±85	Bulk sediment	E298
Moss Peak Lake	14	50±25	Bulk sediment	117352
Moss Peak Lake	42	1530±25	Bulk sediment	117353
Twin Lake	63	510±20	Plant debris	128398
Twin Lake	149	1950±20	Bulk sediment	20141
Twin Lake	193	2490±20	Douglas-fir needle	1284897
Twin Lake	249	3470±25	Charcoal	128408
Twin Lake	339	4990±40	Charcoal	20142
Twin Lake	430	6100±25	Bulk sediment	20143
Twin Lake	519	7633±49 cal yr BP	Mazama tephra	Egan et al., 2015
Twin Lake	534	6474±31	Plant debris	014427
Twin Lake	549	7810±25	Bulk sediment	20152
Twin Lake	631	9440±40	Bulk sediment	20153
Twin Lake	735	11450±45	Bulk sediment	20151
Twin Lake	755	13600±25 cal yr BP	Glacier Peak tephra	Keuhn et al., 2009
Twin Lake	771	12544±50	Bulk sediment	01449
Black Lake	20	305±20	Bulk sediment	14215
Black Lake	30	455±20	Bulk sediment	148216
Black Lake	47	985±30	Wood	117356
Black Lake	61	1030±30	Wood	117354
Black Lake	90	1220±20	Bulk sediment	148217
Black Lake	100	1680±15	Bulk sediment	148219
Black Lake	129	1800±15	Bulk sediment	128401
Black Lake	157	2150±20	Bulk sediment	148218
Black Lake	170	2390±20	Bulk sediment	148220
Black Lake	200	2670±20	Bulk sediment	138221
Black Lake	235	3150±15	Bulk sediment	148223
Black Lake	275	3810±20	Bulk sediment	148222
Black Lake	294	4040±20	Bulk sediment	128396
Black Lake	360	4720±20	Bulk sediment	148224
Black Lake	390	5020±20	Bulk sediment	148225
Black Lake	410	5260±25	Bulk sediment	128403
Black Lake	414	5310±30	Bulk sediment	148228

Table SM4.1 Continued

Black Lake	440	7100±30	Bulk sediment	148226
Black Lake	460	6400±30	Bulk sediment	148227

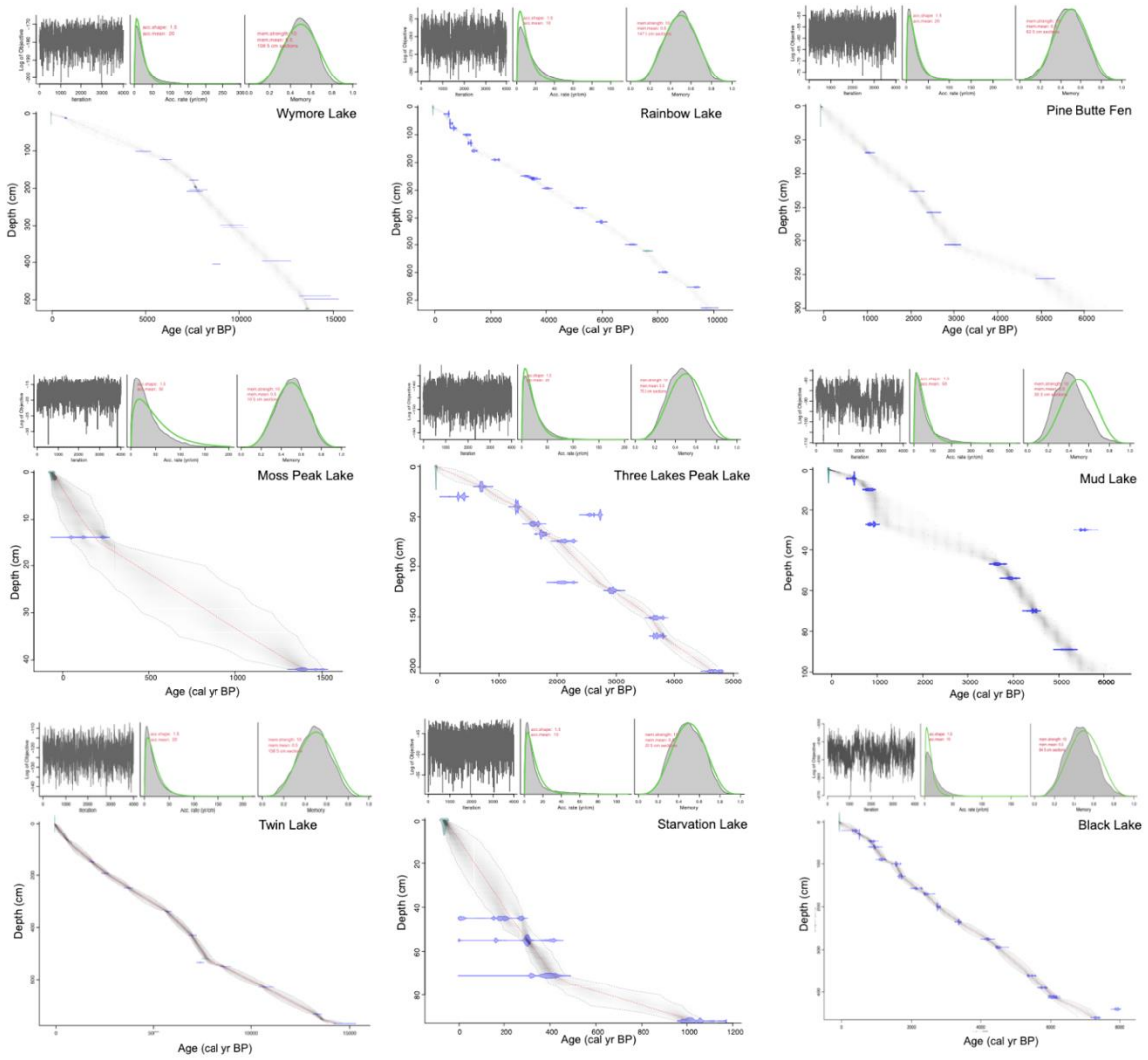


Figure SM4.1. Age-depth models for sites used in the Mission Range study. Light blue represents tephra layers and surface. Purple indicate probability distribution of calibrated 14C dates. Red line shows median ages, and dotted grey lines indicate 95% confidence intervals.

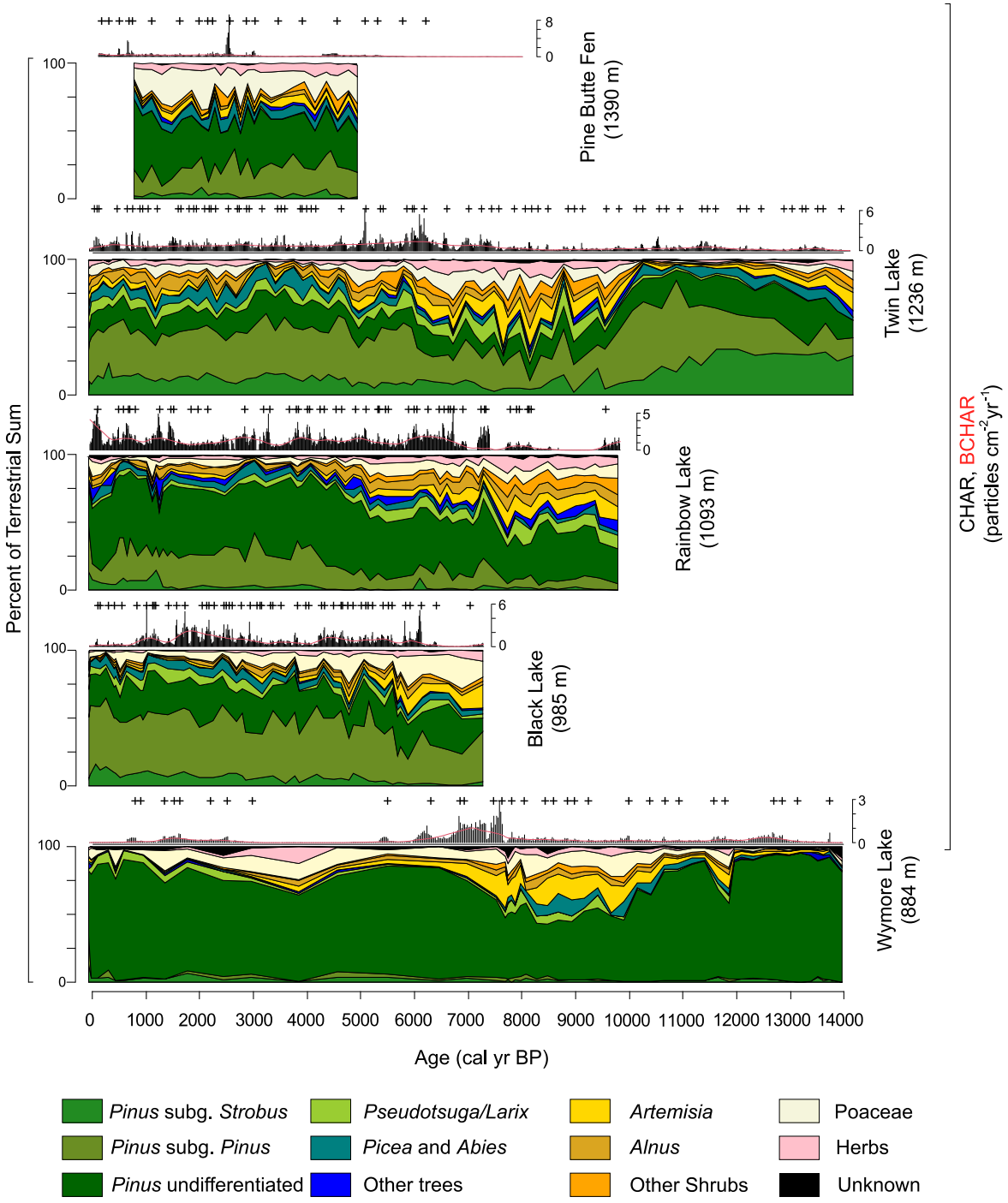


Figure SM4.2. Pollen and charcoal data from low-elevation sites around the Mission Valley and Mission Range. Black bars represent charcoal accumulation rates (CHAR), and red lines are the background charcoal accumulation rates (bCHAR). (+) signs indicate significant fire episodes.

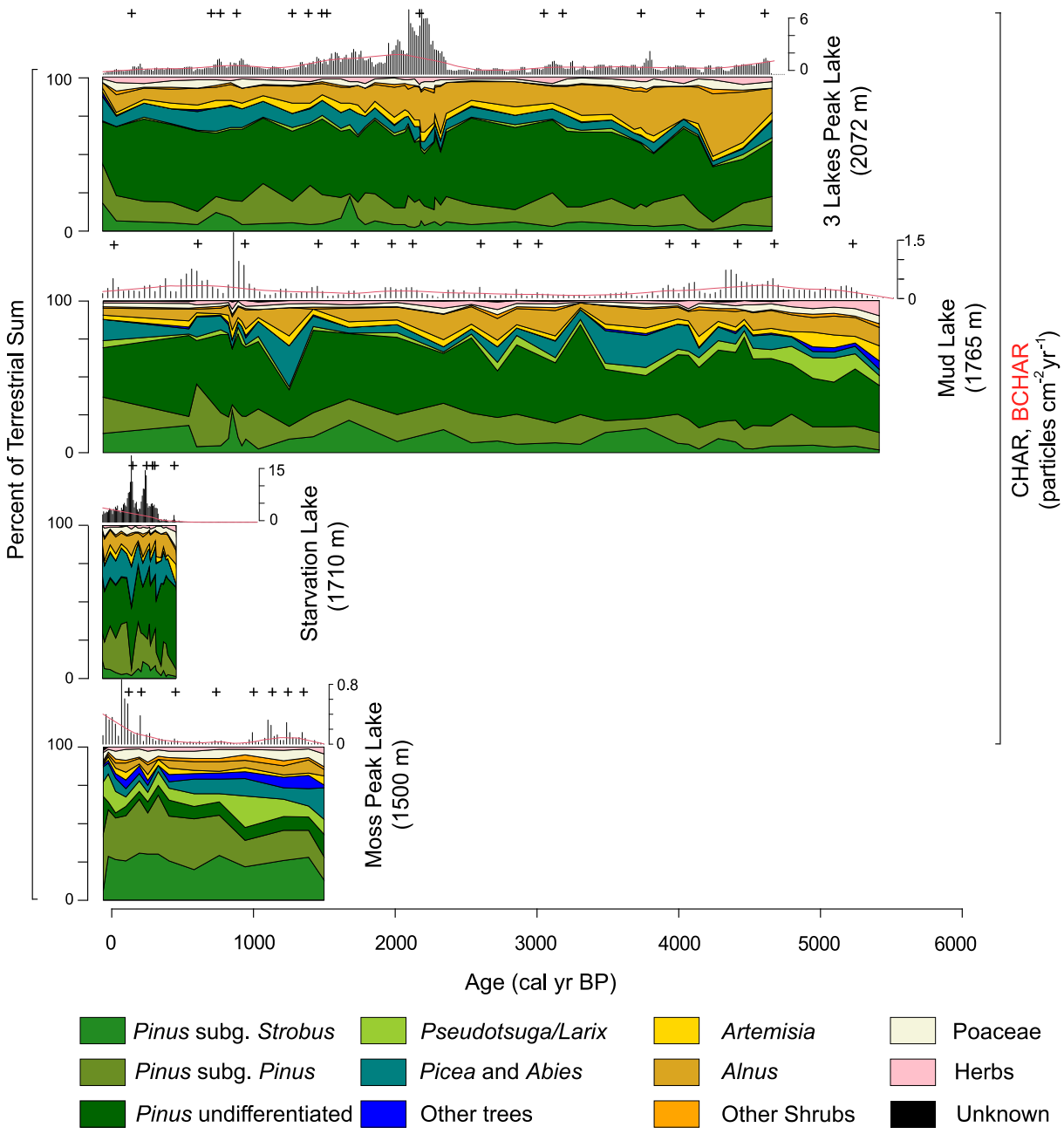


Figure SM4.3. Pollen and charcoal data from high-elevation sites around the Mission Valley. Black bars represent charcoal accumulation rates (CHAR), and red lines are the background charcoal accumulation rates (bCHAR). (+) signs indicate significant fire episodes.