HOLOCENE FIRE, VEGETATION, AND CLIMATE HISTORY OF WESTERN YELLOWSTONE NATIONAL PARK

by

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ABSTRACT

The Greater Yellowstone Ecosystem is the largest intact temperate ecosystem on Earth, spanning 22 million acres. Diverse geo-ecosystem dynamics support an array of vegetation types, large intact predator-prey systems, and the highest concentration of continental thermal features in the world. This area's unique setting and land designation, which permits natural processes to occur with little active management, create unparalleled opportunities to understand how climate, environment, and disturbance interact. Harlequin Lake, located in lodgepole pine forest on the western edge of Yellowstone National Park, preserves a >9,000-year sedimentary record of vegetation, climate, and fire history. Pollen data indicate that Pinus subgen. *Pinus*, attributed to lodgepole pine, has been dominant since the early Holocene, reflecting persistent subalpine forest cover. Charcoal accumulation reveals that high-severity fires occurred regularly (<150 years between fire-episodes) during the early Holocene. Fire frequency declined in the mid-Holocene under cooler, wetter climates and returned to early Holocene patterns during the late Holocene, though some large-magnitude fire episodes occurred during the Medieval Climate Anomaly. Comparisons with paleoenvironmental records from sites within the region suggest that Harlequin Lake has experienced more late-Holocene fire episodes than other rhyolite lodgepole sites on the Yellowstone Plateau, likely due to its position along the western GYE margin, where the effects of interannual climate variability on fire occurrence may be more pronounced. Together, these findings provide a long-term context for evaluating modern and future fire regimes in western Yellowstone, demonstrating the resilience of lodgepole pine forests to past climate variability.

INTRODUCTION

The Greater Yellowstone Ecosystem (referred to as the GYE or simply Yellowstone) is the largest intact temperate ecosystem in the world, spanning over 22 million acres. Its history has been shaped by a long interaction of geologic, climatic, and ecological processes operating across space and time. Following the retreat of the Greater Yellowstone Glacial System after the Pinedale glaciation 22,000-13,000 years ago (Licciardi and Pierce, 2018), the region was initially covered by tundra vegetation, dominated by sagebrush (*Artemesia tridentata*) steppe (Krause and Whitlock, 2013; Millspaugh et al., 2000). Subalpine parkland was followed by lodgepole pine (*Pinus contorta*) forests in the region approximately 11,000 years ago, establishing one of the most extensive subalpine lodgepole pine forest systems in North America (Whitlock, 1993). This paper will explore how geologic, climatic, and ecological processes influence lodgepole pine forests through time in western Yellowstone National Park, an area that has not been well studied.

Although different vegetation types and fire regimes depend on elevation and climate, especially annual precipitation and snowpack (Whitlock and Bartlein, 1993; Millspaugh et al. 2004; West and Young, 2000), lodgepole pine forests at middle elevations in Yellowstone are primarily influenced by soil type. Lodgepole pine has low nutrient requirements and can grow on Quaternary rhyolite flows, which are coarse, sandy, have poor water-holding capacity, and contain only one-third to one-fourth of the nutrient levels found in other soil types (Despain, 1990). In contrast, subalpine fir (*Abies lasiocarpa*) Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) have greater nutritional needs than lodgepole pine and dominate in regions with andesitic and glacial soils. As a result, rhyolitic versus andesitic substrates produce contrasting forest types across the GYE.

In addition to edaphic controls, disturbance regimes (particularly fire regimes) govern lodgepole pine regeneration and its persistence. Regeneration is closely tied to cone serotiny, where seed release requires high temperatures of 45-60°C, typically generated by fire (Perry and Lotan, 1977). The prevalence of lodgepole pine serotiny varies across the GYE (from ~0-48%), with low- to mid-elevation stands (< ~7,800 ft asl) exhibiting higher rates of cone serotiny and shorter fire-return intervals (~180 yrs) and typically regenerating as dense, even-aged cohorts. In contrast, high-elevation stands with longer fire-return intervals tend to favor non-serotinous cones and more mixed-age forest structure (Tinker et al., 1994). Fire severity, stand age, and past disturbance history further influence serotiny levels, and consequently, post-fire seedling density and successional trajectories (Turner et al., 1997). Other disturbance agents like mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoe (*Arceuthobium americanum*) can modify fuels and stand structure (Raffa et al., 2008; Simard et al., 2011; Harvey et al., 2014; Alexander et al., 1975), but at broad spatial and temporal scales, climate remains the primary control on the timing and probability of stand-replacing fires by regulating fuel aridity and fire season length. In recent decades, increased atmospheric aridity is leading to drier fuels over a longer summer season promoting large fires in forests where fire spread was historically limited by moist fuels (Westerling et al., 2006; Westerling, 2016; Abatzoglou and Williams, 2016; Jolly et al., 2015).

Post-fire establishment of lodgepole pine forest is controlled by levels of prefire serotiny and time between fires (Schoennagel et al., 2003; Tinker et al., 1994). Looking forward, mid 21st-century projections for the GYE indicate more frequent, larger fires, and it has been proposed that shortened fire return intervals will not allow sufficient time for lodgepole pine regeneration (e.g., Maple Creek reburn) and, in fact, may eliminate lodgepole pine forests in parts of the GYE by the middle of the 21st century (Turner et al., 2019). In contrast, paleoecological records from the Central Yellowstone Plateau show more frequent stand-replacing fires during warmer and drier intervals in the past, and fewer high-severity fires during cooler, moister periods. Millennial-scale variations in temperature and moisture apparently altered the fire frequency but not the vegetation. Lodgepole pine forest persisted with little change, likely because of its competitive advantage on rhyolite substrates (Whitlock and Bartlein, 1993; Millspaugh et al., 2000). Across the western US, increased anthropogenic warming has driven fuel aridity and nearly doubled cumulative area burned since 1984. A warming climate underscores the need for long-term baselines to assess the resilience of present-day lodgepole pine forests to emerging fire regimes (Westerling et al., 2006; Abatzoglou and Williams, 2016).

The vegetation history of the GYE has been studied extensively (Whitlock, 1993; Whitlock and Bartlein, 1993; Millspaugh and Whitlock, 1995; Millspaugh et al., 2000; Krause and Whitlock, 2013; Huerta et al., 2009; Higuera et al., 2010; Iglesias et al., 2018; Mumma et al., 2012; Whitlock et al., 1995; Whitlock et al., 2012; Brown et al., 2021), but few paleoecological records are available from the western GYE (with the exception of Schiller et al. 2021). This gap limits our ability to evaluate whether current fire-climate-vegetation interactions in western Yellowstone fall within the range of variation seen in other records or represent emerging novel conditions. To address this gap, we reconstruct the Holocene vegetation and fire history for a basin surrounded by lodgepole pine forest in western Yellowstone National Park, based on pollen and charcoal analysis of sediment a core from Harlequin Lake, and compare the site's history with other paleoecologic records from rhyolite terrain in the GYE. Our objective was to answer the following questions:

1. What is the Holocene fire, climate, and vegetation history of a non-hydrothermal watershed dominated by lodgepole pine in western Yellowstone?
2. How does the Harlequin Lake paleoecological record compare to other records in rhyolite terrain in the GYE?
3. How does the Harlequin Lake paleofire record inform our understanding of future fire activity and lodgepole pine resilience?

Site Description

Harlequin Lake (44°38'38.9"N, 110°53'28.0"W; elev. 2,101 m; 4.2 ha; 3.4 m water depth) is located in Madison Canyon, western Yellowstone National Park, between a steep, south-facing rhyolitic talus slope at the base of the canyon wall to the north and the Madison River to the south (Fig. 1).

The north wall of Madison Canyon is primarily composed of Pleistocene Lava Creek Tuff, Member A (Christiansen and Blank, 1974). The basin is underlain by Quaternary surficial sediments and bordered to the south by the Harlequin Lake rhyolite flow. Paleomagnetic data and K-Ar dates on sanidine indicate an early Pleistocene age for the Harlequin Lake rhyolite flow (~0.84-0.93 Ma), predating the collapse of the Yellowstone caldera (Obradovich, 1992). To the north, the canyon rim is part of the Lava Creek caldera formed by the most recent caldera-forming eruption in Yellowstone (631 ± 4 ka, Matthews et al., 2015), which emplaced the Lava Creek Tuff.

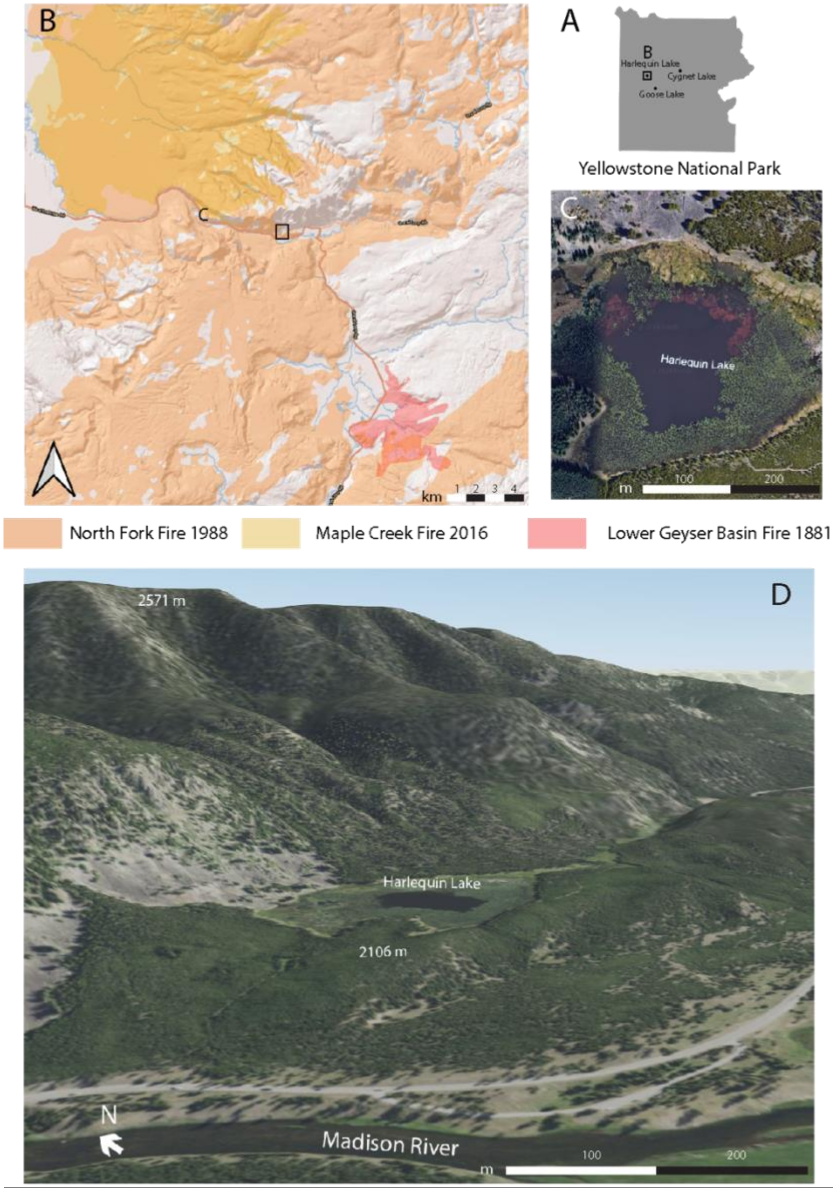

Figure 1. (A) Location of Harlequin Lake locale within Yellowstone National Park, Wyoming, USA, and with respect to Cygnet and Goose lakes (Millspaugh et al., 2000, Schiller et al., 2021). (B) Harlequin Lake location within Madison Canyon, with legend representing extent of historical fires. (C) Satellite view of Harlequin Lake in its basin (Google Earth). (D) 3D view of Harlequin Lake. Arrows showing extinct inflow and outflow channels.

During the Pinedale glaciation (22-13 ka), the Greater Yellowstone Glacial System covered the area surrounding Harlequin Lake. Deglaciation likely occurred in Madison Canyon by ~14 ka based on correlation with dated recessional moraines to the north (Licciardi and

Pierce, 2018). Postglacial mass movement produced talus along the north wall of the canyon that form the immediate hillslopes upslope of Harlequin Lake (Waldrop and Pierce, 1975).

Despite its location on the margin of the Yellowstone Caldera, Madison Canyon largely lacks the hydrothermal activity that defines and shapes the vegetation communities of nearby geyser basins. The nearest notable hydrothermal feature is Terrace Springs (~3.5 km east) (Lowenstern, 2016). According to the Natural Resources Conservation Service's Soil Survey Geographic Database (SSURGO), the soils at Harlequin Lake's margin are Typic Cryaquolls (Gallatin and Grayslake soil families), while surrounding lodgepole pine forests occur on excessively drained loess over glacial till derived from rhyolite (Toldy and Bottle soil families) (Despain, 1990). Currently, the lake is ground-water fed with extinct outflow channels at the west and east ends. The location of these extinct channels suggest that the lake lies in an abandoned channel of the Madison River. The geomorphology, stratigraphy, and age of the lake suggest it formed when one or more landslides off the caldera rim to the north blocked stream flow. A large landslide deposit occurs on the northwest side of the lake (Fig. 1).

Present-day Climate

The climate of the western Yellowstone is strongly influenced by topography and elevation, and Harlequin Lake lies within a "summer-dry/winter-wet" seasonal precipitation regime (Whitlock and Bartlein, 1993). Most of the annual precipitation is received in winter and spring (December-February 264 mm; March-May 243 mm; June-August 134 mm; September-November 184 mm) for a total average annual precipitation at of 825 mm (ratio of summer/winter precipitation (JJA/DJF)=.51) based on 30-year normals (PRISM Climate Group, 2025). Winter precipitation is primarily delivered by Pacific storm systems funneled up the Snake River Plain, whereas summer precipitation is limited by the northeastern Pacific subtropical high-pressure system and comes mainly from convective storms (Liccardi and Pierce, 2018).

Mean annual temperature at Harlequin Lake is 2°C; mean maximum summer temperature (June-August) is 22°C; and mean minimum summer temperature is 4°C. Mean minimum winter temperature (December-February) is -15°C; and mean maximum winter temperature is -3°C. Temperature data are 30-year averages from 1991-2020 (Fig. 2).

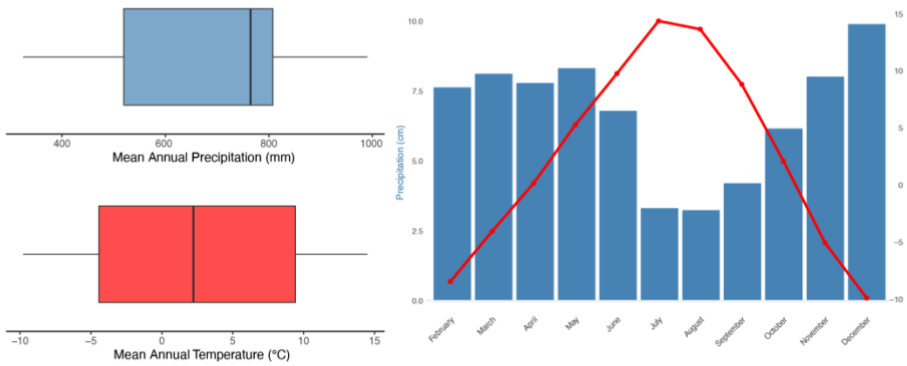

Figure 2. Mean monthly precipitation and average monthly temperature box-and-whisker plot from 1991-2020 for Harlequin Lake, WY (PRISM Climate Group, 2025). Average monthly precipitation (blue) and average monthly temperature (red) from 1991-2020 for Harlequin Lake, WY (PRISM Climate Group, 2025).

Present-day Vegetation

The forests on the west, east, and south sides of Harlequin Lake are dominated by even-aged lodgepole pine stands established largely after the 1988 fires. A sparse shrub and herbaceous understory in the lodgepole pine forest includes *Lupinus argenteus, Juniperus communis, Selaginella wallacei*, *Carex geyeri, Amelanchier alnifolia, Epilobium angustifolium, Vaccinium scoparium*, *Arctostaphylos uva-ursi, Fragaria virginiana*, *Antennaria rosea*, *Berberis repens*, *Campanula petiolata*, *Chamaenerion angustifolium*, and *Rosa woodsii*. Along the steep, south-facing talus slopes on the north are scattered large Douglas-fir (*Pseudotsuga menziesii),* quaking aspen (*Populus tremuloides)* stands. *Artemisia tridentata*, *Ribes aureum*, *Rubus* spp. and *Dasiphora fruticosa*, and herbs in the Asteraceae, Rosaceae, Lamiaceae, Fabaceae, Caryophyllaceae, Ranunculaceae, and Plantaginaceae families were also present on the talus. Douglas-fir's thick bark resists low severity fire, and the trees were able to survive the 1988 fires on rocky slopes with discontinuous fuel cover. The aspen regenerated primarily by post-fire resprouting.

In the wetter outlet areas, riparian vegetation includes *Salix* (spp.), *Betula occidentalis*, *Alnus incana*; *Rubus idaeus*, *Sambucus racemosa*, *Ribes lacustre*, *Pedicularis groenlandica*, *Stellaria longipes*, *Ranunculus* (spp.), *Kalmia microphylla*, *Spiraea douglasii*, and *Potentilla* (spp.). Around the margin of the lake and in shallow water grows *Juncus* (spp.), *Myriophyllum* (spp.), *Potamogeton* (spp.), *Polygonum amphibium*, *Carex* (spp.), *Nuphar polysepala*, *Typha latifolia*, and *Schoenoplectus* (spp.).

To the south of Harlequin Lake lies the floodplain of the Madison River, which is dominated by *Carex* (spp.) and *Poaceae* (spp.). On glacial outwash, *Artemisia tridentata* steppe is common. Additional species found on this glacial ridge include *Eriogonum umbellatum*, *Rumex* (spp.), *Madia glomerata*, *Berteroa incana*, and *Lupinus argenteus.*

Present-day Fire Regime

In 1988, ~793,880 acres (~36%) of Yellowstone National Park and ~1.2 million acres across the GYE burned (Fig. 3), prompting review of fire management policy and research efforts to better understand how fire regimes shape lodgepole pine regeneration and patterns on the landscape (van Wagtendonk, 1991; Turner et al., 1997; Turner et al., 1999; Schoennagel et al., 2003).

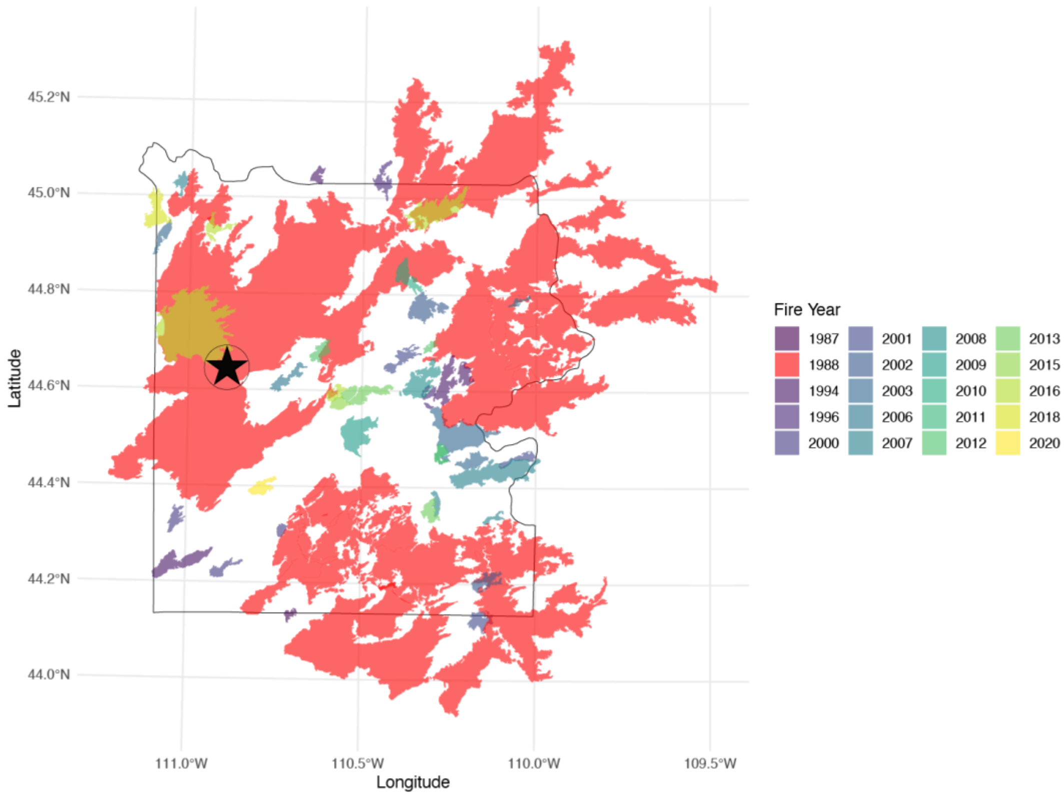

Figure 3. Annual fire area burned in/around Yellowstone National Park from 1987-2020. Circled black star shows the location of Harlequin Lake. Red area shows the extent of the 1988 Yellowstone fires.

Tree-ring and fire-scar chronologies indicate that subalpine lodgepole pine forests in Yellowstone have experienced infrequent, stand-replacing fires (every ~100-300 years) over the past several centuries (Romme, 1982). In contrast, charcoal records (e.g., Cygnet Lake; ~14,000-year record) indicate that intervals between fire episodes occasionally shortened to as little as ~75 years during warmer, drier Holocene intervals, emphasizing long-term climate control on fire activity. Burn behavior in recent fires is typically high-severity crown fire spread through continuous fuels, creating burn patches ranging from tens to thousands of hectares (Barrett, 1994; Romme and Despain, 1989). Fire timing and size is most strongly associated with warm, dry conditions, often following multi-year drought and warm summers. Because conditions for large fire spread in Yellowstone's lodgepole pine forests are largely governed by climate and weather, not fuel availability, the impact of 20th-century fire suppression on large fire spread is comparatively limited relative to many lower-elevation systems.

Recent fires have resulted in lower post-fire seedling densities and higher regeneration failure than occurred from late-20th-century fires, consistent with increasing likelihood of more open forest states under warm-dry conditions in the coming decades (Stevens-Rumann et al., 2018). Serotinous lodgepole pine is partly buffered by canopy seedbanks that release seeds after fire, but post-fire lodgepole seedling densities have been shown to be lower in increasingly warm-dry climate conditions (Harvey et al., 2016; Kiel et al., 2025). However, within Yellowstone's post-1988 landscape, sites with reproductively mature lodgepole pine trees (10-20 years) and adequate seed supply have attained very high tree densities.

METHODS

Core Collection

In August 2023, five 5-cm diameter lake sediment core sections were collected from a platform anchored at the deepest point of Harlequin Lake with a modified Livingstone square-rod-piston coring device (Wright et al., 1983). Core sections were extruded in the field and wrapped in plastic wrap and aluminum foil to prevent contamination and oxidation. They were then transported to the Montana State University cold room where they were stored prior to laboratory analysis.

Laboratory

All core sections were sent to the Continental Drilling Facility (CSD) at the University of Minnesota, where they were split longitudinally into working and archival halves. The working half of each section was then photographed at high resolution, lithologically described, measured for magnetic susceptibility (MS), and measured for x-ray fluorescence (XRF). MS provides information on allochthonous clastic input to the lake, which can be used to better understand the timing of erosional events (Gedye et al., 2000). XRF is a non-destructive analytical technique to measure the elemental composition of the core. The archival halves were wrapped in plastic and stored in core tubes at the CSD, and the working halves were transported to Montana State University where they were analyzed for charcoal, pollen, and macrofossils.

Charcoal

Charcoal data were analyzed from the core top to 338 cm sediment depth. The top and bottom drives of the core were sampled at 0.5 cm continuous intervals, and the remainder was sampled at 1 cm continuous intervals. Following Whitlock and Larsen (2001), 2 cm^3 subsamples at each interval were soaked in a solution of bleach (NaClO) and sodium hexametaphosphate ($Na_6[(PO_3)_6]$) for 24 hours to deflocculate sediment and wet-screened through a 125-µm mesh. Charcoal particles >125 µm in diameter in the residue were counted with a stereomicroscope. This size fraction was selected because it best represents local fire episodes. Charcoal counts were analyzed using CharAnalysis (https://sites.google.com/site/charanalysis/) following Higuera et al. (2009). Charcoal counts were converted to charcoal accumulation rates (CHAR, particles cm^{-2} yr^{-1}) and interpolated to uniform time steps to minimize the effects of variable sedimentation rates. Background charcoal accumulation (BCHAR) was estimated using a locally weighted regression (LOWESS) smoother, smoothed over 500 year windows, and charcoal peaks were identified as positive deviations from BCHAR. A Gaussian mixture model was applied to the residuals, and peaks exceeding the 99th percentile threshold and separated by >25 years were classified as fire episodes, defined as one or more local fires occurring within the span of a peak. Fire episode frequency was calculated using a moving average of 1000 years.

Pollen

Vegetation history was based on pollen analysis following standard procedures (Bennett and Willis 2001). At 8-cm intervals, 0.5 cm^3 samples were taken, resulting in an approximate average sample resolution of 200 years. Pollen analysis was undertaken at a closer interval above and below two prominent charcoal peaks at 18.5-20.5 and 224-235 cm depth. Pollen was mounted onto slides using silicon oil and counted using a Nikon Eclipse 50i compound microscope at 400x and 1000x magnifications, with a minimum of 300 terrestrial pollen grains counted per sample. A known concentration of *Lycopodium* was added to each sample to calculate sample pollen concentration (grains cm^{-3}). Pollen percentages were obtained by dividing pollen counts for each terrestrial taxon by total terrestrial pollen sums, and aquatic taxa were converted to percentages based on the total terrestrial and aquatic sums. *Pinus* pollen grains were identified as either *Pinus* subgen. *Strobus* (haploxylon-type) and *Pinus* subgen. *Pinus* (diploxylon-type) when the distal membrane was intact and visible. Haploxylon-type *Pinus* grains are attributed to *P. albicaulis* and *P. flexilis*, and *Pinus* subgen. *Pinus* grains are attributed to *P. contorta*. *Juniperus*-type pollen may have come from either *J. communis*, *J. scopulorum*, or *J. horizontalis*. Degraded, crumpled, broken, or otherwise unidentifiable pollen grains were labeled as “Indeterminate”. Pollen grains that were intact but could not be identified were labeled as “Unknown”. Terrestrial taxa were classified as falling into either “Arboreal” (AP) or “Non-arboreal” (NAP) categories to better understand ecological shifts in forest density in the watershed surrounding Harlequin Lake over time. The ratio of AP to NAP was calculated using the formula (AP-NAP)/(AP+NAP). Pollen grains were identified to the lowest taxonomic group possible. Note that *Artemisia* was put in the non-arboreal category, given its prevalence in steppe vegetation, and Cyperaceae was considered an aquatic taxon.

RESULTS

Lithology

The composite lake sediment core was 4.1 m in length and composed primarily of organic sapropels and peat (Fig. 4). In Core A, Unit 1 (0-280 cm depth) sediments consisted primarily of peaty, fragmented herbaceous sapropel with thin inorganic silt layers at 34-35 cm and 156-158 cm depth, interpreted as minor clastic input from the adjacent rhyolite talus slope. Sediment color transitioned from black sapropel in the upper 156 cm to dark brown sapropel below. Unit 1 was characterized by low magnetic susceptibility, indicating limited allochthonous input. Unit 2 (80-410 cm depth) was composed of massive sapropelitic silts with diatoms and sapropelitic diatom oozes with silt from 280-343 cm depth. Sediment is primarily composed of sand- to gravel-sized clastic inorganic sediments with some sapropel, silt, and diatomaceous ooze from 343-410 cm depth. Unit 2 exhibited high magnetic susceptibility, reflecting increased allochthonous input. Because of the presence of gravels and the location of Harlequin Lake at the base of a steep talus slope, this gravel is likely an indicator of the mass movement. Charcoal and pollen analysis was not performed after this lithology change.

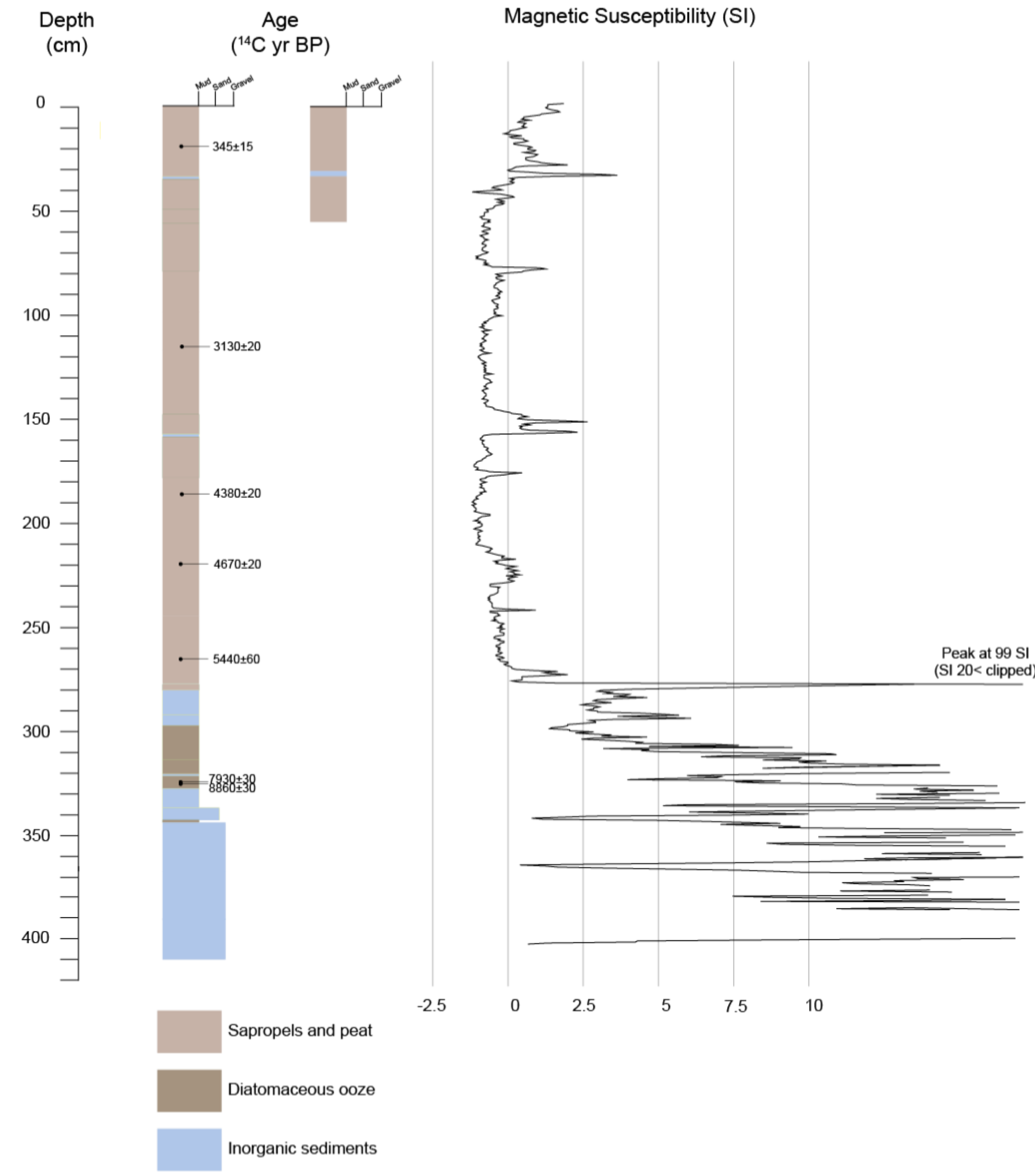

Figure 4. Lithology of cores from Harlequin Lake, magnetic susceptibility data, and uncalibrated radiocarbon dates.

Age-depth Chronology

The chronology of Harlequin Lake (Fig. 5) was based on seven accelerator mass spectrometry (AMS) ^{14}C dates from terrestrial plant remains and charcoal particles. Mazama ash was not visually observed in the sediment cores. Bayesian ACcumulatiON histories were calculated for the Harlequin Lake sediment core using BACON version 3.5.2 in RStudio. ^{14}C dates were calibrated automatically from calendar years by BACON.

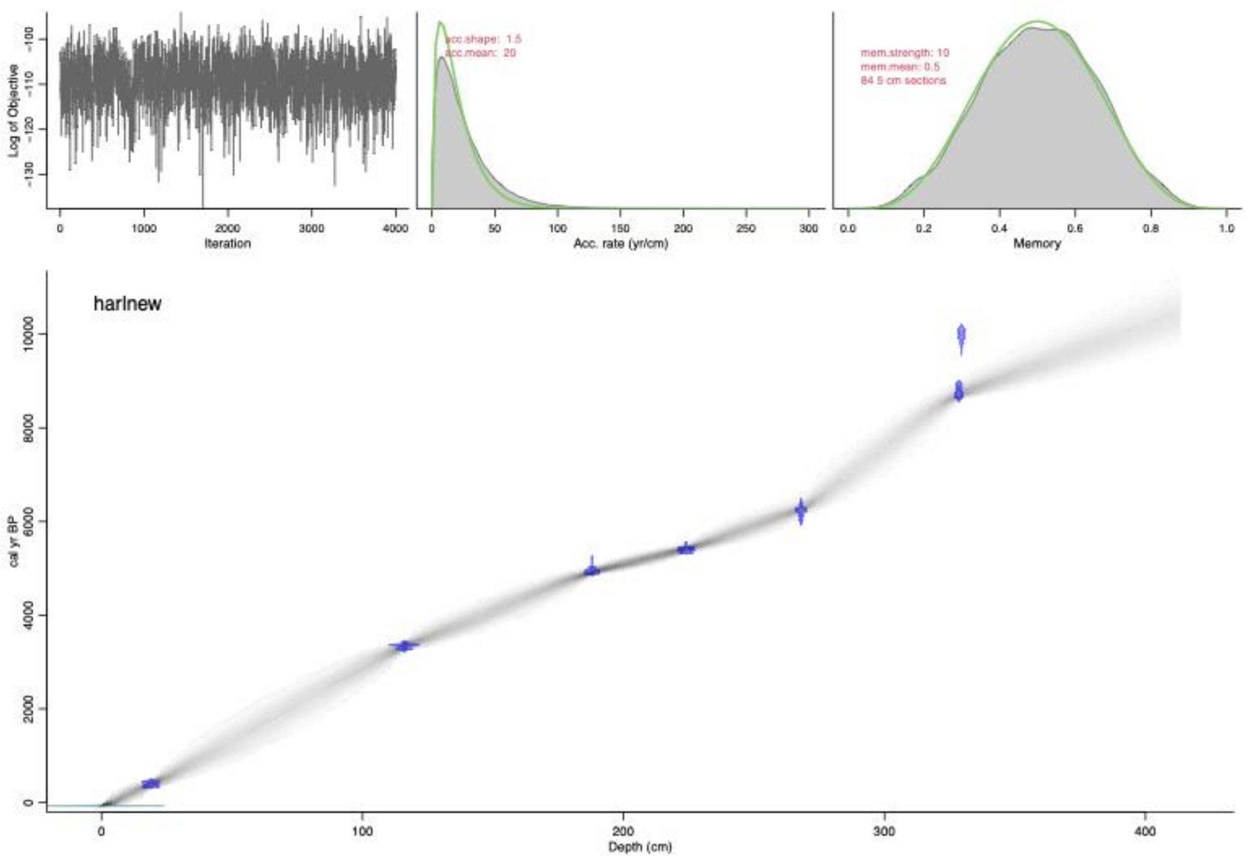

Figure 5. Age-depth model for Harlequin Lake. Blue points along the age-depth line represent calibrated radiocarbon dates. The top left panel shows the fit of the Markov Chain Monte Carlo (MCMC) iterations of the run. The top middle panel shows sedimentation time in yr/cm. The top right panel shows distributions for how much sedimentation time varied between depths.

Table 1. Radiocarbon dates for Harlequin Lake.

CSD Core ID	Composite Depth (cm)	Lab Reference Number	Material Dated	Uncalibrated Age (C yr BP)	Calibrated Age Range (Cal yr BP)
LGB-6A-1L-1-W	19	OS-177405	Charcoal	345±15	310-475
LGB-6A-2L-1-W	114	OS-181221	Charcoal	3130±20	2253-3798
LGB-6A-3L-1-W	186	OS-181222	Terrestrial plant material	4380±20	4115-5815
LGB-6A-3L-1-W	222	OS-181202	Terrestrial plant material	4670±20	5121-6736
LGB-6A-3L-1-W	266	OS-181247	Terrestrial plant material	5440±60	6365-7836
LGB-6A-4L-1-W	326.5	OS-177406	Charcoal	7930±30	8518-8970
LGB-6A-4L-1-W	327.5	OS-177407	Charcoal	8860±30	8577-8980

Charcoal and Pollen Data

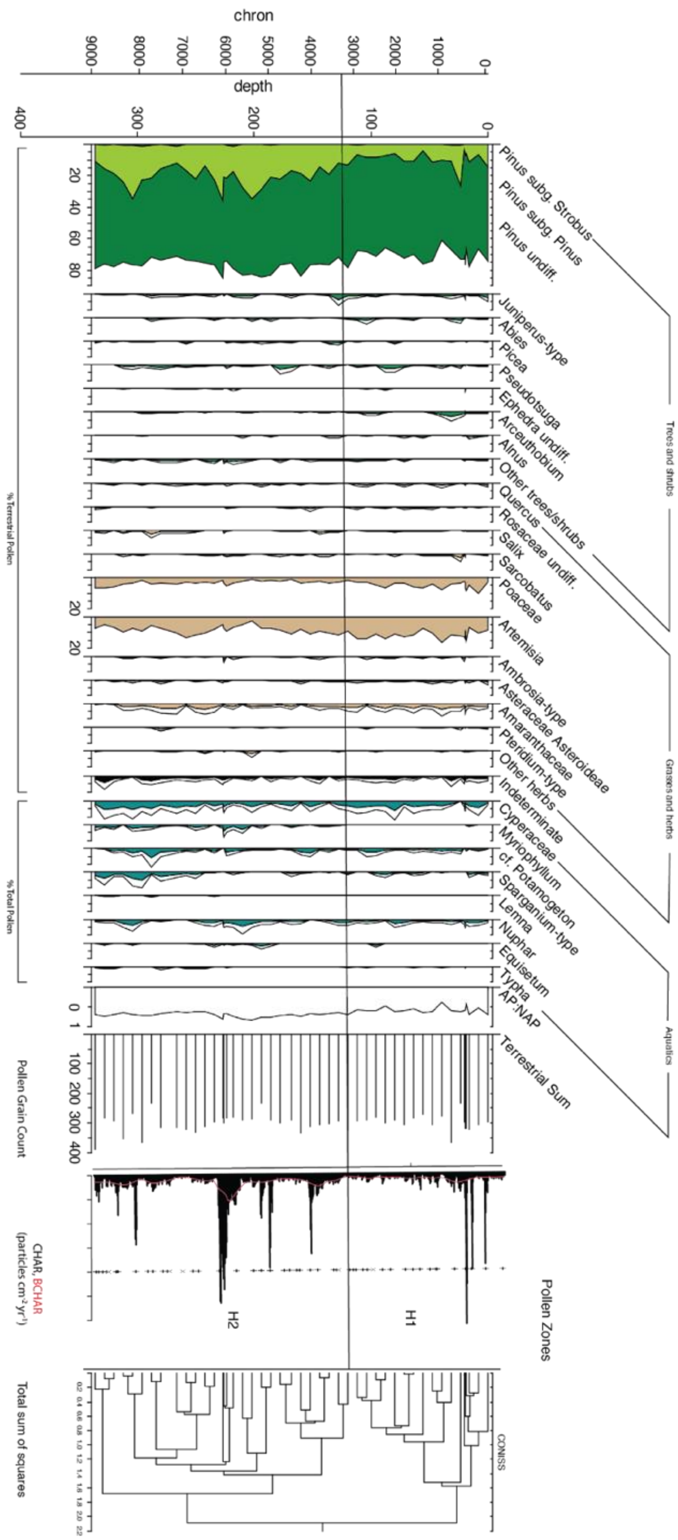

Figure 6. Pollen percentage diagram for Harlequin Lake showing selected taxa and charcoal data (closed line graphs represent percentage data, open line graphs represent 2x exaggeration for better visualization of trends throughout time).

Pollen percentage data (Fig. 6) was divided into two pollen zones using a constrained cluster analysis and visual inspection (CONISS, Grimm, 1987).

Zone H2: 325-120 cm depth; 9000-3200 cal yr BP

Zone H2 was dominated by high percentages of *Pinus* subgen. *Pinus* pollen (~75-85%), indicating the watershed supported lodgepole pine forest. Minor percentages (<2%) from *Picea*, *Abies*, and *Pseudotsuga* likely reflect pollen transport from other nearby or regional sources. Herbaceous taxa were present but not dominant (*Poaceae* ranging from ~2-5% and *Artemisia* from ~5-10%), suggesting a predominantly closed forest with occasional openings that may have been maintained by fire. Aquatic taxa such as *Potamogeton*, *Myriophyllum*, and *Sparganium*-type pollen were present in relatively high abundances (up to 6%), consistent with broad littoral zones that support emergent aquatics. This pollen assemblage and elevated charcoal values during this interval are consistent with modern pollen samples from closed lodgepole pine forests in the GYE (Whitlock, 1993; Fall et al. 1995; Iglesias et al. 2017). The zone corresponds with peak charcoal accumulation rates (CHAR and BCHAR), suggesting frequent, high-severity fires at this time.

Zone H1: 120-0 cm depth; 3200 cal yr BP-present day

In general, there was little change in vegetation from Zone H2. Zone H1 had lower percentages of *Pinus* subgen. *Pinus* pollen (~65-75%) than Zone H2. Despite a ~10% decrease in pollen percentages, Zone H1 was still dominated by *Pinus* subgen. *Pinus* pollen, indicating a lodgepole pine forest that was possibly less dense than during Zone H2 time. Again, minor percentages (<2%) from *Picea*, *Abies*, and *Pseudotsuga* likely reflect pollen transport from other nearby or regional sources. There was an increase in herbaceous taxa from Zone H2, although values are still low (*Poaceae* ~5-10%; *Artemisia* ~10-15%). Aquatic taxa such as *Potamogeton*, *Myriophyllum*, and *Sparganium*-type pollen were present in low abundances (0-5%), suggesting relatively fewer aquatics in the late Holocene compared to the early- and mid-Holocene. This pollen assemblage and elevated charcoal accumulation rates during this interval are consistent with modern pollen samples from closed lodgepole pine forests in the GYE (Whitlock, 1993; Fall et al. 1995; Iglesias et al. 2017). This zone corresponds with peak charcoal accumulation rates (CHAR and BCHAR), suggesting frequent or high-severity fires during this interval.

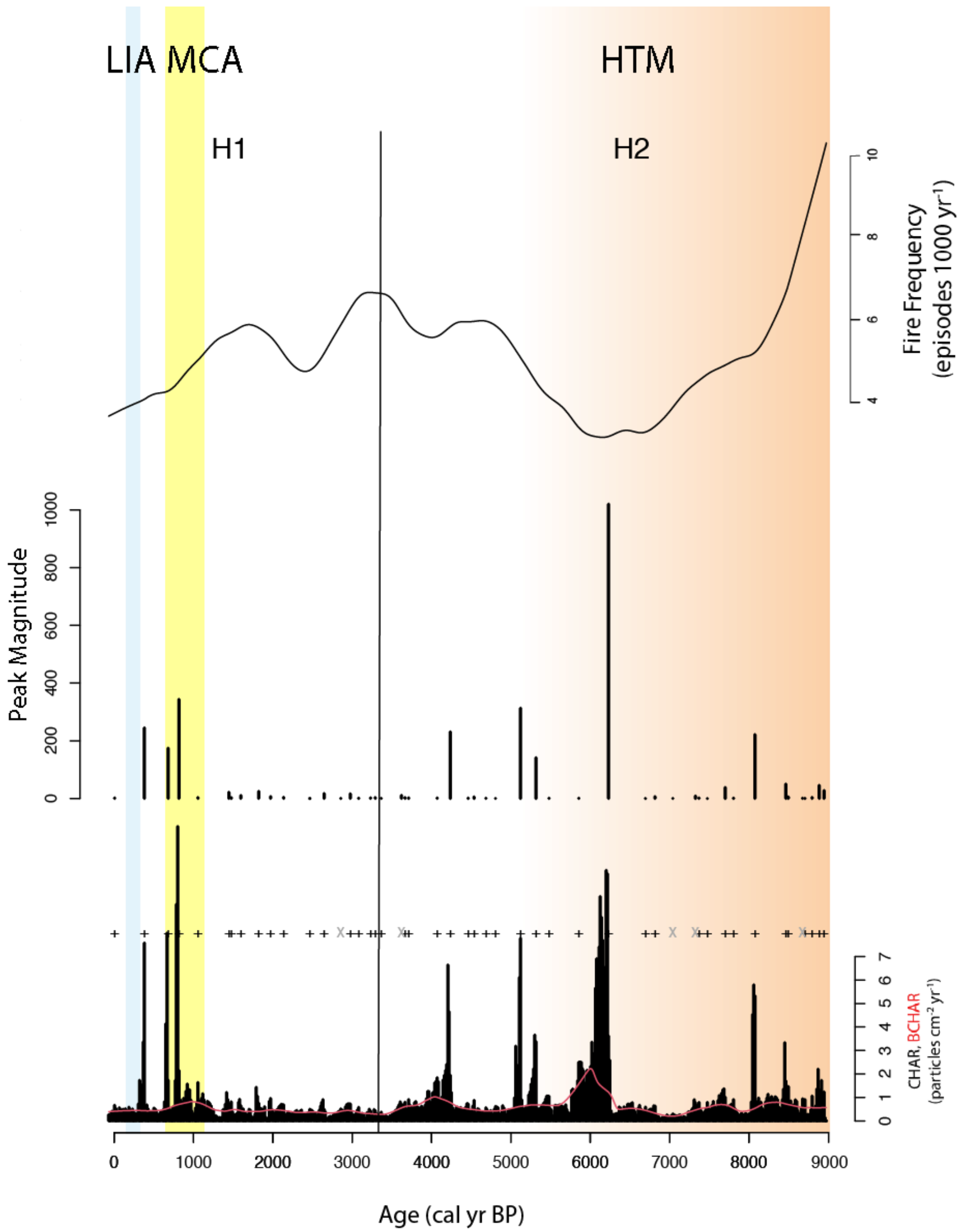

Figure 7. Charcoal diagram with pollen zones (H1, H2) for Harlequin Lake, Wyoming. Blue shading indicates the Little Ice Age (~100-300 cal yr BP), yellow shading highlights the Medieval Climate Anomaly (~650-1,100 cal yr BP), orange shading highlights the Holocene Thermal Maximum (~3,500-11,000 cal yr BP).

The charcoal record for Harlequin Lake (Fig. 7) reveals a fire regime characterized by low-frequency, high-magnitude fire episodes throughout the Holocene. Charcoal influx (CHAR) values varied through time but remained moderate to high, with 39 fire episodes identified across the full record. These fire episodes likely represent one or more high-severity fire events typical of subalpine lodgepole pine forests in the Greater Yellowstone Ecosystem. This interpretation is supported by the fact that most charcoal particles were from burned wood.

The charcoal record shows its highest fire episode frequency occurring ~9,000 cal yr BP with over 10 fire episodes every 1,000 years. Fire-episode frequency reached a minimum at ~6,000 cal yr BP with up to 4 fire episodes per 1,000 years. Fire-episode frequency gradually increased moving into the late-Holocene, reaching another relative maximum at ~3,000 cal yr BP with approximately 7 fire episodes per 1,000 years. In the last 3000 years, fire-episode frequency experienced a negative trend, reaching a minimum of less than for fire episodes per 1,000 years.

An inverse trend between fire-episode frequency and CHAR was observed in the Harlequin record. Two time-intervals record the lowest fire episode frequency and have the highest CHAR values, ~6,000 cal yr BP and ~1,000 cal yr BP to present. The fire episode at ~6,000 cal yr BP had a large peak magnitude value in addition to high CHAR values before and after the episode. From ~1,000 cal yr BP to present, there were three notable fire episodes with high CHAR and peak magnitude values. Two of these fire episodes fell within the timing of the Medieval Climate Anomaly (MCA). Other notable peaks in CHAR throughout the record, including between ~9,000-8,000 cal yr BP which has many small to moderate increases in CHAR associated with fire episodes, and ~5,500-4,000 cal yr BP which has three fire episodes with notable CHAR of at least 3-4 particles cm^{-2} yr^{-1}. Between ~4,000-1,000 cal yr BP, fire episodes were identified by CHAR and peak magnitudes are low.

DISCUSSION

The paleoenvironmental reconstruction at Harlequin Lake reinforces the strong role of climate in mediating fire activity in lodgepole pine forests in the GYE and highlights the remarkable stability of these forests despite changes in Holocene fire activity. The Harlequin Lake pollen and charcoal records are compared with two other records on rhyolitic terrain in the GYE (one of which is also a lodgepole pine forest record) to evaluate differences and identify possible topographic and geologic drivers.

Table 2. Data for sites in regional study.

Site Name	Latitude/ Longitude	Elevation (m)	JJA ppt (cm)	DJF ppt (cm)	Present-day Vegetation	Record Age	Citation
Harlequin Lake	44.644 N/ 110.891 W	2101	13.4	24.7	Lodgepole pine forest	9,000 years	(This paper)
Cygnet Lake	44.663 N/ 110.617 W	2530	12.8	22.2	Lodgepole pine forest	17,000 years	Millspaugh et al., 2000
Goose Lake	44.542 N/ 110.843	2196	12.3	19.6	Lodgepole forest and steppe	11,000 years	Schiller et al., 2021

Harlequin Lake Record

The pollen and charcoal records capture long-term shifts in subalpine forest composition and fire regime dynamics over the past ~9,000 years. The Harlequin pollen data are consistently dominated by *Pinus* pollen, with particularly high proportions of *Pinus* subgen. *Pinus*, indicating a long-term presence of lodgepole pine forest in western Yellowstone likely since its establishment ~11,000 years ago on the Yellowstone plateau seen in other records (Millspaugh et al., 2000). Minor pollen contributions from *Picea*, *Abies*, and *Pseudotsuga* reflect local presence of these conifers in low abundance or long-distance pollen transport from regional sources. Today, *Pseudotsuga* is restricted to drier south-facing talus slopes and *Picea* and *Abies* are found at high-elevation forests surrounding the basin. Herbaceous and aquatic taxa occur throughout the record, with aquatic pollen types including *Potamogeton*, *Myriophyllum*, and *Sparganium*-type reaching their highest abundances in the early to mid-Holocene. These taxa depend on photic littoral zones and can increase in abundance with an expansion of the littoral zone. Aquatic taxa decline in abundance in the upper part of the record, suggesting a shift toward lower aquatic productivity, which could be driven by an increase in water depth that decreases light availability for submerged macrophytes like *Potamogeton* and *Myriophyllum. Pinus* subgen. *Pinus* pollen is more consistently identified and abundant in Zone H2, suggesting a closed lodgepole pine forest, whereas Zone H1 shows a modest decline in *Pinus* and increased presence of herbs and shrubs indicating forest openings or expanded meadows in recent millennia.

In contrast to the vegetation history inferred from the pollen record, the charcoal record shows a complex fire history. Time between fire episodes ranges from ~100 to 400 years (Fig. 12), aligning with time between fire episodes seen elsewhere in lodgepole pine forests on the Yellowstone Plateau (Romme, 1982), with an average time between episodes of ~231 years. Harlequin's fire history displays variability in both the frequency and magnitude of charcoal peaks throughout time, suggesting fluctuations in fire activity linked to climatic changes and internal ecosystem processes such as fuel accumulation.

In the early- to mid-Holocene (Zone H2), fire episodes were relatively frequent, peaking at >10 fire episodes per 1,000 years at ~9,000 cal yr BP, and decreased throughout this time until reaching a minimum at ~6,000 cal yr BP of <4 fire episode per 1,000 years. There are numerous large peaks between ~4,000-9,000 cal yr BP and an average overall time between fire episodes of approximately 200 years. This period coincides with the Holocene Thermal Maximum, caused by stronger summer insolation in the Northern Hemisphere ~11-5 ka, with a peak near ~9-10 ka (Berger, 1978). Higher-than-present summer insolation led to conditions up to 2 degrees Celsius warmer than pre-industrial levels (Bartlein et al., 1998). High CHAR values and repeated, short interval charcoal peaks during this time indicate frequent, severe fires, and high percentages of *Pinus* subgen. *Pinus* pollen (~75-85%) suggests that this fire regime maintained closed lodgepole pine forest (Fig. 11).

During the mid- to late-Holocene (Zone H1), fire episode frequency and CHAR influx vary. From ~3,200-1,100 cal yr BP, the time between fire episodes decreased relative to Zone H2 (Fig. 12), with an average time between fire episodes of ~160 years, but with generally smaller magnitude charcoal peaks. This period features cooler and wetter conditions than previously as summer insolation declined. Previous research suggests oscillations between wet and dry periods were muted, possibly linked to reduced ENSO intensity during the early and mid-Holocene (Barron et al., 2010; Steinman et al., 2016).

In contrast, from ~1,100 cal yr BP to present, time between fire episodes increased to an average ~220 years. CHAR values are moderate to high, and peak magnitudes increased, especially between 700-800 cal yr BP, a period that coincides with the Medieval Climate Anomaly (MCA). During the MCA (~1000 to 700 cal yr BP) (Fig. 12), climate conditions in the Greater Yellowstone region are inferred to have been relatively warm and dry based on increased frequency of fire episodes at Slough Creek Lake (Millspaugh et al., 2004), fire-triggered sedimentation events (Meyer et al., 1995), reduced beaver activity (Persico and Meyer, 2009), and the cessation of regular eruptions at Yellowstone's Old Faithful Geyer believed to reflect diminished hydrothermal recharge during a prolonged regional drought (Hurwitz et al., 2020). The Harlequin record contains three large CHAR peaks identified as fire episodes during this time.

In the Harlequin Lake charcoal record, the MCA interval has some of the largest charcoal peaks, with longer intervals between fire episodes. This pattern suggests that fires may have been more extensive in area burned likely due to lower moisture availability and fuel desiccation leading up to fire episodes after prolonged periods of cool, wet summers and fuel build-up. These conditions are consistent with the hydroclimatic conditions by the Old Faithful record and other regional proxy drought records.

During the LIA (~1550-1850 CE, Viau et al., 2012), the GYE experienced cooler-than-present summers, persistent above-average snowpack, and higher moisture than today (Gray et al., 2017; Pederson et al., 2011). Harlequin Lake's charcoal record shows a decline in charcoal peak magnitudes during the LIA compared to the preceding MCA. This pattern is consistent with expectations of fire behavior under cooler and wetter conditions, as elevated fuel moisture suppresses fire ignition, spread, and severity. The suppression of large fires during the LIA suggests that the fuel loads in the lodgepole pine forest surrounding Harlequin were too wet to experience severe fires.

High-resolution pollen analysis was conducted above and below two prominent charcoal peaks at 18.5-20.5 and 224-235 cm depth at Harlequin Lake to evaluate vegetation composition before and after fire episodes and assess whether fire episodes, including prolonged fire episodes with high CHAR values that provide evidence for large amounts of biomass burning (such as the one at 224-235 cm depth, from 5961-6256 cal yr BP), trigger significant shifts in vegetation composition and forest structure. However, no clear or sustained compositional change was observed.

Regional Analysis

Cygnet Lake lies in lodgepole pine forest and steppe on the central Yellowstone Plateau and provides a useful benchmark for comparison with Harlequin Lake (Whitlock, 1993; Millspaugh et al., 2000). Like Harlequin, Cygnet Lake's pollen record indicates persistent lodgepole pine dominance through the Holocene, reflecting the strong edaphic control of rhyolitic substrates that limit the establishment of spruce and fir. As a result, changes in the Cygnet Lake charcoal record are interpreted as climate-driven fire regime shifts. The Cygnet Lake record indicates that fire-episode frequency was moderate (4 fire episodes/1000 yr) during the late-glacial period and reached highest values in the early Holocene when climate conditions were warm and dry (>10 fire episodes/1000 yr) between ~11,000-7,000 cal yr BP, aligning with peak summer insolation and the attendant Holocene Thermal Maximum (Whitlock and Bartlein, 1993). In the middle and late Holocene, summer insolation decreased and conditions became cooler and wetter in the summer-dry regions of Yellowstone (Whitlock and Bartlein, 1996). The Cygnet Lake record shows a decrease in fire activity after 7000 cal yr BP and by late-Holocene time (the past ~2,000-3,000 years), the fires at Cygnet Lake had declined to ~2-4 fire episodes 1000^{-1} yr (i.e. 250–500 years between fire episodes), comparable to the modern pre-1988 fire regime on the Central Plateau (Romme and Despain, 1989). Vegetation composition was relatively insensitive to these Holocene climate shifts, in contrast to the fire regime.

The charcoal records at Harlequin and Cygnet lakes differ in the last ~1,000 years. While both sites record broadly similar patterns of fire-episode frequency across the Holocene, Harlequin Lake registered several exceptionally high charcoal accumulation peaks during the MCA. By contrast, the Cygnet Lake record shows consistently smaller peak magnitudes over the same interval, with only one peak exceeding ~7 charcoal particles cm^{-2} yr^{-1}. In contrast, Harlequin Lake records multiple charcoal peaks, including the largest magnitude peak of the ~9,000 year record at 796 cal yr BP.

Because charcoal peak magnitude is related to fire severity and biomass burned (Whitlock and Larsen, 2001), the comparison of the two lakes suggests that large or severe fire events were more common at Harlequin Lake than at Cygnet Lake in the last millennium. Cygnet Lake, located at higher elevation and deeper within the Yellowstone Plateau, may have experienced persistently cooler and moister conditions in the last millennium, reducing the likelihood of fuel desiccation. In contrast, Harlequin Lake's position along the western margin of the plateau may have exposed it more directly to interannual and interdecadal hydroclimatic variability, particularly related to the strengthening of ENSO during the late

Holocene. In addition, Harlequin Lake's location in a confined canyon and at the edge of the Snake River Plain and western edge of the Yellowstone Plateau, may have focused fire spread.

Multiple paleoclimate records from the American West demonstrate that ENSO amplitude increased in the late Holocene, particularly in the last millennium, leading to heightened inter-decadal climate variability. Increased frequency and severity of wet-dry oscillations was observed in oxygen isotope records and charcoal data from lakes in the Pacific Northwest (Steinman et al., 2016; Mark et al., 2024). In western Yellowstone, interannual variability would have promoted fuel build-up during wetter periods and enhanced fire potential during subsequent droughts. The large-magnitude charcoal peaks during the MCA record at least 3 extreme fire episodes, which may have been driven by increased interannual or interdecadal climate variability.

Although the records from Harlequin and Cygnet lakes indicate a fire regime strongly governed by variations in climate, marked by high fire frequency during the early Holocene and Holocene Thermal Maximum, and declining fire activity as the climate cooled with decreasing summer insolation, the late-Holocene record at Harlequin Lake suggests that lodgepole pine forests along the western margin of the Yellowstone plateau may have been more sensitive to climate-driven fuel build-up and drying during the late Holocene compared to more central sites like Cygnet Lake.

Goose Lake, located in the hydrothermally active Lower Geyser Basin, offers a contrasting fire history record (Schiller et al., 2021). Unlike Harlequin and Cygnet lakes, Goose Lake lies in a hydrothermally active basin with open lodgepole pine forest. Sediment records indicate that from 10,300-3,800 cal yr BP, Goose Lake supported more forest than is present at the site today (Schiller et al., 2021). During this interval, pollen and charcoal records from Goose and Harlequin lakes show broadly similar trends, with both sites recording maximum arboreal pollen and charcoal influx between ~6,000 and 5,000 cal yr BP near the end of the Holocene Thermal Maximum. After ~3,800 cal yr BP, Goose Lake records a transition toward increased grass and sagebrush abundance, signaling a shift from forested to a more open landscape. The timing of this transition corresponds with geochemical indicators that suggest an opening of the vegetation at the same time as a hydrothermal rearrangement (Schiller et al. 2021).

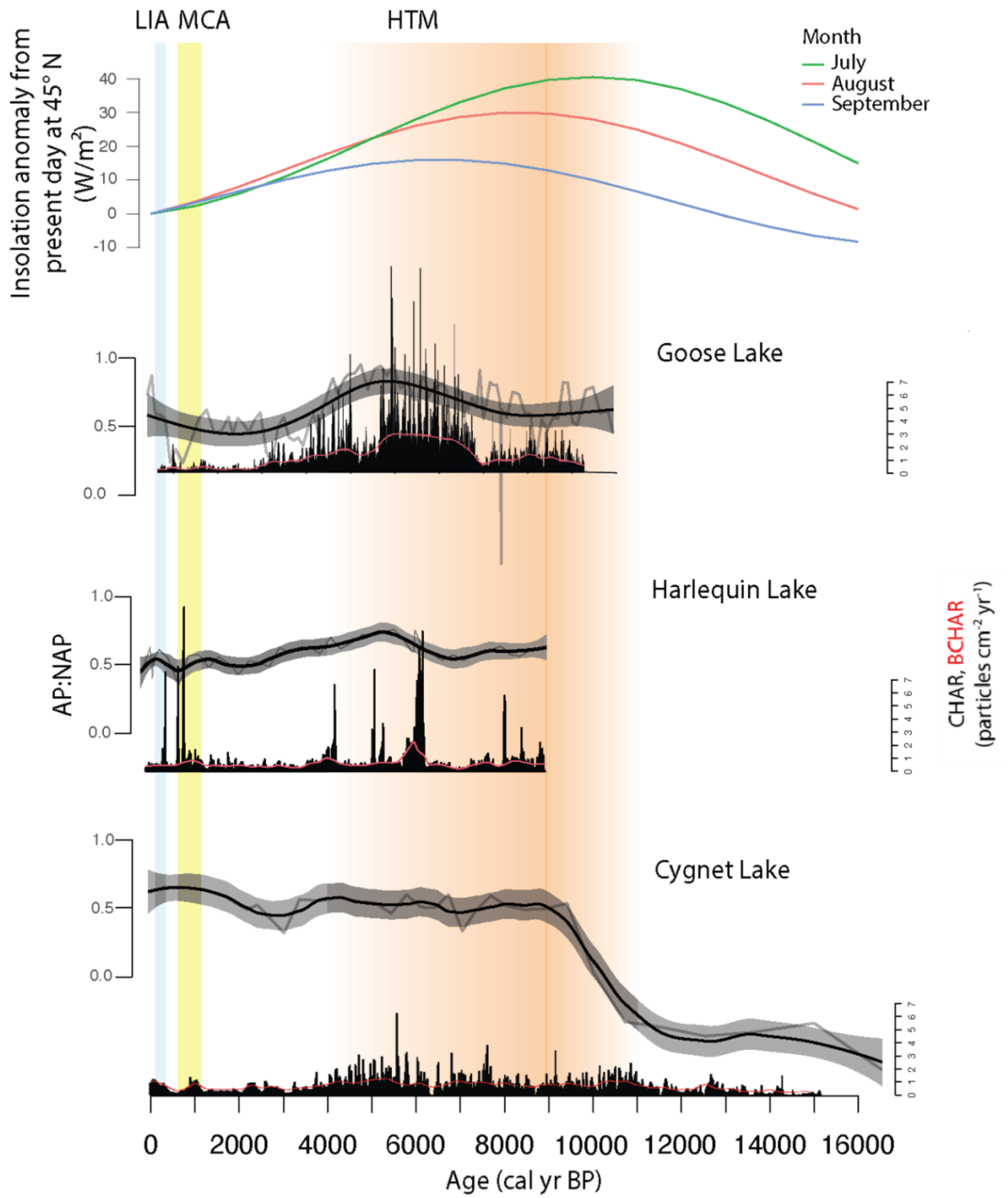

Figure 8. Insolation anomaly curves for July, August, and September, smoothed AP:NAP ratios and CHAR, BCHAR showing changes in forest cover and fire activity for Harlequin, Goose, and Cygnet lakes in the GYE. Blue shading highlights the Little Ice Age (~100-300 cal yr BP), yellow shading highlights the Medieval Climate Anomaly (~650-1,100 cal yr BP), orange shading highlights the Holocene Thermal Maximum (~11,000-5000 cal yr BP).

Regional Climate and Implications for Future Fire Regimes

The Harlequin Lake record provides a long-term baseline for understanding natural variability in Yellowstone's fire regime and forest resilience. Over the last ~9,000 years, lodgepole pine forests in western Yellowstone have experienced fire episodes that ranged in frequency from 10 episodes/1000 years to 4 episodes/1000 years. These fires did not change the composition of the forest and may, in fact, promote lodgepole pine dominance. Pollen data suggest forests recovered rapidly from each fire episode, with no significant shifts in vegetation from forest to non-forest states even during pronounced warm periods like the early Holocene or Medieval Climate Anomaly. This resilience is attributed to lodgepole pine's life-history traits (serotinous cones, rapid re-establishment after fire) that allowed stands to re-establish and dominate rhyolitic substrates in the time between fires (Turner et al., 1994). The paleorecords suggest that as the climate varied, fire episodes burned larger areas and happened more frequently, yet lodgepole pine forests remained remarkably stable throughout the Holocene (Whitlock, 1993; Schiller et al., 2021).

Emerging fire dynamics in the 21st century may challenge the long-standing stability of lodgepole pine forests, as illustrated by recent short-interval fires such as the 2016 Maple Fire, which reburned areas affected by the 1988 fires (Turner et al., 2019). However, because fire episodes in lake-sediment charcoal records are defined as peaks that represent several years and are separated by ~25 years, the Harlequin Lake record cannot resolve short interval fire return intervals. Instead, the paleoecological record constrains the characteristics of fire regime in lodgepole pine under a wide range of Holocene climate conditions, showing that even during the warmest and driest intervals, fire episodes were generally separated by decades to centuries.

Hence, the paleoenvironmental record from Harlequin Lake shows that lodgepole pine forests are resilient to climate variability within the envelope of past Holocene climatic and disturbance patterns.

Future Climate-Fire Interactions in YNP Lodgepole Pine Forests on Rhyolitic Substrates

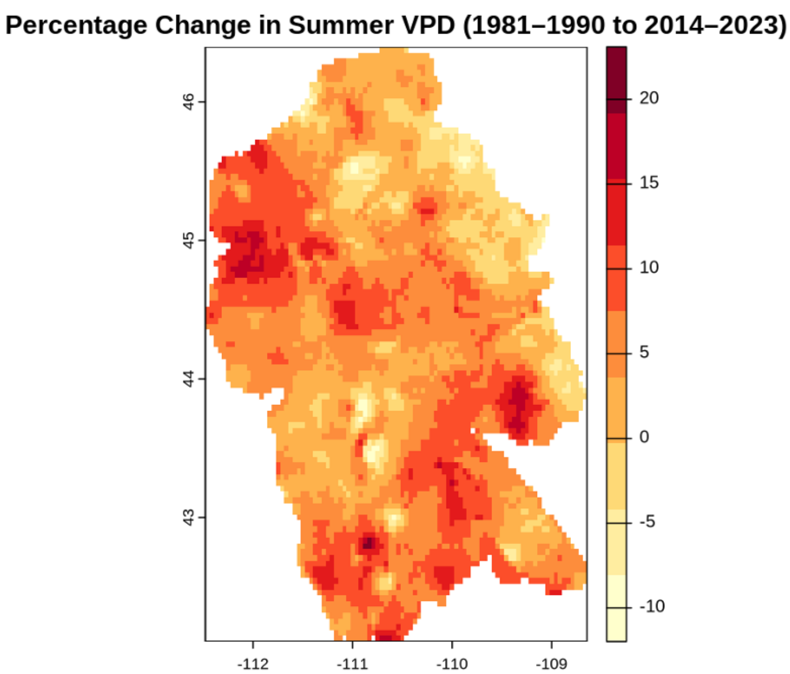

Figure 9. Percent change in average maximum summer vapor pressure deficit in the GYE from (1981-1900) to (2014-2023).

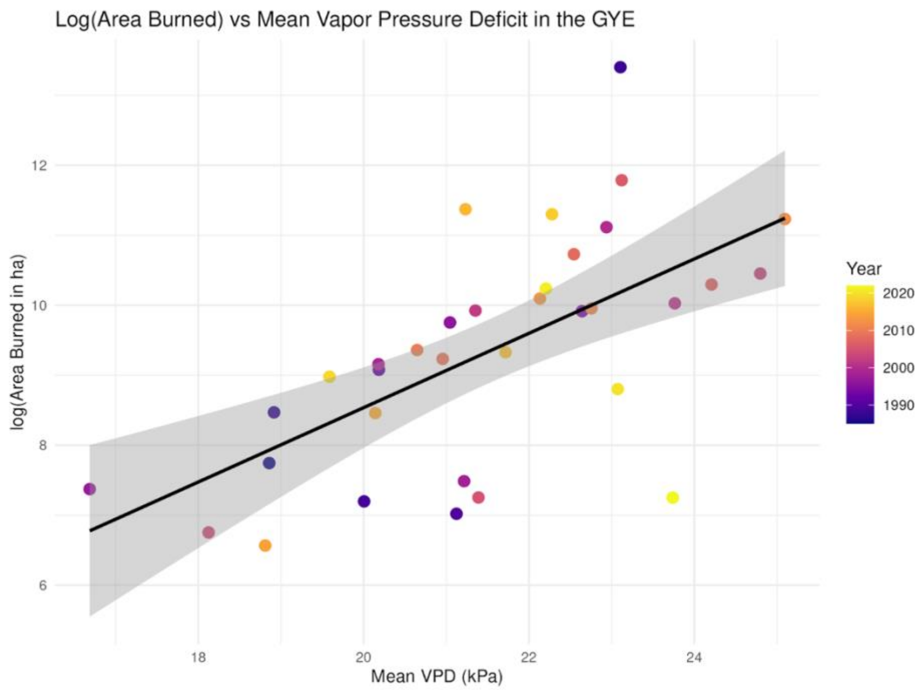

Figure 10. Log(Area Burned) vs. mean maximum vapor pressure deficit in the GYE by year from 1987-2020.

From 1981-2023, vapor pressure deficit (VPD), a fuel aridity metric that measures the difference between moisture in air and how much moisture the air can hold, has risen (Fig. 9). Rising summer VPD has increased fuel aridity, and annual area burned in the GYE is strongly correlated with mean summer VPD, with the largest fire years occurring during periods of highest atmospheric moisture demand (Fig. 10). Climate models project that VPD will continue to rise through the mid-21st century under high-emissions greenhouse gas scenarios, increasing the frequency and duration of conditions conducive to large fires, even if winter precipitation increases modestly (Abatzoglou and Williams, 2016; Shuman et al., 2018; Hostetler et al. 2021). These patterns suggest that the GYE is transitioning into a climate-fire regime where large fire years become increasingly common. Elevated VPD also constrains postfire regeneration by increasing seedling moisture stress and lengthening the seasonal window of unfavorable establishment conditions (Kiel et al., 2025). Across the GYE and Northern Rockies, high-severity fires occurring under warm, dry postfire climates are increasingly associated with regeneration failure and transitions to shrub- or grass-dominated vegetation (Stevens-Rumann et al., 2018; Turner et al., 2019).

The Harlequin Lake record provides a long-term baseline by extending fire history beyond the limits of recent observations and historical documentation. Although charcoal data have less spatial and temporal specificity than historical observations or tree-ring reconstructions, they uniquely allow changes in fire and vegetation to be evaluated across a wide range of Holocene climatic conditions. At Harlequin Lake, lodgepole pine forest persisted through warm, dry intervals with repeated fire episodes over the last ~9,000 years without major compositional change. High-resolution pollen sampling conducted immediately above and below the largest charcoal peaks likewise shows no clear vegetation compositional change following stand-replacing fire episodes, underscoring the long-term resilience of lodgepole pine forests under past climate variability. Continued warming and drying in the future may exceed this Holocene range of conditions allowing lodgepole pine forests to re-establish after high intensity, short-interval fires, possibly reducing the long-term resilience of lodgepole pine forest.

CONCLUSIONS

The Holocene paleoecological record from Harlequin Lake documents long-term interactions between climate, fire, and vegetation in subalpine lodgepole pine forests on the western margin of the Yellowstone Plateau. Several key findings emerge from the Harlequin Lake record that expand our knowledge of Yellowstone's past:

- Lodgepole pine forest has been dominant and remarkably stable at Harlequin Lake site for the last ~9,000 years despite shifts in fire activity throughout the Holocene. Maximum forest density occurred between ~7,000-3,200 cal yr BP.
- The charcoal record at Harlequin Lake suggests that fire episodes occurred every ~231 years on average.
- The pollen record indicates that the vegetation did not change in the face of increasing or decreasing fire activity.
- Regional rhyolite records across the GYE show a warm, dry early Holocene and a cooler, wetter mid-Holocene, while the Harlequin Lake record contains three large charcoal peaks in the last millennium that cluster around the MCA.
- The differences between the three sites reinforces that while regional climate exerts a dominant influence on subalpine fire regimes, local geologic and topographic factors modulate climatic controls, creating spatial heterogeneity in fire activity in Yellowstone within specific watersheds.
- Modern climate trends for GYE include greater climate variability, rising summer VPD, increasing area burned, and <30 year reburns, which raise questions about the future

resilience of GYE forests. The Harlequin Lake record shows long-term lodgepole pine resilience to Holocene climate variability.

Dominated throughout by *Pinus* subgen. *Pinus* pollen, the Harlequin Lake record shows that for the last ~9000 years, lodgepole pine dominated the rhyolitic substrates of Yellowstone, with a fire regime characterized by infrequent, stand-replacing fires at intervals averaging ~231 years. This edaphic setting appears to be a major driver of long-term lodgepole pine forest stability. Charcoal-influx data reveal these fires were not evenly distributed throughout time: the early and late Holocene were characterized by high-magnitude charcoal peaks and shorter time between fire episodes, corresponding to periods of greater interdecadal climate variability and regional aridity. In contrast, the mid-Holocene was characterized by longer fire intervals and lower charcoal peak magnitudes, consistent with a cooler, wetter, more climatically stable period. The Harlequin Lake record affirms the long-standing role of fire as a key ecosystem process in Yellowstone's lodgepole pine forests while also demonstrating that both fire frequency and extent/severity varied in response to variable climate conditions. Although Harlequin Lake shows no major compositional shifts during past warm-dry intervals, a strong regional pine signal and smoothing of the data may obscure short-term (<100 years) vegetation compositional change. Thus, the long-term record of lodgepole pine forest stability at Harlequin Lake does not necessarily preclude the possibility of both short-term vegetation composition change post-fire, or the sensitivity of lodgepole pine forests to novel fire-climate conditions at Harlequin Lake. Overall, the Harlequin Lake record highlights the resilience of lodgepole pine forests to past climatic and fire-regime variability, while underscoring the value of additional high-resolution charcoal and pollen records for better resolving vegetation responses to changing fire regimes and climate across the Greater Yellowstone Ecosystem, in complement to ongoing modeling efforts.

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APPENDICES

APPENDIX A

RAW CHARCOAL COUNTS

Table A1. Raw charcoal counts

Surface	Charcoal count		Total char	Char conc	Age			
Top (cm)	Grass	> 125 u			cal yr BP			
					min	max	median	mean
0	1	11	12	6	-74	-55	-69	-68
0.5	1	9	10	5	-70	-36	-58	-57
1	2	7	9	4.5	-68	-9	-48	-45
1.5	3	11	14	7	-67	19	-38	-34
2	0	12	12	6	-65	48	-28	-23
2.5	0	18	18	9	-64	78	-19	-11
3	0	10	10	5	-62	107	-9	0
3.5	4	24	28	14	-61	137	1	11
4	4	22	26	13	-60	167	11	23
4.5	0	23	23	11.5	-59	196	21	34
5	8	16	24	12	-58	226	31	45
5.5	0	16	16	8	-43	233	44	57
6	8	18	26	13	-35	241	58	70
6.5	2	33	35	17.5	-29	250	71	82
7	2	21	23	11.5	-23	259	86	94
7.5	2	23	25	12.5	-19	268	100	106

8	5	21	26	13	-14	279	113	118
8.5	0	12	12	6	-10	292	126	131
9	2	28	30	15	-6	311	139	143
9.5	1	16	17	8.5	-2	333	151	155
10	0	22	22	11	1	356	164	167
10.5	0	21	21	10.5	20	361	177	179
11	3	29	32	16	36	366	189	192
11.5	4	20	24	12	48	372	202	204
12	3	20	23	11.5	57	378	215	216
12.5	3	24	27	13.5	67	384	230	228
13	2	20	22	11	79	391	243	240
13.5	1	12	13	6.5	85	398	255	253
14	1	23	24	12	90	408	269	265
14.5	0	10	10	5	96	419	282	277
15	1	10	11	5.5	103	435	294	289
15.5	0	25	25	12.5	135	438	305	302
16	2	33	35	17.5	164	441	315	314
16.5	2	81	83	41.5	195	445	325	326
17	2	72	74	37	223	450	335	339

17.5	7	45	52	26	248	454	346	351
18	0	51	51	25.5	273	459	356	363
18.5	4	25	29	14.5	294	465	367	376
19	1	628	629	314.5	310	475	378	388
19.5	0	21	21	10.5	321	493	390	400
20	0	32	32	16	326	517	404	413
20.5	1	45	46	23	340	532	418	427
21	0	21	21	10.5	349	550	433	440
21.5	0	18	18	9	356	578	449	454
22	2	23	25	12.5	362	609	463	468
22.5	2	17	19	9.5	365	646	476	482
23	0	11	11	5.5	369	686	489	496
23.5	1	25	26	13	374	730	501	510
24	2	17	19	9.5	377	772	512	523
24.5	1	22	23	11.5	380	810	523	537
25	3	21	24	12	383	851	533	551
25.5	2	13	15	7.5	395	867	547	564
26	0	12	12	6	404	883	562	578
26.5	1	16	17	8.5	410	897	574	591

27	2	15	17	8.5	416	914	586	604
27.5	1	27	28	14	422	932	600	618
28	0	8	8	4	427	951	613	631
28.5	1	30	31	15.5	432	970	625	644
29	1	33	34	17	435	996	638	658
29.5	2	130	132	66	440	1025	650	671
30	1	561	562	281	444	1057	663	684
30.5	1	132	133	66.5	457	1072	677	698
31	4	14	18	9	469	1087	691	712
31.5	6	31	37	18.5	478	1103	704	725
32	5	10	15	7.5	484	1127	717	739
32.5	2	12	14	7	492	1146	731	753
33	4	29	33	16.5	501	1172	743	767
33.5	3	25	28	14	508	1191	756	781
34	4	57	61	30.5	514	1221	770	794
34.5	2	203	205	102.5	519	1254	783	808
35	0	1029	1029	514.5	524	1277	796	822
35.5	0	221	221	110.5	540	1292	809	835
36	4	51	55	27.5	551	1304	822	848

36.5	3	47	50	25	562	1321	837	862
37	7	38	45	22.5	568	1336	851	875
37.5	1	36	37	18.5	578	1349	865	888
38	4	48	52	26	585	1366	878	902
38.5	3	33	36	18	594	1380	891	915
39	1	44	45	22.5	600	1398	905	928
39.5	1	108	109	54.5	605	1414	917	942
40	3	38	41	20.5	610	1439	930	955
40.5	5	87	92	46	624	1453	943	969
41	2	66	68	34	636	1469	957	983
41.5	0	36	36	18	647	1484	972	997
42	4	17	21	10.5	654	1503	985	1011
42.5	0	17	17	8.5	664	1520	1001	1025
43	0	16	16	8	673	1530	1016	1038
43.5	1	31	32	16	684	1551	1029	1052
44	0	45	45	22.5	691	1571	1042	1066
44.5	12	82	94	47	700	1595	1056	1080
45	4	39	43	21.5	706	1613	1070	1094
45.5	1	44	45	22.5	720	1627	1082	1107

46	10	39	49	24.5	732	1643	1096	1120
46.5	8	45	53	26.5	740	1656	1110	1134
47	9	53	62	31	751	1674	1122	1147
47.5	1	41	42	21	759	1690	1135	1160
48	1	24	25	12.5	770	1708	1148	1173
48.5	1	15	16	8	781	1728	1160	1186
49	2	37	39	19.5	787	1750	1174	1199
49.5	3	43	46	23	793	1773	1186	1212
50	3	40	43	21.5	799	1807	1199	1226
50.5	8	35	43	21.5	816	1812	1214	1240
51	2	28	30	15	829	1825	1228	1254
51.5	5	21	26	13	840	1836	1242	1268
52	3	20	23	11.5	851	1855	1256	1282
52.5	0	9	9	4.5	861	1875	1268	1297
53	2	13	15	7.5	870	1893	1283	1311
53.5	0	10	10	5	877	1913	1299	1325
54	0	6	6	3	883	1940	1314	1339
54.5	1	10	11	5.5	888	1960	1331	1353
55	0	6	6	3	895	1977	1346	1368

55.5	0	8	8	4	911	1991	1360	1381
56	12	16	28	14	930	2003	1372	1395
56.5	3	28	31	15.5	937	2020	1386	1409
57	3	32	35	17.5	949	2039	1402	1423
57.5	10	59	69	34.5	956	2053	1415	1437
58	6	28	34	17	964	2076	1427	1450
58.5	14	55	69	34.5	971	2096	1440	1464
59	5	12	17	8.5	981	2108	1453	1478
59.5	5	25	30	15	989	2132	1467	1492
60	2	45	47	23.5	997	2150	1480	1506
60.5	4	12	16	8	1011	2161	1493	1519
61	5	10	15	7.5	1025	2173	1506	1533
61.5	4	11	15	7.5	1037	2183	1521	1546
62	5	10	15	7.5	1047	2199	1535	1559
62.5	4	12	16	8	1057	2208	1549	1573
63	12	14	26	13	1067	2232	1563	1586
63.5	9	44	53	26.5	1076	2247	1575	1600
64	11	42	53	26.5	1082	2271	1586	1613
64.5	5	26	31	15.5	1091	2284	1603	1627

65	1	22	23	11.5	1099	2302	1618	1640
65.5	2	25	27	13.5	1112	2317	1630	1654
66	3	14	17	8.5	1129	2333	1643	1667
66.5	4	11	15	7.5	1141	2350	1657	1680
67	6	11	17	8.5	1150	2364	1669	1694
67.5	1	9	10	5	1159	2384	1683	1707
68	5	10	15	7.5	1168	2401	1696	1720
68.5	15	25	40	20	1178	2420	1709	1734
69	2	12	14	7	1186	2436	1723	1747
69.5	0	9	9	4.5	1194	2457	1737	1761
70	3	4	7	3.5	1203	2478	1751	1774
70.5	1	5	6	3	1220	2489	1765	1787
71	1	13	14	7	1237	2501	1775	1801
71.5	2	69	71	35.5	1249	2511	1790	1814
72	5	56	61	30.5	1264	2530	1801	1827
72.5	1	41	42	21	1273	2553	1815	1840
73	1	34	35	17.5	1283	2579	1826	1854
73.5	0	19	19	9.5	1293	2589	1839	1867
74	0	30	30	15	1301	2604	1851	1880

74.5	0	20	20	10	1309	2621	1865	1894
75	14	6	20	10	1313	2643	1876	1907
75.5	27	22	49	24.5	1333	2651	1891	1921
76	1	10	11	5.5	1351	2666	1906	1935
76.5	1	3	4	2	1362	2681	1921	1948
77	0	8	8	4	1376	2695	1934	1962
77.5	0	4	4	2	1385	2711	1949	1976
78	6	65	71	35.5	1393	2732	1961	1990
78.5	3	35	38	19	1404	2760	1977	2004
79	0	26	26	13	1417	2782	1989	2018
79.5	0	22	22	11	1427	2793	2005	2032
80	6	13	19	9.5	1437	2807	2017	2045
81	6	21	27	13.5	1461	2835	2047	2072
82	2	28	30	15	1487	2855	2075	2099
83	4	33	37	18.5	1515	2891	2100	2126
84	5	32	37	18.5	1527	2922	2126	2153
85	6	8	14	7	1540	2945	2153	2180
86	5	15	20	10	1575	2964	2184	2206
87	2	13	15	7.5	1596	2996	2211	2232

88	3	12	15	7.5	1620	3023	2236	2259
89	5	16	21	10.5	1638	3067	2262	2285
90	1	26	27	13.5	1658	3108	2291	2311
91	3	15	18	9	1692	3139	2321	2340
92	3	23	26	13	1714	3168	2349	2368
93	3	13	16	8	1735	3195	2377	2397
94	0	18	18	9	1755	3236	2405	2425
95	1	14	15	7.5	1771	3268	2438	2454
96	2	24	26	13	1796	3287	2462	2482
97	2	21	23	11.5	1818	3323	2488	2509
98	0	19	19	9.5	1853	3350	2514	2537
99	2	8	10	5	1872	3384	2541	2564
100	0	20	20	10	1896	3401	2567	2592
101	3	31	34	17	1923	3430	2595	2620
102	0	49	49	24.5	1944	3476	2622	2648
103	1	22	23	11.5	1969	3498	2649	2676
104	0	5	5	2.5	1992	3547	2678	2705
105	0	11	11	5.5	2017	3575	2709	2733
106	1	10	11	5.5	2043	3596	2737	2761

107	0	15	15	7.5	2081	3621	2767	2789
108	1	16	17	8.5	2103	3660	2794	2818
109	0	25	25	12.5	2125	3687	2822	2846
110	0	30	30	15	2147	3714	2853	2874
111	3	16	19	9.5	2176	3728	2882	2901
112	3	27	30	15	2204	3751	2910	2927
113	4	37	41	20.5	2231	3779	2935	2954
114	2	43	45	22.5	2253	3798	2963	2980
115	0	13	13	6.5	2277	3837	2994	3007
116	1	10	11	5.5	2302	3857	3018	3034
117	0	19	19	9.5	2327	3881	3043	3062
118	0	29	29	14.5	2355	3923	3072	3089
119	0	14	14	7	2372	3949	3097	3117
120	1	17	18	9	2398	3984	3125	3145
121	0	7	7	3.5	2431	4013	3153	3172
122	0	21	21	10.5	2454	4037	3185	3200
123	0	28	28	14	2477	4069	3215	3228
124	0	9	9	4.5	2491	4092	3243	3256
125	0	28	28	14	2513	4110	3273	3284

126	0	19	19	9.5	2544	4137	3302	3312
127	0	12	12	6	2575	4171	3334	3339
128	0	21	21	10.5	2607	4194	3360	3367
129	0	11	11	5.5	2623	4223	3388	3394
130	0	12	12	6	2639	4254	3419	3422
131	0	7	7	3.5	2668	4280	3445	3449
132	0	11	11	5.5	2701	4309	3471	3475
133	0	13	13	6.5	2724	4338	3497	3502
134	0	18	18	9	2739	4370	3521	3529
135	0	25	25	12.5	2765	4404	3549	3556
136	1	29	30	15	2800	4421	3575	3583
137	2	42	44	22	2829	4449	3600	3610
138	0	37	37	18.5	2848	4493	3627	3637
139	4	39	43	21.5	2870	4520	3657	3665
140	3	21	24	12	2888	4545	3684	3692
141	1	41	42	21	2920	4568	3711	3719
142	2	23	25	12.5	2945	4591	3734	3745
143	1	35	36	18	2974	4621	3761	3772
144	1	41	42	21	2994	4657	3790	3799

145	5	28	33	16.5	3023	4689	3815	3825
146	0	24	24	12	3044	4705	3842	3853
147	0	39	39	19.5	3076	4731	3867	3881
148	0	30	30	15	3116	4758	3898	3909
149	3	43	46	23	3136	4788	3929	3937
150	2	68	70	35	3166	4832	3953	3965
151	2	41	43	21.5	3189	4866	3980	3993
152	0	71	71	35.5	3223	4900	4009	4020
153	2	89	91	45.5	3247	4922	4039	4048
154	4	110	114	57	3263	4952	4067	4076
155	1	42	43	21.5	3281	4989	4098	4104
156	2	49	51	25.5	3316	5013	4124	4131
157	1	99	100	50	3342	5041	4149	4159
158	1	128	129	64.5	3374	5064	4175	4187
159	1	331	332	166	3399	5086	4205	4215
160	2	107	109	54.5	3426	5123	4230	4243
161	1	31	32	16	3447	5150	4258	4269
162	3	20	23	11.5	3470	5177	4286	4296
163	3	28	31	15.5	3500	5201	4313	4322

164	0	26	26	13	3529	5223	4339	4349
165	1	32	33	16.5	3555	5252	4364	4375
166	0	19	19	9.5	3579	5274	4393	4403
167	1	33	34	17	3604	5299	4420	4431
168	0	39	39	19.5	3627	5328	4449	4459
169	1	22	23	11.5	3650	5356	4474	4487
170	0	20	20	10	3670	5390	4502	4514
171	2	40	42	21	3701	5411	4528	4540
172	1	15	16	8	3729	5434	4552	4566
173	1	30	31	15.5	3745	5473	4579	4592
174	3	12	15	7.5	3763	5486	4609	4618
175	0	21	21	10.5	3791	5515	4631	4644
176	0	19	19	9.5	3818	5535	4658	4672
177	0	27	27	13.5	3859	5561	4686	4700
178	2	19	21	10.5	3879	5589	4710	4728
179	1	22	23	11.5	3898	5617	4739	4756
180	0	16	16	8	3915	5654	4765	4783
181	0	41	41	20.5	3961	5680	4796	4812
182	0	33	33	16.5	3997	5710	4829	4841

183	0	8	8	4	4032	5738	4858	4870
184	1	38	39	19.5	4056	5765	4889	4898
185	0	21	21	10.5	4083	5793	4919	4927
186	0	13	13	6.5	4115	5815	4944	4954
187	3	25	28	14	4139	5844	4971	4982
188	0	26	26	13	4173	5873	5001	5009
189	1	27	28	14	4202	5910	5029	5036
190	4	168	172	86	4223	5950	5058	5063
191	1	53	54	27	4250	5973	5085	5090
192	2	418	420	210	4281	5991	5110	5117
193	0	31	31	15.5	4305	6020	5137	5144
194	0	27	27	13.5	4332	6041	5169	5171
195	3	36	39	19.5	4355	6065	5195	5198
196	0	58	58	29	4381	6085	5226	5226
197	5	83	88	44	4398	6114	5252	5253
198	2	100	102	51	4430	6139	5280	5280
199	7	193	200	100	4454	6176	5303	5308
200	0	29	29	14.5	4473	6206	5329	5335
201	0	28	28	14	4500	6225	5357	5363

202	0	38	38	19	4539	6244	5385	5391
203	0	46	46	23	4569	6268	5414	5419
204	3	52	55	27.5	4600	6297	5443	5446
205	0	59	59	29.5	4622	6317	5469	5474
206	1	26	27	13.5	4660	6331	5497	5501
207	1	9	10	5	4691	6354	5525	5528
208	1	35	36	18	4723	6385	5554	5554
209	1	35	36	18	4749	6424	5581	5581
210	2	35	37	18.5	4773	6451	5609	5607
211	2	31	33	16.5	4798	6469	5636	5635
212	4	26	30	15	4835	6478	5662	5662
213	4	29	33	16.5	4874	6503	5688	5689
214	0	20	20	10	4898	6539	5712	5716
215	0	17	17	8.5	4917	6562	5739	5744
216	2	75	77	38.5	4951	6586	5767	5771
217	2	61	63	31.5	4990	6616	5795	5799
218	3	74	77	38.5	5017	6637	5822	5826
219	4	136	140	70	5038	6668	5851	5854
220	1	129	130	65	5060	6698	5879	5882

221	4	111	115	57.5	5094	6715	5905	5909
222	1	90	91	45.5	5121	6736	5932	5936
223	3	118	121	60.5	5150	6772	5961	5964
224	1	97	98	49	5172	6799	5989	5991
225	1	180	181	90.5	5189	6833	6016	6018
226	2	130	132	66	5214	6869	6043	6045
227	0	345	345	172.5	5245	6890	6070	6071
228	2	384	386	193	5266	6913	6095	6098
229	3	494	497	248.5	5299	6932	6123	6124
230	6	410	416	208	5323	6963	6149	6151
231	9	301	310	155	5348	6984	6176	6177
232	1	614	615	307.5	5381	7005	6202	6203
233	2	186	188	94	5407	7022	6230	6229
234	1	21	22	11	5431	7054	6256	6255
235	0	14	14	7	5448	7075	6281	6281
236	4	12	16	8	5485	7094	6310	6308
237	3	17	20	10	5518	7112	6336	6335
238	1	31	32	16	5559	7141	6367	6363
239	1	19	20	10	5586	7164	6393	6390

240	1	29	30	15	5621	7186	6422	6417
241	2	24	26	13	5660	7208	6447	6443
242	1	38	39	19.5	5691	7231	6472	6469
243	0	35	35	17.5	5712	7252	6499	6495
244	1	41	42	21	5734	7287	6524	6522
245	0	24	24	12	5765	7325	6551	6548
246	0	13	13	6.5	5798	7334	6580	6575
247	1	32	33	16.5	5828	7363	6610	6603
248	1	27	28	14	5845	7390	6634	6630
249	1	15	16	8	5874	7421	6661	6657
250	0	32	32	16	5903	7460	6688	6685
251	1	16	17	8.5	5928	7479	6715	6711
252	2	29	31	15.5	5957	7486	6744	6738
253	2	25	27	13.5	5986	7510	6775	6764
254	1	36	37	18.5	6011	7536	6802	6790
255	1	10	11	5.5	6027	7565	6830	6817
256	0	10	10	5	6059	7585	6856	6844
257	0	3	3	1.5	6105	7616	6882	6871
258	0	8	8	4	6137	7639	6908	6899

259	0	6	6	3	6170	7665	6932	6926
260	0	14	14	7	6201	7698	6960	6953
261	1	8	9	4.5	6222	7713	6987	6980
262	0	9	9	4.5	6258	7728	7013	7007
263	1	16	17	8.5	6295	7754	7036	7034
264	1	13	14	7	6311	7788	7064	7061
265	0	10	10	5	6334	7813	7095	7088
266	0	14	14	7	6365	7836	7120	7115
267	0	8	8	4	6399	7853	7147	7142
268	1	10	11	5.5	6433	7879	7175	7169
269	0	7	7	3.5	6453	7899	7205	7197
270	0	20	20	10	6482	7930	7234	7224
271	2	17	19	9.5	6517	7952	7260	7250
272	0	28	28	14	6550	7978	7286	7276
273	1	44	45	22.5	6569	7996	7311	7302
274	0	30	30	15	6591	8014	7336	7328
275	1	40	41	20.5	6618	8031	7363	7354
276	1	21	22	11	6654	8047	7389	7381
277	0	19	19	9.5	6699	8067	7415	7407

278	0	22	22	11	6720	8082	7444	7434
279	2	42	44	22	6754	8104	7471	7461
280	0	9	9	4.5	6780	8134	7499	7488
280.5	1	29	30	15	6794	8142	7511	7501
281	0	29	29	14.5	6811	8144	7526	7515
281.5	0	46	46	23	6832	8152	7541	7529
282	2	35	37	18.5	6856	8163	7556	7542
282.5	1	24	25	12.5	6878	8174	7567	7556
283	0	33	33	16.5	6898	8180	7581	7569
283.5	0	10	10	5	6913	8189	7594	7583
284	5	38	43	21.5	6925	8201	7609	7597
284.5	7	48	55	27.5	6938	8213	7622	7610
285	4	58	62	31	6950	8225	7636	7624
285.5	0	33	33	16.5	6975	8235	7648	7638
286	8	101	109	54.5	6997	8248	7663	7651
286.5	1	39	40	20	7015	8260	7679	7665
287	0	86	86	43	7031	8268	7692	7679
287.5	2	37	39	19.5	7055	8284	7704	7692
288	0	31	31	15.5	7068	8296	7716	7706

288.5	1	30	31	15.5	7083	8312	7730	7720
289	0	36	36	18	7095	8316	7745	7733
289.5	0	22	22	11	7109	8332	7758	7747
290	2	41	43	21.5	7121	8338	7771	7761
290.5	1	35	36	18	7139	8355	7783	7774
291	0	29	29	14.5	7160	8369	7799	7788
291.5	3	59	62	31	7183	8381	7813	7802
292	0	14	14	7	7199	8391	7825	7815
292.5	0	27	27	13.5	7213	8403	7838	7829
293	2	17	19	9.5	7228	8413	7852	7843
293.5	0	10	10	5	7245	8430	7866	7856
294	0	14	14	7	7256	8446	7881	7870
294.5	0	18	18	9	7270	8467	7896	7884
295	0	18	18	9	7285	8482	7911	7897
295.5	0	11	11	5.5	7309	8488	7924	7910
296	0	13	13	6.5	7326	8493	7939	7923
296.5	1	13	14	7	7342	8498	7951	7936
297	1	14	15	7.5	7361	8504	7963	7949
297.5	1	14	15	7.5	7385	8508	7974	7962

298	0	12	12	6	7404	8514	7987	7975
298.5	0	16	16	8	7412	8522	7999	7987
299	1	14	15	7.5	7425	8529	8012	8000
299.5	0	18	18	9	7439	8537	8025	8013
300	2	58	60	30	7452	8549	8038	8026
300.5	1	308	309	154.5	7473	8555	8050	8039
301	1	304	305	152.5	7493	8568	8064	8053
301.5	2	294	296	148	7507	8577	8077	8066
302	1	47	48	24	7529	8586	8091	8079
302.5	0	19	19	9.5	7554	8597	8104	8092
303	0	52	52	26	7571	8607	8118	8106
303.5	1	34	35	17.5	7587	8616	8130	8119
304	0	25	25	12.5	7599	8624	8141	8132
304.5	1	41	42	21	7606	8633	8155	8145
305	0	32	32	16	7618	8651	8166	8159
305.5	0	13	13	6.5	7643	8657	8180	8172
306	0	18	18	9	7668	8665	8195	8186
306.5	0	36	36	18	7688	8673	8207	8199
307	1	47	48	24	7712	8680	8220	8213

307.5	1	49	50	25	7734	8688	8232	8227
308	0	53	53	26.5	7749	8698	8245	8240
308.5	0	34	34	17	7758	8710	8256	8254
309	2	54	56	28	7778	8726	8269	8267
309.5	0	52	52	26	7789	8735	8283	8281
310	0	65	65	32.5	7800	8746	8297	8295
310.5	0	26	26	13	7828	8755	8309	8308
311	1	31	32	16	7848	8766	8322	8322
311.5	2	61	63	31.5	7870	8772	8337	8336
312	0	52	52	26	7888	8777	8348	8349
312.5	0	58	58	29	7906	8782	8362	8363
313	0	25	25	12.5	7921	8784	8378	8377
313.5	0	31	31	15.5	7935	8794	8390	8390
314	0	26	26	13	7950	8799	8404	8404
314.5	1	47	48	24	7970	8816	8419	8418
315	0	54	54	27	7983	8826	8433	8432
315.5	0	76	76	38	8006	8831	8445	8445
316	0	207	207	103.5	8033	8837	8456	8458
316.5	0	48	48	24	8065	8842	8469	8471

317	0	27	27	13.5	8084	8848	8480	8484
317.5	2	83	85	42.5	8104	8856	8494	8498
318	0	39	39	19.5	8127	8863	8505	8511
318.5	0	26	26	13	8146	8874	8517	8524
319	0	51	51	25.5	8164	8879	8530	8537
319.5	2	20	22	11	8177	8892	8543	8551
320	3	26	29	14.5	8189	8903	8557	8564
320.5	0	28	28	14	8217	8910	8567	8577
321	0	27	27	13.5	8246	8914	8578	8591
321.5	0	49	49	24.5	8275	8919	8590	8604
322	1	38	39	19.5	8301	8926	8602	8618
322.5	0	28	28	14	8331	8930	8613	8631
323	0	15	15	7.5	8353	8936	8625	8645
323.5	0	11	11	5.5	8375	8940	8640	8658
324	0	22	22	11	8390	8945	8652	8672
324.5	0	36	36	18	8406	8951	8666	8686
325	0	51	51	25.5	8420	8958	8680	8699
325.5	0	30	30	15	8454	8963	8692	8712
326	0	48	48	24	8489	8966	8703	8726

326.5	1	22	23	11.5	8518	8970	8714	8739
327	0	8	8	4	8548	8976	8723	8752
327.5	0	14	14	7	8577	8980	8735	8766
328	0	13	13	6.5	8597	8993	8747	8779
328.5	0	13	13	6.5	8612	9001	8760	8792
329	0	20	20	10	8625	9022	8774	8806
329.5	4	26	30	15	8638	9059	8787	8819
330	1	59	60	30	8645	9101	8801	8833
330.5	1	15	16	8	8655	9108	8812	8843
331	1	8	9	4.5	8662	9123	8822	8854
331.5	0	29	29	14.5	8669	9136	8832	8864
332	0	15	15	7.5	8672	9158	8844	8875
332.5	0	86	86	43	8676	9182	8854	8885
333	0	11	11	5.5	8681	9204	8866	8896
333.5	0	135	135	67.5	8683	9235	8876	8906
334	0	59	59	29.5	8688	9264	8887	8917
334.5	0	28	28	14	8693	9290	8898	8927
335	0	19	19	9.5	8698	9316	8908	8938
335.5	0	91	91	45.5	8707	9324	8919	8949

336	0	36	36	18	8715	9333	8929	8959
336.5	2	23	25	12.5	8724	9345	8938	8970
337	0	67	67	33.5	8731	9370	8949	8981
337.5	1	4	5	2.5	8737	9389	8960	8991
338	0	20	20	10	8742	9405	8972	9002

APPENDIX B

POLLEN KEY

Table B1. Pollen key

Haploxylon	H
Diploxylon	D
Pinus undiff.	P
Picea abies	PI
Pseudotsuga/Larix Tsuga	PL
Tsuga	TS
Cupressaceae	CU
Alnus	AL
Salix	SA
Populus	PO
Quercus	QU
Amelanchier-type	AM
Acer glabrum	AC
Ceanothus	CE
Arceuthobium	AR
Sarcobatus	SA
Poaceae	POA
Artemesia	ART
Amaranthaceae	AMT
Eriogonum	ERI
Polygonum bistortoides	PB
Brassicaceae	BR
Rosaceae	ROS
Spirea	SP
Ericaceae	ER
Ambrosia	AMB
Ephedra	EPH

Betulaceae	BET
Ranunculaceae	RAN
Pteridium undiff.	PTE
Indeterminate	IND
Unknown	UNK
Plantago	PLA
Rumex	RU
Apiaceae	AP
Prunus virginiana	PV
Shepherdia canadensis	SC
Cyperaceae	CYP
Polygonum amphibium	PGA
Myriophyllum	MYR
Potamogeton	POT
Equisetum	EQU
Typha	TYP
Nuphar	NUP
Lycopodium	LY
Bistorta bistortoides-type	PB
Polygonum californicum-type	PCAL
Dodecatheon -type	DOD
Thalictrum	THA
Galium-type	GAL
Potamogeton	POTCF
Sparganium-type	SPAR
Lemna	LEM
Pesicaria amphibium	PGA

APPENDIX C

RAW POLLEN COUNTS

Table C1. Raw pollen counts

Age (cal yr BP)	-69	113	315	367	390	404	418	512	717	930
Depth (cm)	0	8	16	18.5	19.5	20	20.5	24	32	40
LY	105	61	103	83	109	50	66	31	97	93
CU	7	2	2	1	2	5	2	2	6	3
PI	2	2	1			1	1	4	5	
P	1			1					1	
D	43	22	37	19	23	20	11	60	38	29
H				1				1	2	
P	180	189	221	195	212	211	208	108	211	145
PL	2	2	1			1		3	1	3
TS							1			
P										
EPH					3					
AR	2	2	2	2		3	3	4	11	4
AL	1	2	4	1			1			
BET	1					1				
BET										
QU										
QU	4	1		1		2	1		3	5
ROS										
SP										
ROS		1		1		1	1		2	
CE		1			1					
SC										
AM	1									
PO			1	1			1			

SA	1	1	1	1			1			1
AC										
SA	2	1				3	1	6	2	2
POA	9	32	16	28	21	10	8	8	16	22
CYP	4	14	9	6	4	11	5		6	8
ART	26	33	23	49	26	45	39	28	42	46
AMB			1			2	5		2	2
AMB	5		3	2	3	3			4	2
AMB				1		1	1			
AMT	5	7	4	7	9	6	4	6	9	11
AP			1							
BR										
BR										
PLA										
PB										
PCAL										
RU										
THA										
RAN										1
GAL										
MYR			2	1						
POTCF	1	3	1	3	1			4	4	5
SPAR	3	2	6							1
LEM										
NUP	3	6	8	5	8	9	5	2	6	3
EQU										
PGA										

TYP					1					1
PTE	2	1	1		1			2		1

Age (cal yr BP)	1148	1372	1586	1810	2017	2236	2462	2678	2910	3125
Depth (cm)	48	56	64	72	80	88	96	104	112	120
LY	93	98	51	92	88	59	55	45	61	56
CU	2	2	1	1		1	3	2	4	5
PI			3	2	1	1	2	6	3	2
P					3				1	
D	35	12	32	33	18	22	24	24	19	45
H					1			1	2	
P	198	200	174	193	193	182	181	180	186	218
PL	2	1	1	3	7	7	1	2	3	
TS										
P										
EPH						2		1		
AR	2					1	3	3	1	1
AL		2	1	2	1			1		
BET										
BET										
QU										
QU	2		1	4	1		1	4	3	
ROS										
SP			1	1						
ROS										

CE				2		1	1	1	1	
SC										
AM	3	2	1	2		2	1		3	1
PO									1	2
SA	1	1	1	1	2	1	1	1		
AC										
SA	2	2			3		1			1
POA	14	19	17	11	11	20	14	9	9	7
CYP	8	8	11	6	18	10	8	11	12	10
ART	32	21	34	40	33	43	32	42	43	31
AMB		2	1		2	2	1	3		
AMB	4	2	1	2	2	1	2	2	3	2
AMB							1			
AMT	6	4	9	6	5	9	6	2	8	8
AP										
BR										
BR										
PLA										
PB										
PCAL										
RU										
THA										
RAN										
GAL										
MYR										
POTCF	4	2	4	2	2	4	7	8	2	2
SPAR		2	3	1	2	5	3			3

LEM										
NUP	3	2	3	6	8	1	3	4	3	7
EQU							4			
PGA										
TYP			1					1		1
PTE	1	1						2		

Age (cal yr BP)	3360	3575	3790	4009	4230	4449	4710	4944	5169	5385
Depth (cm)	128	136	144	152	160	168	178	186	194	202
LY	82	55	87	86	64	91	130	81	107	211
CU	11	2	1		1	4	1			4
PI	1			1		1	1	4	1	4
P	4	3				2	1	2	2	1
D	36	58	44	76	63	50	67	60	68	104
H	1		1				1	2		
P	179	175	193	171	218	176	168	180	131	142
PL	1	4	2		1	6	9		1	2
TS										
P										
EPH										
AR		1	1		1					1
AL	2	2						1		
BET										
BET										
QU										

QU		1	1		2		2	1	3	1
ROS										
SP										
ROS										
CE	1		1	1	1		2			1
SC										
AM			1	5	1	2	1			
PO		1		1			1			
SA	2	2	4		1	1	1			
AC										
SA		3	3		2	1	3	2		
POA	9	11	7	10	12	4	8	5	6	4
CYP	7	2	6	11	2	9	6	3	4	11
ART	34	32	29	35	26	32	27	22	17	8
AMB		1	3	2		1	1			
AMB	2	2	1	1	4	1	1	1		
AMB	1									1
AMT	5	5	7	4	1	6	3	4	3	5
AP										
BR										
BR										
PLA										
PB										1
PCAL										
RU										
THA										
RAN							1			4

GAL										
MYR	1	2	2		1	3			3	1
POTCF	1	4	2	9	7	2	1	2	1	2
SPAR		1		1	2	4				
LEM										
NUP	6	3	1		5	5	2	5	4	8
EQU								3	5	2
PGA										
TYP										
PTE							1		1	

Age (cal yr BP)	5609	5822	5989	6043	6070	6256	6472	6688	6908	7120
Depth (cm)	210	218	224	226	227	234	242	250	258	266
LY	110	82	85	104	68	105	84	87	96	90
CU	4	3		2		3	2	1	2	3
PI		1		1	1	3	1			1
P	2	1	2						3	
D	80	46	61	65	105	68	44	75	55	35
H	1	3	2	1		1		1	1	5
P	164	174	152	166	142	165	194	179	186	195
PL	2	1	3	1	1	1	2	2	3	2
TS										
P										
EPH		2			1	1		1	1	1
AR	1						1			1

AL	2									
BET		1								
BET										
QU										
QU		1	3	1	1	1	2	1	2	3
ROS										
SP										
ROS			1							
CE	1	2	2	3		1	1		1	2
SC										
AM		1	1							
PO	2	1				2			1	1
SA			1	3				2	3	3
AC		1		1		1	1			
SA	2	2	3	2	1	2	2	1	1	
POA	7	10	15	12	5	11	10	12	11	14
CYP	5	3	6	11	5	9	4	13	9	13
ART	15	19	26	23	15	25	32	39	43	34
AMB	1	3		6			1		1	
AMB			2	2	3		1	2		
AMB	1									
AMT	1	5	4	3	2	8	11	10	2	11
AP										1
BR										
BR										
PLA										
PB				1						

PCAL							1			
RU										
THA										
RAN							2			
GAL										
MYR	9	4	7	13	3		4	7	2	1
POTCF	3	5	7			5	1	4	3	5
SPAR	1	2	1			1	1	7	4	6
LEM						1				
NUP	15	8	7	8	3	7	6	4		
EQU	1	2	1	2	1	4	1	1		
PGA	1								1	
TYP			1				2	2	2	
PTE		1								

Age (cal yr BP)	7499	7716	7939	8141	8348	8557	8747	8929
Depth (cm)	280	288	296	304	312	320	328	336
LY	85	33	58	35	60	52	60	64
CU	3	3	1		1	1	1	
PI	2	3						
P		1	1	1		1		2
D	49	50	82	97	86	56	46	41
H	1	2	5	2	2	1	2	1
P	189	122	206	119	187	181	182	270
PL	5	3	3	4	4			

TS			1					
P								
EPH					1			
AR	1	1	2					
AL			1					
BET				1	1	2		
BET								
QU								
QU	1		3			2	1	
ROS								
SP								
ROS							1	4
CE	3					1		1
SC								
AM		1					1	
PO		1					1	
SA	3	6	1	1	4		3	3
AC								
SA			2	1	3			
POA	11	11	7	10	15	19	20	26
CYP	8	11	13	16	14	14	17	6
ART	24	14	35	20	35	20	14	28
AMB	2	1	1	2	3			1
AMB	4	1	1	3	1	2		1
AMB								
AMT	10	5	6	6	8	1		2
AP								

BR								
BR								
PLA								
PB								1
PCAL								
RU								
THA								
RAN	1							
GAL								
MYR	2	4	8	7		5	3	7
POTCF	9	16	8	9	4	5	1	
SPAR	10	2	21	14	6	5	13	8
LEM		1				1	1	
NUP	3	1	6	12	10	3	3	3
EQU				2	1		2	
PGA				1			1	2
TYP	3					2	2	1
PTE	4	1						

APPENDIX D

STATISTICS FOR LINEAR REGRESSION

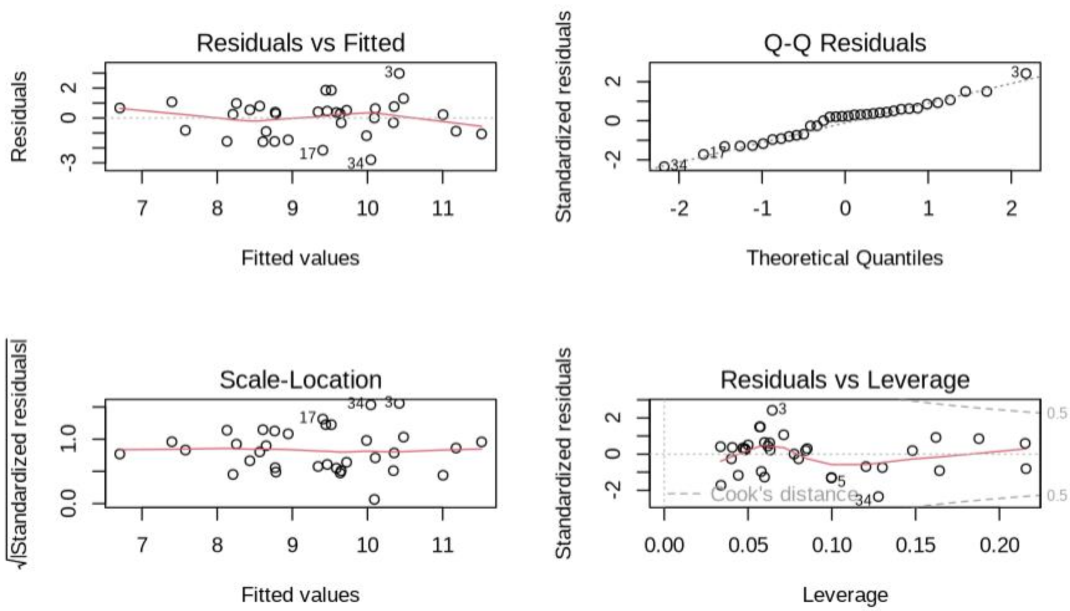

Figure D1. Residuals vs Fitted, Q-Q Residuals, Scale-Location, Residuals vs Leverage plots for linear regression.

```{r}
# Model area burned as a function of mean and SD VPD
lm_model <- lm(log_area_burned ~ mean_vpd + sd_vpd, data = yearly_fire_vpd)

# View model summary
summary(lm_model)
```

```
Call:
lm(formula = log_area_burned ~ mean_vpd + sd_vpd, data = yearly_fire_vpd)

Residuals:
    Min      1Q  Median      3Q     Max 
-2.7936 -0.9008  0.2875  0.6575  2.9790 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.6097     2.4748  -0.650 0.520197    
mean_vpd      0.4689     0.1206   3.889 0.000497 ***
sd_vpd        0.1925     0.1227   1.568 0.127037    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.272 on 31 degrees of freedom
Multiple R-squared:  0.4388,	Adjusted R-squared:  0.4026 
F-statistic: 12.12 on 2 and 31 DF,  p-value: 0.0001292
```

Figure D2. Statistics for linear regression of Log(Area Burned) vs. mean maximum vapor pressure deficit in the GYE by year from 1987-2020.