Vegetation response to wildfire and climate forcing in a Rocky Mountain lodgepole pine forest over the past 2,500 years

by

Barrie Victoria Chileen

B.A., Augustana College, 2017

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF ARTS

Department of Geography
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2019

Approved by:

Major Professor
Dr. Kendra K. McLauchlan

Copyright

Abstract

Wildfire is a ubiquitous disturbance agent in Rocky Mountain subalpine forests. Lodgepole pine (*Pinus contorta*), a dominant tree species in subalpine forests of western North America, is largely resilient to high-severity fires. However, the resilience of lodgepole forests may be compromised with predicted changes to climate and moisture availability. While the modern post-fire dynamics of these systems are well studied, less is known about post-fire responses of lodgepole forests over the past few centuries and millennia. Thus, I investigated fire occurrence and post-fire vegetation change in a lodgepole forest over the past two millennia to understand ecosystem responses to variability in wildfire activity and climate. I reconstructed vegetation composition over the past 2,500 years in the small basin of Chickaree Lake, Colorado, U.S.A., in Rocky Mountain National Park. Pollen samples (n=52) were analyzed to characterize both broad-scale (centennial to millennial) trends in pollen assemblages associated with climate, and short-term (decadal) changes associated with multiple high-severity fire events previously reconstructed through charcoal analysis.

Pollen assemblages were dominated by *Pinus* throughout the record. The primary broad-scale change in pollen composition characterized by an increase *Artemisia* and *Rosaceae*, and a decrease in mean *Pinus* and extra local pollen (*Quercus*, *Salix*, and *Sarcobatus*), which occurred around 1,155 calibrated years before present (cal yr BP). This change is coincident with a shift towards increased winter precipitation which characterizes modern climate identified from δO^{18} and lake level data. Wildfire occurrence resulted in significant decreases in *Pinus* pollen following the zone break at 1,155 cal yr BP, suggesting that impacts of fire on the composition of lodgepole pine forests may depend on underlying climate conditions. Throughout the past 2,500 years, vegetation composition returned to pre-fire conditions within 75 years, indicating

overall resilience of Rocky Mountain lodgepole forests to fire activity despite some variability in post-fire vegetation recovery.

Table of Contents

List of Figures

List of Table*s*

Acknowledgements

I would first like to thank my advisor, Dr. Kendra McLauchlan (Kansas State University Department of Geography), for her paleoecological wisdom, humor, and guidance throughout this project. I couldn't have made it through these past two years without your compassion and understanding throughout the tougher times of my thesis. I would also like to extend my sincerest gratitude to Dr. Shawn Hutchinson and Dr. Arnaud Temme (Kansas State University Department of Geography) for serving on my committee and their feedback on this manuscript. I'd also like to thank Sara Baugh, Abbey Marcotte, Jennifer Roozeboom, and past and current graduate students at Kansas State University, for their friendship and for providing a sounding board for both personal and thesis related challenges and of course, happy hours. Next, I would like to thank Dr. Matthew Fockler (Augustana College) for his mentoring and his continued support and guidance over the years. Additional thanks go to Dr. Philip Higuera (University of Montana), Dr. Bryan Shuman (University of Wyoming), Meredith Parish, and Kyra Wolf and the rest of the Big Burns Team who provided valuable feedback on this manuscript.

Dr. Erin Herring (University of Oregon) prepared the pollen and Vania Stefanova at the University of Minnesota National Lacustrine Core Facility provided training in pollen counting. This research was funded by NSF DEB-1655179, the Steven Kale Graduate Fellowship, the Geography Graduate Research Grant, the Marston Muddy Boots Scholarship, and the Kansas Association of Mappers John Cowan Scholarship.

A thousand thanks go to my family, especially my dad, Scot Chileen, for instilling within me a love for nature, plants, and the outdoors, and my twin sister, Kaylyn Chileen, my younger brother, Cole Chileen, and my godmother/aunt, Marie Apke, for their encouragement and love

during one of the most challenging periods of my life. I love you all and couldn't have made it here without your phone calls along the way.

Lastly, I'd like to thank my boyfriend, Brian Martinez, for his compassion, love, support, humor, and patience over these past two years. Thank you for teaching me the value of work-life balance, your attempts to understand and offer research advice, talking to me during seemingly endless hours of pollen counting, and for believing in me when things got tough. You are incredible, and I couldn't have gotten through this without you by my side (even though you were like 500 miles away the whole time).

Dedication

This thesis is dedicated to the memory of my mother, Louise Apke Chileen

August 10th 1961 - August 1st 2018

Even though you did not get to see the final product, I could not have made it to this point without the lifetime of love and support you showed me along the way. Not a day goes by where I don't miss you and I'll always be looking for you in the stars.

Love always,
Barrie (the dirt major)

Chapter 1 - Literature Review

Wildfire is a ubiquitous disturbance agent in lodgepole pine (*Pinus contorta*) forests across western North America, and this and many other regions are experiencing an increase in wildfire frequency and severity due to increased warmth and fuel aridity (Abatzoglou and Williams, 2016; Dennison et al., 2014; Schoennagel et al., 2017; Westerling, 2016). Increased wildfire activity has important impacts on ecological and social systems, as wildfires not only shape fundamental ecosystem processes, but also threaten human values, including housing, lives, and economies (Dale et al., 2001; Mietkiewicz et al., 2018; Moritz et al., 2014; Smith et al., 2016). The wildfires of the western U.S. are well-documented in news stories and public interest in fires seems to grow with each severe fire season. 2017 was one of the most expensive fire seasons on record and over nine million acres of land burned in the United States (Mietkiewicz et al., 2018; "National Interagency Fire Center," 2017). As the damage to both the land and property has increased over the years, so has the interest in studying the causes and consequences of wildfires in the dominant regional landscape feature: The Rocky Mountains.

While there has been a considerable amount of research conducted on the vegetative successional trajectories of modern post fire landscapes, less is known about how these systems will respond to changes in both future climate scenarios and future fire driven disturbance regimes. To better understand the future of these Rocky Mountain forests, a long-term perspective is needed. This study reconstructs wildfire and vegetation dynamics in the Rocky Mountains using paleoecological proxies from lacustrine sediment cores. In doing this, this research adds to an existing network of reconstructions throughout the region that can be used to improve understanding of how wildfire and vegetation dynamics change throughout time and in differing climate settings.

Relevance to Geography

The field of geography has been described through multiple approaches from the simple study of “space and place” to the complex four traditions of Pattison (Pattison, 1964). While there have been many attempts to characterize the nature and scope of the field of geography (Committee and Council, 1997; Lawrence, 1971; Murphy, 2014; Pattison, 1964; Tuason, 1987), most describe geography as a broad field known for its interdisciplinary approaches and ability to integrate multiple perspectives to tackle a given problem (Committee and Council, 1997; Fosberg, 1976; Murphy, 2014). While this thesis may seem better suited for a biology department due to its focus on ecological concepts and questions, it best falls within the biogeography subfield of geography because of its alignment with the Earth science tradition of Pattison’s four traditions, its need for interdisciplinary approaches, and its focus on temporal ecological change.

Paleoecology incorporates the disciplines of geology, ecology, and biology (Edwards, 1983; Lawrence, 1971; Rull, 2010) to reconstruct past environmental conditions. These disciplines are classic examples of Pattisons’ definition of the Earth sciences. Paleoecological studies rely on the Earth science topic of uniformitarianism in the sense that modern site conditions are interpreted to be the culmination of the long term influence of natural processes and ecosystem change (Rull, 2010). In paleoecological research, past ecological change is traced through a variety of environmental proxies that collect in lacustrine sediments (Lawrence, 1971), using concepts from a variety of disciplines. Research in paleoecology, due to the variety of Earth science disciplines it pulls from, is interdisciplinary.

While most consider the field of geography to be the study of spatial relationships, subdisciplines within geography also address temporal relationships (Hill, 1975). One of the subdisciplines that most heavily addresses temporal relationships and ecosystem change is biogeography/historical biogeography. Biogeography is defined as the study of the spatial and temporal distributions of plants and animals (Cowell and Parker, 2004; Fosberg, 1976; Hill, 1975). Biogeography is a bridge discipline between biology/ecology and geography (Tuason, 1987) (Figure 1.1) and allows for long-term reconstructions of ecological dynamics (Dawson et al., 2013). Contemporary ecology is limited in its ability to address long-term change, as most ecologists define "long-term" as spanning decades to centuries (Dawson et al., 2013; Lawrence, 1971; McLauchlan et al., 2014; Rull, 2010) due to the methods they use in research. This thesis focuses on investigating vegetation response to ecological disturbance regimes at a lake in the Rocky Mountain National Park over the past 2,500 years, a time-frame that is not possible to address with modern ecological methods. It is for this reason that biogeographical approaches are used.

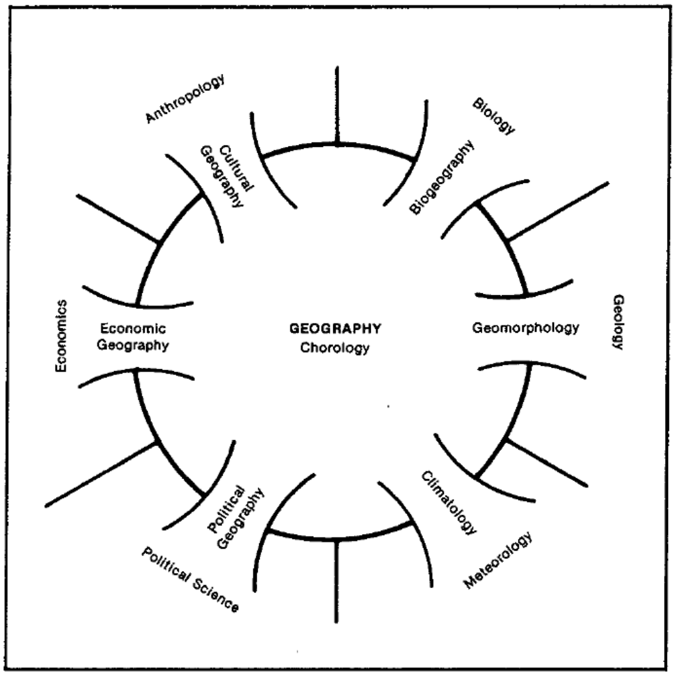


Figure 1.1 Tuason's model of geography as a bridge discipline

Paleoecological research has developed its own unique identity within the field of geography and biogeography (Figure 1.2A) (Stallins, 2007) and has become more readily accepted within the American Association of Geographers with the development of its own “Paleoenvironmental Change” specialty group. This thesis focuses on the use of pollen as a proxy for past vegetation. Palynology, the study of pollen, has always been deeply rooted in geography. Lennart von Post, the founding father of palynology, used pollen preserved in peat bogs to reconstruct vegetation over time and some of his earliest applications included mapping vegetation change from across Europe (Birks et al., 2016; Edwards, 1982). Von Post’s motto “think horizontally, work vertically” (Figure 1.2B) (Edwards et al., 2017) lies very much within the field of geography and biogeography. By working vertically, through depth/time in the case of paleorecords, paleoecologists can then combine multiple paleoecological reconstructions to think horizontally, or spatially, across the landscape.

Few high-resolution paleoecological reconstructions of post-fire vegetation exist within the western United States. This thesis research not only contributes towards improved understanding of past ecology, but also increases the spatial coverage of paleoecological studies in the western United States. Paleoecology has found a home within Geography departments because of the field’s ties to Pattison’s Earth Science tradition, its reliance on interdisciplinary approaches, and its ability to investigate both spatial and temporal realms of change. I think that geographers can also relate to the motto “Think horizontally, work vertically” because it is the very nature of geographic thought and acts as a bridge between geography and all the fields it encompasses. The research interests of time and place tie paleoecology and geography together and allow for paleoecological reconstructions to have found a well-earned home in the field of geography.

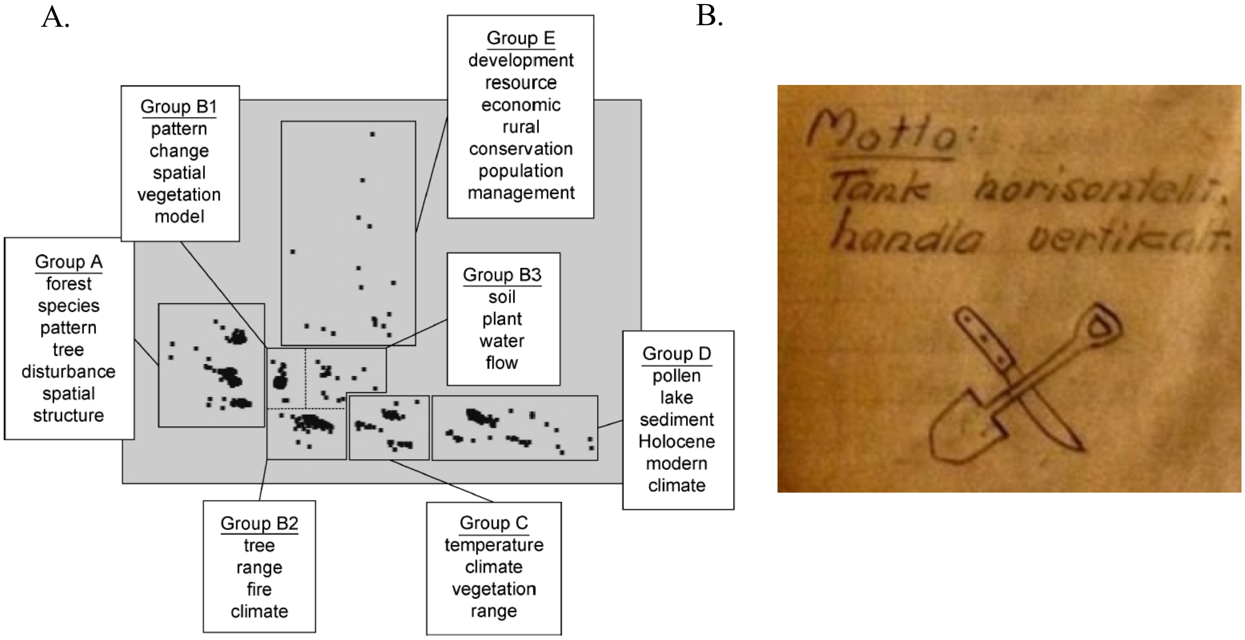


Figure 1.2 A. Publishing space for the AAG Biogeography specialty group, Group D captures paleoecological reconstructions (Stallins, 2007).

B. A page of Lennart von Post's notebook with "Think horizontally; work vertically" sketched in Swedish (Edwards et al., 2017).

Introduction to Rocky Mountain Subalpine Forests

The subalpine forests of the Rocky Mountains are susceptible to changes in disturbance regimes as there is often an intricate balance between climate, vegetation, and fire (Schoennagel et al., 2004). These high elevation forests are generally found at elevations 2,750 meters above sea level and are characterized by mixed conifer forests of Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*) and sometimes limber pine (*Pinus flexilis*) (Peet, 1981), hereafter referred to by common nomenclature. These species all have different responses to disturbance following fire events and play distinct roles in the successional patterns of subalpine forests in the Rocky Mountains (Veblen et al., 1991). Wildfire within subalpine forests are characterized as catastrophic, infrequent, and stand replacing(Veblen et al., 1991; Whitlock et al., 2003).

However, the vegetation of these forest systems is often well adapted to these disturbance events and can regenerate in post-burn landscapes. Lodgepole pines, for example, are fire-adapted due to their serotinous cones that open to disperse seeds when exposed to high temperatures, which makes them successful in the current fire regime of subalpine forests (Peet, 1981; Whitlock et al., 2003).

Fire Ecology and Management in the Southern Rocky Mountains

The increase of fire events during the past five decades is well documented in the Rocky Mountain region of the American West (Schoennagel et al., 2004; Westerling et al., 2011; Whitlock et al., 2003). In response to the increase in frequency of wildfire, there has been an influx of research in investigating the drivers of these fire events to guide future management efforts. One of the most active regions of interest is the subalpine forests of the Rocky Mountain region. Following the Big Burn of 1910 Common Era (CE), the driving management policy of the National Forest Service was to suppress all fires, which has initiated new pathways of secondary succession and novel, densely forested ecosystems that have not been previously observed. Fire in the western United States is a vital component to maintaining the subalpine forests of the Rocky Mountain region (Westerling et al., 2011). Following the acknowledgement that fire is necessary to maintain western forests, the rigid wildfire suppression practices of the National Forest Service have been altered and some fires are now allowed to burn in forests to fulfill their role as necessary ecosystem processes. Despite this change in management practice, the legacy of suppression has left its impacts on the structure of subalpine forests across the Rocky Mountain region.

Subalpine Vegetative Succession Patterns in the Southern Rocky Mountains

The forests of the Colorado Rocky Mountains are generally dominated by mosaics of Engelmann spruce, subalpine fir, quaking aspen, and lodgepole pine (Gill et al., 2017; Peet, 1981). These species are spatially distributed along elevational gradients with some blending between vegetation communities at elevational boundaries (Figure 1.3). Modern post-disturbance successional studies in the region are focused on sampling vegetation composition and structure to explore successional patterns of vegetation following the disturbances of fire, bark beetle outbreaks, and blowdowns (Gill et al., 2017; Peet, 1981). Historically, studies have generally found that subalpine forests are resilient to high severity fire events, with a return to the pre-fire vegetation structure of overstory lodgepole pine forest within two decades. In addition to modern day post-fire studies, dendrochronological studies also reconstruct vegetation response to fire, climate, blowdowns, and bark beetle activity using tree rings over longer time frames. These dendrochronological studies have found that fire history in the southern Rocky Mountains is characterized as infrequent and stand replacing (Sibold et al., 2006) and that disturbances that occurred several centuries prior can still impact the resilience of subalpine forests (Kulakowski and Veblen, 2002). These centennial-scale dendrochronological studies can extend the temporal range of post-fire successional vegetation trends that is often missed in modern day post-disturbance studies.

Based on both modern-day ecological studies and dendrochronological studies, the post-fire successional pattern of subalpine forests is that quaking aspen and lodgepole pine are first to establish after a wildfire (Gill et al., 2017; Kulakowski and Veblen, 2002; Peet, 1981). These systems are then later dominated by lodgepole pine as the climax species, as lodgepole pine outcompetes quaking aspen following multiple fire events (Peet, 1981). The success of lodgepole pine in high severity fire regimes can be attributed both to its ability to quickly reestablish following a fire due to an extensive seed bank, and its ability to outcompete quaking aspen after multiple fire episodes. This understanding of succession has been interpreted to imply that the subalpine forests of the Rocky Mountains are resilient and can regenerate following multiple fire events. However, it is important to note that these ecological studies can only span from a few decades to centuries at their longest temporal scale and are only applicable to current climate conditions (Whitlock, 2004) which can create challenges in using these records for ecological restoration and management. There has been an identified need to use records that span longer time scales to guide the management of subalpine forest of the Rocky Mountains in future climate scenarios (Gill et al., 2017; Sibold et al., 2006; Whitlock, 2004). Paleoecological records have been effective in reconstructing the interactions between fire, climate, and vegetation and will be implemented in this study to better understand the drivers of shifts in disturbance regimes in the Rocky Mountain.

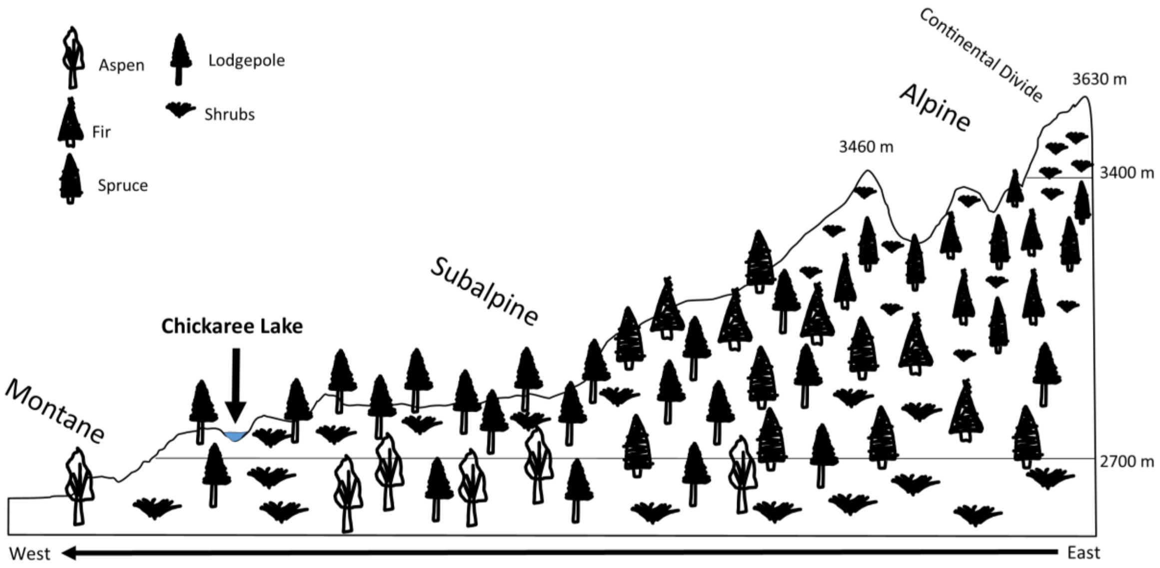


Figure 1.3 A diagram of the elevational distribution of vegetation in a forest in Rocky Mountain National Park

Pollen as a Proxy for Long-Term Vegetation Change

Paleoecological proxies can be used to reconstruct past ecosystems. Lacustrine sediment cores are especially useful in paleoecological studies because they often contain multiple proxies, including pollen and charcoal, which can be used to reconstruct vegetation and fire over time (Birks et al., 2016; Gavin et al., 2007; McLauchlan et al., 2014; Whitlock and Larsen, 2001). Plants produce pollen with the ultimate goal of reproduction and the majority of wind-transported pollen produced ends up depositing within lakes or on the earth's surface (MacDonald, 1988). When pollen falls into the lake, it accumulates in layers and is buried annually by sediments (Bunting et al., 2013; MacDonald, 1988), and this process occurs over decades, centuries, and millennia. Pollen grains are highly resistant to decay and degradation when buried in lake sediments because their structure consists of a chemically inert biological compound named "Sporopollenin", which is resistant to strong acids including Hydrofluoric Acid (Bunting et al., 2013; Halbritter et al., 2018). Pollen grains are often well preserved and can be identified through morphological structures (Halbritter et al., 2018; Kapp, 1969; MacDonald, 1988), often down to the taxa level, which provides a robust snapshot of past vegetation surrounding the lake basin (Figure 1.4). Though pollen analysis has its limitations and pollen counting is a time-consuming process (Green, 1983), it still stands as the strongest paleoecological proxy in reconstructing the presence of past vegetation.

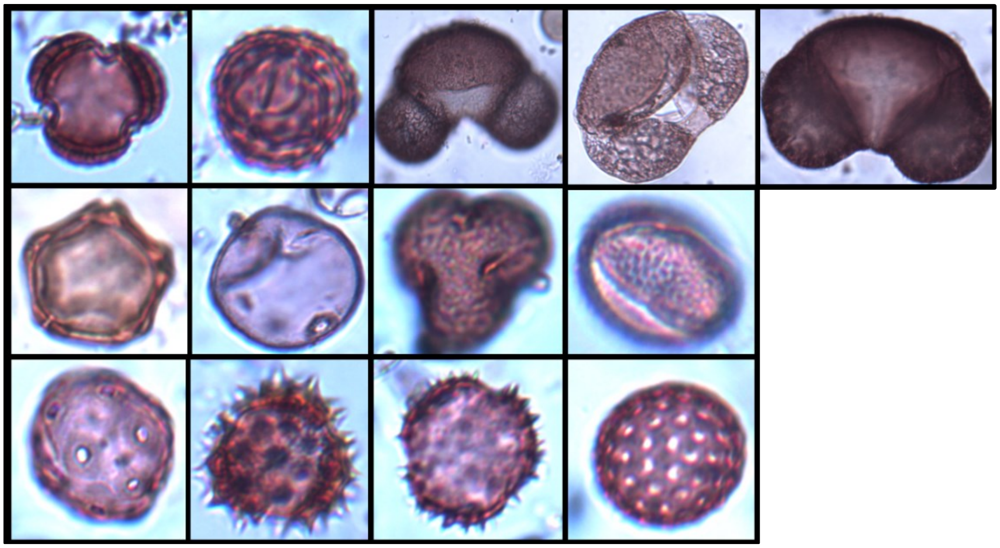


Figure 1.4 Photographs of pollen under a microscope at 400x showing their wide range of morphologies and sizes. Pollen taxa from left to right starting from the top: *Artemisia*, *Ambrosia*, *Pinus*, *Picea*, *Abies*, *Alnus*, Poaceae, *Quercus, Salix*, *Sarcobatus*, Asteraceae, *Arceuthobium*, and Chenopodiaceae. Sizes range from 20 -80 μm. Photos are provided by the author.

Lacustrine cores are often used as the sampling source for quaternary pollen analysis because the anoxic environment of lakes are well suited to preserve pollen at millennial time-scales (Bunting et al., 2013; MacDonald, 1988). Pollen is collected by subsampling sediment from lacustrine cores and subsampling for pollen occurs when the sediment within the core is still wet so that the pollen can be preserved. Samples are then taken at varying depth intervals ranging from 2 cm to 20 cm and, generally, 1 cc of sediment is extracted from cores at each interval for pollen analysis (MacDonald, 1988). Chronologies are developed for core records which are derived through ^{14}C and ^{210}Pb dating of materials found at different depths within the core (Birks and Berglund, 2018; Green, 1983; Green and Dolman, 1988). The resulting ^{14}C and ^{210}Pb derived ages are then plotted by their corresponding depths. Traditionally, linear models were used to interpolate the dates for samples with unknown ages (Blaauw, 2010; Green and Dolman, 1988; MacDonald, 1988), however; advancements in Bayesian modeling approaches and the use of bootstrapping in chronology development have allowed for more environmentally realistic chronologies (Blaauw and Christen, 2011). These Bayesian accumulation models, referred to as “Bacon” in the paleoecology community, produce sediment accumulation rates which can allow for improved inferences about the environmental processes that can drive changes in sediment deposition within lakes (Blaauw and Christen, 2011; Goring et al., 2012). Once the chronology is established, it is possible to map the changes in vegetation over time by comparing the change in pollen composition with relation to their depth/age (Bennett and Willis, 2001; Birks and Birks, 2006; Bunting et al., 2013; Seppä and Bennett, 2003). Quaternary pollen analysis is heavily dependent on the ability to establish a chronology because it is difficult to understand the absolute and relative timing of paleoecological processes and events. Since pollen is subsampled from lacustrine sediment cores, it is possible to pair pollen data with other core-based proxies like charcoal, magnetic susceptibility (MS), and elemental composition from X-Ray Fluorescence (XRF) (Birks and Birks, 2006; Birks et al., 2012; Birks and Berglund, 2018; McLauchlan et al., 2014; Morris et al., 2015), which then allows for more robust reconstructions of past environments.

Once the sample has been chemically processed and mounted on a slide in silicon oil, pollen grains are counted under a microscope at 400x magnification (MacDonald, 1988). Pollen grains are then identified first by genus and then species, if possible, based on their morphologies. Published pollen keys (Kapp, 1969; McAndrews et al., 1973) and in-house reference collections are used to aid in identification. With technological advances, there has been an increase in the number of online pollen identification resources and open forums (e.g. Martin and Harvey, 2017; Weber and Ulrich, 2017), which can improve the quality of pollen identifications because it allows for researchers to collaborate to identify challenging pollen grains. Once grains have been properly identified for each subsample, they are then represented graphically in the form of pollen diagrams. In pollen diagrams, pollen counts are converted to percentages and then plotted by their depth or by their radiocarbon-derived age (Birks and Berglund, 2018; Edwards et al., 2017). While pollen diagrams alone can provide insight to past vegetation communities, one of the advantages of pollen analysis is that pollen diagrams can be matched with other proxies from within lacustrine cores to capture catchment-wide trends and map ecological impacts that would otherwise be missed if each proxy was analyzed individually (Birks and Birks, 2006; Meadows, 2014; Seppä and Bennett, 2003).

Quaternary pollen analysis is often used to reconstruct past ecosystems, model paleoclimates, reconstruct fire history, and map past biogeographical distributions (McLauchlan et al., 2014; Morris et al., 2015; Seppä and Bennett, 2003). Recent developments in the creation of online databases, like Neotoma (Goring et al., 2015), have allowed for an open platform for paleoecological data sharing. The increased availability of paleoecological data has given researchers the ability to conduct biogeographical studies that can map vegetation change on continental and global scales (Reitalu et al., 2014), which was impossible prior due to the time and effort needed to conduct multiple paleoecological studies. Major findings from pollen analysis include the recognition of climate change as a driver in vegetation change over millennial timescales as well as identifying the spatially inconsistent shifts in vegetation zones on the scale of individual species (Edwards et al., 2017). Pollen analysis provides a much-needed millennial perspective to ecology that can only further develop the field. By implementing the use of pollen analysis coupled with a well-established chronology and related proxies, it is possible to explore the drivers of ecological change over millennial timescales.

Paleoecological Findings from Rocky Mountain Subalpine Lakes

There have been multiple paleoecological studies in the southern Rocky Mountain region, all with varying proxies and purposes (Figure 1.5 and Table 1.1). These paleoecological reconstructions all have differing timescales. Some reconstructions are focused on capturing post glacial vegetation establishment with paleoecological datasets that span the entire Holocene (~ 11,000 years) (e.g. Anderson et al., 2015; Carter et al., 2013; Jiménez-Moreno et al., 2011; Jiménez-Moreno and Anderson, 2013; Minckley et al., 2012), while other datasets are centered around smaller timeframes to capture specific events like the Medieval Climate Anomaly, Little Ice Age, and other brief periods of climate variation during the late Holocene from about 7000 calibrated years before 1950 AD (cal yr BP) to present (e.g. Caffrey and Doerner, 2012; Calder and Shuman, 2017; Dunnette et al., 2014; Leys et al., 2016).

The temporal frames of focus for paleoecological studies can often impact the resolution of the proxies used. For example, studies that focus on longer temporal frames (i.e. 11,000 years) often sample at lower temporal intervals (i.e. every 200 years) for vegetation reconstruction. These lower temporal resolution reconstructions of vegetation are often unable to be paired with charcoal records, which are sampled at high temporal resolutions (every 10 years), to capture post-fire changes in vegetation. The difference in temporal resolution between pollen and charcoal data creates temporal offsets between charcoal-inferred fire events and vegetation change inferred through pollen (Birks and Birks, 2006; Birks, 2012; MacDonald et al., 1991; McLauchlan et al., 2014; Morris et al., 2015; Whitlock and Larsen, 2001); however, it is possible to reduce this temporal offset by increasing the sample resolution of pollen data.

Table 1.1 Paleoecological studies and proxies in the Rocky Mountain region

Study	**Lake Name**	**Elevation**	**Proxies Used**	**Pollen Depth Resolution**
Anderson, Brunelle & Thompson, 2015	Bison Lake	3,445 m	$\delta^{18}O$, pollen, XRF, charcoal,	4 cm- <30 cm 8 cm-> 30 cm
Caffrey & Doerner, 2012	Bear Lake	2,888 m	Pollen, charcoal	5 cm intervals
Calder & Shuman. 2017	Summit Lake	3,149 m	Pollen, charcoal, C:N, $\delta^{13}C$	~2 cm intervals
Carter et al. 2013	Long Lake	2,700 m	Pollen, charcoal	4-8 cm intervals
Shuman et al. 2009	Hidden Lake	2,710 m	Lake Level, Pollen, Charcoal	~5 cm intervals
Dunnette et al. 2014, Leys et al. 2016	Chickaree Lake*	2,796 m	Pollen, charcoal, XRF	7 cm- <175 cm 12 cm- >175 cm
Jiménez-Moreno & Anderson, 2013	Kite Lake	3,665 m	Pollen, plant macrofossils	2 cm intervals
Jiménez-Moreno et al. 2011	Tiago Lake	2,700 m	Pollen, charcoal, $\delta^{13}C$	2 cm intervals
Minckley et al. 2012 Minckley and Shriver, 2011	Little Windy Hill Pond	2,980 m	Charcoal, pollen	4-8 cm intervals

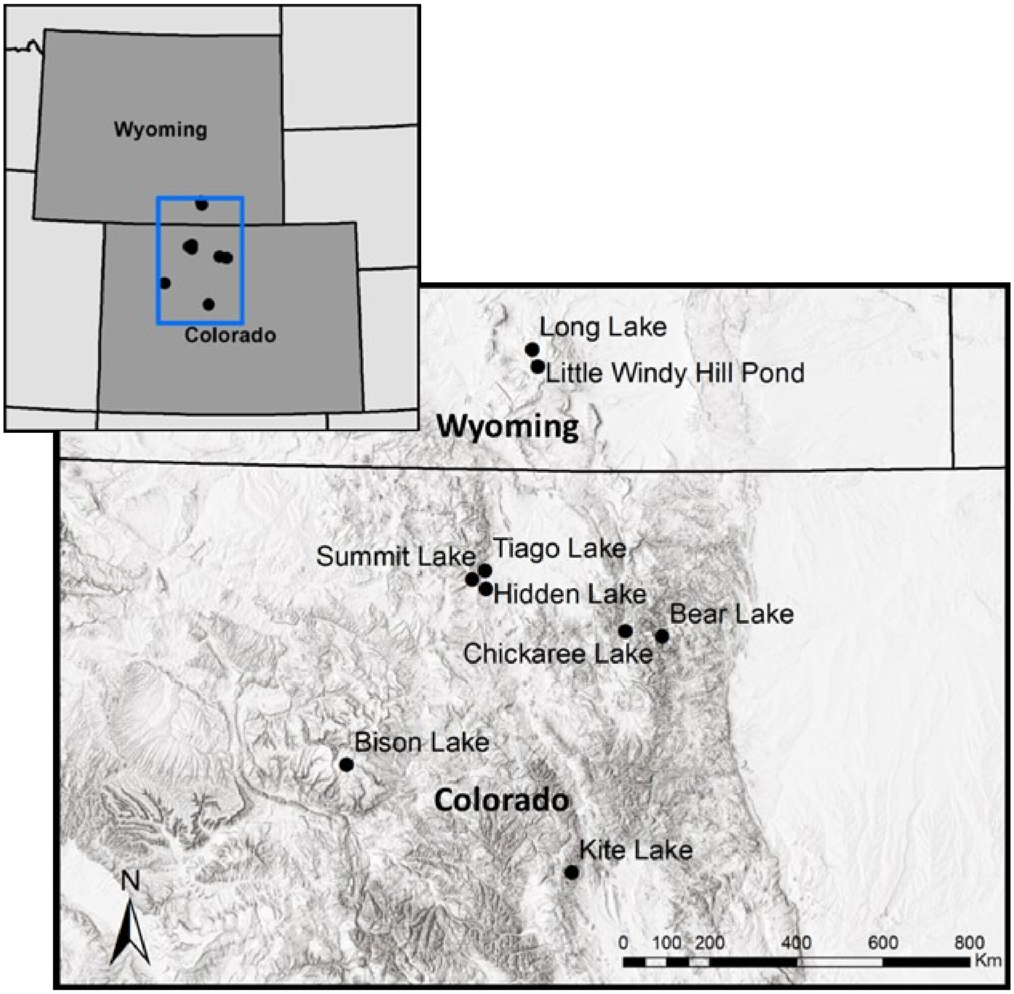


Figure 1.5 Location of key studies mentioned in this research.

High-Resolution Paleoecological Reconstructions of Vegetation

Holocene length reconstructions of vegetation often occur at lower temporal resolutions than late-Holocene reconstructions. However, some studies have reconstructed high resolution vegetation records for the entirety of the Holocene. Jiménez-Moreno et al. 2011 and Jiménez-Moreno & Anderson, 2013 implement high-resolution pollen sampling (~2 cm increments) in paleoecological reconstructions with the intent of capturing shifts in tree line (Jiménez-Moreno and Anderson, 2013) and climate-driven changes in vegetation during the Holocene (Jiménez-Moreno et al., 2011). Vegetation in subalpine forests were found to have been highly sensitive to changes in climate and correlated strongly with global climate reconstructions. However, in high resolution vegetation reconstructions, subalpine forests were found to be resilient to the increase in fire frequency during the late Holocene (Minckley et al., 2012). Paleoecological reconstructions have found that the late Holocene (i.e. past 3,000 years) did not experience significant vegetation turnover (i.e. major shift in dominant vegetation from grassy to densely forested) in the subalpine Rockies (Anderson et al., 2015; Carter et al., 2013; Jiménez-Moreno et al., 2011), however; the response of these vegetation communities over smaller temporal ranges and following multiple fire events is lesser known and has been the subject of paleoecological reconstructions with smaller ranges of temporal focus.

Climate Reconstructions from Paleoecological Records in the Rocky Mountains

Paleoecological reconstructions during the late Holocene are often focused on capturing vegetation shifts in response to recent climate anomalies like the Medieval Climate Anomaly (MCA) from 1,200-850 cal yr BP (Cook et al., 2007) and the Little Ice Age (LIA) from 500-100 cal yr BP (Trouet et al., 2013) (e.g. Caffrey and Doerner, 2012; Calder and Shuman, 2017). In the western United States, the Medieval Climate Anomaly was characterized by increased prevailing drought conditions, as inferred through tree ring datasets (Cook et al., 2007), which has been interpreted to have driven the increases in regional wildfire activity around 1,000 cal yr BP (Calder et al., 2015; Marlon et al., 2006; Whitlock et al., 2003) observed in paleoecological reconstructions. Globally and in North America, pollen and multiproxy-based temperature reconstructions characterize the Medieval Climate Anomaly as a period of higher mean annual temperatures than the Little Ice Age (Mann et al., 2009; Trouet et al., 2013; Viau et al., 2012). Regional reconstructions from mountain regions in western North America, however; do not show significant variations in temperature (Parish et al. in prep, Viau et al., 2012), which indicates that the temperature influences of the Little Ice Age and the Medieval Climate Anomaly may vary throughout North America.

Climate throughout the Holocene was variable which had a substantial influence on fire activity and vegetation composition (Anderson et al., 2015; Carter et al., 2013; Jiménez-Moreno et al., 2011; Jiménez-Moreno and Anderson, 2013). During the early and middle Holocene, climate inferred from paleoecological studies in the Rocky Mountain region was characterized as warm with increased precipitation. This period of warming was followed by cooling with increases in winter precipitation during the late Holocene (Anderson, 2011; Anderson et al., 2015, 2016; Calder et al., 2019; Jiménez-Moreno et al., 2011; Jiménez-Moreno and Anderson, 2013). These findings were consistent with other reconstructions in the Rocky Mountain region (Table 1.2), and these studies attribute the combined effects of orbital oscillations and the El Niño Southern Oscillation (ENSO) as the main driver of changes in temperature and precipitation balance throughout the Holocene (Anderson et al., 2016; Jiménez-Moreno et al., 2011). Climate setting is often attributed as the main driver of wildfire activity throughout the Holocene, and while much work has been done on understanding the influence of climate on vegetation, less is known about the post-fire vegetative feedbacks that relate to broader scale climate dynamics in Rocky Mountain lodgepole pine forests.

Table 1.2 Pollen-inferred climate reconstructions from the Southern Rocky Mountains (Adapted from Carter et al. 2013)

Site Name	**Elevation (m)**	**cal yr BP (k) 12**	**11**	**10**	**9**	**8**	**7**	**6**	**5**	**4**	**3**	**2**	**1**	**0**
Long Lake	2,700	Cold/dry *Artemisia*		*Pinus* warm/wet		peat dry	Warmer *Populus*					Warm/wet *Pinus*		
Tiago Lake	2,700	Cold/dry	Warm/wet *Pinus-Picea-Abies* mixed conifer forests				Warm/wet *Populus*			Cool/wet *Pinus*				
Bear Lake	2,888	Not Covered in Study					Warm/wet *Picea-Pinus*				Cool/wet *Artemisia*		Cooler/wet *Pinus*	
Little Windy Hill Pond	2,980	Cold/dry	Warm/dry *Picea-Pinus*			Cool/wet *Picea-Pinus* Forest								
Summit Lake	3,149	Not Covered in Study									Cool/wet *Picea-Pinus*		Cool/wet *Artemisia*	
Bison Lake	3,445	Cold/dry		Warm/dry *Picea-Pinus* forest			Warmer *Populus*		Cool/wet *Picea-Pinus*				Cool/wet	
Kite Lake	3,665	Cold/dry	Warm/dry *Picea-Abies*	Warm/dry *Picea-Pinus*								Cool/ wet	Cool/wet *Artemisia*	

New Developments and Approaches in Paleoecological Reconstruction

To better capture changes in vegetation, fire, and climate, paleoecological reconstructions have shortened the temporal frame of focus from tens of thousands of years to thousands of years in length. In Holocene length reconstructions, some studies have chosen to increase sampling resolution during the period from ~2,000 cal yr BP to present to better understand the interactions between fire, climate and vegetation over smaller timeframes (Anderson et al., 2015). Recent paleoecological studies in the southern Rocky Mountain region (i.e. over the past 5 years) have started to focus on the temporal range of ~ 7,000 years ago to present. Reconstructing this temporal range of focus has been aided by new developments in paleoecological data analysis that allow for higher resolution reconstructions of fire, climate, and vegetation. XRF analysis has now allowed for paleoecological reconstructions to incorporate biogeochemical cycling (Anderson et al., 2015; Leys et al., 2016) and the development of CHARAnalysis (Higuera et al., 2009) allows for the identification of local fire events by identifying peaks in charcoal against background data. Multiproxy studies can aid in improved interpretations of past fire activity, an example of which is when the results of CHARAnalysis are paired with Magnetic Susceptibility data, a lacustrine core-based proxy for catchment erosion pulses (Dunnette et al., 2014; Morris et al., 2015; Whitlock et al., 2003). High severity fires can trigger mass-wasting events that are captured through peaks in magnetic susceptibility in paleoecological records (Whitlock et al., 2003), and these peaks in erosion can then be paired with charcoal peak data to interpret the severity of a wildfire (e.g. Dunnette et al., 2014). Despite these developments in reconstructing and characterizing fire events and capturing biogeochemical impacts of fire, a gap has been identified in reconstructing vegetation. Pollen analysis, which acts as the proxy for vegetation reconstruction, is often not conducted at the same temporal resolution as the other, newly developed proxies which creates challenges in comparing highly temporally resolved records of fire, biogeochemistry, and erosion to past vegetation.

Chapter 2 - Introduction

The ecological health of subalpine forests in the Rocky Mountain region has been a topic of growing interest due to their susceptibility to changes in wildfire activity and climate under modeled future climate scenarios. Studies have been conducted exploring the elevational distribution dynamics of these Rocky Mountain forest systems (Coop et al., 2010; Peet, 1981) and have explored forest regeneration in response to disturbances like bark beetle, blowdown, changing climate, and fire over decadal timescales (Bigler et al., 2005; Falk et al., 2011; Gill et al., 2017; Kulakowski and Veblen, 2002; Sibold et al., 2006; Veblen et al., 1991). However, these studies are often unable to capture long-term disturbance dynamics due to the temporal limitations of modern ecological sampling approaches.

Despite the paradigm of a predictable successional sequence in lodgepole pine forests, it has not been tested whether the variability in the timing and pattern of post-fire succession is affected by changing climate conditions. The current lack of reconstructions that focus exclusively on post-fire vegetation succession over millennial timescales creates challenges interpreting present day changes to disturbance regimes in subalpine forests. The resiliency, or the system's ability to withstand change recover following a disturbance (Holling, 1973), of lodgepole pine forests to wildfires could also be misunderstood in its present climate context (Calder and Shuman, 2019). Further, an increase in fire frequency could redefine the relationship between climate, fire, and vegetation (Dale et al., 2001; Mietkiewicz et al., 2018) in subalpine lodgepole pine forests, which can create pressure on ecosystem services and can cause management challenges in post-fire scenarios in the future.

One approach to explore the long-term interactions between fire, climate, and vegetation is to use paleoecological records from lacustrine sediments (Heinselman and Jr, 1973; Whitlock et al., 2003; Whitlock and Bartlein, 2003). Lacustrine sediment cores contain remnants of both past fire events and vegetation in the form of microscopic charcoal fragments and fossilized pollen grains (Bennett and Willis, 2001; Birks et al., 2012; Brunelle and Whitlock, 2003; Whitlock and Larsen, 2001). When paired with radiocarbon derived chronologies, lacustrine sediment cores can be used to reconstruct long-term variation in both vegetation and fire with relation to changing climate. Paleoecological reconstructions in the Rocky Mountain region have characterized the dynamics of vegetation communities (e.g. Anderson et al., 2015; Calder and Shuman, 2017; Jiménez-Moreno et al., 2011), quantified past fire regimes (e.g. Caffrey and Doerner, 2012; Carter et al., 2017), assessed the impacts of fire on biogeochemical cycling (Dunnette et al., 2014; Leys et al., 2016; McLauchlan et al., 2014), and captured long-term changes in vegetation following the glacial retreat of the region (e.g. Brunelle et al., 2005; Lynch, 1996; MacDonald et al., 1991; Minckley et al., 2012). However, less is known about the direct relationships between fire and vegetation in differing climates because of the time and effort required to produce high-resolution vegetation records over longer temporal periods.

Objectives

The purpose of this study is to assess the millennial-scale impacts of changes in wildfire frequency and climate on the vegetation composition of lodgepole pine forests of the southern Rocky Mountain region. To do this, I build on an existing paleorecord of fire history at a high temporal resolution (4 years/sample) for Chickaree Lake, a site in Rocky Mountain National Park, U.S.A. (Dunnette et al. 2014). While a low temporal resolution (~94 years/sample) pollen record had been produced for the past 2,500 years, the existing temporal resolution of the record was not sufficient to detect successional vegetation change after fire events (see Appendix C.3). Thus, I increased the temporal resolution of the pollen record to 50 years/sample and paired it with reconstructions of fire activity and climate to better understand post-fire vegetation patterns in a subalpine lake catchment in Rocky Mountain National Park over the past 2,500 years.

The main objectives of this study are:

1. To investigate the long-term (centennial) post-fire vegetation response of lodgepole pine forests to determine if a predictable (decadal) post-fire vegetation trajectory exists following fire events.
2. To identify the influence of climate setting on vegetation dynamics over millennial timescales.

In addressing these objectives, this study can provide a methodological framework that could be applied to other lakes in the southern Rocky Mountain region to better capture regional trends in post-fire vegetation responses to changes in climate. With higher resolution reconstructions, there will be an increased understanding of the impacts of changing wildfire regimes and this understanding could then be used to guide future ecological restoration plans to help aid in the preservation of these subalpine forest systems.

Hypotheses

Based on the research objectives, I have the following hypotheses:

H1 Characterizing millennial vegetation dynamics through pollen: **Over the past two millennia, there will not be significant species turnover and the Chickaree Lake pollen record will be dominated by pine.** Based on the existing work at Chickaree Lake, the low-temporal resolution pollen record does not capture any major species turnover (i.e. changes from open grassland to forest) over the past 2,500 years. Other studies in the region that focus on lodgepole pine forests have also found that modern stand dynamics have been established within the past 3,000 years (Carter et al., 2013; Minckley et al., 2012).

H2 Characterizing post-fire vegetation dynamics: **Following fire events, there will be an observable decrease in tree pollen species, followed by post-fire increases in herbaceous/understory pollen species. Tree pollen concentrations will recover to pre-fire conditions within 75 years following a charcoal inferred fire event.**

This hypothesis is based on what is understood from modern post-fire vegetation dynamics in Rocky Mountain lodgepole pine forests. An extensive dendrochronological study from Rocky Mountain National Park that included Chickaree Lake as a study site found that lodgepole stand structure was able to recover following disturbance about 75 years after the initial event (Sibold et al., 2007). Herbaceous and understory species are generally able to recover faster in post-fire landscapes than tree species (Coop et al., 2010) so it is expected that there will be higher amounts of herbaceous and understory pollen in post-fire samples.

H3 Climate influence on vegetation composition: **There will be a muted climate signal captured through temperature reconstructions and pollen data with increased temperature anomalies between 1,200 and 850 cal yr BP during the Medieval Climate Anomaly (MCA) and cooler temperatures from ~500-100 cal yr BP during the Little Ice Age (LIA).**

This hypothesis is based on similar lake studies in the region that used high-resolution pollen to reconstruct climate. A study conducted in the Mount Zirkel Wilderness (Calder et al., 2017) found distinct climate signal of warming was observed through increases in *Artemisia* and declines in arboreal species. However; previous studies in the Rocky Mountains (Dunnette et al., 2014; Higuera et al., 2014) that reconstructed vegetation through pollen at lower temporal resolutions have found that most of the climate effects on these ecosystems can be captured through charcoal-based fire activity reconstructions.

Chapter 3 - Study Area

Study Area

Chickaree Lake is located on the western side of the continental divide in Rocky Mountain National Park, Colorado, U.S.A. at 40.334249°N, 105.847270°W (Figure 3.1). The lake is 2,830 meters above sea level and surrounded by an even aged stand of lodgepole pine (*Pinus contorta* Douglas ex London) forest dating back to a 1782 Common Era (CE) stand replacing fire (Sibold et al., 2007). Less-dominant overstory species include Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) with a mixed understory including *Sheperdia canadensis*, *Rosa,* and *Artemisia*. Chickaree Lake has a surrounding watershed of ~31 hectares and is a small, deep lake with a surface area of 1.5 hectares and a maximum depth of 7.9 meters. Chickaree Lake has an ephemeral inlet and outlet within the catchment. The well-drained sandy soils surrounding the lake are derived from granite, gneiss, and schist and are covered by a thin duff/litter layer (US Department of Agriculture NRCS Soil Survey Staff, 2006). The fire regime at Chickaree is classified as infrequent (~200 years between fires) and stand replacing. The climate in nearby Grand Lake (8 km from the lake) is continental, with average January and July temperatures of −8.5 °C and 14 °C, and the average total annual precipitation is 482 mm, with an average annual snowfall of 3,503 mm (Western Regional Climate Center 1940–2016 observations).

European settlement impacts on the fire history and natural environment surrounding Chickaree Lake has been minimized due to the protections associated with the National Park designation. The Ute tribe roamed the region prior until the late 1700s (Kornfeld and Frison, 2000; Vale, 2013) and most activity was concentrated to lower lying valleys and plains (Husted, 1965; United States National Park Service, 2019). These tribes were known to ignite fires in the lower lying grassy environments, however; these fires did not occur at the same frequency as lightning ignited fires (Baker, 2002; Vale, 2013; Veblen et al., 2000), and lighting was the main source of fire ignitions prior to European settlement. European settlers arrived in the region in the 1850's, however due the rugged landscape of the Front Range of the Colorado Rockies, they were unable fully to develop settlements at higher elevation sites (United States National Park Service, 2019), so human activity was mainly concentrated in the valleys (Buchholtz, 1984). Rocky Mountain National Park was created in 1919 CE. Fire suppression in the park began in 1920 CE and was changed to allow naturally-ignited wildfires to burn in 1972 CE (Hess, 1993). This decision was reversed in 1978 CE after a large fire occurred in the park and active suppression has been enacted as a response (Hess, 1993). Even though there was human activity in the region prior to Rocky Mountain National Parks designation in 1919 CE (United States National Park Service, 2019), it had minimal influence on both the fire history and the natural landscape over the past 2,500 years which makes Chickaree Lake a relatively pristine site for paleoecological reconstruction.

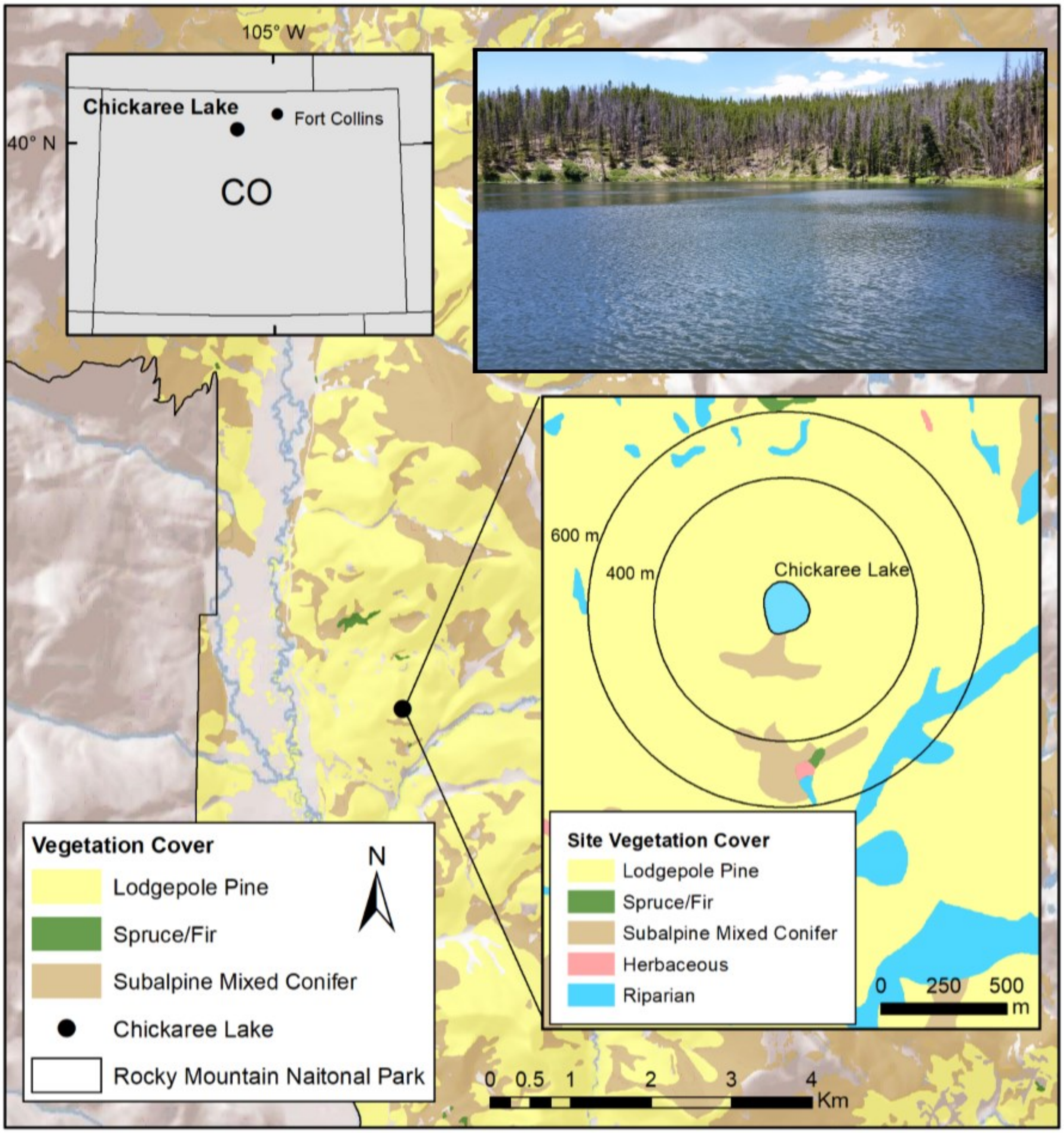


Figure 3.1 Site map of Chickaree Lake in Rocky Mountain National Park, U.S.A. Circular buffers around the lake perimeter indicate distances of 400 m and 600 m which are likely to correspond to pollen source area in this landscape (Sugita, 1994)

Map data source: Rocky Mountain National Park and the U.S. Bureau of Reclamation Remote Sensing and Geographic Information Group (USBR/RSGIG). Vegetation data source: Rocky Mountain National Park vegetation GIS dataset. Data acquired on 03/1/2019.

Chapter 4 - Methods

Existing Data from Chickaree Lake

This study adds to previous work from Chickaree Lake published by Dunnette et al. (2014) and Leys et al. (2016), which included a high-resolution record of fire history and biogeochemical change (i.e., 5-50 yr sampling interval), and a lower resolution record of vegetation change based on fossil pollen (i.e., 20-275 yr sampling interval). For the studies, two parallel, overlapping sediment cores were collected from Chickaree Lake at 7.9-meter water depth in August 2010 with a modified Livingstone piston corer (Wright et al., 1984). The full extent of the core spans 6,200 cal yr BP. This lake core record has a high sedimentation rate of an average of 15 cm yr $^{-1}$ (4 years per 0.5-cm thick sample) and well-established age-depth chronology based on both ^{14}C (n=25) and ^{210}Pb dates (n=13) (See Appendix C.1) (Dunnette et al., 2014). Since Chickaree Lake is small (1.5 ha surface area of water), it can be used to reconstruct local changes in vegetation composition, since smaller lakes capture more local pollen sources (Davis, 2000; Fall, 1992; Sugita, 1994).

New analyses

This study focuses on the past 2,500 years. This time period was selected because I hypothesized that it would contain two short-term variations in climate observed in regional paleoclimate records: the Medieval Climate Anomaly (MCA) from ~700-1,000 cal yr BP when temperatures were warmer and the Little Ice Age (LIA) when climate shifted towards cooler temperatures from ~650-250 cal yr BP (Mann et al., 2009; Trouet et al., 2013). The range of 2,500 years BP to present also captures multiple fire events that have been observed in both charcoal datasets (Dunnette et al. 2014) and dendrochronological reconstructions from the region (Sibold et al. 2007).

Charcoal Data

Contiguous sediment subsamples (1.5-3 cm^3) were sampled at 0.5-cm intervals and were prepared for charcoal analysis. Charcoal particles were counted under a microscope and converted to charcoal accumulation rates (CHAR) based on the chronology. The CHAR data were then used as input for CharAnalysis (Higuera et al., 2009) to identify peaks in charcoal, which were then interpreted as fire events. Magnetic susceptibility (MS), which acts as a proxy for erosion in lake catchments, was also measured continuously for the core in 0.5-cm intervals using a Bartington MS3 meter and MS2E core logging sensor (Bartington Instruments, Oxford, UK). Dunnette et al. (2014) identified "high-severity catchment fires" as CHAR and MS peaks that coincided within 10-20 years of each other and other CHAR-inferred fires were interpreted as "lower severity/extra local fires." Full details are described by Dunnette et al. (2014) and are summarized briefly here.

Pollen Analysis

For the Dunnette et al. study at Chickaree lake, pollen samples (1 cm^3) were subsampled from the sediment cores at 7.5-cm intervals for the upper 175 cm of the core and taken at 25-cm intervals for the lower portion of the core. The existing temporal resolution of the pollen data was improved in this study through the addition of 22 samples over the past 2,500 cal yr BP. The archived wet sediment (1 cm^3) was processed through acid digestion following standard methods modified from Faegri and Iversen, 1975. A known marker of *Lycopodium* spores was then added to each sample to act as an exotic tracer to later calculate pollen concentrations per cc of sediment. Pollen residue was suspended in silicon oil and the samples were counted under a microscope to the standard sum of 300 terrestrial pollen grains at 400x magnification. Samples were identified to the lowest taxonomic resolution possible using existing pollen keys (Kapp, 1969; McAndrews et al., 1973). Pollen counts were converted to percentages by dividing the raw counts of individual samples by the sum of the counts of terrestrial pollen, which excludes unknown pollen, indeterminate pollen, and wetland taxa. To aid in interpretation of vegetation community response to wildfire, pollen data were binned intro three categories: arboreal (canopy), shrub (understory) and herbaceous (understory) (Table 4.1). *Arceuthobium*, a mistletoe species that targets lodgepole pine, was classified as herbaceous/understory because while it does effect lodgepole pine health and is found in the canopy, it is ecologically classified as a perennial herbaceous species (Hawksworth and Johnson, 1989; Hawksworth and Wiens, 1994).

Table 4.1 Dominant pollen taxa surrounding Chickaree Lake categorized to aid in interpretations of fire driven vegetation dynamics.

Arboreal (canopy)	Shrub (understory)	Herbaceous (understory)
Pinus	*Quercus*	*Artemisia*
Picea	*Alnus*	*Ambrosia*
Abies	*Salix*	Asteraceae
Pseudotsuga	*Sarcobatus*	Chenopodiaceae
		Poaceae
		Rosaceace
		Arceuthobium

Statistical Analysis

I used four different methods to assess the impacts of wildfire on vegetation structure in paleoecological datasets. To characterize millennial scale vegetation dynamics, I used Cluster Zone Analysis to determine the Constrained Incremental Sum-of-Squares (CONISS) and Nonmetric Multidimensional Scaling (NMDS) to identify distinct changes in pollen compositional structure over the past 2,500 years. To quantify fire-driven vegetation changes, I used pollen ratios and a rate of change analysis to determine if there was a significant impact of fire on shorter term (decadal) vegetation change. To place the Chickaree Lake pollen record in a regional climate context, I compared reconstructed climate data from Chickaree Lake to existing regional records of moisture availability.

To prepare the data for statistical analysis, pollen types that occurred in at least 20 of the total samples (n=52) and had total abundance of >1% were included in the analysis. The threshold of inclusion was reduced from the standard 5% to 1% to include lower-productivity plant taxa, as *Pinus* is a prolific producer of pollen and its large abundances can often mask shifts in minor taxa that could represent post-fire successional sequences (Fall, 1992; Higuera et al., 2014; Minckley et al., 2008). *Pinus* pollen was often too degraded to differentiate between haploxylon and diploxyon types, so all *Pinus* pollen grains and pairs of *Pinus* bladders were combined and classified as "*Pinus* undifferentiated". Since the lake is surrounded by a stand of lodgepole pine, which is diploxylon-type, and almost all *Pinus* pollen grains identifiable to the subgenus level were diploxylon (98%), I assume that *Pinus* pollen represents the subgenus *Pinus* rather than *Strobus*. The raw pollen counts were converted to percentages using a pollen sum that included all upland pollen types. Fire events from Dunnette et al., 2014 were denoted as either high-severity catchment fires or lower-severity/extra local fires and the cumulative number of years following fire events were also included for future analysis. To aid in the interpretation of post-fire vegetation impacts, pollen samples were binned into two classifications based on their relationship to charcoal peaks. Pollen samples were classified as “fire” if they came from a sample that was coincident with (≤ 5 years prior) or immediately following (≤ 35 years after) a charcoal sample with an identified charcoal peak year. Pollen samples were classified as “non-fire” if they were not associated with an identified charcoal peak and fell at least 35-yr after an identified charcoal peak. A 35-year buffer was used to avoid sampling post-fire successional recovery (Peet, 2000). Cumulative time between fire events was also used for analysis with the following temporal bins: 0-75 years since fire, 75-150 years since fire, and >150 years since fire. These bins were selected due to their ability to capture important periods of interest in lodgepole pine stand development in terms of biogeochemical recovery and forest regeneration (Coop et al., 2010; Dunnette et al., 2014; Peet and Hill, 2012; Sibold et al., 2007)

First, to characterize millennial scale temporal periods (“zones”) of distinct vegetation composition, a stratigraphically constrained cluster zone analysis was conducted using CONISS (Grimm, 1987) carried out through the rioja package (Juggins, 2015) in the R programming platform on the most abundant taxa. This analysis is based on the square chord dissimilarity measure, a common distance metric used when working with pollen data (Gavin et al., 2003; Overpeck et al., 1985). The number of optimal zones to include was identified through the use of a broken-stick model (Bennett, 1996; Seppä and Bennett, 2003) which ensures that the resulting zonation is based on the data structure and not random chance. The broken-stick model compares the variance captured by the clustering to randomized modeled variances for each additional zone. When the clustering curve surpasses the randomized curve, the addition of groups accounts for noise rather than true clustering within the dataset. The resulting optimal number of zones are then used to describe the dominant long-term (centennial to millennial) patterns in the pollen data.

Second, to investigate the relationships between vegetation compositional change over time and to interpret the response of pollen assemblages to fire events over millennial scales, I used Kruskal's nonmetric multidimensional scaling (NMDS) to reduce the dimensionality of the dataset and map vegetation change (Alroy, 2015). This analysis was carried out using the MASS package in R and pollen data was transformed using the Bray-Curtis distance measure, a common distance metric in ecological research (Beals, 1984). Pollen types from lower elevations with long ranges of transport (*Sarcobatus, Quercus, Salix*) (Lynch, 1996) were excluded from analysis. NMDS is a multivariate ordination technique that reduces the dimensionality of the dataset into a series of orthogonal dimensions (axes) though multiple iterations. Dimensions are added only if they reduce the final "stress" (goodness-of-fit) by 5% or more and for the data from Chickaree Lake, two axes were determined optimal based on their stress value of 19%. For this analysis, I used 20 iterations and fit the data to k=2 axes and the analysis uses a Principal Component Analysis (PCA) rotation on the ordination results so that the maximum variance is captured by Axis 1.

The relationship between the pollen abundance data and the NMDS axis scores was quantified through Pearson correlations and pollen types with $r > 0.3$ for either the first or second axis were presented in NMDS ordination space. To compare the NMDS scores of pollen samples with relation to fire activity, I conducted significance tests by using a bootstrapping permutational multivariate analysis of variance test (perMANOVA) (Anderson, 2017) from the vegan package in R. This test used the binary fire and non-fire pollen sample associations and the cumulative years since fire to determine if there was a significant influence of fire activity on how the samples plotted in NMDS space. Time series of the NMDS results were also created to aid in the interpretation of potential drivers in the pollen dataset.

Third, to interpret post-fire shifts in forest composition, I used two ratios that reflect impacts of fire on the balance between overstory and understory vegetation coverage. I use the ratio of arboreal to non-arboreal pollen grains (AP:NAP) to represent the ratio of overstory to understory taxa contributing to a pollen sample. This ratio was calculated using $[a - b]/ [a + b]$, where a is the sum of arboreal pollen taxa counts (summarized as “canopy” in Table 1) and b is the sum of non-arboreal pollen taxa counts (summarized as “understory” in Table 1). I interpret higher ratios as indicating higher abundances of overstory species including *Pinus, Picea,* and *Abies* which indicates a denser forest presence around Chickaree Lake. The ratio of conifer pollen to local understory pollen (Conifer:LNAP) can also be useful in subalpine forest settings as it can offer insight about local-scale disturbance dynamics (Calder et al., 2019; Lynch, 1996). For example, it is expected that after a fire, conifer pollen would decrease and allow for increases in pollen production from local understory components. This ratio was calculated using the same approach above, where a is the sum of *Pinus, Picea,* and *Abies* pollen grains and b is the sum of *Artemisia*, Asteraceae, Chenopodiaceae, Poaceae, and Rosaceae pollen grains. Higher values indicate higher amounts of arboreal pollen. To assess post-fire impacts on vegetation, each pollen ratio was statistically compared based on their association with the binary fire or non-fire sampling scheme. In addition to the two ratios, raw percent data from *Pinus* and *Artemisia* were also statistically compared by their fire association to offer insight into taxa-specific fire impacts. A Wilcox non-parametric ANOVA was used to assess difference in mean ratios between fire and non-fire pollen samples, and samples were considered significantly different if the associated p-value was ≤ 0.05.

Fourth, a rate of change analysis was used to quantify the rate of community compositional change following fire events. The Bray-Curtis distance measure was used calculate the dissimilarity between all adjacent pollen samples. The resulting Bray-Curtis value was then divided by the time between samples (yr) and multiplied by 100 to obtain % change over time (% change per year), following approaches outlined in Crausbay et al., 2017. The resulting rate of change values were then statistically compared based on their association with the cumulative years following fire events from 0-75 years post fire, 75-150 years post fire, and >150 years post fire through the Kruskal Wallis test. A plot comparing rate of change values to cumulative years since fire was constructed as well. It is expected that following a fire event, the dissimilarity/rate of change between samples would be higher for samples 0-75 years post fire than when compared to samples associated with longer non-fire intervals (i.e. >75 years). In doing this, I capture the impacts of wildfire as an agent of change within pollen assemblages, where higher values indicated greater post-fire rates of change.

Finally, to address the second objective and to place the Chickaree pollen record within a regional climate context, I used the Modern Analogue Technique to reconstruct precipitation for the past 2,500 years from the Chickaree Lake fossil pollen record. The Modern Analogue Technique compares modern pollen datasets with fossil pollen datasets and uses the present day climate associated with modern pollen assemblages to infer past climate (Minckley et al., 2008; Overpeck et al., 1985). The reconstruction was created through the analogue package in R and was based on chi square dissimilarities from the Chickaree fossil pollen record and modern pollen records from the central Rocky Mountains and methods are described in detail in Parish et al. in prep. I visually compared the precipitation reconstruction from Chickaree Lake to lake level, δO^{18}, and tree ring inferred precipitation reconstructions from other studies within the region (Anderson et al., 2015; Cook et al., 2007; Shuman et al., 2009). These reconstructions serve two purposes as they place Chickaree in a regional climate context and allow us to investigate the impact of climate forcing on wildfire and vegetation in the central Rocky Mountain region.

Lake level reconstructions are often used to capture past precipitation balances where higher lake levels indicate increased periods of precipitation (Shuman et al., 2009). δO^{18} records form lake sediments can be used to trace water source and the seasonality of precipitation (Anderson, 2011). Tree-ring inferred precipitation reconstructions are useful because they exist at annual temporal resolutions and are especially effective at capturing drought conditions(Cook et al., 2007). Through tree-ring datasets, it is possible to reconstruct Palmers Drought Severity Index (PDSI) which is a measure of the balance between soil moisture and temperature (Cook et al., 2007). Since PDSI exists at annual resolutions, it is often smoothed using a moving average approach to capture longer-term dynamics in precipitation between dry and wet conditions. By using multiple proxies for precipitation, this study will be able to place the Chickaree Lake reconstruction within the regional context of hydrological studies from within the Rocky Mountain region.

Chapter 5 - Results

Fire History

Over the past 2,500 years, four high-severity catchment fires and 11 lower severity/extra local fires were identified in the Chickaree Lake charcoal record (see Appendix C.2) (as presented by Dunnette et al. 2014). The most recent charcoal peak occurred c. 161 cal yr BP, coincident with the 1782 CE stand replacing fire identified through dendrochronology (Sibold et al., 2007). When comparing the charcoal peak-inferred fire history to the pollen data, there were 21 pollen samples that were associated with fire events (fire samples), and 31 pollen samples that were classified as non-fire events (non-fire samples). All samples, except for a sample at 94 cal yr BP, were samples immediately following a charcoal peak inferred fire event (average time lag = 27 yr). The sample at 94 cal yr BP was classified as a fire event because it is the sample that is most closely related to the 1872 CE surface fire and, while the event did not appear in the charcoal record, it could have still had an impact on the local pollen source. When comparing the cumulative years following a fire event, there is a temporal offset due to the differences in sampling resolution between the charcoal peak inferred fire events and the pollen data (Figure 5.1). Average lag time between charcoal peak inferred fire events and pollen data was decreased from 87 years to 27 years (Table 5.2) with the addition of the samples used for this study.

Table 5.1 Comparison of temporal offsets between fire and pollen samples for existing and improved Chickaree Lake pollen record

Chickaree Pollen Record	Mean Temporal Offset (cal yr BP)	Standard Deviation (cal yr BP)
Existing (n=30)	87	72
Improved (n=52)	27	14

Pollen abundance and cluster zone analysis

A total of 52 samples were used in this study, with an average of 318 pollen grains counted per sample (range= 256-432). Overall, 31 pollen types occurred in the record, and of the 31 pollen types, 14 had a maximum abundance of >1% and occurred in more than half of the samples (Figure 5.1). Dominant pollen types throughout the record include *Pinus* (mean=75% range=46%-88%), *Picea* (mean=4% range=0%-13%), *Artemisia* (mean=10% range=3%-24%) and Chenopodiaceae (mean=3% range=.3%-9%); however, less-dominant species including *Arceuthobium* (mean=0.414% range= 0%-1.6%), Rosaceae (mean=0.32% range=0%-2%), and Poaceae (mean=0.86% range=0%-3%) also contributed to the long-term trends identified through cluster analysis.

Cluster analysis and the broken-stick model (See Appendix B.2) identified two distinct pollen zones: Zone 2 from 2,500-1,155 cal yr BP, and Zone 1 from 1,155 cal yr BP to present (Figure 5.1). Zone 2 is characterized by high percentages of *Pinus* (pine) (mean=77% max=88%), Poaceae (grass family) (mean= 1% max=3%), *Abies* (fir) (mean=1% max= 3%), *Ambrosia* (ragweed) (mean=1% max=2%), *Alnus* (alder) (mean=1% max=1%), and *Sarcobatus* (greasewood) (mean=1% max=3%) pollen. Fire frequency was the higher in Zone 2 than Zone 1, with nine events identified, two of which were high severity catchment fires, and the remaining seven classified as extra local/lower severity fires. The mean fire return interval (FRI) for this period was 158 years between all fire events.

Zone 1, from 1,155 cal yr BP to present, was characterized by higher Rosaceae (rose family) (mean=1% max=2%) and *Arceuthobium* (Dwarf Mistletoe) (mean=1% max=2%) pollen percentages than in Zone 2. *Picea* (spruce) (mean=5% max=13%), Asteraceae (sunflower family) (mean=1% max=3%) and *Artemisia* (sagebrush) (mean=13% max=24%) also show increases during this zone, relative to Zone 2. Notably, mean *Pinus* abundance decreases to 71% and the lowest *Pinus* abundance for the entirety of the record is observed in this zone, after the most-recent high-severity catchment fire in 1782. Lower-elevation and extra-local pollen types, including *Salix* (willow), *Sarcobatus* (greasewood) and *Quercus* (oak), also decrease during this period. Six fire events occurred in Zone 1, including two high severity catchment fires and four extra local/lower severity fires. The mean FRI for this period was 159 years, including all fire events.

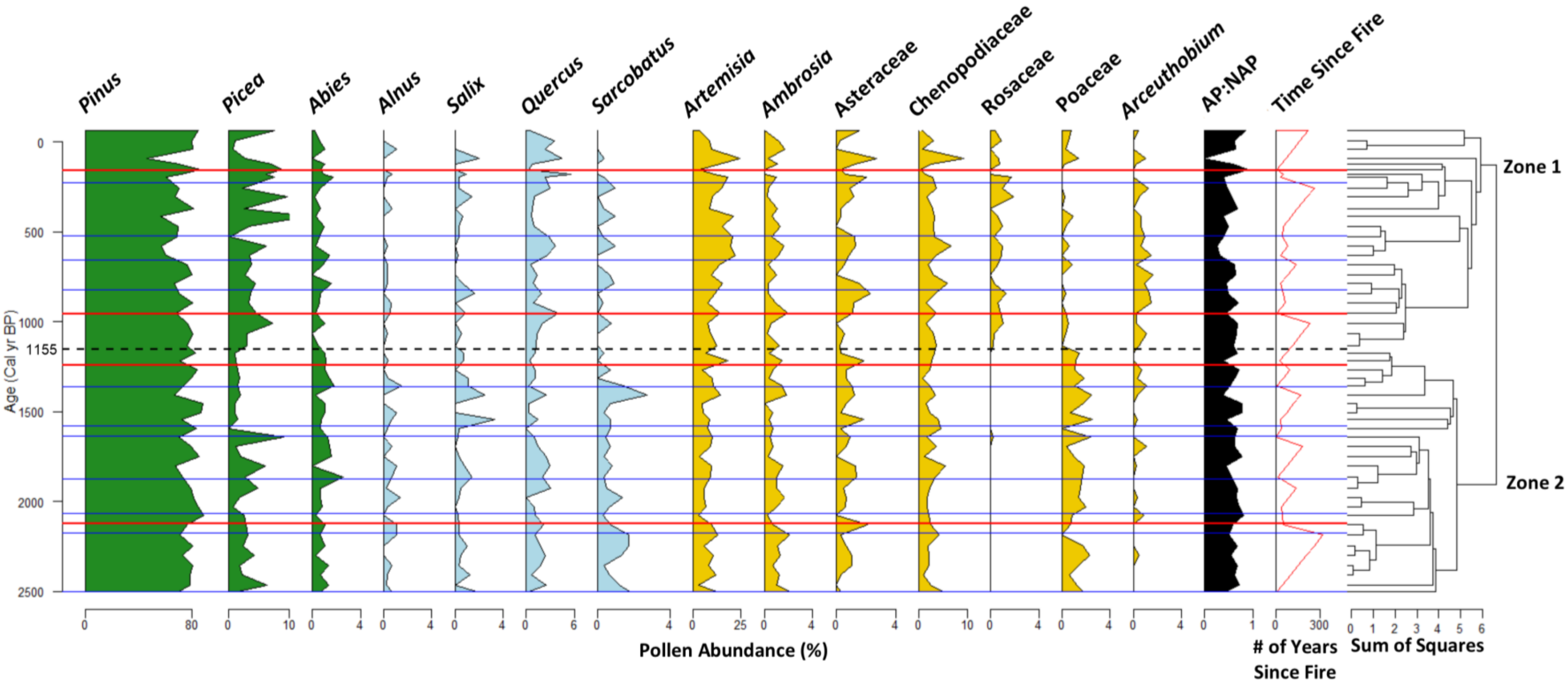


Figure 5.1 Stratigraphic diagram of selected pollen taxa. CONISS dendrogram included to right of plot with zone break delineated in a black dashed line. High severity catchment fire events are depicted in red lines and lower severity/extra local fire events are included in blue. Time since fire may not line up directly with fire events due to differences in sample resolution between pollen and charcoal data.

Ordination

The NMDS analysis converged after 20 restarts and resulted in a final stress value of 0.19. The data were plotted based on the first two dimensions (Figure 5.2) and this plot represents the Bray-Curtis distance-based relationships between individual samples (points), time since fire (color), and zonation (shape) in a two-dimensional space. NMDS1 captures the difference in pollen assemblages between Zone 1 and Zone 2, with Pearson correlations of *Pinus* (*r* =0.56) driving the positive values of Axis NMDS1 and *Artemisia* (*r*= -0.57), Rosaceae (*r*= -0.71), Asteraceae (*r*= -0.39), and *Arceuthobium* (*r*= -0.7) driving the negative values of Axis NMDS1. Axis NMDS2 was mainly driven by high correlations of *Alnus* (*r* =0.59) and *Ambrosia* (*r* =0.49) in the positive direction and higher correlations of Poaceae (*r* =-0.31) and *Picea* (*r*= -.33) in the lower direction (Table 5.1).

Table 5.2 Pearson correlation coefficients of Chickaree Lake pollen taxa and NMDS axis scores

Taxa	NMDS1	NMDS2
Pinus	0.56	-0.21
Picea	-0.28	-0.33
Abies	0.36	-0.01
Alnus	0.43	0.59
Artemisia	-0.57	0.32
Ambrosia	0.13	0.49
Asteraceae	-0.39	0.08
Chenopodiaceae	-0.38	0.36
Rosaceae	-0.71	-0.06
Arceuthobium	-0.70	0.22
Poaceae	0.29	-0.31

When looking at the time series of NMDS1, it was driven by the zone break identified through CONISS. Although the NMDS analysis used the Bray-Curtis distance metric, the zone break is consistent with the square-chord distance-based zonation of CONISS and is consistent with other distance metrics (see Appendix B.1). The samples from 0-75 years following a fire tended to plot towards the positive values of NMDS2 while samples that were greater than 75 years following fire tended to be more dispersed between NMDS1 and NMDS2. I interpret NMDS2 as reflecting the variability of post-fire vegetation impacts as the high severity catchment fires and lower severity/extra local catchment fires appeared to have different magnitudes of influence on pollen spectra. The perMANOVA results indicate significant differences in the dissimilarity between the binary association of fire and non-fire samples (p-value= .037) while cumulative years following fire had no significant influence on pollen in NMDS space (p-value=.5).

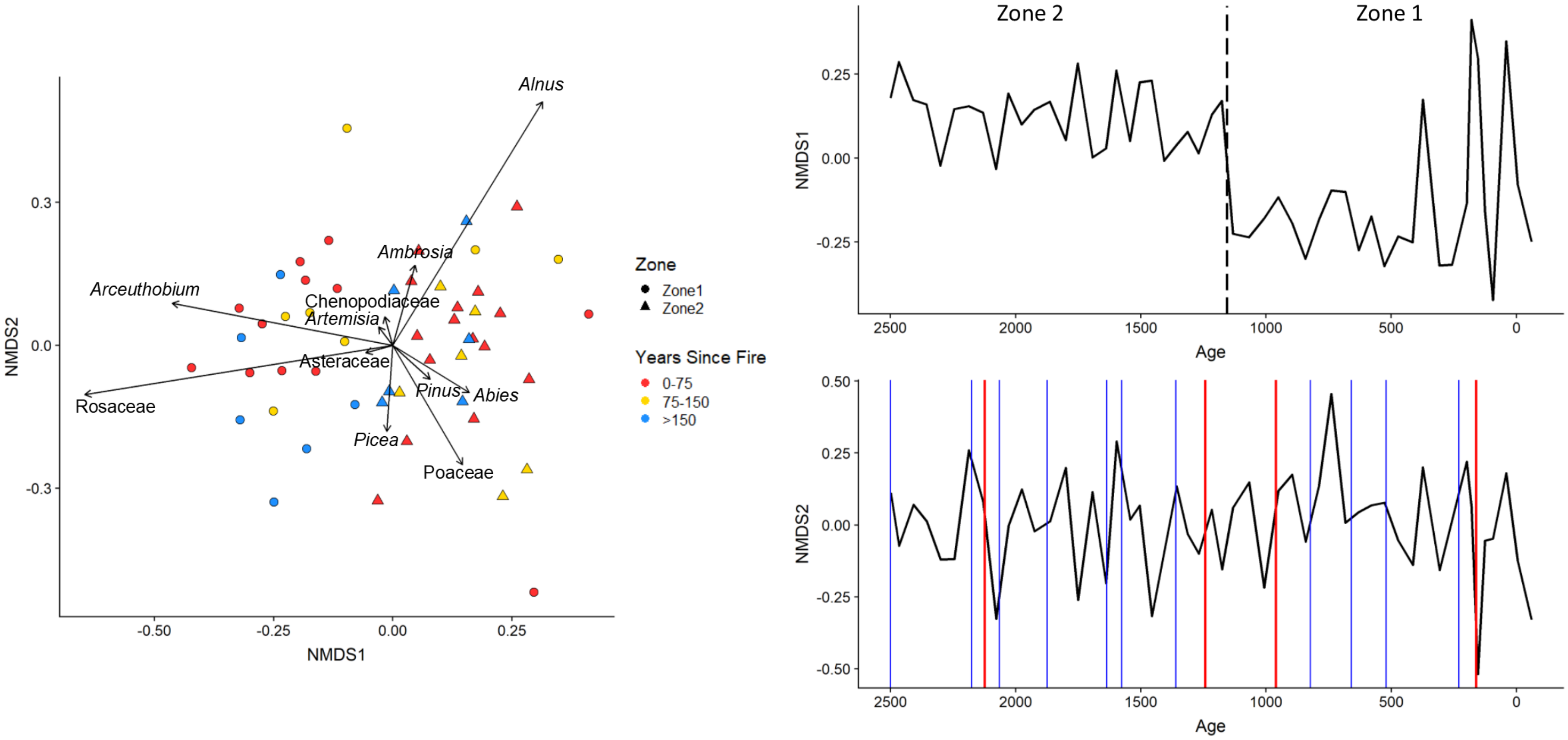


Figure 5.2 Nonmetric multidimensional scaling ordination plot of Chickaree pollen percent data of selected taxa. Zone breaks are denoted by the point shape and cumulative time since fire for each sample is denoted by color scheme. NMDS1 accounts for the most variance based on PCA rotation of ordination results and the zone break is included as a dashed line. NMDS2 has high severity fire events denoted in red and lower severity/extra local fire events denoted in blue.

Pollen ratios

Pollen assemblages varied significantly between fire (n=21) and non-fire samples (n=31) (Figure 5.3). When comparing the AP:NAP, fire samples had significantly lower ratios than non-fire samples (p=0.029). The median ratio of conifer pollen to local non-arboreal pollen was also significantly lower for fire samples than non-fire samples (p=0.019). Fire samples for the record were characterized by lower amounts of median arboreal pollen (median= 0.52) and median conifer pollen (median= 0.62) while non-fire samples had higher amounts of median arboreal pollen (median= 0.62) and higher amounts of median conifer pollen (median= 0.71). When comparing the median percentages of *Pinus* and *Artemisia* by fire association, fire samples had nearing significantly lower amounts of *Pinus* pollen (p=.06) and higher amounts of *Artemisia* pollen (p=.07). Median percentages of *Pinus* pollen were lower for fire samples (median=72%) while median percentages of *Artemisia* pollen were higher for fire samples (median=12%).

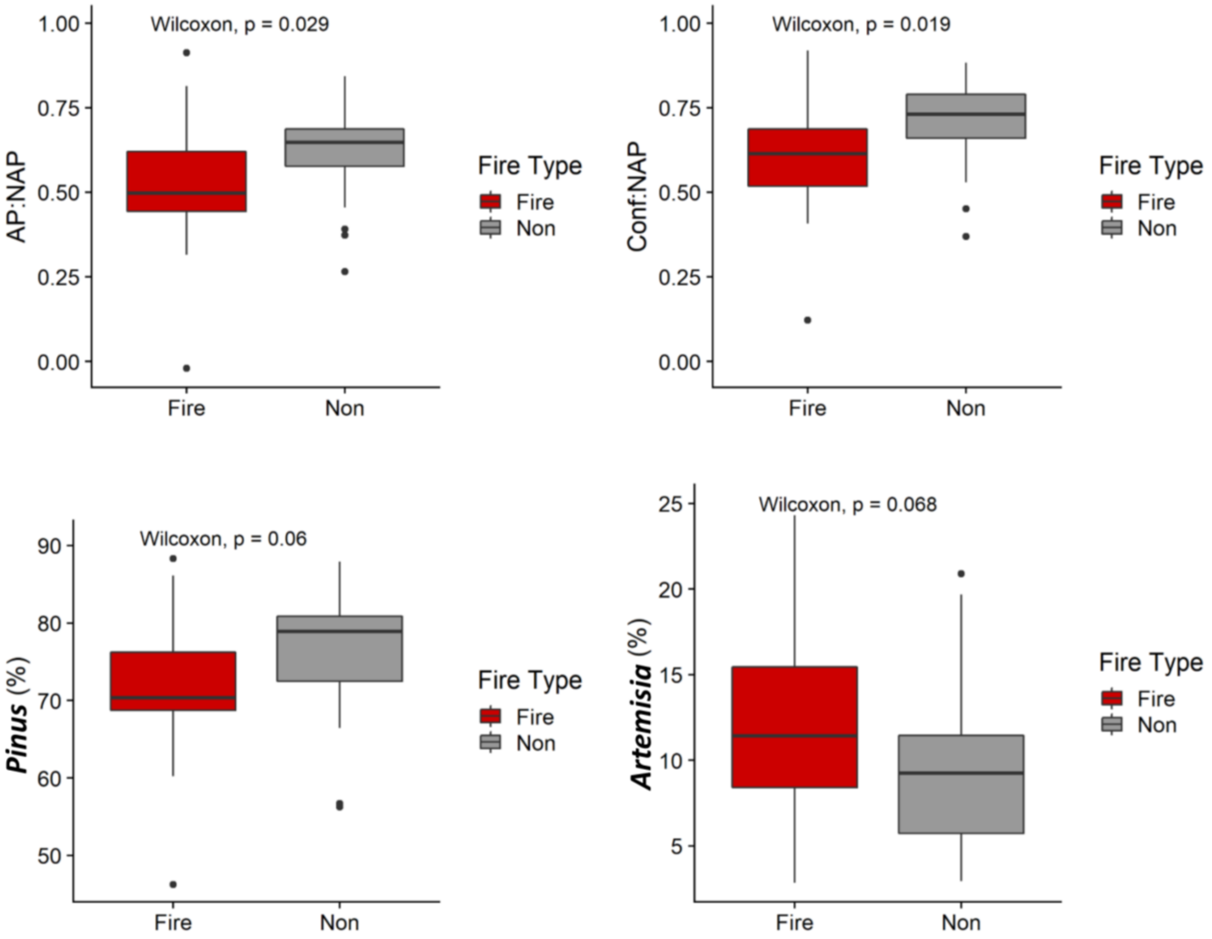


Figure 5.3 Boxplots of selected pollen ratios, red indicates post-fire pollen samples and grey indicates samples that are not associated with fire events. Wilcoxon test p-values are included.

Rate of Change

The rate of change time series captured the variability in species compositional change over the past 2,500 years (Figure 5.4). The rate of change in pollen assemblages following some fire events increased above the median (background) level of 27%. The highest rate of change value was observed at 94 cal yr BP, as 88%. Notably, this follows the 1782 CE stand-replacing fire. There was no significant difference (p-value=.09) between the median rate of change values for samples when compared by time since fire based on the Kruskal test. While this result may not be significant, the range of rate of change values reflected time since fire as samples from 0-75 years postfire had a range of 11%-88% change, samples from 75 years-150 years had a range of 6%-70%, and samples >150 years postfire had rate of change values from 8%-20% change.

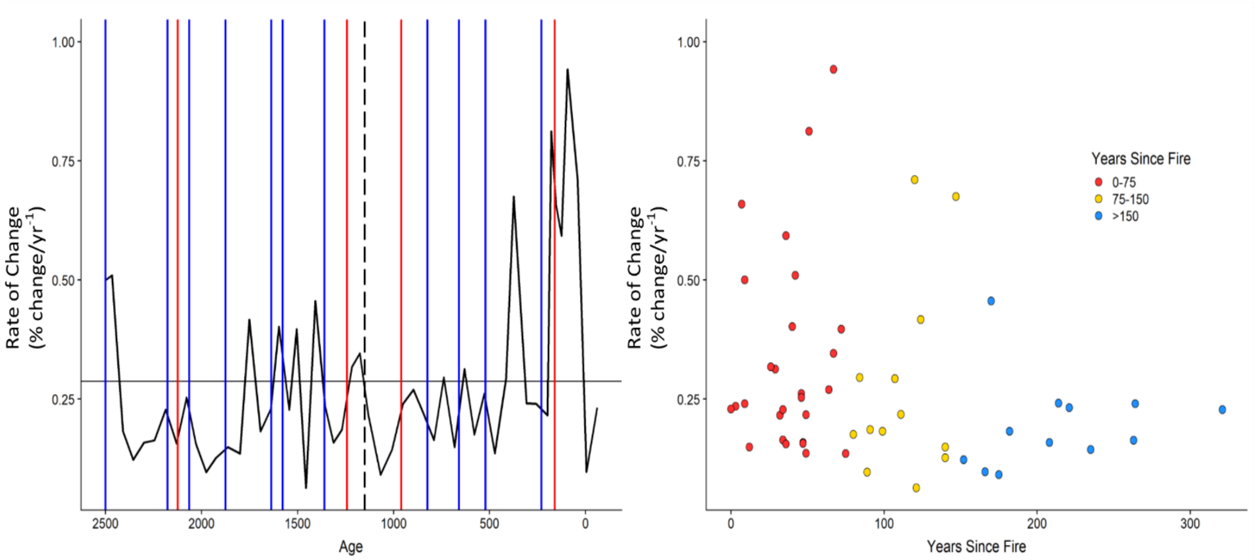


Figure 5.4 Rate of Change analysis using square chord distance measures between consecutive samples. Red lines indicate high severity fire events and blue lines indicate lower severity/extra local fire events from Dunnette et al. 2014. A biplot of cumulative years since fire and rate of change is also included and points are colored by cumulative time since fire.

Temperature and Precipitation Reconstructions

The reconstruction of temperature and precipitation captured broad trends in past climate. Mean annual temperature over the past 2,500 years was consistent with other reconstructions throughout the region (Parish et al. in prep) as there were no significant changes in reconstructed temperature prior to a spike in temperature anomaly around 94 cal yr BP, which was most likely forced by using a singular pollen record rather than actual climate conditions (See Appendix B.3). I instead chose to focus on the precipitation reconstructions from Chickaree Lake as they offer better insight towards site level climate forcing on vegetation dynamics (Figure 5.5). While reconstructed summer precipitation anomalies show no significant changes from the mean (Figure 5.5 A), winter precipitation was static prior to the zone shift at 1,155 cal yr BP and increased up to 150 mm annually towards present (Figure 5.5 B), indicating increased amounts of winter precipitation at Chickaree Lake. The δO^{18} reconstruction (Figure 5.5 C) of precipitation seasonality shows an increase in winter precipitation following the zone break, as indicated by increasingly negative values. Lake levels increased towards present (Figure 5.5 D) and PDSI shows increases towards wetter conditions (Figure 5.5 E).

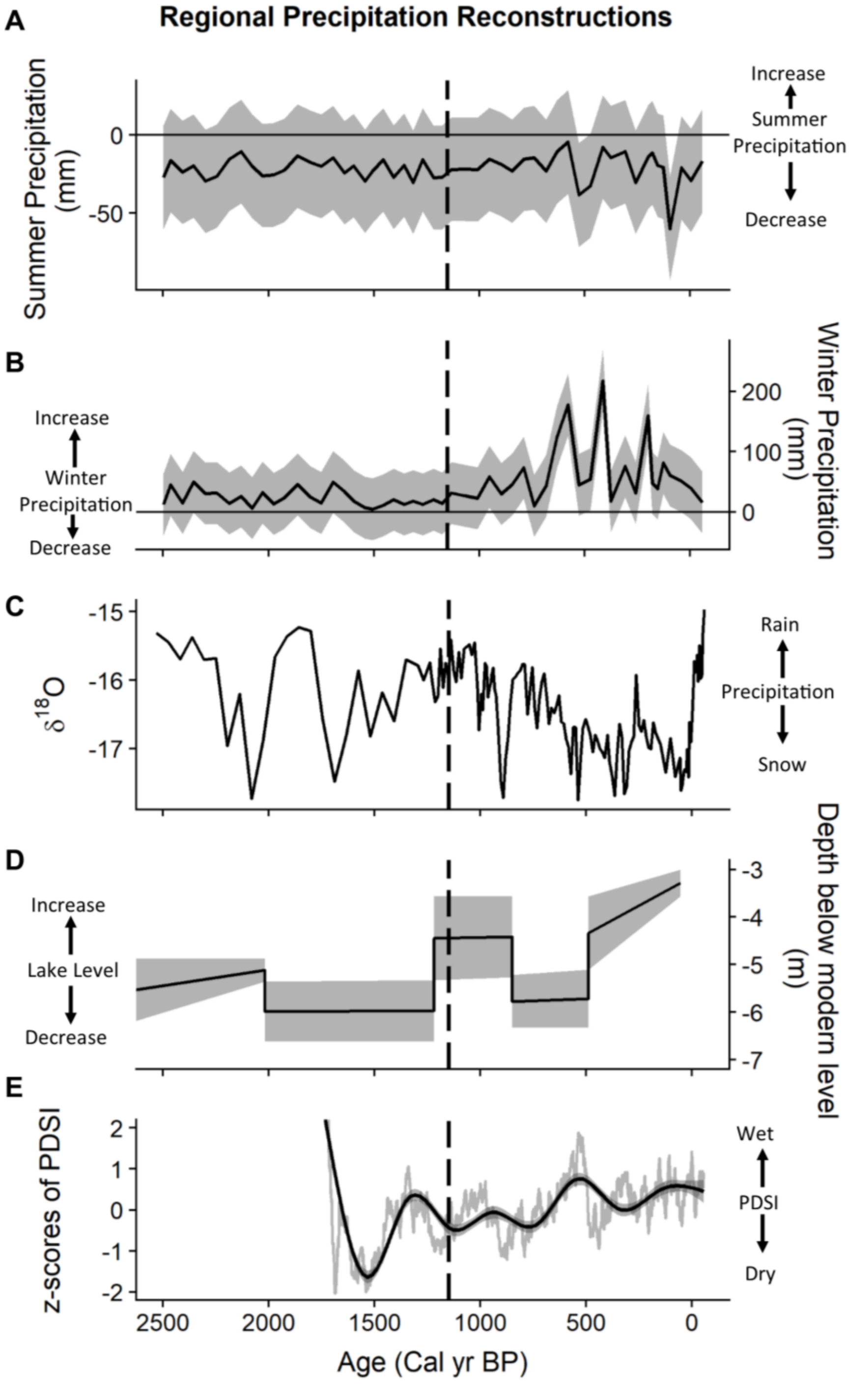


Figure 5.5 Chickaree MAT fossil-pollen based reconstruction of summer precipitation (A), winter precipitation (B), Bison lake $\delta^{18}O$ (C) (Anderson et al., 2015), Hidden Lake Water Level (D) (Shuman et al., 2009), and tree-ring derived Palmer Drought Severity Index (PDSI) (E) (Cook et al., 2007). Black dashed line indicates zone break from Chickaree pollen record. Z-scores of PDSI was smoothed using moving average to 125-year intervals. Precipitation anomalies were calculated for the Chickaree reconstructions using the 30-year normal precipitation mean from nearby Grand Lake, Colorado.

Chapter 6 - Discussion

Pollen data from high elevation small lakes are best able to capture local changes in vegetation structure (Fall, 1992), and since Chickaree Lake was a small lake, this study was able to address localized impacts of wildfire and climate change at Chickaree Lake. Previous paleoecological studies in the region considered Rocky Mountain subalpine lodgepole forests to be stable ecosystems due to the ongoing presence of pine over the past 3,000 years (Dunnette et al., 2014; Minckley et al., 2012). Even though the vegetation reconstructions surrounding Chickaree Lake show a similar trend of pine dominance over this shorted temporal interval of analysis, local non-dominant taxa offered some insights towards compositional changes throughout the record. For example, the zonation, which is interpreted as millennial scale vegetation dynamics, was mainly driven by the less abundant taxa (Rosaceae and *Arceothobium*) rather than changes in *Pinus* composition (Figure 5.1, Figure 5.2). While the period of 2,500 cal yr BP to present is generally associated with the establishment of modern day climate and forest composition in paleoecological records from the region (Caffrey and Doerner, 2012; Fall, 1997; Higuera et al., 2014; Minckley et al., 2012), there are some changes in forest density with relation to different fire regimes and climate setting at Chickaree Lake.

By increasing the temporal resolution to a median of 50 years between samples, this study was better able to characterize the influence of wildfire and climate and capture post-fire vegetation dynamics that would otherwise be missed when using longer temporal windows. The increased temporal resolution better reflected the post-fire successional sequences understood in modern contexts. When comparing the existing Chickaree pollen record to the newly developed record from this study (see Appendix C.3), the average temporal offset between pollen samples and fire events was reduced from 87 years to 27 years which offers better insight towards post-fire vegetation signals that could otherwise be muted by the longer temporal offsets between pollen-based vegetation observations and a charcoal-based fire observations.

Millennial-scale fire and vegetation dynamics

As hypothesized, *Pinus* was the dominant species throughout the record, however; understory taxa were able to offer insight towards millennial changes at Chickaree Lake due to their role in driving the zone break. Changes in vegetation inferred from the Chickaree Lake pollen record were driven by the increase in *Picea*, Asteraceae, *Artemisia*, *Arceuthobium*, and Rosaceae following the zone break at 1,155 cal yr BP (Figure 5.1, Figure 5.2). Arboreal density surrounding Chickaree Lake decreased over the past 2,500 years which allowed for extra local pollen sources to increase. The increased abundance of herbaceous taxa like *Artemisia* and Rosaceae indicate that extra local pollen input is increasing at Chickaree Lake since *Artemisia* is associated with lower elevations and Rosaceae tends to be found at higher elevations (Fall, 1992). These taxa are also associated with drier environmental settings in Rocky Mountain National Park (Peet, 1981), which could be reflective of increases in hotter, drier summer conditions towards present throughout the region (Abatzoglou and Williams, 2016; Dennison et al., 2014; Westerling, 2016). While *Pinus* was dominant throughout the record, I interpreted the increase in *Picea* and decrease in *Pinus* towards present as an additional proxy of local forest thinning since *Picea* is found at higher elevations and is not locally abundant around Chickaree Lake (Figure 1.3).

Wildfire activity also decreased slightly towards present following the zone break at 1,155 cal yr BP. Despite this decrease in fire frequency, it appeared that fires following the zone break had a more substantial impact on vegetation composition as *Pinus* reached its lowest abundances (46%). Prior to the zone shift, *Pinus* had reached its maximum abundance (88%)

despite the increased number of fire events, which is consistent to what has been observed in other studies throughout the southern Rocky Mountain region (Calder et al., 2019; Minckley et al., 2012). While it is expected that the increased fire frequency prior to the zone shift would reduce pine pollen abundances, lodgepole pine forests are known to exist in settings that experience high severity stand replacing fires about every 200 years and their seed dispersal relies on fire activity (Peet, 1981; Veblen et al., 1991). The fires that occurred prior to the zone shift were classified as lower severity/extra local fires (Figure 5.1), which could reflect why *Pinus* was not as impacted by wildfire activity prior to 1,155 cal yr BP. This distinction is important in interpreting the millennial scale vegetation response to fire because, while these lower severity/extra local fire events do produce charcoal, they may not have a significant impact on the arboreal compositional structure of the forest.

Arceuthobium and lasting legacies of wildfire decrease

Notably, an increase in *Arceuthobium* acted as one of the millennial drivers of the zone break at 1,155 cal yr BP. *Arceuthobium,* or dwarf mistletoe, is a species of interest in Rocky Mountain pine forests as it is a parasite that can cause substantial damage to lodgepole forest health. The increased abundances of *Arceuthobium* pollen following the zone break captures increased ecological stress on lodgepole pines. *Arceuthobium* pollen can only be distributed over a short spatial range (Player, 1979) and the spread of the species is controlled by fire activity as it is more abundant during fire-free intervals (Hawksworth and Johnson, 1989). Lower-severity fires have been found to have little impact on *Arceuthobium* communities and infestations of the parasite are expected to grow with the absence of high-severity stand replacing fires (Kipfmueller and Baker, 1998) which could be indicative of the lasting impacts of decreases in wildfire activity.

Ecologically, dwarf mistletoe can decrease overall growth and productivity in lodgepole pine forests with the increase of fire-free periods (Hawksworth and Johnson, 1989; Kipfmueller and Baker, 1998; Wicker and Leaphart, 1976). While the overall percent increase of *Arceuthobium* pollen towards present is low with the total abundance within the record not reaching beyond 1.6%, it is still indicative of the presence of mistletoe around Chickaree Lake due to its short range of pollen dispersal. Increases in fire-free periods can perpetuate the spread of dwarf mistletoe and other fire-prone pests, like bark beetle, which increases the ecological stress on existing lodgepole pine stands. Without high severity stand replacing fires, the lodgepole pine forest surrounding Chickaree Lake could be more susceptible to disturbances like mistletoe and bark beetle and, in projected climate scenarios, Chickaree Lake could actually benefit from increased fire activity due to its role in controlling pests that cause mortality in lodgepole pines (Lotan et al., 1985).

Decadal post-fire vegetation response

When comparing the composition of pollen samples between fire associations, there were significant influences of fire on pollen composition. These results support the hypothesis that while fire frequency was reduced following the zone break, the fires that did occur had significant impacts on the ratios of arboreal pollen to non-arboreal pollen as well as conifer pollen to local nonarboreal pollen (Figure 5.3). Samples following fire events had significantly lower mean ratios of total arboreal pollen and conifer pollen and nearing significant decreases in *Pinus* pollen. *Artemisia* pollen was higher for fire samples than non-fire samples, which is indicative of increases in extra local/lower elevation pollen following fire. Generally, when fires occurred within the catchment of Chickaree lake, the arboreal tree cover (*Pinus*, AP, Conifer) was reduced from the landscape which allowed for extra local species (*Artemisia*, NAP, LNAP) to increase in the pollen record. Samples from 0-75 years since fire for Zone 1 plotted closer to each other in NMDS space (Figure 5.3) than samples in Zone 2, which captures similar responses in pollen composition as a factor of time since fire. When comparing the rate of change values to the cumulative years since fire (Figure 5.4), samples from 0-75 years and 75-150 years post fire had generally higher rate of change values than samples that were >150 years post fire, which captures the legacy of impact of wildfires on pollen data. While it is challenging to characterize the long-term influences of fire based on a continuous sampling approach, comparing pollen data from immediately post-fire samples to non-fire samples allowed for statistical inference of the influence of wildfire on pollen assemblages.

Climate forcing of coupled vegetation and fire dynamics

By using the Modern Analog Technique, I was able to reconstruct temperature and precipitation based on the Chickaree pollen record. To interpret these reconstructions, they must be compared to other sites to provide regional climate context (Figure 5.5). The pollen-based temperature reconstruction from Chickaree Lake does not appear to have the signature of the Medieval Climate Anomaly or the Little Ice Age captured in other proxy-based reconstructions from the region (Mann et al., 2009; Trouet et al., 2013), and the influence of climate setting on the Chickaree pollen record mainly manifests in the form of increased snow driven precipitation. This result rejects my initial hypothesis that there would be an increase in temperature during the Medieval Climate Anomaly and decreases in temperature during the Little Ice Age. The zone break observed in the Chickaree pollen record is consistent with other short term (~2,500 year) pollen studies in the region (Calder et al., 2017, 2019) and captures the shift towards increased winter/snow driven precipitation as inferred through various precipitation proxies from the central Colorado Rocky Mountain region. Lower $\delta^{18}O$ values, increases in lake level, and higher

PDSI values from about 1,155 cal yr BP to present (Anderson, 2011; Cook et al., 2007; Shuman et al., 2009) are consistent with both the zone break and the pollen-inferred winter precipitation reconstruction at Chickaree Lake.

Climate has been found to be one of the main drivers of changes in wildfire activity over the past few millennia in subalpine forests in the Western United States (Marlon et al., 2012; Schoennagel et al., 2004, 2007; Sibold and Veblen, 2006; Whitlock et al., 2003) and this also holds true for Chickaree Lake. Since wildfire frequency only slightly declined following the zone break, and there were only three less fire events following 1,155 cal yr BP, I interpret the zone break from the Chickaree Lake pollen record as reflecting the regionally observed changes of precipitation balance rather than changes in wildfire activity or temperature. Climate is the ultimate control on wildfire activity, so even if there were significant increases in wildfire towards presents, climate would still act as the ultimate driving force because it controls fuel abundance and ignition conditions (Abatzoglou and Williams, 2016; Carter et al., 2018; Mietkiewicz et al., 2018; Schoennagel et al., 2004). The regional increase in winter precipitation over the past 1,155 years is attributed to both El Niño Southern Oscillation (ENSO) dynamics which drives snowpack development in the Rocky Mountain region (Anderson, 2012) and regional-scale interactions between oceanic and atmospheric currents driven by orbital forcing and insolation (Anderson et al., 2016). Localized-impacts of these broader scale climate controls can vary based on topographic position and spatial orientation on the landscape, so this study helps to improve the understanding of the localized climatic impacts of ENSO and oceanic controls in the Rocky Mountains.

In the central Rocky Mountains in Colorado, the drier La Niña phase of the El Niño Southern Oscillation (ENSO) and the cool phase of the Pacific Decadal Oscillation (PDO) have been found to drive the dry spring conditions associated with fire-heavy years (Schoennagel et al., 2005; Sibold and Veblen, 2006; Veblen et al., 2000). The interplay between winter precipitation and dry spring conditions can have significant impacts on the severity and frequency of crown fires in subalpine forests (Mietkiewicz et al., 2018; Schoennagel et al., 2004; Veblen et al., 2000) as the increased fuel load brought upon by winter precipitation is more susceptible to ignition during dry spring conditions. While this may seem counterintuitive, increased winter precipitation followed by warm and dry summer conditions can result in significant wildfire activity, as experienced during the fire season of 2017 (Mietkiewicz et al., 2018). Increased winter precipitation drives snowpack development in the subalpine forests of the Rocky Mountains, and snowpack development is crucial in determining water availability during dry summer months (Gergel et al., 2017). Early spring melting of snowpack has been found to be a driving factor of wildfire frequency and intensity during increasingly arid and warming summer conditions (Mietkiewicz et al., 2018; Westerling, 2016; Westerling et al., 2006). Future climate scenarios predict increasingly warm and dry summer conditions in the western United States (Abatzoglou and Williams, 2016; Dennison et al., 2014; Schoennagel et al., 2017; Westerling, 2016) which, when following periods of increased precipitation, could be conducive to driving the intense fire seasons observed in recent decades.

Reconstruction of ecological disturbance through paleoecological proxies

Paleoecological proxies can provide valuable insights towards past wildfire activity, climate setting, and vegetation however; some of the limitations of this research is that some disturbances common to lodgepole pine forests are unable to be reconstructed through lacustrine records. Bark beetle outbreaks and windthrow can have substantial impacts on lodgepole pine forest density by killing off pine trees and fire activity by increasing available fuel loads (Bigler et al., 2005; Veblen, 2000). These disturbances, though important to fire dynamics in the Rocky Mountains, are unable to be quantified in paleoecological reconstructions (e.g. Morris and Brunelle, 2012). While paleoecological reconstructions can extend our understanding of modern ecological dynamics, they are still limited in the disturbances that they are able to reconstruct. Also, pollen taxa represented in lake sediments can be sourced from long distances which could influence lake catchment level interpretations of vegetation change (Bunting et al., 2004; Davis, 2000; Matthias and Giesecke, 2014; Sugita, 1994), this however can often be mitigated by using smaller lake basins for paleoecological studies as done for this study. For future studies, I would like to conduct vegetation surveys at the sites chosen for localized paleoecological reconstructions to better calibrate pollen taxa selection and ensure that the species used for analysis best capture site-specific environmental change.

By increasing the temporal sampling resolution of pollen from ~100 years between samples to ~50 years between samples, I was able to better understand the influence of changes in fire and climate setting on vegetation surrounding Chickaree Lake. While the metrics used had varying degrees of success, increased sampling resolution of the pollen data allowed for more temporally robust reconstructions of post-fire vegetation dynamics. High resolution temporal reconstructions of vegetation and wildfire history are becoming increasingly relevant as wildfire occurrence and severity increases in the western United States (Calder and Shuman, 2019), and these types of reconstructions can offer baselines that can be used to contextualize modern fire dynamics and guide future management efforts. While it is unrealistic to expect that the past provides perfect analogues for future climate scenarios, these long-term reconstructions can allow us to better understand how these systems have responded to past changes in climate and fire regimes which can be used to improve future management efforts. There are many low temporal resolutions that exist within the Western United States and many of these cores are still archived, and it is worth going back to improve these records as they offer further insight towards how our environment has changed in the past. Pollen analysis is a time intensive process, however; it still stands as the best proxy for vegetation reconstruction beyond centennial timeframes and can offer insights about vegetation change that have been missed in prior reconstructions due to low temporal sampling resolution.

Chapter 7 - Conclusion

This study applied a variety of methods to quantify the coupled influence of wildfire and climate on a lodgepole pine forest system in Rocky Mountain National Park. Few paleoecological studies have focused exclusively on reconstructing fire and vegetation relationships (Crausbay et al., 2017; Minckley et al., 2012; Minckley and Shriver, 2011), and even fewer have focused on creating high temporal resolution reconstructions of vegetation over shorter timeframes (Calder et al., 2019; Calder and Shuman, 2017), but these type of paleoenvironmental reconstructions are necessary to assess the resiliency of regions increasingly threatened by changes to coupled interactions between wildfire and climate (Calder and Shuman, 2019). By looking at a shorted temporal interval and increasing the temporal sampling resolution of existing paleoecological datasets, this study was able to characterize the relationships between fire, vegetation, and climate setting over the past two millennia within a subalpine lodgepole pine forest.

In recent decades, the western US has been experiencing increases in wildfire activity and severity due to the coupled effects of increased winter precipitation and drier summers and autumns (Mietkiewicz et al., 2018; Schoennagel et al., 2004). Increased winter precipitation increases the amount of fuels available and, when ignited during the drier summers and falls, these climate conditions could result in an increase in increased fire severity and decreased forest recovery in the western United States. Lodgepole pine seedling recovery has been found to be declining in post-fire drought conditions (Andrus et al., 2018; Hansen et al., 2018; Hansen and Turner, 2019; Harvey et al., 2016; Stevens-Rumann et al., 2018), which indicates that the coupled interactions of increased fire activity and post-fire drought conditions could threaten the resiliency of lodgepole pine forests in predicted climate scenarios. The paleoenvironmental reconstruction at Chickaree Lake reflects this trend. The zone break captured in the pollen record was found to reflect the regional increase in winter precipitation after 1,155 cal yr BP and fire frequency decreased towards present. Despite this decline in fire activity, the pollen record exhibited overall declines in *Pinus* pollen and decreased amounts of arboreal pollen, which is indicative of increases in post-fire regeneration challenges most likely driven by increasing aridity and warmth in post-fire landscapes during the summer season. The coupled impacts of increased winter precipitation and fire activity could have resulted in decreased forest recovery as following the shift in climate condition, *Pinus* was unable to recover, and forest density decreased as interpreted through lower ratios of arboreal and conifer pollen. While lodgepole pine forests are generally able to thrive in fire-driven regimes, changes to the balance between fire and climate could have subsequent impacts on vegetation and the ability for these systems to continue to recover in the modeled drier, warmer climate scenarios of the future.

References

Abatzoglou JT and Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences* 113(42): 11770–11775. doi:10.1073/pnas.1607171113.

Agriculture UD of ANSSS (2006) *Soil Survey of Rocky Mountain National Park, Colorado*. .

Alroy J (2015) A simple way to improve multivariate analyses of paleoecological data sets. *Paleobiology*. Cambridge University Press (CUP) 41(03): 377–386. doi:10.1017/pab.2014.21.

Anderson L (2011) Holocene record of precipitation seasonality from lake calcite δ18O in the central Rocky Mountains, United States. *Geology* 39(3): 211–214: doi:10.1130/G31575.1.

Anderson L (2012) Rocky Mountain hydroclimate: Holocene variability and the role of insolation, ENSO, and the North American Monsoon. *Global and Planetary Change*. Elsevier 92–93: 198–208. doi:10.1016/J.GLOPLACHA.2012.05.012.

Anderson L, Berkelhammer M, Barron JA, Steinman BA, Finney BP and Abbott MB (2016) Lake oxygen isotopes as recorders of North American Rocky Mountain hydroclimate: Holocene patterns and variability at multi-decadal to millennial time scales. *Global and Planetary Change*. Elsevier 137: 131–148. doi:10.1016/J.GLOPLACHA.2015.12.021.

Anderson L, Brunelle A and Thompson RS (2015) A multi-proxy record of hydroclimate, vegetation, fire, and post-settlement impacts for a subalpine plateau, central Rocky Mountains, USA. *Holocene* 25(6): 932–943: doi:10.1177/0959683615574583.

Anderson MJ (2017) Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley StatsRef: Statistics Reference Online*. Chichester, UK: John Wiley & Sons, Ltd, 1–15. doi:10.1002/9781118445112.stat07841.

Andrus RA, Harvey BJ, Rodman KC, Hart SJ and Veblen TT (2018) Moisture availability limits subalpine tree establishment. *Ecology*. Wiley Online Library 99(3): 567–575: doi:10.1002/ecy.2134.

Baker WL (2002) Indians and fire in the Rocky Mountains: the wilderness hypothesis renewed. *Fire, native peoples, and the natural landscape*. Island Press Washington, DC 41–76.

Beals EW (1984) Bray-curtis ordination: An effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14(C): 1–55: doi:10.1016/S0065-2504(08)60168-3.

Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*. Wiley Online Library 132(1): 155–170.

Bennett KD and Willis KJ (2001) Pollen BT - Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators. In: Smol JP, Birks HJB, Last WM, Bradley RS and Alverson K (eds) Dordrecht: Springer Netherlands, 5–32. doi:10.1007/0-306-47668-1_2.

Bigler C, Kulakowski D and Veblen TT (2005) Multiple Disturbance Interactions and Drought Influence Fire Severity in Rocky Mountain Subalpine Forests. *Ecology* 86(11): 3018–3029.

Birks HH and Birks HJB (2006) Multi-proxy studies in palaeolimnology. *Vegetation History and Archaeobotany*. Springer-Verlag 15(4): 235–251. doi:10.1007/s00334-006-0066-6.

Birks HJB (2012) Ecological palaeoecology and conservation biology: Controversies, challenges, and compromises. *International Journal of Biodiversity Science, Ecosystem Services and Management* 8(4): 292–304: doi:10.1080/21513732.2012.701667.

Birks HJB and Berglund BE (2018) *One hundred years of Quaternary pollen analysis 1916–2016. Vegetation History and Archaeobotany*. Springer Berlin Heidelberg. doi:10.1007/s00334-017-0630-2.

Birks HJB, Birks HH and Ammann B (2016) The fourth dimension of vegetation. *Science* 354(6311): 412–413. doi:10.1126/science.aai8737.

Birks HJB, Lotter A e F, Juggins S and Smol JP (2012) *Tracking Environmental Change Using Lake Sediments Developments in Paleoenvironmental Research*. .

Blaauw M (2010) Methods and code for 'classical'age-modelling of radiocarbon sequences. *Quaternary Geochronology*. Elsevier 5(5): 512–518.

Blaauw M and Christen JA (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian analysis*. International Society for Bayesian Analysis 6(3): 457–474.

Brunelle A and Whitlock C (2003) Postglacial fire, vegetation, and climate history in the Clearwater Range, Northern Idaho, USA. *Quaternary Research*, 307–318. doi://doi.org/10.1016/j.yqres.2003.07.009.

Brunelle A, Whitlock C, Bartlein P and Kipfmueller K (2005) Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. *Quaternary Science Reviews* 24(20–21): 2281–2300: doi:10.1016/j.quascirev.2004.11.010.

Buchholtz CW (1984) *Rocky Mountain National park: a history*. University Press of Colorado.

Bunting MJ, Farrell M, Broström A, Hjelle KL, Mazier F, Middleton R, et al. (2013) Palynological perspectives on vegetation survey: A critical step for model-based reconstruction of Quaternary land cover. *Quaternary Science Reviews*. Elsevier Ltd 82: 41–55. doi:10.1016/j.quascirev.2013.10.006.

Bunting MJ, Gaillard M, Sugita S, Middleton R and Brostro A (2004) Vegetation structure and pollen source area. (September 2017): doi:10.1191/0959683604hl744rp.

Caffrey MA and Doerner JP (2012) A 7000-Year Record of Environmental Change, Bear Lake, Rocky Mountain National Park, USA. *Physical Geography* 33(5): 438–456. doi:10.2747/0272-3646.33.5.438.

Calder WJ, Parker D, Stopka CJ, Jiménez-Moreno G and Shuman BN (2015) Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. *Proceedings of the National Academy of Sciences* 112(43): 13261–13266. doi:10.1073/pnas.1500796112.

Calder WJ and Shuman B (2017) Extensive wildfires, climate change, and an abrupt state change in subalpine ribbon forests, Colorado. *Ecology* 98(10): 2585–2600: doi:10.1002/ecy.1959.

Calder WJ and Shuman B (2019) Detecting past changes in vegetation resilience in the context of a changing climate. *Biology Letters* 15(3): 20180768. doi:10.1098/rsbl.2018.0768.

Calder WJ, Shuman B, Van De Walle JP, Gavin DG, Brubaker LB, Greenwald DN, et al. (2017) Extensive wildfires, climate change, and an abrupt state change in subalpine ribbon forests, Colorado. *Ecology*. University of Washington 98(2): 2585–2600. doi:10.4996/fireecology.0702066.

Calder WJ, Stefanova I and Shuman B (2019) Climate-fire-vegetation interactions and the rise of novel landscape patterns in subalpine ecosystems, Colorado. *Journal of Ecology*. John Wiley & Sons, Ltd (10.1111). doi:10.1111/1365-2745.13138.

Carter VA, Brunelle A, Minckley TA, Dennison PE and Power MJ (2013) Regionalization of fire regimes in the Central Rocky Mountains, USA. *Quaternary Research (United States)*. University of Washington 80(3): 406–416. doi:10.1016/j.yqres.2013.07.009.

Carter VA, Brunelle A, Minckley TA, Shaw JD, DeRose RJ and Brewer SC (2017) Climate variability and fire effects on quaking aspen in the central Rocky Mountains, USA. *Journal of Biogeography*. John Wiley & Sons, Ltd (10.1111) 44(6): 1280–1293. doi:10.1111/jbi.12932.

Carter VA, Power MJ, Lundeen ZJ, Morris JL, Petersen KL, Brunelle A, et al. (2018) A 1,500-year synthesis of wildfire activity stratified by elevation from the U.S. Rocky Mountains. *Quaternary International* 488: 107–119: doi:10.1016/j.quaint.2017.06.051.

Committee RG and Council NR (1997) *Rediscovering geography: New relevance for science and society*. National Academies Press.

Cook ER, Seager R, Cane MA and Stahle DW (2007) North American drought: Reconstructions, causes, and consequences. *Earth-Science Reviews*. Elsevier 81(1–2): 93–134. doi:10.1016/J.EARSCIREV.2006.12.002.

Coop JD, Massatti RT and Schoettle AW (2010) Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. *Journal of Vegetation Science* 21(3): 472–487: doi:10.1111/j.1654-1103.2009.01154.x.

Cowell CM and Parker AJ (2004) Biogeography in the Annals. *Annals of the Association of American Geographers*. Taylor & Francis 94(2): 256–268.

Crausbay SD, Higuera PE, Sprugel DG and Brubaker LB (2017) Fire catalyzed rapid ecological change in lowland coniferous forests of the Pacific Northwest over the past 14,000 years. *Ecology*. Wiley Online Library 98(9): 2356–2369.

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, et al. (2001) Climate change and forest disturbances. *Bioscience* 51(9): 723–734: doi:CCAFD]2.0.CO;2.

Davis MB (2000) Palynology after Y2K—Understanding the Source Area of Pollen in Sediments. *Annual Review of Earth and Planetary Sciences*. Annual Reviews 4139 El Camino Way, P.O. Box 10139, Palo Alto, CA 94303-0139, USA 28(1): 1–18. doi:10.1146/annurev.earth.28.1.1.

Dawson MN, Algar AC, Antonelli A, Dávalos LM, Davis E, Early R, et al. (2013) An horizon scan of biogeography. *Frontiers of Biogeography*. Europe PMC Funders 5(2).

Dennison PE, Brewer SC, Arnold JD and Moritz MA (2014) Large wildfire trends in the western United States, 1984-2011. *Geophysical Research Letters*. John Wiley & Sons, Ltd 41(8): 2928–2933. doi:10.1002/2014GL059576.

Dunnette P V., Higuera PE, McLauchlan KK, Derr KM, Briles CE and Keefe MH (2014) Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed. *New Phytologist* 203(3): 900–912: doi:10.1111/nph.12828.

Edwards KJ (1982) Palynology and biogeography. *Area*. JSTOR 241–248.

Edwards KJ (1983) Quaternary palynology: consideration of a discipline. *Progress in Physical Geography: Earth and Environment*. SAGE Publications Ltd 7(1): 113–125. doi:10.1177/030913338300700106.

Edwards KJ, Fyfe RM and Jackson ST (2017) The first 100 years of pollen analysis. *Nature Plants*. Macmillan Publishers Limited 3: 17001.

Faegri K and Iversen J (1975) *Textbook of pollen analysis*. Hafner Press.

Falk DA, Heyerdahl EK, Brown PM, Farris C, Fulé PZ, McKenzie D, et al. (2011) Multi-scale controls of historical forest-fire regimes: New insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9(8): 446–454: doi:10.1890/100052.

Fall PL (1992) Pollen accumulation in a montane region of Colorado, USA: a comparison of moss polsters, atmospheric traps, and natural basins. *Review of Palaeobotany and Palynology* 72(3–4): 169–197: doi:10.1016/0034-6667(92)90026-D.

Fall PL (1997) Timberline fluctuations and late Quaternary paleoclimates in the Southern Rocky Mountains, Colorado. *Bulletin of the Geological Society of America* 109(10): 1306–1320: doi:10.1130/0016-7606(1997)109<1306:TFALQP>2.3.CO;2.

Fosberg FR (1976) Geography, ecology, and biogeography. *Annals of the Association of American Geographers*. Taylor & Francis 66(1): 117–123.

Gavin DG, Hallett DJ, Hu FS, Lertzman KP, Prichard SJ, Brown KJ, et al. (2007) Forest fire and climate change in western North America: insights from sediment charcoal records. *Frontiers in Ecology and the Environment*. John Wiley & Sons, Ltd 5(9): 499–506. doi:10.1890/060161.

Gavin DG, Oswald WW, Wahl ER and Williams JW (2003) A statistical approach to evaluating distance metrics and analog assignments for pollen records. *Quaternary Research* 60(3): 356–367: doi:10.1016/S0033-5894(03)00088-7.

Gergel DR, Nijssen B, Abatzoglou JT, Lettenmaier DP and Stumbaugh MR (2017) Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change*. Springer 141(2): 287–299.

Gill NS, Jarvis D, Veblen TT, Pickett STA and Kulakowski D (2017) Is initial post-disturbance regeneration indicative of longer-term trajectories? *Ecosphere* 8(8): doi:10.1002/ecs2.1924.

Goring S, Dawson A, Simpson G, Ram K, Graham R, Grimm E, et al. (2015) Neotoma: A programmatic interface to the Neotoma Paleoecological Database. *Open Quaternary*. Ubiquity Press 1(1).

Goring S, Williams JW, Blois JL, Jackson ST, Paciorek CJ, Booth RK, et al. (2012) Deposition times in the northeastern United States during the Holocene: establishing valid priors for Bayesian age models. *Quaternary Science Reviews*. Elsevier 48: 54–60.

Green DG (1983) The ecological interpretation of fine resolution pollen records. *New Phytologist* 94(3): 459–477.

Green DG and Dolman GS (1988) Fine resolution pollen analysis. *Journal of Biogeography*. JSTOR 685–701.

Halbritter H, Ulrich S, Grímsson F, Weber M, Zetter R, Hesse M, et al. (2018) *Illustrated Pollen Terminology*. doi:10.1007/978-3-319-71365-6.

Hansen WD, Braziunas KH, Rammer W, Seidl R and Turner MG (2018) It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. *Ecology*. John Wiley & Sons, Ltd 99(4): 966–977. doi:10.1002/ecy.2181.

Hansen WD and Turner MG (2019) Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. *Ecological Monographs* 89(1). doi:10.1002/ecm.1340.

Harvey BJ, Donato DC and Turner MG (2016) High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography* 25(6): 655–669: doi:10.1111/geb.12443.

Hawksworth FG and Johnson DW (1989) Biology and management of dwarf mistletoe in lodgepole pine in the Rocky Mountains. *US Dept. of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station* (RM-169).

Hawksworth FG and Wiens D (1994) Viscaceae: Mistletoe Family. *Journal of the Arizona-Nevada Academy of Science*. JSTOR 241–246.

Heinselman ML and Jr HEW (1973) The ecological role of fire in natural conifer forests of western and northern North America--introduction. *Quaternary Research* 3: 319–328.

Hess K (1993) *Rocky times in Rocky Mountain National Park: an unnatural history*. University Press of Colorado.

Higuera PE, Briles CE and Whitlock C (2014) Fire-regime complacency and sensitivity to centennial through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA. *Journal of Ecology* 102(6): 1429–1441: doi:10.1111/1365-2745.12296.

Higuera PE, Brubaker LB, Anderson PM, Hu FS and Brown TA (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*. John Wiley & Sons, Ltd 79(2): 201–219. doi:10.1890/07-2019.1.

Hill AR (1975) Biogeography as a sub-field of geography. *Area*. JSTOR 156–161.

Holling CS (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*. Annual Reviews 4139 El Camino Way, PO Box 10139, Palo Alto, CA 94303-0139, USA 4(1): 1–23.

Husted WM (1965) Early occupation of the Colorado front range. *American Antiquity*. Cambridge University Press 30(4): 494–498.

Jiménez-Moreno G and Anderson RS (2013) Pollen and macrofossil evidence of Late Pleistocene and Holocene treeline fluctuations from an alpine lake in Colorado, USA. *Holocene* 23(1): 68–77: doi:10.1177/0959683612450199.

Jiménez-Moreno G, Anderson RS, Atudorei V and Toney JL (2011) A high-resolution record of climate, vegetation, and fire in the mixed Conifer forest of Northern Colorado, USA. *Bulletin of the Geological Society of America* 123(1–2): 240–254: doi:10.1130/B30240.1.

Juggins S (2015) rioja: Analysis of Quaternary science data. Newcastle University.

Kapp RO (1969) *How to know pollen and spores*. W.C. Brown Co.

Kipfmueller KF and Baker WL (1998) Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. *Forest ecology and management*. Elsevier 108(1–2): 77–84.

Kornfeld M and Frison GC (2000) Paleoindian occupation of the high country: the case of Middle Park, Colorado. *Plains Anthropologist*. Taylor & Francis 45(172): 129–153.

Kulakowski D and Veblen TT (2002) Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. *Journal of Ecology* 90(5): 806–819: doi:10.1046/j.1365-2745.2002.00722.x.

Lawrence DR (1971) The nature and structure of paleoecology. *Journal of Paleontology*. JSTOR 593–607.

Leys B, Higuera PE, McLauchlan KK and Dunnette P V. (2016) Wildfires and geochemical change in a subalpine forest over the past six millennia. *Environmental Research Letters* 11(12): 125003. doi:10.1088/1748-9326/11/12/125003.

Lotan JE, Brown JK and Neuenschwander LF (1985) Role of fire in lodgepole pine forests. . pp. 133-152 in D. Baumgartner et al. (eds) Lodgepole pine the species and its management Symposium Proceedings. Washington State University, Pullman.

Lynch EA (1996) The ability of pollen from small lakes and ponds to sense fine-scale vegetation patterns in the central Rocky Mountains, United States. *Review of Palaeobotany and Palynology* 94(3–4): 197–210: doi:10.1016/S0034-6667(96)00040-1.

MacDonald GM (1988) Methods in Quaternary Ecology# 2. Palynology. *Geoscience Canada* 15(1).

MacDonald GM, Larsen CPS, Szeicz JM and Moser KA (1991) The reconstruction of boreal forest fire history from lake sediments: A comparison of charcoal, pollen, sedimentological, and geochemical indices. *Quaternary Science Reviews* 10(1): 53–71: doi:10.1016/0277-3791(91)90030-X.

Mann ME, Zhang Z, Rutherford S, Bradley RS, Hughes MK, Shindell D, et al. (2009) Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. *Science* 326(5957): 1256 LP-1260: doi:10.1126/science.1177303.

Marlon J, Bartlein PJ and Whitlock C (2006) Fire-fuel-climate linkages in the northwestern USA during the Holocene. *Holocene* 16(8): 1059–1071: doi:10.1177/0959683606069396.

Marlon JR, Bartlein PJ, Gavin DG, Long CJ, Anderson RS, Briles CE, et al. (2012) Long-term perspective on wildfires in the western USA. *Proceedings of the National Academy of Sciences* 109(9): E535–E543. doi:10.1073/pnas.1112839109.

Martin AC and Harvey WJ (2017) The Global Pollen Project: a new tool for pollen identification and the dissemination of physical reference collections. *Methods in Ecology and Evolution*. Wiley Online Library 8(7): 892–897.

Matthias I and Giesecke T (2014) Insights into pollen source area, transport and deposition from modern pollen accumulation rates in lake sediments. *Quaternary Science Reviews*. Pergamon 87: 12–23. doi:10.1016/J.QUASCIREV.2013.12.015.

McAndrews JH, Berti AA and Norris G (1973) *Key to the quaternary pollen and spores of the Great Lakes region*. Royal Ontario Museum.

McLauchlan KK, Higuera PE, Gavin DG, Perakis SS, Mack MC, Alexander H, et al. (2014) Reconstructing disturbances and their biogeochemical consequences over multiple timescales. *Bioscience* 64(2): 105–116: doi:10.1093/biosci/bit017.

Meadows ME (2014) Recent methodological advances in Quaternary palaeoecological proxies. *Progress in Physical Geography* 38(6): 807–817: doi:10.1177/0309133314540690.

Mietkiewicz N, Balch J, Schoennagel T, Williams A, Abatzoglou J, Cattau M, et al. (2018) Switching on the Big Burn of 2017. *Fire*. Multidisciplinary Digital Publishing Institute 1(1): 17: doi:10.3390/fire1010017.

Minckley TA, Bartlein PJ, Whitlock C, Shuman BN, Williams JW and Davis OK (2008) Associations among modern pollen, vegetation, and climate in western North America. *Quaternary Science Reviews*. Pergamon 27(21–22): 1962–1991. doi:10.1016/J.QUASCIREV.2008.07.006.

Minckley TA and Shriver RK (2011) Vegetation Responses to Changing Fire Regimes in a Rocky Mountain Forest. *Fire Ecology*. Springer International Publishing 7(2): 66–80. doi:10.4996/fireecology.0702066.

Minckley TA, Shriver RK and Shuman B (2012) Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17 000 years. *Ecological Monographs* 82(1): 49–68: doi:10.1890/11-0283.1.

Moritz MA, Batllori E, Bradstock RA, Gill AM, Handmer J, Hessburg PF, et al. (2014) Learning to coexist with wildfire. *Nature*. Nature Publishing Group 515(7525): 58.

Morris JL and Brunelle A (2012) Pollen accumulation in lake sediments during historic spruce beetle disturbances in subalpine forests of southern Utah, USA. *Holocene* 22(9): 961–974: doi:10.1177/0959683612437870.

Morris JL, McLauchlan KK and Higuera PE (2015) Sensitivity and complacency of sedimentary biogeochemical records to climate-mediated forest disturbances. *Earth-Science Reviews* 148: 121–133: doi:10.1016/j.earscirev.2015.06.001.

Murphy AB (2014) Geography's Crosscutting Themes: Golden Anniversary Reflections on "The Four Traditions of Geography." *Journal of Geography* 113(5): 181–188: doi:10.1080/00221341.2014.918639.

National Interagency Fire Center (2017). Available at: https://www.nifc.gov/fireInfo/nfn.html. Accessed 10/20/2018.

Overpeck JT, Webb T and Prentice IC (1985) Quantitative Interpretation of Fossil Pollen Spectra: Dissimilarity Coefficients and the Method of Modern Analogs. *Quaternary Research*. Cambridge University Press 23(1): 87–108. doi: 10.1016/0033-5894(85)90074-2.

Pattison WD (1964) The Four Traditions of Geography. *Journal of Geography*. Informa UK Limited 63(5): 211–216. doi:10.1080/00221346408985265.

Peet K and Hill C (2012) Forest Vegetation of the Colorado Front Range : Composition and Dynamics Author (s): Robert K . Peet Reviewed work (s): Source : Vegetatio , Vol . 45 , No . 1 , Forest Vegetation of the Colorado Front Range : Composition Published by : Springer JSTOR . 45(1): 3–75.

Peet RK (1981) Forest Vegetation of the Colorado Front Range: Composition and Dynamics. *Vegetation* 45(1): 3–75.

Peet RK (2000) Forests and meadows of the Rocky Mountains. *North American terrestrial vegetation*. Cambridge University Press Cambridge, UK 2: 75–122.

Player G (1979) Pollination and wind dispersal of pollen in Arceuthobium. *Ecological Monographs*. Wiley Online Library 49(1): 73–87.

Reitalu T, Kuneš P and Giesecke T (2014) Closing the gap between plant ecology and Quaternary palaeoecology. *Journal of Vegetation Science* 25(5): 1188–1194: doi:10.1111/jvs.12187.

Rull V (2010) Ecology and palaeoecology: two approaches, one objective. *The Open Ecology Journal* 3(1).

Schoennagel T, Balch JK, Brenkert-Smith H, Dennison PE, Harvey BJ, Krawchuk MA, et al. (2017) Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences* 114(18): 4582–4590. doi:10.1073/pnas.1617464114.

Schoennagel T, T. TV and H. WR (2004) The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. *Bioscience* 54(7): 661–676: doi:TIOFFA]2.0.CO;2 [doi].

Schoennagel T, Veblen TT, Kulakowski D and Holz A (2007) Multidecadal climate variability and climate interactions affect subalpine fire occurrence, Western Colorado (USA). *Ecology* 88(11): 2891–2902: doi:10.1890/06-1860.1.

Schoennagel T, Veblen TT, Romme WH, Sibold JS and Cook ER (2005) ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain subalpine forests. *Ecological Applications*. Wiley Online Library 15(6): 2000–2014.

Seppä H and Bennett KD (2003) Quaternary pollen analysis: Recent progress in palaeoecology and palaeoclimatology. *Progress in Physical Geography* 27(4): 548–580. doi:10.1191/0309133303pp394oa.

Shuman B, Henderson AK, Colman SM, Stone JR, Fritz SC, Stevens LR, et al. (2009) Holocene lake-level trends in the Rocky Mountains, U.S.A. *Quaternary Science Reviews*. Pergamon 28(19–20): 1861–1879. doi:10.1016/J.QUASCIREV.2009.03.003.

Sibold JS and Veblen TT (2006) Relationships of subalpine forest fires in the Colorado Front Range with interannual and multidecadal-scale climatic variation. *Journal of Biogeography* 33(5): 833–842: doi:10.1111/j.1365-2699.2006.01456.x.

Sibold JS, Veblen TT, Chipko K, Lawson L, Mathis E and Scott J (2007) Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. *Ecological Applications* 17(6): 1638–1655.

Sibold JS, Veblen TT and González ME (2006) Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography* 33(4): 631–647: doi:10.1111/j.1365-2699.2005.01404.x.

Smith AMS, Kolden CA, Paveglio TB, Cochrane MA, Bowman DMJS, Moritz MA, et al. (2016) The science of firescapes: achieving fire-resilient communities. *Bioscience*. Oxford University Press 66(2): 130–146.

Stallins JA (2007) The biogeography of geographers: A content visualization of journal publications. *Physical Geography*. Taylor & Francis 28(3): 261–275.

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, et al. (2018) Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters* 21(2): 243–252: doi:10.1111/ele.12889.

Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of ecology*. JSTOR 82(4): 881–897. doi:10.2307/2261452.

Trouet V, Diaz HF, Wahl ER, Viau AE, Graham R, Graham N, et al. (2013) A 1500-year reconstruction of annual mean temperature for temperate North America on decadal-to-multidecadal time scales. *Environmental Research Letters*. IOP Publishing 8(2): 024008. doi:10.1088/1748-9326/8/2/024008.

Tuason JA (1987) Reconciling the unity and diversity of geography. *Journal of Geography*. Taylor & Francis 86(5): 190–193.

United States National Park Service (2019) *A Brief History of Rocky Mountain National Park*. . Available at: https://www.nps.gov/romo/learn/historyculture/brief.htm.

Vale T (2013) *Fire, native peoples, and the natural landscape*. Island Press.

Veblen TT (2000) Disturbance patterns in southern Rocky Mountain forests. In: *Forest Fragmentation in the Southern Rocky Mountains*. Boulder: Colorado University Press, pp. 31–54.

Veblen TT, Hadley KS and Reid MS (1991) Disturbance and Stand Development of a Colorado Subalpine Forest. *Journal of Biogeography* 18(6): 707–716. doi:10.2307/2845552.

Veblen TT, Kitzberger T and Donnegan J (2000) Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications*. Wiley Online Library 10(4): 1178–1195.

Viau AE, Ladd M and Gajewski K (2012) The climate of North America during the past 2000 years reconstructed from pollen data. *Global and Planetary Change*. Elsevier 84: 75–83.

Weber M and Ulrich S (2017) PalDat 3.0–second revision of the database, including a free online publication tool. *Grana*. Taylor & Francis 56(4): 257–262.

Westerling AL (2016) Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B: Biological Sciences*. The Royal Society 371(1696): 20150178.

Westerling AL, Hidalgo HG, Cayan DR and Swetnam TW (2006) Warming and earlier spring increase Western U.S. forest wildfire activity. *Science* 313(5789): 940–943: doi:10.1126/science.1128834.

Westerling AL, Turner MG, Smithwick EAH, Romme WH and Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences* 108(32): 13165–13170. doi:10.1073/pnas.1110199108.

Whitlock C (2004) Forests, fires and climate. *Nature* 432(7013): 28–29: doi:10.1038/432028a.

Whitlock C and Bartlein PJ (2003) Holocene fire activity as a record of past environmental change. *Developments in Quaternary Sciences* 1: 479–490.

Whitlock C and Larsen C (2001) Charcoal as a Fire Proxy BT - Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators. In: Smol JP, Birks HJB, Last WM, Bradley RS and Alverson K (eds) Dordrecht: Springer Netherlands, 75–97. doi:10.1007/0-306-47668-1_5.

Whitlock C, Shafer SL and Marlon J (2003) The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. *Forest Ecology and Management* 178(1): 5–21: doi:10.1016/S0378-1127(03)00051-3.

Wicker EF and Leaphart CD (1976) Fire and dwarf mistletoe (Arceuthobium spp.) relationships in the northern Rocky Mountains. *Proceedings, 1974 Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida*, 279–298.

Wright HE, Mann DH and Glaser PH (1984) Piston corers for peat and lake sediments. *Ecology* 65(2): 657–659.

Appendix A-Raw Pollen Counts

The samples highlighted in blue indicate the newly generated samples used in this study

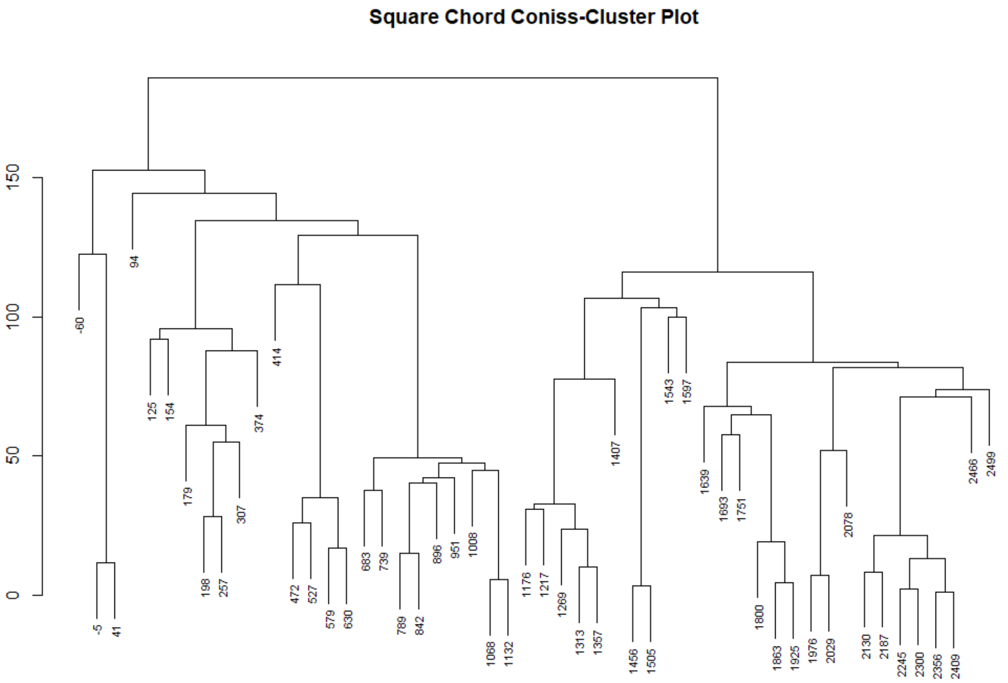
sample ID	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
sample #	1	2	44	60	70	80	90	105	120	135	150	127	142	157	172	187	202	217	232	247	262	277	292	307	322
Depth (cm)	0.8	16.5	24	32.7	38.1	43.5	48.3	52.2	63.1	70.8	75	85.5	93	100	106.5	113	120	127.5	134.5	142	149.5	157	164.5	172	179.5
age_yrBP	-60	-5	41	94	125	154	179	198	257	307	374	414	472	527	579	630	683	739	789	842	896	951	1008	1068	1132
Pinus	216	275	233	135	266	255	219	176	219	285	229	175	212	220	173	206	260	240	214	214	267	243	295	290	301
Picea	19.5	3.5	2	8	27	26	19	22	7	41	7	41	10	1	19	12	13	8	14	11	11	16	28	11	12
Abies	0.5	2	3	0	4	2	3	5	2	1	2	1	3	2	1	5	3	0	5	2	2	1	4	0	2
Pseudotsuga/Larix	0	0	0	1	1	0	1	1	2	5	0	0	1	1	0	2	1	0	1	2	1	0	0	0	1
Populus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Juniperus* -type**	0	2	0	12	1	0	2	3	2	12	1	0	3	0	0	3	0	0	0	1	0	1	2	0	1
Alnus	0	0	3	0	0	0	2	1	0	0	2	0	0	0	1	0	1	1	1	0	2	2	0	1	0
Corylus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Betula	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Salix	0	0	0	6	0	0	3	1	1	6	0	2	1	1	0	1	0	0	2	5	0	3	0	2	0
Quercus	1	12	7	13	3	1	17	7	9	4	2	2	3	9	11	9	2	4	3	6	3	14	8	5	5
Acer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosaceae	1	3	0	2	3	0	0	5	3	10	0	3	7	1	3	4	2	0	1	6	2	3	6	1	2
Ceanothus	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Shepherdia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arceuthobium	1	0	0	3	1	0	0	0	4	2	0	2	2	3	2	5	1	5	3	4	5	1	1	4	2
Ephedra	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sarcobatus	0	0	0	1	0	0	0	1	3	0	1	3	0	1	3	0	0	2	3	0	1	0	3	0	0
Poaceae	2	2	1	4	1	0	0	0	0	1	0	3	1	0	2	0	3	0	0	1	0	1	2	1	0
Cyperaceae	0	0	0	2	0	0	0	2	0	0	2	1	0	0	0	0	0	0	3	0	0	1	0	0	0
Artemisia	9	30	28	71	52	10	33	52	46	43	24	65	47	65	60	75	47	29	49	35	25	49	29	32	48
Ambrosia	0	4	5	1	4	0	0	3	1	1	3	2	4	2	5	4	1	3	1	1	3	7	2	1	5
Asteraceae	4	1	0	8	5	1	2	6	3	5	1	1	0	4	4	3	2	0	5	7	4	4	0	2	1
Chenopodiaceae	2	10	2	27	10	1	4	8	11	7	8	10	9	10	20	12	6	9	19	10	5	13	6	11	14
Thalictrum	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Brassicaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Berberis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indeterminate-type	0	4	9	4	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown	0	4	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Dung_spores	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charcoal	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN
EU	841	100	9	243	342	97	206	335	419	693	12	319	188	192	461	327	193	310	256	483	212	422	227	283	220
Terrestrial Sum	256	344.5	289	292	378	296	305	291	313	424	282	311	304	320	305	342	342	301	321	306	331	358	387	361	395
AP	236	280.5	238	144	298	283	242	204	230	332	238	217	226	224	193	225	277	248	234	229	281	260	327	301	316
NAP	20	64	51	150	80	13	63	89	83	92	46	95	78	96	112	117	65	53	90	77	50	99	60	60	79
Conifer	236	280.5	238	143	297	283	241	203	228	327	238	217	225	223	193	223	276	248	233	227	280	260	327	301	315
LNAP	18	46	31	112	71	12	39	71	63	66	33	82	64	80	89	94	60	38	74	59	36	70	43	47	65

sample ID	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**
sample #	77	86	97	106	115	125	135	145	153	165	175	189	7	25	51	75	92	107	120	133	147	161	175	190	102	25	37
Depth (cm)	184.5	189	194.5	199	203.5	208.5	213.5	218.5	222.5	228.5	233.5	240.5	249.5	258.5	271.5	283.5	292	299.5	306	312.5	319.5	326.5	333.5	341	348.9	358.5	364.5
age_yrBP	1176	1217	1269	1313	1357	1407	1456	1505	1543	1597	1639	1693	1751	1800	1863	1925	1976	2029	2078	2130	2187	2245	2300	2356	2409	2466	2499
Pinus	228	189.5	234.5	217	206	217	248	242	196.5	236	300.5	222	246	257.5	210.5	308.5	236.5	250	310.5	218	201	229	282.5	230	247	321	196
Picea	3	3	4	5	4	6.5	3	3	4	0	39	3.5	5.5	23	8	19	5	2	9	8	9	7	16.5	5	7	26	4
Abies	3	3	3	4	5	1	3	3	2	2	5.5	4	4.5	0	7.5	2.5	2	2.5	1	3	2	3	1	4	2	5.5	2
Pseudotsuga/Larix	1	0	0	0	2	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Populus	0	0	1	1	0	1	1	0	1	2	1	0	1	0	1	0	0	0	1	0	3	2	0	0	0	0	0
***Juniperus* -type**	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	9	0
Alnus	0	1	0	1	4	0	0	3	2	1	0	2	0	4	2	1	4	1	0	3	3	0	0	2	1	1	2
Corylus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Betula	0	0	0	0	1	0	0	0	2	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1
Salix	2	2	0	3	3	8	0	0	9	1	1	0	1	3	4	2	1	0	1	1	1	3	2	1	4	0	5
Quercus	3	1	3	3	1	8	1	1	4	0	4	4	7	11	6	12	0	3	4	6	3	5	9	5	2	10	1
Acer	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Rosaceae	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Ceanothus	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1
Shepherdia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Arceuthobium	0	0	2	1	3	1	0	0	1	0	0	3	0	1	0	0	1	0	3	0	0	0	2	0	0	0	0
Ephedra	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Sarcobatus	1	0	2	0	4	9	2	1	2	2	2	2	1	3	1	2	4	2	1	2	5	5	5	1	2	5	5
Poaceae	4	3	3	5	3	8	5	2	7	0	10	1	3	7	5	6	4	6	3	2	0	5	9	4	2	5	5
Cyperaceae	5	11	2	7	4	2	4	0	6	3	5	0	0	4	0	1	0	0	3	3	1	0	4	0	0	4	1
Artemisia	19	48	13	28	29	46	13	14	23	21	42	26	10	37	26	22	17	20	10	27	37	16	40	23	38	12	35
Ambrosia	1	4	2	1	4	6	0	2	1	2	2	2	1	6	3	4	5	3	1	2	6	3	5	2	4	4	6
Asteraceae	1	5	2	2	3	4	2	1	5	1	4	2	0	5	4	2	2	2	0	6	1	2	4	3	1	0	1
Chenopodiaceae	9	7	6	2	6	11	4	6	11	13	7	10	3	21	10	9	5	5	7	7	12	5	8	6	3	10	14
Thalictrum	0	0	0	0	1	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Brassicaceae	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Polygonaceae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berberis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Plantago	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indeterminate-type	19	21	19	19	18	0	14	21	23	14	0	18	13	0	10	0	7	5	0	11	13	3	0	14	0	0	17
Unknown	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	2	0	0	1	0	2
Dung_spores	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charcoal	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN	NaN
EU	33	21	12	29	12	50	15	21	16	22	160	16	30	68	34	62	18	19	20	20	16	17	83	10	10	48	20
Terrestrial Sum	276	268.5	279.5	274	279	326.5	282	280	273.5	283	427	281.5	288	381.5	290	391	291.5	296.5	351.5	286	285	286	386	286	314	408.5	279
AP	235	195.5	242.5	227	217	225.5	255	248	203.5	240	350	229.5	257	280.5	227	331	243.5	254.5	321.5	229	215	241	301	239	256	352.5	202
NAP	46	84	39	54	66	103	31	32	76	46	82	52	31	105	63	61	48	42	33	61	71	45	89	47	58	60	78
Conifer	234	195.5	241.5	226	215	224.5	254	248	202.5	238	345	229.5	256	280.5	226	330	243.5	254.5	320.5	229	212	239	300	239	256	352.5	202
LNAP	33	63	24	37	41	69	24	23	46	35	64	39	16	71	45	39	28	33	20	43	50	28	61	36	44	27	55

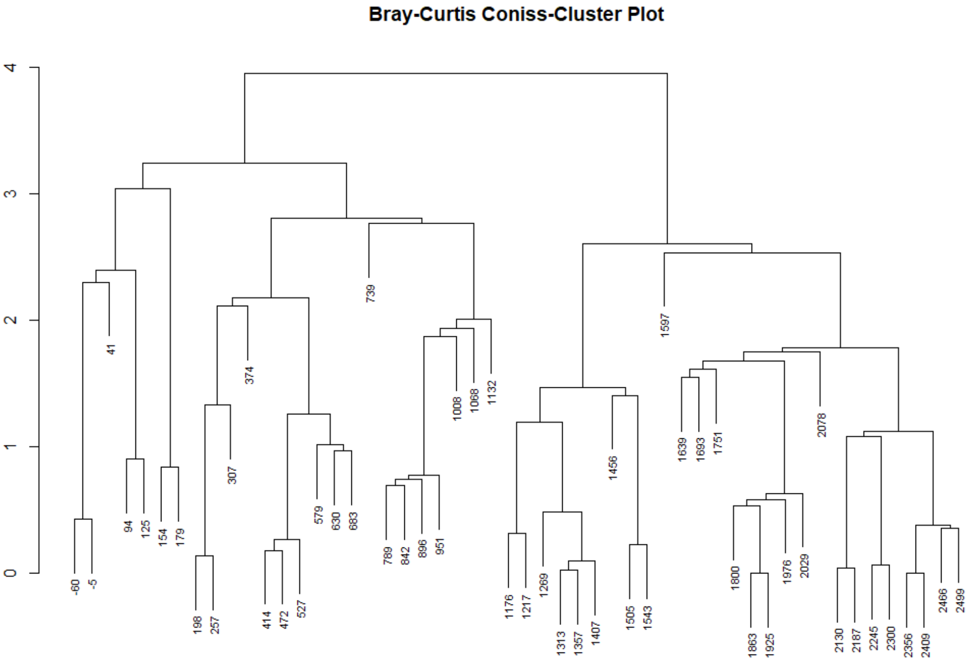
Appendix B-Supplemental Figures

B.1 Comparison of zonation across distance metrics

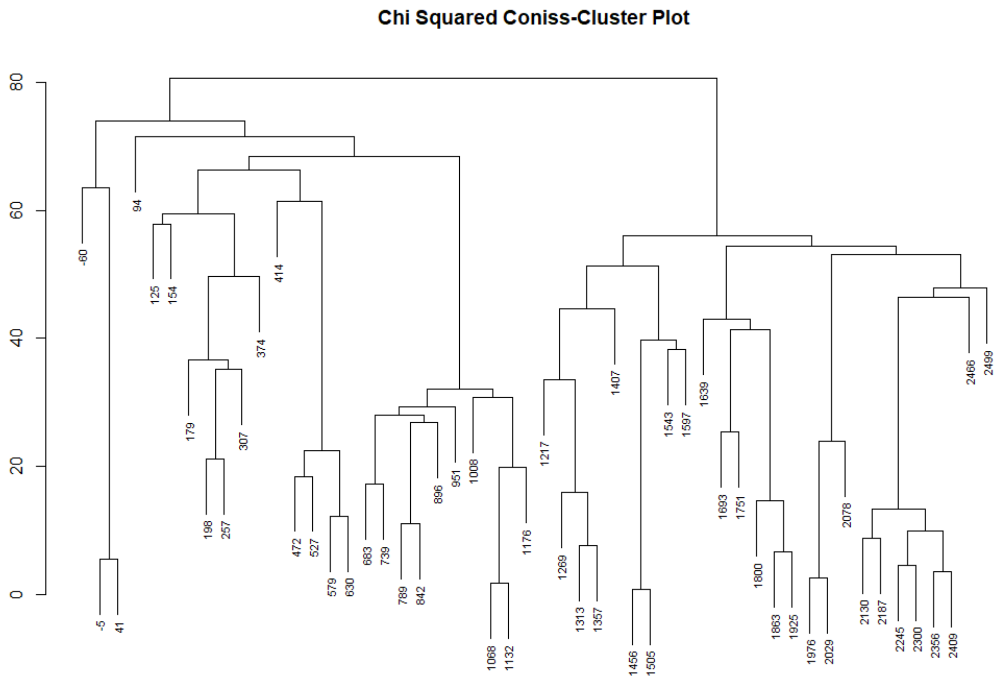
Square Chord



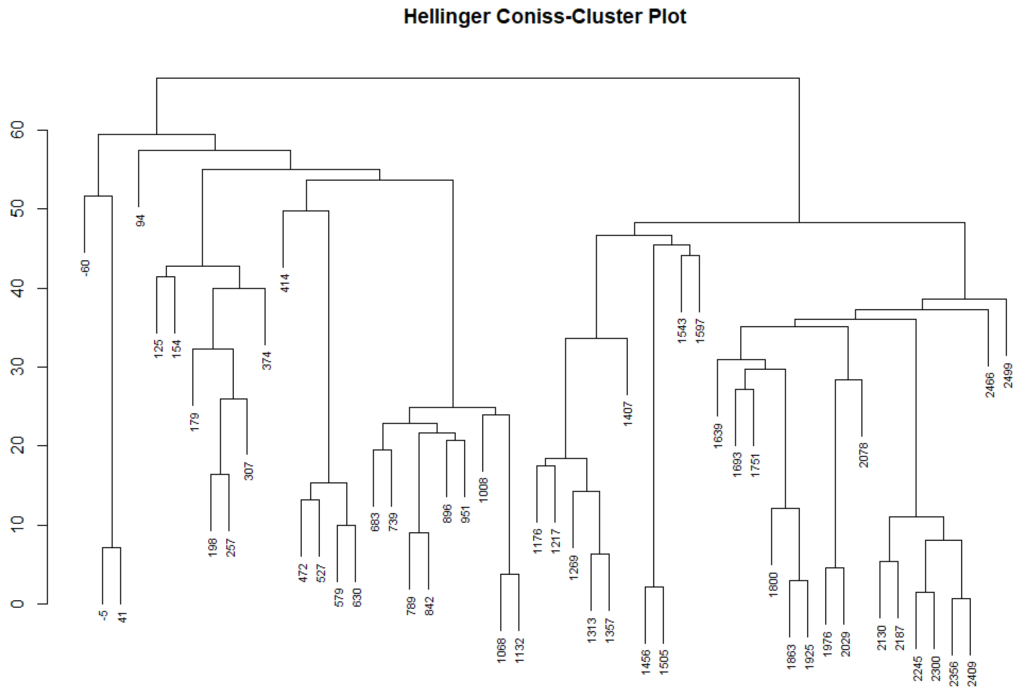
Bray-Curtis



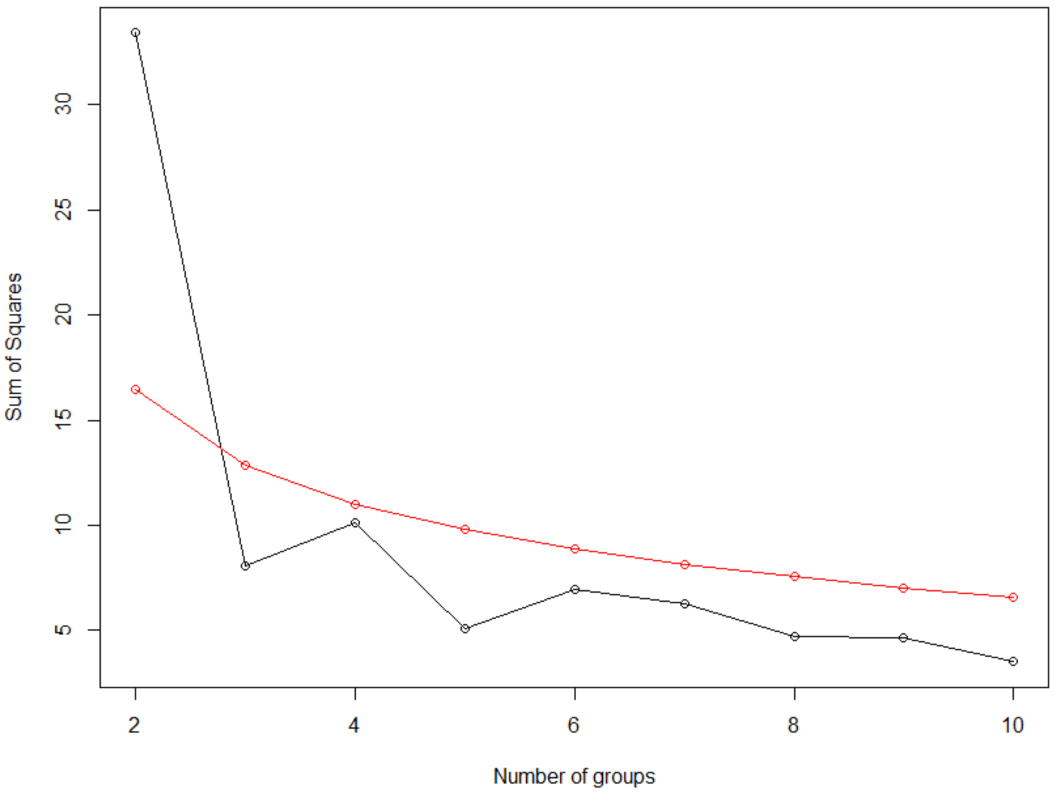
Chi Squared



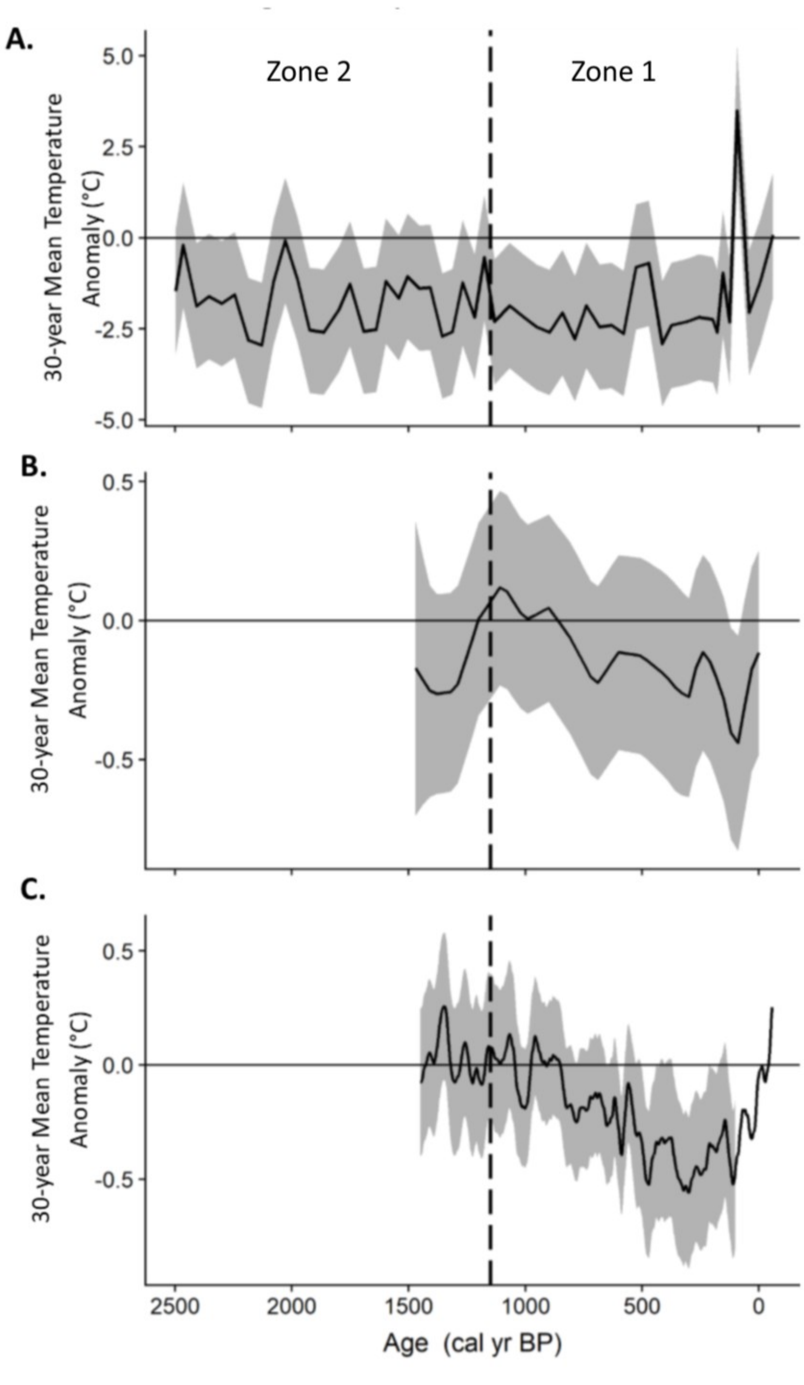
Hellingers



B.2 Broken Stick Model



B.3 Regional Temperature Reconstructions

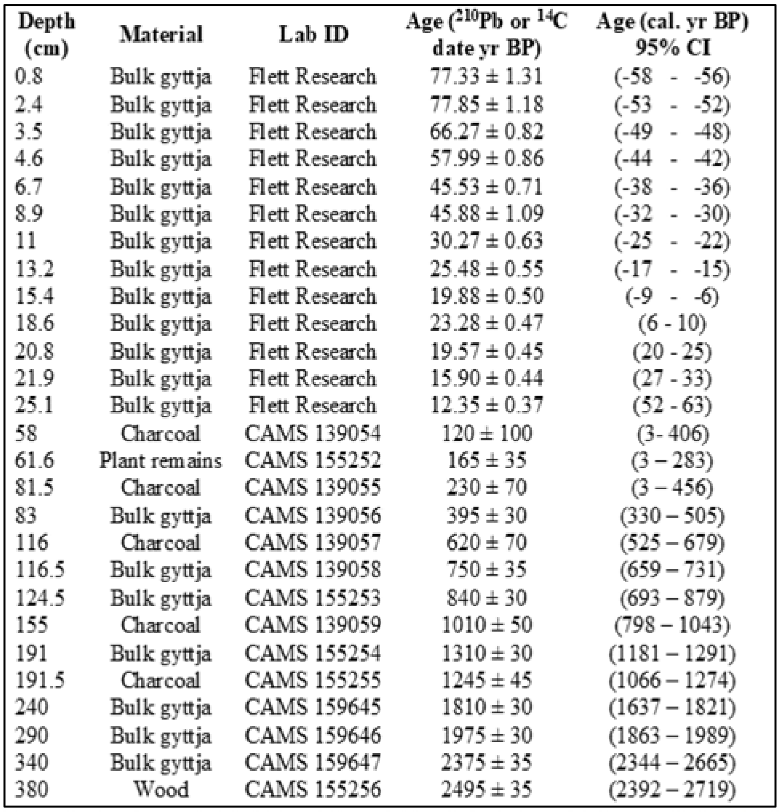


B.3.A. 30-year mean temperature anomaly reconstructed through Chickaree fossil pollen data. B. North American reconstruction of 30 year mean temperature through pollen (Trouet et al., 2013) C. Northern hemisphere reconstruction of 30 year mean temperature anomaly from multiple proxies including tree-ring, ice core, coral and sediment data. (Mann et al., 2009)

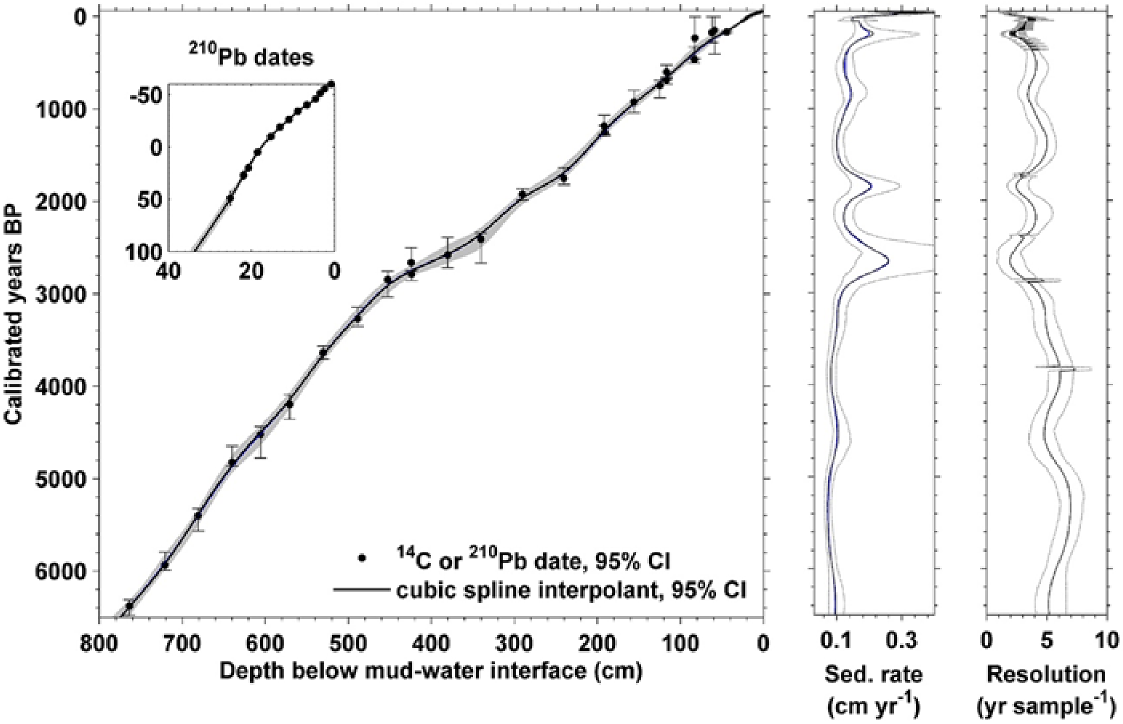
Appendix C- Existing Chickaree Lake data used in this study

C.1 Radiocarbon dates and age-depth model

unmodified from Dunnette et al., 2014:

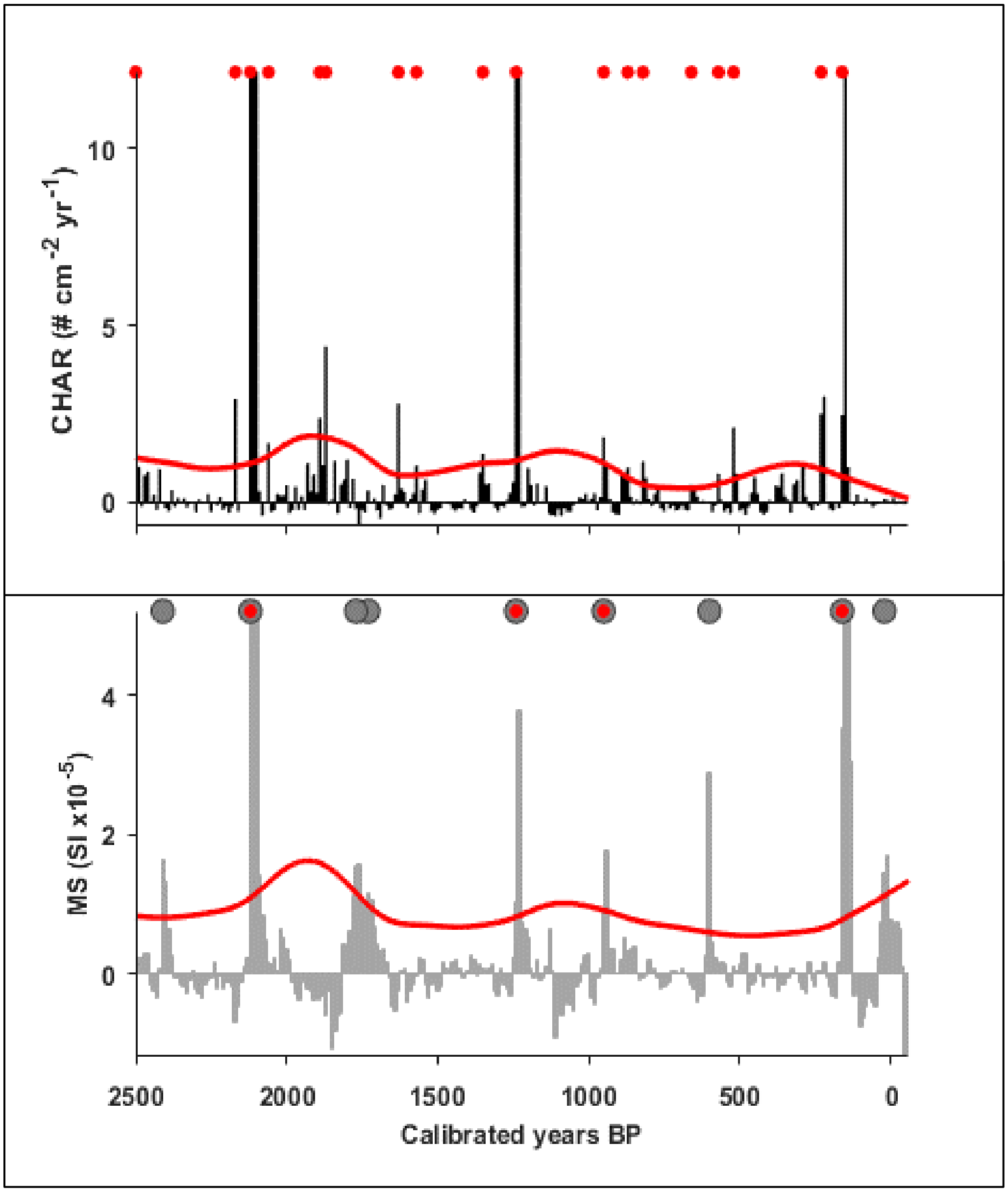


Depth (cm)	Material	Lab ID	Age (^{210}Pb or ^{14}C date yr BP)	Age (cal. yr BP) 95% CI
0.8	Bulk gyttja	Flett Research	77.33 ± 1.31	(-58 - -56)
2.4	Bulk gyttja	Flett Research	77.85 ± 1.18	(-53 - -52)
3.5	Bulk gyttja	Flett Research	66.27 ± 0.82	(-49 - -48)
4.6	Bulk gyttja	Flett Research	57.99 ± 0.86	(-44 - -42)
6.7	Bulk gyttja	Flett Research	45.53 ± 0.71	(-38 - -36)
8.9	Bulk gyttja	Flett Research	45.88 ± 1.09	(-32 - -30)
11	Bulk gyttja	Flett Research	30.27 ± 0.63	(-25 - -22)
13.2	Bulk gyttja	Flett Research	25.48 ± 0.55	(-17 - -15)
15.4	Bulk gyttja	Flett Research	19.88 ± 0.50	(-9 - -6)
18.6	Bulk gyttja	Flett Research	23.28 ± 0.47	(6 - 10)
20.8	Bulk gyttja	Flett Research	19.57 ± 0.45	(20 - 25)
21.9	Bulk gyttja	Flett Research	15.90 ± 0.44	(27 - 33)
25.1	Bulk gyttja	Flett Research	12.35 ± 0.37	(52 - 63)
58	Charcoal	CAMS 139054	120 ± 100	(3- 406)
61.6	Plant remains	CAMS 155252	165 ± 35	(3 – 283)
81.5	Charcoal	CAMS 139055	230 ± 70	(3 – 456)
83	Bulk gyttja	CAMS 139056	395 ± 30	(330 – 505)
116	Charcoal	CAMS 139057	620 ± 70	(525 – 679)
116.5	Bulk gyttja	CAMS 139058	750 ± 35	(659 – 731)
124.5	Bulk gyttja	CAMS 155253	840 ± 30	(693 – 879)
155	Charcoal	CAMS 139059	1010 ± 50	(798 – 1043)
191	Bulk gyttja	CAMS 155254	1310 ± 30	(1181 – 1291)
191.5	Charcoal	CAMS 155255	1245 ± 45	(1066 – 1274)
240	Bulk gyttja	CAMS 159645	1810 ± 30	(1637 – 1821)
290	Bulk gyttja	CAMS 159646	1975 ± 30	(1863 – 1989)
340	Bulk gyttja	CAMS 159647	2375 ± 35	(2344 – 2665)
380	Wood	CAMS 155256	2495 ± 35	(2392 – 2719)



C.2 CHARAnalysis and Magnetic Susceptibility

unmodified from Dunnette et al., 2014:



C.3 Original Chickaree Pollen Record