DISENTANGLING ANTHROPOGENIC AND NATURAL DRIVERS OF CHANGE IN VEGETATION AND FIRE HISTORY ALONG THE FOREST-GRASSLAND ECOTONES OF THE CENTRAL UNITED STATES AND PATAGONIA

by

William Parashar Nanavati

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Ecology and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2020

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Dr. Cathy Whitlock, for an amazing opportunity to learn and be part of her lab. Dr. Whitlock provided a wealth of guidance and support without which, none of this research would have been possible. Many thanks to my committee members, Dr. Ben Poulter, Dr. Dave McWethy, and Dr. Greg Pederson, for offering valuable comments and suggestions in class and throughout the Ph.D. process. I also thank my dear friends, Dr. Eric Grimm and Pietra Mueller, for their guidance and success at turning me into a paleoecologist. I am thankful for the friendships formed with Dr. Bob Gresswell, Dr. Valeria Outes, Dr. Gustavo Villarosa, Dr. María Marta Bianchi, Dr. Thomas Kitzberger, Dr. Juan Gowda, Dr. Andrés Holz, Dr. Jed Kaplan and many others during discussions and collaborations throughout this process.

It truly takes a community to make a Ph.D. happen and this is certainly the case for me. Many thanks to my amazing family and friends for supporting me every step of the way. Our time discussing theory in the lab, ecology on the trails, and important life goals at home were all vital in making me who I am. Also, warmest regards to Robert and the team at Granny's Donuts: your warm and fluffy donuts made this central Illinoian feel right at home.

Mrs. Beth Nanavati, I love you and thank you for your unwavering support. I look forward to our many travels and adventures.

TABLE OF CONTENTS

TABLE OF CONTENTS - CONTINUED

TABLE OF CONTENTS - CONTINUED

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES - CONTINUED

LIST OF FIGURES - CONTINUED

LIST OF FIGURES - CONTINUED

LIST OF FIGURES - CONTINUED

LIST OF FIGURES - CONTINUED

ABSTRACT

Disentangling anthropogenic and natural drivers of vegetation and fire history at different spatiotemporal scales is a fundamental challenge in Earth Systems science. To better understand the role of past human ignition in altering long-term ecosystem dynamics, we rely on the anthropogenic fire regime conceptual model proposed by Guyette et al. (2002) in the central U.S. Ozarks. The synthesis of new and existing pollen and charcoal records, and their integration with archaeological, ethnographic, and independent paleoclimate records is used to test the anthropogenic fire regime conceptual model at a longer time scale in the central U.S. Ozarks. Following its validation, this conceptual model is applied to the forest-steppe ecotone east of the Patagonian Andes (38-55°S) for the first time. Although it is well established that Patagonian vegetation and fire history for most of the postglacial period was governed by the strength and position of the Southern Westerly Wind (SWW) storm tracks, the influence of land use since the arrival of American Indians to the region ~12,000 years ago remains unclear. From the late glacial to early Holocene, region-wide increases in fire were associated with aridity while the SWW were weakened and south of their present position. Between ~7000-4000 cal yr BP, increased arboreal taxa and decreased fire throughout Patagonia suggest wet conditions as the SWW moved northward to their present position. After ~4000 cal yr BP, a combination of increased land use and greater climate variability, led to spatially heterogeneous but generally rising fire activity along the forest-steppe ecotone. When trends in the vegetation and fire history of individual sites are compared to each other and to the archaeological record, however, it becomes apparent that American Indians may have served as an important source of ignition, locally increasing landscape heterogeneity since their arrival. During the last 100 years, increased Euro-American settlement and land clearance in Patagonia led to native forest loss, more disturbance, and the spread of introduced taxa along the eastern flanks of the Andes. These ecological changes in the recent century far outweigh thousands of years of American Indian influence on fire and vegetation history.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Introduction

Humans and pre-human hominids have used fire as a tool for at least the last 400,000 years to cook, clear and fertilize land, facilitate hunting, communicate, and wage war (Sauer 1950, Pyne 1982, Denevan 1992, Karkanas et al. 2007). During the last 2000-3000 years, biomass burning has increased worldwide as human populations have grown and relied on fire as a means to clear forests for extensive crop- and pasturelands (Marlon et al. 2013, Ruddiman 2013). In recent decades, increases in large uncontrollable wildfires in the western United States of America have led to over $4 billion of spending per year in firefighting and protection efforts at the state and federal level (Gorte 2013). Recent analyses suggest that in the U.S., humans are responsible for 90% of the recent surge in wildfire (Balch et al. 2017) and that increased fire size and severity are attributed to warming (Jolly et al. 2015, Abatzoglou and Williams 2016) and fire management (Whitlock et al. 2003, Hessburg et al. 2005, Marlon et al. 2012). To better predict and manage our increasingly fire-prone landscapes, it is necessary to understand the roles of human activity and climate change as drivers of past fire events (Bowman et al. 2009, Schoennagel et al. 2017, Kelley et al. 2019, McWethy et al. 2019). This understanding requires examination of fire, people, and climate over multiple spatial and temporal scales.

Understanding the spatial and temporal scales at which prehistoric anthropogenic and natural fire activity becomes separable is fundamental to Earth System science and geography (Bowman et al. 2011, Seddon et al. 2014, Roos et al. 2019). At the local to landscape scales, humans actively suppress or eliminate fires, alter ignition location, frequency, and seasonality, and change the flammability and spatial contiguity of fuels (McWethy et al. 2010, Whitlock et al. 2014, Bird et al. 2016, Nanavati and Grimm 2020). In contrast, at regional to continental scales, climate (i.e., precipitation, relative humidity, lightning, air temperature, and wind) is and has been the primary driver of fire activity through changes in vegetation and fire regimes (e.g., Whitlock and Bartlein 2003, Krawchuk and Moritz 2011, Marlon et al. 2013, Pausas and Ribeiro 2013). However, the relationship between long-term trends in climate and fire activity at all scales broke down with expansion of agriculture across Asia, Europe, and the Americas during the middle and late Holocene (Marlon et al. 2013, Ruddiman 2013). Separating anthropogenic from natural drivers of fire activity is most difficult at intermediate scales, where human influences on fire activity operate at the same scale as climate- and weather-driven controls on ignition, vegetation, fuel and soil moisture, and wind (Whitlock et al. 2010). For example, Iglesias and Whitlock (2014) note that only one of seven sedimentary charcoal records from the northern Patagonian forest-steppe ecotone (41-43°S) showed a positive correlation between biomass burning and American Indian settlement, whereas biomass burning recorded in the remaining six sites was associated with climate conditions that affected fuel availability.

Most of the scientific literature examining relationships between climate, vegetation, humans, and fire conclude that climate-vegetation interactions drove fire activity at larger spatial and longer temporal scales, but at local spatial and shorter temporal scales, humans and interannual climate variability could have played an important role. Local variations in anthropogenic fire activity show a complex, non-linear trend between demography (often summarized as population density) and fire activity (Fig. 1.1; e.g., Guyette et al. 2002), because there is no single forcer that leads individuals, family groups, communities, or civilizations to change their land use strategies (e.g., Morrison 1994). These findings suggest that the relationship between climate, land use (e.g., use of fire to facilitate hunting, forest clearance for agriculture, etc.), vegetation, and fire is complex and requires further investigation.

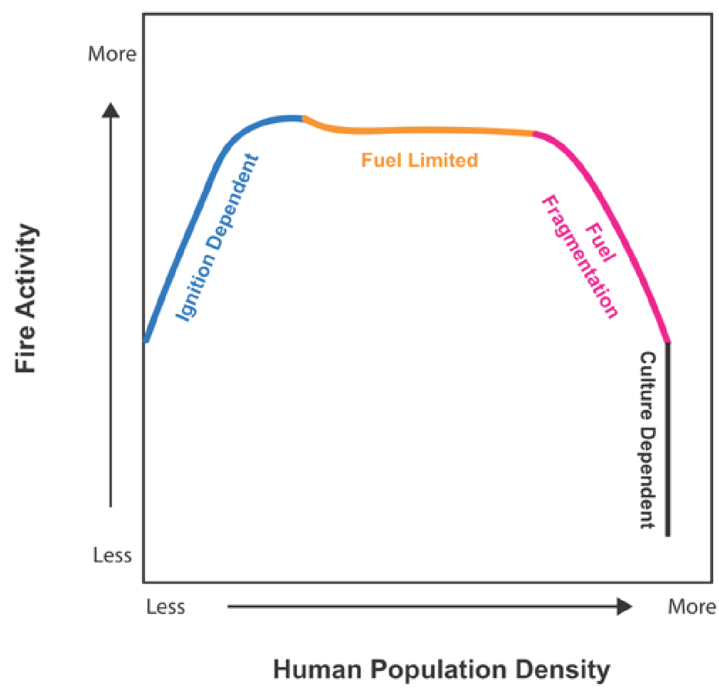

Figure 1.1: Anthropogenic fire regime conceptual model modified from Guyette et al. (2002). This model summarizes the hypothesized, non-linear relationship between human population density (a proxy for anthropogenic ignition frequency) and burned area (here, fire activity). Sections of the curve are color-coded and labeled based on the hypothesized limiting factor of fire activity.

Disentangling anthropogenic and natural drivers of change in vegetation and fire history is imperative for understanding the footprint of pre-European peoples and the expansion of Euro-American land use practices in the Americas (Crutzen and Stoermer 2006, Ruddiman 2013). Therefore, I ask: To what extent did American Indians and later Euro-American settlers alter ecosystems through their use of fire? The knowledge gained from reconstructions of vegetation and fire dynamics provide a better understanding of the mechanisms that have shaped fire regimes through time (i.e. variation and interactions among climate, vegetation, and land use). A more nuanced understanding of climate-human-vegetation-fire interactions is important to (1) interpret how past land use has amplified and/or buffered climate-mediated ecosystem dynamics; (2) provide a better appreciation of past and present socio-ecological interactions; and (3) offer a plausible range of wildfire conditions under which cultures and ecosystems have evolved. This long-term perspective on socio-ecological interactions helps guide current management and conservation of individual species and entire ecosystems, and can also be used to inform projections of ecosystem dynamics under different climate-change scenarios (e.g., Whitlock et al. 2018, Newman 2019).

Conceptual framework

Although it is well established that land use altered ecosystem dynamics of temperate ecosystems in the United States and Patagonia prior to Euro-American settlement, the spatial and temporal scales of their impact is still debated (Munoz et al. 2014, Holz et al. 2016, Gajewski et al. 2017, Nanavati and Grimm 2020). This debate persists because of the intricacies inherent in socioecological systems. As Denevan

(1992) noted, human alteration of the environment by such means as anthropogenic burning is “not simply a process...in response to linear population growth and economic expansion. It is instead interrupted by periods of reversal and ecological rehabilitation as cultures collapse, populations decline, wars occur, and habitats are abandoned”. Furthermore, interpretations of anthropogenic burning are complicated by variations in climate, which can alter the abundance and flammability of fuel biomass. Disentangling anthropogenic from natural drivers in vegetation and fire histories refines our understanding of how changes in culture and climate alter ecosystem dynamics.

Fire activity varies naturally across the landscape and through time as a result of climate-fuel-fire relationships (Fig. 1.2; Whitlock et al. 2010, Hirota et al. 2011, Staver et al. 2011). Terrestrial biomes can be placed along a precipitation and biomass gradient between dry, fuel-limited conditions (e.g., desert and over-grazed pasture) and wet, climate-limited conditions (e.g., rainforest and moorland). Fire activity tends to be low at either end of the gradient and high in biomes that are seasonally dry but maintain ample fuel biomass for fire (e.g., shrubland, savannah, and parkland biomes). Climate-fuel-fire relationships can be greatly altered by land use, where activities that limit disturbance through the removal of grazers or fire may shift an open or disturbed landscape to one with more fuel and, thus, a higher fire activity. Conversely, the clearance of forest or shrubs for agricultural or pastoral land may result in a general decrease in fire activity as fuel is removed from the landscape.

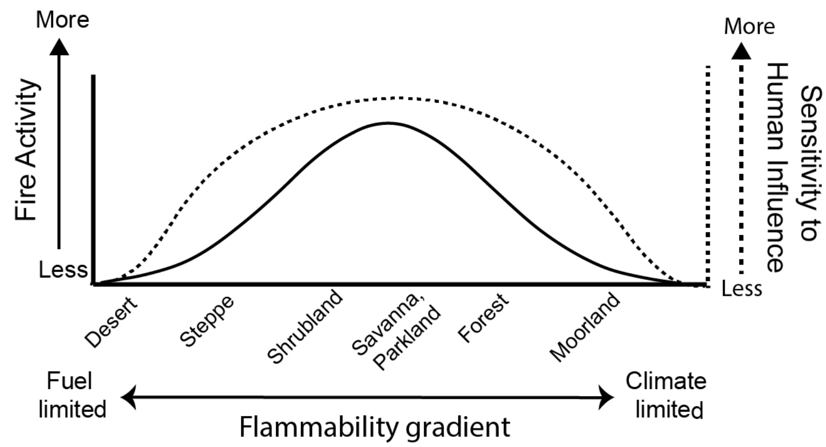

Fig. 1.2: Conceptual model for how natural fire activity (solid line) and biome sensitivity to human influence (dashed line) vary along a generalized flammability and vegetation productivity (biomass) gradient (modified from Whitlock et al. 2010).

Guyette et al. (2002) proposed the "anthropogenic fire regime hypothesis" suggesting that changes in percent of burned sites – as recorded in fire-scar records from parkland and forest in the Ozark Highlands of the central U.S. – occurred in four states that coincided with increased population density (Fig. 1.1). For the purpose of relating the anthropogenic fire-regime hypothesis to our paleoecological records, I simplify the terminology, changing "percent of burned sites" to "fire activity" and generally equating "ignition frequency" with "population density". Ignition-limited landscapes are characterized by sufficient fuel, fuel connectivity, and flammability, increasing anthropogenic ignition also increases fire activity. Fuel-limited landscapes are ones in which increasing anthropogenic ignition does not result in increased fire activity, because biomass produced and consumed are nearly at equilibrium. Fuel-fragmented landscapes are ones in which increased anthropogenic ignition further reduces fuel load and connectivity to the extent that overall fire activity decreases. According to Guyette et al. (2002), once population density reaches a certain threshold, the cultural need for broadcast burning decreases resulting in a drastic decrease in fire activity, thus a culture-dependent landscape. This culture-dependent stage is critically evaluated in the conclusion (Ch. 5) based on the research presented in this dissertation.

Guyette et al. (2002) benefitted from a wealth of highly spatially and temporally resolved fire-scarred tree ring and historical records documenting the last 300 years of fire activity and human history in the central U.S. Ozarks. The appropriateness of the anthropogenic fire-regime hypothesis for longer time scales and in different regions remains untested. Bowman et al. (2011) provides three criteria that are used throughout this dissertation in evaluating the potential role of fire as a driver of change in ecosystem dynamics through time:

1. Are there spatial and/or temporal changes in vegetation and fire history as preserved in the paleoecological record or records?
2. Are changes well explained by climate-fuel-fire relationships or paleoclimate records, without a human component?
3. Do changes coincide spatially and temporally with human presence and/or changes in human history?

Objectives

The objective of this dissertation is to better understand the role of past land use and climate in shaping landscapes in the central U.S. Ozarks and east of the Patagonian Andes (Fig. 1.3) by asking such questions as: (1) What is the vegetation and fire history of these regions?; (2) How have climate and land use driven changes in vegetation and fire history?; (3) How does the Guyette et al. (2002) conceptual framework hold up on longer timescales in the Ozarks, and can it be applied to other regions and spatial scales?; and (4) How do spatial and temporal scales affect our ability to disentangle natural and anthropogenic drivers of change in vegetation and fire history? To address these questions, I rely on the analysis of fossil pollen, charcoal, botanical remains, and geochemistry from sediment cores to recreate local vegetation and fire history. I then integrate these results with those from other paleoecological data, independent paleoclimate records, historical accounts, and archaeological research to assess how changes in land use and climate have influenced environmental history along these forest-grassland transitions from the local to regional scales over the last ~2000 years in the central U.S. Ozarks and the last ~18,000 years in Patagonia.

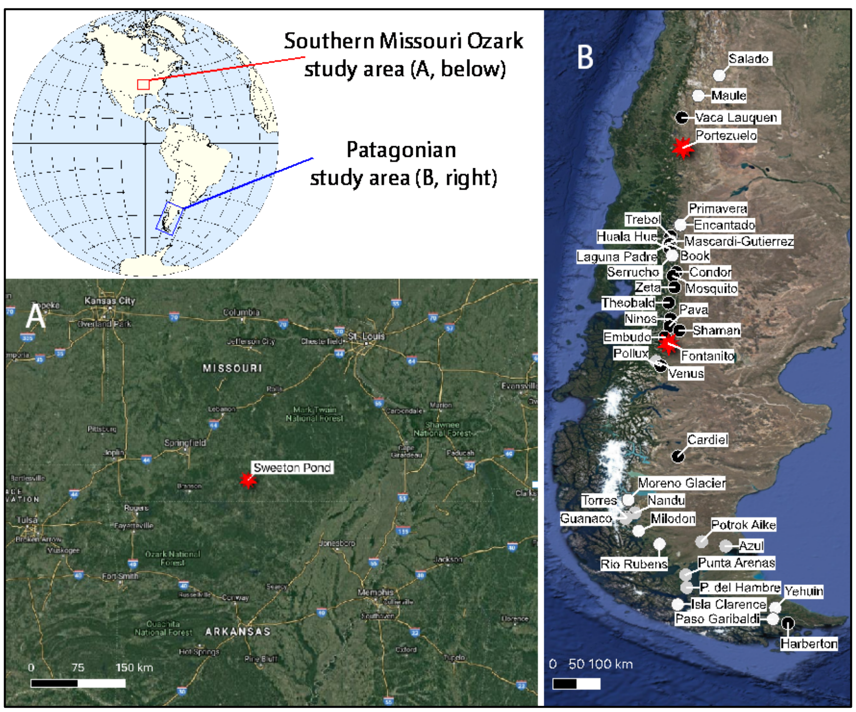

Figure 1.3: Maps of study areas discussed in this dissertation: multiproxy sites presented here (red starts), sites with only charcoal data (white dots), sites with only pollen data (gray dots), sites with both pollen and charcoal data (black dots).

Forest-grassland transitions (or ecotones) in temperate latitudes are regions that are sensitive to rapid fire-mediated changes, where humans, through their use of fire, have long altered natural vegetation, and are thus valuable for understanding ecosystem dynamics under changing climate and disturbance regimes (Veblen and Lorenz 1988, Mayer and Khalyani 2011, Staver et al. 2011, Kitzberger 2012). Humans have long inhabited forest-grassland ecotones, no doubt adapting their technologies and land-use practices to subsist and become a keystone species in these biomes (Hart and Hart 1986, Nicholson 1988, Hope and Golson 1995, Segalen et al. 2007). The forest-steppe ecotone in Patagonia (37-55°S) is one of the most striking examples this transition between biomes. Forest is typically promoted by high levels of moisture and/or low fire activity, whereas in drier settings, steppe is maintained by seasonal or annual moisture deficits and high levels of burning (Bond et al. 2005, Mayer and Khalyani 2011, Kitzberger 2012).

Overview of dissertation

This dissertation presents research published in *The Holocene* (Ch. 2), *Quaternary Science Reviews* (Ch. 4) and submitted to the *Journal of Biogeography* (Ch. 3). The study areas discussed here include the forest-grassland ecotones of the central U.S. Ozarks and Patagonia east of the Andes (Fig. 1.3). This research would not have been possible without the intellectual support of my committee members and the thoughtful contributions of my co-authors and numerous collaborators.

Chapter 2:

A multiproxy study from Sweeton Pond, Ozark County, Missouri, provides a high-resolution 1,900-year history of fire and vegetation in the southern Missouri Ozarks, where the modern vegetation is oak-hickory forest. In this paper, our objectives are two-fold: (1) present the timing of vegetation change and fire activity over the last 1900 years in the southern Missouri Ozarks using the pollen, charcoal, and loss-on-ignition data from Sweeton Pond (36°N, 92°W, 304 m elev.; Fig. 1.3a; Nanavati and Grimm 2020) and (2) assess the role of American Indians in influencing local fire activity and vegetation utilizing historical accounts and archaeological research, particularly concerning the role of the Osage. Understanding the late-Holocene interactions between climate, humans, ecology, and fire in the southern Missouri Ozarks is especially important as it allows for us to examine the validity of Guyette et al. (2002)'s anthropogenic fire-regime hypothesis in the same ecosystem and region, but at a much longer temporal scale.

Pollen and charcoal data from Sweeton Pond are compared to dendrochronological data to assess the role of climate and fire in altering ecosystem dynamics in the southern Missouri Ozarks. Land use, particularly of the Osage American Indians, is assessed from historical and archaeological records. Three cultural periods are superimposed on the paleoenvironmental history: (1) The Pre-Osage period, ending ~1500 CE, was characterized by open oak-hickory forest and frequent low-severity fires, suggesting interannual climate variability as a driver of vegetation and fire occurrence (2) The Osage period (~1500-1820 CE) was characterized by increased fire activity and the expansion of both fire-sensitive and fire-dependent taxa coincident with Osage expansion, suggesting that anthropogenic fire and land use was local in nature and increased landscape heterogeneity prior to Euro-American settlement. (3) The Euro-American period (since ~1820 CE) was characterized by increased disturbance and the loss of pine, resulting from increased Euro-American settlement and extensive agricultural and logging activities. During this period, forest clearance led to fuel fragmentation, reducing fire activity; after 1920 CE, fire was actively eliminated.

Chapter 3:

To test whether the anthropogenic fire regime hypothesis can be applied to the temperate, *Araucaria araucana* forest-steppe ecotone of northernmost Patagonia, lake-sediment cores from Laguna Portezuelo were analyzed for pollen and charcoal (38°S, 71°W, 1730 m elev.; Fig. 1.3b; Nanavati et al. *submitted*). L. Portezuelo provides a 11,100-year history of climate, vegetation, fire, and land use along the *Araucaria araucana* forest-steppe ecotone. *Araucaria* was an important resource for American Indians and is engrained into Mapuche-Pehuenche cultural identity. The pollen record shows that *Araucaria* expanded in the late Holocene with rising human populations and increased climate variability associated with a strengthened El Niño-Southern Oscillation (ENSO). Prior to that, the forest-steppe region supported scattered *Nothofagus* (mostly *N. dombeyi*-type pollen) and moderate-to-high fire activity. Beginning at 6800 cal yr BP, changes in vegetation composition and fire are attributed to increased climate variability and human presence along the ecotone. Increased *Nothofagus* and *Araucaria* pollen and null-to-low fire activity occurred at 1800, 1200, and 800 cal yr BP, in association with increased strength and frequency of wet El Niño events. After 500 cal yr BP, increased abundance of *Plantago*, *Rumex*, and other disturbance taxa (e.g., Apiaceae and Caryophyllaceae) and high fire activity mark Euro-American land use. Non-native *Pinus* pollen in the 20th century indicate the establishment of *Pinus* plantations near Laguna Portezuelo.

Chapter 4:

The role of climate in shaping the postglacial history of Patagonia (41-55°S) east of the Andes is evident in new pollen and charcoal data from Mallín Fontanito (44.91°S, 71.57°W; Fig. 1.3b; Nanavati et al. 2019) and their comparison with other paleoenvironmental records in the region. Between ~17,800-13,000 cal yr BP, evidence of heath-steppe vegetation with some *Nothofagus* and little fire activity at M. Fontanito suggest cold, dry conditions in early late-glacial time. From ~13,000-7000 cal yr BP, increased *Nothofagus* pollen and charcoal levels imply expanding tree cover and more fires, consistent with warming. Between ~7000-4000 cal yr BP, closed *Nothofagus* forest was established at M. Fontanito during a period of low fire activity and effectively wet conditions. Fluctuations in pollen and charcoal levels after ~4000 cal yr BP are consistent with increased submillennial climate variability and, possibly, increased American Indian presence and land use. The environmental history at M. Fontanito is similar to other records from central Patagonia east of the Andes (44-50ºS); however, differences in the timing of fires and human occupation suggest that pre-European burning was local in nature. At a regional scale, composited *Nothofagus* pollen abundance and charcoal data east of the Andes (41-55ºS) reveal latitudinal differences in the timing of forest establishment and fire that relate to changes in the strength and position of the Southern Westerly Winds (SWW) through time. Notably, the SWW were south of their present position between ~14,000-9000 cal yr BP, leading to dry conditions across the region. The present storm-track position was established after ~7000 cal yr BP, when region-wide increases in precipitation occurred.

Chapter 5:

Here, I summarize results and discuss how they advance our understanding of how changes in land use and climate have altered the temperate ecotonal ecosystems of Patagonia for the last ~18,000 years. My findings demonstrate the importance of (1) considering spatial and temporal scales while interpreting the roles of humans and climate as drivers of change in the paleoecological record; (2) study area and paleoecological site selection while investigating past socio-ecological interactions; and (3) understanding cultural changes in the archaeological and ethnohistorical records, not just changes in population size or density.

Contributions

The research presented in Chapter 2 was conceptualized and funded by E. Grimm. Field work was completed by P. Mueller, R.B. McMillan, B. Styles, T. Stafford, and R. Toomey. Initial pollen sampling was completed by P. Mueller. I completed pollen, charcoal, and loss-on-ignition analyses. E. Grimm and I completed the statistical analyses and wrote the manuscript. Useful comments and additional funding were provided by C. Whitlock through the WildFIRE PIRE project (National Science Foundation grant OISE0966472) and NSF award GSS-1461590. The research also benefited from comments by S. Muñoz and an anonymous reviewer.

C. Whitlock and B. Poulter conceptualized and provided funding for the research in Patagonia through the WildFIRE PIRE project (National Science Foundation grant OISE 0966472) and NSF award GSS-1461590, which is described in Chapters 3 and 4. C. Whitlock, R. Gresswell, V. Iglesias, G. Villarosa, V. Outes, D. Quick, and I undertook fieldwork. V. Outes, H. Dailey and D. Quick assisted in the lab. I completed pollen, charcoal, and statistical analyses. V. Iglesias assisted in coding. I wrote the manuscripts with contributions from C. Whitlock, V. Iglesias, M.E. de Porras, V. Outes, and G. Villarosa. The manuscripts benefitted from comments by V. Markgraf, J. Larmon, S. Munoz, and anonymous reviewers. This dissertation benefitted from comments by my advisor, C. Whitlock, and my committee members, D. McWethy, G. Pederson, and B. Poulter.

CHAPTER TWO

HUMANS, FIRE, AND ECOLOGY IN THE SOUTHERN MISSOURI OZARKS

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

Author: William P. Nanavati

Contributions: Defined experimental design, completed lab and statistical analyses, and wrote the manuscript.

Co-Author: Eric C. Grimm

Contributions: Helped defined experimental design, provided funding and lab space, and helped write the manuscript.

Manuscript Information

William P. Nanavati and Eric C. Grimm

The Holocene

Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-reviewed journal
____ Accepted by a peer-reviewed journal
__X_ Published in a peer-reviewed journal

Volume 30, issue 1, pages 125-135, SAGE Journals
https://doi.org/10.1177/0959683619875807

CHAPTER TWO

HUMANS, FIRE, AND ECOLOGY IN THE SOUTHERN MISSOURI OZARKS

Abstract

A multiproxy study from Sweeton Pond, Ozark County, Missouri, provides a high-resolution 1900-year-long history of fire and vegetation in the southern Missouri Ozarks, where the modern vegetation is oak-hickory (*Quercus-Carya*) forest. Pollen and charcoal data are compared to dendroecological data to assess the long-term role of climate and fire in shaping local vegetation history. The activities of humans, particularly the Osage, are assessed from historical accounts and archaeological studies. Three cultural periods are superimposed on the vegetation and fire history: (1) Pre-Osage, ending ~1500 CE, 450 cal yr BP; (2) Osage, ~1500-1820 CE, 450-130 cal yr BP; and (3) Euro-American, since ~1820 CE, 130 cal yr BP. The Pre-Osage period was characterized by open oak-hickory forest and frequent low-severity fires, suggesting interannual climate variability as a driver of vegetation and fire occurrence. At ~1360 CE (590 cal yr BP), mesic tree species began to expand, while fire frequency remained low. During the Osage period beginning ~1500 CE (450 cal yr BP), mesic, fire-sensitive species, especially elm (*Ulmus*), expanded in conjunction with cool, effectively wet conditions in the southern Missouri Ozarks. Despite climate conditions that were seemingly less favorable for fire, the Osage expansion was accompanied by more fires and increased abundance of fire-dependent shortleaf pine (*Pinus echinata*). The expansion of both fire-sensitive and fire-dependent taxa coincident with Osage occupation of the area suggest that anthropogenic

fire and land use was local in nature and increased landscape heterogeneity prior to Euro-American settlement. The Euro-American period was characterized by increases in settlement size and extensive agriculture and logging activities in the area are evidenced by large increases in disturbance pollen types (e.g. *Ambrosia*-type), at the expense of shortleaf pine pollen. During this period, forest clearance led to fuel fragmentation, reducing fire activity; after 1920 CE, fire was actively suppressed.

Introduction

The role of fire in shaping the eastern woodlands of North America has long been debated (Day 1953, Russell 1983, Patterson and Sassaman 1988, Abrams 1992). However, along the western prairie-forest border of this region, ecologists generally agree that fire has had a major influence on forest distribution and composition (e.g. Wuenscher and Valiunas 1967, Grimm 1984, Batek et al. 1999, Williams et al. 2009b). Sedimentary pollen and charcoal records have been used to elucidate the relationship between vegetation and fire along the prairie-forest border in Wisconsin and Minnesota (Grimm 1984, Clark 1990, Camill et al. 2003, Umbanhowar et al. 2006, Williams et al. 2009a) and farther east into the northern conifer and hardwood forests (Lynch et al. 2006, Lynch et al. 2011). In contrast, little is known about the role of fire in shaping the prairie-forest border south of Wisconsin and Minnesota, where prairie borders *Quercus*-*Carya* forest.

Fire histories within predominantly *Quercus-Carya* forests are relatively short, based on historical (e.g., chronicles and Public Land Survey records) and dendroecological records that span the last 300 years (e.g., Cutter and Guyette 1994, Batek et al. 1999, Guyette et al. 2002, Stambaugh and Guyette 2006). In this study, we provide a high-resolution, 1900-year-long vegetation and fire history from *Quercus-Carya* forest in the southern Missouri Ozarks based on pollen and charcoal data from Sweeton Pond (36.7914º N, 92.2231º W, 304 m elev.; Fig. 2.1a-c), as well as published dendroecological data (Guyette and McGinnes 1982, Cutter and Guyette 1994). The high-resolution nature of the Sweeton Pond record is facilitated by a 7.92 m core that spans ~1900 years, with a deposition time averaging ~1-3 yr cm^{-1} (Fig. 2.2).

In this paper, our objectives are two-fold: (1) present a high-resolution 1900-yr-long vegetation and fire history from the southern Missouri Ozarks based on pollen, charcoal, and loss-on-ignition data and (2) assess the influences of American Indians and Euro-Americans on local vegetation and fire history, utilizing historical accounts and archaeological research (Fig. 1a; Schoolcraft 1821, Ponziglione 1882, Bailey 1973, Clayton et al. 1995, McMillan 2014a). To frame the discussion, the vegetation and fire history at Sweeton Pond was divided *a priori* into three sociocultural periods: leading up to the Osage occupation of the region ("Pre-Osage Period", until 1500 CE, ~450 cal yr BP), the Osage occupation and expansion ("Osage Period", 1500-1820 CE, ~450-130 cal yr BP), and following the displacement of the Osage by Euro-Americans ("Euro-American Period", since 1820 CE, ~130 cal yr BP). Dates are presented as Common Era (CE), calendar years before present (BP), and/or calibrated years before present (cal yr BP), where "present" is 1950 CE.

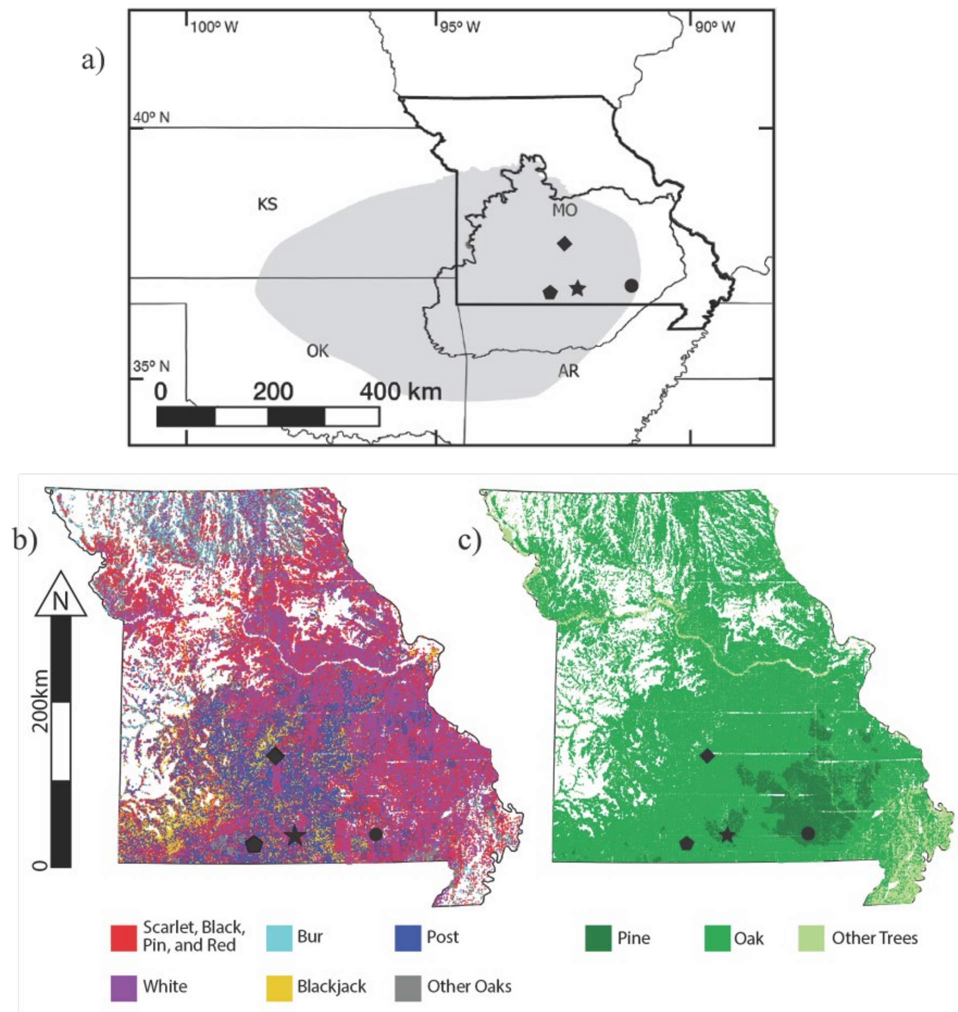

Figure 2.1: (a) Map of Sweeton Pond (star), Cupola Pond (circle, Jones et al. 2017) and dendroecological studies (diamond, Cutter and Guyette 1994; pentagon, Guyette and McGinnes 1984) within the Ozark Highlands (back border not associated with state boundaries), and the extent of Osage occupation (gray, Bailey 2001). (b-c) Map of oak species recorded in Public Land Surveys form 1815-1850 CE (Missouri Spatial Data Information Service, http://msdis.missouri.edu). (b) Scarlet (*Quercus coccinea*), black (*Q. velutina*), pin (*Q. palustris*), and red oak (*Q. rubra*) were grouped (red) because of likely misidentification by surveyors. Bur (*Q. macrocarpa*, light blue), post (*Q. stellata*, dark blue), white (*Q. alba*, purple), blackjack (*Q. marilandica*, yellow), and other oaks (gray) are also plotted. (c) Oak (green), pine (dark green), and other trees (light green) are plotted.

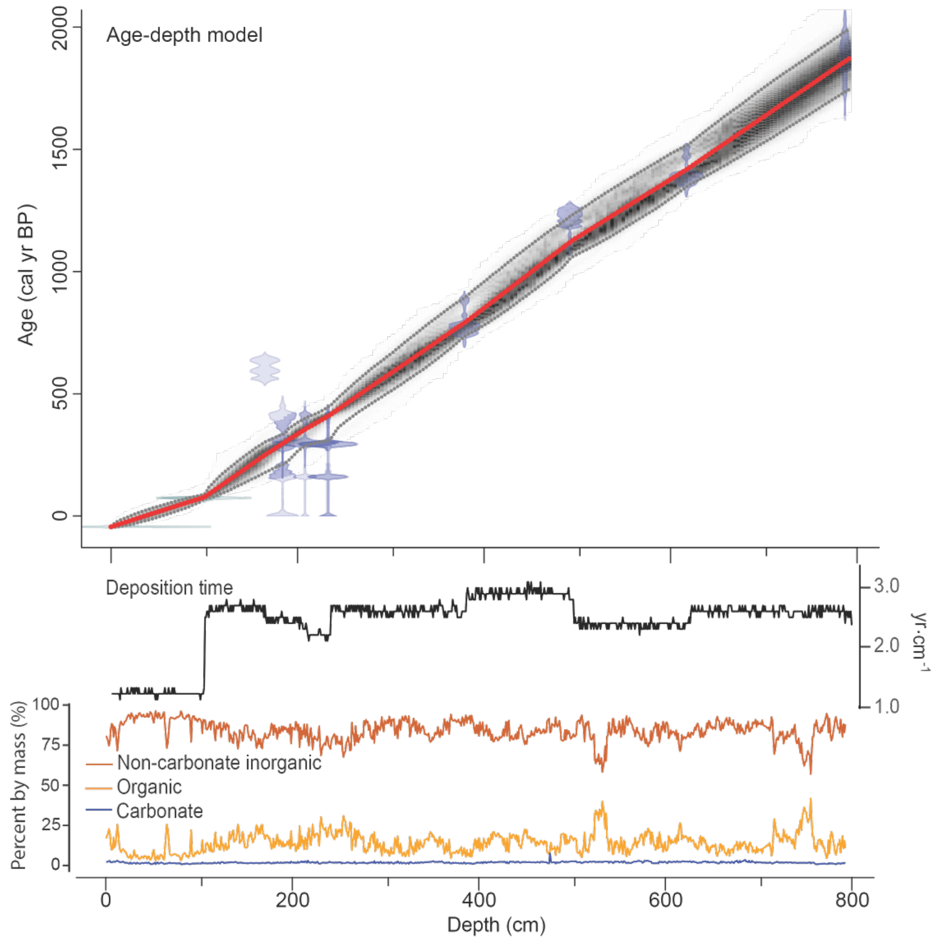

Figure 2.2: Age-depth model for Sweeton Pond using Bacon 2.2 (Blaauw and Christen, 2011). Bayesian priors were: acc.shape = 1.5, acc.mean = 2.5, mem.strength = 4, mem.mean = 0.7, thick = 5) Blue areas represent the probability distributions of the calibrated dates, the dotted red line shows the weighted mean age for each depth, and gray shading and dotted light gray lines depict the most likely age-depth model and 95% confidence intervals. The deposition time rate (yr cm^{-1}), percent composition of organic (light orange), carbonate (blue), non-carbonate inorganic (dark orange), and lithologic units are described in the text.

Study Area

The Ozarks are a dissected highland and biogeographical region located primarily in southern Missouri and northern Arkansas and bordered by the Missouri River to the north and the Arkansas Valley to the south (Fig. 2.1a; King 1973). Between 35-39º N latitude, the Ozarks are the westernmost extension of the Eastern Deciduous Forest, with prairie to the west. Today, the Missouri Ozarks are dominated by *Quercus-Carya* forest (Braun 1950, King 1973, Dyer 2006, Hanberry et al. 2014b). According to Public Land Survey (PLS) from 1815-1850 CE (135-100 BP), *Pinus echinata* was abundant in southeastern Missouri, until it was heavily logged at the end of the 19th century CE (Fig. 2.1c; Braun 1950, Holmes 1968, Dyer 2006).

Sweeton Pond is a small, deep sinkhole pond (0.5 ha, 14.6 m maximum depth) in northern Ozark County, Missouri (Fig. 1). The pond lies in a woodlot dominated *Quercus alba, Carya*, *Ulmus*, *Nyssa sylvatica*, and *Juglans nigra*. *Cephalanthus occidentalis* grows in the littoral zone, and *Salix nigra* is present along the shore. The pond is located near the extreme northwestern limit of *Pinus echinata*. Locally, *Pinus* was concentrated in the valleys of the North Fork River to the east of Sweeton Pond and Bryant Creek to the west until ~1870 CE (80 BP) (Fig. 2.1c; Holmes 1968).

Methods

Two cores, SWP-A and SWP-C, were obtained ~1 m apart with a 5-cm diameter Wright square-rod piston corer (Wright et al. 1984) from an anchored raft in 1994 CE (-44 BP). Cores were extruded in the field, wrapped in plastic wrap and aluminum foil, and transported to Illinois State Museum for storage and study. In the laboratory, cores were split lengthwise and preliminarily sampled for pollen at wide intervals. After initial analysis showed significant changes in pollen assemblages, cores were imaged at the National Lacustrine Core Facility at the University of Minnesota using a Geotek Geoscan-III at a 10 pixel mm^{-1} resolution. The SWP-A and SWP-C cores were then stratigraphically aligned and cut into 1-cm sections to form a continuous 792-cm-long composite core (Grimm et al. 2011).

Organic, carbonate, and non-carbonate inorganic content percent by mass values were estimated throughout the core using loss-on-ignition analysis (LOI; Heiri et al. 2001). Terrestrial plant remains and charcoal were collected for AMS radiocarbon dating. Radiocarbon ages were calibrated using OxCal 4.3 (Bronk Ramsey 2009) based on the IntCal13 calibration curve (Reimer et al. 2013). An age-depth model was developed from a series of two calendar dates and ten uncalibrated AMS radiocarbon dates using Bacon 2.2 (Blaauw and Christen 2011). The calendar ages entered into the Bayesian age-depth model were the core top at 1994 CE (-44 BP), and the rise of *Ambrosia*-type pollen resulting from local Euro-American settlement and land clearance, at 1876 CE (74 cal yr BP, 99.5 cm depth) (Holmes 1968).

Samples for charcoal analysis (1 cm^3 of sediment) were treated with a 10% solution of sodium pyrophosphate ($Na_4P_2O_7$), then gently washed through nested 250 and 180 µm sieves. Charcoal was identified and counted at 10–40× magnification (Whitlock and Larsen 2001). CharAnalysis version 1.1 (Higuera et al. 2009) and REDFIT spectral analysis (Schulz and Mudelsee 2002) were used to interpret charcoal data. Sedimentation rate was interpolated to a constant temporal resolution based on a fourth-order polynomial, fit to the slope of the median values from the Bacon age-depth model. In CharAnalysis, charcoal concentration values (particles cm^{-3}) were divided by an interpolated temporal resolution of 2 yr $sample^{-1}$, the median sampling resolution of the entire record, to provide an interpolated charcoal accumulation rate (CHAR, particles cm^{-}

^{2} yr^{-1}). A 100-yr moving median was used to describe background charcoal (BCHAR). Fire episodes were defined as the positive residual values from interpolated CHAR above the BCHAR values at the 99th percentile. To separate fire-related (i.e., signal) from non-fire related variability (i.e., noise), charcoal peak values had to surpass this percentile of a locally defined Gaussian distribution model (Higuera et al. 2009). CHAR data, calculated separately from CharAnalysis but also using the median values from the Bacon age-depth model, then underwent spectral analysis using REDFIT, to test for frequently re-occurring fire return intervals (FRI: years between fires) (Gilman et al. 1963, Brown et al. 2005).

Samples for pollen analysis were prepared with standard procedures using a microsphere tracer and mounted in silicone oil (Faegri et al. 1989). Pollen were identified and counted at 400–1000× magnification and preservation was noted. Percentages for terrestrial taxa were calculated based on a sum of at least 300 terrestrial pollen and spores, while percentages for aquatic taxa were based on a denominator of total pollen and spores (Grimm 1983, Higuera et al. 2009). Stratigraphic zonation of the pollen data was based on a stratigraphically constrained incremental sum-of-squares cluster analysis (CONISS) (Grimm 1987, Grimm et al. 2011).

PLS surveys first were conducted before legal settlement of the southern Missouri Ozarks and provide a record of tree distributions before intensive forest clearance and habitat modification by Euro-American settlers between 1815 and 1850 CE (135-100 BP). Maps of bearing-tree distributions from the original PLS were created in QGIS 2.8.1-Wein to reconstruct forest composition, including the distribution of *Pinus*, immediately prior to Euro-American settlement. The PLS surveyors partitioned the land into townships ~6 miles (9.66 km) on a side, and these were divided into 36 sections of ~1 square mile (1.6 km^2). To facilitate the reproducibility and future identification the corners, surveyors marked between two and four “bearing trees” at every section corner and two bearing trees at every quarter-section corner midway between the section corners. Surveyors recorded bearing trees in field notes by using the common name, diameter, and distance and bearing from the corner. The bearing-tree data for Missouri are available from the Missouri Spatial Data Information Service (http://msdis.missouri.edu). For this study, the bearing-tree distributions of *Pinus*, common *Quercus* taxa, and other trees were mapped for the entire state of Missouri (Fig. 1b-c).

Results

Chronology and Lithology

Ten macrobotanical samples were submitted from Sweeton Pond for AMS radiocarbon dating (Table 2.1). The age-depth model produced an extrapolated median basal age of the core of ~1872 cal yr BP. One of the 10 radiocarbon dates was rejected as too old (UCIAMS-135272), based on exceeding the 95% confidence interval of the Bayesian model (Fig. 2).

Table 2.1: AMS radiocarbon dates from Sweeton Pond

Lab number	Depth (cm)	Thickness (cm)	^{14}C yr BP	Material dated
UCIAMS-135272	165	1	615 ± 20	Charcoal
UCIAMS-155806	184	1	200 ± 20	Leaf fragments
UCIAMS-155807	184	1	300 ± 20	Charcoal
UCIAMS-135273	208	1	255 ± 20	Charcoal
UCIAMS-155808	232	1	240 ± 20	Charcoal
UCIAMS-155809	233.5	1	240 ± 20	Wood twig
UCIAMS-135274	379	1	870 ± 20	Deciduous tree leaf fragment
UCIAMS-135275	492	1	1265 ± 20	*Brasenia* seeds
UCIAMS-135276	617	1	1510 ± 20	Wood twig, partly charcoalized
CAMS-15293	787	1	1940 ± 60	Wood

Sediment from SWP-A and SWP-C was generally an organic-rich silty-clay with woody fragments and plant macrofossils throughout the core. LOI values (percent by mass) varied from 2.8 to 41.6% organic content, from 0.7 to 7.5% carbonate content, and from 57.0 to 96.3% non-carbonate inorganic (Fig. 2.2). Between 792-773 cm depth (~1870-1820 cal yr BP), the lithology was an organic-rich silty-clay with scattered gravel; deposition time was 2.7 yr cm^{-1} (Fig. 2.2). A twig recovered at 787 cm depth dated to 2038-1720 cal yr BP (Table 1). Between 773-234 cm depth (~1810-420 cal yr BP), the lithology consisted of organic-rich silty-clay loam with woody fragments and plant macrofossils; deposition time was 2.6 yr cm^{-1}. Between 234-139 cm depth (~420-

180 cal yr BP), the lithology was composed of coarsely laminated with gravel, woody fragments, and layers of plant macrofossils at 166-163 cm, 181-175 cm, and 234-233 cm depth; deposition time was 2.5 yr cm^{-1}. Between 139-0 cm depth (~180 to -44 cal yr BP), the sediment was an organic-rich silty-clay with woody fragments and plant macrofossils throughout; sedimentation rate increased to 1.6 yr cm^{-1}.

PLS vegetation reconstruction

PLS maps show that southern and southeastern Missouri were heavily forested prior to intensive Euro-American settlement, whereas northern and western Missouri supported a mosaic of forest and prairie, with trees mainly along river valleys and grassland generally in upland (Fig. 2.1b-c). *Quercus* was common in upland forested areas, but not in the riparian forest along Missouri and Mississippi rivers. *Pinus* grew on the more rugged terrain of southeastern Missouri located west of the Mississippi floodplain. Significant disjunct populations of *Pinus* occurred along the North Fork River and Bryant Creek, which lie ~5 km east and west of Sweeton Pond, respectively (Fig. 2.1c). Small populations of *Pinus* occurred in scattered locations across southern Missouri.

Because the individual maps for *Quercus coccinea*, *Q. velutina*, *Q. palustris*, and *Q. rubra* showed considerable variability and misidentification by surveyors, these were grouped together in Figure 1b. *Quercus alba* and the *Q. coccinea*, *Q. velutina*, *Q. palustris*, and *Q. rubra* group were common throughout Missouri. *Q. macrocarpa* occurred across the landscape in northern Missouri and in mainly riparian habitats throughout the rest of the state. However, the rectangular shape of the *Q. macrocarpa* distribution in northern Missouri and complete absence in extreme northeastern Missouri suggest that many surveyors misidentified it as *Q. alba*. Nevertheless, a geographic pattern does exist in the distribution of *Quercus* species favoring different growing environments. For example, the ecologically and morphologically similar *Q. stellata* replaced *Q. macrocarpa* on the uplands in central and southern Missouri. *Quercus alba* was particularly abundant in southcentral Missouri, including the area around Sweeton Pond, while *Q. marilandica* was most common in southwestern Missouri.

Pollen and charcoal results

Based on the CONISS cluster analysis, five stratigraphic zones (SWP-1 to SWP-5) were defined (Fig. 2.3).

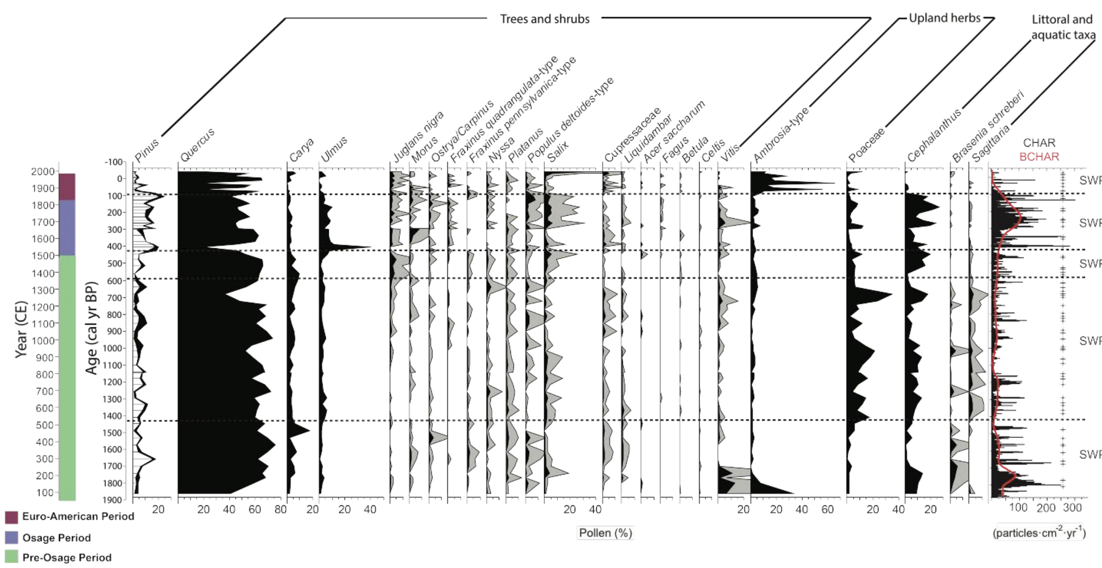

Figure 2.3: Pollen percentage diagram from Sweeton Pond showing dominant pollen taxa and charcoal data. Rarer taxa are provided with a 5x exaggeration (gray). Pollen zones were identified based on CONISS analysis (Grimm 1987). Charcoal accumulation rates (CHAR, black line) and background CHAR (red line) describe variations in fire activity, and significant charcoal peaks (+) represent fire episodes. Sociocultural periods used to discuss the record are provided and explained in the text.

Zone SWP-1 (792-628 cm depth, ~1870-1430 cal yr BP) was dominated by *Quercus* (41.6-76.4%), *Carya* (1.9-18.0%), and *Pinus* (2.8-18.0%) after an initial period between 792-724 cm (~1870-1620 cal yr BP) of elevated *Vitis* (<1.0-12.9%), *Ambrosia*-type (<1.0-34.0%), *Brasenia schreberi* (<1.0-5.9%), and *Cephalanthus* (4.0-13.9%).

Between 792 and 780 cm depth (between ~1870 and 1840 cal yr BP), CHAR ranged from 18.9 to 67.7 particles cm^{-2} yr^{-1} (Fig. 2.3). CHAR was elevated between 18.5 and 276.5 particles cm^{-2} yr^{-1} from 780 to 758 cm depth (from ~1840 to 1780 cal yr BP), decreased to 2.2 particles cm^{-2} yr^{-1} at 668 cm depth (~1540 cal yr BP) and was between 1.3 and 130.8 particles cm^{-2} yr^{-1} at the top of Zone SWP-1. BCHAR increased from 25.5 to 95.9 particles cm^{-2} yr^{-1} from 792 to 751 cm depth (from ~1870 to 1760 cal yr BP) and decreased to 7.0 particles cm^{-2} yr^{-1} at 628 cm depth (~1440 cal yr BP). FRI averaged 27.1 yr $fire^{-1}$ and 16 peaks were recorded (Fig. 4). Peak magnitude (particles cm^{-2} $peak^{-1}$) was between 4.7 and 6488.3 particles cm^{-2} $peak^{-1}$, with a median of 176.5 particles cm^{-2} $peak^{-1}$ (Fig. 2.4).

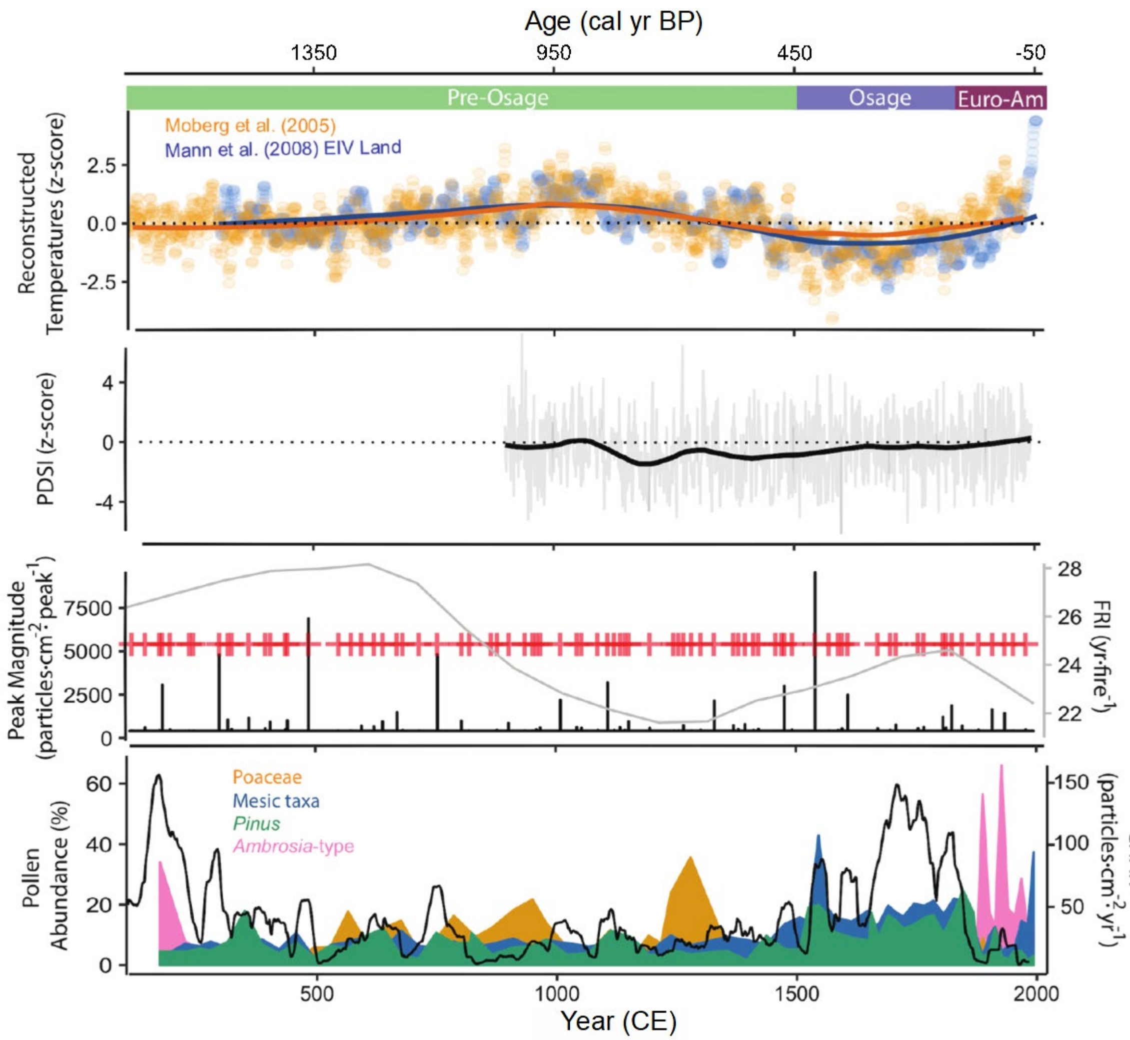

Figure 2.4. Temperature reconstructions from Moberg et al. (2005) (orange) and Mann et al. (2008) (blue, EIV land) are plotted by z-score. The annual (gray) and smoothed (black) PDSI for the Ozark region is provided, beginning 899 CE (*ca.* 1051 cal yr BP) (Cook et al. 2010). Significant peaks are plotted (red +) with their magnitudes (black) and fire return intervals (gray). Percent pollen abundance of Poaceae (orange), mesic taxa (i.e., *Ulmus*, *Fraxinus quadrangulata*-type, *Juglans nigra*, *Morus, Ostrya/Carpinus,* and *Populus deltoides*-type combined; blue), *Pinus* (green), and *Ambrosia*-type (pink) are overlaid and plotted with charcoal accumulation rate (black).

Zone SWP-2 (628-304 cm depth, ~1430-590 cal yr BP) featured increased Poaceae (2.1-35.6%), *Cephalanthus* (1.8-17.8%), and *Sagittaria* (<1.0-3.2%) and lower percentages *Quercus* (36.5-74%).

In Zone SWP-2, CHAR was between 0.0 and 178.6 particles cm^{-2} yr^{-1} (Fig. 3). BCHAR was between 5.9 and 26.8 particles cm^{-2} yr^{-1}, FRI averaged 24.2 yr fire^{-1}, and 39 peaks were recorded (Fig. 4). Peak magnitude ranged from 1.3 to 4404.1 particles cm^{-2} peak^{-1}, with a median of 130.3 particles cm^{-2} peak^{-1}.

Zone SWP-3 (304-229 cm depth, ~590-400 cal yr BP) was marked by increased values of *Salix* (<1.0-5.0%), *Nyssa* (<1.0-1.4%), and *Juglans nigra* (<1.0-5.1%), while Poaceae (3.7-12.5%), *Brasenia schreberi* (2.3-20.2%), and *Sagittaria* (<1.0%) decreased.

In Zone SWP-3, CHAR rose to between 0.4 and 378.3 particles cm^{-2} yr^{-1} (Fig. 3). BCHAR was between 16.2 and 22.5 particles cm^{-2} yr^{-1} FRI was 22.3 yr fire^{-1} and 13 peaks were identified (Fig. 4). Peak magnitude ranged from 1.9 to 9132.6 particles cm^{-2} peak^{-1}, with a median of 115.3 particles cm^{-2} peak^{-1}.

In Zone SWP-4 (229-102 cm depth, ~400-80 cal yr BP), *Pinus* (8.1-24.8%), *Ulmus* (3-40%), *Populus deltoides*-type (<1.0-7.8%), *Salix* (<1.0-6.2%) and *Fagus* (<1%) increased in abundance; while Poaceae (1.0-13.1%), *Brasenia schreberi* (<1%), and *Sagittaria* (<1%) continued to decrease.

In Zone SWP-4, CHAR was between 2.9 and 414.5 particles cm^{-2} yr^{-1} (Fig. 3). BCHAR ranged from 15 to 21 particles cm^{-2} yr^{-1} and averaged 14 particles cm^{-2} yr^{-1}. Sixteen peaks were identified and the FRI was 16.3 yr fire^{-1} (Fig. 4). Peak magnitude was between 11.2 and 2084.7 particles cm^{-2} $peak^{-1}$, with a median of 184.9 particles cm^{-2} $peak^{-1}$.

In Zone SWP-5 (102-0 cm depth, ~80- -44 cal yr BP), *Ambrosia*-type increased (10.3-66.0%), and *Pinus* (1.7-12.2%), *Quercus* (16.6-65.6%) and *Cephalanthus* (<1-2.8%) decreased. This pollen assemblage resembled modern surface samples taken elsewhere in the Ozarks (Peterson 1978).

In Zone SWP-5**,** CHAR decreased to between 0 and 190 particles cm^{-2} yr^{-1} (Fig. 3). BCHAR during this period ranged from 3 to 21 particles cm^{-2} yr^{-1}, and averages 6 particles cm^{-2} yr^{-1}, with a FRI of 22.3 yr $fire^{-1}$ and six peaks in CHAR (Fig. 4). Peak magnitude in Zone SWP-5 was between 16.1 and 1237.8 particles cm^{-2} $peak^{-1}$, with a median of 79.4 particles cm^{-2} $peak^{-1}$.

REDFIT spectral analysis of the CHAR data from Sweeton Pond shows that fire-episode frequencies varied throughout the record, surpassing a chi-squared test with 90%, 95%, and 99% confidence intervals (CI; Fig. 2.5). Significant FRIs (above a CI of 95%) occurred at intervals of between 5 and 10 yr $fire^{-1}$. Highly significant FRIs (above CI of 99%) occurred at 6 and 8 yr $fire^{-1}$. The only FRI to surpass the 99.87% false alarm CI occurred at 7 yr $fire^{-1}$.

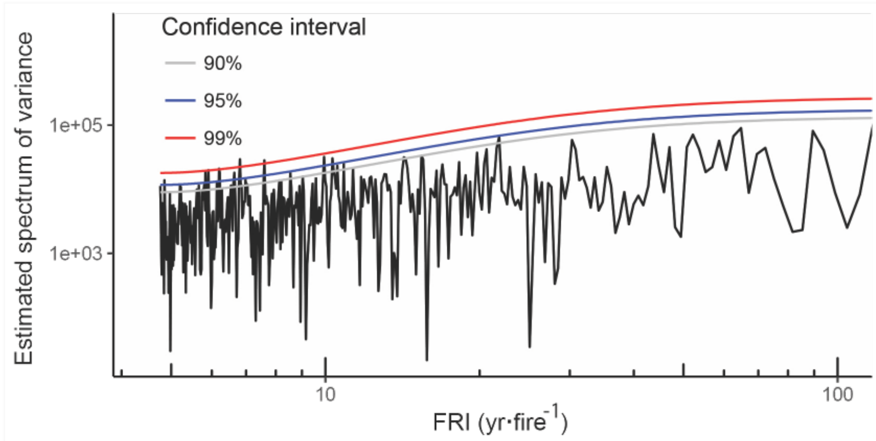

Figure 2.5: Results of REDFIT spectral analysis are plotted. CI is provided and a false alarm CI of 1-n^{-1} – where n is the number of data points – is used in the text to highlight frequencies with the least probability of being the result of red noise (Thomson 1990, Schulz and Mudelsee 2002). Here, the false alarm CI is 99.87% (n=792).

Discussion

Northern Hemispheric temperature reconstructions show a significant warming trend from 600 to 1350 CE (~1350-600 cal yr BP) encompassed the Medieval Climate Anomaly (~950-1250 CE, 1000-700 cal yr BP; MCA). This period of warming was followed by cooler temperatures from 1350 to 1900 CE (~600 to 50 cal yr BP), that encompassed the Little Ice Age (~400-1750 CE, 550 to 250 cal yr BP, LIA) (Fig. 2.4; Moberg et al. 2005, Mann et al. 2008). The local Palmer Drought Severity Index (PDSI) is available from 899 CE (~1051 cal yr BP) (Fig. 2.4; Cook et al. 2010). Smoothed PDSI values decreased from 1060 to 1190 CE (~890-760 cal yr BP) suggesting that aridity increased. After 1190 CE (~760 cal yr BP) smoothed PDSI increased to zero by 1930 CE (~20 cal yr BP) suggesting that although conditions remained dry, aridity decreased through present.

El Niño-Southern Oscillation (ENSO) was also a driver of climatic conditions throughout the Sweeton Pond record, especially given that ENSO frequency has been elevated since ~50 BCE (2000 cal yr BP) (Moy et al. 2002). Modern atmospheric and climatic research show that El Niño events are associated with increased summer precipitation, which can lead to increased fuel biomass, while La Niña events are associated with earlier, warmer, and drier summers across Missouri, which increases fuel flammability (Ratley and Lupo 2002, Newberry et al. 2016, Henson et al. 2017).

Synthesizing the paleoecological, historical, and archaeological records with independent climate data allows us to address how changes in climate and land use have altered vegetation and fire history in the Missouri Ozark ecosystem. Here, we delineate three socioecological periods: (1) Pre-Osage, ending as early as 1500 CE (~450 cal yr BP); (2) Osage, 1500-1820 CE (~450-130 cal yr BP); and (3) Euro-American, since 1820 CE (~130 cal yr BP).

Pre-Osage period

(ending 1500 CE, ~450 cal yr BP)

From ~110 to 1500 CE (1840-450 cal yr BP), high percentages of *Quercus* and *Carya* pollen indicate that the Sweeton Pond was surrounded by *Quercus-Carya* forest (Fig. 3). High pollen values of the littoral shrub *Cephalanthus* and aquatic *Brasenia* at the base of the core (~110-500 CE, 1840-1400 cal yr BP; Zone SWP-1), and the presence of *Sagittaria* pollen between ~550 and 1200 CE (1400-750 cal yr BP), suggest that the pond was initially shallow. At ~550 CE (1400 cal yr BP; Zone SWP-2), Poaceae pollen abundance increased while that of *Quercus* decreased but remained dominant, suggesting formation of either prairie openings, savanna, or parkland vegetation coincident with the warm and dry conditions (Fig. 2.3 and 2.4) (Moberg et al. 2005, Mann et al. 2008, Cook et al. 2010). Poaceae pollen reached its highest abundance in the record by ~1200 CE (750 cal yr BP), then abruptly declined as percentages of pollen from mesic taxa, *Juglans nigra*, *Nyssa*, and *Salix*, increased through ~1360 CE (590 cal yr BP) (Zone SWP-3, Fig. 3; Fig. 4). After ~1200 CE (750 cal yr BP), pollen from littoral shrub *Cephalanthus* and aquatics *Brasenia* and *Sagittaria* decrease, suggesting that water depth increased at Sweeton Pond. These changes in the pollen record suggest the development of mesic vegetation and a shift to more humid conditions between ~1200-1360 CE (750-590 cal yr BP), coincident with a cool and effectively wet climate (Fig. 2.3; Fig. 2.4) (Moberg et al. 2005, Mann et al. 2008, Cook et al. 2010). Following a brief period of elevated CHAR from ~120 to 280 CE (1830-1670 cal yr BP), CHAR was continuous but low from ~280 to 1500 CE (1670-450 cal yr BP), suggesting low-severity fires typical of modern surface fires in open *Quercus*-*Carya* forest (Fig. 4).

Prior to ~1500 CE (450 cal yr BP), human occupation of the region was likely by small, seasonal hunting parties (Wood and McMillan 1976, McMillan 2014a). Archaeological sites in the Ozarks, such as the Big Eddy site (37.72ºN, 93.72ºW; 168 km from Sweeton Pond) and Rodgers Shelter (38.09ºN, 93.35ºW; 178 km from Sweeton Pond), demonstrate transient populations in the region throughout the Paleoindian (~9000-7600 BCE, 10,950-9550 cal yr BP), Archaic (~7600-550 BCE, 9550-2500 cal yr BP), and Woodland (~550 BCE - 900 CE, 2500-1050 cal yr BP) periods (Wood and McMillan 1976, Klippel et al. 1978, Ray et al. 1998, Wolverton 2005). Although the

Mississippi and Ohio River valleys were heavily populated by agricultural Mississippian societies after 900 CE (1050 cal yr BP; peaking by ~1120 CE, 830 cal yr BP), the Ozark Highlands were not heavily occupied until major Euro-American settlement in the 19th century CE (Holmes 1968, Pauketat 2003, Bird et al. 2017). Human influence on the landscape in the southern Missouri Ozarks was indistinguishable from that created by natural disturbance processes (e.g., lightning-started fires), in contrast with the great influence of the large Mississippian populations on the landscapes of the Mississippi and Ohio River valleys (Muñoz et al. 2014, Bird et al. 2017).

Osage Period

(1500-1820 CE ~450-130 cal yr BP)

Between ~1500 and 1820 CE (450-130 cal yr BP; Zones SWP-3 and SWP-4), pollen from mesic taxa expanded, particularly *Ulmus*, but also *Fraxinus quadrangulata*-type, *Juglans nigra*, *Morus, Ostrya/Carpinus,* and *Populus deltoides*-type; while *Quercus*, *Carya*, and Poaceae pollen declined (Fig. 2.3 and Fig. 2.4). These mesic taxa likely grew primarily in riparian habitats or on moist soils, and expanded in mesic habitats, coincident with a cool and effectively wet climate (Fig. 4) (Moberg et al. 2005, Mann et al. 2008, Cook et al. 2010). At the same time, *Pinus* subgen. *Pinus* pollen abundance increased, suggesting that fire-dependent *Pinus* (most likely *P. echinata*) also expanded in the North Fork and Bryant Creek valleys on either side of Sweeton Pond, forming mixed *Quercus-Carya-Pinus* forest.

At Cupola Pond, which lies within the main range of *Pinus* in the Ozarks to the east of Sweeton Pond (Fig. 2.1), a slight increase in *Pinus* about ~3050 BCE (5000 cal yr

BP) may represent establishment of small *Pinus* populations in the region; however, the certain establishment of *Pinus* in the Ozarks occurred less than 2000 years ago, when *Pinus* pollen increased to about 20% (Jones et al. 2017). At Sweeton Pond, *Pinus* pollen abundance fluctuated between 5% and 10% until ~1550 CE (400 cal yr BP), when it reached values of 15-20%, similar to those at Cupola Pond. Low values of *Pinus* prior to ~1550 CE (400 cal yr BP) may have come from small local populations or long-distance transport from the main Ozark range to the east. The subsequent increase after ~1550 CE (400 cal yr BP) is attributed to local establishment of *P. echinata* near Sweeton Pond. The modern range of *Pinus echinata* is in the warm, humid southeastern United States, where January temperatures range from 0-12°C, and 25-30°C in July, with an annual precipitation of 102-152 cm yr^{-1} (Lawson 1990, Webb et al. 1993, Williams et al. 2006). The species is shade intolerant and highly dependent on fire for regeneration (Lawson 1990, Guyette et al. 2007).

Increased CHAR from ~1550 to 1820 CE (400-130 cal yr BP) suggests that fire activity increased concomitant to the formation of mixed *Quercus*-*Carya*-*Pinus* forest near Sweeton Pond and a climate that was cooler and effectively wetter than before (Fig. 2.3 and 2.4). Increased fire activity despite effectively wetter conditions could have resulted from greater fuel biomass and/or increased ignition. Although fuel loads and fire activity in shortgrass prairie are positively correlated with moisture (Nelson et al. 2004, Grimm 2011), this relationship may not hold for higher biomass vegetation types, such as tall-grass prairie and savanna (Nelson et al. 2006). Indeed, within the forest but near the prairie-forest border in northwestern Minnesota, Clark (1988a, 1990) documented decreased fire frequency with increased humidity over the past 750 years, suggesting that increased fire ignition was an important driver of increased fire activity after ~1550 CE (400 cal yr BP).

Notably, fire activity did not increase with the initial expansion of mesic species ~1350 CE (600 cal yr BP; Zone SWP-3), but with Osage expansion 150-200 years later. Archaeological and historical evidence suggests that the Osage arrived into the region between the end of the 15th and the beginning of the 16th centuries CE (Bailey 2001, McMillan 2014b) (Fig. 2.1a). The Osage subsisted on mixed hunter-gatherer-horticulturist strategies, living primarily in permanent villages on the prairie-forest border (Bailey 1973). Osage hunting parties were short, seasonal ventures into the prairie for bison and into the Ozark woodlands for elk and deer. Following French contact at ~1680 CE (270 cal yr BP), the Osage expanded their territory and increased the scale of their hunting and warring to provide game and slaves in exchange for French goods, likely utilizing fire in the process (Schoolcraft 1821, Schoolcraft 1853, Ponziglione 1882).

Given that this region has few lightning fires (<1 per 4000 km^2 annually, accounting for ~1% of fire occurrences in recent decades) (Schroeder and Buck 1970, Guyette et al. 2002, Stambaugh and Guyette 2008) and that the arrival of the Osage coincided with increased CHAR and *Pinus* pollen, we propose that the combination of increased humidity and ignition fires by the Osage promoted the expansion of *P. echinata* in the North Fork and Bryant Creek valleys. The expansion of both fire-sensitive and fire-dependent vegetation coincident with Osage occupation of the area suggest that anthropogenic fire and land use was local in nature and increased landscape heterogeneity prior to Euro-American settlement. This hypothesis supports that of Stambaugh and Guyette (2008), who documented decreasing fire activity with distance from the rivers, which were foci for human habitation and travel in the Current River watershed of southeastern Missouri, between 1620 and 1850 CE (330-170 cal yr BP).

Euro-American Period

<u>(1820 CE, ~130 cal yr BP, to present)</u>

After about ~1820 CE (130 cal yr BP), pollen from disturbance taxa, *Ambrosia*-type, increased dramatically at the expense of *Pinus*, *Quercus*, and *Carya* pollen, concomitant to the forced removal of the Osage from the Missouri Ozarks and Euro-American settlement and population growth following the end of the U.S. Civil War, from 1861 to 1865 CE (89-85 BP) (Fig. 2.3; Holmes 1968, Bailey 2001). The timber and mining industries spurred Euro-American immigration to the post-war Missouri Ozarks. By 1880 CE (70 BP), most of the *P. echinata* in Ozark county had been removed by logging (Holmes 1968), which is clearly represented by a sharp decline in *Pinus* pollen from ~1850-1890 CE (100-60 cal yr BP; from 24.8% to 2.4%). At Sweeton Pond, charcoal is nearly absent after ~1890 CE (60 cal yr BP), pre-dating the active suppression of wildfires that began in the 1920s CE (after 30 BP; Fig. 2.3 and 2.4). Early absence of fire on the landscape probably relates to fuel fragmentation around Sweeton Pond (Guyette and McGinnes 1982, Cutter and Guyette 1994, Guyette et al. 2002). Since the beginning of fire suppression efforts, fire-intolerant broadleaf species have been replacing *Quercus*-*Carya*-*Pinus* forest throughout the Missouri Ozarks (Hanberry et al. 2014a, Hanberry et al. 2014c).

In addition, row-crop farming for wheat and corn led to an increase in soil runoff into the Sweeton Pond catchment, which is visible after ~1880 CE (70 cal yr BP), when deposition time and non-carbonate inorganic content percent by mass increased (Fig. 2). As erosive row-crop farming was replaced by first by pasturing and then zero-till practices, organic content percent by mass rebounded and non-carbonate inorganic content decreased nearly 15% to pre-Euro-American settlement levels.

Summary of fire severity and return interval

Despite the variation in vegetation and the magnitude of charcoal peaks throughout the record (Fig. 2.3 and 2.4), the CharAnalysis-reconstructed FRI remained relatively invariant, between 22 and 28 years fire^{-1}, which suggests that variation in fuel load was not the primary factor driving fire-episode frequency, as it was, for example, in northwestern Minnesota, where FRI varied as much as 35 years fire^{-1} with changes in vegetation and climate (Clark 1988b, 1990). REDFIT spectral analysis of the CHAR data showed that FRI was close to 5-10 yr fire^{-1} (Fig. 2.5). The 5-10 yr fire^{-1} FRI from REDFIT is supported by nearby fire scar records, which suggest a FRI of between 3 and 4 yr fire^{-1} prior to Euro-American settlement (Guyette and McGinnes 1982, Cutter and Guyette 1994). The 5-10 yr periodicity in FRI recorded at Sweeton Pond falls within the ENSO band (Moy et al. 2002), which suggests that ENSO has been a driving factor for moisture variability for the past 1900 years in the Ozark region (Guyette et al. 2006).

Charcoal peak magnitude (particles cm^{-2} peak^{-1}) is a measure of the amount of charcoal accumulated in a given peak and can be affected by fire episode size, severity, proximity to the catchment area, and/or taphonomic processes (Whitlock and Millspaugh

1996, Clark et al. 1998, Higuera et al. 2007, Walsh et al. 2010). Given the overestimation of FRI by CharAnalysis as compared to that from REDFIT spectral analysis and nearby fire-scar records, we assume that the charcoal peaks identified by CharAnalysis were produced by fire episodes in close proximity to Sweeton Pond. The local source area (<3 km radius from the site) of charcoal peaks has been noted in other studies (Higuera et al. 2010, Kelly et al. 2011). Furthermore, we doubt that erosion played a significant role in peak magnitude because non-carbonate inorganic content varies little until the establishment of row cropping ~1880 CE (70 cal yr BP), suggesting that the influx of soil surrounding the pond was minimal and that any re-deposition of charcoal particles was likely registered as BCHAR. We therefore interpret high peak magnitudes as fire episodes of greater size and/or severity, as compared to fire episodes with of low peak magnitude (Higuera et al. 2014).

Median charcoal-peak magnitude was highest in Zones SWP-1 (~80-520 CE, 1870-1430 cal yr BP; 176.5 particles cm^{-2} peak^{-1}) and SWP-4 (~1550-1870 CE, 400-80 cal yr BP; 184.9 particles cm^{-2} peak^{-1}), indicating greater size and/or severity of fire episodes during these times (Fig. 2.4). During Zones SWP-2 and SWP-3 (~520-1550 CE, 1430-400 cal yr BP), median peak magnitude was lower, but still contained 8 of the recorded 14 largest charcoal peaks (>1000 particles cm^{-2} peak^{-1}). Zones SWP-2 and SWP-3 coincide with a period of increased Northern Hemisphere temperature from ~900 to 1400 CE (1050-550 cal yr BP) (Moberg et al. 2005, Mann et al. 2008, Mann et al. 2009), encompassing the MCA. Increased Poaceae pollen abundance at the expense of arboreal pollen taxa during Zones SWP-2 and SWP-3, higher Northern Hemisphere temperatures, and low smoothed PDSI values suggest that this period was warm and effectively dry. The occurrence of high individual peak magnitudes amidst generally lower CHAR and median peak magnitudes during Zones SWP-2 and SWP-3 suggests that surface fires were punctuated by large and/or severe fire episodes between ~520 and 1550 CE (1430-400 cal yr BP).

The highest peak in the record (9132.6 cm^{-2} $peak^{-1}$, at ~1540 CE, 410 cal yr BP) occurred in Zone SWP-3 and was followed by increased BCHAR during Zone SWP-4, suggesting that fire activity increased between ~410 and 80 cal yr BP. Somewhat paradoxically, increased abundance of mesic arboreal taxa and low reconstructed temperatures suggest that this period was cooler and wetter than before, coincident with LIA (Moberg et al. 2005, Mann et al. 2008, Mann et al. 2009). High BCHAR in Zone SWP-4 and decreased FRIs reconstructed from fire scars (Guyette et al. 2002) between ~1550 and 1870 CE (400-80 cal yr BP) suggest that fire activity increased that likely as a result of increased fire ignition near Sweeton Pond. Given the extremely low modern occurrence of lightning-started fires in the region, we ascribe the increase in fire activity during this period first to the Osage, who extensively occupied the area until ~1820 CE (130 cal yr BP) (Bailey 1973, 2001), and then later to Euro-American land clearance.

Conclusion

Multi-proxy data from Sweeton Pond combined with published dendroecological, archaeological, and historical records, demonstrate that the vegetation and fire history of the southern Missouri Ozarks was altered by past changes in climate and land use over the last 1900 years. Interannual climate variability was the primary driver of changes in vegetation and fire activity prior to ~1500 CE (450 cal yr BP), when a generally warmer and drier climate than at present favored open *Quercus-Carya* woodland. After ~1500 CE (450 cal yr BP), cool temperatures led to an expansion of mesic *Quercus-Carya* forest. The hunting and warring efforts of the Osage, especially following French contact, led to high fire activity between ~1540 and 1820 CE (410 and 130 cal yr BP) despite independent evidence of cool and less arid conditions coeval with the Little Ice Age. These climate conditions, along with increased fire activity facilitated the spread of *Pinus echinata* at the time of Osage occupation. Fire activity declined after ~1870 CE (80 cal yr BP) following displacement of the Osage and expansion of Euro-American agricultural, logging, and mining activities. The change in fire activity to levels well below the range of fire activity from the last 1900 years is attributed to fuel fragmentation and later fire suppression efforts. The Sweeton Pond case study provides an example of how both American Indian and Euro-American populations helped shape the local vegetation and fire history through changes in land use practices.

Acknowledgements

This article benefitted from research supported by the WildFIRE PIRE project (National Science Foundation [NSF] grant OISE 0966472) and NSF award GSS-1461590, as well as extensive input from C. Whitlock. Acknowledgement goes to P. Mueller for initial pollen preparation and analysis and to K. Gates for assistance in the design of Figure 1a-c. Field assistance was provided by P. Mueller, R.B. McMillan, B. Styles, T. Stafford, and R. Toomey. The Sweeton Pond cores are deposited at the National Lacustrine Core Facility (LacCore) at the University of Minnesota. The pollen and charcoal data are deposited in the Neotoma Paleoecology Database (www.neotomadb.org): Dataset IDs 46128-46132.

CHAPTER TREE

A HOLOCENE HISTORY OF *Araucaria araucana* IN NORTHERNMOST PATAGONIA

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: William P. Nanavati

Contributions: Defined experimental design, completed field, lab, and statistical analyses, and wrote the manuscript.

Co-Author: Cathy Whitlock

Contributions: Helped defined experimental design, provided funding and lab space, and helped write the manuscript.

Co-Author: Valeria Outes

Contributions: Completed field, lab, and statistical analyses, and provided comments on manuscript.

Co-Author: Gustavo Villarosa

Contributions: Completed field, lab, and statistical analyses, and provided comments on the manuscript.

Manuscript Information

William P. Nanavati, Cathy Whitlock, Valeria Outes, Gustavo Villarosa

Journal of Biogeography

Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
_X_ Officially submitted to a peer-reviewed journal
____ Accepted by a peer-reviewed journal
___ Published in a peer-reviewed journal

Submitted 10 Feb. 2020

CHAPTER THREE

A HOLOCENE HISTORY OF *Araucaria araucana* IN NORTHERNMOST PATAGONIA

Abstract

In this chapter we evaluate the Holocene vegetation and fire dynamics of northernmost Patagonia (Argentina and Chile; 37-40°S) within the modern range of *Araucaria araucana* and describe how changes in climate and land use have influenced the local and regional environmental history. The local Holocene vegetation and fire history was reconstructed using sedimentary pollen and charcoal from Laguna Portezuelo (37.9°S, 71.0°W; 1730 m). These results were compared with other paleoecological sites in the region, independent paleoclimate records, and the regional human history. Steppe and moderate fire activity dominated the L. Portezuelo area throughout the Holocene. However, punctuated increases in *Nothofagus* pollen occurred after ~6590 cal yr BP, suggesting brief increases in forest cover and moisture in association with increased El Niño frequency. *Araucaria* pollen appeared at L. Portezuelo at ~6380 cal yr BP, but was low in abundance until ~340 cal yr BP, when it increased with elevated levels of charcoal. This increase in *Araucaria* and fire activity coincided with the influx of Mapuche American Indians into the region, who were known for *Araucaria* orcharding. Old-World pollen (e.g., *Plantago* and *Rumex*) increased in abundance prior to local Euro-American settlement. *Nothofagus* deforestation and the arrival of *Pinus* silviculture marked the 19th and 20th century Euro-American settlement. We conclude that: (1) Although *Araucaria* may have dominated glacial refugia, rapid warming and drying in

northernmost Patagonia during the late-glacial and early-Holocene periods decreased the species' abundance prior to ~7000 cal yr BP. In the middle and late Holocene, ENSO event frequency increased, increasing precipitation variability in the region. (2) Increased *Araucaria* and fire activity at L. Portezuelo after 460 cal yr BP suggest increased land use following an influx of the Mapuche American Indians into the region. (3) The early appearance of nonnative pollen taxa in the L. Portezuelo record indicates that the spread of Old-World weeds outpaced local Euro-American settlement.

Introduction

Although it is well established that climate and fire have greatly influenced the long-term dynamics of the Patagonian forest-steppe ecotone south of 41°S (Whitlock et al. 2006, Iglesias et al. 2014, Nanavati et al. 2019), the vegetation and fire history of Patagonia north of this latitude is poorly understood, given the paucity of well-dated records (i.e., Fletcher and Moreno 2012b, Abarzúa et al. 2014) (Table 1; Fig. 1). Here, we present a 11,100-year-long record of climate, vegetation, fire, and land use from Laguna Portezuelo (37.91°S, 71.04°W; 1733 m elev.; 1.66 ha; 5.6 m maximum water depth), along the forest-steppe ecotone of northernmost Patagonia (here defined as, 37-40°S).

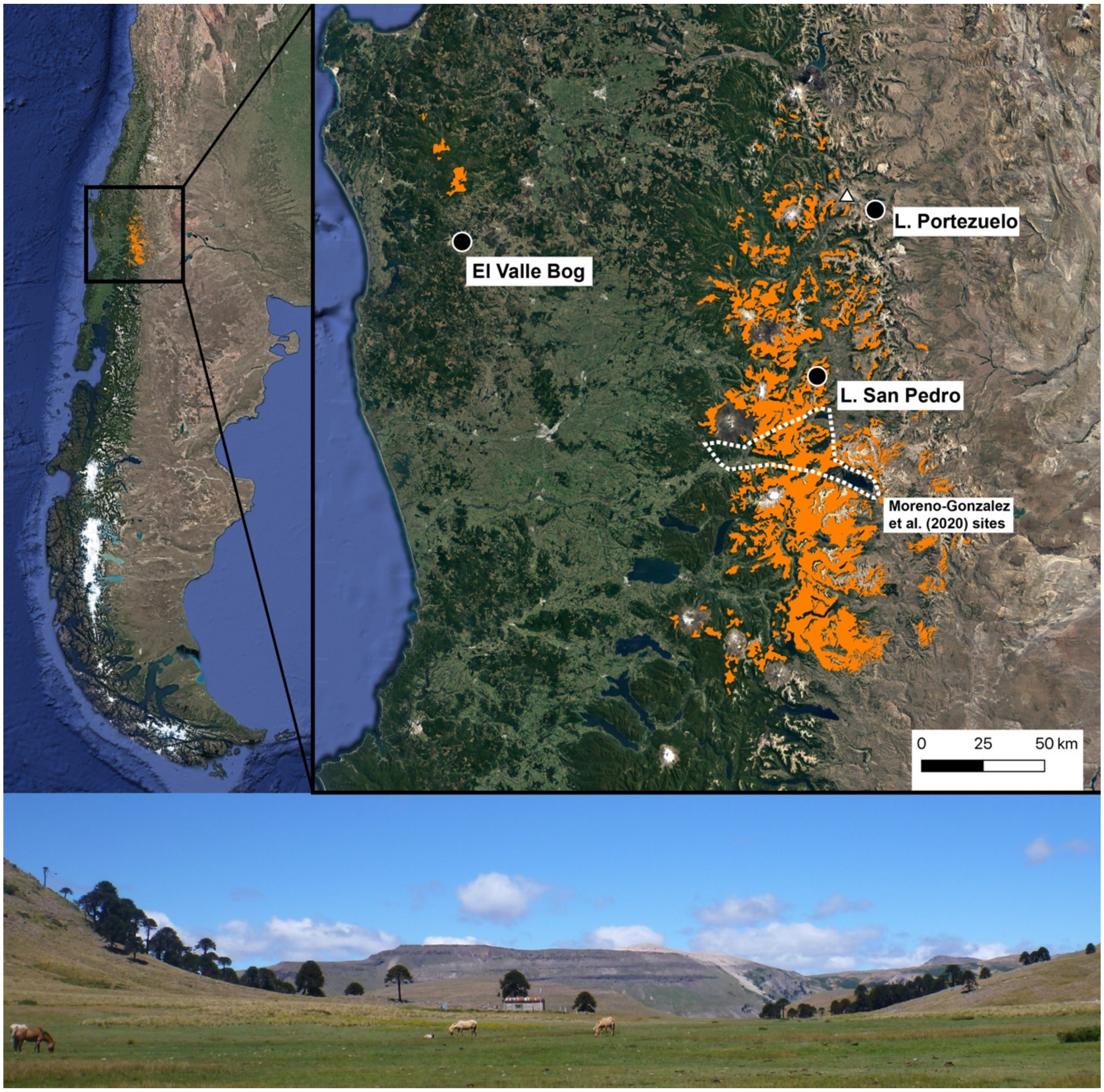

Fig 3.1. Map of southern South America, showing a conservative *Araucaria araucana* species distribution (orange; CONAF-CONAMA 1999, Lara et al. 1999). The inset map shows the location of L. Portezuelo and other sites discussed in the text (i.e., Fletcher and Moreno 2012b, Abarzúa et al. 2014, Moreno-Gonzalez et al. 2020). The triangle northwest of L. Portezuelo marks the Copahue stratovolcano. Satellite map data: Google, Maxar Technologies. Photo taken from L. Portezuelo (2013) facing a stand of *Araucaria araucana* about 0.5 km south of the site.

Table 3.1. Pollen and charcoal records discussed in text.

Site name	Lat. (°S)	Long. (°W)	Elev. (m)	Temporal range (~BP)	Pre-European vegetation**	Citation
Lagunas las Tortas	37.8	73.1	1225	6200 to 0	Valdivian forest with Araucaria	Villagrán (2001)
El Valle Bog*	38.1	73.0	70	26,500 to 0	*Nothofagus* forest with very few, scattered *Araucaria*	Abarzúa et al. (2014)
Lomocura	38.8	71.8	1015	75 to -66	*Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Laguna San Pedro*	38.4	71.3	913	1500 to -59	*Araucaria-Nothofagus* forest	Fletcher and Moreno (2012b)
Quinquen	38.6	71.3	1690	220 to -66	*Araucaria-Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Los Piñones	38.8	71.3	1280	70 to -66	*Araucaria-Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Koywija	38.9	71.2	1189	-5 to -60	*Araucaria-Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Paso del Arco	38.9	71.1	1200	2500 to 0	*Araucaria-Nothofagus* forest	Heusser et al. (1988)
Relem*	39.0	71.1	1265	360 to	Steppe with patches of *Araucaria*	Moreno-Gonzalez et al. (2020)
Laguna Portezuelo*	37.9	71.0	1730	11,100 to -62	Steppe with patches of *Araucaria*	This manuscript
Lonco Luan	38.6	71.0	1230	-30 to -64	Steppe with patches of *Araucaria*	Moreno-Gonzalez et al. (2020)

This northernmost Patagonia is home to the endemic and endangered *Araucaria araucana* tree, which presently grows along the Andes of Chile and Argentina (37-40°S) and in disjunct populations in the Cordillera de Nahuelbuta, Chile (Fig. 1) (Premoli et al. 2013). L. Portezuelo lies at the northeastern limit of *A. araucana* distribution, where the conifer forms an ecotone with Patagonia steppe. *A. araucana* trees at their northeastern limit grow on moist, south- and east-facing slopes in rocky settings. This conifer is a shade-intolerant species that tolerates surface fire, but has a limited capacity for seed dispersal (Veblen 1982, Sanguinetti and Kitzberger 2009, González et al. 2010). Members of the genus *Araucaria* were present throughout the Gondwanan supercontinent in the Mesozoic Era, when the Patagonian land area supported subtropical to warm-temperate conditions (Baldoni 1980, Kunzmann 2007). Since then, its distribution has become steadily restricted by Cenozoic cooling and aridity (Kunzmann 2007). Since the late 19th century CE, Euro-American settlement resulted in increased fire severity, logging, and livestock grazing in northernmost Patagonia, decreasing *A. araucana* distribution by ~60% to occupy a present area of less than 400 km^2 (González et al. 2010, Mundo et al. 2013, Premoli et al. 2013). This recent decline of *A. araucana* warranted its listing as an endangered species by the International Union for Conservation of Nature (Premoli et al. 2013).

The L. Portezuelo reconstruction is compared with independent climate, paleoecological, archaeological, and historical information from northernmost Patagonia to address three questions: (1) What is the Holocene vegetation and fire history of northernmost Patagonia, east of the Andes? (2) What is the history of *A. araucana* at its northeastern limit? (3) How have climate and humans influenced the dynamics of *A. araucana* through time? Below, all dates are provided in calibrated radiocarbon years before 1950 Common Era (henceforth, BP) and/or in years Common Era (CE).

Study Area

L. Portezuelo lies in an ice-block depression formed on a lateral moraine of late-Pleistocene age. It is fed by a spring from the southwest and has a small outflowing stream that drains into the Lago Caviahue. The site is 13 km southeast of the active Copahue stratovolcano (Fig. 1).

Along the Patagonian Andes (36-55°S), annual precipitation ranges from >3000 mm yr^{-1} at the crest of the Andes to <100 mm yr^{-1} in the steppe to the east (Garreaud et al. 2013). The resulting precipitation gradient produces a transition in vegetation from wet forest in the western Andean foothills, to alpine heathland at high elevations, dry forest along the eastern foothills, and steppe at low elevations. Near L. Portezuelo, average annual temperature is 8.8°C, with an average winter temperature of 2.8°C (DJF) and 15.1°C in summer (JJA) (University of East Anglia Climatic Research Unit; Harris 2017). The area receives most of its annual precipitation, between May and August (average of 93.5 mm $month^{-1}$). The climate is influenced by El Niño-Southern Oscillation (ENSO), where El Niño events result in increased winter precipitation and warmer-than-average annual temperature, and La Niña results in decreased winter precipitation and cooler-than-average annual temperature (Garreaud et al. 2009).

The lake is surrounded by heavily grazed steppe with native taxa including *Acaena*, *Azorella trifulata*, *Berberis empetrifolia*, *Colliguaja integerrima*, *Chusquea*, *Fabiana* spp., *Stipa* spp., and members of Rhamanaceae (including *Ochetophila trinervis*). *A. araucana* grows above 1660 m elev. and less than a kilometer from the site (Fig. 1). *Nothofagus antarctica* is present in moist and protected habitats. *Scirpus* grows along the margin of L. Portezuelo, and *Myriophyllum* and *Potamogeton* are present as aquatics.

Humans were present in coastal Patagonia by ~14,500 BP (Dillehay et al. 2015) and east of the Andes by ~11,200 BP (Arias et al. 2012). The archaeological record suggests that groups were small in number, dispersed, and reliant on nomadic hunter-gather subsistence strategies until the late Holocene (Barberena et al. 2015, Perez et al. 2017). According to 19th-century travelers, American Indians in Patagonia used fire to signal distant parties, facilitate hunting, and improve grazing (Cox 1863, Musters 1871, Moreno 1897). The ethnographic record and isotopic analysis of human remains suggest that *Araucaria araucana* has been an important food source in northernmost Patagonia since ~11,000 years ago and that surface fires were used to promote tree establishment and facilitate piñón collection (Aagesen 2004, dos Reis et al. 2014, Gordón et al. 2016).

Methods

Three cores were collected February 2013 from the center of L. Portezuelo (LP13A-LP13C) with a 5-cm-diameter modified Livingstone piston corer and extruded in the field. Cores were wrapped in cellophane and aluminum foil for transport to the laboratory. A fourth core, LP13D, was retrieved with a polycarbonate tube using a UWITEC gravity corer. In the laboratory, cores were split longitudinally, lithology and tephra layers described (Villarosa et al. in prep). Organic, carbonate, and non-carbonate inorganic content was measured on 1 cm^3 samples with by weight-loss analysis. (LOI; Heiri et al. 2001). Cores LP13D and LP13A were correlated based on stratigraphy, chronology, and LOI results to create a composite core that was 719-cm long.

A Bacon Bayesian age-depth model was developed based on 11 AMS radiocarbon dates calibrated in Bacon using the SHCal13 calibration curve (Blaauw and Christen 2011, Hogg et al. 2016), the initial rise in *Pinus* (indicative of the arrival of *Pinus* plantations, ~1960 CE), tephra from the 2012 CE Copahue eruption, and 2013 CE collection date (Table 1). Tephra layers ≥0.5 cm in thickness were treated as instantaneous deposition events (i.e., "slump" in rbacon; Blaauw and Christen 2011). Mean accumulation rate was set to 20 yr cm^{-1} and section thickness was set to 10 cm. To address the age uncertainty of important events in the L. Portezuelo records, we present the 95% highest posterior density (HPD) interval, essentially Bayesian confidence limits calculated in rbacon.

Table 3.2. Calendar and AMS radiocarbon ages from L. Portezuelo.

Lab ID	Depth (cm)	Radiocarbon Age (^{14}C yr BP)	Calibrated Age (BP; 1-σ range)[a]
Core top	0.0	-63 ± 0.1[b]	
Copahue tephra	0.1-0.5	-62 ± 0.5[b]	
Pinus rise[c]	10.0-11.0	-23 ± 5[b]	
OS-144514	29.0-30.0	430 ± 15	495-465
D2	46.5-47.5	1770 ± 30	1700-1648, 1626-1593
Da3	78.0-79.0	2230 ± 30	2304-2235, 2203-2194, 2187-2151
D3	110.0-111.0	2630 ± 30	2757-2716
OS-144384	161.0-162.0	3400 ± 20	3635-3569
D4	251.0-252.0	3930 ± 30	4408-4287, 4264-4259
OS-144385	341.0-342.0	5490 ± 30	6292-6266, 6246-6212
D5	446.0-447.0	6450 ± 30	7415-7353, 7335-7302, 7296-7295
OS-144515[d]	552.0-553.0	9070 ± 40	10,233-10,188
D6	609.0-610.0	8340 ± 40	9415-9258
D7	717.0-718.0	9980 ± 40	11,394-11,255

[a] Calibrated with CALIB 7.10 using the ShCal13 calibration curve (Hogg et al. 2016, Stuiver et al. 2017).
[b] Dates for the core top, Copahue tephra, and *Pinus* rise are in calendar years before present.
[c] *Pinus* rise is indicative of the arrival of *Pinus* plantations to northernmost Patagonia, beginning in the 1970s CE.

[d] Date rejected by the 95% highest posterior density of the Bacon age-depth model.

Pollen was analyzed at 1-cm intervals for the top 39 cm to provide a high-resolution description of vegetation change during the last ~1000 years, and between 2- and 16-cm intervals for the remainder of the composite core. Samples were prepared with standard procedures (Faegri et al. 1989), and a tracer of *Lycopodium* spores was added to each sample to calculate pollen accumulation rates (PAR; grains cm^{-2} yr^{-1}). At least 1000 terrestrial pollen grains were counted for the first 10 cm of the composite core to increase the probability of recording rare taxa. Below 10 cm depth, at least 300 terrestrial pollen grains were tallied. Terrestrial pollen percentages were calculated based on a sum of all terrestrial pollen and spores. Percentages of aquatic and wetland taxa were based on a denominator of all pollen and spores. Local pollen zones were identified by visual inspection and CONISS (Grimm 1987).

Nothofagus dombeyi-type pollen in this region likely comes from *N. antarctica*, *N. dombeyi*, and/or *N. pumilio*. *N. obliqua*-type pollen includes *N. alpina*, *N. glauca*, and/or *N. obliqua* from extralocal sources. We used established modern pollen-vegetation relationships from east of the Andes between 40 and 45°S to discriminate major vegetation formations: steppe (<41% *N. dombeyi*-type pollen), shrubland or open forest (41-67% *N. dombeyi*-type pollen), and closed forest (>67% *N. dombeyi*-type pollen) (Iglesias et al. 2017). Poaceae pollen includes species from steppe, forest, and tundra, including bamboo (*Chusquea* spp.). Cupressaceae pollen, which was present in low percentages, is attributed to long-distance transport from *Fitzroya cupressoides* growing the temperate rainforest to the west or *Austrocedrus chilensis* in dry forests between 39 and 43°S (Pastorino et al. 2006). *Araucaria araucana* is not an abundant pollen producer nor disperser and thus generally underrepresented in pollen records (Heusser et al. 1988, Paez et al. 2001). Modern surface samples within the present distribution of *A. araucana* often show less than 5% abundance in ecotonal regions east of the Andes (Paez et al. 2001, Moreno-Gonzalez et al. 2020). Its pollen, even in low percentages, is a conservative indicator for species' presence in the watershed. Human-indicator taxa include native and non-native taxa. Although Asteroideae subfamily Cichorioideae (henceforth, Cichorioideae) and *Rumex* pollen types include native and non-native species, their marked increase following European arrival suggests non-native *Taraxacum* species and *R. acetosella* as the pollen source.

Samples for charcoal analysis (1 cm^3) were taken from contiguous 1-cm intervals from the composite core and treated with a 10% solution of tetrasodium diphosphate ($Na_4P_2O_7$), then gently washed through a 125-µm mesh sieve to reconstruct local fire history following procedures in (Whitlock and Larsen 2001). CharAnalysis version 1.1 (Higuera et al. 2009) was used to identify statistically significant increases in charcoal accumulation rate (CHAR, particles cm^{-2} yr^{-1}) that denote fire peaks (fire episodes within the catchment area). Prior to the analysis, the sedimentation rate was interpolated to a constant temporal resolution based on a cubic spline fitted to mean ages of the adjusted depth provided by the age-depth model. In CharAnalysis, charcoal concentration values (particles cm^{-3}) were divided by 16 years cm^{-1}, the median sampling resolution, to provide an interpolated CHAR. A moving median with an 800-year window was used to describe background charcoal (BCHAR) and maximize signal to noise. Fire episodes were identified by charcoal peaks (i.e., the positive residuals of CHAR-BCHAR) that surpassed the 95th percentile of a locally defined Gaussian distribution model by a probability of at least 0.3 (minCountP).

Results

Lithology and chronology

Sediment from L. Portezuelo consisted of brown clayey silt intercalated by 54 tephra layers ≥0.5 cm in thickness (Fig. 2). Based on LOI, organic content varied from 1 to 25% of dry mass, carbonate content from 0-6%, and non-carbonate inorganic content from 42-99%. The AMS radiocarbon dating results produced an extrapolated mean basal age of ~11,100 BP (Table 2, Fig. 2). One date (OS-144515) was rejected as too old based on exceeding the 95% confidence interval of the Bayesian model (Fig. 2). Deposition time was generally between ~8 and 25 yr cm^{-1}, except for a period of low deposition, 40-29.5 cm depth (1120-430 BP), where deposition time increased to ~100 yr cm^{-1}.

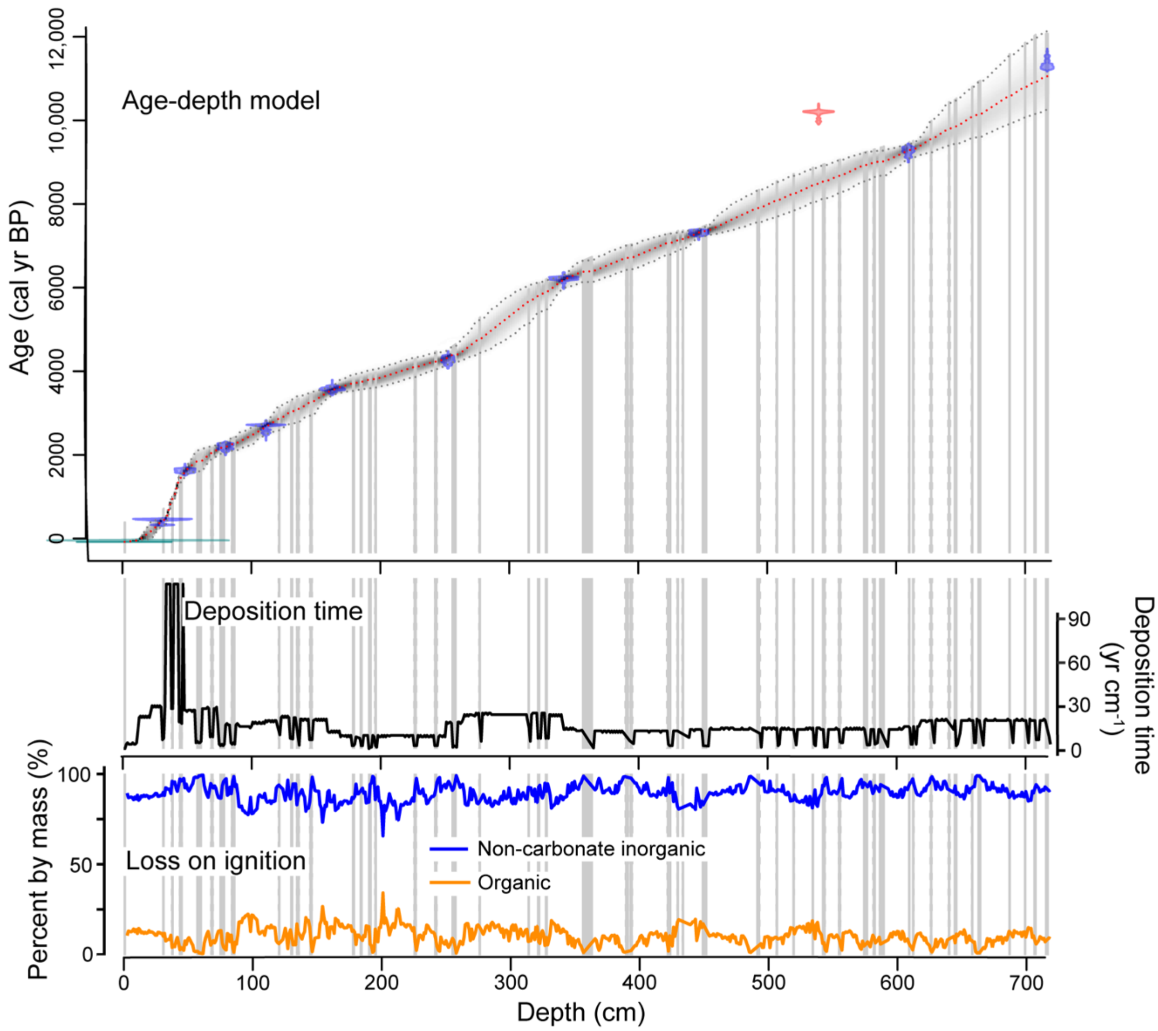

Fig 3.2. Age-depth model for Laguna Portezuelo using Bacon 2.2 (Blaauw and Christen, 2011). Green areas represent the calendar ages provided for different layers (see Table 2), blue areas represent the probability distributions of the calibrated dates, the red area represents the Bacon-rejected date (OS-144515), the dotted red line shows the weighted mean age, and dotted light gray lines depict the 95% highest posterior density intervals. Vertical gray bars show the location and thickness of tephra layers (≥0.5 cm thickness). The deposition time (black), percent composition of non-carbonate inorganic (blue), and organic (orange) are described in the text.

Pollen and charcoal record

The L. Portezuelo record (Fig. 3) is divided into four local pollen zones:

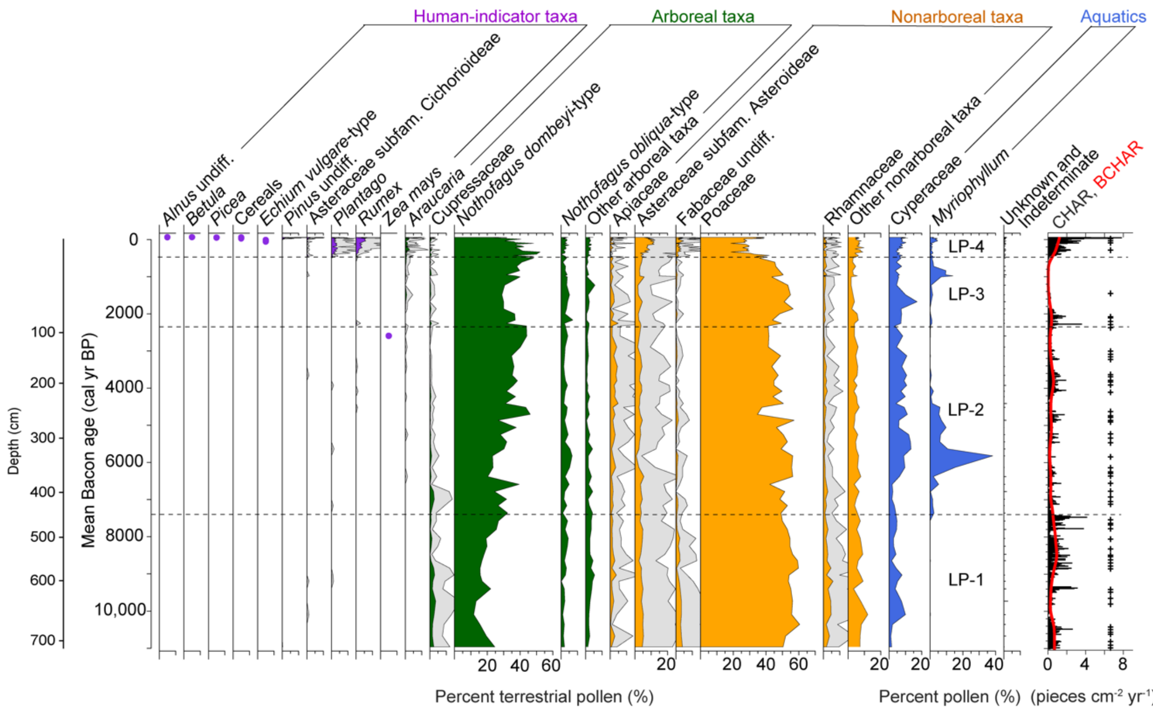

Fig 3. Pollen percentage diagram from Laguna Portezuelo showing pollen taxa and zones discussed in the text. Charcoal accumulation rates (CHAR; black) and background CHAR (BCHAR; red) describe variations in fire activity, and significant charcoal peaks (+) represent fire episodes.

Zone LP-1 (710-448 cm depth; ~10,960-7360 BP) featured an increase in *Nothofagus dombeyi*-type pollen (from 12 to 33%) at the expense of Cupressaceae (from 4 to <1%), Poaceae (from 61 to 50%), Fabaceae (from 4 to <1%), and Rhamnaceae (from 6 to 1%). Cyperaceae was present (1-10%) and Myriophyllum was scarcely present (<1-2%). Trends in PAR at L. Portezuelo were strongly governed by deposition time (Fig. 2) and will not be discussed further. CHAR in Zone LP-1 was low-to-moderate, between 0 and 5 particles cm^{-2} yr^{-1} and featured 24 significant peaks.

Zone LP-2 (448-82 cm depth; ~7360-2260 BP) featured a continued, but punctuated increase in *Nothofagus dombeyi*-type pollen to 48% at the expense of Cupressaceae and steppe pollen taxa (i.e., Poaceae, Fabaceae, and Rhamnaceae). *Araucaria* pollen first appeared at 354 cm depth (~6380 BP), but its low and discontinuous representation (<1%) does not confirm local occurrence. Cyperaceae increased from 2 to 13%. *Myriophyllum* was elevated (2.0-38.3%) between 378 and 264 cm depth (~6600-4520 BP). Trends in PAR at L. Portezuelo were strongly governed by deposition time (Fig. 2) and will not be discussed further. CHAR in Zone LP-2 was low, between 0 and 2 particles cm^{-2} yr^{-1} and featured 30 significant peaks.

Zone LP-3 (82-30 cm depth; ~2260-460 BP) was characterized by an increase in Poaceae percentages from 34 to 55% at the expense of *Nothofagus dombeyi*-type (from 44 to 29%) and Ranunculaceae (<2%), by 45 cm depth (~1490 BP) (Fig. 3). Although low in abundance (<1%), *Araucaria* pollen was consistently present above 57 cm depth (by ~1870 BP). At 33 cm depth (~500 BP), *N. dombeyi*-type pollen abundance increased from 29 to 48% at the expense of Poaceae (from 55 to 36%). Cyperaceae was slightly elevated throughout Zone LP-3 with a brief increase to 17% at 49 cm depth (~1670 BP). *Myriophyllum* pollen was abundant (7-14%) between 39 and 36 cm depth (~1000-840 BP). CHAR data decreased to 0 particles cm^{-2} yr^{-1} and only six significant peaks. Between 58 and 30 cm depth (~1860-455 BP), CHAR was negligible with no significant peaks.

Zone LP-4 (30-0 cm depth; ~460 to -13 BP) featured a steady increase in *Araucaria* pollen abundance until 10 cm depth (~30 BP; 0-3%) that was followed by a decrease to 2% by the top of the core (~-63 BP), as well as increased native disturbance taxa (i.e., Apiaceae, Asteraceae subfamily Asteroideae (henceforth, Asteroideae), and Fabaceae) and non-native taxa (e.g., Cichorioideae, *Echium vulgare*, *Plantago*, *Pinus*, and *Rumex*) at the expense of *Nothofagus dombeyi*-type (from 47.8 to 24.7%) (Fig. 3). Poaceae pollen abundance decreased between 29 and 17 cm depth (~430-100 BP) from 42 to 19%. Poaceae values increased to 27% at 16 cm depth (~80 BP), largely at the expense of *N. dombeyi*-type, and remained high (26-39%). *Pinus* appeared in the record at 12 cm depth (~-9 BP), and remained low and infrequent (≤1%) until 7 cm depth (~-40 BP), when values increased to 5% by present. CHAR increased to 1 particle cm^{-2} yr^{-1} (30-26 cm depth; ~460-340 BP), before decreasing to <1 particle cm^{-2} yr^{-1} at 20 cm depth (~170 BP) (Fig. 3). CHAR then increased to 4 particles cm^{-2} yr^{-1} at 10 cm depth (~-30 BP) and was followed by a large decrease in CHAR to present (to <1 particle cm^{-2} yr^{-1}). Three significant peaks in CHAR were recorded in Zone LP-3, at 26 cm (~340 BP), 17 cm (~100 BP), and 10 cm depth (~-30 BP).

Discussion

The vegetation and fire history of *Araucaria araucana* at L. Portezuelo is compared with other well-dated sites from northernmost Patagonia (37.3-40.3°S) (Table 1; Fig. 1 and 4; i.e., Fletcher and Moreno 2012b, Abarzúa et al. 2014, Moreno-Gonzalez et al. 2020), and examined in light of changes in seasonal insolation (Berger and Loutre 1991), sea surface temperature (Chilean coast, 41°S; Kaiser et al. 2005), El Niño history (Moy et al. 2002), and dendroclimatology from *A. araucana* forest (Mundo et al. 2013) (Fig. 4). The vegetation and fire reconstruction is also compared with regional archaeological and ethnohistorical records (Aagesen 2004, dos Reis et al. 2014, Barberena et al. 2015, Perez et al. 2017) to assess past human influence (Fig. 4).

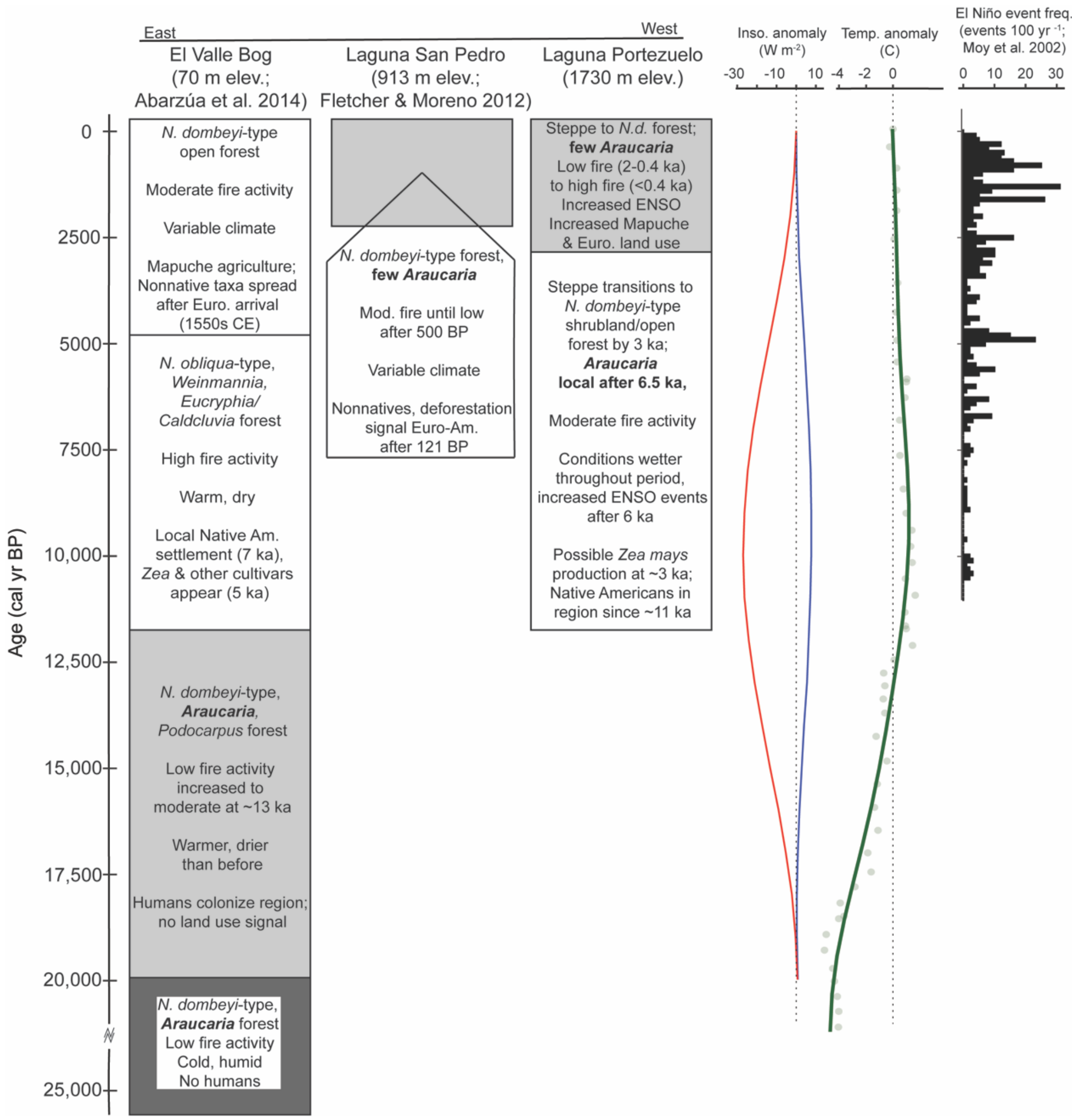

Fig 3.4. Vegetation, fire, climate, and human history based on published interpretations. Darker shades denote greater inferred abundance of *Araucaria araucana*. Summer (DJF; red) and winter (JJA; blue) insolation values are from Berger and Loutre (1991), temperature values (green; anomalies from present) are from Kaiser et al. (2005), and El Niño event frequency (black) are from Moy et al. (2002).

Vegetation and fire history at L. Portezuelo

Steppe vegetation generally dominated at L. Portezuelo throughout the Holocene, however; increasing *N. dombeyi*-type pollen suggests expanding shrubland through time, likely dominated by *N. antarctica*. CHAR levels were moderate between ~11,050 and 6590 BP with a slight increase between ~9480 and 7970 BP, suggesting moderate-to-high fire activity (Fig. 3 and 4). After ~6590 BP, increased abundance of Cyperaceae and *Myriophyllum* pollen indicate an expanded riparian area and higher water levels. Between ~6590 and 2330 BP, fire activity declined and *Araucaria* first appeared in the pollen record.

Between ~2330 and 720 BP, the vegetation shifted back to steppe contemporaneous with increased fire activity, including fire prominent fire episodes between ~2140 and 1900 BP (Fig. 3 and 4). Decreased CHAR from ~1900 to 1640 BP and increased in *Nothofagus dombeyi*-type pollen suggests an expansion of shrubland. Consistent presence of *Araucaria* pollen since 1870 BP marks establishment of *A. araucana* near the site. After ~1640 BP, increased CHAR indicates low-to-moderate fire activity until ~460 BP, when fire activity increased to moderate-to-high in association with increased Nothofagus and *Araucaria* between ~460 and 340 BP (1490-1610 CE). This increase in fire activity and arboreal taxa suggest that increased moisture may have led to more fuel biomass at this time.

Evidence of land use near L. Portezuelo began at ~410 BP (1540 CE), when native and non-native disturbance pollen taxa increased along with fire activity (Fig. 4). This increase precedes Euro-American settlement of the area (1870s CE; Moreno 1897) and coincides with the translocation of Mapuche peoples into the region from west of the

Andes (Ortelli 1996). Mapuche-Pehuenche peoples use *Araucaria* as a source of food, fuel, and timber and practice orcharding, planting and protecting stands of *Araucaria* (Aagesen 2004, dos Reis et al. 2014, Gordón et al. 2016). *Araucaria* near L. Portezuelo either unintentionally benefited from the increase in anthropogenic fire or was intentionally supported following the arrival of Mapuche-Pehuenche peoples. Between ~70 and 14 BP (1880-1936 CE), fire-scar records from *Araucaria* <10 km north of L. Portezuelo suggest that fires were as frequent as 6 yr $fire^{-1}$ (Mundo et al. 2013). Subsequent increases in non-native taxa and decline of *Nothofagus* at ~60 BP (1890 CE) are associated with Euro-American settlement. Decreased *Araucaria* after ~30 BP (1920 CE) may have occurred with grazing and logging prior provincial, federal, and international efforts to protect the species in 1948 CE (CITES 2007, González et al. 2010, Premoli et al. 2013). Non-native *Pinus* pollen appeared at ~-10 BP (1960 CE), marking establishment of *Pinus* plantations near the site.

Environmental history of *Araucaria araucana*
<u>(37.3-40.3°S)</u>

In addition to L. Portezuelo, other well-dated Holocene or late Holocene paleoecological records lie within the modern range of *Araucaria araucana*: Laguna San Pedro, beginning at ~1500 BP (38.43°S, 71.32°W; 913 m elev.; Fletcher and Moreno 2012b), and El Valle Bog, beginning at ~26,500 BP (38.05°S, 72.97°W; 70 m elev.; Abarzúa et al. 2014) (see Table 1; Fig. 1 and Fig. 4). The charcoal record from El Valle differs from L. Portezuelo and L. San Pedro in presenting microscopic charcoal concentrations (particles cm^{-3}) instead of macroscopic charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}). This type of data is complicated by variations in the deposition time through the core and its larger fire source (Carcaillet et al. 2001, Whitlock and Larsen 2001). Sites presented by Moreno-Gonzalez et al. (2020) provide a useful characterization of the last few hundred years of environmental history along the forest-steppe ecotone of northernmost Patagonia. Two other pollen records from the region (Table 1) have poorly constrained Holocene chronologies, making comparison difficult; they will not be discussed further.

<u>Late Pleistocene and early Holocene (~20,000-7000 BP)</u>: Winter insolation increased and summer insolation decreased from 20,000 to 10,000 BP (Berger and Loutre 1991) (Fig. 4), resulting in low seasonality throughout northern Patagonia (Renssen et al. 2005, Whitlock et al. 2007). ODP-1233 sea-surface temperature reconstructions off the Chilean coast (41°S) suggests that temperatures quickly warmed from ~20,000 to 10,000 BP, reaching slightly warmer conditions than present by 11,500 BP (Kaiser et al. 2005). Composited pollen and CHAR records between 41 and 44°S east of the Andes suggest that this period was warmer and drier than present in that region (Nanavati et al. 2019).

During the last glaciation, *Araucaria-Nothofagus* forest dominated and fire activity was low at El Valle, suggesting a likely refugia for *Araucaria* in the central valley of Chile and generally cool and wet conditions (Fig. 4) (Heusser 1984, Villagrán 1991, Marchelli and Gallo 2004, Ruiz et al. 2007, Abarzúa et al. 2014). A decrease in *Araucaria* and an increase in Poaceae and warm-temperate arboreal taxa (e.g., *Prumnopitys* and Myrtaceae) at El Valle suggest a shift to open warm-temperate forest and increased fire activity between ~20,000 and 12,000 BP. Between ~12,000 and 7000 BP, El Valle was dominated by warm-temperate forest, whereas L. Portezuelo was dominated by steppe; both records featured moderate-to-high fire activity during a period that was likely warmer and drier than before. Null-to-low levels of *Araucaria* pollen at both El Valle and L. Portezuelo between ~12,000 and 7000 BP suggest that *Araucaria* was scarce and/or not close to the sites. Increased fire activity during the early Holocene at El Valle and L. Portezuelo has been noted throughout southern South America in association with the possible southward shift and/or weakening of the SWW (Fletcher and Moreno 2012a, Moreno et al. 2012, Nanavati et al. 2019).

Middle Holocene (~7000-4000 BP): Winter insolation decreased and summer insolation increased, resulting in a gradual increase in seasonality from previous conditions and a decrease in average annual temperature during this period (Fig. 4) (Berger and Loutre 1991, Kaiser et al. 2005). Precipitation increased across Patagonia, as storm tracks associated with the SWW reached modern position and intensity (strongest between 40 and 60°S) (Fletcher and Moreno 2012a, Garreaud et al. 2013, Nanavati et al. 2019). Increased El Niño frequency after ~6800 BP (Moy et al. 2002) likely led to increased fall, winter, and spring moisture by shifting the storm tracks northward into the latitudes of El Valle and L. Portezuelo (Veblen and Kitzberger 2002, Garreaud et al. 2009, Garreaud et al. 2013).

During this period, El Valle and L. Portezuelo show an increase in arboreal pollen taxa (i.e., *Eucryphia*/*Caldcluvia* and *Nothofagus dombeyi*-type, respectively), consistent with increased moisture (Fig. 4). Decreased charcoal levels at El Valle and L. Portezuelo suggest a shift from high to low-to-moderate fire activity by 4000 BP. Although increased moisture throughout the region favored *Nothofagus* near L. Portezuelo, local vegetation remained fairly open and fire activity was likely fuel limited. At El Valle, increased *Eucryphia*/*Caldcluvia* suggests an expansion of temperate humid forest with moderate fire activity (Abarzúa et al. 2014). Between ~7000 and 4000 BP, *Araucaria* was slightly more abundant at El Valle (at ~7500 BP) and first appeared in the L. Portezuelo record (at ~6380 BP), suggesting few, scattered *Araucaria* near both sites with increased moisture.

American Indian presence, although low in population, was nearly continuous after ~7000 BP from the Chilean coast to the Argentine steppe in northernmost Patagonia (Barberena et al. 2015, Perez et al. 2016). Despite increased human presence (and, likely, anthropogenic ignitions) between ~7000 and 4000 BP (Quiroz and Sánchez 2004, Barberena et al. 2015), the fire histories at El Valle and L. Portezuelo point to differences in fuel biomass and/or land use at this time in Patagonia (Fig. 4). The appearance of *Zea mays* pollen at El Valle at ~5000 BP suggests the arrival of maize and increased land use west of the Andes, but there is no evidence of maize east of the Patagonian Andes at this time.

Late Holocene (since ~4000 BP): High summer and low winter insolation compared to the past periods (Berger and Loutre 1991), and similar-to-present sea-surface temperatures mark the establishment of present-day climate conditions after ~4000 BP (Garreaud et al. 2013). Changes in the position and intensity of the SWW-related storm tracks in recent millennia have been attributed to strengthened interannual climate variability across Patagonia (Holz et al. 2012, Iglesias et al. 2014, Nanavati et al. 2019).

Pollen and charcoal data from El Valle, between ~4000 and 1500 BP suggest increasingly open conditions and decreased fire activity (Fig. 4) (Abarzúa et al. 2014). At L. Portezuelo, however, shrubland expanded from ~4000 to 2500 BP with fire activity that was similar to the previous period, suggesting increased moisture. Between ~2500 and 1500 BP, steppe expanded with decreased fire activity, implying dry conditions and limited fuel biomass. Between ~1500 and 800 BP, shrubland and forest expanded at El Valle , L. Portezuelo, and L. San Pedro with increased moisture (Fletcher and Moreno 2012b, Abarzúa et al. 2014). Shrubland and forest expansion at all sites coincided with three large increases in El Niño frequency (to 16-31 events 100 yr^{-1}) at ~1600-1500, 1300-1200, and 900-600 BP (Moy et al. 2002).

From ~4000 to 800 BP, *Araucaria* was not present at El Valle (Abarzúa et al. 2014), and occurred in low abundance at L. Portezuelo (Fig. 4). L. San Pedro had the highest *Araucaria* pollen abundance of the three sites (1-6%) between ~1500 and 800 BP, reflecting its location in the center of *Araucaria*-*Nothofagus* forest distribution. Thus, *Araucaria* decreased in abundance around El Valle, but was continually present near L. San Pedro and L. Portezuelo during the late Holocene.

After ~800 BP at El Valle, sclerophyllous vegetation replaced *Nothofagus* forest and was associated with the onset of dry conditions (Fig. 4) (Abarzúa et al. 2014). At L. San Pedro, closed forest of *Nothofagus* and *Araucaria* persisted until Euro-American deforestation at ~100 BP (Fletcher and Moreno 2012b). Charcoal data from L. San Pedro suggest that fire activity decreased from moderate-to-high to low levels between ~900 and 500 BP. At L. Portezuelo, *Nothofagus* declined while *Araucaria* and fire activity increased after ~340 BP. Between ~800 and 300 BP at L. San Pedro, *Araucaria* decreased with the expansion of *N. dombeyi*-type with low fire activity, suggesting that *Nothofagus* may have out-competed *Araucaria* in wetter, less fire-prone settings prior to Euro-American deforestation at ~100 BP (Fletcher and Moreno 2012b).

Increased American Indian land use is evident at El Valle with the frequent appearance of *Zea mays* pollen. Decreased fire activity after ~5000 BP suggests land clearance for agriculture near El Valle, preceding local agricultural intensification within the last 1000 years (Fig. 4) (Dillehay et al. 2007, Abarzúa et al. 2014). The appearance of a single *Zea mays* pollen grain at L. Portezuelo may be explained by contamination, a rare long-distance dispersal event, or a brief attempt at local maize agriculture. No *Zea mays* was recorded at L. San Pedro (Fletcher and Moreno 2012b).

Clear evidence for land use at L. Portezuelo began ~1540 CE (410 BP), as indicated by increased native and non-native disturbance taxa (i.e., *Plantago lanceolata* and *Rumex acetosella*) in conjunction with moderate-to-high fire activity. Pollen and charcoal records throughout northernmost Patagonia demonstrate similar increases in non-native disturbance taxa within the last 200 years and *Pinus*, after ~1950 CE (0 BP) (Fletcher and Moreno 2012b, Abarzúa et al. 2014, Moreno-Gonzalez et al. 2020). Interestingly, fire activity during the last century in northernmost Patagonia varied greatly by site, likely demonstrating local differences in fuel, catchment area, and/or intensity of land use along the west-to-east moisture gradient (Fletcher and Moreno 2012b, Abarzúa et al. 2014, Moreno-Gonzalez et al. 2020). Similar variability in fire activity within *Araucaria* forest and woodland is noted by Mundo et al. (2013), which show that although fire return intervals generally decreased with Euro-American settlement and then increased to present, the timing and magnitude of change differed from west to east between 1632 and 2007 CE.

Conclusions

1) At L. Portezuelo, steppe with moderate-to-high fire activity transitioned to *Nothofagus* shrubland with low-to-moderate fire activity between ~11,100 and 2260 BP. Increased arboreal taxa is attributed to increased moisture, which was likely facilitated by strengthened ENSO in the middle Holocene. Between ~2260 and 1900 BP at L. Portezuelo, shrubland was replaced by steppe and fire activity decreased consistent with dry conditions. Increased arboreal pollen and few fires between ~1900 and 460 BP occurred during peak El Niño events with associated wet conditions.

2) *Araucaria* was likely present in glacial refugia west of the Andes, and late-glacial to early-Holocene warming witnessed a large loss in its abundance. *Araucaria* pollen first appeared in the L. Portezuelo record at ~6380 BP but was sporadic and in low abundance until ~1670 BP, suggesting few *Araucaria* in the area. Moderate levels of *Araucaria* pollen were present at L. San Pedro until decreased fire activity allowed *Nothofagus* to outcompete *Araucaria* between ~800 and 300 BP.

3) Increased *Araucaria* pollen abundance and fire activity at L. Portezuelo after ~1490 CE (460 BP) imply increased American Indian land use following an influx of the Mapuche-Pehuenche peoples into the region, fleeing the Spanish

conquest of the Chilean coast beginning in the 1550s CE. This hypothesis warrants further testing through extensive archaeological survey and excavation near L. Portezuelo.

4) Increased abundance of *Plantago* and *Rumex* pollen in the L. Portezuelo record beginning at ~1580 CE (370 BP) predates the arrival of Spanish into the area, suggesting that the spread of Old-World weeds outpaced local Euro-American settlement. Throughout northernmost Patagonia Euro-American settlement was marked by increased non-native and steppe taxa at the expense of *Nothofagus*. During this period, fire increased with initial settlement of the region and decreased with farming, pastoralism, and fire elimination after ~1960 CE.

Acknowledgements

Research was supported by grants from the National Science Foundation (OISE0966472, GSS1461590), Fondo para la Investigación Científica y Tecnológica (PICT 2011 2046), and the Neuquén Volcanic Hazards Assesment, CONICET-Legislatura Provincial de Neququén. We would like to acknowledge collaboration from Copahue Provincial Park, Neuquén Province, Argentina. D. Quick assisted with lab work. J. Larmon provided useful comments on the manuscript.

CHAPTER FOUR

POSTGLACIAL VEGETATION, FIRE, AND CLIMATE HISTORY ALONG THE EASTERN ANDES, ARGENTINA AND CHILE (LAT. 41-55°S)

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: William P. Nanavati

Contributions: Defined experimental design, completed field, lab, and statistical analyses, and wrote the manuscript.

Co-Author: Cathy Whitlock

Contributions: Helped defined experimental design, provided funding and lab space, and helped write the manuscript.

Co-Author: Virginia Iglesias

Contributions: Helped complete statistical analyses, and provided comments on manuscript.

Co-Author: María Eugenia de Porras

Contributions: Provided data and comments on the manuscript.

Manuscript Information

William P. Nanavati, Cathy Whitlock, Virginia Iglesias, María Eugenia de Porras

Quaternary Science Reviews

Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
__ Officially submitted to a peer-reviewed journal
____ Accepted by a peer-reviewed journal
_X__ Published in a peer-reviewed journal

Volume 207, pages 146-160, Elsevier B.V.
https://doi.org/10.1016/j.quascirev.2019.01.014

CHAPTER FOUR

POSTGLACIAL VEGETATION, FIRE, AND CLIMATE HISTORY ALONG THE EASTERN ANDES, ARGENTINA AND CHILE (LAT. 41-55°S)

Abstract

The role of climate in shaping the postglacial history of Patagonia (41-55°S) east of the Andes is evident in new pollen and charcoal data from Mallín Fontanito (44.91ºS, 71.57ºW) and their comparison with other paleoenvironmental records in the region. Between 17,800-13,000 cal yr BP, evidence of heath-steppe vegetation with some *Nothofagus* and little fire activity at M. Fontanito suggest cold, dry conditions in early late-glacial time. From 13,000-7000 cal yr BP, increased *Nothofagus* pollen and charcoal levels imply expanding tree cover and more fires, consistent with warming. Between 7000-4000 cal yr BP, closed *Nothofagus* forest was established at M. Fontanito during a period of low fire activity and effectively wetter conditions than before. Fluctuations in pollen and charcoal levels after 4000 cal yr BP are consistent with increased submillennial climate variability. The environmental history at M. Fontanito is similar to other records from central Patagonia east of the Andes (44-50ºS); however, differences in the timing of fires and human occupation suggest that pre-European burning was local in nature. At a regional scale, composited *Nothofagus* pollen abundance and charcoal data east of the Andes (41-55ºS) reveal latitudinal differences in the timing of forest establishment and fire that relate to changes in the strength and position of the Southern Westerly Winds (SWW) through time. Notably, the SWW were south of their present position between 14,000-9000 cal yr BP, leading to dry conditions across the region. The

present storm-track position was established after 7000 cal yr BP, when region-wide increases in precipitation occurred.

Introduction

The forest-to-steppe ecotone on the east side of the Andes in southern South America is one of the most dramatic vegetation boundaries in the world. It responds to a steep west-to-east precipitation gradient that is governed by the orographic influence of the Andes on Pacific storm tracks, as well as the position and strength of the Southern Westerlies (SWW) (Veblen et al. 1996, Garreaud et al. 2013). Paleoenvironmental reconstructions show that the postglacial history of the forest-steppe ecotone has been dynamic both longitudinally and latitudinally over the last 20,000 years, as a result of large-scale changes in the storm-track location and intensity (Iglesias et al. 2016a) and the local effects of fire (Whitlock et al., 2007).

Although the vegetation, fire, and climate history has been well studied in many parts of Patagonia (e.g., Markgraf et al. 2003, Moreno 2004, Whitlock et al. 2006, Iglesias et al. 2014), the central region (44-50ºS) east of the Andes has received relatively little attention. Understanding the paleoecological history of this particular region is important for several reasons. First, central Patagonia is the position of the present-day core of the SWW and receives high levels of precipitation year-round, whereas regions to the north and south experience greater seasonal variability in moisture (Garreaud et al. 2013). Although the influence of the SWW has been studied west of the Andes in central Patagonia (Moreno 2004, Moreno et al. 2012), the influence of the SWW on postglacial vegetation and fire history east of the Andes is unclear (as discussed in, Heusser 1983, Markgraf 1987, 1989, Fletcher and Moreno 2012a). Second, humans have been present in central Patagonia since ~12,000 cal yr BP, and both archaeological and paleoecological records suggest deliberate use of fire in the region; however, the extent and influence of burning on vegetation patterns are not known (Méndez et al. 2016). Third, this region lies beyond the southern limit of *Austrocedrus chilensis*, an important conifer of dry forests in northern Patagonia. The presence of *Austrocedrus* in northern Patagonia, a well-studied region, likely altered the disturbance dynamics of the forest-steppe ecotone in ways that were different from regions farther south, but the long-term history of these interactions is not well known.

To increase our knowledge of the environmental history of the forest-steppe region of central Patagonia, we present a new 18,000-yr-old record of vegetation and fire history from Mallín Fontanito (44.91°S, 71.57°W; 940 m elev, 0.58 km^2). The reconstruction builds on other records in central Patagonia, including those with known human presence (e.g., Markgraf et al. 2007, de Porras et al. 2012, de Porras et al. 2014, Iglesias et al. 2016a). To better understand the postglacial climate history east of the Andes, we also developed a composite record of *Nothofagus* pollen abundance and charcoal accumulation rate that allowed us to compare the environmental history of central Patagonia with (1) that of regions to the north and south and (2) independent paleoclimate proxies from the Southern Hemisphere (Fig. 4.1).

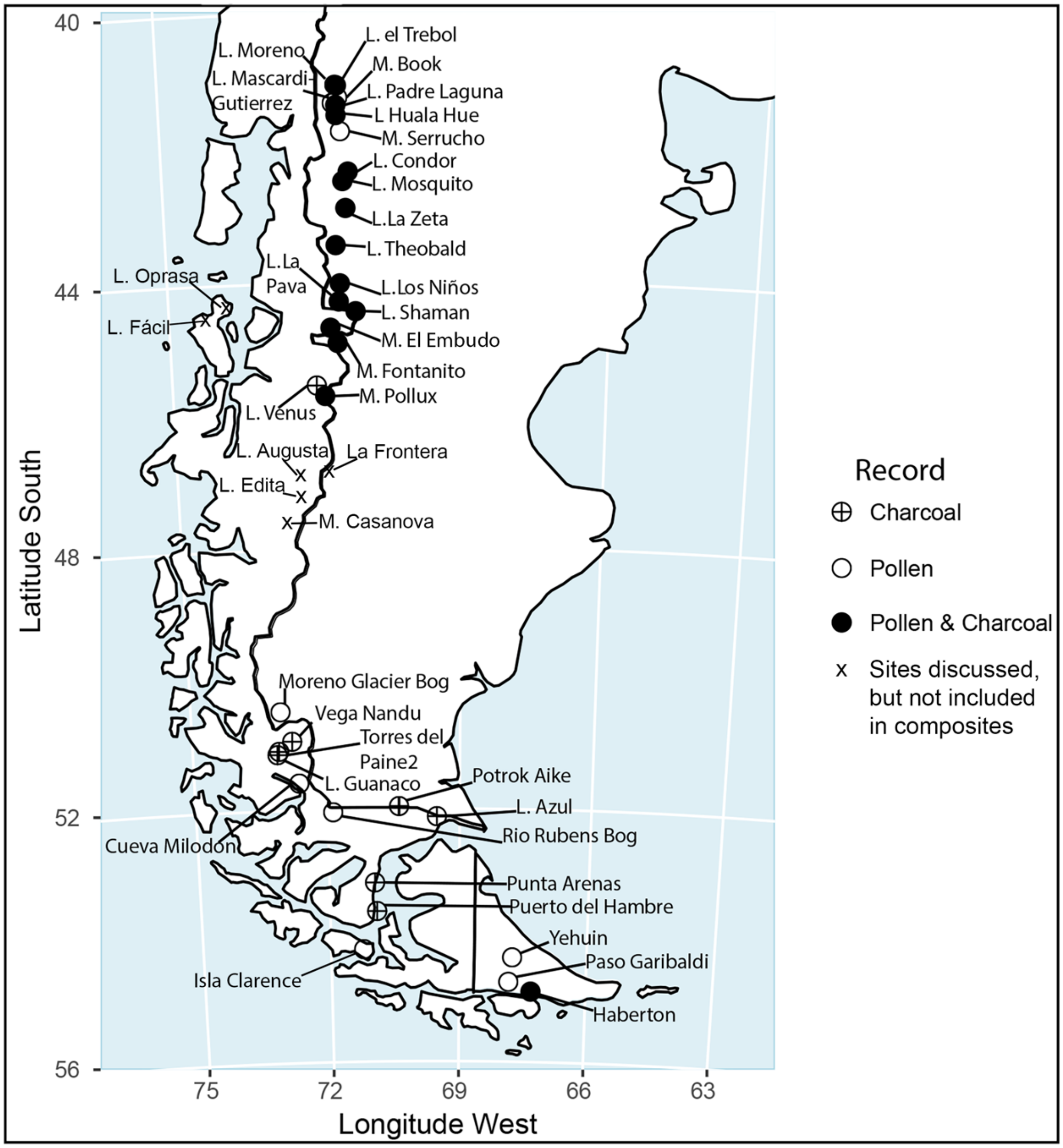

Figure 4.1: Map of southern South America, showing the location of Mallín Fontanito and other pollen and charcoal records described in the text and/or used in the composite analyses. Some sites have only pollen or charcoal data, whereas others have both. The inset satellite map highlights the position of pollen and charcoal records in Central Patagonia (44.0-45.7°S), in relation to the modern forest-steppe ecotone. Archaeological sites discussed in the text are plotted in the inset map: RGV = Río Genoa Valley (Scheinsohn et al. 2017), RPV = Río Pico Valley (Scheinsohn et al. 2016), RCV = Río Cisnes Valley (Méndez et al. 2016), 1 El Chueco 1, 2 Cueva de la Vieja (Méndez et al. 2018a), 3 Baño Nuevo 1 (Mena et al. 2003), and 4 Casa de Piedra Roselló (Castro Esnal et al. 2017).

Throughout Patagonia east of the Andes, annual precipitation ranges from >1000 mm/yr at the Andean crest to <100 mm/yr in the steppe (Garreaud et al. 2013). In the vicinity of M. Fontanito, average annual temperature is 5.8°C, average austral winter temperature is 0.7°C (June, July, and August of 1901-2016), and average austral summer temperature is 10.7°C (December, January, and February of 1901-2016) (University of East Anglia Climatic Research Unit; Harris 2017). The SWW are presently centered at ~50°S, but seasonally and annually span latitudes from 30-70°S, generally shifting storm tracks north during the austral winter and south during the austral summer.

M. Fontanito is located along the south margin of L. Fontana in mixed *Nothofagus pumilio* and *N. antarctica* forest, approximately 25 km west of steppe vegetation. The wetland may have originated as an embayment of the larger proglacial lake or formed in an isolated ice-block depression along the lateral moraine system. Upper treeline lies above 1300 m elevation to the west and includes *N. pumilio*, *Berberis illicifolia*. East of M. Fontanito, the forest is replaced by shrubland that includes *N. antarctica*, *Schinus*, *Berberis serratodentata*, and *Baccharis patagonica.* Grass-shrub steppe to the east is dominated by tussock grasses (e.g., *Stipa*, *Poa*) intermingled with cushion shrubs (e.g., *Mulinum spinosum*, *Adesmia boronioides, Senecio filaginoides, Nassauvia darwinii*), and herbs (e.g., Asteraceae subfamily Asteroideae, *Arenaria*, *Geum magellanicum*). Forest cover at the site was extensively reduced by 19th- and 20th-century land clearance, fire, and livestock grazing. Disturbed areas support *N. antarctica*, *Escallonia alpina*, *Gunnera chilensis*, *Acaena splendens*, and *A. magellanica*, as well as introduced weeds (e.g., *Taraxacum officinalis*, *Holcus lanatus*, *Rumex acetosella*).

Humans first arrived east of the Andes in central Patagonia at ~12,000 cal yr BP as small, nomadic, and dispersed populations (Méndez et al. 2016). Guillermo E. Cox (1863) and George Chaworth Musters (1871) traveled the forest-steppe region in the late 19th century, and their journals describe frequently burned landscapes that they attribute to American Indian burning practices. In the late 19th century, Euro-Americans settled the area and used fire to clear forests for pasture (Veblen and Lorenz 1988, Kitzberger 2012).

Methods

Field and laboratory

Cores were taken with a modified Livingstone piston sampler from the wetland surface, extruded, and wrapped in cellophane and aluminum foil in the field, and transported back to the laboratory for refrigeration and sampling. In the laboratory, cores were split longitudinally and described. Color assignment was based on the Munsell system.

For the purpose of AMS radiocarbon dating, 15 sediment samples were processed for pollen with the Schulze reagent and without use of any compounds containing carbon (i.e., no sodium bicarbonate, alcohols, acetic acid, or acetic anhydride). These samples were subsequently calibrated using CALIB 7.1, based on the SHCal13 calibration curve (Hogg et al. 2016, Stuiver et al. 2017). A Bayesian age-depth model was developed based on an adjusted depth that excluded tephra layers >1 cm in thickness on the grounds that they were deposited instantaneously (Blaauw and Christen, 2011). Maximum depth of the age-depth model was set to the deepest radiocarbon date (518 cm depth), mean sedimentation rate was set to 36 yr cm^{-1}, and section thickness was set to 10 cm.

Pollen was analyzed at 3- to 18-cm intervals, and samples were prepared with standard procedures (Faegri et al. 1989). A tracer of *Lycopodium* was added to each sample to calculate pollen concentration (grains cm^{-3}). At least 300 terrestrial pollen grains were counted for each sample. Terrestrial pollen percentages were calculated based on a sum of terrestrial pollen and spores. Percentages of aquatic and wetland taxa were based on a denominator of total pollen and spores. Local pollen zones were identified by visual inspection of the resulting sum of squares from constrained cluster analysis (CONISS; Grimm 1987).

Nothofagus dombeyi-type pollen constitutes pollen from *N. dombeyi*, *N. antarctica*, and *N. pumilio*, but only *N. antarctica* and *N. pumilio* are currently present in the local forest. *N. dombeyi*, *N. antarctica*, and *N. pumilio* produce large amounts of wind-dispersed pollen that often travels long distances from its source; we therefore rely on *Nothofagus* percentage data from modern pollen studies to inform interpretations of local steppe (<41%), shrubland or open forest (41-67%), and closed *Nothofagus* forest (>67%) (Mancini et al. 2012, Iglesias et al. 2017). Poaceae pollen includes species from the steppe, forest, and tundra, including the forest bamboo, *Chusquea*. Cupressaceae pollen, which was present in low percentages, is attributed to long-distance transport from *Fitzroya cupressoides* and *Pilgerodendron uviferum*, which grow in the temperate rainforest to the west and, less likely, *Austrocedrus chilensis*, a dominant taxon of dry forests north of 43°S.

Macroscopic charcoal particles (>125 µm in size) were analyzed to reconstruct local fire history following procedures in Whitlock and Larsen (2001). Subsamples of 1-2 cm^3 were taken from contiguous 1-cm intervals spanning the core and treated with a 10% solution of tetrasodium diphosphate ($Na_4P_2O_7$), then gently washed through a 125-µm mesh sieve. Charcoal was identified and counted at 10–40x magnification. CharAnalysis version 1.1 (Higuera et al., 2009) was used to reconstruct the fire history. Prior to the analysis, the sedimentation rate for each depth was interpolated to a constant temporal resolution based on a cubic spline fitted to the estimated weighted-mean ages. In CharAnalysis, charcoal concentration values (particles cm^{-3}) were divided by 30 years $sample^{-1}$, which is the median sampling resolution of the M. Fontanito record, to provide an interpolated charcoal accumulation rate (CHAR, particles cm^{-2} yr^{-1}). A locally-weighted scatter plot smoother (LOWESS) with a 500-year window was used to describe background charcoal (BCHAR). Fire episodes were identified as charcoal peaks (i.e., the positive residuals of the LOWESS model) that surpassed the 95th percentile of a locally defined Gaussian distribution model by a probability of at least 0.3 (minCountP).

Regional data synthesis

To examine the changes in vegetation, fire, and climate history along the eastern Andes, we divided Patagonia into three regions, northern (41-44°S, 11 pollen and 7 charcoal records), central (44-50°S, 6 pollen and 7 charcoal records) and southern (50-55°S, 7 pollen and 8 charcoal records) (Table 4.1, Figure 4.1). For the composite analyses, we used only records from sites east of the Andean crest that were available from open Neotoma Paleoecology and the Global Charcoal databases, and where

Nothofagus dombeyi-type pollen exceeded 41% of the terrestrial pollen sum. This cut-off is based on modern pollen studies that establish this percentage as the lower limit for inferring *Nothofagus* shrubland or open forest (Iglesias et al., 2016b; Mancini et al., 2012). (Note: sites not meeting these criteria are discussed, but their data were not incorporated into the composites).

Following the compositing strategies of Marlon et al. (2008) and Daniau et al. (2012), *Nothofagus* pollen (including *N. dombeyi*-type and *N. obliqua*-type) and CHAR time series from individual sites were MinMax-, Box-Cox-, and Z-score- transformed. A base period of 4000-200 cal yr BP was used for the transformation of both data types because it spans the period of modern vegetation prior to extensive land use. *Nothofagus* and CHAR data were then binned into non-overlapping 20-yr windows, from 18,000 to -50 cal yr BP, so that records with high-sample resolution were not overrepresented in the composite record and data from lower resolution records were not interpolated. After records were binned, LOWESS was used with a 1000-yr smoothing window. A 95% confidence interval was calculated by 1000 bootstrapped replicates and smoothed using a LOWESS smoother with a 1000-yr window (Blarquez et al. 2014).

Table 4.1: Information about the sites used in this study

Region	Site Name	Lat. (°S)	Lon. (°W)	Elevation (m elev)	Youngest Age (cal yr BP)	Oldest Age (cal yr BP)	Data Type[1]	Present Vegetation	Publication
Northern Patagonia	Lago Moreno	41.06	71.52	800	651	17,681	P	*Nothofagus dombeyi-Austrocedrus chilensis forest*	Valenciano et al. (1985)
	Laguna El Trébol	41.07	71.49	758	117	18,767	P, C	*Nothofagus dombeyi-Austrocedrus chilensis forest*	Whitlock et al. (2006), Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
	Lago Mascardi-Gutierrez	41.25	71.47	800	129	11,857	P	*Nothofagus dombeyi-Austrocedrus chilensis forest*	Markgraf (1983)
	Mallín Book	41.33	71.58	800	358	16,937	P	*Nothofagus dombeyi-Austrocedrus chilensis forest*	Markgraf (1983)
	Laguna Padre Laguna	41.36	71.51	880	-58	4978	P, C	*Nothofagus dombeyi-Austrocedrus chilensis forest*	Iglesias et al. (2012), Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
	Lago Huala Hué	41.51	71.51	849	57	12,577	P, C	*Nothofagus dombeyi-Austrocedrus chilensis forest*	Iglesias et al. (2012), Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
	Mallín Serrucho	41.75	71.43	995	-47	15,838	P	Scirpus-*Empetrum* wetland, surrounded by stands of Nothofagus antarctica, Pilgerodendron uviferum and Fitzroya cupressoides	Markgraf et al. (2013)
	Laguna del Cóndor	42.35	71.29	818	78	10,064	P, C	*Austrocedrus chilensis-Nothofagus dombeyi* woodland and steppe	Iglesias et al. (2012), Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
	Lago Mosquito	42.49	71.40	556	142	9230	P, C	*Austrocedrus chilensis-Nothofagus dombeyi* woodland and steppe	Whitlock et al. (2006), Iglesias et al. (2012), Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
	Laguna La Zeta	42.89	71.35	781	-31	19,582	P, C	*Austrocedrus chilensis-Nothofagus dombeyi* woodland and steppe	Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
	Lago Theobald	43.44	71.56	640	-46	12,104	P, C	*Austrocedrus chilensis-Nothofagus dombeyi* woodland and steppe	Iglesias (2013), Iglesias and Whitlock (2014a), Iglesias et al. (2014b)
Central Patagonia	Lago Los Niños	44.01	71.49	1023	-68	18,520	P, C	*Nothofagus antarctica* and *N. pumilio* forest	Iglesias et al. (2016)
	Laguna La Pava	44.28	71.52	760	30	14,222	P, C	*Nothofagus antarctica* and *N. pumilio* forest	Iglesias et al. (2016)
	Laguna Fácil*	44.33	74.28	10	0	16,200	P, C	*Nothofagus betuloides-Pilgerodendron forest*	Haberle and Bennett (2004)
	Laguna Oprasa*	44.36	73.66	50	0	17,300	P, C	*Nothofagus betuloides-Pilgerodendron forest*	Haberle and Bennett (2004)
	Lago Shaman	44.43	71.18	919	-56	16,712	P, C	*Nothofagus antarctica* shrubland and steppe	de Porras et al. (2012)
	Mallín El Embudo	44.67	71.70	686	-61	11,875	P, C	*Nothofagus pumilio* forest	de Porras et al. (2014)
	Mallín Fontanito	44.91	71.57	940	-58	18,050	P, C	*Nothofagus pumilio* forest	*This Manuscript*
	Laguna Venus	45.53	72.01	634	-34	1650	C	*Nothofagus nitida* and *N. pumilio* forest	Szeicz et al. (1998)
	Mallín Pollux	45.69	71.84	640	-47	17,619	P, C	*Nothofagus pumilio* forest	Markgraf et al. (2007)
	La Frontera**	46.89	71.88	997	350	8210	P, C	*Nothofagus antarctica* and *N. pumilio* forest	McCulloch et al. (2017)
	Lago Augusta**	47.08	72.38	440	0	16,000	P, C	*Nothofagus antarctica* and *N. pumilio* forest	Villa-Martínez et al. (2012)
	Lago Edita**	47.13	72.42	570	8940	19,000	P, C	*Nothofagus antarctica* and *N. pumilio* forest	Henríquez et al. (2017)
	Mallín Casanova*	47.64	72.98	126	-57	9950	P, C	*Nothofagus betuloides-Pilgerodendron forest*	Iglesias et al. (2018)

[1] P = Pollen data, C = Charcoal data

*Sites west of the Andean crest that were discussed, but not included in composite analyses

**Sites east of the Andean crest that were discussed, but data were not available for composite analyses

Table 4.1 cont.

Region	Site Name	Lat. (°S)	Lon. (°W)	Elevation (m elev)	Youngest Age (cal yr BP)	Oldest Age (cal yr BP)	Data Type[1]	Present Vegetation	Publication
Southern Patagonia	Moreno Glacier Bog	50.47	73.00	200	0	10,802	P	*Nothofagus pumilio* forest	Mercer and Ager (1983)
	Vega Ñandú	50.93	72.76	208	110	12,432	C	Open *Nothofagus antarctica* and *N. pumilio* forest and steppe	Villa-Martínez and Moreno (2007)
	Torres del Paine 2	51.08	73.06	88	57	13,127	C	Open *Nothofagus antarctica* and *N. pumilio* forest and steppe	Heusser (1995)
	Lago Guanaco	51.13	73.10	215	-39	3697	C	Steppe with scatered *Nothofagus antarctica*	Moreno et al. (2009a)
	Cueva Milodón	51.58	72.63	50	12,839	16,009	P	Open *Nothofagus pumilio* forest	Salmi (1955), Markgraf (1985)
	Potrok Aike	51.96	70.38	152	-42	437	C	Graminoid steppe with scatered *Nothofagus antarctica*	Haberzettl et al. (2005, 2006)
	Río Rubens Bog	52.04	71.88	220	-43	16,844	P	Open *Nothofagus antarctica* and *N. pumilio* forest and steppe	Huber and Markgraf (2003a, 2003b), Huber et al. (2004), Markgraf and Huber (2010)
	Laguna Azul	52.12	69.52	131	-14	1151	C	Graminoid steppe with scatered *Nothofagus antarctica*	Mayr et al. (2005)
	Punta Arenas	53.15	70.95	106	8	16,669	C	*Empetrum* steppe with scattered *Nothofaus betuloides*	Heusser (1995)
	Puerto del Hambre	53.60	70.91	3	47	13,417	C	*Nothofagus pumilio-N. betuloides* forest	McCulloch and Davies (2001)
	Isla Clarence	54.20	71.23	10	400	11,017	P	*Nothofagus betuloides* forest	Markgraf (1983)
	Yehuin	54.33	67.75	100	557	11,728	P	Open *Nothofagus antarctica* and *N. pumilio* forest and steppe	Markgraf (1983)
	Paso Garibaldi	54.72	67.83	550	-37	13,551	P	Open *Nothofagus antarctica* and *N. pumilio* forest	Markgraf (1993), Markgraf and Huber (2010)
	Harberton	54.87	67.30	20	-34	15,279	P, C	*Nothofagus betuloides-N. pumilio* forest	Markgraf (1991), Markgraf (1993a, 1993b), Markgraf and Kenny (1997), Markgraf et al. (2001)

[1] P = Pollen data, C = Charcoal data

*Sites west of the Andean crest that were discussed, but not included in composite analyses

**Sites east of the Andean crest that were discussed, but data were not available for composite analyses

Results

Chronology

Fifteen pollen samples were submitted from M. Fontanito for AMS radiocarbon dating (Table 4.2). The age-depth model produced an extrapolated mean basal age of the core of ~18,300 cal yr BP (Fig. 2). Five of the 15 radiocarbon dates were rejected as too old (OS-110935, OS-98575, and OS-135864) or too young (OS-110938 and OS-98861), based on exceeding the 95% confidence interval of the Bayesian model (Fig. 4.2). Anomalously old dates are attributed to contamination by groundwater, whereas anomalously young dates may be a result of younger material dragged down in the core.

Table 4.2. Radiocarbon dates from M. Fontanito.

Adjusted Depth (cm)	Lab ID[1]	Radiocarbon Age (^{14}C yr BP)	Age Error (yr)	Calibrated Age (cal yr BP; 1-sigma range)
0	Surface	Inferred	NA	-60
83	OS-98581	1030	20	820-929
104	OS-110935*	2290	35	2180-2337
115	OS-110936	2060	20	1932-2004
115.5	OS-135862	1950	20	1833-1880
123	OS-110937	1850	20	1706-1784
127	OS-98575*	7270	30	7977-8151
239	OS-110938*	2480	30	2364-2680
248.5	OS-130201	3930	20	4291-4406
287	OS-98861*	785	25	662-716
305.5	OS-135863	9080	45	10,189-10,238
320.5	OS-130202	9520	35	10,601-10,619
383	OS-98576	10850	60	12,685-12,740
402.5	OS-135864*	14000	85	16,770-17,095
482	OS-98588	13550	65	16,136-16,371
518	OS-130422	15800	85	18,893-19,111

[1] Pollen samples were submitted to the National Ocean Sciences Accelerator Mass Spectrometry facility for radiocarbon dating.
* Samples excluded from the age-depth model based on their position outside the 95% confidence interval of the chronology

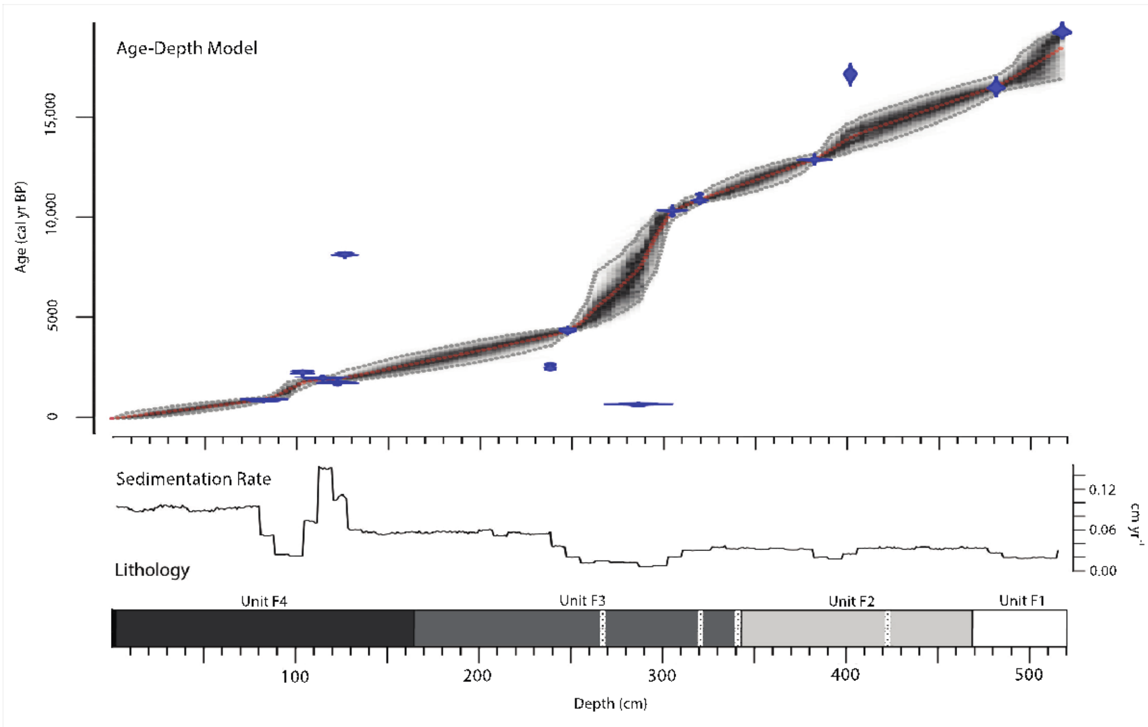

Figure 4.2: Age-depth model for Mallín Fontanito using Bacon 2.2 (Blaauw and Christen 2011). Blue areas represent the probability distributions of the calibrated dates, the dotted red line shows the weighted mean age for each depth, and gray shading and dotted light gray lines depict the most likely age-depth model and 95% confidence intervals. The sedimentation rate (cm yr^{-1}) and lithologic units are described in the text. Tephra layers > 1 cm in thickness are shown as white dotted bands. Depths are given in true core measurements, not the adjusted depths used to develop the chronology.

Lithology

At M. Fontanito, four lithologic units were identified (Fig. 4.2). Unit F1 (518-469 cm depth; ~18,900-16,000 cal yr BP) was composed of gray to dark-gray clay containing fine organic matter. The median sedimentation rate during Unit F1 was 0.017 cm yr^{-1} until 495 cm depth (~16,900 cal yr BP), when it increased to 0.034 cm yr^{-1}. Unit F1 was overlain by Unit F2 (469-343 cm depth; ~16,900-11,500 cal yr BP), which consisted of dark gray-to-grayish brown gyttja, interrupted by layers of black clay containing fine organic matter (469.5-469 and 416-380 cm depth) and a tephra layer (425-421 cm depth, ~14,600 cal yr BP). Sedimentation rate was stable through Unit F2 (median 0.03 cm yr^{-1}), except for a brief decrease at 407-392 cm depth (~14,000-13,000 cal yr BP) to 0.021-0.014 cm yr^{-1}. Unit F3 (343-165 cm depth; ~11,500-2600 cal yr BP) was characterized by very dark brown gyttja, with layers of black and white coarse tephra (343-340 cm depth, ~11,500 cal yr BP), black fine-grained tephra (322-321 cm depth, ~10,800 cal yr BP, and 268-267 cm depth, ~5700 cal yr BP), and gray fine-grained tephra (253-251 cm depth, ~4700 cal yr BP). The median sedimentation rate greatly decreased between 311 and 256 cm depth (~10,400-4550 cal yr BP) to 0.010 cm yr^{-1}. Unit F4 (165-147 cm depth; ~2600-2300 cal yr BP) was a dark grayish brown coarse-detritus gyttja (165-147 cm depth). Median sedimentation rate decreased to 0.052 cm yr^{-1} during the deposition of Unit F4. Unit F5 (147-0 cm depth; ~2300 cal yr BP to present) was a black fibrous sandy peat. The sedimentation rate of Unit F5 increased greatly to a median of 0.167 cm yr^{-1} between 127-112 cm depth (~2000-1900 cal yr BP), decreased to a median of 0.039 cm yr^{-1} between 112-80 cm depth (~1900-800 cal yr BP), and increased to a median of 0.087 cm yr^{-1} above 80 cm (~800 cal BP to present). Units F3 and F5 contained four radiocarbon dates that were rejected for having exceeded the 95% confidence interval of the Bayesian age-depth model. In general, the lithologic sequence suggests a hydrologic evolution from an open-water unproductive system (F1), to a more productive lake (F2-F3), then a shallow small lake (F4), and finally the present wetland (F5).

<u>Pollen and charcoal record</u>

The M. Fontanito record (Fig. 4.3) was divided into three local pollen zones:

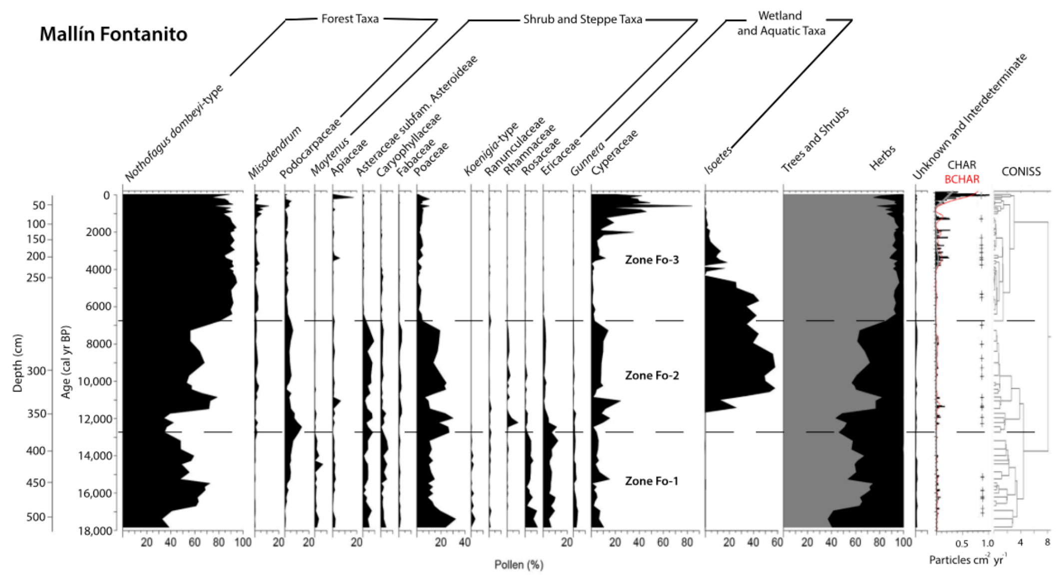

Figure 4.3: Pollen percentage diagram from Mallín Fontanito (Core Fo10B) showing dominant pollen taxa and charcoal data. Pollen zones were identified based on CONISS analysis (Grimm 1987). Charcoal accumulation rates (CHAR) and background CHAR (red line) describe variations in fire activity, and significant charcoal peaks (+) represent fire episodes.

Zone Fo-1 (511-391 cm depth; ~17,800-12,900 cal yr BP) was characterized by initially low percentages of *Nothofagus dombeyi*-type pollen (32.6-40.9%) until 490 cm depth (~16,600 cal yr BP). Between 490-391 cm depth (~16,600-12,900 cal yr BP), *N. dombeyi*-type pollen averaged 55.1% (ranging from 32.6 to 72.5%). Intervals of high *N. dombeyi*-type (61.0-72.5%) between 490-454 cm depth (16,600-15,500 cal yr BP) were associated with low percentages of herbaceous pollen taxa, including Poaceae (decreased from 32.0% to 8.9% through Fo-1), Asteraceae subfamily Asteroideae (0.3-5.4%), and Caryophyllaceae (0.3-5.0%). *Misodendrum* percentages were <0.6%. *Maytenus* pollen was at its highest abundance of the record (<0.1-6.6%), and pollen of Ericaceae (4.7-

12.3%), *Gunnera* (0.7-3.9%), *Koenigia*-type (<0.1-3.4%), and Rosaceae (<0.1-10.2 %) were well represented. Cyperaceae was present at values between 0.7-10%. Podocarpaceae percentages increased in Zone Fo-1 to the base of Fo-2 (from 0 to 14.2%).

CHAR in Zone Fo-1 was <0.07 particles cm^{-2} yr^{-1}. Between 500-411 cm depth (~17,300-15,000 cal yr BP), CHAR levels were slightly elevated and contained six significant peaks (Fig. 4.3). Little charcoal was recorded between 410 and 391 cm depth (~15,000-12,800 cal yr BP), and CHAR levels were negligible at the top of Zone Fo-1.

Zone Fo-2 (391-285 cm depth; ~12,900-7000 cal yr BP) was characterized by a brief increase in the abundance of *Nothofagus dombeyi*-type pollen (from 34 to 78%) at the expense of Poaceae pollen (from 30 to 6%) between 343-324 cm depth (~12,000-10,900 cal yr BP). This event was followed by an abrupt increase in Poaceae pollen (from 6 to 24%) at the expense of *N. dombeyi*-type pollen (from 78 to 57%) at 312 cm depth (~10,400 cal yr BP). Between 312-285 cm depth (~10,400-7000 cal yr BP), *N. dombeyi*-type pollen averaged 58% (53-68%) and Poaceae averaged 20% (14-24%). *Misodendrum* (<0.1-3.3%), Asteraceae subfamily Asteroideae (1.7-9.1%), Fabaceae (<0.1% -2.2%), and Rhamnaceae (<0.1-9.2%) were present in low abundance, and *Maytenus* (<0.01-2.0%), Ericaceae (0.6-11.2%), and Rosaceae (<0.1-0.4%) decreased (Fig. 3). Cyperaceae pollen increased from 0.9 to 24.6%. *Isoetes* appeared in the record and increased abruptly between 351-312 cm depth (~11,700-10,400 cal yr BP; averaged 49%).

Zone Fo-2 was characterized by a negligible level of CHAR until 369 cm depth (~12,300 cal yr BP), when CHAR increased with five significant peaks between 369-312 cm depth (~12,300-10,400 cal yr BP) (Fig. 4.3). CHAR levels decreased between 312-287 cm depth (~10,400-7700 cal yr BP) and remained low (0-0.06 particles cm^{-2} yr^{-1}) with five significant peaks. No charcoal was recorded between 287-285 cm depth (~7700-7000 cal yr BP).

Zone Fo-3 (285-0 cm depth; since ~7000 cal yr BP) featured a rise in *Nothofagus dombeyi*-type percentages (73.7-95.0%), and *Misodendrum* values were also elevated (0.4-11.7%). *N. dombeyi*-type and *Misodendrum* percentages increased at the expense of the nonarboreal taxa (e.g., Asteroideae (<0.1-0.9%), Caryophyllaceae (<0.1-1.8%), and Poaceae (0.7-10.3%)). Percentages of Apiaceae peaked (7.7-17.3%) at 17-9 cm depth (~135-48 cal yr BP) and a peak of Poaceae pollen (to 10.3%) coincided with increased Apiaceae percentages at 9 cm depth (~48 cal yr BP). Cyperaceae values were at their lowest level (0.4-3.2%) at the base of Zone Fo-3, increased above 206 cm depth (~3400 cal yr BP), and peaked (84%) at 59 cm depth (~600 cal yr BP). *Isoetes* decreased after 272 cm depth (~590 cal yr BP) and accounted for <1% by 88 cm depth (~1000 cal yr BP).

CHAR values in Zone Fo-3 were low (0-0.05 particles cm^{-2} yr^{-1}) between 285-233 cm depth (~7000-3900 cal yr BP) and varied above that (0-1.04 particles cm^{-2} yr^{-1}). Seven significant peaks in CHAR occurred from 250-150 cm depth, between ~3900 and 2500 cal yr BP (at ~3900, 3600, 3400, 3200, 3000, 2800, and 2400 cal yr BP). A large peak in CHAR also occurred at 95 cm depth (~1400 cal yr BP). Between 64-16 cm depth (~680-100 cal yr BP), CHAR levels increased to 0.07-1.04 particles cm^{-2} yr^{-1}, with highest values between 44-16 cm depth (~420-100 cal yr BP), and a large peak in CHAR at 20 cm depth (~150 cal yr BP). Above 10 cm depth (~100 cal yr BP to present), CHAR levels decreased to 0.07-0.78 particles cm^{-2} yr^{-1}.

Discussion

The postglacial vegetation and fire history east of the Andes in central Patagonia (44-50°S) is discussed based on pollen and charcoal records from M. Fontanito, and its comparison with five sites along the forest-steppe ecotone that lie within 100 km of M. Fontanito: Lago Los Niños, Laguna La Pava, Lago Shaman, Mallín El Embudo, and Mallín Pollux (Fig. 4.1, Table 4.1) (sites summarized in Table 1; Markgraf et al. 2007, de Porras et al. 2012, de Porras et al. 2014, Iglesias et al. 2018). The central Patagonia reconstruction is then compared with records from northern and southern Patagonia in order to better understand how *Nothofagus* history and past fire activity east of the Andes responded to large-scale changes in the climate system (Fig. 4.1, Table 4.1).

Vegetation and fire history at M. Fontanito

Between ~17,800 and 16,900 cal yr BP in Zone Fo-1, the presence of cold- and drought-tolerant heath-steppe at M. Fontanito suggests conditions that were cooler and drier than at present (Fig. 4.3). Drought-tolerant *Maytenus* was present in the pollen record along with elevated levels of Poaceae, Ericaceae (most likely *Empetrum*), Rosaceae, and Asteraceae subfamily Asteroideae (hereafter Asteraceae) (Fig. 4.3). Initially low pollen percentages of *Nothofagus dombeyi*-type also suggest few *N. antarctica* and/or *N. pumilio*. Early *Nothofagus* establishment may have been facilitated by *Empetrum* shrubs as occurs today in low-productivity settings following glacial retreat

(Henríquez and Lusk 2005). Alternatively, long-distance pollen transport from glacial refugia near the Andes may explain the persistent low occurrence of *N. dombeyi*-type that characterizes many early late-glacial pollen records (Markgraf et al. 1995, Premoli 1997, de Porras et al. 2012).

The abundance of *N. dombeyi*-type pollen was elevated (to an average of 59%) along with that of *Maytenus* and other shrub taxa (e.g., Asteraceae, Caryophyllaceae, and Rosaceae) until the end of Zone Fo-1, suggesting an expansion in *Nothofagus* shrubland or open forest from ~16,900 to 12,900 cal yr BP. Between ~15,900 and 15,500 cal yr BP, *N. dombeyi-type* pollen increased to 68-72%. Based on modern pollen data (Mancini et al. 2012, Iglesias et al. 2016b), the local vegetation at M. Fontanito after ~16,900 cal yr BP was likely *Nothofagus* shrubland or open forest, with a brief period of more-closed *Nothofagus* forest from ~15,900-15,500 cal yr BP. Podocarpaceae pollen increased throughout Zone Fo-1 and is attributed *Podocarpus nubigenus* and/or *Lepidothamnus fonkii*, the product of long-distance transport from west of the Andean crest. Low but present levels of *Gunnera* pollen during Zone Fo-1 come from *G. chilensis* and/or *G. magellanica*, which grow in locally disturbed wet habitats.

Although CHAR increased slightly between ~17,300 and 15,000 cal yr BP at M. Fontanito, CHAR was generally low (<0.07 particles $cm^{-2}\ yr^{-1}$) through Zone Fo-1, suggesting that fire activity was low, likely as a consequence of cold conditions and low fuel biomass. The slight increase in CHAR between ~17,300 and 15,000 cal yr BP co-occurred with the brief increase in *Nothofagus dombeyi-type* percentages, suggesting that fire activity was fuel limited.

Between *ca.*12,900 and 11,700 cal yr BP, the Zone Fo-2 pollen record featured high percentages of Poaceae and Asteraceae and a decrease in *Nothofagus dombeyi*-type (to <41%)*,* indicative of a grass-steppe with sparse tree cover (Fig. 4.3). This interval was followed by increasing *N. dombeyi*-type percentages (to 78%) between ~12,000 cal yr BP and 10,400 cal yr BP, which suggests a brief period of closed *Nothofagus* forest. Between ~10,400 and 7000 cal yr BP, Poaceae increased and *N. dombeyi*-type percentages decreased (to 41-67%), suggesting a return levels similar to modern shrubland and open forest (Iglesias et al. 2017). Increased Cyperaceae values suggest lower water levels, and along with decreased Gunnera percentages, imply conditions that were effectively drier than before. *Isoetes* microspores increased in abundance abruptly between ~11,700 and 10,400 cal yr BP. Although it has been used as a proxy for high lake level at some sites (Moreno et al. 2018b), studies of modern *Isoetes* ecology in southern South America provide conflicting information about its preferred environment (i.e., water depth and temperature) (Hickey et al. 2003); thus, we do not interpret this taxon.

Increased CHAR at the beginning of Zone Fo-2 suggests that fire activity was higher from ~12,300-10,400 cal yr BP than before. Increased fire activity co-occurred with a brief transition from shrubland or open forest to closed forest near M. Fontanito. After 10,400 cal yr BP, *Nothofagus dombeyi*-type and CHAR levels were low until ~7000 cal yr BP, suggesting a return of open vegetation and low fire activity until the end of Zone Fo-2. Pollen and charcoal data from this zone suggest that warming and drying led to longer growing and fire seasons, especially between ~12,300 and 10,400 cal yr BP, and that fire activity was fuel limited.

The beginning of Zone Fo-3 (~7000-4000 cal yr BP) is characterized by increased *Nothofagus dombeyi*-type pollen to nearly 95%, at the expense of steppe taxa (i.e., Poaceae, Asteraceae, Fabaceae, Ericaceae, and Rhamnaceae), marking the establishment of closed forest in the M. Fontanito watershed. Low levels of Cyperaceae between ~7000 and 3400 cal yr BP suggest a time of reduced littoral area and higher lake levels. During this period, CHAR was at its lowest and fire activity was minimal. Forest closure, increased lake levels, and low fire activity suggest effectively wetter than the early Holocene.

After ~4000 cal yr BP (Zone Fo-3), *Nothofagus dombeyi*-type pollen dominated the M. Fontanito pollen record (>73.7%) but fluctuations with Poaceae and/or Apiaceae were registered at ~3400, 3200, 1000, 800, 600, 200, and 100 cal yr BP (Fig. 4.3). CHAR levels were elevated, suggesting overall high fire activity. Periods of highest CHAR values align with decreased *N. dombeyi*-type percentages at ~3700-3300 cal yr BP, 2400-1800 cal yr BP, and after 1400 cal yr BP, implying that fire episodes led to short-term openings in forest canopy. The large increase in Cyperaceae between ~3400 and 500 cal yr BP probably marks formation of the modern wetland. Fluctuations in the pollen record between forest and disturbance taxa and increased fire activity are consistent with increased submillennial climate variability (i.e., ENSO and SAM) and increased human presence in the region (Méndez et al. 2018a).

Vegetation and fire history of central Patagonia
<u>east of the Andes (44-50°S)</u>

Late-glacial period (> ~13,000 cal yr BP): Pollen data from L. Los Niños indicate the presence of heath-steppe before ~15,500 cal yr BP, grass-steppe between ~15,500 and 14,200 cal yr BP, and open *Nothofagus* forest from ~14,200 to 13,400 cal yr BP (Fig. 4.4; Iglesias et al. 2016a). In the Río Cisnes Valley, L. Shaman shows similar presence of grass-steppe with scattered *Nothofagus* (<40% abundance) prior to ~12,300 cal yr BP (de Porras et al. 2012). M. Fontanito was characterized by heath-steppe until ~16,900 cal yr BP, when *Nothofagus* shrubland and/or forest expanded in the region between ~16,900 and 12,900 cal yr BP. M. Pollux featured grass-steppe before ~10,200 cal yr BP, with a brief expansion of *Nothofagus* between ~14,200-13,800 cal yr BP (Markgraf et al. 2007).

The pollen record from L. Edita shows an Ericaceae (most likely *Empetrum*) heath-steppe between ~19,000 and 16,800 cal yr BP (Henríquez et al. 2017). Pollen data from L. Edita and nearby L. Augusta (Table 4.1, not in the composite) suggest replacement of heath-steppe by grass-steppe at ~13,200 cal yr BP, and establishment of *Nothofagus* forest by ~12,700 cal yr BP at L. Edita, and by ~11,800 cal yr BP at L. Augusta (Villa-Martínez et al. 2012, Henríquez et al. 2017). L. Oprasa and L. Fácil, on the Chonos Archipelago, record presence of rainforest taxa including *Nothofagus,* Cupressaceae (most likely *Pilgerodendron*), and Podocarpaceae after ~15,000 cal yr BP and establishment of closed forest by ~13,500 cal yr BP (Bennett et al. 2000, Haberle and Bennett 2004). According to Haberle and Bennett (2004), this expansion is attributed to rising temperature.

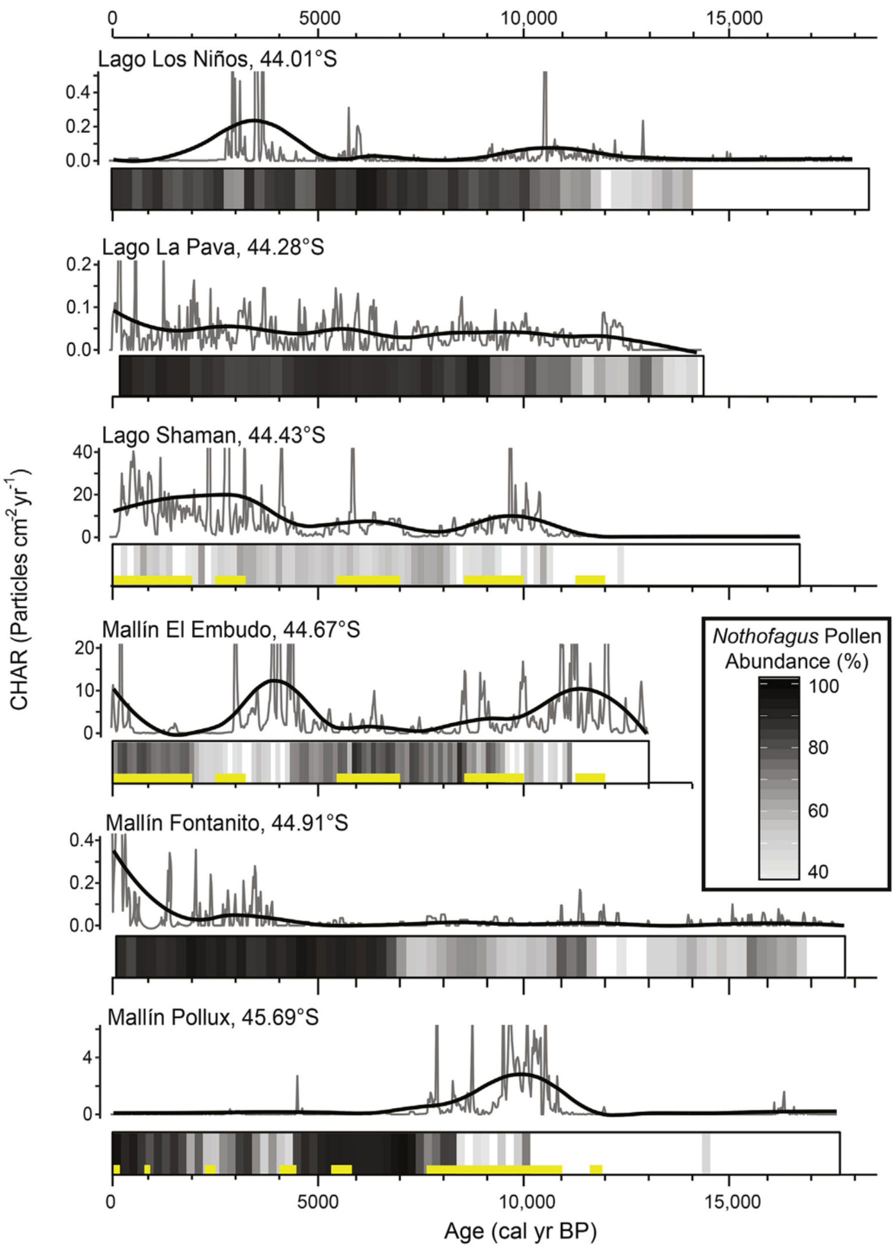

Figure 4.4: Fire and vegetation history for sites east of the Andes in central Patagonia**.** Interpolated charcoal accumulation rate data (CHAR) are shown in gray and black lines depict smoothed (LOWESS with 500-yr window) trends in CHAR. Percent *Nothofagus dombeyi*-type pollen is plotted as a color gradient, from white (<41%) to black (100%). Based on modern pollen studies steppe is <41% *N. dombeyi*-type pollen, *Nothofagus* shrubland or open *Nothofagus* forest is 41-67% *N. dombeyi*-type pollen, and closed *Nothofagus* forest is greater than 67% *N. dombeyi*-type pollen (Mancini et al. 2012, Iglesias et al. 2016b). Radiocarbon-dated human presence, shown as yellow bars, is summarized from Mena et al. (2003), Méndez et al. (2018a), Méndez et al. (2011), and Reyes et al. (2007).

Charcoal data indicate slightly increased fire activity between ~17,000 and 14,000 cal yr BP at M. Fontanito, concomitant with pollen evidence of increased woody fuels, before both fire activity and *Nothofagus* abundance decreased between ~14,000 and 13,000 cal yr BP (Fig. 4.3 and 4.4). At L. Los Niños, fire activity was low throughout the late-glacial period possibly due to sparse fuel cover and/or few ignitions (Iglesias et al. 2016a). According to de Porras et al. (2012), the steppe vegetation at L. Shaman was discontinuous, resulting in negligible fire activity during the late-glacial period. Fire activity was also generally low at L. Edita, L. Augusta, and at L. Oprasa and L. Fácil, west of the Andes (Haberle and Bennett 2004, Villa-Martínez et al. 2012, Henríquez et al. 2017).

<u>Late-glacial to early-Holocene period (~13,000-7000 cal yr BP)</u>: Pollen records from L. Los Niños, L. La Pava, L. Shaman, M. El Embudo, M. Fontanito, and M. Pollux show the beginning of nearly continuous *Nothofagus dombeyi*-type percentages of over 41% beginning between ~14,000 and 10,200 cal yr BP, suggesting the presence of *Nothofagus* shrubland or open forest (41-67% *N. dombeyi*-type), and closed forest (when >67% *N. dombeyi*-type). Similar increases in woody shrub and forest pollen taxa occurred at L. Edita and L. Augusta, between ~13,200 and 11,100 cal yr BP, where *N. dombeyi*-type, Cupressaceae, and *Podocarpus* pollen percentages were high at the expense of Poaceae and *Empetrum* steppe taxa (Villa-Martínez et al. 2012, Henríquez et al. 2017). At La Frontera, *N. dombeyi*-type pollen abundance increased from 25 to 65%, suggesting a shift from steppe to shrubland or open forest at ~7300 cal yr BP (Table 4.1, not included in composites) (McCulloch et al. 2017).

The presence of closed *Nothofagus* forest (>67% *Nothofagus dombeyi*-type) at central Patagonian sites east of the Andes was generally time transgressive from north to south, starting first at ~10,000 cal yr BP at L. Los Niños, then at ~9000 cal yr BP at L. La Pava, ~8000 cal yr BP at M. El Embudo, ~7000 cal yr BP at M. Fontanito, and ~7500 cal yr BP at M. Pollux. The high *Nothofagus* abundance at these sites also suggests that the forest-steppe ecotone occupied a similar-to-present position by the end of the early Holocene. The latitudinal development of closed *Nothofagus* forest in central Patagonia appears to have been time transgressive, but site-specific differences in vegetation history were also governed by moisture limitations along the west-east precipitation gradient. For example, L. Shaman had a lower abundance of *N. dombeyi*-type pollen relative to other sites in the region (reaching 61-63% *Nothofagus* abundance at between ~8000 and 7300 cal yr BP), reflecting its location to the east, where steppe and shrubland taxa were abundant. West of the Andes, the pollen record from M. Casanova was dominated by *N. dombeyi*-type and Cupressaceae until ~8500 cal yr BP, indicating the early establishment of present-day *Nothofagus*-*Pilgerodendron* forest (Iglesias et al. 2018). In contrast, high levels of *Tepualia* and *Weinmannia* pollen at L. Oprasa and L. Fácil from ~12,500 to 6800 cal yr BP indicate a more diverse rainforest than at present.

Fire activity, inferred from CHAR, was elevated throughout central Patagonia between ~13,000 and 10,000 cal yr BP, concomitant with increased *Nothofagus dombeyi*-type percentages. This apparent increase in fire activity and *Nothofagus* abundance could have resulted from warmer winters, which extended the growing season, and effectively drier summers, which increased fire activity (Renssen et al. 2005, Whitlock et al. 2007).

The association of elevated *N. dombeyi*-type percentages and elevated CHAR levels also suggests that *N. antarctica*, which resprouts and spreads rapidly after fire (Kitzberger et al. 2016), was a major component of the vegetation, as opposed to *N. pumilio*, which is sensitive to fire (Mermoz et al. 2005). Decreased CHAR at sites throughout central Patagonia between ~10,000 and 7000 cal yr BP, suggests a reduction of fire activity in the region from earlier levels.

Although earliest occupation of central Patagonia east of the Andes dates to between ~12,060 and 11,760 cal yr BP, human populations were sparse, nomadic, and confined to the steppe (Fig. 4.4; Bellelli et al. 2000, Méndez and Reyes 2008, Perez et al. 2016, Méndez et al. 2018a). During the early Holocene in the Río Cisnes Valley, increased fire activity at L. Shaman and M. El Embudo coincided with the radiocarbon-dated occupation of the nearby El Chueco 1 archaeological site (Fig. 4.1 and 4.4; Reyes et al. 2007, Méndez et al. 2011). Similarly, increased fire activity at M. Pollux and radiocarbon-dated human presence at the nearby Baño Nuevo 1, Cueva de la Vieja, and Casa de Piedra Roselló archaeological sites (40-50 km to the northeast; Fig. 4.1) co-occurred between ~11,000-7800 cal yr BP (Mena et al. 2003, Castro Esnal et al. 2017, Méndez et al. 2018a). Interestingly, a period of null-to-low fire activity between ~8000 and 7000 cal yr BP at M. Fontanito and L. Shaman coincided with the abandonment of the El Chueco 1, Baño Nuevo 1, and the Cueva de la Vieja archaeological sites (de Porras et al. 2012, Méndez et al. 2016, Méndez et al. 2018a), suggesting that fire activity may have been constrained by an effectively wetter climate after 8000 cal yr BP as well as reduced human ignition. Méndez et al. (2016) suggest that increased fuel biomass, a warmer, effectively drier climate than before, and human ignition were responsible for increased fires in central Patagonia during the late-glacial to early-Holocene transition. We suggest that anthropogenic burning was nonetheless localized.

<u>Middle Holocene (~7000-4000 cal yr BP)</u>: Afforestation, decreased CHAR, and increased lake levels occurred during this period throughout central Patagonia east of the Andes (Fig. 4.4; Markgraf et al. 2007, de Porras et al. 2012, de Porras et al. 2014, Iglesias et al. 2016a) and west of the Andes (Bennett et al. 2000, Haberle and Bennett 2004), likely as a result of increased precipitation and point to more Pacific storms in this region.

Interestingly, a unique period of high fire activity occurs at L. Shaman from ~7000 to 5000 cal yr BP (de Porras et al. 2012), coincident with human occupation at the nearby El Chueco 1 archaeological site and elsewhere in the Río Cisnes Valley (Méndez et al. 2016). During this period, M. Fontanito shows no evidence of increased burning even though it was located within 50 km of archaeological sites (i.e., El Chueco 1 and Las Quemas to the north, and Baño Nuevo 1 and Cueva de la Vieja to the south; Méndez et al. 2018a, Méndez et al. 2018b). Similarly, although M. Pollux is <50 km from the Baño Nuevo 1 and Cueva de la Vieja archaeological sites, there is no evidence of increased fires in the charcoal record during this period (Markgraf et al. 2007). This comparison between L. Shaman, M. Fontanito, and M. Pollux suggests that anthropogenic fires continued to be local in extent during this period.

Late Holocene to present (< ~4000 cal yr BP): Nonsynchronous increases in CHAR and decreases in *Nothofagus dombeyi*-type pollen abundance occurred throughout central Patagonia: at L. Los Niños (i.e., at ~3100-2800 cal yr BP), L. Shaman (i.e., at ~4200-2200 cal yr BP, 2000-1600 cal yr BP, and after 600 cal yr BP), M. Fontanito (i.e., at ~3700-3300 cal yr BP, 2400-1800 cal yr BP, and after 1400 cal yr BP), and M. Pollux (i.e., at ~4500-3500 cal yr BP, 3000-2200 cal yr BP, and after 100 cal yr BP) (Fig. 4.4) (Markgraf et al. 2007, de Porras et al. 2012, Iglesias et al. 2016a). Similarly, La Frontera registered a period of decreased *N. dombeyi*-type percentages from ~3800 to 1800 cal yr BP, associated with an increase in microcharcoal between ~2800 and 2600 cal yr BP (McCulloch et al. 2017). M. El Embudo shows a period of low-to-moderate levels of *N. dombeyi*-type pollen between ~4200 and 2100 cal yr BP that was associated with high CHAR between ~4500 and 3000 cal yr BP (de Porras et al. 2014). Similar forest closure and low fires occurred at M. Pollux between ~2200 and 100 cal yr BP (Fig. 4.4). L. Augusta registered low fire activity and *Nothofagus* forest closure through the late Holocene until ~650 cal yr BP (Villa-Martínez et al. 2012). West of the Andes, fluctuations in disturbance taxa (e.g., Poaceae and Apiaceae) and increased fires occurred after ~2000 cal yr BP at M. Casanova (Iglesias et al. 2018). On the Chonos Archipelago, fire activity increased after ~2800 cal yr BP, with little change in rainforest taxa (Haberle and Bennett 2004). Taken together the central Patagonia records show increased fire activity at ~4500-2800 and 2400-1600 cal yr BP, in association with relatively open vegetation. Less fire activity and more *N. dombeyi*-type pollen are registered at ~2800-2400 cal yr BP and after 1600 cal yr BP.

Overall levels of *Nothofagus dombeyi*-type pollen in central Patagonia during the late Holocene suggest vegetation similar to the middle Holocene; however, subtle fluctuations in pollen and charcoal at most sites are consistent with independent evidence of increased interannual climate variability, resulting from a strengthening of the El Niño-Southern Oscillation (ENSO; Moy et al. 2002) and Southern Annual Mode (SAM; Villalba et al. 2012, Moreno et al. 2018a). Aridity associated with La Niña events is a strong driver of fire activity in northern Patagonia (Kitzberger et al. 1997, Veblen et al. 1999, Whitlock et al. 2007), and a positive phase of SAM has been shown explained fire occurrence south of 42°S (Garreaud et al. 2009, Holz and Veblen 2011b, Holz et al. 2012). Dendrochronological research on *N. pumilio* south of 44°S shows that positive SAM during the austral spring and summer, when SWW are shifted poleward, is associated with warmer, drier conditions and region-wide burning (Garreaud et al. 2009, Holz and Veblen 2011b, Mundo et al. 2017b).

The late Holocene is also characterized by increased human populations, which may have contributed to fluctuations in fire activity (Méndez et al. 2016) (Fig. 4.4). Human presence near in the Río Cisnes Valley increased after ~3500 cal yr BP (Bellelli et al. 2000, Méndez and Reyes 2008, Méndez et al. 2018a), and co-occurred with periods of elevated fire activity at M. El Embudo and L. Shaman (de Porras et al. 2014, Méndez et al. 2016). In both the Río Cisnes Valley and on the Chonos Archipelago, people were likely taking advantage of heightened climate variability, including periods of drier, more fire-conducive conditions. Interestingly, at L. Los Niños and L. La Pava, fire activity does not increase during this period even though the Río Pico and Genoa valleys (10-40 km away) had late-Holocene occupation (Fig. 4.1; Scheinsohn et al. 2016, Scheinsohn et al. 2017). We believe this highlights the heterogeneous nature of pre-European land use.

The Euro-American influence in central Patagonia is evident at some but not all sites. In the Chonos Archipelago, L. Fácil shows increased charcoal levels and decreased *Pilgerodendron* after ~600 cal yr BP during initial Spanish exploration and colonization (Szeicz et al. 2003, Haberle and Bennett 2004). Loss of forest at L. Augusta occurred at ~650 cal yr BP. At M. Fontanito, high values of Apiaceae and Poaceae and the highest fire activity of the record are registered after ~140 cal yr BP with Euro-American settlement and forest clearance (Fig. 4.3). Similar evidence of anthropogenic disturbance in recent centuries is also found at L. Shaman, M. El Embudo, M. Pollux, and M. Casanova as an increase in disturbance taxa at the expense of *Nothofagus dombeyi*-type pollen (Markgraf et al. 2007, de Porras et al. 2012, de Porras et al. 2014, Iglesias et al. 2018).

Environmental history of Patagonia (39-55°S)
<u>along the eastern Andes</u>

Postglacial climate histories of southern South America have greatly focused on the strength and position of the Southern Westerly Winds (SWW) through time (Garreaud et al. 2013). Although the influence of SWW dynamics has been inferred from sites west of the Andes (Moreno 2004, Moreno et al. 2012), their role in governing Pacific storm tracks and therefore shaping the postglacial vegetation and fire history east of the Andes is still unclear. Moreno et al. (2012) suggest that the SWW were south of their present position between ~15,000 and 11,500 cal yr BP based on the fire history of southwestern Patagonia. In contrast, Iglesias et al. (2016a) used *Nothofagus* pollen abundance to suggest that the SWW initially lay farther north and gradually shifted southward through the late-glacial period and early Holocene. During the Antarctic Cold Reversal (~14,500-12,800 cal yr BP; ACR), precipitation increased throughout Patagonia (Moreno et al. 2012), with an inferred southward shift and/or strengthening of the SWW. During the Younger Dryas Chronozone (~13,000-11,700 cal yr BP; YDC), moisture levels decreased in northern and central Patagonia and increased in southern Patagonia, implying a further southward shift of SWW (Moreno et al. 2012, Iglesias et al. 2016a). Evidence of decreased precipitation throughout Patagonia from ~11,700 to 8000 cal yr BP is attributed to a weakening and/or more southerly position of the SWW during the early Holocene (Whitlock et al. 2007, Moreno et al. 2012), After ~8000 cal yr BP, the establishment of modern vegetation west of the Andes implies that the SWW were generally at their present position and strength (Fletcher and Moreno 2012a).

To understand how the vegetation and fire history of Patagonia east of the Andes was governed by the position and strength of the SWW, *Nothofagus* and CHAR composites from selected sites from 41° to 55°S (Fig. 4.1; Table 4.1) were compared with independent paleoclimate data, including a deuterium-based temperature reconstruction from the EPICA Antarctic Dome C ice core (Jouzel et al. 2007) and sea-surface temperature (SST) reconstructions off the Chilean coast (Kaiser et al. 2005) (Fig. 5).

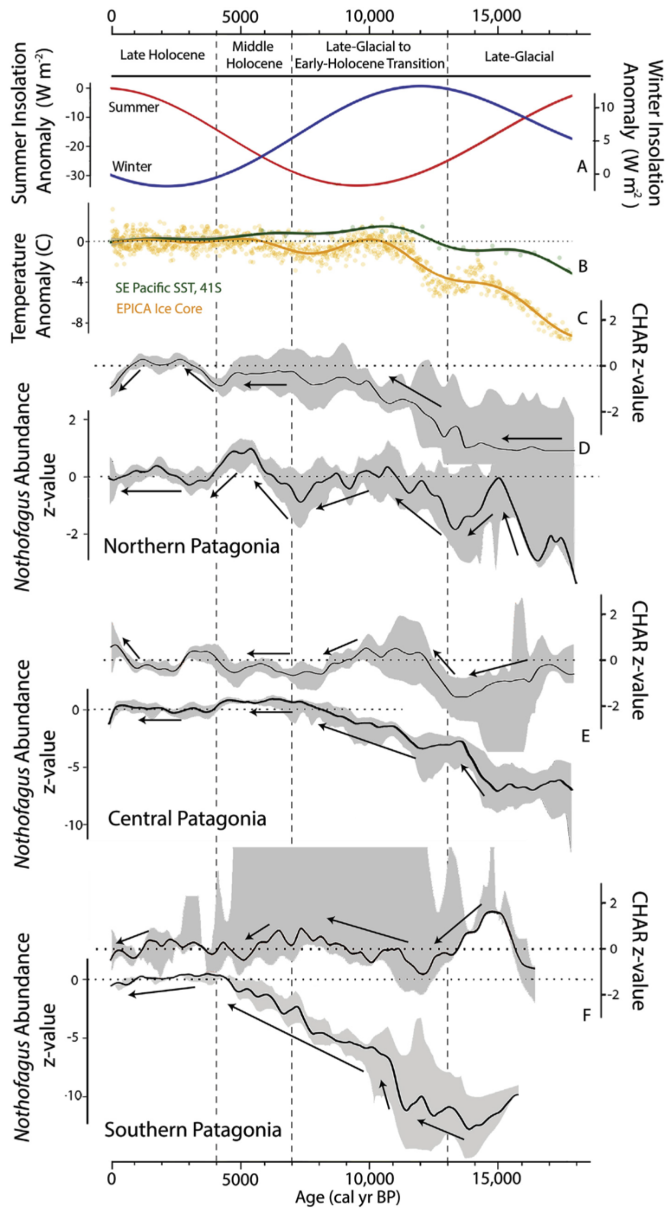

Figure 4.5: Comparison of forest and fire history in northern, central, and southern Patagonia, east of the Andes, with independent paleoclimate information. (A) Summer (red) and winter (blue) insolation anomalies from present (Alder and Hostetler 2014) (B) Alkenone-based SST anomalies (dark green) (Kaiser et al. 2005). (C) Deuterium-based temperature reconstructions (yellow) (Jouzel et al. 2007). Composite CHAR and *Nothofagus* abundance are presented as z-values for sites in (D) northern Patagonia (41-44°S), (E) central Patagonia (44-50°S), and (F) southern Patagonia (50-55°S). (D-F) 95% confidence intervals (shaded in gray) were based on bootstrap resampling by site 1000 times. The black lines represent data smoothed using a LOWESS robust to outliers. Arrows denote discussed trends and, for reference, dashed horizontal lines show the boundary between positive and negative anomalies for each series.

Late-glacial period (>~ 13,000 cal yr BP): From ~18,000 to 13,000 cal yr BP, winter insolation increased ~7 Wm^{-2} and summer insolation decreased ~20 Wm^{-2}, resulting in less seasonality than present (Alder and Hostetler 2014). Independent climate data show rapid warming until ~15,000 cal yr BP, followed by little change in temperatures between ~15,000 and 13,000 cal yr BP. Antarctic Dome C ice-core and sea-surface temperature (SST) reconstructions indicate rapid warming by about 5°C from ~18,000 to 15,000 cal yr BP in association with increasing winter and annual insolation (Fig. 4.5) (Kaiser et al. 2005, Jouzel et al. 2007, Caniupán et al. 2011). The Patagonian Icecap decreased in area by nearly 20% between ~18,000 and 15,600 cal yr BP and then receded to near-present size by ~14,000 cal yr BP (~80% loss since the LGM) (McCulloch et al. 2005, Boex et al. 2013).

During the late-glacial period, northern, central, and southern Patagonia east of the Andes differed in *Nothofagus* pollen and charcoal abundance, suggesting regional differences in *Nothofagus* cover and fire activity (Fig. 4.5). In northern Patagonia (41-44°S), *Nothofagus* pollen increased between ~16,000 and 15,000 cal yr BP (-4.0 - -0.5 z-value) and then decreased until ~13,000 cal yr BP (-1.7 z-value). Fire activity was low in northern Patagonia (-4.0 - -2.5 z-value) throughout the late-glacial period, potentially facilitating an early expansion of *Nothofagus*. Central Patagonia east of the Andes was largely treeless prior to ~17,000 cal yr BP (-7.5 - -6.2 z-value). Fire activity was elevated between ~18,000 and 17,000 cal yr BP (-0.5 - -0.3 z-value), decreased to lower-than-base levels between ~17,000 and 14,500 cal yr BP (-0.3 - -1.3 z-value), and further decreased at ~13,000 cal yr BP (-1.7 z-value). *Nothofagus* became somewhat more abundant in central Patagonia between ~14,500 and 13,000 cal yr BP, when fire activity decreased, although the pollen records at most sites indicate steppe vegetation. Southern Patagonia (50-55°S) also had few *Nothofagus* (-12 - -10 z-value) during the late-glacial period, but small increases in *Nothofagus* occurred between ~14,000 and 13,000 cal yr BP. Fire activity was higher than the base period (0-1.5 z-value), especially between ~16,000 and 13,000 cal yr BP, and decreased at ~12,000 cal yr BP (to -1.5 z-value). Thus, vegetation east of the Andes was generally steppe during the late-glacial period, but small increases in *Nothofagus* abundance occurred at all latitudes after ~14,000-13,000 cal yr BP, concomitant with low or decreasing fire activity.

The regional differences in *Nothofagus* abundance and fire activity suggest that conditions were wetter in the north than in the south, consistent with a more northerly position of the SWW storm tracks during the early late-glacial period (Iglesias et al. 2016a, Moreno et al. 2018b). Low fire activity and early expansion of *Nothofagus* in northern Patagonia contrast with higher levels of charcoal and later expansion of *Nothofagus* in central and southern Patagonia. During the ACR, fire activity was low or decreasing east of the Andes, and *Nothofagus* abundance decreased in northern Patagonia and increased in central and southern Patagonia. Colder, wetter conditions in central and southern Patagonia are also evidenced by glacial re-advances in Torres del Paine (51°S) between ~14,800 and 12,600 cal yr BP (Moreno et al. 2009b, García et al. 2012). Increased moisture south of 44°S co-occurring with cold, dry conditions in the north and the increasing *Nothofagus* abundance in the south, is consistent with a strengthening and southward shift of storm tracks and the position of the SWW.

Late-glacial to early-Holocene period (~13,000-7000 cal yr BP): During the late-glacial to early-Holocene period winter insolation anomaly reached a maximum (~12 Wm^{-2}) at ~12,000 cal yr BP, before slowly decreasing to 5 Wm^{-2} by ~7000 cal yr BP; summer insolation anomaly reached a minimum by ~9500 cal yr BP, and was ~-30 Wm^{-2} throughout the period (Alder and Hostetler 2014). Seasonality during this period would have been lowest at ~13,000-9000 cal yr BP, then slowly increased through the end of the period. Independent climate data show a period of increasing temperature between ~13,000 and 10,000 cal yr BP (Kaiser et al. 2005, Jouzel et al. 2007). SST data from 41°S indicate warmer-than-present conditions by ~12,000 cal yr BP (Kaiser et al. 2005). By ~11,500 cal yr BP, reconstructed Antarctic temperatures were warmer than present (Jouzel et al. 2007). SST at 41°S and Antarctic temperature reconstructions decrease slightly from ~9000 to 7000 cal yr BP (Kaiser et al. 2005, Jouzel et al. 2007).

The late-glacial to early-Holocene period was characterized by higher-than-present fire activity and large differences in *Nothofagus* abundance between northern, central, and southern Patagonia. In northern Patagonia, *Nothofagus* levels increased from ~13,000 to 10,000 cal yr BP (from -1.0 to 0.5 z-value) and then decreased from ~10,000 to 7000 cal yr BP (from 0.5 to -0.7 z-value). Fire activity increased but remained below base levels between ~13,000 and 7000 cal yr BP (from -2 to -0.5 z-value). In central Patagonia, *Nothofagus* became more abundant (increasing from -4 to 0 z-score), reaching base levels at ~8000 cal yr BP, and surpassing base levels by ~7000 cal yr BP (z-values reaching 0.5). Fire activity was elevated between ~12,500 and 10,000 cal yr BP (0 to 0.5 z-value), then decreased (from 0.5 to -0.5 z-score) by ~8000 cal yr BP. In southern

Patagonia, *Nothofagus* abundance increased abruptly at ~11,500-11,000 cal yr BP (from -10 to -6 z-value) and then gradually from ~11,000 to 8000 cal yr BP (from -6 to -5 z-value). Fire activity increased (from -1 to 0.5 z-value) between ~12,000 and 7000 cal yr BP.

Increased *Nothofagus* abundance and fire activity throughout Patagonia between ~13,000 and 10,000 cal yr BP is attributed to decreased seasonality caused by higher winter insolation and lower summer insolation (Renssen et al. 2005, Whitlock et al. 2007). Between ~10,000 and 7000 cal yr BP, decreased *Nothofagus* abundance, increased fire activity, and higher-than-present temperatures suggest that increased effective aridity may have facilitated a shift towards open vegetation (Moreno 2004). In contrast, *Nothofagus* abundance continued to increase in central and southern Patagonia after ~10,000 cal yr BP, concomitant with decreased fire activity in central Patagonia and increased fire activity in southern Patagonia. The continued *Nothofagus* expansion to base levels in central Patagonia and just below base levels in southern Patagonia suggest an effectively wetter climate than in northern Patagonia. The paleoecological data east of the Andes support the hypothesis that storm tracks weakened throughout Patagonia between ~13,000-10,000 cal yr BP. During this period, either the SWW were weakened and/or shifted far south of their present position (Moreno 2004, Whitlock et al. 2007, Fletcher and Moreno 2012a, Kilian and Lamy 2012). Between ~10,000-7000 cal yr BP, the paleoecological data suggest that storm tracks became stronger in central and southern Patagonia than in northern Patagonia. This is consistent with the hypothesis that by ~7000 cal yr BP, the SWW strengthened and/or shifted north from the previous

(~13,000-10,000 cal yr BP) position (Moreno 2004, Whitlock et al. 2007, Fletcher and Moreno 2012a, Kilian and Lamy 2012).

Middle Holocene (~7000-4000 cal yr BP): Throughout Patagonia, the middle Holocene marks the onset of cooler, effectively wetter conditions than during the early Holocene, in association with decreasing winter and increasing summer insolation (Fig. 4.5) (Kaiser et al. 2005, Jouzel et al. 2007, Fletcher and Moreno 2012a, Alder and Hostetler 2014). The SWW strengthened and shifted to the present position by ~7000 cal yr BP, therefore strengthening and focusing storm tracks at the latitude of central Patagonia. Cool, effectively wet middle-Holocene conditions resulted in the Neoglacial expansion of the Northern and Southern Patagonian Icecaps, from ~5800 to 4900 cal yr BP (Porter 2000, Rojas and Moreno 2011).

During this period, *Nothofagus* abundance increased throughout Patagonia in association with decreased fire activity. In northern and central Patagonia, *Nothofagus* abundance was highest by ~6000 cal yr BP (~1 z-value), in association with relatively low fire activity between ~7000 and 4000 cal yr BP. In southern Patagonia, *Nothofagus* abundance was highest at 4000 cal yr BP (0.2 z-value), and fires were at base levels (from 0.75 to -0.5 z-value). These results support a strengthening of storm tracks throughout Patagonia and a "moisture maximum" from ~7000 to 4000 cal yr BP, associated with a strengthening and shifting of the SWW to the present position (Fletcher and Moreno 2012a).

Late Holocene to present (<~ 4000 cal yr BP): During the late Holocene, the summer insolation anomaly increased 15 Wm^{-2} to present level, and the winter insolation anomaly reached a minimum of -2 Wm^{-2} (Alder and Hostetler 2014), suggesting increasing seasonality to present levels. SST data from 41°S and Antarctic reconstructed temperatures are similar to modern throughout the late Holocene (Kaiser et al. 2005, Jouzel et al. 2007). During this period, precipitation increased at Lago Aculeo, in central Chile (33°S; Jenny et al. 2003), and at Laguna Potrok Aike, in Tierra del Fuego (53°S; Anselmetti et al. 2009), and decreased in northern Patagonia (41°S), as inferred from pollen records (Moreno 2004, Iglesias et al. 2012). These differences in regional precipitation suggest that the latitude of storm tracks were influenced by the strengthening of ENSO and probably SAM after ~4000 cal yr BP (Kitzberger et al. 1997, Holz and Veblen 2012, Moreno et al. 2014, Mundo et al. 2017b).

The late Holocene in Patagonia east of the Andes is characterized by high *Nothofagus* abundance and the formation the forest-steppe ecotone. In northern Patagonia, a pronounced decrease in *Nothofagus* abundance (from 0.8 to -0.2 z-value) after ~3500 cal yr BP is a result of the added presence of *Austrocedrus* in low-elevation dry forests (Whitlock et al. 2006). Between ~4000-2000 cal yr BP, central and southern Patagonia show very little regional-scale variability. After ~2000 cal yr BP, fire activity declined in northern and southern Patagonia (by 1.5 and 0.5 z-value, respectively) and rose in central Patagonia (by 1.0 z-value). These results suggest that northern and southern Patagonia were wetter than central Patagonia, consistent with increased climate variability.

In the last ~1000 years, *Nothofagus* abundance increased in northern Patagonia, but decreased in central and southern Patagonia. Concurrently, fire activity increased in central Patagonia and decreased in northern and southern Patagonia (Fig. 4.5). Recent fire activity has generally been attributed to interannual shifts between dry and wet periods (Holz et al. 2012) and possibly increased use of fire by rising human populations (Méndez et al. 2016). Although the composite records presented here cannot distinguish short-term variability (e.g., the interannual climate variability associated with ENSO and SAM), individual records in all regions show fluctuations in fire activity associated with greater climate variability and increased human presence in the late Holocene (de Porras et al. 2012, de Porras et al. 2014, Iglesias and Whitlock 2014, Méndez et al. 2016).

Conclusions

The postglacial vegetation and fire history of Patagonia was reconstructed from pollen and charcoal records east of the Andes, including a new record from M. Fontanito. The M. Fontanito record, its comparison to other sites in central Patagonia, and a more generalized description of *Nothofagus* abundance and fire activity were used to better understand the environmental history of Patagonia east of the Andes, including the role of climate and humans. Major findings from this study are:

1. M. Fontanito was characterized by heath-steppe with low fire activity prior to ~16,900 cal yr BP, suggesting cold, dry conditions. Between ~16,900 and 13,000 cal yr BP, local *Nothofagus antarctica* and/or *N. pumilio* formed a shrubland, but brief periods of forest and increased fire activity suggest fluctuations in effective moisture as temperatures increased. After ~13,000 cal yr BP, the local vegetation

transitioned to grass-steppe and fire activity was low until ~11,500 cal yr BP. Between ~11,500 and 7000 cal yr BP, the local vegetation was *Nothofagus* shrubland or open forest and fire activity increased, suggesting that warming and drying led to longer growing and fire seasons. Between ~7000 and 4000 cal yr BP, closed *Nothofagus* forest established and fires were infrequent, suggesting an effectively wetter climate than before. After ~4000 cal yr BP, fluctuations in *Nothofagus* abundance and increased fire activity attest to increased submillennial climate variability and human presence.

2. The late-glacial vegetation of Patagonia east of the Andes was largely treeless at all latitudes, but *Nothofagus* was more abundant in northern Patagonia than in central and southern Patagonia. Fire activity was initially low in northern Patagonia but elevated in central Patagonia at ~18,000-16,000 cal yr BP and in southern Patagonia at ~16,000-13,000 cal yr BP. These regional differences imply that conditions were wetter in the north than in the south during the early late-glacial period and support a more northern position for the SWW storm tracks at this time.
3. *Nothofagus* abundance increased in a north-to-south pattern east of the Andes. It was first abundant in northern Patagonia at ~15,000 cal yr BP (and again at ~12,500-12,000 cal yr BP), then in central Patagonia at ~8000 cal yr BP, and finally in southern Patagonia at ~4500 cal yr BP. The vegetation history suggests that the SWW storm tracks lay north of their present position in the early late-

glacial period, and shifted southward during the late-glacial to early-Holocene period (Moreno et al. 2018b).

4. Paleoecologic records from central Patagonia generally show highest fire activity during an increase in *Nothofagus* abundance from ~12,500 to 8000 cal yr BP. These conditions are attributed to higher-than-before temperatures and weakened and/or southward shifted storm tracks (Whitlock et al. 2007, Moreno et al. 2009a, Fletcher and Moreno 2012a, Iglesias et al. 2016a)
5. Elevated levels of *Nothofagus* and low fire activity between ~7000-4000 cal yr BP mark the establishment of the forest-steppe ecotone at its present position throughout Patagonia east of the Andes. These changes are consistent with evidence that the SWW strengthened and moved to the present position by the middle Holocene.
6. High but variable *Nothofagus* abundance and fire activity after ~4500 cal yr BP in central Patagonia east of the Andes are attributed to increased interannual climate variability and/or increased pre-European burning. In particular, periods of high fire activity were associated with increased disturbance taxa at ~4500-2800 and 2400-1600 cal yr BP, and decreased fire activity and disturbance activity occurred at ~2800-2400 cal yr BP and 1600-150 cal yr BP.
7. In central Patagonia east of the Andes, human occupation was sporadic and associated with evidence of local increases in fire. Euro-American forest clearance is evidenced in pollen records in the last ~150 years in all regions as a

decrease in *Nothofagus* abundance and increase in disturbance and introduced taxa (e.g., *Rumex acetosella* and *Plantago* spp.).

Acknowledgements

Research was supported by National Science Foundation grants (OISE0966472, GSS1461590). G. Villarosa and R. Gresswell helped with field work. H. Dailey and D. Quick assisted with lab work. This paper benefitted from the comments of J. Larmon, V. Markgraf, and three anonymous reviewers.

CHAPTER FIVE

CONCLUSIONS

Summary of findings

In this dissertation, I examine how changes in land use and climate have altered ecosystem dynamics along forest-grassland ecotones in the central U.S. and east of the Patagonian Andes. Following its validation on longer timescales in the southern Missouri Ozarks (Ch. 2; Nanavati and Grimm 2020), we use the "anthropogenic fire regime hypothesis" posed by Guyette et al. (2002) to discuss how climate and land use have interacted to shape the ecology of the Patagonia forest-steppe ecotone prior to the arrival and expansion of Europeans. In Chapter 3 (Nanavati et al. *submitted*), we discuss how changes in land use and climate-mediated fuel flammability and availability at L. Portezuelo altered fire activity along the *Araucaria araucana* forest-steppe ecotone, where anthropogenic fire and orcharding may have helped resource-rich *A. araucana* to outcompete other arboreal taxa. To understand the spatial and temporal scales at which changes in land use and climate have altered ecosystem dynamics along the Patagonian forest-steppe ecotone, the vegetation and fire history of individual sites was compared to their regional trends, independent climate records, and archaeological evidence in Chapter 4 (Nanavati et al. 2019). These comparisons show that pre-European land use was an important driver of ecosystem dynamics at local spatial scales, but the top-down constraints of climate and bottom-up limitations of biomass growth (e.g., topography and soil characteristics) governed ecosystem dynamics at larger scales for at least the last

~18,000 years (Fig. 5.1). Importantly, changes in the position and intensity of the Southern Westerly Winds (SWW) and their associated storm tracks through time have had a strong impact on the flammability (wet/dry) and availability of fuel biomass along the Patagonian forest-steppe ecotone (Ch. 4; Nanavati et al. 2019).

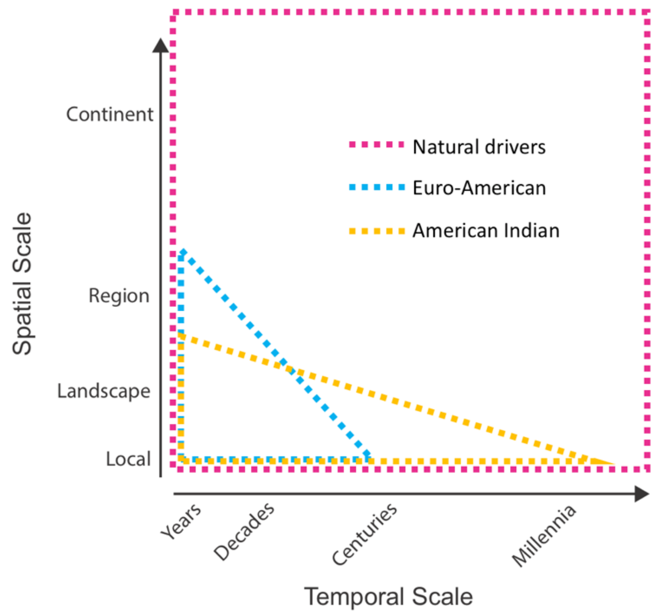

Figure 5.1: Conceptualization of the spatial and temporal scales at which natural drivers (i.e., climate and fuel biomass; pink) and land use alter ecosystem dynamics in the central U.S. Ozarks and along the Patagonian forest-steppe ecotone east of the Andes. Land use is broken into two categories: American Indian (i.e., traditional American Indian land use; yellow) and Euro-American (i.e., expansion of European and American agricultural and ranching strategies; blue).

Late Holocene vegetation and fire history of the
<u>central U.S. Ozarks</u>

Interannual climate variability was the primary driver of changes in vegetation and flammability near Sweeton Pond between ~1870 and 590 cal yr BP, when a generally warmer and drier climate than at present favored open *Quercus-Carya* parkland (Fig. 5.1). Fire activity during this period was likely limited by fuel flammability and the timing and frequency of ignition. Between ~590 and 450 cal yr BP, cool temperatures led to an expansion of *Quercus-Carya* forest and mesic other mesic taxa, but fire activity remained similar to before. The hunting and warring efforts of the Osage American Indians, especially following French contact, led to high fire activity between ~410 and 100 cal yr BP (1540-1820 CE) despite independent evidence of cool and less-arid conditions coeval with the Little Ice Age. These climate conditions, along with increased fire activity during Osage occupation, increased landscape heterogeneity and facilitated the spread of *Pinus echinata* in the area; both findings suggest that fire activity was ignition-limited. Fire activity declined after ~1880 CE (~70 cal yr BP) following displacement of the Osage and expansion of Euro-American agricultural, logging, and mining activities, suggestive of fuel fragmentation limiting fire activity. Fire activity declined to levels well below the previous range of fire activity by 30 cal yr BP (1920 CE) as a result of fuel fragmentation and later fire suppression/elimination efforts.

Vegetation and fire history of Patagonia east of the Andes

Regional differences in *Nothofagus* forest and fire activity during the late-glacial period in Patagonia imply that conditions were wetter in the north than in the south during the early late-glacial period and support a more northern position for the SWW storm tracks at this time (Table 5.1). The drier central and southern Patagonia landscape supported sufficient fuels to maintain fire activity at this time, whereas fire activity in northern Patagonia was limited by fuel flammability and/or ignition. The vegetation history of Patagonia suggests that the SWW storm tracks shifted southward during the late-glacial to early-Holocene period (Moreno et al. 2018b). Elevated levels of

Nothofagus and low fire activity between ~7000-4000 cal yr BP mark the establishment of the forest-steppe ecotone at its present position throughout Patagonia east of the Andes. These changes are consistent with evidence that the SWW strengthened and moved to their present position by the middle Holocene. High but variable fire activity after ~4000 cal yr BP throughout Patagonia east of the Andes is attributed to increased interannual climate variability (namely, ENSO) and, possibly, increased American Indian-set ignitions.

Euro-American contact in Patagonia was associated with the spread of Old World diseases and violent conflict that accelerated at the hands of the Chilean and Argentine militaries in the late 19th century (Hasbrouck 1935, Ortelli 1996). The precipitous decline in American Indian population likely reduced fire activity along parts of the ecotone, in some cases leading to the encroachment of shrubs into the steppe (Veblen and Lorenz 1988, Veblen and Markgraf 1988). Euro-American use of fire to open forest for agriculture, pastoralism, and settlement was common in the late 19th and early 20th century CE (Kitzberger and Veblen 1999, Holz and Veblen 2011a, Méndez et al. 2016). The establishment of the Argentine and Chilean National Park system in the 1930s and 1940s CE, was associated fire suppression efforts (Kitzberger 2012). However, since the 1970s CE, fires have increased in size and severity with increased anthropogenic ignition, warmer climate, and the expansion of nonnative pine plantations (Schlichter and Laclau 1998, Holz and Veblen 2011b, Gowda et al. 2012, Kitzberger 2012). Increased fire activity and deforestation of native forest for timber and non-native pine plantations took a major toll on the spatial extent of *Araucaria araucana*, which was reduced by nearly

60% following Euro-American settlement (Mundo et al. 2017a). Although American Indian land use was likely an important driver of local ecosystem dynamics since their early-Holocene arrival to the region (Méndez et al. 2016, Nanavati et al. 2019), historic and modern Euro-American land use has altered ecosystem dynamics to a greater extent and at larger spatial scales (Huber and Markgraf 2003; Nanavati et al. submitted; Ch. 3) (Fig. 5.1).

Advancements in method and theory

This dissertation supports the hypothesis that pre-European land use locally altered vegetation and fire history, increasing landscape heterogeneity along forest-grassland ecotones in the central U.S. Ozarks and east of the Patagonian Andes prior to the arrival of Euro-American settlement, agriculture, and ranching. These findings further show that humans can greatly alter climate-fire-vegetation feedbacks that naturally govern forest-grassland ecotones (Hirota et al. 2011, Mayer and Khalyani 2011, Staver et al. 2011), either by changing the frequency of ignitions or altering fuel structure through such processes as grazing and silviculture (Veblen et al. 2011, Gowda et al. 2012, Paritsis et al. 2018). Furthermore, although pre-European land use was likely an important driver of ecosystem dynamics locally, historic and modern Euro-American land use has altered ecosystem dynamics to a greater extent and at larger spatial scales through the clearance of forest for agriculture and ranching, and through the introduction of nonnative taxa (Fig. 5.1; Table 5.1).

Table 5.1. Summary of reconstructed biome, fire activity, main limiting factors for fire, and anthropogenic fire regime characterization for when humans are present for each study area.

Region	Site or composite	Time period	Time (cal yr BP)	Reconstructed biome	Reconstructed fire activity	Main limiting factors for fire	Anthropogenic fire regime categorization
Central U.S.	Sweeton Pond	Late Holocene	<30	*Quercus-Carya* forest surrounded by ag.	Null-to-low	Connectivity and suppression	Culture-dependent
			130-30	*Quercus-Carya* forest surrounded by ag.	High immediately followed by null-to-low	Fuel and connectivity	Fuel limited followed by fuel fragmentation
			590-130	*Quercus-Carya-Pinus* forest	Moderate-to-high	Flammability and ignition	Ignition limited
			1870-590	*Quercus-Carya* parkland	Moderate	Flammability and ignition	Ignition limited
Northernmost Patagonia	L. Portezuelo	Late Holocene	<-10	Heavily grazed *Araucaria* parkland and steppe	Low	Fuel, connectivity, and ignition	Culture-dependent
			460- -10	*Araucaria* parkland and steppe	Moderate-to-high	Flammability and ignition	Ignition limited
			1670-460	*Nothofagus* shrub steppe	Null-to-low	Flammability and ignition	Ignition limited
		Middle-to-Late Holocene	6800-1670	*Nothofagus* shrub steppe	Low	Fuel and ignition	Ignition limited
		Early-to-Middle Holocene	11,100-6800	Poaceae steppe with scattered *Nothofagus*	Low-to-moderate	Fuel and ignition	Ignition limited
Northern Patagonia	Composite	Late Holocene	<4000	*Nothofagus-Austrocedrus* forest	Moderate-to-high	Flammability and ignition	Ignition limited
		Middle Holocene	7000-4000	*Nothofagus* forest	Moderate	Flammability and ignition	Ignition limited
		Early Holocene	12,000-7000	*Nothofagus* forest	Low-to-moderate	Fuel and ignition	Ignition limited
		Late Glacial	18,000-12,000	*Nothofagus* shrubland to forest	Low	Fuel and ignition	
Central Patagonia	Composite	Late Holocene	<4000	*Nothofagus* forest	Moderate-to-high	Flammability and ignition	Ignition limited
		Middle Holocene	7000-4000	*Nothofagus* forest	Moderate	Flammability and ignition	Ignition limited
		Early Holocene	12,000-7000	*Nothofagus* shrubland to forest	Moderate-to-high	Fuel and ignition	Ignition limited
		Late Glacial	18,000-12,000	Steppe to *Nothofagus* shrubland	Low-to-moderate	Fuel and ignition	
	L. Fontanito	Late Holocene	<100	*Nothofagus* forest	Low	Fuel, connectivity, and ignition	Fuel fragmentation and culture-dependent
			420-100	*Nothofagus* forest	Very high	Fuel and ignition	Fuel limited
			4000-420	*Nothofagus* forest	Moderate-to-high	Fuel and ignition	Ignition limited
		Middle Holocene	7000-4000	*Nothofagus* forest	Low	Fuel and ignition	Ignition limited
		Early Holocene	12,000-7000	*Nothofagus* shrubland to forest	Low	Fuel and ignition	Ignition limited
		Late Glacial	18,000-12,000	Steppe to *Nothofagus* shrubland	Low	Fuel and ignition	
Southern Patagonia	Composite	Late Holocene	<4000	*Nothofagus* forest	Moderate-to-high	Flammability and ignition	Ignition limited
		Middle Holocene	7000-4000	Steppe to *Nothofagus* forest	Moderate-to-high	Fuel and ignition	Ignition limited
		Early Holocene	12,000-7000	Steppe	Moderate-to-high	Fuel and ignition	Ignition limited
		Late Glacial	18,000-12,000	Steppe	High	Fuel and ignition	

Bowman et al. (2011)'s criteria for considering anthropogenic alteration of ecosystem dynamics in paleoecological records are clearly met at Sweeton Pond (36.8°N, 92.2°W; Ch. 2; Nanavati and Grimm 2020), where despite cool, mesic conditions not conducive to fire, expansion of the Osage American Indians in the region between 1540 and 1820 CE was accompanied by increased fire activity. Fire activity at Sweeton Pond declined after ~1880 CE following displacement of the Osage and the expansion of Euro-American agricultural, logging, and mining activities. This rapid and extensive change in land use resulted in fuel fragmentation that preceded national fire suppression and elimination efforts.

Suggesting that increased fire activity recorded at paleoecological sites resulted from anthropogenic fires along Patagonia forest-steppe ecotone is facilitated by (1) remarkably low frequency lightning strikes at present (a major source of natural ignition) (Garreaud et al. 2014); (2) the long fire-return intervals evident in many charcoal records prior to the arrival of American Indians near the paleoecological sites (Whitlock et al. 2006, Iglesias et al. 2014, Nanavati et al. 2019); and (3) anomalously high fire activity recorded at individual sites as compared to regional trends (Iglesias and Whitlock 2014, Nanavati et al. 2019). Unfortunately, where lighting strikes are more frequent (e.g., northernmost Patagonia, 37-40°S), less archaeological research has been done, and/or there are few paleoecological sites with which to compare vegetation and fire history, it is much harder to differentiate between natural, climate-vegetation-fire dynamics and anthropogenic fire activity.

Based on Guyette et al. (2002)'s anthropogenic fire-regime framework, increased population density would have increased fire activity where (and when) flammable fuel biomass was sufficient until fires were suppressed or eliminated from the landscape in response to a change in a culture's use of fire. Guyette et al. (2002)'s framework generally holds true along the Ozark and Patagonian forest-grassland ecotones, but its focus on population density as an independent variable is reductionist and ahistorical. The use of fire by humans, whether to cook, signal neighboring parties, procure food, or in ritual is greatly influenced by changes in cultural practice and subsistence strategies, thus –to repurpose one of Guyette et al. (2002)'s stages– all anthropogenic fire is *culture-dependent*. For example, near the Cahokia archaeological complex in the Mississippi River Valley of the central U.S., fire activity decreased prior to the densely populated Mississippian Period (1050-1350 CE) and appeared to respond to changes in subsistence strategies from hunter-gatherer (Middle Woodland, 200 BCE – 500 CE; low-to-moderate fire), to swidden agricultural (Late Woodland, 500-1050 CE; high fire), and to permanent agricultural (Mississippian; low-to-moderate fire) subsistence strategies (Munoz 2015). Acknowledging the role of cultural changes in anthropogenic fire not only provides a more nuanced understanding of socioecological past, but can also facilitate the selection of study areas and spatial and temporal scales that may be best suited to describe changes in anthropogenic fire activity.

The socioecological interpretation from the Sweeton Pond record in the central U.S. Ozarks is facilitated by a wealth of archaeological and ethnohistorical research that suggests important shifts in cultural practice and/or subsistence strategies (Klippel et al.

1978, Ray et al. 1998, Bailey 2001, Wolverton 2005). The 15th century CE arrival of the Osage American Indians to the region signaled a shift from the transient hunter-gatherer occupations of the previous ~10,000 years to one that had permanent hunter-gatherer-horticulturalist settlements along the prairie-forest ecotone. Even then, a sustained increase in fire activity did not occur until after ~1680 CE, when the Osage expanded their hunting and warring to procure goods and slaves for trade with the French (Bailey 1973). Such significant shifts in cultural practice and/or subsistence strategies east of the Patagonian Andes did not occur until the arrival of Euro-American settlement, agriculture, and pastoralism, aside from the rapid influx of Mapuche American Indians east of the northernmost Patagonian Andes following the arrival of the Spanish conquistadores to central Chile (1550-1850 CE) (Scheinsohn 2003). This is an important distinction to make because even though evidence supports an increase in American Indian population in Patagonia prior to Euro-American arrival and settlement (Barberena et al. 2015, Perez et al. 2016), the lack of significant changes in cultural practice and/or subsistence strategies may have muted anthropogenic signals in the paleoecological record.

Furthermore, the Guyette et al. (2002) anthropogenic fire-regime hypothesis appears to breakdown at larger spatial and longer temporal scales in Patagonia, where the relationship between periods of archaeological occupation and increased fire activity as recorded at the local and landscape spatial scales is not clear in regional composites that generally follow larger-scale trends in temperature, moisture (resulting from changes in the strength and position of the SWW), and fuel biomass. The amplification or muting of fire activity by the combination of anthropogenic ignition and climate variability at the local-to-landscape levels, and the apparent breakdown of this relationship at larger spatial and longer temporal scales suggests that although land use may have played an important role in local- and landscape-level ecosystem dynamics, climatic constraints on fuel biomass govern larger scale ecosystem dynamics along the Patagonian forest-steppe border in the past (Fig. 5.1).

This discussion highlights methodological and theoretical considerations for future research. Importantly, changes in cultural practice and/or subsistence strategies may provide a clearer signal in paleoecological records than changes in human population alone. There are four ways to advance our understanding of climate-human-vegetation-fire interactions in paleoecological research: (1) focus on regions or individual paleoecological sites with sufficiently documented archaeological and ethnohistorical research that suggests local- or landscape-scale changes in cultural practice and/or subsistence strategies; (2) combine archaeological-paleoecological research at a single location, where archaeological survey and excavation within the catchment area of paleoecological sites can jointly shed light on changes in human, vegetation, and fire history; (3) use a well-constrained chronology and increase the sampling resolution for pollen and charcoal analyses during periods when changes in cultural practice and/or subsistence strategies are expected, so that changes at shorter, human time scales may become evident; and (4) discuss changes in raw charcoal accumulation rates and/or background charcoal accumulation rates that may better represent the cooler, smaller fires associated with land use, than large, statistically significant "peaks" in the fire record.

Future directions and final remarks

One of the most important considerations provided by Bowman et al. (2011) is that changes in the paleoecological record or records that are not well explained by climate-fuel-fire relationships provide the best indication of anthropogenic effects. Given the extensive work of dynamic global vegetation modelers to simulate past, present, and future climate-fuel-fire relationships in northern Patagonia (Ogunkoya 2020), the next logical step is to undertake landscape- to regional- scale data-model comparisons. Such a project can be done by comparing changes in vegetative composition and fire activity from individual and composited pollen and charcoal records, with LPJ-GUESS simulations of ecosystem dynamics. Comparison between paleoecological records and postglacial simulations of northern Patagonian landscape could determine where and when the vegetation and fire history of individual sites does not match simulated climate-fuel-fire relationships, per Bowman et al. (2011). Anomalous events recorded in the paleoecological data could be compared with the archaeological record to determine if land use (assumed from human presence) could explain the deviation from the model and if so, to what extent land use alter the simulated natural ecosystem dynamics.

The evidence presented in this dissertation suggests that the Patagonian forest-steppe ecotone experienced limited anthropogenic alteration prior to Euro-American settlement, agriculture, and pastoralism. This raises an important concern about the protection of these iconic ecosystems and their biodiversity. Currently, the Patagonian forest-steppe ecotone faces pressures from the introduction of non-native species, livestock grazing, timber extraction, rapid urbanization, and climate change (Veblen et al.

2011, Gowda et al. 2012, Blackhall et al. 2015, Paritsis et al. 2018). More can be understood about the context of these socioecological changes if we have high-resolution data for the last 1000 years of vegetation and fire history from different sites along the forest-steppe ecotone east of the Patagonian Andes. This information would better categorize socioecological change following the regional and local arrival of Europeans, the formation of Spanish colonies, the independence of Argentina and Chile, and the expansion of modern Euro-American land use strategies. By providing a better understanding how land use has altered natural ecosystem dynamics through time, we will be able to better interpret management goals in the face of future disturbance and climate change. Recognizing the Patagonian forest-steppe ecotone as a mosaic of nearly-pristine and humanized landscapes can provide a pragmatic guide for land management strategies and intensities, where natural processes can be left to play out in nearly-pristine landscapes, while active management of humanized landscapes can either restore ecosystems to nearly-pristine states or preserve cultural landscapes dependent on the decisions of stakeholders (Whitlock et al. 2018). As land use increases throughout Patagonia and anthropogenic global warming changes climate conditions at an alarming rate, combined paleoecological-archaeological efforts can help inform projections of future ecosystem dynamics and guide conservation and management decisions to protect native ecosystems.

REFERENCES CITED

Aagesen, D. 2004. Burning monkey-puzzle: native fire ecology and forest management in northern Patagonia. Agriculture and Human Values **21**:233-242.

Abarzúa, A. M., A. G. Pinchicura, L. Jarpa, A. Martel-Cea, M. Sterken, R. Vega, and M. Pino. 2014. Environmental responses to climatic and cultural changes over the last 26,000 years in Purén-Lumaco valley (38ºS).

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences **113**:11770-11775.

Abrams, M. D. 1992. Fire and the development of oak forests. BioScience:346-353.

Alder, J., and S. Hostetler. 2014. Global climate simulations at 3000 year intervals for the last 21 000 years with the GENMOM coupled atmosphere-ocean model. Climate of the Past Discussions **10**.

Anselmetti, F. S., D. Ariztegui, M. De Batist, A. Catalina Gebhardt, T. Haberzettl, F. Niessen, C. Ohlendorf, and B. Zolitschka. 2009. Environmental history of southern Patagonia unravelled by the seismic stratigraphy of Laguna Potrok Aike. Sedimentology **56**:873-892.

Arias, P., P. Fernández Sánchez, A. Hajduk, M. Lezcano, E. Crivelli, E. P. Pérez, A. M. Chauvín, A. Albornoz, J. T. Sagarna, and A. A. Gutiérrez. 2012. El poblamiento temprano del noroeste de la Patagonia argentina. Informes y Trabajos 19-41.

Bailey, G. A. 1973. Changes in Osage social organization, 1673-1906. Dept. of Anthropology, University of Oregon, Eugene.

Bailey, G. A. 2001. Osage. Pages 476-496 *in* W. C. Sturtevant, editor. Handbook of North American Indians. Smithsonian Institute, Washington D.C.

Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. Proceedings of the National Academy of Sciences **114**:2946-2951.

Baldoni, A. 1980. Análisis de algunas tafofloras jurásicas y eocretácicas de Argentina y Chile. Pages 15-39 *in* 2º Congreso Argentino de Paleontología y Bioestratigrafía y 1º Congreso Latinoamericano de Paleontologia.

Barberena, R., L. Prates, and M. Eugenia de Porras. 2015. The human occupation of northwestern Patagonia (Argentina): Paleoecological and chronological trends. Quaternary International **356**:111-126.

Batek, M. J., A. J. Rebertus, W. A. Schroeder, T. L. Haithcoat, E. Compas, and R. P. Guyette. 1999. Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri Ozarks. Journal of Biogeography **26**:397-412.

Bellelli, C., V. Scheinsohn, P. Fernández, F. Pereyra, M. Podestá, and M. Carballido. 2000. Arqueología de la Comarca Andina del Paralelo 42º. Localidad de Cholila. Primeros resultados. Desde el país de los gigantes. Perspectivas arqueológicas en Patagonia:587-602.

Bennett, K. D., S. G. Haberle, and S. H. Lumley. 2000. The last glacial-Holocene transition in southern Chile. Science **290**:325-328.

Berger, A., and M.-F. Loutre. 1991. Insolation values for the climate of the last 10 million years. Quaternary Science Reviews **10**:297-317.

Bird, B. W., J. J. Wilson, W. P. Gilhooly, III, B. A. Steinman, and L. Stamps. 2017. Midcontinental Native American population dynamics and late Holocene hydroclimate extremes. Sci Rep **7**:41628.

Bird, R. B., D. W. Bird, and B. F. Codding. 2016. People, El Nino southern oscillation and fire in Australia: fire regimes and climate controls in hummock grasslands. Philosophical Transactions of the Royal Society B-Biological Sciences **371**:20150343.

Blaauw, M., and J. A. Christen. 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis **6**:457-474.

Blackhall, M., E. Raffaele, and T. T. Veblen. 2015. Efectos combinados del fuego y el ganado en matorrales y bosques del noroeste patagónico. Ecología Austral **25**:1-10.

Blarquez, O., B. Vannière, J. R. Marlon, A.-L. Daniau, M. J. Power, S. Brewer, and P. J. Bartlein. 2014. paleofire: an R package to analyse sedimentary charcoal records from the Global Charcoal Database to reconstruct past biomass burning. Computers & Geosciences **72**:255-261.

Boex, J., C. Fogwill, S. Harrison, N. F. Glasser, A. Hein, C. Schnabel, and S. Xu. 2013. Rapid thinning of the Late Pleistocene Patagonian Ice Sheet followed migration of the Southern Westerlies. Sci Rep **3**:2118.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without fire. New Phytol **165**:525-537.

Bowman, D. M., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio, R. Defries, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, M. Mack, M. A. Moritz, S. Pyne, C. I. Roos, A. C. Scott, N. S. Sodhi, T. W. Swetnam, and R. Whittaker. 2011. The human dimension of fire regimes on Earth. J Biogeogr **38**:2223-2236.

Bowman, D. M., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D'Antonio, R. S. Defries, J. C. Doyle, S. P. Harrison, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, J. B. Marston, M. A. Moritz, I. C. Prentice, C. I. Roos, A. C. Scott, T. W. Swetnam, G. R. van der Werf, and S. J. Pyne. 2009. Fire in the Earth system. Science **324**:481-484.

Braun, E. L. 1950. Deciduous forests of eastern North America. Deciduous forests of Eastern North America.

Bronk Ramsey, C. 2009. Bayesian analysis of radiocarbon dates. Radiocarbon **51**:337-360.

Brown, K. J., J. S. Clark, E. C. Grimm, J. J. Donovan, P. G. Mueller, B. C. S. Hansen, and I. Stefanova. 2005. Fire cycles in North American interior grasslands and their relation to prairie drought. Proceedings of the National Academy of Sciences of the United States of America **102**:8865-8870.

Camill, P., C. E. Umbanhowar, R. Teed, C. E. Geiss, J. Aldinger, L. Dvorak, J. Kenning, J. Limmer, and K. Walkup. 2003. Late-glacial and Holocene climatic effects on fire and vegetation dynamics at the prairie-forest ecotone in south-central Minnesota. Journal of Ecology **91**:822-836.

Caniupán, M., F. Lamy, C. B. Lange, J. Kaiser, H. Arz, R. Kilian, O. Baeza Urrea, C. Aracena, D. Hebbeln, C. Kissel, C. Laj, G. Mollenhauer, and R. Tiedemann. 2011. Millennial-scale sea surface temperature and Patagonian Ice Sheet changes off southernmost Chile (53°S) over the past ~60 kyr. Paleoceanography **26**:n/a-n/a.

Carcaillet, C., M. Bouvier, B. Fréchette, A. C. Larouche, and P. J. Richard. 2001. Comparison of pollen-slide and sieving methods in lacustrine charcoal analyses for local and regional fire history. The Holocene **11**:467-476.

Castro Esnal, A., C. B. Pérez de Micou, and M. L. Casanueva. 2017. Early Holocene Occupation of the Forest-Steppe Ecotone of Southern South America: Evidence from Casa de Piedra de Roselló Cave (Chubut, Patagonia Argentina). PaleoAmerica **3**:276-282.

CITES. 2007. Consideration of proposals for amendment of appendices I and II. Convention on International Trade in Endangered Species of Wild Fauna and Flora.

Clark, J. S. 1988a. Effect of Climate Change on Fire Regimes in Northwestern Minnesota. Nature **334**:233-235.

Clark, J. S. 1988b. Particle Motion and the Theory of Charcoal Analysis - Source Area, Transport, Deposition, and Sampling. Quaternary Research **30**:67-80.

Clark, J. S. 1990. Fire and Climate Change during the Last 750 Yr in Northwestern Minnesota. Ecological Monographs **60**:135-159.

Clark, J. S., J. Lynch, B. J. Stocks, and J. G. Goldammer. 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. Holocene **8**:19-29.

Clayton, L. A., V. J. Knight, and E. C. Moore. 1995. The De Soto Chronicles : the Expedition of Hernando de Soto to North America in 1539-1543. University of Alabama Press, Tuscaloosa.

CONAF-CONAMA. 1999. Catastro y evaluación de los recursos vegetacionales nativos de Chile. Proyecto CONAF-CONAMA-BIRF. Informe Nacional con Variables Ambientales, Santiago, Chile.

Cook, E. R., R. Seager, R. R. Heim Jr, R. S. Vose, C. Herweijer, and C. Woodhouse. 2010. Megadroughts in North America: Placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. Journal of Quaternary Science **25**:48-61.

Cox, G. E. 1863. Viaje en las Rejiones Septentrionales de la Patagonia: 1862-1863. Imprenta Nacional Calle de la Moneda.

Crutzen, P. J., and E. F. Stoermer. 2006. The "Anthropocene". Pages 13-18 Earth system science in the anthropocene. Springer.

Cutter, B. E., and R. P. Guyette. 1994. Fire Frequency on an Oak-Hickory Ridgetop in the Missouri Ozarks. American Midland Naturalist **132**:393-398.

Daniau, A. L., P. J. Bartlein, S. P. Harrison, I. C. Prentice, S. Brewer, P. Friedlingstein, T. I. Harrison-Prentice, J. Inoue, K. Izumi, J. R. Marlon, S. Mooney, M. J. Power, J. Stevenson, W. Tinner, M. Andric, J. Atanassova, H. Behling, M. Black, O. Blarquez, K. J. Brown, C. Carcaillet, E. A. Colhoun, D. Colombaroli, B. A. S. Davis, D. D'Costa, J. Dodson, L. Dupont, Z. Eshetu, D. G. Gavin, A. Genries, S. Haberle, D. J. Hallett, G. Hope, S. P. Horn, T. G. Kassa, F. Katamura, L. M. Kennedy, P. Kershaw, S. Krivonogov, C. Long, D. Magri, E. Marinova, G. M. McKenzie, P. I. Moreno, P. Moss, F. H. Neumann, E. Norstrom, C. Paitre, D. Rius, N. Roberts, G. S. Robinson, N. Sasaki, L. Scott, H. Takahara, V. Terwilliger, F. Thevenon, R. Turner, V. G. Valsecchi, B. Vanniere, M. Walsh, N. Williams, and Y. Zhang. 2012. Predictability of biomass burning in response to climate changes. Global Biogeochemical Cycles **26**:n/a-n/a.

Day, G. M. 1953. The Indian as an Ecological Factor in the Northeastern Forest. Ecology **34**:329-346.

de Porras, M. E., A. Maldonado, A. M. Abarzúa, M. L. Cárdenas, J. P. Francois, A. Martel-Cea, C. R. Stern, C. Méndez, and O. Reyes. 2012. Postglacial vegetation, fire and climate dynamics at Central Chilean Patagonia (Lake Shaman, 44 S). Quaternary Science Reviews **50**:71-85.

de Porras, M. E., A. Maldonado, F. Quintana, A. Martel-Cea, O. Reyes, and C. Méndez. 2014. Environmental and climatic changes in central Chilean Patagonia since the late glacial (Mallín El Embudo, 44 S). Climate of the Past **10**:1063-1078.

Denevan, W. M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers **82**:369-385.

Dillehay, T. D., C. Ocampo, J. Saavedra, A. O. Sawakuchi, R. M. Vega, M. Pino, M. B. Collins, L. Scott Cummings, I. Arregui, X. S. Villagran, G. A. Hartmann, M. Mella, A. Gonzalez, and G. Dix. 2015. New Archaeological Evidence for an Early Human Presence at Monte Verde, Chile. Plos One **10**:e0141923.

Dillehay, T. D., M. P. Quivira, R. Bonzani, C. Silva, J. Wallner, and C. Le Quesne. 2007. Cultivated wetlands and emerging complexity in south-central Chile and long distance effects of climate change. Antiquity **81**:949-960.

dos Reis, M. S., A. Ladio, and N. Peroni. 2014. Landscapes with Araucaria in South America: evidence for a cultural dimension. Ecology and Society **19**.

Dyer, J. M. 2006. Revisiting the Deciduous Forests of Eastern North America. BioScience **56**:341-352.

Faegri, K., P. E. Kaland, and K. Krzywinski. 1989. Textbook of Pollen Analysis. John Wiley & Sons Ltd.

Fletcher, M.-S., and P. I. Moreno. 2012a. Have the Southern Westerlies changed in a zonally symmetric manner over the last 14,000 years? A hemisphere-wide take on a controversial problem. Quaternary International **253**:32-46.

Fletcher, M.-S., and P. I. Moreno. 2012b. Vegetation, climate and fire regime changes in the Andean region of southern Chile (38ºS) covaried with centennial-scale climate anomalies in the tropical Pacific over the last 1500 years. Quaternary Science Reviews **46**:46-56.

Gajewski, K., B. Kriesche, M. A. Chaput, R. Kulik, and V. Schmidt. 2017. Human–vegetation interactions during the Holocene in North America. Vegetation History and Archaeobotany:1-13.

García, J. L., M. R. Kaplan, B. L. Hall, J. M. Schaefer, R. M. Vega, R. Schwartz, and R. Finkel. 2012. Glacier expansion in southern Patagonia throughout the Antarctic cold reversal. Geology **40**:859-862.

Garreaud, R., P. Lopez, M. Minvielle, and M. Rojas. 2013. Large-Scale Control on the Patagonian Climate. Journal of Climate **26**:215-230.

Garreaud, R. D., M. Gabriela Nicora, R. E. Bürgesser, and E. E. Ávila. 2014. Lightning in western Patagonia. Journal of Geophysical Research: Atmospheres **119**:4471-4485.

Garreaud, R. D., M. Vuille, R. Compagnucci, and J. Marengo. 2009. Present-day south american climate. Palaeogeography, Palaeoclimatology, Palaeoecology **281**:180-195.

Gilman, D., F. Fuglister, and J. Mitchell Jr. 1963. On the power spectrum of "red noise". Journal of the Atmospheric Sciences **20**:182-184.

González, M. E., T. T. Veblen, and J. S. Sibold. 2010. Influence of fire severity on stand development of Araucaria araucana–Nothofagus pumilio stands in the Andean cordillera of south-central Chile. Austral Ecology **35**:597-615.

Gordón, F., S. I. Perez, A. Hajduk, M. Lezcano, and V. Bernal. 2016. Dietary patterns in human populations from northwest Patagonia during Holocene: an approach using Binford's frames of reference and Bayesian isotope mixing models. Archaeological and Anthropological Sciences:1-12.

Gorte, R. 2013. The rising cost of wildfire protection. Headwater Economics, Bozeman, MT.

Gowda, J. H., T. Kitzberger, and A. C. Premoli. 2012. Landscape responses to a century of land use along the northern Patagonian forest-steppe transition. Plant ecology **213**:259-272.

Grimm, E. C. 1983. Chronology and Dynamics of Vegetation Change in the Prairie-Woodland Region of Southern Minnesota, USA. New Phytologist **93**:311-350.

Grimm, E. C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs **54**:291-311.

Grimm, E. C. 1987. Coniss - a Fortran-77 Program for Stratigraphically Constrained Cluster-Analysis by the Method of Incremental Sum of Squares. Computers & Geosciences **13**:13-35.

Grimm, E. C. 2011. High-Resolution Age Model Based on Ams Radiocarbon Ages for Kettle Lake, North Dakota, USA. Radiocarbon **53**:38-52.

Grimm, E. C., J. J. Donovan, and K. J. Brown. 2011. A high-resolution record of climate variability and landscape response from Kettle Lake, northern Great Plains, North America. Quaternary Science Reviews **30**:2626-2650.

Guyette, R. P., and E. A. McGinnes. 1982. Fire History of an Ozark Glade in Missouri. Transactions of the Missouri Academy of Science **16**:85-93.

Guyette, R. P., R.-M. Muzika, and S. L. Voelker. 2007. The historical ecology of fire, climate, and the decline of shortleaf pine in the Missouri Ozarks. SHORTLEAF PINE RESTORATION:8.

Guyette, R. P., R. M. Muzika, and D. C. Dey. 2002. Dynamics of an anthropogenic fire regime. Ecosystems **5**:472-486.

Guyette, R. P., M. A. Spetich, and M. C. Stambaugh. 2006. Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. Forest Ecology and Management **234**:293-304.

Haberle, S. G., and K. D. Bennett. 2004. Postglacial formation and dynamics of North Patagonian Rainforest in the Chonos Archipelago, southern Chile. Quaternary Science Reviews **23**:2433-2452.

Hanberry, B. B., D. C. Dey, and H. S. He. 2014a. The history of widespread decrease in oak dominance exemplified in a grassland-forest landscape. Sci Total Environ **476-477**:591-600.

Hanberry, B. B., D. T. Jones-Farrand, and J. M. Kabrick. 2014b. Historical Open Forest Ecosystems in the Missouri Ozarks: Reconstruction and Restoration Targets. Ecological Restoration **32**:407-416.

Hanberry, B. B., J. M. Kabrick, and H. S. He. 2014c. Densification and State Transition Across the Missouri Ozarks Landscape. Ecosystems **17**:66-81.

Hart, T. B., and J. A. Hart. 1986. The Ecological Basis of Hunter-Gatherer Subsistence in African Rain-Forests - the Mbuti of Eastern Zaire. Human Ecology **14**:29-55.

Hasbrouck, A. 1935. The Conquest of the Desert. The Hispanic American Historical Review **15**:195-228.

Heiri, O., A. F. Lotter, and G. Lemcke. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of paleolimnology **25**:101-110.

Henríquez, J., and C. H. Lusk. 2005. Facilitation of Nothofagus antarctica (Fagaceae) seedlings by the prostrate shrub Empetrum rubrum (Empetraceae) on glacial moraines in Patagonia. Austral Ecology **30**:877-882.

Henríquez, W. I., R. Villa-Martínez, I. Vilanova, R. D. Pol-Holz, and P. I. Moreno. 2017. The Last Glacial Termination on the eastern flank of the central Patagonian Andes (47 S). Climate of the Past **13**:879-895.

Henson, C., P. Market, A. Lupo, and P. Guinan. 2017. ENSO and PDO-related climate variability impacts on Midwestern United States crop yields. International journal of biometeorology **61**:857-867.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management **211**:117-139.

Heusser, C. J. 1983. Quaternary pollen record from laguna de tagua tagua, chile. Science **219**:1429-1432.

Heusser, C. J. 1984. Late-glacial-Holocene climate of the Lake District of Chile. Quaternary Research **22**:77-90.

Heusser, C. J., J. Rabassa, A. Brandani, and R. Stuckenrath. 1988. Late-Holocene vegetation of the Andean Araucaria region, province of Neuquén, Argentina. Mountain Research and Development:53-63.

Hickey, R. J., C. Macluf, and C. W. Taylor. 2003. A re-evaluation of Isoetes savatieri Franchet in Argentina and Chile. American Fern Journal **93**:126-136.

Higuera, P. E., C. E. Briles, and C. Whitlock. 2014. Fire-regime complacency and sensitivity to centennial-through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA. Journal of Ecology **102**:1429-1441.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu, and T. A. Brown. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs **79**:201-219.

Higuera, P. E., D. G. Gavin, P. J. Bartlein, and D. J. Hallett. 2010. Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. International Journal of Wildland Fire **19**:996-1014.

Higuera, P. E., M. E. Peters, L. B. Brubaker, and D. G. Gavin. 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. Quaternary Science Reviews **26**:1790-1809.

Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer. 2011. Global resilience of tropical forest and savanna to critical transitions. Science **334**:232-235.

Hogg, A. G., Q. Hua, P. G. Blackwell, M. Niu, C. E. Buck, T. P. Guilderson, T. J. Heaton, J. G. Palmer, P. J. Reimer, R. W. Reimer, C. S. M. Turney, and S. R. H. Zimmerman. 2016. SHCal13 Southern Hemisphere Calibration, 0–50,000 Years cal BP. Radiocarbon **55**:1889-1903.

Holmes, J. A. 1968. History of Ozark County, Missouri, to 1865. University of Kansas.

Holz, A., T. Kitzberger, J. Paritsis, and T. T. Veblen. 2012. Ecological and climatic controls of modern wildfire activity patterns across southwestern South America. Ecosphere **3**:1-25.

Holz, A., C. Méndez, L. Borrero, A. Prieto, F. Torrejón, and A. Maldonado. 2016. Fires: the main human impact on past environments in Patagonia? Past Global Change Magazine **24**:72-73.

Holz, A., and T. T. Veblen. 2011a. The amplifying effects of humans on fire regimes in temperate rainforests in western Patagonia. Palaeogeography, Palaeoclimatology, Palaeoecology **311**:82-92.

Holz, A., and T. T. Veblen. 2011b. Variability in the Southern Annular Mode determines wildfire activity in Patagonia. Geophysical Research Letters **38**.

Holz, A., and T. T. Veblen. 2012. Wildfire activity in rainforests in western Patagonia linked to the Southern Annular Mode. International Journal of Wildland Fire **21**:114.

Hope, G., and J. Golson. 1995. Late quaternary change in the mountains of New Guinea. Antiquity **69**:818-830.

Huber, U. M., and V. Markgraf. 2003. European impact on fire regimes and vegetation dynamics at the steppe-forest ecotone of southern Patagonia. The Holocene **13**:567-579.

Iglesias, V., S. G. Haberle, A. Holz, and C. Whitlock. 2018. Holocene Dynamics of Temperate Rainforests in West-Central Patagonia. Frontiers in Ecology and Evolution **5**.

Iglesias, V., V. Markgraf, and C. Whitlock. 2016a. 17,000 years of vegetation, fire and climate change in the eastern foothills of the Andes (lat. 44°S). Palaeogeography, Palaeoclimatology, Palaeoecology **457**:195-208.

Iglesias, V., F. Quintana, W. Nanavati, and C. Whitlock. 2016b. Interpreting modern and fossil pollen data along a steep environmental gradient in northern Patagonia. The Holocene.

Iglesias, V., F. Quintana, W. Nanavati, and C. Whitlock. 2017. Interpreting modern and fossil pollen data along a steep environmental gradient in northern Patagonia. The Holocene **27**:1008-1018.

Iglesias, V., and C. Whitlock. 2014. Fire responses to postglacial climate change and human impact in northern Patagonia (41-43 degrees S). Proc Natl Acad Sci U S A **111**:E5545-5554.

Iglesias, V., C. Whitlock, M. M. Bianchi, G. Villarosa, and V. Outes. 2012. Climate and local controls of long-term vegetation dynamics in northern Patagonia (Lat 41°S). Quaternary Research **78**:502-512.

Iglesias, V., C. Whitlock, V. Markgraf, and M. M. Bianchi. 2014. Postglacial history of the Patagonian forest/steppe ecotone (41–43°S). Quaternary Science Reviews **94**:120-135.

Jenny, B., D. Wilhelm, and B. Valero-Garcés. 2003. The Southern Westerlies in Central Chile: Holocene precipitation estimates based on a water balance model for Laguna Aculeo (33 50′ S). Climate Dynamics **20**:269-280.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications **6**:7537.

Jouzel, J., V. Masson-Delmotte, O. Cattani, G. Dreyfus, S. Falourd, G. Hoffmann, B. Minster, J. Nouet, J. M. Barnola, J. Chappellaz, H. Fischer, J. C. Gallet, S. Johnsen, M. Leuenberger, L. Loulergue, D. Luethi, H. Oerter, F. Parrenin, G. Raisbeck, D. Raynaud, A. Schilt, J. Schwander, E. Selmo, R. Souchez, R. Spahni, B. Stauffer, J. P. Steffensen, B. Stenni, T. F. Stocker, J. L. Tison, M. Werner, and E. W. Wolff. 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years. Science **317**:793-796.

Kaiser, J., F. Lamy, and D. Hebbeln. 2005. A 70-kyr sea surface temperature record off southern Chile (Ocean Drilling Program Site 1233). Paleoceanography **20**:n/a-n/a.

Karkanas, P., R. Shahack-Gross, A. Ayalon, M. Bar-Matthews, R. Barkai, A. Frumkin, A. Gopher, and M. C. Stiner. 2007. Evidence for habitual use of fire at the end of the Lower Paleolithic: Site-formation processes at Qesem Cave, Israel. Journal of Human Evolution **53**:197-212.

Kelley, D. I., I. Bistinas, R. Whitley, C. Burton, T. R. Marthews, and N. Dong. 2019. How contemporary bioclimatic and human controls change global fire regimes. Nature Climate Change **9**:690-696.

Kelly, R. F., P. E. Higuera, C. M. Barrett, and F. S. Hu. 2011. A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. Quaternary Research **75**:11-17.

Kilian, R., and F. Lamy. 2012. A review of Glacial and Holocene paleoclimate records from southernmost Patagonia (49-55 degrees S). Quaternary Science Reviews **53**:1-23.

King, J. E. 1973. Late Pleistocene Palynology and Biogeography of the Western Missouri Ozarks. Ecological Monographs **43**:539-565.

Kitzberger, T. 2012. Ecotones as complex arenas of disturbance, climate, and human impacts: The trans-Andean forest-steppe ecotone of northern Patagonia. Pages 59-88 Ecotones between forest and grassland. Springer.

Kitzberger, T., G. L. W. Perry, J. Paritsis, J. H. Gowda, A. J. Tepley, A. Holz, and T. T. Veblen. 2016. Fire-vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. New Zealand Journal of Botany **54**:247-272.

Kitzberger, T., and T. T. Veblen. 1999. Fire-induced changes in northern Patagonian landscapes. Landscape Ecology **14**:1-15.

Kitzberger, T., T. T. Veblen, and R. Villalba. 1997. Climatic influences on fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. Journal of Biogeography **24**:35-47.

Klippel, W. E., G. Celmer, and J. R. Purdue. 1978. The Holocene naiad record at Rodgers Shelter in the western Ozark Highland of Missouri. The Plains Anthropologist:257-271.

Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. Ecology **92**:121-132.

Kunzmann, L. 2007. Araucariaceae (Pinopsida): aspects in palaeobiogeography and palaeobiodiversity in the Mesozoic. Zoologischer Anzeiger-A Journal of Comparative Zoology **246**:257-277.

Lara, A., D. Bran, P. Rutherford, A. Perez, S. Clayton, D. Barrios, J. Ayesa, M. Gross, and G. Iglesias. 1999. Mapeo de la Ecoregión de los Bosques Valdivianos de Argentina y Chile, en escala 1: 500,000. Boletın Técnico FVSA.

Lawson, E. R. 1990. Silvics of North America: Volume 1. Conifers. United States Department of Agriculture (USDA), Forest Service, Agriculture Handbook **654**.

Lynch, E. A., R. Calcote, and S. Hotchkiss. 2006. Late-Holocene vegetation and fire history from Ferry Lake, northwestern Wisconsin, USA. Holocene **16**:495-504.

Lynch, E. A., S. C. Hotchkiss, and R. Calcote. 2011. Charcoal signatures defined by multivariate analysis of charcoal records from 10 lakes in northwest Wisconsin (USA). Quaternary Research **75**:125-137.

Mancini, M. V., M. E. de Porras, and F. P. Bamonte. 2012. Southernmost South America steppes: vegetation and its modern pollen-assemblages representation. Steppe Ecosystems: Dynamics, Land Use and Conservation, edited by: Germanno, D., NOVA publishers, New York:141-156.

Mann, M. E., Z. Zhang, M. K. Hughes, R. S. Bradley, S. K. Miller, S. Rutherford, and F. Ni. 2008. Proxy-based reconstructions of hemispheric and global surface temperature variations over the past two millennia. Proc Natl Acad Sci U S A **105**:13252-13257.

Mann, M. E., Z. Zhang, S. Rutherford, R. S. Bradley, M. K. Hughes, D. Shindell, C. Ammann, G. Faluvegi, and F. Ni. 2009. Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. Science **326**:1256-1260.

Marchelli, P., and L. A. Gallo. 2004. The combined role of glaciation and hybridization in shaping the distribution of genetic variation in a Patagonian southern beech. Journal of Biogeography **31**:451-460.

Markgraf, V. 1983. Late and postglacial vegetational and paleoclimatic changes in subantarctic, temperate, and arid environments in Argentina. Palynology **7**:43-70.

Markgraf, V. 1987. Paleoenvironmental changes at the northern limit of the subantarctic Nothofagus forest, Lat 37 S, Argentina. Quaternary Research **28**:119-129.

Markgraf, V. 1989. Reply to CJ Heusser's “Southern westerlies during the last glacial maximum”. Quaternary Research **31**:426-432.

Markgraf, V., J. P. Bradbury, A. Schwalb, S. J. Burns, C. Stern, D. Ariztegui, A. Gilli, F. S. Anselmetti, S. Stine, and N. Maidana. 2003. Holocene palaeoclimates of southern Patagonia: limnological and environmental history of Lago Cardiel, Argentina. Holocene **13**:581-591.

Markgraf, V., V. Iglesias, and C. Whitlock. 2013. Late and postglacial vegetation and fire history from Cord?n Serrucho Norte, northern Patagonia. Palaeogeography, Palaeoclimatology, Palaeoecology **371**:109-118.

Markgraf, V., M. Mcglone, and G. Hope. 1995. Neogene Paleoenvironmental and Paleoclimatic Change in Southern Temperate Ecosystems - a Southern Perspective. Trends in ecology & evolution **10**:143-147.

Markgraf, V., C. Whitlock, and S. Haberle. 2007. Vegetation and fire history during the last 18,000 cal yr BP in Southern Patagonia: Mallin Pollux, Coyhaique, Province Aisen (45 degrees 41 ' 30 " S, 71 degrees 50 ' 30 " W, 640 m elevation). Palaeogeography Palaeoclimatology Palaeoecology **254**:492-507.

Marlon, J. R., P. J. Bartlein, C. Carcaillet, D. G. Gavin, S. P. Harrison, P. E. Higuera, F. Joos, M. J. Power, and I. C. Prentice. 2008. Climate and human influences on global biomass burning over the past two millennia. Nature Geoscience **1**:697-702.

Marlon, J. R., P. J. Bartlein, A. L. Daniau, S. P. Harrison, S. Y. Maezumi, M. J. Power, W. Tinner, and B. Vanniere. 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. Quaternary Science Reviews **65**:5-25.

Marlon, J. R., P. J. Bartlein, D. G. Gavin, C. J. Long, R. S. Anderson, C. E. Briles, K. J. Brown, D. Colombaroli, D. J. Hallett, M. J. Power, E. A. Scharf, and M. K. Walsh. 2012. Long-term perspective on wildfires in the western USA. Proc Natl Acad Sci U S A **109**:E535-543.

Mayer, A. L., and A. H. Khalyani. 2011. Ecology. Grass trumps trees with fire. Science **334**:188-189.

McCulloch, R. D., M. J. Figuerero Torres, G. L. Mengoni Goñalons, R. Barclay, and C. Mansilla. 2017. A Holocene record of environmental change from Rio Zeballos, central Patagonia. The Holocene **27**:941-950.

McCulloch, R. D., C. J. Fogwill, D. E. Sugden, M. J. Bentley, and P. W. Kubik. 2005. Chronology of the last glaciation in central Strait of Magellan and Bahia Inutil, southernmost South America. Geografiska Annaler Series a-Physical Geography **87a**:289-312.

McMillan, R. B. 2014a. Holocene Range Extension of Pronghorn into the Southern Prairie Peninsula. The Wisconsin Archaeologist **95**:289-283.

McMillan, R. B. 2014b. Migration Legends and the Origins of Missouri's Siouan-Speaking Tribes. The Missouri Archaeologist **75**:5.

McWethy, D. B., T. Schoennagel, P. E. Higuera, M. Krawchuk, B. J. Harvey, E. C. Metcalf, C. Schultz, C. Miller, A. L. Metcalf, and B. Buma. 2019. Rethinking resilience to wildfire. Nature Sustainability **2**:1-8.

McWethy, D. B., C. Whitlock, J. M. Wilmshurst, M. S. McGlone, M. Fromont, X. Li, A. Dieffenbacher-Krall, W. O. Hobbs, S. C. Fritz, and E. R. Cook. 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proceedings of the National Academy of Sciences **107**:21343-21348.

Mena, F., O. Reyes, T. W. Stafford, and J. Southon. 2003. Early human remains from Bano Nuevo-1 cave, central Patagonian Andes, Chile. Quaternary International **109**:113-121.

Méndez, C., M. E. De Porras, A. Maldonado, O. Reyes, A. Nuevo Delaunay, and J.-L. Garcia. 2016. Human effects in Holocene fire dynamics of Central Western Patagonia (~ 44° S, Chile). Frontiers in Ecology and Evolution **4**:100.

Méndez, C., A. N. Delaunay, O. Reyes, I. L. Ozán, C. Belmar, and P. López. 2018a. The initial peopling of Central Western Patagonia (southernmost South America): Late Pleistocene through Holocene site context and archaeological assemblages from Cueva de la Vieja site. Quaternary International **473**:261-277.

Méndez, C., O. Reyes, A. Nuevo Delaunay, V. Trejo, R. Barberena, and H. Velásquez. 2011. Ocupaciones humanas en la margen occidental de Patagonia Central: eventos de poblamiento en alto río Cisnes. Magallania (Punta Arenas) **39**:223-242.

Méndez, C., C. R. Stern, A. N. Delaunay, O. Reyes, F. Gutiérrez, and F. Mena. 2018b. Spatial and temporal distributions of exotic and local obsidians in Central Western Patagonia, southernmost South America. Quaternary International **468**:155-168.

Méndez, C. A., and O. R. Reyes. 2008. Late Holocene human occupation of the Patagonian forests: A case study in the Cisnes river basin. Antiquity **82**:560.

Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology **86**:2705-2715.

Moberg, A., D. M. Sonechkin, K. Holmgren, N. M. Datsenko, W. Karlen, and S. E. Lauritzen. 2005. Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data. Nature **433**:613-617.

Moreno, F. P. 1897. Reconocimiento de la region andina de la República Argentina: 1. Apuntes preliminares sobre una excursión a los territorios del Neuquen, Rio Negro, Chubut y Santa Cruz. Talleres de Publicaciones del Museo.

Moreno, P., I. Vilanova, R. Villa-Martínez, R. Dunbar, D. Mucciarone, M. Kaplan, R. Garreaud, M. Rojas, C. Moy, and R. De Pol-Holz. 2018a. Onset and evolution of southern annular mode-like changes at centennial timescale. Scientific Reports **8**:3458.

Moreno, P. I. 2004. Millennial-scale climate variability in northwest Patagonia over the last 15 000 yr. Journal of Quaternary Science **19**:35-47.

Moreno, P. I., J. P. Francois, R. P. Villa-Martinez, and C. M. Moy. 2009a. Millennial-scale variability in Southern Hemisphere westerly wind activity over the last 5000 years in SW Patagonia. Quaternary Science Reviews **28**:25-38.

Moreno, P. I., M. R. Kaplan, J. P. Francois, R. Villa-Martinez, C. M. Moy, C. R. Stern, and P. W. Kubik. 2009b. Renewed glacial activity during the Antarctic cold reversal and persistence of cold conditions until 11.5 ka in southwestern Patagonia. Geology **37**:375-378.

Moreno, P. I., J. Videla, B. Valero-Garcés, B. V. Alloway, and L. E. Heusser. 2018b. A continuous record of vegetation, fire-regime and climatic changes in northwestern Patagonia spanning the last 25,000 years. Quaternary Science Reviews **198**:15-36.

Moreno, P. I., I. Vilanova, R. Villa-Martinez, R. D. Garreaud, M. Rojas, and R. De Pol-Holz. 2014. Southern Annular Mode-like changes in southwestern Patagonia at centennial timescales over the last three millennia. Nature Communications **5**.

Moreno, P. I., R. Villa-Martínez, M. L. Cárdenas, and E. A. Sagredo. 2012. Deglacial changes of the southern margin of the southern westerly winds revealed by terrestrial records from SW Patagonia (52°S). Quaternary Science Reviews **41**:1-21.

Moreno-Gonzalez, R., T. Giesecke, and S. L. Fontana. 2020. The impact of recent land-use change in the Araucaria araucana forest in northern Patagonia. The Holocene:0959683620913918.

Morrison, K. D. 1994. The intensification of production: archaeological approaches. Journal of Archaeological Method and Theory **1**:111-159.

Moy, C. M., G. O. Seltzer, D. T. Rodbell, and D. M. Anderson. 2002. Variability of El Nino/Southern Oscillation activity at millennial timescales during the Holocene epoch. Nature **420**:162-165.

Mundo, I. A., A. Holz, M. E. González, and J. Paritsis. 2017a. Fire History and Fire Regimes Shifts in Patagonian Temperate Forests. Pages 211-229 Dendroecology. Springer.

Mundo, I. A., T. Kitzberger, F. A. Roig Juñent, R. Villalba, and M. D. Barrera. 2013. Fire history in the Araucaria araucana forests of Argentina: human and climate influences. International Journal of Wildland Fire **22**:194-206.

Mundo, I. A., R. Villalba, T. T. Veblen, T. Kitzberger, A. Holz, J. Paritsis, and A. Ripalta. 2017b. Fire history in southern Patagonia: human and climate influences on fire activity in Nothofagus pumilio forests. Ecosphere **8**.

Munoz, S. E. 2015. Forests, fields, and floods: A historical ecology of the Cahokia region, Illinois, USA. The University of Wisconsin-Madison.

Munoz, S. E., D. J. Mladenoff, S. Schroeder, and J. W. Williams. 2014. Defining the spatial patterns of historical land use associated with the indigenous societies of eastern North America. Journal of Biogeography **41**:2195-2210.

Muñoz, S. E., S. Schroeder, D. A. Fike, and J. W. Williams. 2014. A record of sustained prehistoric and historic land use from the Cahokia region, Illinois, USA. Geology **42**:499-502.

Musters, G. C. 1871. At home with the Patagonians: a year's wanderings over untrodden ground from the straits of Magellan to the Rio Negro. John Murray, London.

Nanavati, W. P., and E. C. Grimm. 2020. Humans, fire, and ecology in the southern Missouri Ozarks, USA. Holocene **30**:125-135.

Nanavati, W. P., C. Whitlock, V. Iglesias, and M. E. de Porras. 2019. Postglacial vegetation, fire, and climate history along the eastern Andes, Argentina and Chile (lat. 41–55°S). Quaternary Science Reviews **207**:145-160.

Nelson, D. M., F. S. Hu, E. C. Grimm, B. B. Curry, and J. E. Slate. 2006. The influence of aridity and fire on holocene prairie communities in the eastern Prairie Peninsula. Ecology **87**:2523-2536.

Nelson, D. M., F. S. Hu, J. Tian, I. Stefanova, and T. A. Brown. 2004. Response of C3 and C4 plants to middle-Holocene climatic variation near the prairie-forest ecotone of Minnesota. Proc Natl Acad Sci U S A **101**:562-567.

Newberry, R. G., A. R. Lupo, A. D. Jensen, and R. A. R. Zalipynis. 2016. An analysis of the spring-to-summer transition in the West Central Plains for application to long range forecasting. Atmospheric and Climate Sciences **6**:375.

Newman, E. A. 2019. Disturbance ecology in the Anthropocene. Front. Ecol. Evol. 7: 147. doi: 10.3389/fevo **7**.

Nicholson, B. A. 1988. Modeling Subsistence Strategies in the Forest Grassland Transition Zone of Western Manitoba during the Late Prehistoric and Early Historic Periods. Plains Anthropologist **33**:351-365.

Ogunkoya, A. G. 2020. Understanding the present and past climate-fire-vegetation dynamics of southern south america (40 – 45° s). Montana State University, Bozeman, MT.

Ortelli, S. 1996. La «araucanización» de las pampas:¿ realidad histórica o construcción de los etnólogos? Anuario IEHS: Instituto de Estudios histórico sociales:203-225.

Paez, M. M., F. Schäbitz, and S. Stutz. 2001. Modern pollen–vegetation and isopoll maps in southern Argentina. Journal of Biogeography **28**:997-1021.

Paritsis, J., J. B. Landesmann, T. Kitzberger, F. Tiribelli, Y. Sasal, C. Quintero, R. D. Dimarco, M. N. Barrios-García, A. L. Iglesias, and J. P. Diez. 2018. Pine plantations and invasion alter fuel structure and potential fire behavior in a Patagonian forest-steppe ecotone. Forests **9**:117.

Pastorino, M. J., M. M. Fariña, D. Bran, and L. A. Gallo. 2006. Extremos geográficos de la distribución natural de Austrocedrus chilensis (Cupressaceae). Boletín de la Sociedad Argentina de Botánica **41**:307-311.

Patterson, W. A., and K. E. Sassaman. 1988. Indian fires in the prehistory of New England. Pages 107-135 Holocene human ecology in northeastern North America. Springer.

Pauketat, T. R. 2003. Resettled farmers and the making of a Mississippian polity. American Antiquity **68**:39-66.

Pausas, J. G., and E. Ribeiro. 2013. The global fire–productivity relationship. Global Ecology and Biogeography **22**:728-736.

Perez, S. I., M. B. Postillone, and D. Rindel. 2017. Domestication and human demographic history in South America. Am J Phys Anthropol **163**:44-52.

Perez, S. I., M. B. Postillone, D. Rindel, D. Gobbo, P. N. Gonzalez, and V. Bernal. 2016. Peopling time, spatial occupation and demography of Late Pleistocene–Holocene human population from Patagonia. Quaternary International **425**:214-223.

Peterson, G. 1978. Pollen spectra from surface sediments of lakes and ponds in Kentucky, Illinois and Missouri. American Midland Naturalist:333-340.

Ponziglione, P. M. 1882. Kansas. Letter from Fr. P.M. Ponziglione, Dec. 31, 1881. Pages 164-165 Woodstock Letters.

Porter, S. C. 2000. Onset of neoglaciation in the Southern Hemisphere. Journal of Quaternary Science: Published for the Quaternary Research Association **15**:395-408.

Premoli, A., P. Quiroga, and M. Gardner. 2013. Araucaria araucana. The IUCN red list of threatened species:2013-2011.

Premoli, A. C. 1997. Genetic variation in a geographically restricted and two widespread species of south American Nothofagus. Journal of Biogeography **24**:883-892.

Pyne, S. J. 1982. Fire in America. A cultural history of wildland and rural fire. Princeton University Press.

Quiroz, D., and M. Sánchez. 2004. Poblamientos iniciales en la costa septentrional de la Araucanía (6.500-2.000 ap). Chungara (Arica) **36**:289-302.

Ratley, C. W., and A. R. Lupo. 2002. Determining the spring to summer transition in the Missouri Ozarks using synoptic scale atmospheric data. Transactions of the Missouri Academy of Science **38**:55-62.

Ray, J. H., N. H. Lopinot, E. R. Hajic, and R. D. Mandel. 1998. The Big Eddy site: a multicomponent Paleoindian site on the Ozark border, southwest Missouri. The Plains Anthropologist:73-81.

Reimer, P. J., E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. B. Ramsey, C. E. Buck, H. Cheng, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, H. Haflidason, I. Hajdas, C. Hatte, T. J. Heaton, D. L. Hoffmann, A. G. Hogg, K. A. Hughen, K. F. Kaiser, B. Kromer, S. W. Manning, M. Niu, R. W. Reimer, D. A. Richards, E. M. Scott, J. R. Southon, R. A. Staff, C. S. M. Turney, and J. van der Plicht. 2013. Intcal13 and Marine13 Radiocarbon Age Calibration Curves 0-50,000 Years Cal Bp. Radiocarbon **55**:1869-1887.

Renssen, H., H. Goosse, T. Fichefet, V. Masson-Delmotte, and N. Koç. 2005. Holocene climate evolution in the high-latitude Southern Hemisphere simulated by a coupled atmosphere-sea ice-ocean-vegetation model. The Holocene **15**:951-964.

Reyes, O., C. Méndez, V. Trejo, and H. Velásquez. 2007. El Chueco I: un asentamiento multicomponente en la estepa occidental de Patagonia Central (11.400 A 2.700 años Cal. AP,-44° S). Magallania (Punta Arenas) **35**:107-119.

Rojas, M., and P. I. Moreno. 2011. Atmospheric circulation changes and neoglacial conditions in the Southern Hemisphere mid-latitudes: insights from PMIP2 simulations at 6 kyr. Climate Dynamics **37**:357-375.

Roos, C. I., G. J. Williamson, and D. M. Bowman. 2019. Is anthropogenic pyrodiversity invisible in paleofire records? Fire **2**:42.

Ruddiman, W. F. 2013. The Anthropocene. Annual Review of Earth and Planetary Sciences, Vol 41 **41**:45-68.

Ruiz, E., F. González, C. Torres-Díaz, G. Fuentes, M. Mardones, T. Stuessy, R. Samuel, J. Becerra, and M. Silva. 2007. Genetic diversity and differentiation within and among Chilean populations of Araucaria araucana (Araucariaceae) based on allozyme variability. Taxon **56**:1221-1228.

Russell, E. W. B. 1983. Indian-Set Fires in the Forests of the Northeastern United-States. Ecology **64**:78-88.

Sanguinetti, J., and T. Kitzberger. 2009. Efectos de la producción de semillas y la heterogeneidad vegetal sobre la supervivencia de semillas y el patrón espacio-temporal de establecimiento de plántulas en Araucaria araucana. Revista chilena de historia natural **82**:319-335.

Sauer, C. O. 1950. Grassland climax, fire, and man. Journal of Range Management **3**:16-21.

Scheinsohn, V. 2003. Hunter-gatherer archaeology in South America. Annual Review of Anthropology **32**:339-361.

Scheinsohn, V., S. L. Dahinten, J. G. Otero, F. Rizzo, S. Leonardt, P. Tchilinguirián, A. G. Millán, N. Kuperszmit, M. C. González, and B. Beroqui. 2017. La antigüedad de la ocupación humana en el centro-oeste del Chubut: nuevos datos del valle del Genoa. Arqueología **23**:109-124.

Scheinsohn, V., P. M. Fernández, F. Garrone, L. Catelli, M. Longaray, M. Romero, M. Salado, M. G. Fernández, P. Tchilinguirián, and C. Vullo. 2016. Identificación taxonómica mediante Citocromo b: Su aplicación a un caso arqueológico patagónico. Intersecciones en antropología **17**:281-289.

Schlichter, T., and P. Laclau. 1998. Ecotono estepa-bosque y plantaciones forestales en la Patagonia norte. Ecología Austral **8**:285-296.

Schoennagel, T., J. K. Balch, H. Brenkert-Smith, P. E. Dennison, B. J. Harvey, M. A. Krawchuk, N. Mietkiewicz, P. Morgan, M. A. Moritz, and R. Rasker. 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences **114**:4582-4590.

Schoolcraft, H. R. 1821. Journal of a Tour into the Interior of Missouri and Arkansas, from Potosi, or Mine A'burton, in Missouri Territory, In a South-West Direction, Toward the Rocky Mountains; Peformed In the Years 1818 and 1819.

Schoolcraft, H. R. 1853. Scenes and Adventures in the Semi-alpine Region of the Ozark Mountains of Missouri and Arkansas: Which Were First Traversed by De Soto, in 1541. Lippincott, Grambo.

Schroeder, M., and C. Buck. 1970. Fire Weather, Agricultural Handbook 360. USDA Forest Service: Washington, DC.

Schulz, M., and M. Mudelsee. 2002. REDFIT: estimating red-noise spectra directly from unevenly spaced paleoclimatic time series. Computers & Geosciences **28**:421-426.

Seddon, A. W. R., A. W. Mackay, A. G. Baker, H. J. B. Birks, E. Breman, C. E. Buck, E. C. Ellis, C. A. Froyd, J. L. Gill, L. Gillson, E. A. Johnson, V. J. Jones, S. Juggins, M. Macias-Fauria, K. Mills, J. L. Morris, D. Nogues-Bravo, S. W. Punyasena, T. P. Roland, A. J. Tanentzap, K. J. Willis, M. Aberhan, E. N. van Asperen, W. E. N. Austin, R. W. Battarbee, S. Bhagwat, C. L. Belanger, K. D. Bennett, H. H. Birks, C. B. Ramsey, S. J. Brooks, M. de Bruyn, P. G. Butler, F. M. Chambers, S. J. Clarke, A. L. Davies, J. A. Dearing, T. H. G. Ezard, A. Feurdean, R. J. Flower, P. Gell, S. Hausmann, E. J. Hogan, M. J. Hopkins, E. S. Jeffers, A. A. Korhola, R. Marchant, T. Kiefer, M. Lamentowicz, I. Larocque-Tobler, L. Lopez-Merino, L. H. Liow, S. McGowan, J. H. Miller, E. Montoya, O. Morton, S. Nogue, C. Onoufriou, L. P. Boush, F. Rodriguez-Sanchez, N. L. Rose, C. D. Sayer, H. E. Shaw, R. Payne, G. Simpson, K. Sohar, N. J. Whitehouse, J. W. Williams, and A. Witkowski. 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. Journal of Ecology **102**:256-267.

Segalen, L., J. A. Lee-Thorp, and T. Cerling. 2007. Timing of C4 grass expansion across sub-Saharan Africa. J Hum Evol **53**:549-559.

Stambaugh, M. C., and R. P. Guyette. 2006. Fire regime of an Ozark wilderness area, Arkansas. American Midland Naturalist **156**:237-251.

Stambaugh, M. C., and R. P. Guyette. 2008. Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. Forest Ecology and Management **254**:463-473.

Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. Science **334**:230-232.

Stuiver, M., P. Reimer, and R. Reimer. 2017. CALIB 7.1 [WWW program] at http://calib.org.

Szeicz, J. M., S. G. Haberle, and K. D. Bennett. 2003. Dynamics of North Patagonian rainforests from fine-resolution pollen, charcoal and tree-ring analysis, Chonos Archipelago, Southern Chile. Austral Ecology **28**:413-422.

Thomson, D. 1990. Time series analysis of Holocene climate data. Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences **330**:601-616.

Umbanhowar, C. E., P. Camill, C. E. Geiss, and R. Teed. 2006. Asymmetric vegetation responses to mid-Holocene aridity at the prairie-forest ecotone in south-central Minnesota. Quaternary Research **66**:53-66.

University of East Anglia Climatic Research Unit; Harris, I. C. J., P.D. . 2017. CRU TS4.01: Climatic Research Unit (CRU) Time-Series (TS) version 4.01 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901- Dec. 2016).*in* C. f. E. D. Analysis, editor.

Valencio, A., K. Creer, A. Sinito, M. Mazzoni, M. Alonso, and V. Markgraf. 1985. Palaeomagnetism, sedimentology, radiocarbon age determinations and palynology of the Llao area, southwestern Argentina (lat. 41 S, long. 71.3 W): paleolimnological aspects. Quaternary of South America and Antarctic Peninsular **3**:109-148.

Veblen, T. T. 1982. Regeneration patterns in Araucaria araucana forests in Chile. Journal of Biogeography:11-28.

Veblen, T. T., R. S. Hill, and J. Read. 1996. The ecology and biogeography of Nothofagus forests. Yale University Press.

Veblen, T. T., A. Holz, J. Paritsis, E. Raffaele, T. Kitzberger, and M. Blackhall. 2011. Adapting to global environmental change in Patagonia: What role for disturbance ecology? Austral Ecology **36**:891-903.

Veblen, T. T., and T. Kitzberger. 2002. Inter-hemispheric comparison of fire history: the Colorado front range, USA, and the northern Patagonian Andes, Argentina. Plant ecology **163**:187-207.

Veblen, T. T., T. Kitzberger, R. Villalba, and J. Donnegan. 1999. Fire History in Northern Patagonia: The Roles of Humans and Climatic Variation. Ecological Monographs **69**:47-67.

Veblen, T. T., and D. C. Lorenz. 1988. Recent Vegetation Changes Along the Forest Steppe Ecotone of Northern Patagonia. Annals of the Association of American Geographers **78**:93-111.

Veblen, T. T., and V. Markgraf. 1988. Steppe expansion in Patagonia? Quaternary Research **30**:331-338.

Villa-Martínez, R., and P. I. Moreno. 2007. Pollen evidence for variations in the southern margin of the westerly winds in SW Patagonia over the last 12,600 years. Quaternary Research **68**:400-409.

Villa-Martínez, R., P. I. Moreno, and M. A. Valenzuela. 2012. Deglacial and postglacial vegetation changes on the eastern slopes of the central Patagonian Andes (47 S). Quaternary Science Reviews **32**:86-99.

Villagrán, C. 1991. Historia de los bosques templados del sur de Chile durante el Tardiglacial y Postglacial. Revista chilena de historia natural **64**:447-460.

Villagrán, C. 2001. Un modelo de la historia de la vegetación de la Cordillera de La Costa de Chile central-sur: la hipótesis glacial de Darwin. Revista chilena de historia natural **74**:793-803.

Villalba, R., A. Lara, M. H. Masiokas, R. Urrutia, B. H. Luckman, G. J. Marshall, I. A. Mundo, D. A. Christie, E. R. Cook, R. Neukom, K. Allen, P. Fenwick, J. A. Boninsegna, A. M. Srur, M. S. Morales, D. Araneo, J. G. Palmer, E. Cuq, J. C. Aravena, A. Holz, and C. LeQuesne. 2012. Unusual Southern Hemisphere tree growth patterns induced by changes in the Southern Annular Mode. Nature Geoscience **5**:793-798.

Walsh, M. K., C. Whitlock, and P. J. Bartlein. 2010. 1200 years of fire and vegetation history in the Willamette Valley, Oregon and Washington, reconstructed using high-resolution macroscopic charcoal and pollen analysis. Palaeogeography Palaeoclimatology Palaeoecology **297**:273-289.

Webb, T., P. J. Bartlein, S. P. Harrison, and K. H. Anderson. 1993. Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. Global climates since the last glacial maximum:415-467.

Whitlock, C., and P. J. Bartlein. 2003. Holocene fire activity as a record of past environmental change. Developments in Quaternary Sciences **1**:479-490.

Whitlock, C., M. M. Bianchi, P. J. Bartlein, V. Markgraf, J. Marlon, M. Walsh, and N. McCoy. 2006. Postglacial vegetation, climate, and fire history along the east side of the Andes (lat 41–42.5°S), Argentina. Quaternary Research **66**:187-201.

Whitlock, C., D. Colombaroli, M. Conedera, and W. Tinner. 2018. Land-use history as a guide for forest conservation and management. Conserv Biol **32**:84-97.

Whitlock, C., P. E. Higuera, D. B. McWethy, and C. E. Briles. 2010. Paleoecological perspectives on fire ecology: revisiting the fire-regime concept. The Open Ecology Journal **3**:6-23.

Whitlock, C., and C. Larsen. 2001. Charcoal as a fire proxy. Pages 75-97 Tracking environmental change using lake sediments. Springer.

Whitlock, C., D. B. McWethy, A. J. Tepley, T. T. Veblen, A. Holz, M. S. McGlone, G. L. W. Perry, J. M. Wilmshurst, and S. W. Wood. 2014. Past and Present Vulnerability of Closed-Canopy Temperate Forests to Altered Fire Regimes: A Comparison of the Pacific Northwest, New Zealand, and Patagonia. BioScience **65**:151-163.

Whitlock, C., and S. H. Millspaugh. 1996. Testing the assumptions of fire history studies: An examination of modern charcoal accumulation in Yellowstone National Park, USA. Holocene **6**:7-15.

Whitlock, C., P. I. Moreno, and P. Bartlein. 2007. Climatic controls of Holocene fire patterns in southern South America. Quaternary Research **68**:28-36.

Whitlock, C., S. L. Shafer, and J. Marlon. 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**:5-21.

Williams, J. W., Bryan Shuman, J. W. Patrick J. Bartlein, Konrad Gajewski, Michael Sawada, Thomas Minckley, Sarah Shafer, Andre E. Viau, Thompson Webb III, Patricia Anderson, Linda Brubaker, Cathy Whitlock, and O. K. Davis. 2006. An atlas of pollen-vegetation-climate relationships for the United States and Canada. American Association of Stratigraphic Palynologists Foundation.

Williams, J. W., B. Shuman, and P. J. Bartlein. 2009a. Rapid responses of the prairie-forest ecotone to early Holocene aridity in mid-continental North America. Global and Planetary Change **66**:195-207.

Williams, J. W., B. Shuman, and P. J. Bartlein. 2009b. Rapid responses of the prairie-forest ecotone to early Holocene aridity in mid-continental North America. Global and Planetary Change **66**:195-207.

Wolverton, S. 2005. The effects of the hypsithermal on prehistoric foraging efficiency in Missouri. American Antiquity **70**:91-106.

Wood, W. R., and R. B. McMillan. 1976. Prehistoric man and his environments: a case study in the Ozark Highland. Academic Press, Inc., New York.

Wright, H. E., D. H. Mann, and P. H. Glaser. 1984. Piston Corers for Peat and Lake-Sediments. Ecology **65**:657-659.

Wuenscher, J. E., and A. J. Valiunas. 1967. Presettlement forest composition of the River Hills region of Missouri. American Midland Naturalist:487-495.