HOLOCENE CLIMATE-VEGETATION-FIRE LINKAGES ALONG THE PATAGONIAN FOREST/STEPPE ECOTONE (41 – 43˚S)

by

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of

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ABSTRACT

Patagonian vegetation has dramatically changed in composition and distribution since the Last Glacial Maximum. Although patterns of vegetation change are relatively clear, our understanding of the processes that produce them is limited. In this study, I reconstructed the vegetation and fire history of the North Patagonian forest-steppe ecotone (lat. 41 - 43°S) and linked vegetation changes to variations in the fire regime, large-scale synoptic controls of climate, and human activity. Postglacial vegetation and fire dynamics were inferred from seven high-resolution pollen and charcoal records from lakes located along the forest-steppe ecotone. Regional trends in vegetation composition and biomass burning were compared to independent records of climate to assess long-term climate-vegetation-fire linkages. Pollen data indicate that late-glacial steppe was replaced by parkland in the early Holocene and by shrubland and forest in the middle and late Holocene. Fire activity was lowest during the late-glacial/early-Holocene transition and gradually increased throughout the Holocene. Based on current knowledge of human settlement in the area, there is no evidence that indicates that increased aboriginal population densities resulted in higher biomass burning at regional scales. Instead, results show that climate was the main driver of Holocene ecological change, either by its direct effects on vegetation or its indirect effects on fire. Watershed vegetation flammability explains much of the fine-scale variability in the fire regime, which, in turn can amplify or override the direct influence of climate on ecotone composition. During the late Holocene, in particular, oscillations in forest dominance were largely driven by changes in humidity, possibly associated with the onset or strengthening of ENSO. At intermediate-moisture levels fire became an important control of community composition. These findings emphasize the importance of biophysical feedbacks in ecosystem dynamics and suggest that these relations must be understood in the context of millennial-scale climate variations that shape broad patterns of vegetation and fire in the region.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Terrestrial ecotones are amongst the world most dynamic ecosystems and expected to undergo rapid and pronounced shifts in position and composition in response to climate changes (di Castri et al., 1988; Kitzberger, 2012). Forest-steppe boundaries are areas of especial interest because, since prehistoric times, they have been sites of human activity. During the last decade, unprecedented rates of change attributed to increased climate variability and land use have been observed in these ecosystems (Nielson, 1991). As the composition of ecotones shifts, so too do surface energy and water balances, erosion rates, and nutrient cycling, resulting in complex environmental feedbacks that can potentially amplify the effects of climate alone. These changes in environmental properties are likely to affect not only regional biodiversity and ecotone dynamics, but also a wide range of ecosystem services including carbon storage, forage production, enhanced water supply and quality, crop pollination, and outdoor recreation (Kupfer and Cairns, 1996).

A longstanding assumption in plant ecology has been that, in the absence of disturbance, vegetation eventually reaches a climate-dependent climax condition in which its structure does not change significantly over time (Clements, 1936). Moderate- to large-scale disturbance agents, however, are omnipresent in natural ecosystems, inasmuch as fires, floods, windstorms, and insect outbreaks regularly alter climate-vegetation linkages (Clark, 1996). Fire, for example, has been proposed to be an

important trigger of past biotic reorganizations (Christensen, 1993), whose properties (i.e., intensity, frequency, temperature) can potentially amplify or override the direct effects of climate on vegetation (Higuera et al., 2009) and maintain biomes such as grasslands and forests as alternative stable states (Staver et al., 2011).

In a given year, successful spread of fires requires a combination of low fuel moisture and high fuel accumulation and continuity (Agee, 1993). Fuel characteristics are in turn determined by complex interactions between short-term weather conditions and the vegetation history of the area (Christensen, 1993). Such climate-vegetation-fire linkages operating at multiple spatiotemporal scales result in complex ecosystem dynamics. There is therefore a need for ecologists and policymakers to go beyond equilibrium estimates of biosphere change and consider transient responses of ecosystems to environmental variability.

Along the southeastern Andes, a sharp ecotone separates North Patagonian forest dominated by the evergreen tree species *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*, from low-elevation steppe. The modern geographic position of the ecotone is largely determined by effective moisture, which in turn is broadly governed by the strength and latitudinal position of the Southern Westerlies and southeastern Pacific subtropical high-pressure system. The orographic effects of the Andes on western moisture sources sharpen the west-to-east gradient resulting in a 90% decline in precipitation between the Andean crest and the Patagonian steppe, located 100 km to the east (Villalba and Veblen, 1997; Villalba et al, 2003). Recent widespread mortality of *Nothofagus* in the face of drought and large fires evidence the high

sensitivity of the forest-steppe ecotone to seasonal, annual and decadal changes in precipitation (Kitzberger and Veblen, 2003; Veblen et al, 2011). Pronounced effects of disturbance have been observed along the ecotone, where decades of fire suppression have allowed the fire-sensitive conifer *Austrocedrus chilensis* to expand eastwards into the steppe (Veblen and Markgraf, 1989). Deliberate burning, deforestation, heavy livestock grazing, extensive plantations of non-native conifers (Veblen and Lorenz, 2005) and large-scale water-diversion projects designed to support development and expansion of the urban-wildland interface have altered natural ecotone dynamics since European colonization (Mermoz et al., 2005).

It is becoming increasingly clear that forest/steppe ecotone dynamics respond to a multivariate set of biophysical conditions, such as temperature, effective moisture, soil, and disturbance, whose relative importance changes as critical thresholds are reached (Kitzberger, 2012). Understanding ecosystem processes requires disentangling regional drivers from more-local feedbacks involving vegetation, fire and human activities. Such feedbacks have evolved over millennia and been shaped by dramatic changes in climate ranging from Quaternary glacial-interglacial transitions to interannual variability of ENSO. For this reason, evaluations of long-term climate-fire vegetation linkages are necessary for estimating the natural variability of north Patagonian ecosystems and inferring local responses to regional climate change, such as those predicted to occur in the future (IPCC, 2007).

Objectives

My research aims to better understand climate-vegetation-fire linkages that have evolved since the last glacial maximum (i.e., 23,000 cal yr BP) at the forest-steppe ecotone in a core region from lat. 41 to 43˚S. In particular, the objectives of this dissertation are to: (1) reconstruct the postglacial environmental history along the forest/steppe ecotone and estimate watershed- and regional-scale trends in vegetation and fire; (2) infer the relationship between the postglacial vegetation history of the lower treeline and the biogeography of the keystone species *Austrocedrus chilensis*; (3) assess the spatiotemporal dynamics of climate-vegetation-fire linkages across scales, and identify the relative importance of local versus regional drivers of Holocene ecological change; and (4) evaluate the role of humans as drivers of pre-European environmental change.

To address these objectives, I have focused on the acquisition of new high-resolution charcoal and pollen records from a transect of sites along the North Patagonian forest-steppe ecotone from lat. 41 to 43˚S. Lakes and bogs collect sediment from neighboring slopes, volcanic ash, charcoal produced by fires, and pollen from local and regional vegetation, providing a continuous record of environmental change extending to the beginning of the lake/bog. The study area is particularly sensitive to changes in effective moisture associated with the strength and latitudinal position of the Southern Westerlies and ENSO-related variability. For this reason, a north-to-south transect along the foothills of the Andes allowed me to evaluate how the precipitation regime was affected by large-scale changes in climate and assess the effects that those changes had

on both local ecosystems and the regional evolution of the ecotone. From north to south, the sites are as follows (Fig 1.1):

- Laguna el Trébol (Rio Negro Province; 41˚15’’S; 71˚32’W; 977 m elev.) is a glacial lake (Whitlock et al., 2006) that provides a record of post-glacial environmental change. Currently, the basin lies in the transition forest dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis* and is moderately affected by recreation and tourism.

- Laguna Padre Laguna (Rio Negro, Nahuel Huapi National Park; 41˚30’S; 71˚ 32’W; 735 m elev.), dammed by a broad postglacial alluvial fan, is surrounded by co-dominated *Nothofagus-Austrocedrus* forest. A ca. 5,000-year vegetation and fire record was obtained at this site.

- Lago Huale Hué (Río Negro, Nahuel Huapi National Park; 41˚30’S, 71˚ 30’W, 849 m elev.) is blocked on its east side by a prominent glacial delta associated with late-Pleistocene meltwater from ice complexes from the north (Caldenius, 1932). A ca. 13,000-year-old vegetation and fire history from low-elevation forests of *Nothofagus dombeyi* and Austrocedrus was reconstructed for this watershed.

- Laguna del Cóndor (Chubut, near Cholila; 42˚20’S; 71˚17’W; 818 m elev.) lies at the forest margin in a heavily grazed region and provides fire and vegetation histories that span the last ca. 11,000 years.

- Lago Mosquito (also known as Lago Pellegrini; Chubut, near Cholila; 42˚29’S; 71˚24’W; 551 m. elev.) is dammed by Holocene alluvial fans (Whitlock et al., 2006). It is currently located within the transition zone from open *Austrocedrus* woodland to steppe,

and the landscape that surrounds it is heavily grazed by sheep. Ca. 9000 years of local environmental history were obtained from this lake.

- Laguna La Zeta (Chubut, near Esquel; 43˚17'S; 71˚53'W; 774 m elev.) is situated on a high plain that was glaciated several times during the Pleistocene (Schaebitz, 1994). Although the native vegetation is dominated by shrubs and grasses, pines have been planted to reforest the surroundings of the lake. A ca. 23,000 year-old record of environmental change was collected from this site.

- Lago Theobal (Chubut, near Corcovado; 43˚12'S; 71˚40'W; 678 m elev.). This lake was formed in either an ice-block depression or glacial scour depression. It currently lies at the *Nothofagus-Austrocedrus* forest/steppe boundary, and provides a postglacial record of fire and vegetation changes for the region.

Chronologies for the paleoenvironmental reconstructions come from radiocarbon-dated plant material in the sediment cores, and from identifying the volcanic ashes preserved in the sediments and tracing them to known eruptions (Naranjo and Stern, 1998; 2004; Villarosa et al., 2006). Pollen interpretation is based on modern pollen studies from Patagonia (Páez et al., 2001; Markgraf et al., 1981). Time series of macroscopic charcoal, examined in continuous core sections, were developed to reconstruct local fire histories at each watershed. I worked closely with tree-ring collaborators to calibrate our charcoal data against known fires (Kitzberger et al., 1997; Veblen et al., 2003), and with modern ecologists and fire management specialists (Guillermo de Fossé, CIEFAP, Dirección de Bosques de Esquel) for information on present fire regimes. Further environmental change information was provided by lithology, magnetic susceptibility,

loss on ignition and sediment density measurements performed at LacCore (University of Minnesota). By analyzing a network of sites, my intention was to override the effects of chaotic and ecology-independent random processes operating on the vegetation and fire history at each site, and obtain a reliable reconstruction of past environmental changes in the area. I compared these reconstructions with paleoenvironmental data (e.g., Lamy et al., 2001; Moy et al., 2003; Whitlock et al., 2006; 2007; Markgraf et al., 2007; 2008; Moreno et al., 2010) to increase our understanding of the regional history of the ecotone as well as its relationship to past climate changes.

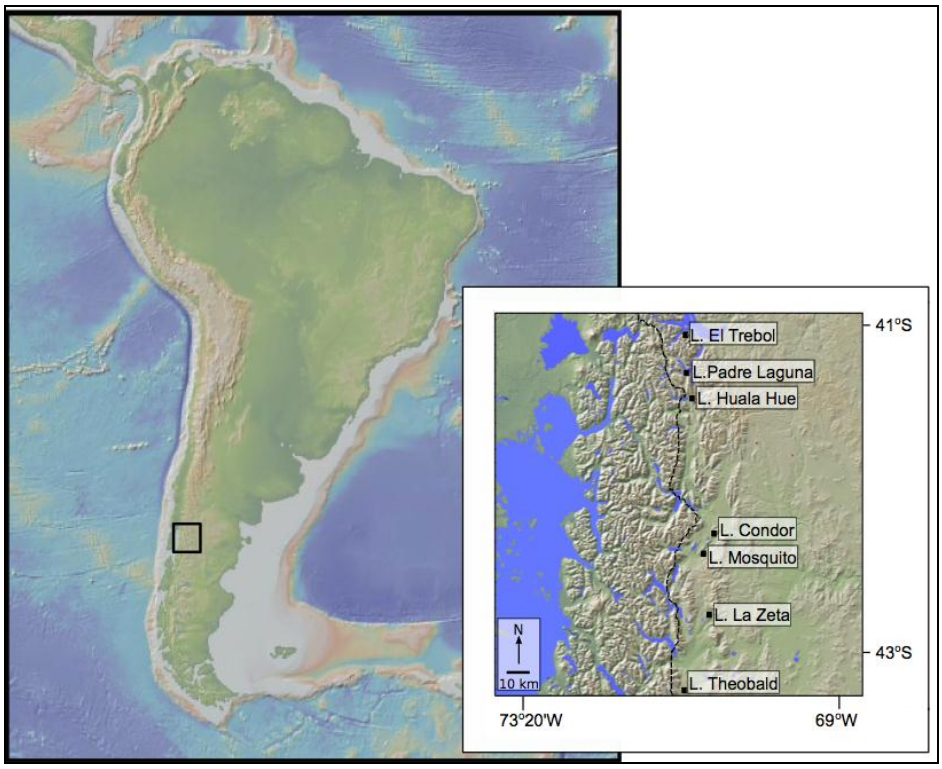


Figure 1.1: Study area and location of L. el Trébol, L. Padre Laguna, L. Huala Hué, L. Cóndor, L. Mosquito, L. La Zeta and L. Theobald. The dashed line shows the international border between Argentina and Chile.

Overview of Dissertation

In my dissertation, I examine post-glacial climate-vegetation-fire linkages at the Patagonian forest/steppe ecotone as reconstructed from lithology, pollen and charcoal data. By identifying the natural variability of Patagonian ecosystems and its responses to changes in climate and disturbance regimes, this work provides a basis for evaluation of current environmental trends and helps link ecological responses to variations in large-scale synoptic controls of regional climate.

Holocene climate variability and environmental history at lat. 42˚S is provided in Chapter 2. L. el Cóndor (42˚20'S; 71˚17'W) and L. Mosquito (42˚29'S; 71˚24'W) are two sites that lie in close proximity near the terminal Pleistocene moraine that lies at the present-day forest-steppe ecotone (Caldenius, 1932). Pollen, charcoal and lithological analyses of these sites provided a detailed spatial reconstruction of environmental changes at lat. 42˚S for the last ca. 10,000 years and insights into the biogeographic history of *Austrocedrus chilensis*. Sediments from both lakes preserve evidence of explosive Holocene eruptions of large stratovolcanoes in the southern portion of the Andean Southern Volcanic Zone (lat. 41.5°-46°S; Stern, 2004). Inductively coupled plasma mass spectrometry (ICP-MS) analyses on five tephra samples undertaken by my collaborators helped in the characterization of Holocene tephrochronology.

In Chapter 3, I discuss climatic and local controls of long-term vegetation dynamics in the Río Manso drainage (northern Patagonia; lat. 41°S). Most of the large lakes in the Río Manso drainage are dammed by recessional moraines from eastward-flowing late-Pleistocene glaciers. The small low-elevation sites considered in this section,

however, are blocked by prominent glacial deltaic complexes associated with late-Pleistocene meltwater (i.e., L. Huala Hué [41˚30'S, 71˚ 30'W], Caldenius, 1932), or dammed by broad postglacial alluvial fans (i.e., L. Padre Laguna [41˚30'S; 71˚ 32'W]). The Holocene history of the area is presented and compared with records from nearby sites to identify the relative importance of local and regional drivers of ecosystem dynamics. I also focus on the last 5000 years of environmental change at the forest/steppe ecotone to contribute to better understanding of the dynamics of modern ecosystems and the drivers of ecological variability. The late Holocene is of special interest for ecologists and policy-makers because it is the time of establishment of modern climates and plant communities in northern Patagonia.

Vegetation and fire history of the forest/steppe ecotone between lat. 41 and 43°S since the Last Glacial Maximum (ca. 23,000 cal yr BP) as well as the biogeography of *Austrocedrus chilensis* are discussed in Chapter 4. I link past changes in vegetation to variations in the fire regime, large-scale controls of climate, and human activity. Postglacial vegetation and fire dynamics are inferred from high-resolution pollen and charcoal records from seven lakes located along the forest-steppe ecotone in the eastern flanks of the Andes (i.e., L. el Trébol [41˚15''S; 71˚32'W], L. Padre Laguna [41˚30'S; 71˚ 32'W], L. Huala Hué [41˚30'S, 71˚ 30'W], L. el Cóndor [42˚20'S; 71˚17'W], L. Mosquito [42˚29'S; 71˚24'W], L. La Zeta [43˚17'S; 71˚53'W] and L. Theobald [43˚12'S; 71˚40'W]). Mixed Generalized Additive Models (Wood, 2004) were fit to the pollen and charcoal time series to estimate regional trends in vegetation composition and biomass burning. Under the premise that large-scale ecological variability is driven by top-down

controls (Huber et al., 2004), I assessed long-term vegetation-fire-climate linkages by comparing the estimated trends in vegetation and fire with independent paleoclimate data. Following a similar approach, I evaluated the role of aboriginal peoples, as inferred from archeological data, in altering the position and composition of the forest/steppe boundary. The effects of watershed vegetation flammability on fine-scale variability in the fire regime were estimated through regression of local fire anomalies on pollen data.

Finally, in Chapter 5, I provide a summary of the major results from each chapter and discuss how they influence our current understanding of the environmental history of temperate Patagonia, the regional fire history, paleo-dynamics of the forest-steppe ecotone, and response of regional environments to global climate change. My findings emphasize the importance of biophysical feedbacks in ecosystem dynamics and suggest that these relations must be understood in the context of millennial-scale climate variations that shape broad patterns of vegetation and fire in the region.

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CHAPTER TWO

HOLOCENE CLIMATE VARIABILITY AND ENVIRONMENTAL HISTORY AT THE PATAGOANIAN FOREST/STEPPE ECOTONE: LAGO MOSQUITO (42 29’37.89”S, 71 24’14.57”W) AND LAGUNA DEL CONDOR (42 20’47.22”S, 71 17’07.62”W)

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, and 4

Author: Virginia Iglesias

Contributions: Defined the experimental design, described the sediment cores from L. del Cóndor, measured magnetic susceptibility, loss-on-ignition and other lithological properties of the cores, counted charcoal and pollen samples from L. del Cóndor, analyzed the data and wrote the manuscript.

Co-Author: Cathy Whitlock

Contributions: Supported this research under the National Science Foundation grants ATM-0714061 and OISE-0966472, helped define the experimental design, participated in fieldwork, discussed the results and implications and edited the manuscript.

Co-Author: María Martha Bianchi

Contributions: Participated in fieldwork, counted pollen samples from L. Mosquito and commented on the manuscript.

Co-Author: Gustavo Villarosa

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MANUSCRIPTS IN CHAPTERS TWO, THREE AND FOUR

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Abstract

Along the eastern Andes, a sharp ecotone separates steppe from North Patagonian forest dominated by *Nothofagus* spp. and *Austrocedrus chilensis*. The longitudinal position of the ecotone is largely determined by effective moisture, which in turn is partly governed by the strength and latitudinal position of the Southern Westerlies. As a result, changes in the ecotone provide an opportunity to examine past climate variations. Holocene environmental history at two sites in close proximity is inferred from pollen and high-resolution charcoal data. Prior to 9000 cal yr BP, vegetation resembled a steppe, in accordance with widespread aridity. Fires were infrequent, likely as a consequence of fuel discontinuity associated with low vegetation cover. At 9000 cal yr BP, forest taxa expanded into steppe and fires became frequent, indicating that summers were arid enough to support fires but winter moisture was sufficient for *Nothofagus* spp. to expand. A two-step increase in effective moisture is inferred for the middle Holocene. The first step occurred at 8500 cal yr BP, as interpreted from the increase in *A. chilensis* in the region, probably as a consequence of an eastward migration from glacial refugia. The second step at 5500 cal yr BP is based on a *Nothofagus* spp. expansion into the steppe. Steppe readvances into the forest between 5250 and 3000 cal yr BP indicate decreased temperatures and/or effective moisture. The last 3000 years are characterized by expansions of *A. chilensis* and an eastward shift of the ecotone, suggesting more humid conditions. European settlement is reflected in the establishment of non-native species and disturbance-adapted taxa.

Introduction

Along the eastern Andes, a sharp ecotone separates low-elevation steppe from North Patagonian forest dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*. The geographic position of the ecotone is largely determined by effective moisture, which in turn is broadly governed by the strength and latitudinal position of the Southern Westerlies (SW), and the orographic effects of the Andes (Villalba et al., 2003). As a result, changes in the position, sharpness, and composition of the Patagonian forest-steppe ecotone provide an opportunity to examine past climate variations.

Previous work in the Andes (Bianchi and Ariztegui, this issue; Huber and Markgraf, 2003; Markgraf, 1984; Whitlock et al., 2006) has shown that climate-induced vegetation change occurs through the direct effects of climate on plant fitness, and indirectly through altered disturbance regimes, such as insect breakouts and fires. Fire is an intrinsic element of the forest-steppe border with large effects on vegetation composition and landscape structure (Veblen et al., 1999). In recent decades, a human-induced change in the fire regime has led to an increase in re-sprouting shrubs (i.e. *Nothofagus antarctica*, *Discaria* spp.) at expense of trees, and this shift has contributed to the observed shrinkage of the *Nothofagus dombeyi* forest (Mermoz et al., 2005). Evaluations of climate-fire vegetation linkages are therefore critical for understanding ecosystem dynamics and local responses to regional climate change, such as those predicted to occur in the future (IPCC, 2007).

In order to improve our understanding of forest-steppe ecotone dynamics, we reconstruct the vegetation, fire, and climate history based on pollen, charcoal, and

lithologic records contained in sediment cores from Lago Mosquito (also known as Lago Pellegrini, lat. 42 29'37.89"S, long. 71 24'14.57"W, 556 m elevation, 8-m coring water depth, 461 ha surface area, surface runoff from Arroyo Mosquito) and Laguna del Cóndor (also known as Laguna Escondida, lat. 42 20'47.22"S, long. 71 17'07.62"W, 818 m elevation, 8.5-m coring water depth, ca. 175 ha surface area, no incoming streams). These lakes are 18 km apart along a west-east precipitation transect and located within the transition from open *Austrocedrus chilensis* woodland to steppe, near the town of Cholila (Chubut Province) in western Patagonia (Fig. 2.1). Their sediments preserve evidence of explosive Holocene eruptions of large stratovolcanoes from the southern portion of the Andean Southern Volcanic Zone (lat. 41.5°-46°S; Stern, 2004). Both lakes lie close to terminal Pleistocene moraines (Caldenius, 1932), but the origin of L. Mosquito is related to Holocene alluvial fans that dammed westward flowing streams and created the lake upvalley (Whitlock et al., 2006). By analyzing two proximal sites, we expect to override the effects of chaotic (Bennett, 1993; Ives et al., 2008; May, 1976) and ecology-independent random processes (Hubbell, 2001) operating on the vegetation history at each site, and obtain a reliable reconstruction of past environmental changes in the area (Blaauw et al., 2010; Briles et al., 2008), increasing our understanding of the ecotonal history as well as its relationship to past climate changes.

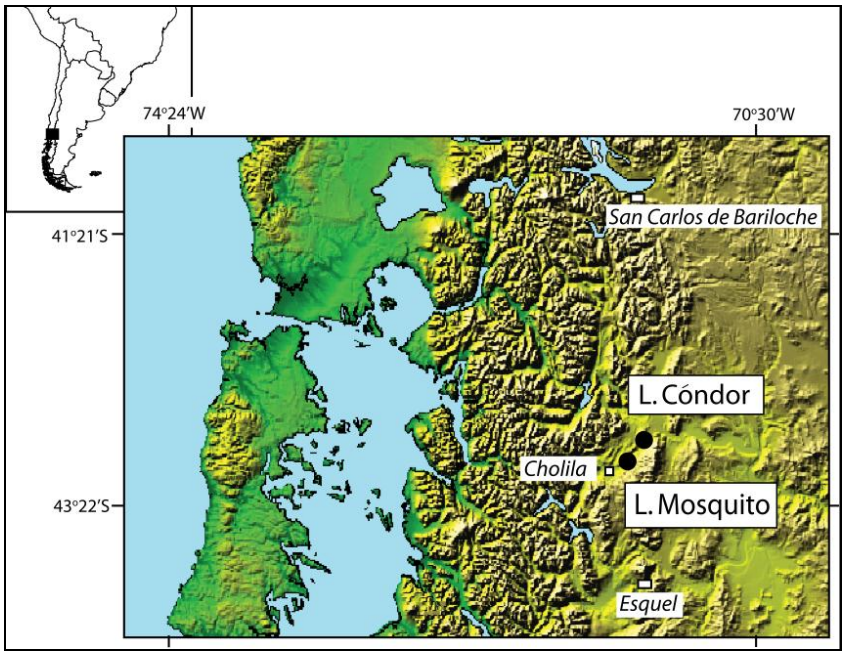


Figure 2.1: Location of L. Mosquito and L. Cóndor.

Modern Setting

A latitudinal and altitudinal gradient dominates Patagonian temperatures and precipitation. In northern Patagonia, mean annual temperatures range from 12°C in the intermountain valleys, to 6°C in the subalpine deciduous forest near the treeline (Villalba et al., 2003). Precipitation in the area is related to frontal systems associated with migratory surface cyclones. Pacific cyclones migrate eastwards along the storm tracks, whose main position follows the jet stream (Garreaud et al., 2003). Prevailing strong SW are the main characteristic that delimits Patagonia as a uniform climatic region (Garreaud et al., 2003). A west wind component occurs at least 75% of the time along the entire Chilean coast (Miller, 1976), and 50 to 70% of the time in the eastern plains (Prohaska, 1976). The Andes constitute an effective barrier to tropospheric flow. The uplift of low-

level winds over the western slope of the Andes produces continental orographic precipitation (Villalba et al., 2003), and forced subsidence over the Argentine flanks of the Andes causes an adiabatic warming of the air masses, resulting in dry conditions in eastern Patagonia (Paruelo et al., 1998). As a consequence, precipitation decreases from 4000-6000 mm/yr in Chile, to 700 mm/yr at San Carlos de Bariloche airport, located approximately 60 km east of the crest of the Andes (Villalba et al., 2003).

Seasonal and annual precipitation variability is influenced by changes in intensity and latitudinal position of the SW, which result in shifts in the storm tracks. In northern Patagonia, storm frequency is highest in winter, when 40% of the precipitation occurs (Miller, 1976). Above 1000 m elevation, winter precipitation is usually in the form of snow. In the foothills and the steppe, distance from the Andes explains over 90% of the spatial variability of mean annual precipitation, and interannual precipitation variability is greatest at the dry end of the humidity gradient (Jobbágy et al., 1995).

The latitudinal position of the SW is governed by the strength and position of the southeastern Pacific high-pressure cell and the subpolar low-pressure trough centered along the Antarctic Circle (Mayr et al., 2005). These circulation systems show latitudinal shifts related to seasonal changes in the temperature gradient between the equator and the poles. The pronounced summer pole-to-equator pressure gradient leads to strongest SW, whose core focuses at lat. 45°- 50°S. In winter, the intensification of the subpolar low and the equatorward displacement of the southeastern Pacific high-pressure cell result in jet stream migration to lower latitudes (lat. 40°S; Paruelo et al., 1998), whereas the low-level

component expands equatorward but weakens, particularly at lat. 50°S (Garreaud et al., 2008).

The steep west-to-east precipitation gradient in the eastern Andes is reflected in a vegetation transition from rainforests to xerophytic forests to steppe (Hajec and di Castri, 1975; Jobággy, 1996) that occurs in <50 km. The montane slopes of the Andes are dominated by tall forests of the evergreen *Nothofagus dombeyi*. Further east, where annual precipitation declines to 1500 mm, *Austrocedrus chilensis* and *N. dombeyi* form extensive co-dominant stands. Under the more xeric conditions to the east, *A. chilensis* forms pure dense stands at its western limit, and open woodlands with abundant sclerophyllous shrubs and small trees (e.g., *Lomatia hirsuta*, *Schinus patagonicus*, *Embothrium coccineum*, *Maytenus sp.*, and the deciduous *Nothofagus antarctica*) towards the east. Further east where precipitation is <500 mm, *A. chilensis* is replaced by steppe characterized by spiny shrubs (*Adesmia* spp., *Mulinum* sp., *Berberis* sp.) and bunchgrasses (*Stipa spp*. and *Festuca spp*.; Seibert, 1982).

Fire is an intrinsic element of Patagonian ecosystems with large effects on vegetation composition and landscape structure (Veblen et al., 1999). *Nothofagus* forests, dominated by evergreen and broadleaved species that tend to act as biologic fire breaks, experience infrequent drought-induced stand-replacing fires (Kitzberger et al., 1997). In contrast, the fine fuels of the steppe desiccate quickly and are commonly dry enough to support frequent surface fires. Vegetation discontinuity limits fires in these dry areas, where dry years of fire occurrence are often preceded by wet years of fuel accumulation (Huber et al., 2004). Shrubs and bunch grasses are the dominant fuels in the ecotonal *A.*

chilensis forests. Their fire regime is characterized by relatively frequent low-severity surface fires (Kitzberger et al., 1997; Veblen et al., 1999). Many decades of fire exclusion, livestock grazing, escarpment from non-native forestry plantations, however, have allowed woody fuels to accumulate sufficiently to increase the potential of crown fires (Veblen et al., 2008).

Methods

Sediment cores were collected from the center of the L. Mosquito and L. Cóndor basins with a modified Livingston piston sampler from a floating, anchored platform. Cores were extruded in the field and wrapped in cellophane and aluminum foil to protect them from contamination and oxidation, and shipped to Montana State University, where they were stored and refrigerated. In the laboratory, cores were split longitudinally into a working half and an archive. The working half was lithologically described, photographed, and analyzed for magnetic susceptibility (MS), sequential loss on ignition (LOI) and charcoal and pollen content. Inductively coupled plasma mass spectrometry (ICP-MS) analyses were performed to five tephra samples for characterization and stratigraphic correlation purposes. Their major oxide, trace and rare earth elements (REE) were determined.

Description of the lithology was based on identification of sedimentary structures, mineralogy, and biological components, following Schnurrenberger et al. (2003). MS was measured at 0.5-cm intervals with a spot-reading sensor (MS2E) directly on the split-surface of the core. The data were used as an approximation of sediment magnetic mineral concentration (Gedye et al. 2000), which provides information on allochthonous

clastic sediment inputs from erosion and volcanic eruptions. LOI analysis was carried out on 1-cm^3 samples taken at 2-cm intervals. Samples were dried at 90°C for 24 hours, and then ignited at 550°C and 900°C. The weight loss between each step measures water, organic matter and carbonate content of the sediment, respectively (Dean, 1974).

Nine samples from the L. Cóndor LC06A, and 19 samples from the L. Mosquito Mos03A and Mos03C cores were submitted for AMS dating (Table 2.1). Chronologies were developed from modeling sediment age as a function of sediment depth. Two-sigma calibrated ages and probability distributions were determined for each radiocarbon date using CALIB 6.0.1 (Stuiver et al., 2005). Calibration was performed with the Southern Hemisphere radiocarbon calibration data set for samples <11,000 cal yr BP (McCormac et al., 2004) and the IntCal09 Calibration Curve for samples >11,000 cal yr BP (Reimer et al., 2009). Core depth was corrected for sediment compaction and adjusted by excluding volcanic ash layers >1.5 cm thick, which are assumed to have been rapidly deposited. Uncertainties in age determinations were considered in the age-depth model by using Monte Carlo sampling (1000 iterations) to generate cubic splines through the calibrated probability distributions of all the dates (Higuera et al., 2009). The importance of each age in the fitted spline was weighted based on its standard deviation, such that ages with larger associated errors had less influence in the models (Telford et al., 2005). The final age-depth models were based on the median of all the runs (Fig. 2.2).

We developed seven alternative age-depth models for L. Mosquito by including all dates, and then excluding individual dates from three levels that had been dated twice. All the models passed through the 95% confidence interval of the ^{14}C dates, and in no

case did the overall nature of the age-depth relationship change. Given that the lithology of the Mos03A core did not suggest changes in sedimentation, for this study we consider the model that yielded least abrupt changes in sedimentation rates.

Three ^{14}C dates from the LC06A core were not included in the age-depth model. The oldest date (17,500 cal yr BP) corresponded to a peat layer at 277 cm depth, and overlying gyttja yielded an age of 10,046 cal yr BP at 247.25 cm depth. This discrepancy suggests a hiatus of approximately 7200 years in sedimentation between the deposition of the peat layer and the creation of the lake. For this reason, the date obtained from the peat layer was not used in the chronology and the overlying date was extrapolated to the gyttja-peat contact. A date at 24.5 cm depth (7040 cal yr BP) was older than ages defined by other three ^{14}C dates obtained from deeper levels and excluded from the model, and so was one at 203.75 cm (7620 cal yr BP) whose inclusion in the model would have resulted in a dramatic change in sedimentation rate that was not reflected in the lithology. The resulting chronology was well constrained.

Charcoal analysis was performed on 2 cm^3 volume samples, taken at contiguous 0.5-cm intervals, following the methodology outlined by Whitlock and Larsen (2001) to reconstruct local fire histories. The material was wet-screened through a 125-mm-mesh sieve and charcoal particles were tallied under a stereomicroscope. Grass and wood charcoal were tallied separately. Charcoal counts were converted to charcoal concentration (particles cm^{-3}), and then to charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}). In order to account for variable sampling intensity with time and override the effects of dynamic sedimentation rates, the CHAR time series was interpolated to its

median resolution. A low frequency component of the series (background CHAR) was defined by smoothing the record with a locally weighted regression (Higuera et al., 2009). The L. Mosquito record was smoothed with a moving average. Because of the presence of outliers, a moving median was chosen for the L. Cóndor CHAR series. Background CHAR integrates charcoal contributions from across the landscape (Long et al. 1998) and reflects area burned (Higuera et al., 2010). The positive residuals of the model include fire episodes (one or more local fires during the time span of the charcoal peak; Whitlock and Anderson 2003) as well as noise. Local thresholds were used to identify significant fire-related peaks from noise (Higuera et al. 2005). Fire frequency was calculated as fire events/time and smoothed over a time window of 1000 years. Grass-to-total charcoal ratios were used to infer the relative contribution of grass and woody fuels, allowing provisional classification of fires into surface fires (grass-to-total charcoal ratio>0.5) and crown fires (grass-to-total charcoal ratio <0.5). *Chusquea* spp. seem unlikely or minor contributors to the grass charcoal, given that they do not grow in the Mosquito-Cóndor area at present.

For pollen analysis, 1 cm^3 of sediment was taken at 8-cm intervals and prepared with standard techniques (Faegri and Iversen, 1989). A known amount of *Lycopodium* tracer spores was added to each sample to allow calculation of pollen accumulation rate (PAR; grains cm^{-2} yr^{-1}), which was interpreted as a crude measure of plant abundance. Pollen grains were identified at 400x magnification, using a reference collection and published atlases (Heusser, 1987; Markgraf and D'Antoni, 1978). In all cases, counts exceeded 300 terrestrial grains, excluding Cyperaceae, aquatic taxa and spores.

Terrestrial pollen percentages were based on the sum of trees, shrubs and herbs and plotted using C2 (Juggins, 2007).

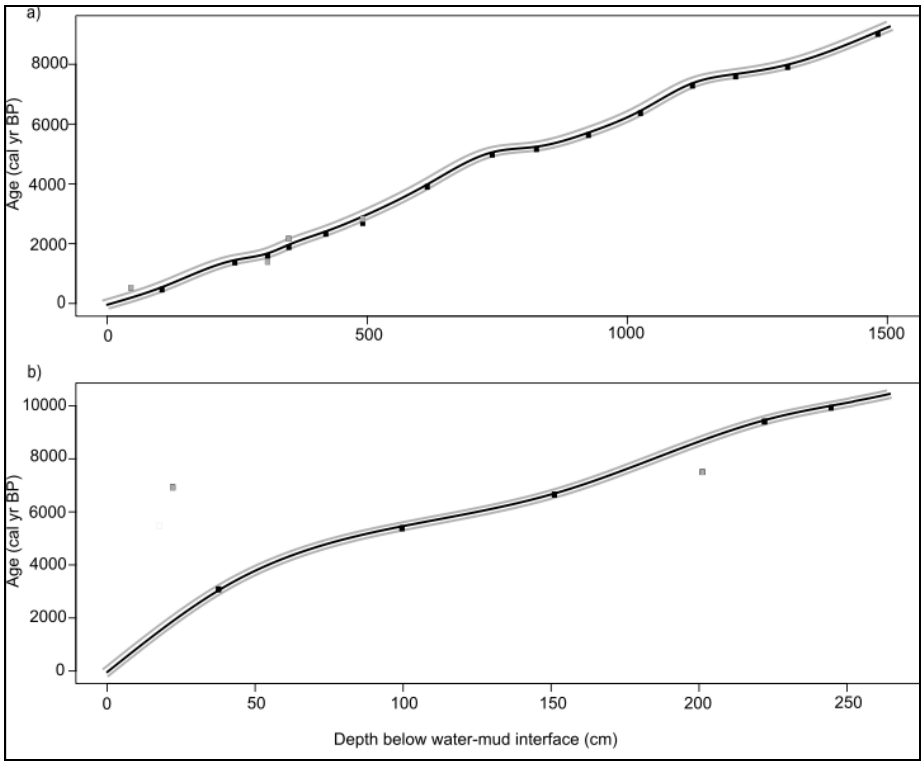


Figure 2.2: Age-depth model for a) L. Mosquito, and b) L. Cóndor. 95% Confidence intervals are shown in gray. Black squares are calibrated dates used to develop the models and gray squares are dates that were not included in the models. See Table 2.1 for more information.

The pollen diagram was grouped according to modern affinities of the probable pollen contributors. The resulting pollen groups were 'Rainforest taxa', 'Xerophytic forest taxa', and 'Shrubland / steppe taxa'. Taxa whose pollen percentages remained low (<2%) throughout the core were assigned to two pollen categories: 'Other rainforest taxa' (i.e. *Fuchsia* sp., *Drimys* sp., *Gevuina* sp., *Weinmannia* sp.) and 'Other shrubland/steppe taxa' (i.e. Solanaceae, Caryophyllaceae, *Galium* sp.). *Nothofagus dombeyi*-type pollen

includes the closed forest trees *N. dombeyi* and *N. pumilio*, and the disturbance-adapted open-forest tree *N. antarctica*. Cupressaceae pollen is attributed largely to *Austrocedrus chilensis*, although *Fitzroya cupressoides* and *Pilgerodendron uviferum* are potential long-distance contributors. Rhamnaceae pollen is likely to come from species of the genera *Discaria* sp. and/or *Colletia* sp.

A regional composite forest-to-steppe taxa ratio was constructed and interpreted as a measurement of the position of the forest-steppe ecotone relative to its mean Holocene position. Pollen percentages from L. Mosquito and L. Cóndor were normalized to stabilize the variance and standardized to prevent overrepresented taxa from dominating the signal, making the values comparable across the two sites. Forest-to-steppe taxa ratios were calculated with the transformed pollen data from each watershed. The composite record was constructed by combining the forest-to-steppe taxa ratios from both sites and extracting the low frequency component of the resulting time series with a smoothing cubic spline (smoothing parameter=0.675, lambda=3.457, equivalent degrees of freedom=10.644). Unless otherwise indicated, all the graphs and statistical analyses were performed with R (R Development Core Team, 2010).

Table 2.1: Radiocarbon and calibrated radiocarbon dates from Lago Mosquito and Laguna del Condor.

Core	Depth (cm)	Adjusted midpoint depth (cm)[a]	Lab no.	Material	^{14}C yr BP	Corrected ^{14}C yr error	Median probability age (cal yr BP)[b]
Lago Mosquito							
Mos03A	0-0.1	0.5	n/a	inferred	0		-53
Mos03A*	45-46	45.5	AA58860	sediment	645	33	606
Mos03A	105-106	105.5	AA58861	sediment	577	32	540
Mos03A	245-246	245.5	AA58862	sediment	1600	33	1444
Mos03A*	308-309	308.5	AA58874	charcoal	1610	150	1471
Mos03A	308-309	308.5	AA58863	sediment	1818	34	1670
Mos03A	349-350	349.5	AA58864	sediment	2066	34	1961
Mos03A*	348.5-349.5	349	AA58875	charcoal	2300	160	2245
Mos03A	420-421	420.5	AA58865	sediment	2421	34	2405
Mos03A	491-492	491.5	AA58876	charcoal	2699	76	2762
Mos03A*	491-492	491.5	AA58866	sediment	2859	35	2906
Mos03A	615-616	615.5	AA58867	sediment	3711	37	3978
Mos03A	740-741	740.5	AA59431	sediment	4495	40	5051
Mos03A	825-826	825.5	AA58868	sediment	4629	39	5237
Mos03A	925-926	925.5	AA58869	sediment	5038	39	5710
Mos03A	1025-1026	1025.5	AA58870	sediment	5714	47	6441
Mos03A	1125-1126	1125.5	AA58871	sediment	6499	43	7362
Mos03A	1208-1209	1208.5	AA58872	sediment	6892	45	7668
Mos03A	1308-1309	1308.5	AA58873	sediment	7218	51	7983
Mos03C	1482	1482	AA58903	wood	8200	47	9091
Laguna del Cóndor							
LC06A	0-0.05	0.5	n/a	inferred	0		-56
LC06A*	24-25	24.5	AA81902	charcoal	6195	49	7040
LC06A	39.5-40.5	40	AA84187	sediment	3057	38	3198
LC06A	101.5-102.5	102	AA81900	charcoal	4819	55	5501
LC06A	153-154	153.5	AA81904	charcoal	5993	55	6767
LC06A*	203-204	203.5	AA81901	charcoal	6818	64	7618
LC06A	263.5-264.5	224.5	AA81905	charcoal	8601	55	9524
LC06A	286-287	247	AA81467	sediment	8988	52	10,046
LC06A	305-306	261.5	AA81467	sediment	14,669	79	17,845

[a] Adjusted depths were used to calculate the age-depth model.
[b] Calibrated ages were based on CALIB 6.0 (Stuiver et al., 2005; http://radiocarbon.pa.qub.ac.uk/calib/calib.html).
*Not included in the chronologies.

Results

Lithology

The Lago Mosquito record –whose lithology was composed of a basal unit of laminated silty organic clay (1506 – 1421 cm), overlained by fine detritus gyttja (1421 – 0cm) with several tephras- was published by Whitlock et al. (2006). Given that the authors provide a detailed description of the cores (Mos03A and Mos03C), we only present the lithology of the LC06A core retrieved from L. Cóndor. For consistency, the radiocarbon dates from Mos03A and Mos03C were re-calibrated and a new chronology was developed for L. Mosquito using the same techniques employed in the L. Cóndor age model (Table 2.1).

Three lithological units were identified in the 289-cm-long LC06A core (Fig. 2.3). The basal unit, 289-279 cm depth, was composed of laminated clay. It was overlain by a decomposed 1.5-cm peat layer (279-277.5 cm depth) and a unit of fine-detritus gyttja (277.5-0 cm depth). The gyttja unit contained a black scoria tephra at 273-268.5 cm depth (CT-1), a thick white pumiceous tephra at 230.5-213.5 cm depth (CT-2), and a thin ash layer at 209-208 cm depth (CT-3).

Tephra CT-2 was composed of white pumice lapilli of rhyolitic composition (74% SiO2) and, according to the chronology proposed for L. Cóndor, was deposited at 9212 ± 100 cal yr BP. This tephra is correlated with a white to yellow rhyolite pumice fall layer exposed in several road cuts in the surroundings of the Chilean town of Chaitén that overlies a 9370-year-old pyroclastic surge deposit (Fig. 2.4, a). That pumice fall layer has

been the only reported deposit from Chaitén volcano prior to the 2008 eruption (Naranjo & Stern, 2004). The geochemistry of Tephra CT-2 matches the characteristic major, trace

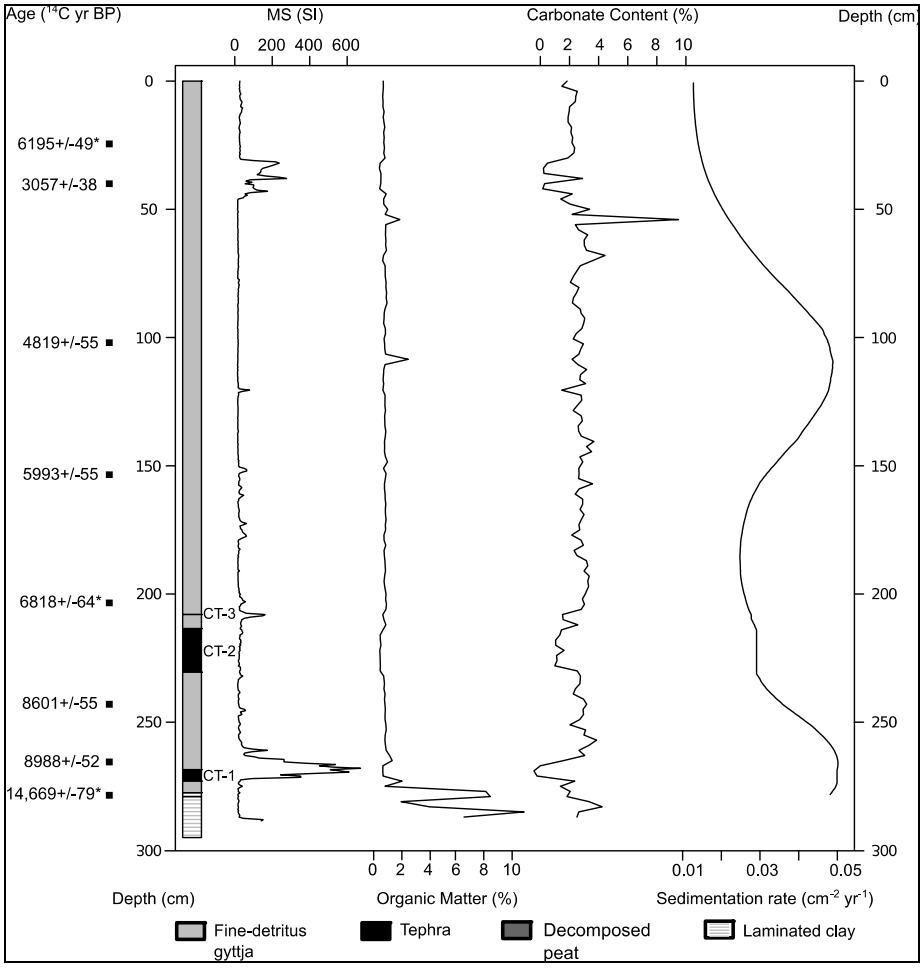


Figure 2.3: Lithologic, MS and LOI data, and sedimentation rates for the LC06A core. Radiocarbon dates are shown.

and REE composition of the lower white pumice tephra present in the L. Mosquito core (1506 cm depth; 9263 ± 101 cal yr BP). It also matches other rhyolitic tephra units found in sediment records and surface exposures in Argentina, including the white to yellow pumice lapilli tephra unit exposed in several road cuts along the Los Alerces National

Park (Fig 2.4, a and b), which has previously been attributed to the Michinmahuida volcano (Naranjo & Stern, 2004). The major element composition of Tephra CT-2 is similar to that of the Chaitén 2008 ash (Horwell et al., 2008, Alfano et al., 2010), indicating that this volcano, the only known source of rhyolitic products in the area, has likely been more active than previously reported.

Except for the tephra layers and a gyttja unit from 48 to 35 cm depth, which had low organic and carbonate content and high MS, the organic content of the sediment showed little variation, with values ranging from 0.4 to 4% (Fig. 2.3). Sediment carbonate content was highest in the laminated-clay unit (0.6-0.9 %), declined to 0.3 % at the clay-to-peat transition, and remained low in the gyttja unit (0.1-0.5 %). We suggest that the laminated clay unit was deposited in a periglacial environment, and the decomposed peat layer indicates the presence of a wetland soon after deglaciation.

The Pollen and Charcoal Records

Pollen zones were defined by visually inspecting the L. Cóndor pollen diagram (Fig. 2.5). The main features of the L. Mosquito vegetation and fire history are described in association with contemporaneous L. Cóndor pollen zones in order to infer regional patterns of vegetation and fire. Only the dominant pollen types are shown. For further details on the L. Mosquito pollen record, see Whitlock et al. (2006).

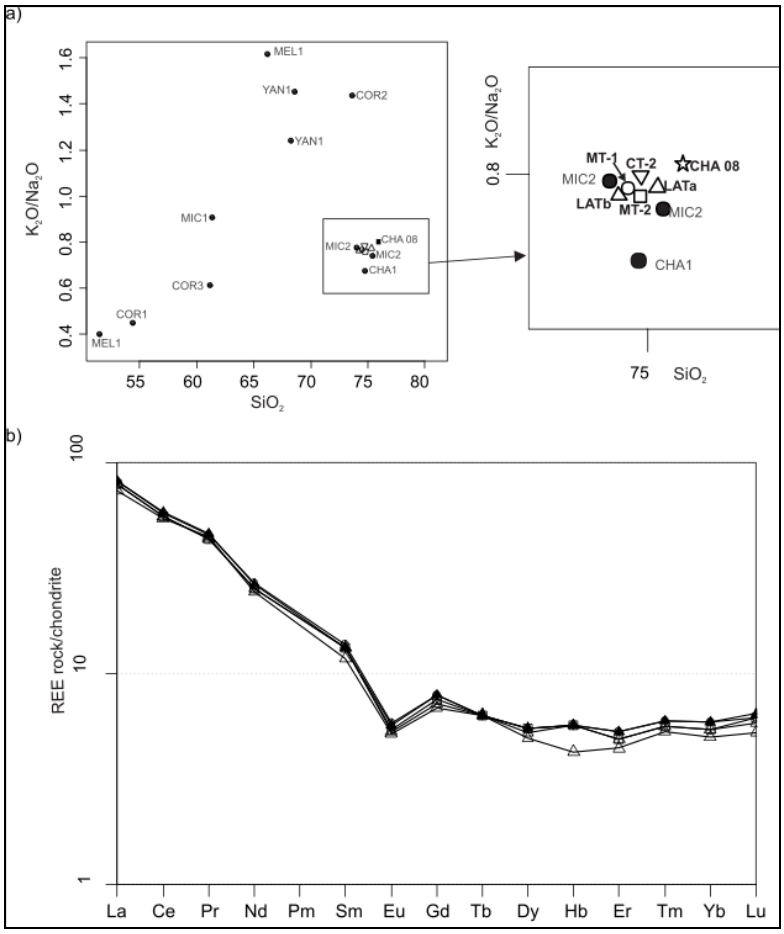


Figure 2.4: a) K_2O/Na_2O vs SiO_2 content of tephra layers (open symbols) in Lago Mosquito (MT) and L. Cóndor (CT-2) sediment cores, road-cuts in Los Alerces National Park (LAT), ashfall from the Chaitén 2008 eruption (CHA 08) and tephras from volcanoes from the study area (solid symbols CHA: Chaitén; COR: Corcovado; MEL: Melimoyu; MIC: Michinmahuida and YAN: Yanteles from Naranjo and Stern, 2004). Right: detail of the cluster of samples interpreted as derived from Chaitén volcano, including two tephras previously attributed to Michinmahuida volcano. b) Chrondrite-normalized REE patterns for selected rhyolitic tephra samples from L. Mosquito and L. Cóndor cores and road-cuts along Los Alerces National Park.

Zone Co-1 (249.5-210 cm depth; >9150 cal yr BP) was characterized by nonarboreal taxa, primarily Poaceae (>30%). Steppe/shrubland taxa, including Asteraceae (>3%), Chenopodiaceae (>10%) and Apiaceae (>10%), were abundant, and *Maytenus* sp. reached values of 9%. The assemblage resembled modern pollen spectra

from the steppe (Markgraf, 1981; Páez et al., 2001), and low PAR values (40-60 grains cm^{-2} yr^{-1}) indicate sparse vegetation cover. Background CHAR levels were high (0.7 particles cm^{-2} yr^{-1}), but charcoal peaks displayed a frequency of ca. 1 fire episode per 200 years, suggesting that local fire was not an important element of the ecosystem.

The vegetation that grew near L. Mosquito was very similar to that at L. Cóndor in terms of community composition. *Nothofagus dombeyi*–type pollen percentages were lower at L. Mosquito (20%) than at L. Cóndor, where they reached 45%. *N. dombeyi*-type pollen influx (not shown), however, was lower at L. Cóndor (<124 grains cm^{-1} yr^{-1}) than at L. Mosquito (<765 grains cm^{-1} yr^{-1}), suggesting that *Nothofagus* spp. are unlikely to have been present at L. Cóndor and the observed pollen is from sources to the west. Higher PAR values at L. Mosquito (200-480 grains cm^{-2} yr^{-1}) indicate that vegetation cover was greater than at L. Cóndor, implying a west-to-east productivity gradient. Background CHAR values of up to 48 particles cm^{-2} yr^{-1} suggest maximum Holocene biomass burning, and forest-to-steppe taxa ratios indicate the steppe reached its westernmost position during this interval.

Zone Co-2 (210-91.5 cm depth; 9150-5250 cal yr BP) featured a sharp increase in *N. dombeyi*-type (to 65%) at the bottom of the zone, and a rise of Cupressaceae (to 15%) at ca. 8500 cal yr BP. Steppe/shrubland taxa, Poaceae and Asteraceae were less abundant than before (<25%, <5% and <3%, respectively), and PAR values increased to 250 particles cm^{-2} yr^{-1}. The assemblage compares well with modern samples from sclerophyllous shrubland and steppe (Markgraf, 1981; Páez et al., 2001). Background CHAR, which initially was 1.5 particles cm^{-2} yr^{-1}, rose to 5 particles cm^{-2} yr^{-1} at 6250 cal

yr BP and remained high for the following 2500 years, implying a trend towards increased biomass burning. A similar pattern was observed for fire-episode frequency, as charcoal peaks gradually increased in frequency from near-absence at the bottom of the zone to 1 episode per 100 years at 6250 cal yr BP.

Following an initial increase in *N. dombeyi*-type pollen percentages at ca. 8900 cal yr BP, the L. Mosquito pollen assemblage suggests a shrubland with elements from the forest and significant areas of steppe. Background CHAR at L. Mosquito decreased from 48 particles cm^{-2} yr^{-1} at the bottom of the zone, to 5 particles cm^{-2} yr^{-1} at 6500 cal yr BP, the same values registered at L. Cóndor at this time. These CHAR levels indicate decreased biomass burning, and total-to-grass charcoal ratios, ranging between 0.01 and 0.39, suggest primarily woody fuels. An eastward expansion of the forest can be inferred from forest-to-steppe ratios.

Zone Co-3 (91.5-27 cm; 5250-2200 cal yr BP) contained high values of open-forest taxa, such as Cuppresaceae (up to 17%) and Rhamnaceae (7%), and lower amounts of *N. dombeyi*-type pollen (<55%) than the previous zone. The highest percentages of steppe/shrubland taxa (>7%) in the record were observed in this zone. This assemblage is comparable to modern pollen samples from the *A. chilensis* forest/steppe ecotone (Markgraf, 1981; Páez et al., 2001). PAR values declined at the base of the zone (to 60 grains cm^{-2} yr^{-1}) and remained low until the top of the zone, indicating open vegetation prevailed throughout the period. Background CHAR and fire-episode frequency were low, reaching zero values between 3500 and 2700 cal yr BP, implying negligible fire activity for the period.

The L. Mosquito pollen assemblage featured a trend towards decreased *N. dombeyi*-type pollen and increased Poaceae as well. Increases in Cupressaceae pollen mark the beginning of local *A. chilensis* expansion into forest. Grass-to-total charcoal ratios suggest a rapid shift from canopy to surface fires at 4500 cal yr BP. Forest-to-steppe taxa ratios suggest a westward steppe expansion into the forest.

Zone Co-4 (27-0 cm depth; 2200 cal yr BP to present) had higher pollen values of *N. dombeyi*-type (>65%) and epiphytic *Misodendrum* sp. (to 6%), and lower values of Rhamnaceae (less than 1%), Poaceae (< 35%) and other shrubland/steppe taxa (less than 1%) than the previous zone. PAR increased abruptly with respect to the previous zone, reaching the maximum values of the record (600 grains cm^{-2} yr^{-1}) at the top. Comparison with modern pollen assemblages suggests an open xerophytic forest (Markgraf, 1981; Páez et al.2001). Background CHAR remained very low (<1 particles cm^{-2} yr^{-}) and charcoal peaks were virtually absent, indicating local fires were rare. *Austrocedrus chilensis* populations west of the L. Mosquito area are inferred from the increase of Cupressaceae pollen at the expense of *N. dombeyi*-type in the L. Mosquito record. During the last 200 years, *Rumex* sp. (*R. acetosella*-type), and *Pinus* spp. (not shown) were present in small amounts, reflecting the effects of European settlement on vegetation composition.

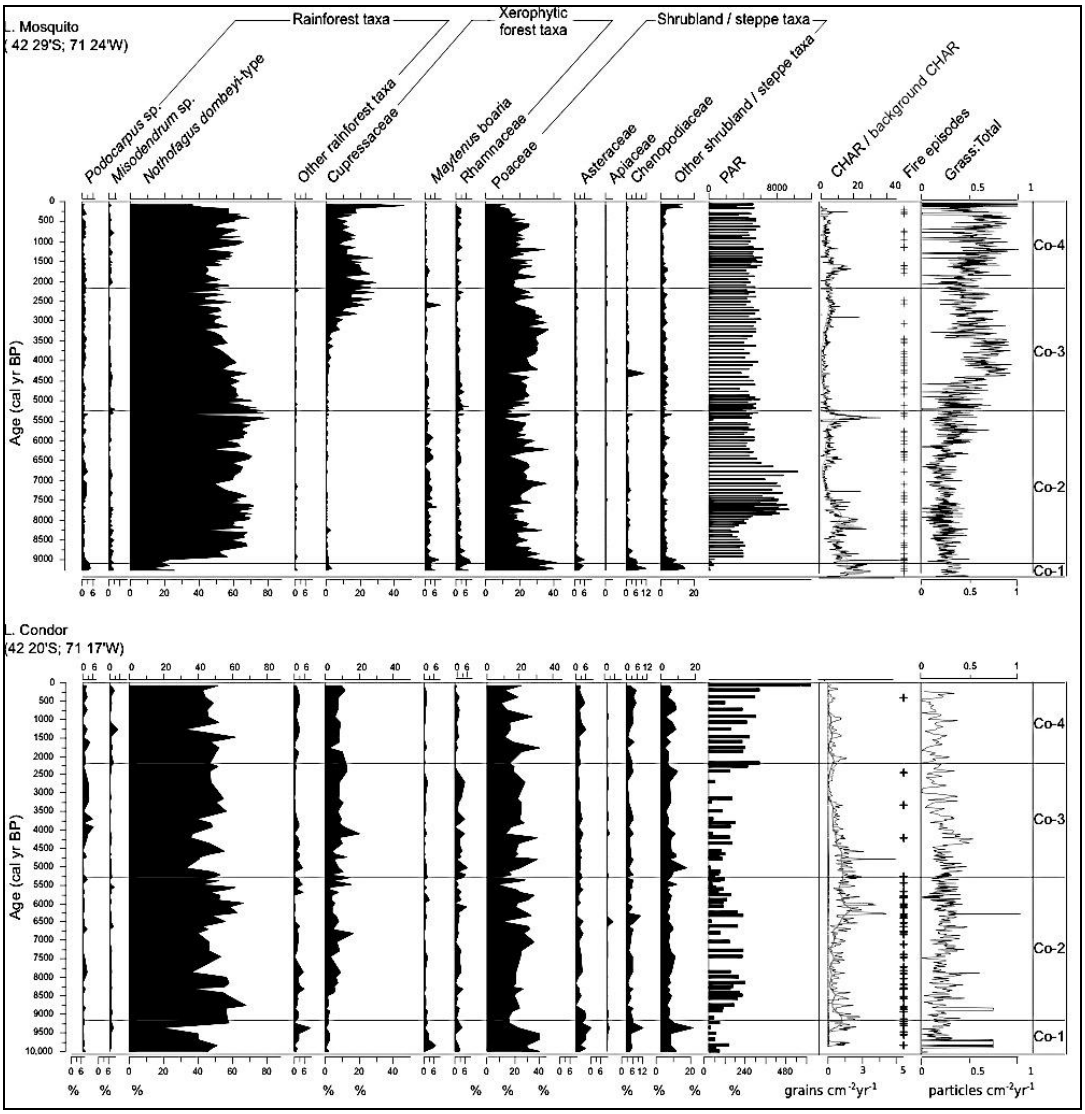


Figure 2.5: Lithology, selected pollen percentages, PAR, CHAR, background CHAR, local fire episodes and grass-to-total charcoal ratio for L. Mosquito, and L. Cóndor.

Discussion

Holocene vegetation, climate and fire history of the forest-steppe ecotone at lat. 42°S, based on the pollen and charcoal records at Lago Mosquito and Laguna del Cóndor, is summarized in Figure 2.6. A cubic spline was fit to the forest-to steppe taxa records from both sites to develop a composite record, which was used to infer the west-

east position of the ecotone relative to its mean Holocene location. Positive anomalies relative to the mean position for the last 10,000 years indicate eastward shifts of the ecotone; negative anomalies represent westward expansions of steppe at the expense of forest. The paleovegetation reconstruction was compared with changes in fire frequency and fuel composition at each site to understand the role of fire in promoting ecotonal shifts. In addition, the climate implications of the vegetation and fire regime changes in Mosquito-Cóndor region (Fig. 2.6) are discussed in light of other paleoclimatic records from southern South America.

Early Holocene (>9000 cal yr BP)

Prior to 9000 cal yr BP, the forest-steppe ecotone was located west of its mean Holocene position, such that both L. Mosquito and L. Cóndor supported steppe vegetation (Figs. 2.5 and 2.6) dominated by grasses, Chenopodiaceae, Asteraceae and Apiaceae. The pollen data suggest drought-tolerant shrubs and trees, such as Rhamnaceae, *Maytenus* sp. and possibly *Nothofagus Antarctica*, grew in the area, probably on south-facing slopes and cool deep Andean valleys, where the water balance would have been more positive. These re-sprouting shrubs burned frequently at L. Mosquito, the westernmost site, and less often at L. Cóndor, likely reflecting lower fuel loads and/or fuel discontinuity associated with sparser vegetation in the east (Huber et al., 2004). Along with high fire activity, *Nothofagus* spp. began to expand at both sites at 9000 cal yr BP, coupled with a reduction of steppe taxa, suggesting that summers were arid enough to dry fuels and support fires, while winter moisture was sufficient for forest expansion (Markgraf et al, 2003).

Evidence of dry summers in the early Holocene has been found throughout Patagonia. East of the Andes, vegetation was structurally more open than today, with steppe-tundra in the south (lat. 52°S; Fesq-Martin et al., 2004), parkland between lat. 49-54°S (Huber et al., 2004), xerophytic forest at lat. 41° S (Whitlock et al., 2006) and steppe in the north (lat. 40°S; Markgraf and Bianchi, 1999). Patagonian records between lat. 40 and 56°S on both sides of the Andes show high fire activity (Whitlock et al., 2007), and Chilean sites between lat. 35 (Jenny et al., 2002) and 40°S (Bertrand et al., 2008) indicate lower-than-present lake levels. Regional aridity has been attributed to the effects of higher-than-present winter and annual insolation (Berger and Loutre, 1991) on temperature and atmospheric circulation patterns. Increased annual insolation led to higher temperatures and evapotranspiration. Reduced seasonality weakened and/or latitudinally shifted the SW and storm tracks south of their present position (Moreno et al., 2010; Whitlock et al., 2007), resulting in decreased precipitation throughout Patagonia. In the Mosquito-Cóndor region, the early onset of the fire season combined with the high flammability and rapid regrowth of steppe shrubs (Mermoz et al., 2005) would have made the ecotone especially prone to fire.

Middle Holocene (9000 - 5250 cal yr BP)

During the middle Holocene, the forest-steppe ecotone in the Mosquito-Cóndor region was located east of its early Holocene position and dominated by scherophyllous shrubs, likely as a consequence of lower-than-before temperatures and /or higher effective moisture. PAR indicates that vegetation cover was greater at L. Mosquito than at L. Cóndor, suggesting a west-to-east vegetation gradient, with more productive

communities towards the west. Higher charcoal peak frequency and background CHAR at L. Mosquito indicate that fires episodes (Figs. 2.5 and 2.6) were more frequent and fuel biomass was greater west of the Mosquito-Cóndor area. Low grass-to-total charcoal ratios suggest that such fires were fueled by woody vegetation.

Throughout the middle and southern latitudes of Chile and Argentina, the onset of cooler and/or effectively wetter-than-before conditions in the middle Holocene has been inferred from multiple climate proxies and attributed to changes in insolation. Decreasing annual insolation and amplification of the seasonal cycle of insolation (Berger and Loutre, 1991) increased seasonality and resulted in lower-that-before annual temperatures. As a consequence, sedimentological and/or geochemical evidence from lat. 35 (Jenny et al., 2003) and 40°S (Bertrand et al., 2009) suggests higher-than-before lake levels, and high-resolution pollen and charcoal records document forest expansions, coupled with reduced fire activity throughout Patagonia (Abarzúa and Moreno, 2008; Markgraf et al., 2007; Moreno, 2004; Whitlock et al., 2007; Wille and Schaebitz, 2009). Cooler and/or effectively wetter conditions explains the advance of mountain glaciers in the middle- and high-latitude Andes (Douglass et al., 2005; Porter, 2000), as well as sea-ice expansion and sea-surface cooling in the Atlantic sector of the Southern Ocean (Lamy et al., 1999; Liu et al., 2003).

Shifts in the relative position of the forest-steppe ecotone in the Mosquito-Cóndor region suggest a two-step increase in effective moisture during the middle Holocene (Fig. 2.6). The first step occurred at 8500 cal yr BP and is inferred from the eastward expansion of *Nothofagus* spp. from L. Mosquito and the higher levels of *Austrocedrus*

chilensis at L. Cóndor, inferred from the rise in Cupressaceae pollen from previously negligible levels (<6%). The second step at 5500 cal yr BP is based on the increase of *Nothofagus* spp. near L. Cóndor, suggesting an advance of forest into the steppe.

The history and ecology of *Austrocedrus chilensis* in this region warrant special attention. Cupressaceae pollen percentages rose to 15 % at L. Cóndor at 8500 cal yr BP, and comparison with modern pollen samples (Markgraf, 1981; Páez et al., 2001) indicates that these values came from small populations. Palynological data (Markgraf, 1980, 1983, 1984, 1987; Markgraf and Bianchi, 1999; Markgraf et al., 1986) and genetic evidence (Pastorino and Gallo, 2002) suggest that *A. chilensis* survived the last glaciation east of the Andes in multiple small refugia, possibly east of its present distribution. Its middle-Holocene presence at L. Cóndor and its delayed appearance at L. Mosquito at 3500 cal yr BP are consistent with postglacial expansion westward from the steppe margin.

Present-day establishment patterns of *Austrocedrus chilensis* vary according to habitat type, associated species, and the influence of fuel cover on fire regimes. At mesic sites, where competition from *Nothofagus* sp. and fire-resistant shrubs is intense, high-severity fire effectively precludes establishment of *A. chilensis* (Veblen et al., 1995). At drier sites, low-severity fire limits *A. chilensis* seedling establishment, but the trees become more resistant to patchy surface fires as they mature. Dendroecological studies reveal that discontinuous age structures are characteristic of *A. chilensis* stands close to the forest-steppe ecotone (Kitzberger et al., 1997). The age gaps reflect intermittent opportunities for seedling establishment during periods of above-average moisture

availability (Villalba and Veblen, 1997). Increased effective moisture during the growing season at 8500 cal yr BP may have allowed a small *A. chilensis* population to establish, possibly in the rocky hills between the two sites or in the L. Cóndor watershed, whereas high severity fires may have limited expansion westward to L. Mosquito and the eastern Andes before 3500 cal yr BP.

Late Holocene (5250 cal yr BP - Present)

Between 5250 and 3000 cal yr BP, steppe vegetation was present in the Mosquito-Cóndor region and the forest-steppe ecotone was sharply defined by the pollen dominance of *Nothofagus dombeyi*-type and Rhamnaceae and low levels of Cuppresaceae. The westward expansion of steppe taxa (Fig. 2.6) implies colder conditions and/or a loss of growing season moisture, especially from 3700 to 3000 cal yr BP. An associated rise in magnetic susceptibility and decreased sediment organic-matter content at L. Cóndor (48 cm depth, 3658 cal yr BP to 35 cm depth, 2844 cal yr BP; Fig. 2.3), suggest increased inorganic input to the lake, possibly as a consequence of greater windiness or more surface run-off from exposed ground.

Evidence of cooler conditions between 3700 and 3000 yr BP is found throughout the mid and high latitudes (lat. 30-53°S), including sedimentological data that indicate low lake paleoproductivity (Bertrand et al., 2008), and paleoecological records that suggest expansions of cold resistant taxa (Villagrán and Varela, 1990; Heusser, 1990, 1995). This period also marks extensive glaciation in the Andes (Douglas et al., 2005; Grosjean et al., 1997, 1998; Mercer, 1998; Moy et al., 2009;). Cooler conditions and

year-round precipitation may have been caused by a northwards migration of the winter polar front and SW from their middle Holocene position (van Geel et al., 2000).

The last 3000 years are characterized by the eastward expansion of the forest-steppe ecotone in the Mosquito-Cóndor region. The expansion was mainly caused by an increase of *Austrocedrus chilensis* population size at both sites, following a shift in the fire regime from intense woody fires to surface fires (Figs. 2.5 and 2.6). This directional change in the position and composition of the ecotone is consistent with wetter springs and/or summers than before that would have promoted *A. chilensis* expansion, as well as surface fire regimes. Increased effective moisture during the growing season has also been inferred from changes in forest composition in the mid-latitudes west of the Andes (Abarzúa and Moreno, 2008; Haberle and Bennett, 2004, Villagrán and Varela, 2000), suggesting that the climate change at lat. 42°S could have resulted from intensified westerly wind activity (Moy et al., 2009).

During the period of European settlement (< ca.1800 AD), a decline of *Nothofagus dombeyi*-type pollen, the appearance of non-native pollen taxa and increased CHAR and/or fire episode frequency have been registered in sediment records throughout Patagonia (Abarzúa and Moreno, 2008; Haberzettl et al., 2006; Huber and Markgraf, 2003; Maidana et al., 2007; Wille et al., 2007). In contrast, neither L. Cóndor or L. Mosquito show pollen or charcoal changes that suggest a dramatic decline of closed-forest taxa or major changes in the fire regime during the last 200 years. Nonetheless, trace amounts of pollen from non-native species such as *Rumex* sp. (*R. acetosella*-type) and *Pinus* spp. were identified in the L. Mosquito record, and the large population of

sweet briar rose (*Rosa rubiginosa*) currently growing at the site suggests that agriculture, forest clearance, and intensive grazing had significant effects in this region, just as they did across the forest-steppe ecotone of Patagonia (Huber and Markgraf, 2003).

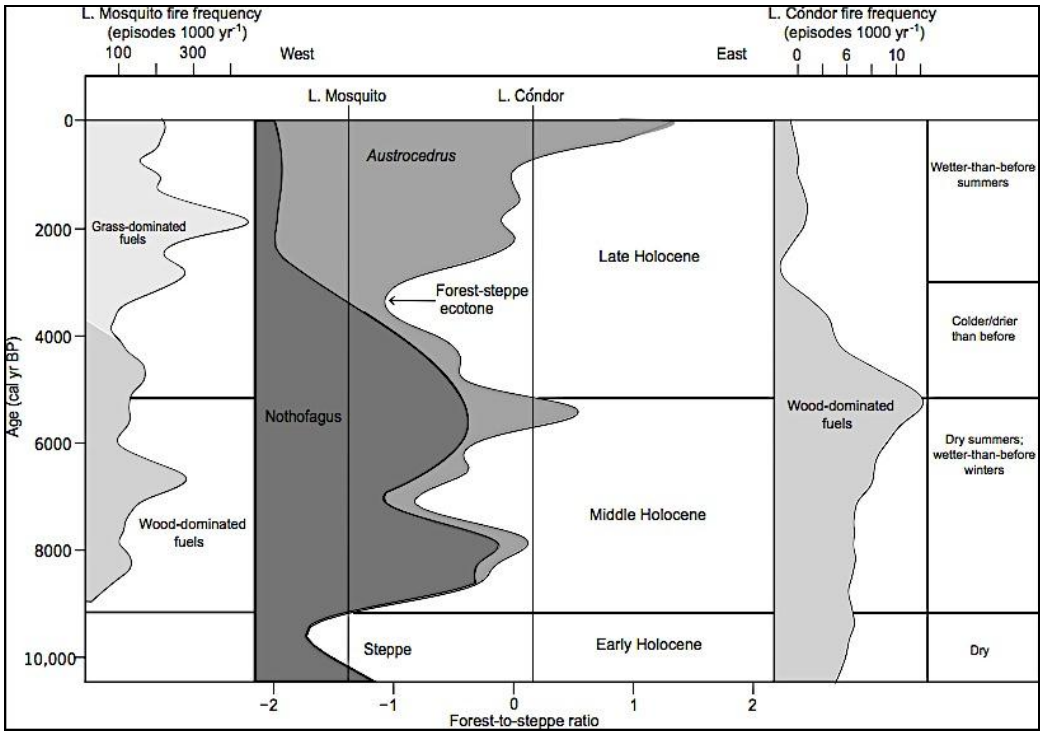


Figure 2.6: Position of the forest-steppe ecotone as inferred from a composite forest-to-steppe taxa ratio record. Present-day position of L. Mosquito and L. Cóndor relative to the ecotone is based on modern forest-to-steppe taxa ratios. The proportion of *Nothofagus* and *Austrocedrus* pollen to total forest taxa pollen, and the fire episode frequency records from both sites are shown.

Conclusions

- During the early Holocene prior to 9000 cal yr BP, the forest-steppe ecotone was located west of its Holocene mean position. Lower-than-present seasonality led to the early onset of the fire season. The high fuel flammability in the western region

(west of L. Mosquito) resulted in frequent fires, but at the eastern limit (near L. Cóndor), low vegetation cover could not support frequent fires, even though the climate was suitable.

- At ca. 9000 cal yr BP, *Nothofagus* spp. and other forest taxa expanded into steppe, resulting in an eastward shift of the ecotone. This change in vegetation is reflected in the fire regime: fire frequency and area burned increased in the study area and also regionally. The middle-Holocene fire and vegetation suggests that summers were arid enough to support fires at the forest-steppe ecotone, and winter moisture was sufficient for *Nothofagus* spp. to expand. About 500 years later, *Austrocedrus chilensis* established near L. Cóndor, probably as part of a westward migration from steppe margin glacial refugia. It is possible that increased effective moisture allowed a small *A. chilensis* population to persist in the rocky hills between the two sites or in the L. Cóndor watershed for 5000 years before its expansion westward to L. Mosquito.
- The 5250 to 3000 cal yr BP period was cold and/or dry, as evidenced by the contraction of forest to the west. Cooling is inferred from marine and terrestrial records in the southern middle and high latitudes and related to a northward shift in the polar front and SW.
- The last 3000 years are characterized by an eastward expansion of the forest-steppe ecotone, with dominance of *Austrocedrus chilensis*. This shift indicates a recent trend towards wetter conditions. European settlement is reflected in the establishment of non-native and disturbance-adapted species.

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CHAPTER THREE

CLIMATIC AND LOCAL CONTROLS OF LONG-TERM VEGETATION DYNAMICS IN NORTHERN PATAGONIA (LAT. 41°S)

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, and 4

Author: Virginia Iglesias

Contributions: Supported this research under a LacCore student grant, defined the experimental design, participated in fieldwork, described the sediment cores, measured magnetic susceptibility, loss-on-ignition and other lithological properties of the cores, counted charcoal and pollen samples from L. Padre Laguna and pollen samples from L. Huala Hué, analyzed the data and wrote the manuscript.

Co-Author: Cathy Whitlock

Contributions: Supported this research under the National Science Foundation grants ATM-0714061 and OISE-0966472, helped define the experimental design, participated in fieldwork, discussed the results and implications and edited the manuscript.

Co-Author: María Martha Bianchi

Contributions: Participated in fieldwork, counted pollen samples from L. Huala Hué and commented on the manuscript.

Co-Author: Gustavo Villarosa

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Abstract

Patagonian vegetation has dramatically changed in composition and distribution over the last 16,000 years. Although patterns of vegetation change are relatively clear, our understanding of the processes that produce them is limited. High-resolution pollen and charcoal records from two lakes located at lat 41°S provide new information on the postglacial history of vegetation and fire activity at the forest-steppe ecotone, and help clarify the relative importance of local and regional drivers of late-Holocene ecological change. Our results suggest that late-glacial parkland was colonized by shrubs at ca. 11,200 cal yr BP and this vegetation persisted until 4900 cal yr BP, when increased humidity allowed for the establishment of *Nothofagus* forest. The late Holocene is characterized by oscillations in forest dominance largely driven by changes in humidity, possibly associated with the onset or strengthening of ENSO. In the last 4900 cal years, humid periods (4900-3800 cal yr BP, 2850-1350 cal yr BP) have promoted *Nothofagus* forest, and drier times (3800-2850 cal yr BP, 1350-450 cal yr BP) have favored *Austrocedrus* expansion. At intermediate-moisture levels, however, the lower forest supported both taxa, and fire became an important control of community composition, with severe, infrequent fires facilitating *Nothofagus* regeneration and high fire frequency and intensity supporting *Austrocedrus*.

Introduction

Paleoenvironmental records from the mid-latitudes (38-42°S) show a trend from early-Holocene aridity towards more humid and variable conditions during the late

Holocene (e.g., Markgraf et al., 2003; Fletcher and Moreno, 2011). These long-term climate changes are attributed to variations in seasonal and annual insolation (Whitlock et al., 2007), the location and strength of the Southern Westerlies (Lamy et al., 2001), and the late-Holocene onset and/or strengthening of El Niño Southern Oscillation (ENSO; Moy et al., 2002). Plant populations responded to regional climate variations by altering their range and density, which, in turn, resulted in shifts in vegetation composition and structure. For example, the late-glacial steppe that was widespread along the eastside of the Andes was gradually colonized by shrub and tree taxa in response to rising temperature and humidity (Markgraf et al., 2007). The early Holocene was characterized by higher-than-present annual and winter insolation and weakened southern westerlies, and the eastern flanks of the Andes supported open, fire adapted woodland. Present-day *Nothofagus* and *Austrocedrus* forests developed ca. 5000 cal yr BP (Whitlock et al., 2006; Bianchi and Ariztegui, in press, Iglesias et al., 2012, Chapter 2), during a time of declining annual insolation and the onset or strengthening of ENSO.

Although long-term vegetation dynamics of the eastern Andes are relatively clear, our understanding of the proximal and distal mechanisms that produce them is limited. In Patagonia, modern plant communities are distributed along a steep west-to-east precipitation gradient, suggesting that climate exerts a significant control over the regional-scale variability in vegetation composition. However, historical studies suggest that natural and anthropogenic disturbances amplify or override the effects of climate on ecosystem processes (Mermoz et al., 2005). At the Patagonian forest-steppe ecotone, for example, decades of fire suppression have allowed fire-sensitive *Austrocedrus* to expand

eastwards into steppe in spite of the relative stability of the climate (Veblen and Markgraf, 1989). This expansion indicates that patterns in ecological communities are determined by a variety of drivers and mechanisms, operating over a range of spatio-temporal scales (Levin, 1992). Understanding ecosystem dynamics requires disentangling regional drivers from more-local feedbacks involving vegetation, fire and human activities.

We present high-resolution pollen and charcoal records from two small low-elevation lakes located in close proximity in the eastern slopes of the Patagonian Andes at the forest-steppe ecotone (Laguna Huala Hué, lat 41°30'24''S, long 71°30'32''W, 849 m elevation; and Laguna Padre Laguna, lat 41°21'34''S, long 71°30'29''W, 1280 m elevation). Our objectives are to (1) reconstruct the postglacial environmental history at the lower forest border; and (2) compare these data with those from nearby sites to identify the relative importance of local and regional drivers of late-Holocene ecological change (Huber et al., 2004). The last 5000 years are of special interest because they are characterized by the establishment of modern climates and plant communities (Moy et al., 2002; Whitlock et al., 2006). By focusing on this period, we expect to better understand the dynamics of modern ecosystems.

Study Area

The study sites are located in the drainage of the Río Manso, south of Volcán Tronador (Fig. 3.1). Most of the large lakes in the Río Manso drainage are dammed by recessional moraines from eastward-flowing late-Pleistocene glaciers. L. Huala Hué, however, is blocked on its east side by a prominent glacial deltaic complex associated

with late-Pleistocene meltwater from ice complexes from the north (Caldenius, 1932). L. Padre Laguna, located 15 km south of L. Huala Hué, is dammed by a broad postglacial alluvial fan.

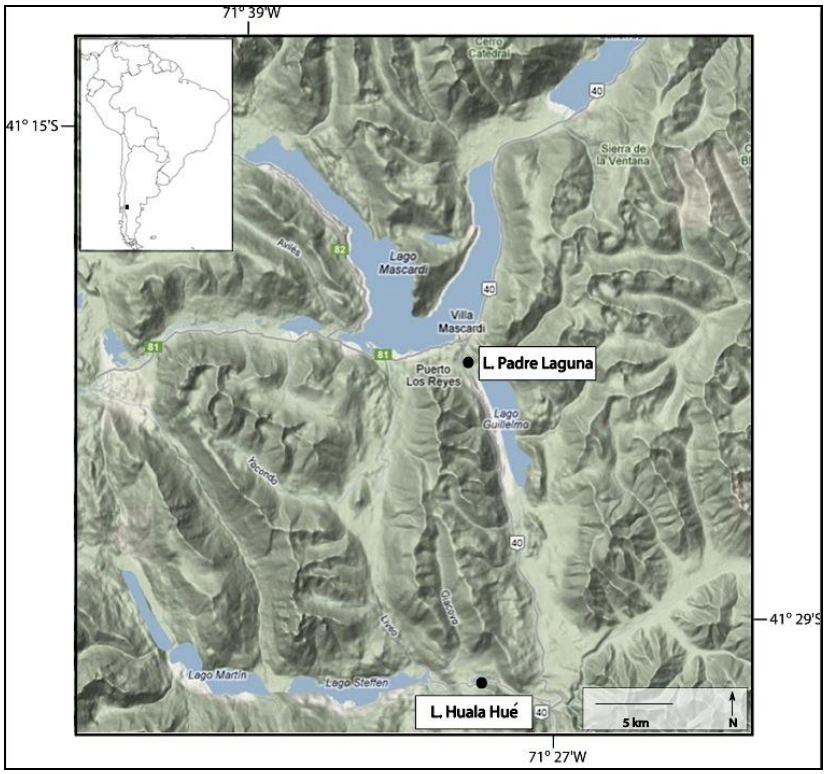


Figure 3.1: Location of L. Huala Hué and L. Padre Laguna.

Mean annual temperatures range from 12°C in the intermountain valleys to 6°C in subalpine forests near the treeline (Villalba et al., 2003). Precipitation is related to frontal systems associated with Pacific cyclones that migrate eastwards along the storm tracks. Annual and seasonal precipitation variability is largely explained by latitudinal shifts of the storm tracks resulting from changes in the strength and position of the Southern Westerlies, which are affected by the Southern Annular Mode and ENSO (Fogt and Bromwich, 2006).

The uplift of low-level winds over the western flanks of the Andes produces continental orographic precipitation, and forced subsidence on the eastern side causes an adiabatic warming of the air masses, leading to dry conditions in eastern Patagonian (Garreaud et al., 2008). As a consequence, precipitation decreases from 4000 mm yr^{-1} in the Chilean Andes to 700 mm yr^{-1} at San Carlos de Bariloche (Villalba et al., 2003).

The west-to-east precipitation gradient (>2800 mm yr^{-1} at the crest of the Andes; <300 mm yr^{-1} in the Argentine steppe) results in a dramatic vegetation transition from humid forests to xerophytic forests to steppe on the eastern flanks, within a distance of <50 km. Above 1500 m elevation on the eastern side, deciduous *Nothofagus pumilio* dominates the modern forest, although its limit has been strongly modified by burning in the last 150 years. Between 1500 and 1000 m elevation, a dense forest of evergreen *Nothofagus dombeyi* is present. From 1000 to 800 m elevation, *Austrocedrus chilensis* grows in mixed stands with *N. dombeyi*, and at lower elevations, it forms pure stands. Xerophytic shrubs and trees, such as *Maytenus* spp, Rhamnaceae (e.g. *Colletia*, *Discaria*) and *Nothofagus antarctica*, are abundant at lower treeline (ca. 700 m elevation). Below treeline, the North Patagonian steppe is characterized by a matrix of cushion shrubs (e.g., *Mulinum spinosum*), tussock grasses (e.g., *Stipa speciosa, Festuca pallenscens*) and herbs (e.g. Asteraceae, Euphorbiaceae).

Methods

A modified Livingston piston sampler was used to take a 731-cm-long core (HH08B) along the west margin of L. Huala Hué, and a 397-cm-long core from the center of L. Padre Laguna (LCar08B). Core segments were wrapped in plastic wrap and

aluminum foil and transported to LacCore Facility, University of Minnesota, for lithologic characterization. High-resolution magnetic susceptibility (SI) was measured at 0.5 cm contiguous intervals in the core to assess changes in inorganic allochthonous sediment input (Gedye et al., 2000). Gamma density (kg cm^{-3}), measured at 1-cm contiguous intervals, was used as an indicator of lithology and porosity changes. Organic and carbonate contents (% dry weight) were determined from weight-loss after ignition at 550° and 900°C of 1 cm^3 samples taken at 1.5 cm intervals (Dean, 1974).

Cores were cut in half, described, subsampled, and archived at the Paleoecology Laboratory at Montana State University. Pollen samples of 0.5-cm^3 volume were taken at intervals that spanned between 15 and 250 years and prepared according to the methods of Bennett and Willis (2001). Pollen identification was based on published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978) and performed at magnifications of 250 and 400x. Pollen percentages and pollen accumulation rates (PAR, grains cm^{-2} yr^{-1}) were calculated based on terrestrial pollen types. Riparian and aquatic taxa percentages were based on a sum of all pollen and spores. The pollen diagrams were plotted with C2 software (Juggins, 2007) and subdivided in pollen zones identified by CONISS (Grimm, 1987).

For this study, only the dominant pollen types are discussed. *Nothofagus dombeyi*-type pollen includes *N. dombeyi, N. pumilio*, and *N. antarctica*. Cupressaceae pollen is attributed largely to *Austrocedrus chilensis*, although rainforest taxa (*Fitzroya, Pilgerodendron*) may have been long-distance contributors. Other taxa were grouped into ecological units: Rainforest taxa (e.g., *Gaulteria*, *Hydrangea*, *Podocarpus*,

Saxegothaea); shrubland (e.g. *Schinus*, Rhamnaceae, *Berberis, Lomatia*, *Maytenus*); steppe (e.g., *Acaena*, *Ephedra*, Chenopodiaceae); and riparian and aquatic taxa (e.g., *Caltha*, Cyperaceae, *Myriophyllum).*

In order to provide a local signal of fire, large charcoal particles (>125 μm in diameter) were extracted from 2-cm^3 samples at contiguous 0.5-cm intervals with standard sieving methods (Whitlock and Larsen, 2001). Grass and wood charcoal particles were tallied separately. A grass-to-total charcoal ratio was used to infer the relative contribution of grass and woody fuels to total biomass burned. Charcoal time series were interpolated to the median resolution of the cores (15 years, L. Huala Hué; 12 years, L. Padre Laguna). Charcoal concentrations and deposition times were calculated and converted to charcoal accumulation rates (CHAR, particles cm^{-2} yr^{-1}). Smoothing techniques (a locally-weighted 1000-year median in the L. Huala Hué record; 750-year lowess smoother robust to outliers in the L. Padre Laguna record) were used to separate the long-term trends (i.e., background CHAR) in the time series from the positive residuals (i.e., charcoal peaks). The latter are inferred to represent fire episodes (i.e., one or more fires occurring during the time span of the peak; Higuera et al., 2009). Fire-episode frequency was calculated in 1000 years windows. The suitability of the records for fire-episode identification was assessed with the signal-to-noise index (SNI) proposed by Kelly et al. (2011). At both sites, 1000-year bandwidths were used to calculate the SNI. Except for the periods 6240-6020 (2.6<SNI<2.9) and 3620-2720 cal yr BP (0.19<SNI<2.9) at L. Huala Hué, and 1200-700 cal yr BP (0.7<SNI<3) at L. Padre

Laguna, the SNI (3<SNI<51) was well above the value expected from records without a signal.

Chronologies were developed from a series of AMS dates (Table 3.1), which were calibrated using CALIB 6.0.1 (Stuiver et al., 1993). For modeling purposes, depths were adjusted by removing volcanic ashes >1 cm in thickness on the assumption that these tephra layers were deposited in a negligible span of time. Age-depth models (Fig. 3.2)

Table 3.1:Radiocarbon and calibrated radiocarbon dates from L. Huala Hué and L. Padre Laguna.

Core	Depth (cm)	Adjusted depth (cm)	Lab no.	Material	^{14}C yr BP	Corrected ^{14}C error	Median probability age (cal yr BP)[b]
L. Huala Hué							
HH08B	0	0	n/a	inferred	n/a	n/a	-58
HH08B	218	214	AA85284	charcoal	2932	37	3094
HH08B	291	277	AA85285	charcoal	4200	37	4732
HH08B	318	303	75270	charcoal	4770	35	5718
HH08B*	342	327	AA85286	bark	386	34	451
HH08B	421	407	AA85287	charcoal	8690	50	9642
HH08B	426	411.5	75271	charcoal	8740	40	9712
HH08B*	475	457	AA85288	leaf	7651	47	8446
HH08B	533	505	AA85289	charcoal	10210	310	11916
HH08B	568	538	AA85290	charcoal	10572	56	12620
HH08B	730.5	700.5	AA83067	bulk sediment	11293	63	13180
L. Padre Laguna							
LCar08B	0	0	n/a	inferred	n/a	n/a	-58
LCar08B	154.5	154.5	75280	charcoal	1890	30	1772
LCar08B	245.5	224.5	75268	charcoal	2290	100	2228
LCar08B	291	267.8	25769	charcoal	2760	30	2851
LCar08B	396	374	AA85086	Bulk sediment	4393	44	4963

Adjusted depths were used to calculate the age-depth models. Only true depths are referred to in text.
[b] Calibrated ages were based on CALIB 6.0 (Stuiver et al., 2005; http://radiocarbon.pa.qub.ac.uk/calib/calib.html).
*Not included in the chronologies.

were constructed with a cubic smoothing spline and bootstrap approach (2000 iterations) that allowed each date to influence the age model through the probability density function of the calibrated age (Higuera et al., 2009). All depths hereafter are given in true core measurements, not adjusted depths. Unless indicated otherwise, analyses were performed with R (R Development Core Team, 2010).

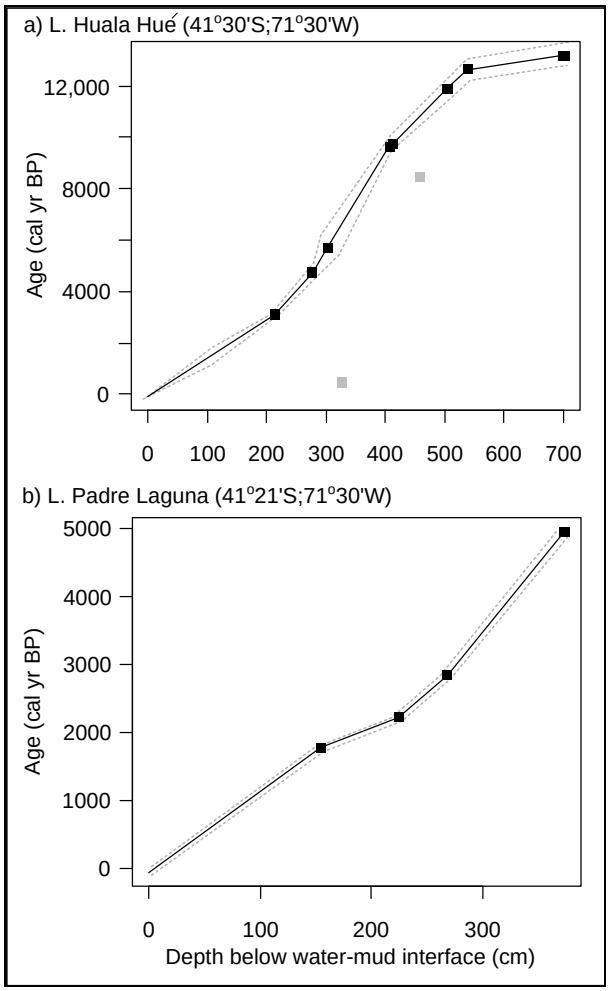


Figure 3.2: Age-depth model for a) L. Huala Hué (41°30'S; 71°30'W) and b) L. Padre Laguna (41°21'S; 71°30'W). 95% confidence intervals are shown in gray. Black squares are calibrated radiocarbon ages used to develop the models, and gray squares are dates that are ages that were not included in the models.

Results

Lithology

L. Huala Hué. Four lithological units were identified in the HH08B core (Fig. 3.3). The basal unit (Unit 1; 731-628.5 cm depth; 13,500-13,300 cal yr BP) was composed of clay with gray and dark gray beds. High bulk density and sedimentation rates suggest that this period featured abundant allochthonous input and poorly developed soils. The magnetic susceptibility profile shows overall high values and variability, with high values associated with dark gray beds and low values with lighter beds. These data suggest periodic changes in sediment source and likely short-term fluctuations in sediment accumulation rates.

Unit 1 was overlain by an organic clay unit (Unit 2; 628.5-570 cm depth; 13,300-12,700 cal yr BP), which represents a transition from dark grayish brown to dark olive brown clay. This trend reflects a gradual increase in organic matter and decrease in carbonate content in the sediment, indicating increased lake productivity. Decreasing sediment accumulation rates, bulk density and magnetic susceptibility are consistent with decreased allochthonous input into the lake. At 570 cm depth, a sharp contact marks the transition to the overlying gyttja unit (Unit 3, 570-62 cm depth; 12,700-630 cal yr BP). The gyttja unit was characterized by relatively stable sedimentation rates and organic matter content and variable magnetic susceptibility and gamma density. Based on changes in color, magnetic susceptibility and gamma density, seven subunits were identified in Unit 3.

The uppermost unit (Unit 4, 62-0 cm depth; 630 cal yr BP- present) consisted of low-density decomposed sedge peat. Eleven volcanic ashes were present and preliminary geochemical data suggest they are from eruptions of Puyehue and Chaitén volcanoes.

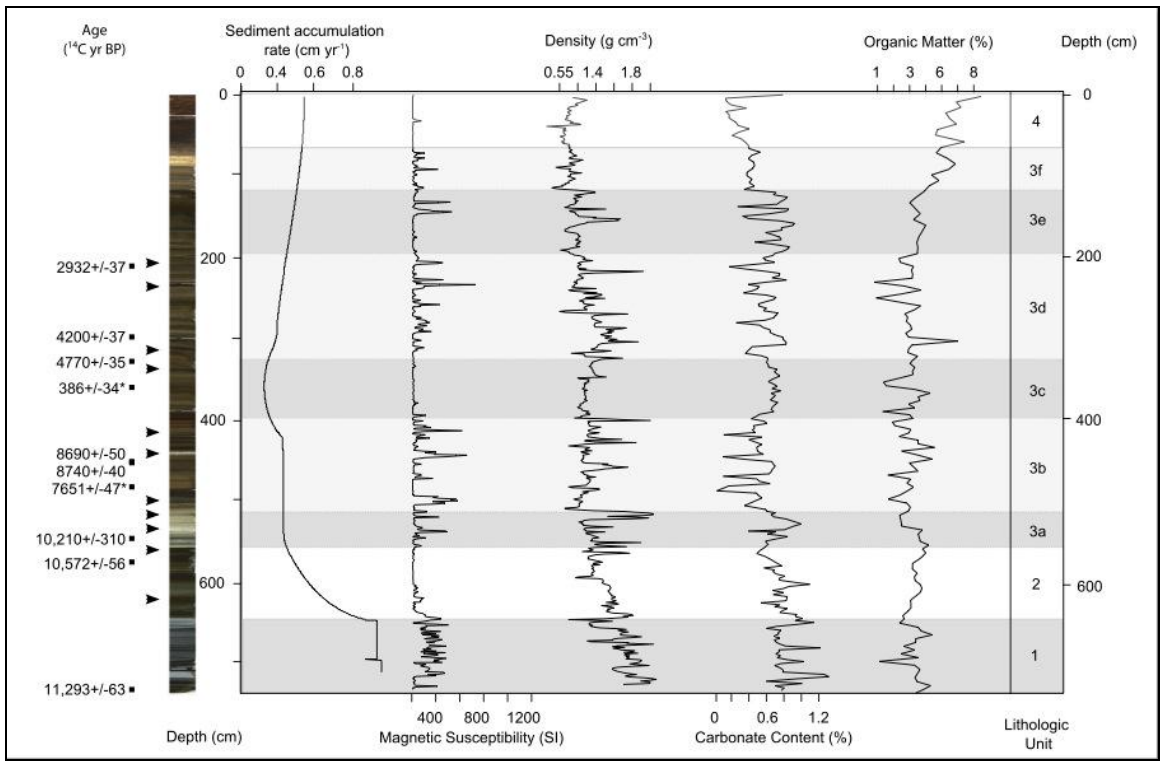


Figure 3.3: Lithology, sediment accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the HH08B core. Black triangles indicate the position of tephra layers and black squares represent radiocarbon years. Asterisks indicate dates that were not used in the chronology.

L. Padre Laguna. LCar08B core sediments consisted of fine-detritus gyttja and thirteen volcanic ashes (Fig. 3.4). Carbonate and organic matter content showed little variability throughout the core. Seven lithological subunits were identified based on color and sedimentation rate changes, variability in the magnetic susceptibility profile, and gamma density.

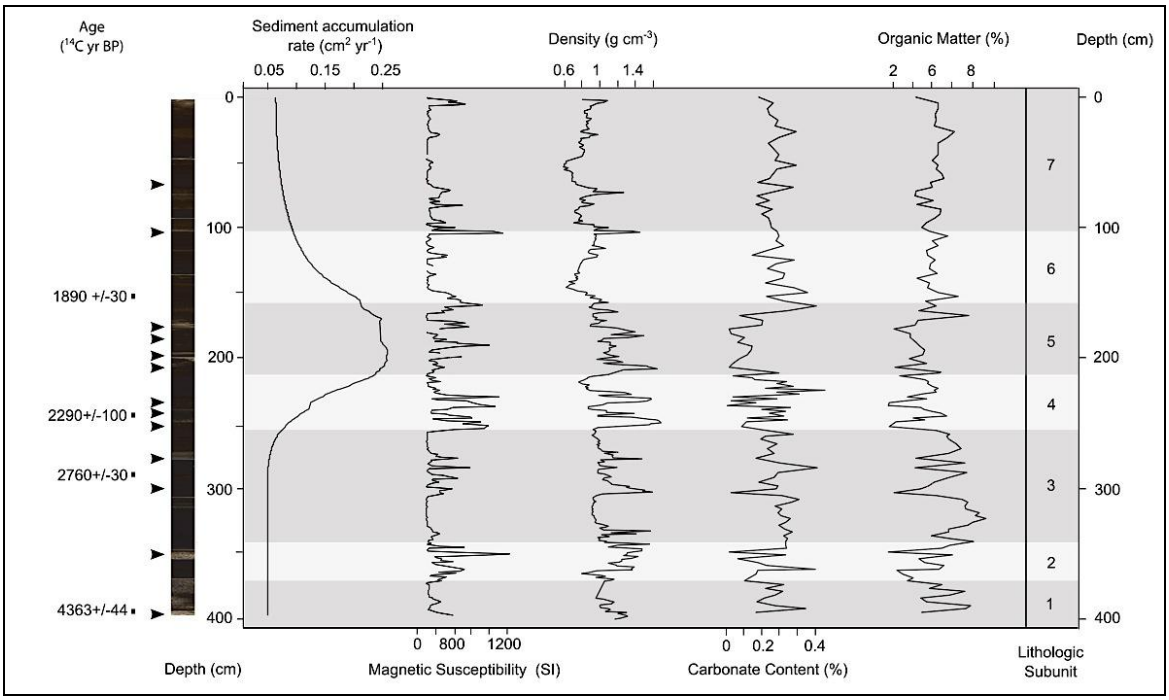


Figure 3.4: Lithology, sediment accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the LCar08B core. Black triangles indicate the position of tephra layers and black squares are radiocarbon years.

Pollen and Charcoal Records

L. Huala Hué (Fig. 3.5). Zone HH-1 (731-472.5 cm depth, 13,500-11,200 cal yr BP). *Nothofagus dombeyi*-type increased from 54 to 86% at 12,907 yr BP and remained high throughout the zone. Pollen of rainforest elements, Cupressaceae (presumely A. chilensis), and shrubland taxa were present in low percentages (<14, <1.37 and <4%, respectively). After reaching the highest values of the record at the bottom of the zone, Poaceae (15%), Asteraceae (7%) and steppe herbs (16%) decreased to 7, <1.5 and <2%. PAR was highly variable, fluctuating between 50 and 4110 grains cm^{-2} yr^{-1}. There are no modern analogs for the Zone HH-1 pollen assemblage, but the percentages of arboreal

and nonarboreal pollen compare most closely with modern samples from the forest/steppe ecotone (Markgraf et al., 1981). CHAR values ranged between 0 and 2.19 particles cm^{-2} yr^{-1}. Fire-episode frequency was initially low and gradually increased to 5.14 episodes 1000 yr^{-1} at the top of the zone. The grass-to-total charcoal ratio was variable, suggesting a mixed fire regime characterized by frequent fires in both grassland and woody vegetation.

Zone HH-2 (472.5-284 cm depth; 11,200-4900 cal yr BP). *Nothofagus dombeyi*-type decreased from 54 to 31%, and *Misodendrum* was abundant (up to 13%). Rainforest taxa, such as *Hydrangea* and *Gaultheria*, attained their highest values in the record (22%). Pollen from present-day shrubland taxa reached 23%. Except for a peak of 21.5% at 6700 cal yr BP, Cupressaceae pollen accounted for <5% of the total pollen sum. Asteraceae and other steppe taxa pollen were at higher levels than in the previous zone (up to 6% in both cases), but Poaceae dropped to <9 %. PAR was low (≤450 grains cm^{-2} yr^{-1}), suggesting an open landscape. The pollen data are most similar to modern pollen spectra from shrubland (Paez et al., 2001). CHAR was <0.5 particles cm^{-2} yr^{-1}, with exception of the intervals at 10,100 - 8500 and 5700 - 4700 cal year BP, when it reached 7 particles cm^{-2} yr^{-1}. Fire frequency declined to <1 episode 1000 yr^{-1}, rose to 5.5 episodes 1000 yr^{-1} during the 7600 to 6700 cal yr BP period, and declined thereafter. Low levels of grass-to-total charcoal (0.1 to 0.28) suggest fires burned predominantly woody fuels.

Zone HH-3 (284-250 cm depth; 4900-3860 cal yr BP). Rainforest elements, *Misodendrum*, and shrubland and steppe taxa declined in this zone. *Nothofagus-dombeyi* type was high at the bottom of the zone (83%) and decreased to 41% at the top.

Cupressaceae -presumably *Austrocedrus*- pollen increased from 3 to 32%. PAR values rose to 1280 grains cm^{-2} yr^{-1}, suggesting an increase in vegetation productivity. The pollen assemblage compares most closely with modern samples from the *Nothofagus* forest. CHAR remained <1.5 particles cm^{-2} yr^{-1}. Fire frequency and the levels of grass-to-total charcoal were initially low and gradually increased to >4 episodes 1000 yr^{-1} and a grass-to-total charcoal ratio of 0.25 at the top of the zone, indicates a shift towards more frequent fires burning more grassy fuels than before.

Zone HH-4 (250-165 cm depth; 3860-2120 cal yr BP). *Nothofagus dombeyi*-type decreased to 38 % and remained low throughout the zone (<61%). Cupressaceae increased to its highest values (up to 44%), and Poaceae rose to 7%. Rainforest, shrubland and steppe taxa percentages did not change from the previous zone. PAR values were relatively high, reaching values of 1200 grains cm^{-2} yr^{-1}. CHAR fluctuated between 0 and 3.37 particles cm^{-2} yr^{-1}, and fire frequency increased from 4 to 6.5 episodes 1000 yr^{-1}. Grass charcoal was well represented and increased in abundance (ratio of 0.65) towards the end of the zone. The pollen and charcoal data suggest an open *Austrocedrus* forest (Markgraf et al., 1981) and a fire regime characterized by frequent fires.

Zone HH-5 (165-117 cm depth; 2120-1350 cal yr BP). *Nothofagus dombeyi*-type percentages reached maximum values (90%), whereas humid forest taxa, *Misodendrum*, Cupressaceae, shrubland taxa, and Poaceae were poorly represented. PAR increased to 1200 grains cm^{-2} yr^{-1}, suggesting high vegetation productivity. CHAR values oscillated between 0 and 4.41 particles cm^{-2} yr^{-1}, and the grass-to-total charcoal ratio steadily

declined from 0.49 to 0.19. Fire frequency increased to highest values at 2000 cal yr BP (<7 episodes 1000 yr^{-1}) and decreased thereafter to 4 episodes 1000 yr^{-1}, suggesting a transition from frequent grass fires to less frequent woody fires. Comparisons with modern pollen studies indicate a shift in forest dominance from *Austrocedrus* to *Nothofagus* (Paez et al., 2001).

Zone HH-6 (117-0 cm depth; 1350 cal yr BP to present). *Nothofagus dombeyi*-type decreased, and Cupressaceae and humid forest taxa increased to 8 and 9%, respectively. Shrubland and steppe taxa, and Asteraceae also became more abundant (10, 8 and 2.5%, respectively). PAR values were initially high (920 grains cm^{-2} yr^{-1}) and decreased to <140 particles cm^{-2} yr^{-1} towards the top of the zone, suggesting that the forest became less productive. After 450 cal yr BP, CHAR values rose and showed prominent peaks, including a value of 7 particles cm^{-2} yr^{-1} at 15 cm depth, that corresponds with a large forest fire event in the watershed at 1761 AD (Veblen et al., 1999). Fire frequency steadily declined to 3.8 episodes 1000 yr^{-1}, and grass-to-total charcoal ratio, which reached 0.80 at the bottom of the zone, decreased to 0 towards the top, indicating a notable shift from surface to crown fires in recent times. The zone marks the establishment of open *Nothofagus-Austrocedrus* forest, and an infrequent but stand-replacing fire regime.

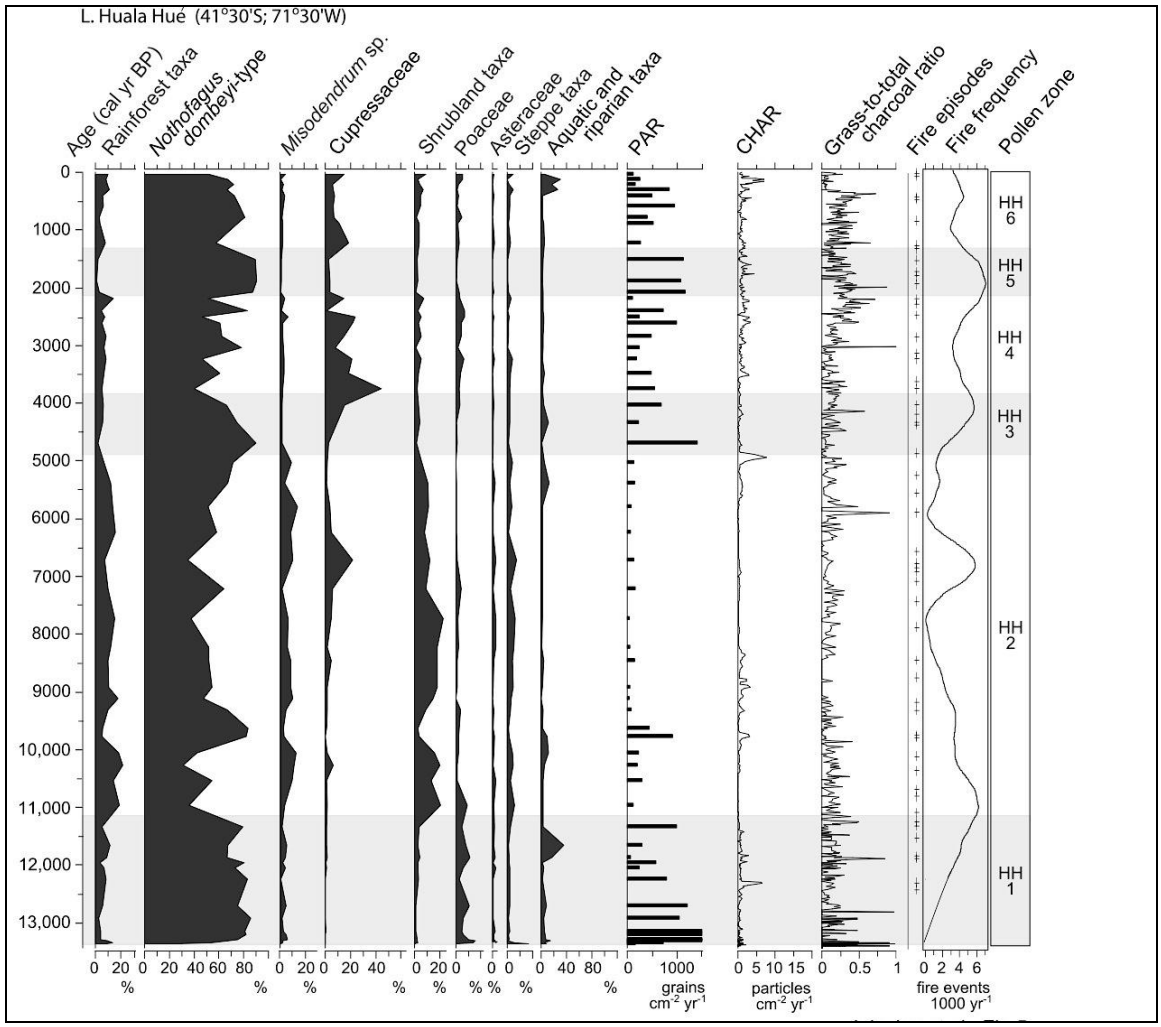


Figure 3.5: Selected pollen and charcoal data for L. Huala Hué.

L. Padre Laguna (Fig. 3.6). Zone PL-1 (397-339 cm; 4910-3860 cal yr BP). *Nothofagus dombeyi*- type was the dominant pollen taxa in the assemblage (up to 80%). Rainforest taxa and *Misodendrum* oscillated between 5 and 7%, except at 4522 cal yr BP (352 cm depth), when they both peaked, reaching values >25%. Shrubland and steppe taxa as well as Poaceae did not exceed 12% of the total pollen sum. PAR was generally high and variable, fluctuating between 40 and 400 grains cm^{-2} yr^{-1}. CHAR and fire-episode frequency were initially low (>1 particles cm^{-2} yr^{-1}, 0 fire episodes 1000 yr^{-1}) and

increased to 2.5 particles cm^{-2} yr^{-1} and ca.1.8 fire episodes 1000 yr^{-1} at the end of the zone. Grass charcoal was poorly represented (grass-total-charcoal ratio <0.23). Pollen and charcoal data suggest a *Nothofagus* forest where fires were infrequent but severe enough to burn predominantly woody vegetation dominated the watershed.

Zone PL-2 (339-289 cm; 3860-2850 cal yr BP). *Nothofagus dombeyi*-type declined to <52% at the expense of Cupressaceae, which increased to 45%. Humid forest elements and *Misodendrum* percentages were slightly lower than before (>4%). PAR and CHAR decreased from 1000 to 10 grains cm^{-2} yr^{-1} and 4.3 to 1.6 particles cm^{-2} yr^{-1}, respectively. Fire-episode frequency increased and peaked at ca.3250 cal yr BP (310 cm depth; 2.8 fire episodes 1000 yr^{-1}). The proportion of grass charcoal was similar to that of the previous zone. The pollen assemblage compares well with modern samples from *Austrocedrus* forest, and the charcoal data indicate a shift towards more frequent fires.

Zone PL-3 (289-134 cm; 2850-1650 cal yr BP). *Nothofagus dombeyi*-type rose to 70% and Cupressaceae decreased to 20%. Humid forest elements, *Misodendrum*, Asteraceae and steppe taxa percentages were indistinguishable from the previous zone. Shrubland taxa showed a slight decline (to 3%). PAR values were generally high, reaching 500 grains cm^{-2} yr^{-1} towards the end of the period. CHAR and fire episode frequency were initially low and rose to 18 particles cm^{-2} yr^{-1} and 3.2 fire episodes 1000 yr^{-1} at the end of the zone. Grass charcoal became more abundant, resulting in grass-to-charcoal values as high as 0.98. The zone marks the establishment of the *Nothofagus-Austrocedrus* forest and a shift in the fire regime from woody to grass fires at 2100 cal yr BP (246.5 cm depth).

Zone PL-4 (134-33 cm; 1650-450 cal yr BP). *Nothofagus dombeyi*-type pollen decreased to 35% whereas that of *Misodendrum*, Cupressaceae and shrubland taxa increased to 7, 48, <48 and 6%, respectively. PAR was low throughout the zone (>100 grains cm^{-2} yr^{-1}). CHAR ranged from 2 to 7 particles cm^{-2} yr^{-1}. After 1350 cal yr BP, fire-episode frequency increased (to 1.5 fire episodes 1000 yr^{-1}) and grass-to-total charcoal ratio decreased (to 0.25), suggesting more frequent and severe fires than before. Pollen percentages match modern samples from mixed *Nothofagus-Austrocedrus* forest (Paez et al., 2001) and are consistent with a shift in dominance from *Nothofagus* to *Austrocedrus.*

Zone PL-5 (33-0 cm; 450 cal yr BP to -present). *Nothofagus dombeyi*-type pollen rose to 76% and *Misodendrum* pollen reached 18%. Cupressaceae pollen ranged from 11 to 19%. Poaceae, Asteraceae, and shrubland and steppe taxa decreased to 8, 1, 3 and 5%, respectively. PAR values were greater than in the previous zone and fluctuated between 15 and 208 grains cm^{-2} yr^{-1}. Except for a local charcoal maximum at 146 cal yr BP (8 particles cm^{-2} yr^{-1}; 12 cm depth), CHAR values were below 2 particles cm^{-2} yr^{-1}. Fire frequency and grass-to-total charcoal ratio increased to 1 fire episode 1000 yr^{-1} and 0.19 towards the top of the zone, suggesting more frequent burning of mixed fuels. The pollen assemblage compares most closely with modern samples from mixed *Nothofagus-Austrocedrus* forest (Paez et al., 2001), which describes well the modern vegetation.

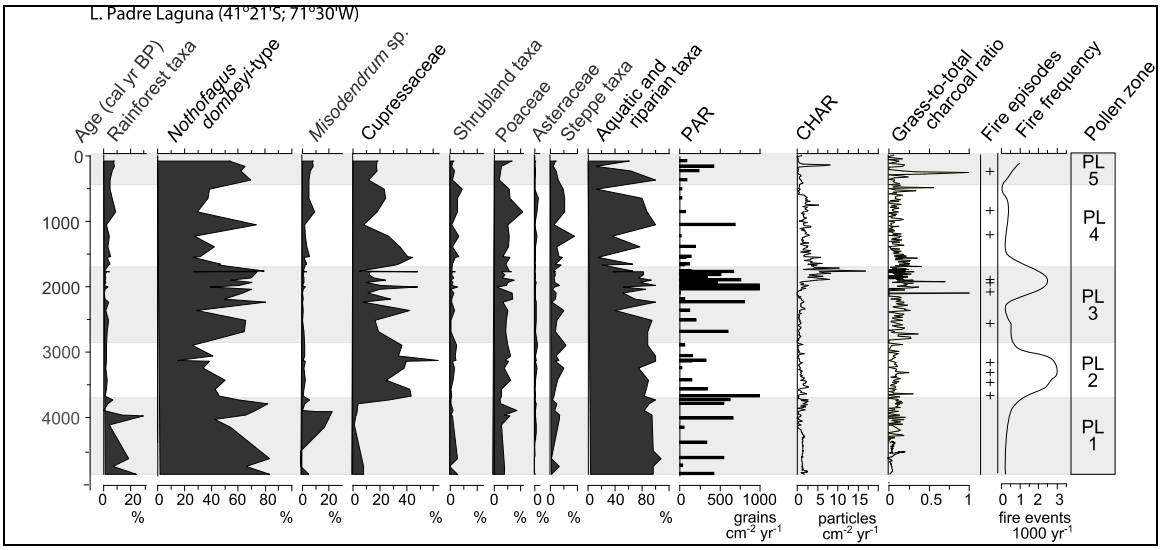


Figure 3.6: Selected pollen and charcoal data for L. Padre Laguna.

Discussion

Regional Vegetation and Fire History

Late-Glacial/Early-Holocene Transition (13,500 - 11,200 cal yr BP). The L. Huala Hué record begins at ca.13,500 cal yr BP following ice recession from the Río Manso valley. Initially, glacial clay was deposited in the basin in a quasi-periodic fashion, reflecting fluctuations in inorganic clastic sediment possibly related to changes in glacial meltwater input. The inorganic sediment contribution to the lake decreased after ca.13,300 cal yr BP and the system became increasingly more productive. This trend towards a more-stable system was reversed between 12,700 and 11,200 cal yr BP, when laminations of carbonate-rich silt were periodically deposited in the lake. The lithological change suggests that the late-glacial/early-Holocene transition was characterized by pronounced fluctuations in sedimentation, a finding that is consistent with independent

evidence of climatic variability at this time throughout Patagonia (Ariztegui et al., 1997; Hajdas et al., 2003, Moreno and León, 2003).

The pollen data indicate that L. Huala Hué lay in open parkland or near the *Nothofagus* (presumably *N. antarctica*) forest/steppe ecotone, but the exact admixture of species has no modern analogs. Vegetation composition was remarkably stable throughout the period, suggesting either that the magnitude of the environmental changes was small relative to the fundamental niche of the dominant species or that detection of environmental change at the time was constrained by the low diversity of pollen types (i.e. *Nothofagus dombeyi*-type, Poaceae). Paleoecological studies indicate that open forest was present in North Patagonia as early as 15,360 cal yr BP (i.e. Bianchi and Ariztegui., in press; Iglesias et al., 2012; Chapter 2; Whitlock et al., 2006). During full-glacial times, low temperatures and moisture levels limited tree establishment and seedling survival. As temperatures rose and the Southern Westerlies migrated south of this region (Whitlock et al., 2007), open forest/shrubland developed on the eastern flanks of the Andes.

Fires were initially rare but became more frequent by 11,200 cal yr BP, occurring approximately every 200 years and burning grassland and woody vegetation. Pollen data provide no evidence of increasing fuel biomass or changes in fuel composition to explain the increased fire activity, suggesting that it was related to increased ignition and decreased effective moisture. Widespread burning has been recorded throughout Patagonia during the late-glacial/early-Holocene transition. Although human activity may explain the shift in the fire regime, it is likely that increased lightning occurrence

associated with more frequent convective storms (Huber et al., 2004) and drier conditions (Whitlock et al., 2006) created conditions conducive for burning throughout the region.

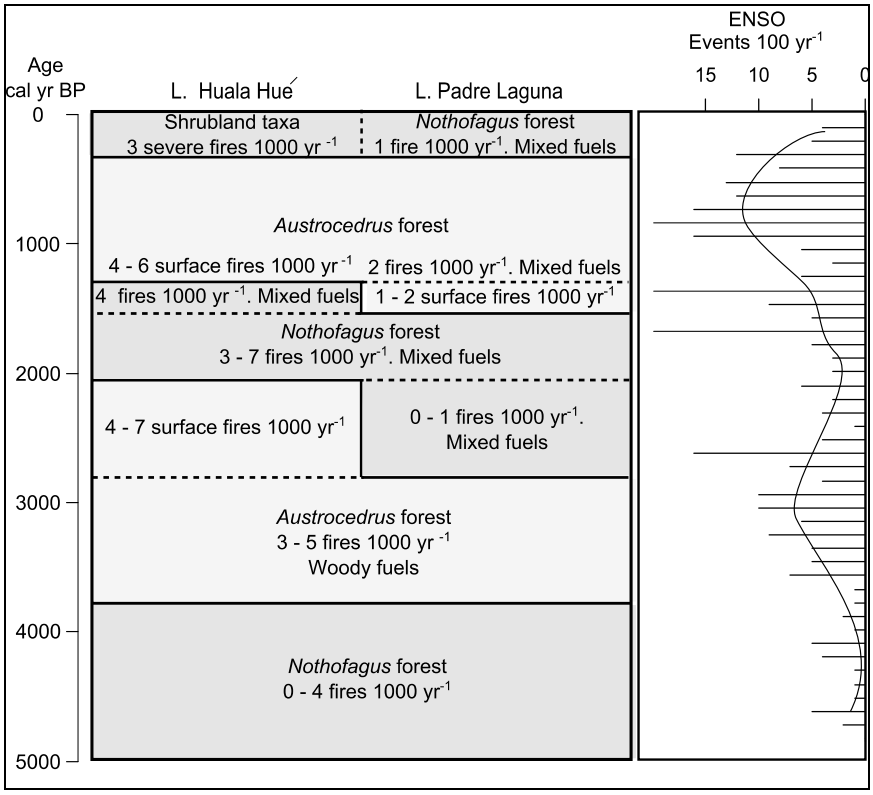


Figure 3.7: Late-Holocene vegetation and fire at L. Huala Hué and L. Padre Laguna and ENSO event frequency (modified from Moy et al., 2002). Note that the y-axis is inverted.

Early and Middle Holocene (11,200 - 4900 cal yr BP). Between 11,200 and 4900 cal yr BP, the L. Huala Hué record suggests establishment of a shrubland dominated by Rhamnaceae, *Nothofagus* (presumably *N. antarctica*) and steppe taxa. Local fire frequency was high at the beginning of the period (5.5 episodes 1000 years^{-1}) and decreased as vegetation cover became more discontinuous. Low CHAR indicates that regional biomass burning was limited except between 10,100 - 8500 and 5700 - 4700 cal year BP. Periods of higher CHAR coincide with short-term fluctuations between

inorganic and organic sediment deposition (lithological units 3b and d), which suggest intermittent pulses of erosionand deposition. Higher-than-average CHAR and episodes of erosion at these times may have been a consequence of multi-decadal variations in effective moisture that resulted in periods of fuel accumulation followed by periods of fuel desiccation, conditions conducive to fire in present-day fuel-limited ecosystems (Whitlock et al., 2010). It is also possible however, that some of the charcoal was secondarily introduced into the lake through erosion.

Increasing effective moisture is implied by the expansion of woody species (e.g. Rhamnaceae*, Maytenus*, *Schinus*) at ca. 11,200 cal yr BP. Shrubland establishment at L. Huala Hué corresponds in time with an eastward shift of the forest-steppe ecotone on the eastern flanks of the Andes (Iglesias et al., 2012; Chapter 2); an expansion of Valdivian forest taxa and an increase in disturbance-adapted species (e.g., *Eucryphia*, *Weinmannia*) in the mid-latitudes of Chile (Moreno and León, 2003; Abarzúa and Moreno, 2008); and higher-than-before lake levels at lat 40°S, on the western flanks of the Andes (Bertrand et al., 2008). Whitlock et al. (2006) attribute widespread fire activity in southern Patagonia (south of lat 42°S) during the early Holocene to a southward or weakening of the Southern Westerlies, related to higher-than-present annual and winter insolation. Conditions became cooler and/or effectively wetter from 11,200 to 5000 cal yr BP probably as a result of decreasing annual and winter insolation and a strengthening of the Southern Westerlies at mid-latitudes. Superimposed on this long-term trend, millennial-scale shifts in the position of the Southern Westerlies led to oscillations in moisture,

vegetation and fire not only in Patagonia but throughout the mid- and high latitudes of the Southern Hemisphere (Huber et al., 2004; Fletcher and Moreno, 2011).

Late Holocene (4900 cal yr BP to Present). Between 5000 and 4700 cal yr BP, *Nothofagus* expanded in the L. Huala Hué and L. Padre Laguna watersheds at the expense of drought-tolerant species, and forest advanced eastward into steppe throughout the northeastern slopes of the Patagonian Andes (Whitlock et al., 2006, Bianchi and Ariztegui, in press; Iglesias et al., 2012; Chapter 2). These vegetation changes, which are abrupt at most sites, suggest that effectively wetter conditions than before allowed an expansion of mesophytic taxa. An increase in effective moisture is also inferred from geochemical records off the coast of Chile and has been ascribed to an intensification and/or shift of the Southern Westerlies to mid-latitudes as well as a strengthening or intensification of ENSO-related climate variability (Lamy et al., 2001; Markgraf et al., 2007).

The development of the forest after 5000 cal yr BP was accompanied by millennial-scale shifts in forest species dominance (i.e. *Nothofagus* and *Austrocedrus*) and fire activity at L. Huala Hué and L. Padre Laguna (Fig. 3.7). Between 4900 and 3860 cal yr BP, a closed *Nothofagus* forest was present in both watersheds, and fires became more frequent towards the end of the period (up to 4 fire episodes 1000 yr^{-1} at L. Huala Hué, and 2.8 fire episodes 1000 yr^{-1} at L. Padre Laguna; Figs. 3.5, 3.6). *Austrocedrus* abundance increased substantially at 3860 cal yr BP, leading to the development of open *Austrocedrus* forest, and local fire frequency (>3 fire episodes 1000 yr^{-1} at L. Huala Hué and 2.8 fire episodes 1000 yr^{-1} at L. Padre Laguna) as well as regional biomass burning

(CHAR>3 particles cm^{-2} yr^{-1}at both sites) were higher than before. The expansion of *Austrocedrus* and concurrent increases in fire activity point to a strong climatic control and, in particular, to decreased effective moisture during the growing season (Villalba et al, 2003).

At 2850 cal yr BP, fires became more frequent and less severe at L. Huala Hué (up to 6.5 fire episodes 1000 yr^{-1}) and burned predominantly Poaceae (grass-to-total charcoal ratio of 0.65). Although the fire regime did not change significantly at L. Padre Laguna at this time, vegetation shifted to a *Nothofagus*-dominated forest. *Nothofagus* replaced *Austrocedrus* as the local dominant tree at L. Huala Hué at 2120 cal yr BP, when vegetation productivity (inferred from high PAR) and grass fuels (grass-to-total charcoal ratio<0.98) reached their maximum. Based on comparisons with modern fire regimes (Kitzberger et al., 1997), it is reasonable to assume that the abundance of grass charcoal particles associated with *Nothofagus*-dominated pollen assemblages originated from fires in bamboo stands (*Chusquea* sp.), widespread in disturbed *Nothofagus* forests, rather than grasslands. The persistence of grass charcoal and high fire frequency until 1650 cal yr BP suggests that short-term climatic variability (i.e., interannual or interdecadal) created conditions suitable for bamboo burning despite the generally wet character of the forest.

Between 1650 and 450 cal yr BP, the forest at L. Padre Laguna was co-dominated by *Austrocedrus* and *Nothofagus*. Fires were rare (0.2 fire events 1000 yr^{-1}) until 1350 cal yr BP and became more frequent and severe afterwards (0.8 fire events 1000 yr^{-1}; grass-to-total charcoal ratio<0.1). At 1350 cal yr BP, *Austrocedrus* expanded in the L.

Huala Hué watershed, marking the establishment of mixed *Nothofagus-Austrocedrus* forest and drier-than-before conditions.

Paleoenvironmental records from the mid- and high latitudes of the Southern Hemisphere reveal increased millennial- to decadal-scale variability during the late Holocene (Fletcher et al., 2011). Our data suggest oscillations between humid periods (4900-3800 cal yr BP and 2850-1350 cal yr BP) and dry periods (3800-2850 cal yr BP and 1350-450 cal yr BP). A similar pattern is inferred from nearby sites on the eastern flanks of the Andes (Iglesias et al., 2012; Chapter 2; Whitlock et al., 2006). Comparison of our records with an ENSO reconstruction (Moy et al., 2002) reveals drier (more humid) periods are concurrent with intensified (decreased) ENSO activity (Fig. 3.7). For example, whereas *Nothofagus* forest is dominant during periods with few ENSO events (i.e., 4900-3800 cal yr BP; 2100-1650 cal yr BP), *Austrocedrus* expands during times of active ENSO (i.e., 3800-2850 cal yr BP; 1350-450 cal yr BP). Mixed forests occur during the transitions between high and low ENSO activity periods (2850-2100 cal yr BP; 1650-1350 cal yr BP; Fig. 3.7).

This association suggests that ENSO variability accounts for some of the late-Holocene vegetation and fire history shifts in northwestern Patagonia. The positive (negative) phase of ENSO has been linked to decreased (increased) spring and summer precipitation and high (low) annual temperatures as a result of a strengthened (weakened) southeastern Pacific subtropical high-pressure system and southward (northward) shift in the position of the Southern Westerlies (Montecinos and Aceituno, 2003). These

atmospheric teleconnections are also influenced by fluctuations in the strength and position of the polar vortex (Cash et al., 2005) but to a degree that is not well understood.

The last 450 cal years are characterized by substantial bog encroachment into L. Huala Hué and increased lake productivity at L. Padre Laguna. The vegetation and fire histories of the two sites diverge at this time. Whereas shrubs and Poaceae became abundant and fire severity increased at L. Huala Hué, a closed forest that rarely burned developed at L. Padre Laguna. These differences cannot be attributed exclusively to effective moisture variability. Paleoecological records throughout Patagonia show pronounced changes in forest composition and burning regimes with the onset of European settlement (ca. 1850 AD; i.e. Haberzettl et al., 2006; Abarzúa and Moreno, 2008). The geographic differences in vegetation and fire could be due to the spatial pattern of anthropogenic burning for forest clearance, livestock grazing, and introduction of exotic species, which are likely to have altered ecosystem dynamics at local scales.

Distal and Proximal Controls of late-Holocene Vegetation History

The relative importance of local non-climatic versus regional climate controls of vegetation and fire activity is often ascribed to the scale of observation, be it a reconstruction from a single site or a regional pattern inferred from multiple sites (e.g., Huber et al., 2004; Williams et al. 2007). Paleoecological studies suggest that local controls can confound the direct effects of climate, and the importance of distal and proximal controls on vegetation can alternate through time (i.e., Cwynar, 1987; Gavin et al., 2006). Our results support this assertion, by showing the significant role of fire in

shaping the vegetation during the last 5000 cal years in creating vegetation changes that climate alone cannot explain.

In the late Holocene at L. Huala Hué and L. Padre Laguna, humid periods are associated with *Nothofagus* forest expansion, and drier times have promoted *Austrocedrus* dominance (Figs. 3.7 and 3.8). The ecological niches of *Austrocedrus* and *Nothofagus* partly overlap along west-to-east moisture gradient, with the former dominating drier environments and the latter prevailing under more humid conditions. At the extremes of the moisture gradient, climate imposes physiological constraints that favor one taxa or the other. Xerophytic adaptations such as reduced leaf surface and thick cuticle make *Austrocedrus* more resistant to water stress than *N. dombeyi*. As a result, climatic conditions that cause *Nothofagus* drought-induced mortality may not have consequences for *Austrocedrus* (Manion, 1981). *N. dombeyi*, on the other hand, is widely distributed along the humid slopes of the eastern Andes. High growth rates under open conditions, effective seed dispersion and longevity enables regeneration of *Nothofagus* in recently disturbed areas, and once established, it can persist for centuries and outcompete *Austrocedrus* (Veblen and Markgraf, 1989).

At intermediate moisture levels, where the niches of *Nothofagus* and *Austrocedrus* overlap, vegetation is characterized by mixed forests. The relative importance of either species in this situation depends upon the characteristics of the fire regime (Staver et al., 2011), which in turn is driven by climate-fuel interactions. Pollmann and Veblen (2004) suggest that *Nothofagus dombeyi* dominates the landscape after coarse-scale disturbances, such as large stand-replacing fires that occur every few

centuries. This hypothesis is consistent with our data, which suggest severe fires during periods when *Nothofagus* was most abundant (i.e. 2800-2100 cal yr BP at L. Padre Laguna and 1650-1360 cal yr BP at L. Huala Hué). The dominance of *Austrocedrus*, on the other hand, is impeded by large-scale disturbance events (Amoroso et al., 2011), but small surface fires promote regeneration of seedlings at the expense of *Nothofagus* and understory bamboos. This observation matches paleoecological data for a fire return interval of 180-300 years when *Austrocedrus* dominated the forest (i.e., 2800-2100 cal yr BP at L. Huala Hué and 1650-1360 cal yr BP at L. Padre Laguna). Thus, climate variability has been the main driver of late Holocene vegetation change, but interactions between available moisture, disturbance regime, and species biology have been crucial in shaping the mosaic of vegetation at lower treeline.

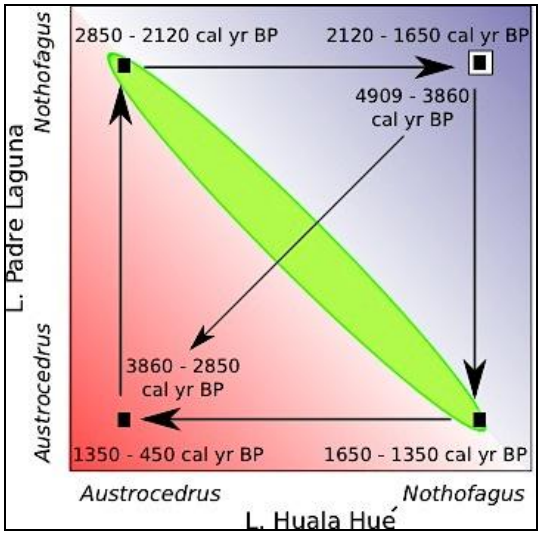


Figure 3.8: Late Holocene vegetation shifts in forest dominance at L. Huala Hué and L. Padre Laguna relative to effective moisture. The white square shows the beginning of the trajectory (4909 cal yr BP) towards modern communities. The red (blue) shade indicates drier (more humid) periods. At intermediate moisture levels (outlined with a dashed oval), either *Austrocedrus* or *Nothofagus* can dominate the ecosystem.

Conclusions

The L. Huala Hué record begins at ca.13,460 cal yr BP following ice recession of the Río Manso valley. Pronounced fluctuations in sedimentation on centennial to decadal timescales between 13,460 and 11,150 cal yr BP are consistent with the late-glacial climatic variability recorded throughout Patagonia. During this period, the site lay in parkland or near the forest/steppe ecotone with no vegetation analogs in the modern landscape. Fires were frequent attesting to the dry conditions at this time.

During the early Holocene, higher-than-present annual and winter insolation and a weakening of the Southern Westerlies led to shrubland development. Conditions became progressively wetter after 11,200 cal yr BP. Higher-than-before effective moisture after ca. 5000 cal yr BP enabled the expansion of *Nothofagus* and *Austrocedrus* at lower treeline. The boundary conditions of the climate system (i.e. insolation, position/strength of the westerlies) have not experienced significant change since this time. However, comparison of shifts in species dominance and fire regimes at L. Huala Hué and L. Padre Laguna suggests that the periods between 4900 and 3800 cal yr BP, and 2850 and 1350 cal yr BP were humid, and the intervals from 3800 to 2850 cal yr BP and 1350 to 450 cal yr BP were relatively dry. This pattern is consistent with millennial-scale oscillations in effective moisture associated with the onset or strengthening of ENSO.

Short-term oscillations in humidity have resulted in alterations of forest types and shifts in fire regime in the last 5000 cal yr. *Nothofagus* expanded during humid periods and *Austrocedrus*-dominated forest prevailed during drier times. At intermediate moisture levels, both taxa co-existed and changes in the size, severity and frequency of fire

explains differences in the relative abundance of species between the sites. Our results therefore provide further evidence that vegetation change is not simply a linear response to climate but rather a consequence of the combined effects of climate and disturbance, whose relative importance changes as critical thresholds are reached.

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CHAPTER FOUR

CLIMATE-VEGETATION-FIRE LINKAGES AT LOCAL TO REGIONAL SCALES ALONG THE PATAGONIAN FOREST-STEPPE ECOTONE (41 – 43˚S)

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, and 4

Author: Virginia Iglesias

Contributions: Supported this research under a LacCore student grant and a Montana Institute on Ecosystems graduate fellowship, defined the experimental design, participated in fieldwork, described the sediment cores, measured magnetic susceptibility, loss-on-ignition and other lithological properties of the cores, counted charcoal and pollen samples, analyzed the data and wrote the manuscript.

Co-Author: Cathy Whitlock

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Abstract

Patagonian ecosystems have dramatically changed in composition, distribution and dynamics since the last glaciation. In this study, we reconstructed the vegetation and fire history of the North Patagonian forest-steppe ecotone (lat. 41 - 43°S) and linked vegetation changes to variations in the fire regime, large-scale synoptic controls of climate, and human activity. Postglacial vegetation and fire dynamics were inferred from seven high-resolution pollen and charcoal records from lakes located along the forest-steppe ecotone in the eastern flanks of the Andes. We fit Generalized Additive Models to the pollen and charcoal time series to estimate regional trends in vegetation composition and biomass burning, and compared them to independent paleoclimate data so as to assess long-term vegetation-fire-climate linkages. Pollen data indicate that late-glacial steppe was replaced by open forest in the early Holocene and by closed forest in the middle and late Holocene. Fire activity was lowest during the late-glacial, rapidly increased in the early Holocene and remained relatively stationary until the late Holocene, when it peaked at ca. 2300 cal yr BP. Based on the current knowledge of human settlement in the area, there is no evidence that indicates that increased aboriginal population densities resulted in higher biomass burning at regional scales. Instead, our results show that climate was the main driver of Holocene ecological change at the forest/steppe ecotone, either by its direct effects on vegetation or its indirect effects on fire, as burning was strongly controlled by climate-driven plant productivity and fire weather. Watershed vegetation flammability explains much of the fine-scale variability in the fire regime, which, in turn can amplify or override the direct influence of climate on

ecotone composition. These findings emphasize the importance of biophysical feedbacks in ecosystem dynamics and suggest that these relations must be understood in the context of millennial-scale climate variations that shape broad patterns of vegetation and fire in the region.

Introduction

Plant communities are complex, non-stationary, interactive systems whose current state is just one realization from a suite of ecological and climate conditions and historical events. Since ecological fitness is dependent on the environment under which plants grow, species are expected to respond individualistically to environmental change (Williams et al., 2007). Metapopulation theory predicts that unfavorable environmental changes lead to local extirpation of plant populations, whereas favorable conditions result in colonization of new locations (Levins, 1969). Such individualistic shifts in range and abundance of plant taxa scale upward to cause compositional shifts within communities, appearances and disappearances of plant associations, and changes in the position, area, composition, and structure of biomes. As a result, ecological change is ubiquitous and continuous, and variability is found on all temporal and spatial scales.

Climate is the main driver of large-scale ecosystem dynamics, as it imposes physiological constraints on species distribution (McKenzie et al., 2003;Williams et al., 2007). Evidence from the paleorecord shows that the profound climatic changes that mark the Quaternary have left an indelible imprint on modern biota through impacts on species distributions. After the Last Glacial Maximum, for example, populations expanded from ice-age refugia to their present habitats, tracking climate and leading to

changes in community composition (Heusser et al., 2003, Anderson et al. 2006; Gavin et al., 2006).

An underlying assumption in 20th-century plant ecology was that, in the absence of disturbance, ecosystems eventually reach a "climax" condition in which the vegetation structure and community composition do not change over time (Clements, 1936). This assumption is belied by the fact that moderate- to large-scale disturbance events, such as fires, floods, windstorms and insect outbreaks, are omnipresent in natural ecosystems (Gleason, 1939). Furthermore, recent studies suggest that watershed-scale shifts in disturbance regimes are sufficient to explain increases in coverage by one plant association at the expense of another (Higuera et al., 2009; Iglesias et al., 2012a; Chapter 2), implying the existence of non-linearities in vegetation responses to climate variability. Thus, disturbance must be understood as an integral component of ecosystems and vegetation dynamics, as a function of species' ability to disseminate, grow and reproduce in constantly changing environments, as well as the feedbacks rendered from the interaction of large-scale synoptic controls of climate and local-scale variability (Clark 1989).

Fire is the primary disturbance agent in many terrestrial ecosystems and its occurrence and characteristics are driven by interactions between top-down (e.g., mean climatic conditions, weather variability, frequency of ignition) and bottom-up (e.g., fuel load, continuity and moisture content, topography, soil characteristics) controls (Christensen, 1993). Climate-vegetation-fire linkages are therefore naturally complex and dynamic. Humans, past and present, have altered these natural linkages causing

environmental changes at scales ranging from watershed to regional and global (e.g., Bowman and Jackson, 1981; IPCC, 2007; Marlon et al., 2009; McWethy et al., 2010).

In northern Patagonia (41 – 43˚S), a sharp forest/steppe ecotone developed over the last ca. 10,000 cal yr, as trees colonized areas that were previously dominated by steppe taxa (Markgraf et al., 2007). Paleoecological data suggest that forest expansion was a response to increased effective moisture associated with insolation-driven shifts in the position of the Southern Westerlies, and changes in the fire regime modified the composition of the ecotone (Iglesias et al., 2012a and b; Chapters 2 and 3). Better understanding of ecosystem dynamics requires disentangling proximal from distal drivers of environmental change at different scales, as well as assessing feedbacks involving climate, vegetation, fire and human activities.

Of special interest is the case of *Austrocedrus chilensis*, a keystone species at present-day lower treeline between lat. 38 and 43˚S, in a region that was glaciated until ca. 17,000 cal yr BP (Flint and Fidalgo, 1964). Its current distribution raises the question about the location of its glacial refugium(a) and the factors that governed its Holocene expansion at both regional and watershed scales. Veblen and Markgraf (1989) proposed that fires are likely to have controlled the current longitudinal range of *Austrocedrus*, which expanded eastwards after decades of fire suppression in the 20th century. In this study, we use pollen and charcoal records to reconstruct the environmental history of the eastern Patagonian forest/steppe ecotone since the Last Glacial Maximum (ca. 23,000 cal yr BP) from lat. 41 to 43˚S in order to (1) estimate watershed- and regional-scale trends in vegetation and fire; (2) provide insights into the biogeography of *Austrocedrus*

chilensis; (3) assess the spatiotemporal dynamics of climate-vegetation-fire linkages across scales; and (4) evaluate the role of humans as drivers of pre-European environmental change. We expect to expose causal linkages by considering a network of sites and thus eliminating the noise of site-specific natural variability.

Study Sites and Regional Setting

We examined sediment cores from seven small lakes and bogs along a ca. 275 km north - south transect in the foothills of the eastern Patagonian Andes, Argentina (Fig. 4.1; Table 4.1). The study lakes are 21 to 461 ha in size, with water depths of 488 to 1050 cm. All sites are currently located at or near the forest/steppe boundary, although in some cases European forest clearance and other economical activities have altered the geographic position of the ecotone. Ashes from Volcan Chaitén (2008) and/or Volcan



Figure 4.1: Study area and location of L. el Trébol, L. Padre Laguna, L. Huala Hué, L. Cóndor, L. Mosquito, L. La Zeta and L. Theobald. The dashed line shows the international border.

Puyehue, which last erupted in 2008 and 2011, respectively, were observed at the sites.

Laguna el Trébol (41˚15’’S; 71˚32’W) is a glacial lake located in the northernmost end of the transect, near the city of San Carlos de Bariloche, Río Negro Province (mean annual temperature=12˚C; mean annual precipitation= 1660 mm [Cordon et al., 1993]) The lake was formed at ca. 14,000 cal yr BP, after Pleistocene deglaciation associated with numerous meltwater spillways and glacio-fluvial deposits in the area (Flint and Fidalgo, 1964; Bianchi et al., 1999). Currently, the lake basin lies in the transition forest dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis* (west of the ecotone).

Laguna Padre Laguna (41˚30’S; 71˚ 32’W) and Lago Huala Hué (41˚30’S, 71˚ 30’W) are located in the drainage of the Río Manso, south of Volcán Tronador (Río Negro Province), where mean annual temperatures range from 12˚C in the intermountain valleys to 6˚C in the subalpine forests (Villalba et al., 2003), and annual precipitation averages 1600 mm (Cordon et al., 1993). Geomorphological evidence suggests that L. Padre Laguna is dammed by a broad postglacial alluvial fan (Iglesias et al., 2012b; Chapter 3) and L. Huala Hué is blocked on its east side by a prominent glacial delta associated with late-Pleistocene meltwater from ice complexes to the north (Caldenius, 1932). Both lakes are located west of the forest / steppe ecotone and surrounded by co-dominated *Nothofagus-Austrocedrus* forest. Both sites are within Nahuel Huapi National Park.

Located in Chubut Province near the town of Cholila (mean annual temperature= 10˚C; mean annual precipitation=750 mm [Cordon et al., 1993]), Laguna del Cóndor

(42˚20'S; 71˚17'W) and Lago Mosquito (also known as Lago Pellegrini; 42˚29'S; 71˚24'W) lie close to the terminal Pleistocene moraines. The origin of L. Mosquito, however, is related to Holocene alluvial fans that dammed westward-flowing streams

(Whitlock et al., 2006; Iglesias et al., 2012a; Chapter 2). The lakes lie within the transition zone from open *Austrocedrus* woodland to steppe, and the landscape that surrounds them is heavily grazed by sheep and used for agriculture.

Laguna La Zeta (43˚17'S; 71˚53'W) is situated on a high plain, west of the city of Esquel, Chubut Province (mean annual temperature= 9˚C; mean annual precipitation= 560 mm [Cordon et al., 1993]). Geomorphological studies carried out by Schaebitz

Table 4.1: Study site information.

Site	Position	Elevation [m]	Lake surface [ha]	Water depth [cm]	Vegetation	Core
L. el Trébol	41˚15'S; 71˚32'W	977	391	1050	*N. dombeyi - A. chilensis* forest	Tre02A
L. Padre Laguna	41˚30'S; 71˚29'W	1280	21	735	*N. dombeyi - A. chilensis* forest	LCar08B
L. Huala Hué	41˚30'S; 71˚30'W	849	101	864	*N. dombeyi - A. chilensis* forest	HH08B
L. Cóndor	42˚20'S; 71˚17'W	818	175	850	*A. chilensis* stands - steppe	LC06A
L. Mosquito	42˚29'S; 71˚24'W	551	461	800	*A. chilensis* stands - steppe	Mos03A
L. La Zeta	43˚17'S; 71˚53'W	774	60	675	*N. dombeyi - A. chilensis-Pine* spp. forest - steppe	LZL09A
			Bog	NA		MLZ09A
L. Theobald	43˚12'S; 71˚40'W	678	416	488	*N.dombeyi - A. chilensis* forest - steppe	TH09A

(1994) indicate that the plain was glaciated several times during the Pleistocene. At the Last Glacial Maximum, a glacier originated on the southwestern slopes of Cordon de Esquel reached at least the southern end of the lake and melted rapidly, exposing the shore at ca. 18,000 cal yr BP. Vegetation, dominated by *Nothofagus dombeyi*, *Austrocedrus*, shrubs and grasses, characterizes the forest/steppe ecotone. Anthropogenic disturbance has been intense since the establishment of Esquel, mostly through land-cover change associated with ranching, agroforestry, and fire. In recent decades, pine trees have been planted to reforest the surroundings of the lake.

The southernmost site of the transect is Lago Theobald (43˚12'S; 71˚40'W). The lake, situated near the town of Corcovado, Chubut Province (mean annual temperature= 9˚C; mean annual precipitation= ca. 530 mm [Servicio Meteorologico Nacional, 2012]), was formed in an ice-block or glacial scour depression. Although it lies at the *Nothofagus-Austrocedrus* forest/steppe boundary, the landscape is open due to recent fires that killed approximately 50% of the trees and favored the establishment of abundant grasses and herbs. The local watershed has been intensively grazed by sheep.

Climate

The year-round presence of strong Southern Westerlies delimits Patagonia as a climatic region, inasmuch as westerly winds occur at least 75% of the time along the entire Chilean coast (Miller, 1976), and 50 to 70% of the time in the eastern plains (Prohaska, 1976). The particular latitude of the Southern Westerlies is governed by the strength of the southeast Pacific high pressure system and a subpolar low-pressure trough centered along the Antarctic Circle (Mayr et al., 2005). These circulation systems show

shifts in latitudinal position and strength related to seasonal changes in the temperature gradient between the Equator and the South Pole. South of 40°S, low-level westerly flow prevails year round in connection with a poleward decrease in pressure. In winter, the intensification of the subpolar low and the equatorward displacement of the Southeast Pacific High Pressure system result in jet stream migration to subtropical latitudes (30°S, [Paruelo et al., 1998]), whereas the low-level component expands equatorward but weakens, particularly at 50°S (Garreaud et al., 2008).

Frontal storm systems tracking the jet stream produce most of the rainfall in Patagonia (Garreaud et al., 2008). The Andes constitute an effective barrier to tropospheric wind flow, as the uplift of low-level winds over the western slope of the Andes results in orographic precipitation at levels that are two to three times greater than oceanic levels at the same latitude. In contrast, forced subsidence on the Argentine flanks of the Andes produces adiabatic warming of the air masses and very dry conditions in eastern Patagonia (Paruelo et al, 1998).

Mechanisms for interannual to decadal climate variability in Patagonia are related to tropospheric forcing of mid-latitude sea surface temperatures, indirect effects of coupled ocean-atmosphere phenomena rooted in the tropical Pacific, and pressure anomalies resulting from the fluctuations in strength and position of the polar vortex (Miller, 1976). El Niño Southern Oscillation (ENSO) dominates variability in the 3- to 6-year band. In northwestern Patagonia, positive precipitation and temperature anomalies have been linked to the positive phase of ENSO and the indirect effects of changes in sea-

surface temperatures at higher latitudes and concurrent changes in evaporation and atmospheric moisture content over Patagonia (Compagnucci and Araneo, 2007).

Modern Vegetation

The vegetation composition of the study sites is largely explained by east - west differences in effective moisture across the area. East of the Andes (40 - 43°S), a steep precipitation gradient results in a well-defined transition from rainforests to xerophytic forests to steppe (Hajec and di Castri, 1975; Jobaggy et al., 1996). This vegetation gradient is also influenced by the transition of soil types from productive volcanic soils in the west (i.e., Andisols, 1000 – 1300 mm annual precipitation), to relatively fertile substrates at intermediate precipitation levels (Alfisols, 500 – 1000 mm annual precipitation) to nutrient poor desert soils (i.e., Aridisols, <500 mm annual precipitation) towards the east (Mazzarino et al., 1998).

Above 1500 m elevation, slopes are dominated by forests of *Nothofagus pumilio* Krass. *Saxegothaea conspicua* Lind., *Fitzroya cupressoides* Johnst. and *N. antarctica* Oerst. are common and interspersed within *N. pumilio* stands. The forest supports an understory of shrubs (e.g., *Drimys winteri* J.R. Forst. et G. Forst., *Berberis* L., *Azara microphylla* Hook. and *Escallonia alpina* Poepp.) and rich herbaceous vegetation (e.g., *Lycopodium paniculatum* Desv. ex Poir., *Gaultheria caespitosa* Poepp. et Endl., *Sisyrinchium* L., *Blechnum auriculatum* Hieron. and Poaceae Barnhart). Along lake shores, mixed communities composed of species of *Equisetum* L., *Juncus* L., *Carex* L., *Arenaria serpens* Kunth and *Pernettya* L. occur.

Between 1500 and 1000 m elevation, 40-to-50-m tall *Nothofagus dombeyi* Mirb. dominates the temperate rainforest. *Saxegothaea conspicua* and *Laurelia philippiana* Looser., whose crowns lie 20 to 25 m above the ground, grow beneath *N. dombeyi* trees. Tree trunks support a rich epiphytic vegetation of mosses, lichens, ferns of the genus *Hymenophyllum* Labill., parasitic species (e.g., widespread *Phrygilanthus tetrandrus* L. and *Misodendron* Agardh.) and lianas (e.g., *Dioscorea brachybotrya* Poepp. and *Hydrangea integerrima* Hook. et Arn.). The ground is covered with a dense mat of bryophytes, many of which are endemic to Patagonia.

Further east, where precipitation declines to ca. 1500 mm, *Austrocedrus chilensis* Florin et Boutelje and *Nothofagus dombeyi* form extensive co-dominant stands. In these forests, a large number of arboreal (e.g., *Gevuina avellana* Molina, *Lomatia hirsuta* Diels ex Macbr. and *Myrceugenia* Berg) and shrubby species (e.g., *Berberis darwinii* Hook., *Baccharis* L., *Buddleja globosa* Hope) occur in association. Bamboos (*Chusquea argentina* Kunth and *C. culeou* Desvaux., in higher elevations) form extensive and almost impenetrable stands. The herbaceous flora, represented by *Calceolaria* L., *Gunnera chilensis* Molina, *Viola* L., and *Blechnum* L., is rich, especially in open areas.

Under more xeric conditions to the east, *Austrocedrus* forms pure stands and then farther east, open woodlands co-dominated by sclerophyllous shrubs and small trees (e.g., *Berberis* L., *Maytenus* Molina, *Escallonia* Mutis ex L.f. and *Embothrium coccineum* J.R. Forst. et G. Forst [Seibert, 1982]). Marginal *Austrocedrus* populations are characterized by scattered, usually multi-stemmed, poorly developed trees on rocky outcrops in the steppe where mean precipitation is as low as 500 mm precipitation annually (Dezzotti

and Sancholuz, 1991). Further east, sparse steppe elements, such as spiny shrubs (e.g., *Colletia* Comm ex Juss., *Discaria* Hook., *Mulinum* Pers.) and bunchgrasses (e.g., *Stipa* L. and *Festuca* L.), dominate the ecosystem.

Modern Fire Regime

Historical records of wildfire activity in Argentine Patagonia begin as early as 1938 but are geographically incomplete. In spite of this limitation, tree-ring records point to moisture deficits during the fire season linked to the positive phase of EL Niño Southern Oscillation as an important driver of fire activity during the last 500 years (Kitzberger et al., 1997). Similarly, area burned has been proposed to be dependent on warmer and drier than average springs associated with the positive phase of the Southern Annular Mode (Holz, 2009). Such linkages suggest a strong correlation between regional biomass burning and inter-annual climate variability.

At watershed scales, variability in fire occurrence is explained by location and frequency of ignitions, topography and local controls on fuel load and flammability. The coarse woody fuels of the temperate rainforest only burn under the most extreme drought. These forests are dominated by evergreen, broadleaved tree species with high water content that tend to act as biological breaks for fires (Kitzberger et al. 2005). Once ignited, however, fire spread is facilitated by fuel continuity, usually resulting in devastating stand-replacing fires.

Shrublands associated with *Nothofagus-Austrocedrus* forests are proportionally more affected by fire than adjacent forests or steppe (Mermoz et al. 2005). In these ecosystems, fire is facilitated by rapid fuel recovery, fuel flammability and vertical

continuity, along with microclimatic conditions created by the architecture of shrubs. *Chusquea* and epiphytes provide additional fine fuels, further facilitating vertical fire spread (Kitzberger et al., 1997).

Changes in land use during the 19th and 20th centuries have had profound impacts on Patagonian ecosystems. Accidental human ignitions as well as deliberate burning associated with European settlement increased the risk of fire in an otherwise ignition-limited ecosystem. In addition, the introduction of livestock and non-native plants, as well as conversion of large areas of native vegetation to plantations of fire-prone species, such as pines and eucalyptus, has further altered the fire regime, leading to higher fire potential in Patagonia (Veblen et al., 2011).

Methods

Sample Collection

A modified Livingstone piston sampler was used to collect sediment cores from the study lakes. In the case of L. La Zeta, we collected a core from the lake (core LZL09A) and a core from the bog located on the northern margin of the lake (core MLZ09A) and correlated them by identifying a thick pumiceous tephra layer. Cores were extruded in the field and wrapped in cellophane and aluminum foil and shipped to LacCore Facility, University of Minnesota, for lithologic characterization. In the laboratory, cores were split longitudinally into a working half and an archive. The working half was lithologically described, photographed, and analyzed for magnetic susceptibility (MS), gamma density, sequential loss on ignition (LOI), charcoal and

pollen content. The archival core and other materials are stored at the Paleoecology Laboratory at Montana State University.

Lithological Analyses

Description of the lithology was based on identification of sedimentary structures, mineralogy, and biological components, following Schnurrenberger et al. (2003). The Munsell system was used to specify color. High-resolution magnetic susceptibility was measured directly on the split-surface of the core at 0.5-cm contiguous intervals to assess changes in inorganic allochtonous sediment input from erosion and volcanic eruptions (Gedye et al., 2000). Gamma density (kg cm^{-3}), measured at 1-cm contiguous intervals, was used as an indicator of lithology and porosity changes. Organic and carbonate contents (% dry weight) were determined from weight-loss after ignition at 550° and 900°C of 1 cm3 samples taken at 1.5-cm intervals (Dean, 1974).

Bulk-sediment samples were taken at lithologic boundaries and submitted to Woods Hole NOSAMS and NSF-Arizona AMS Facility for radiocarbon analyses (Table 4.2). Chronologies were developed from modeling sediment age as a function of sediment depth. Two-sigma calibrated ages and probability distributions were determined for each radiocarbon date using CALIB 6.0.1 (Stuiver et al., 2005). Calibration was performed with the Southern Hemisphere radiocarbon calibration dataset for samples <10,000 cal yr BP and the Northern Hemisphere radiocarbon dataset for samples >10,000 cal yr BP. Core depth was corrected for sediment compaction and adjusted by excluding volcanic ash layers > 1.5 cm in thickness on the assumption that these tephra layers were deposited in a negligible span of time. Age-depth models (Fig. 4.2) were constructed with

cubic smoothing splines and a Monte Carlo sampling approach (2000 iterations) that allows each date to influence the age model through the probability density function of the calibrated age. The final age-depth models were based on the median of all the runs (Higuera et al., 2009).

The chronology for L. La Zeta showed two age reversals when modeled with cubic splines. We do not suspect contamination or have any reasons for rejecting the radiocarbon dates. The final age-model was developed by Monte Carlo sampling of the probability distribution of each calibrated age and linearly interpolating the estimated median probability ages. In the cases where age reversals occurred, values from the 95% confidence intervals of the calibrated dates were used in the interpolation (e.g., samples from 148.5 – 149 and 239.5 – 240 cm depth and 185 – 185.5 and 220.5 – 221 cm depth).

Charcoal and Pollen Analyses

Charcoal analysis was performed on 2-cm^3 volume samples, taken at contiguous 0.5-cm intervals, following the methodology outlined by Whitlock and Larsen (2001) to reconstruct local fire histories. The material was wet-screened through a 125-mm-mesh sieve, and charcoal particles were tallied under a stereomicroscope. Grass and wood charcoal were identified and tallied separately. Charcoal counts were converted to charcoal concentration (particles cm^{-3}) and then to charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}). In order to account for variable sampling intensity with time and override the effects of changing sedimentation rates, the CHAR time series were interpolated to their median resolution (Higuera et al., 2009). Grass-to-total charcoal ratios were used to infer the relative contribution of grass and woody fuels.

Sediment samples of 0.5 cm^3 were taken at <250-year intervals for pollen analysis and prepared according to standard techniques (Faegri et al., 1989). A known amount of *Lycopodium* tracer spores was added to each sample to allow calculation of pollen accumulation rates (PAR; grains cm^{-2} yr^{-1}), which were interpreted as a general measure of plant abundance. Pollen identification was based on a reference collection and published atlases (Markgraf and D'Antoni, 1978; Heusser, 1987) and performed at 250 and 400x magnification. In all cases, counts exceeded 300 terrestrial pollen grains, excluding Cyperaceae, aquatic taxa and spores. Terrestrial pollen percentages were based on the sum of trees, shrubs and herbs and plotted using C2 (Juggins, 2007).

For this study, only the dominant pollen types are discussed. *Nothofagus dombeyi*-type pollen includes *Nothofagus dombeyi*, *N. pumilio*, and *N. antarctica*. Cupressaceae pollen is attributed largely to *Austrocedrus*, although rainforest taxa (*Fitzroya*, *Pilgerodendron*) may have been long-distance contributors. Rhamnaceae pollen is likely to come from species of the genera *Discaria* and/or *Colletia*. Other taxa were grouped into ecological units: Humid forest taxa (e.g., *Hydrangea*, *Podocarpus*, *Saxegothaea*); shrubland (e.g., *Berberis*, *Discaria*, *Lomatia*, *Maytenus*); steppe (e.g., *Acaena*, *Ephedra*, Chenopodiaceae); and riparian and aquatic taxa (e.g., *Caltha*, *Cyperaceae*, *Myriophyllum*). The pollen diagrams were grouped according to modern affinities of the probable pollen contributors. The resulting pollen groups were 'Rainforest taxa', 'Xerophytic forest taxa', and 'Shrubland/steppe taxa'. Pollen zones were defined by visually identifying ecologically significant changes in pollen percentages.

Table 4.2: Radiocarbon and calibrated radiocarbon dates from Laguna La Zeta and Lago Theobald.

Core	Depth (cm)	Adjusted midpoint depth (cm)[a]	Lab no.	Material	^{14}C yr BP	Corrected ^{14}C yr error	Median probability age (cal yr BP)[b]
La Zeta lake							
LZL09A	0-0.1	0.5	n/a	inferred	0		-59
LZL09A	63-63.5	63.25	87557	pollen	835	25	706
LZL09A	148.5-149	148.75	75273	charcoal	2370	150	2352
LZL09A	239-239.5	239.25	82994	charcoal	2440	120	2460
LZL09A	307-307.5	305.75	92995	charcoal	3560	180	3798
MLZ09A	60.5-61	59.25	87549	pollen	5500	30	6243
MLZ09A	111.5-112	110.25	85986	pollen	6130	50	6937
MLZ09A	189-189.5	139.5	87550	pollen	7500	35	8267
MLZ09A	178-178.5	163.75	87551	pollen	9520	50	10713
MLZ09A	185-185.5	171.25	85987	pollen	11050	60	12940
MLZ09A	220.5-221	206.75	87552	pollen	10200	55	11901
MLZ09A	251-251.5	233.75	85988	pollen	13450	45	16636
MLZ09A	314.5-315	297.25	85989	pollen	15600	65	18763
Theobald lake							
TH09A	0-0.05	0.5	n/a	inferred	0		-59
TH09A	34-34.5	34.25	87553	pollen	410	25	452
TH09A*	58.5-59	58.75	85991	pollen	2850	75	2911
TH09A	130-130.5	130.25	85992	pollen	1170	40	1624
TH09A	236-236.5	236.25	85993	pollen	3250	55	3420
TH09A	331-331.5	331.25	85994	pollen	4710	30	5404
TH09A	354-354.5	354.25	87554	pollen	5360	40	6085
TH09A*	471-471.5	471.25	85996	charcoal	1990	130	1883
TH09A	493.5-494	492.25	87556	pollen	9500	45	10680
TH09A	528-528.5	526.25	85997	pollen	10500	50	12273

[a] Adjusted depths were used to calculate the age-depth model. Only true depths are referred to in text.
[b] Calibrated ages were based on CALIB 6.0 (Stuiver et al., 2005; http://radiocarbon.pa.qub.ac.uk/calib/calib.html).
*Not included in the chronologies.

Time-Series Analysis

In recent years, statistical methods have been used to aid in paleoenvironmental reconstructions and hypothesis testing (e.g., Birks, 1997; Marlon et al., 2008; Higuera et al., 2009). Pollen and charcoal are produced in large quantities during the growing/fire

season and accumulated constantly in the sediments (Birks and Gordon, 1985). Their records are therefore potentially biased and present numerous statistical limitations, such as stratigraphically ordered sampling (i.e., autocorrelated data), non-random data, non-linear trends, uneven sampling over time and heterogeneous variance. Thus, vegetation and fire history reconstructions require the use of analytical methods that account for these statistical issues while appropriately reflecting the processes controlling pollen and charcoal accumulation.

We were primarily interested in estimating regional trends in vegetation composition and biomass burning since the last glacial maximum, and assessing climate-vegetation-fire linkages at different scales. Efforts to reconstruct regional composite records and estimate regional trends in vegetation development and fire activity have used several approaches. One approach would be to compare trends in percentages of similar pollen types at each site, recognizing that they have different temporal resolutions (Zhao et al. 2009). A second approach, used in global reconstructions of charcoal time series (Power et al., 2008; Daniau et al., 2012), is to standardize and interpolate stratigraphic data into evenly spaced time intervals and fit cubic splines in order to estimate regional trends.

In this study, we constructed regional composite records of vegetation and fire activity by fitting Generalized Additive Models (GAM) to our forest taxa (i.e., forest pollen types to total terrestrial pollen ratio) and charcoal time series (Table 4.3). We focused on GAMs because they allow specification of the distribution of the response variable (i.e., Forest $taxa_i$ and $CHAR_i$) and the link function (i.e., the relationship between

the mean value of the response and the systematic component), and do not assume linearity (Wood, 2006). The trends provided by the GAMs overcome the limitations of compounded single-site interpretations, do not require data interpolation or standardization, and account for autocorrelation, thus avoiding the common violation of the independent-residual assumption in regression modeling.

In an attempt to achieve an optimal compromise between goodness-of-fit and parsimony, GAMs were fitted to the pollen and charcoal time series by penalized likelihood maximization, such that the model likelihood was modified by the addition of a penalty for each smooth function (Wood and Austin, 2002). All calculations and figures were made using R-programming language (R Core team, 2012) with the package mgcv, version 1.7-22 (Wood, 2002). Our response variables were based on counts (i.e., count of forest pollen types x terrestrial pollen sum^{-1} and CHAR). Poisson rate models were applied to our count data (i.e., pollen grains per sample and number of charcoal particles), which were assumed to be Poisson-distributed with means μ_i x Terrestrial pollen sum_i^{-1} and μ_i x Accumulation $rate_i$. We used a logarithmic link between the means of the pollen count and charcoal data and time to ensure that the fitted values were always non-negative. Because overdispersion was observed (i.e., the variance was larger than the mean), we also assessed the performance of models considering a negative binomial distribution. By fitting these models, we were able to highlight regional trends in vegetation composition and biomass burning, smooth site-specific variability that may reflect edaphic controls or local responses to disturbance, and overcome the limitations of sedimentary data.

Table 4.3: Model selection results.

Model	Family	AIC
Forest taxa data		
$\alpha + f(Time_i) + Site_i + \log(\text{Terrestrial pollen sum}^{-1})_i + \varepsilon_i$	Poisson	20,134
$\alpha + f(Time_i) + \log(\text{Terrestrial pollen sum}^{-1})_i + \varepsilon_i$	Poisson	29,960
$\alpha + f_1(Time_i) + Site_i + \log(\text{Terrestrial pollen sum}^{-1})_i + \varepsilon_i$	Neg. binomial	7056
$\alpha + f(Time_i) + \log(\text{Terrestrial pollen sum}^{-1})_i + \varepsilon_i$	Neg. binomial	7114
$\alpha + \beta \times Time_i + Site_i + \log(\text{Terrestrial pollen sum}^{-1})_i$	Neg. binomial	7078
Charcoal data		
$\alpha + f(Time_i) + Site_i + \log(\text{Accumulation rate})_i + \varepsilon_i$	Poisson	438,797
$\alpha + f(Time_i) + \log(\text{Accumulation rate})_i + \varepsilon_i$	Poisson	240,686
$\alpha + f(Time_i) + Site_i + \log(\text{Accumulation rate})_i + \varepsilon_i$	Neg. binomial	54,665
$\alpha + f(Time_i) + \log(\text{Accumulation rate})_i + \varepsilon_i$	Neg. binomial	58,960
$\alpha + \beta \times Time_i + Site_i + \log(\text{Accumulation rate})_i$	Neg. binomial	56,512

where forest taxa and charcoal have been modeled as smoothing functions of the concatenated time data of all sites [$f(Time_i)$] and the nominal variable $Site_i$. α is the intercept for the baseline site, $\log(\text{Terrestrial pollen sum}^{-1})_i$ and $\log(\text{Accumulation rate})_i$ are the offsets of the pollen and charcoal models, respectively, and ε_i is the i^{th} residual.

We compared the models fitted to the pollen and charcoal data based on their Akaike's Information Criterion values (AIC) and preferred the ones with lowest AIC values (Table 4.3). The AIC is a measure of the relative goodness of fit of a statistical model defined as -2 x log(likelihood) + 2p, where 2p is the number of parameters estimated in the model . The AIC attempts to optimize goodness of fit while avoiding overfitting (Akaike, 1973). Following Burnham and Anderson (2002), we considered models within two AIC units to have equal predictive ability. Although data exploration did not show clear linear patterns between initial Poisson models for either the pollen or charcoal data and time, we verified the assumption of non-linearity by also comparing the performance of our best models to that of Generalized Linear Models (GLM) with similar specifications.

Under the premise that regional long-term trends in ecosystem dynamics respond to large-scale controls, we assessed the role of climate in driving ecological change at regional scales by visually comparing the estimated trends in Holocene vegetation composition and biomass burning with independent paleoclimatic evidence. We also considered the archeological record in the region to evaluate the influence of aboriginal populations on past fire regimes.

Results

Chronologies

Nine pollen samples and three charcoal samples from the L. La Zeta site were submitted for AMS radiocarbon dating analysis. Four samples came from the lake core LZL09A and eight samples came from the bog core MLZ09A. At L. Theobald, nine pollen samples and one charcoal sample from the TH09A core were submitted for AMS dating (Table 4.2). We developed five alternative chronologies for L. La Zeta by using cubic splines and linear interpolation, and excluding individual dates from three levels, and selected a linear interpolation model which allowed for changes in sedimentation rate with different lithology (Fig. 4.2, a).

Four models were fitted to the age-depth data from L. Theobald by including all dates, and then excluding individual dates from two levels. The date corresponding with the 471 - 471.5 cm depth level was discarded as too young. We assumed it had been contaminated with modern carbon during coring or sampling (Table 4.2). All the models passed through the 95% confidence interval of the ^{14}C dates, and in no case did the overall nature of the age-depth relationship change. Given that the lithology of the

TH09A core does not suggest major changes in lithology, we selected the model that yielded the least abrupt changes in sedimentation rates (Fig. 4.2, b).

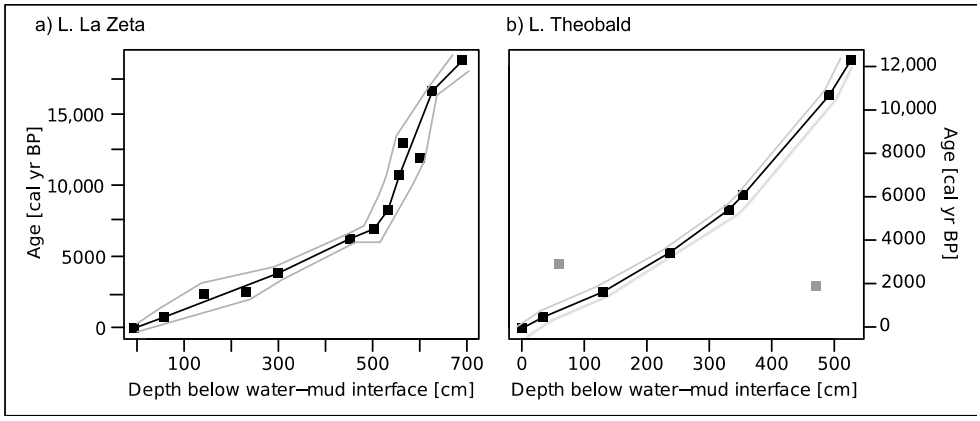


Figure 4.2: Age-depth models for a) La Zeta and b) L. Theobald. 95% confidence intervals are shown in gray. Black squares are calibrated radiocarbon ages used to develop the models, and gray squares are dates that were not included in the models.

Chronologies from L. el Trébol, L. Huala Hué, L. Padre Laguna, L. Cóndor and L. Mosquito have been published by Whitlock et al. (2006), Iglesias et al., (2012b; Chapter 3), Iglesias et al. (2012b; Chapter 3), Iglesias et al. (2012a; Chapter 2) and Whitlock et al., (2006), respectively, and their construction is not shown or discussed in this study. Comparison of the chronologies from all sites suggests that sedimentation rates are variable among lakes. A steady trend from low sedimentation rates during the late-glacial/early-Holocene transition to higher deposition in the late Holocene, however, was observed at all sites (Fig. 4.3), suggesting that sedimentation rates have increased throughout the Holocene across the region.

Lithology

L. La Zeta. Three lithological units were identified in the bog core MLZ09A (Fig. 4.3). The basal unit (Unit M1; 393 - 355.5 cm depth; 22,870 - 21,550 cal yr BP) was composed of clay and sand beds. High bulk density and magnetic susceptibility suggest that this interval was characterized by abundant allochthonous input and poorly developed soils. Unit M1 was overlain by a laminated inorganic clay unit (Unit M2; 355.5 - 270 cm depth; 21,550 - 18,770 cal yr BP), which represents a transition from dark grayish brown to dark olive brown clay. This trend reflects a gradual decrease in density and magnetic susceptibility, indicating decreased allochthonous input and changes in sediment source. At 270 cm depth, a diffuse contact marked the beginning of the uppermost gyttja unit (Unit M3, 270 - 0 cm depth; 18,770 - 5800 cal yr BP). The gyttja unit was characterized by relatively stable sedimentation rates and variable magnetic susceptibility and gamma density. The organic matter content was low at the bottom of the unit and gradually increased throughout the unit. The carbonate content profile shows overall low values. At 25 cm depth (6350 cal yr BP), these values increased to reach the maximum values of the core, and remained high until the top. The increase in carbonate content coincided with a decrease in magnetic susceptibility and gamma density and an

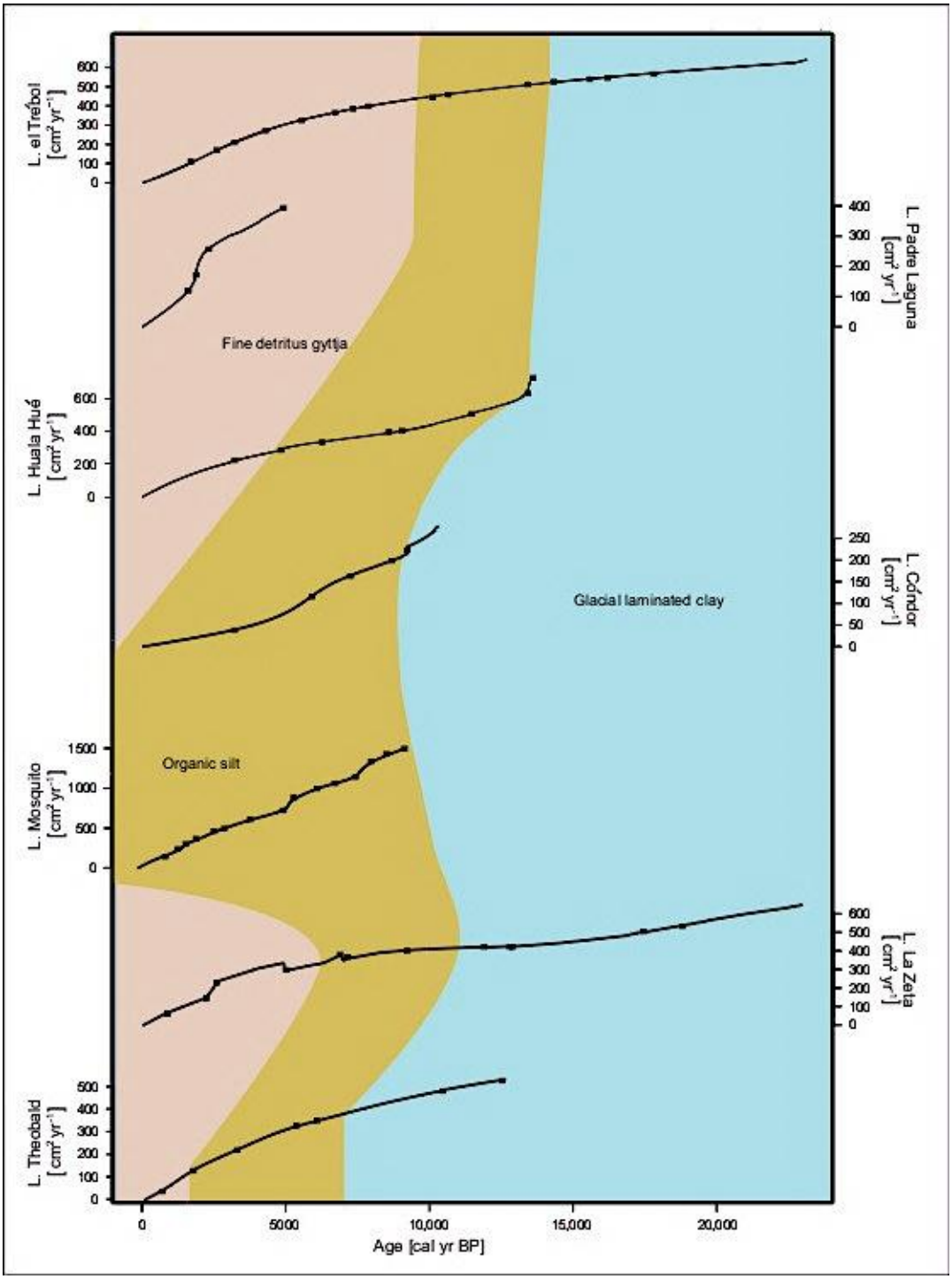


Figure 4.3: Comparative sediment accumulation rates and lithology for the L. el Trébol, L. Padre Laguna, L. Huala Hué, L. Cóndor, L. Mosquito, L. La Zeta and L. Theobald cores. Black squares show calibrated radiocarbon ages used to develop the models.

increase in organic matter content and sedimentation rates, possibly reflecting lower lake levels and the imminent establishment of the modern bog. Nineteen ash layers were identified in the core, and attributed to eruptions of Chaitén, Corcovado, Michinmahuida and possibly other volcanoes from the Andean Southern Volcanic Zone (Naranjo and Stern, 2004).

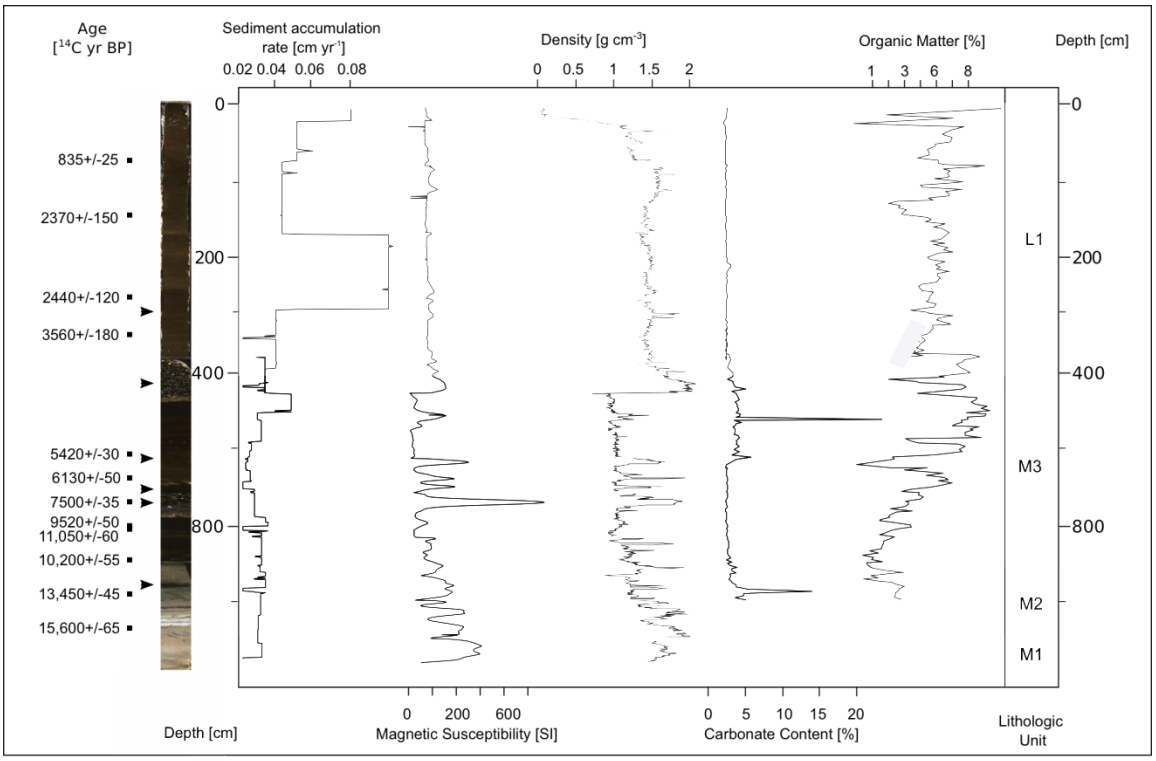


Figure 4.4: Lithology, sediment accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the LZL09A and MLZ09A cores. Black triangles indicate the position of tephra layers and black squares represent radiocarbon years. Asterisks indicate dates that were not used in the chronology.

The LZ09A lake core consisted of fine-detritus gyttja and three ash layers (Unit L1; 370 - 0 cm depth; 5930 cal yr BP - present). The magnetic susceptibility and gamma density as well as carbonate and organic matter content of the sediments showed little

variability throughout the core. A white pumiceous tephra layer in the top 5 cm of the MLZ09A core and at 368 - 370 cm depth in the LZ09A core was used to correlate the cores.

L. Theobald. L. Theobald core TH09B was composed of fine-detritus gyttja (Fig, 4.4). Based on changes in color, magnetic susceptibility, gamma density, carbonate and organic matter content, three lithological units were identified. The basal unit (Unit 3, 532 - 290 cm depth; 12,450 - 4430 cal yr BP) consisted of high-density, magnetically enriched dark brown sediments with very dark grayish brown beds. Sedimentation rates were low, and carbonate and organic matter content was variable. The basal unit was overlain by magnetically poor very dark brown silt (Unit 2, 290 - 108 cm depth; 4430 - 1340 cal yr BP). Sedimentation rates and carbonate content of the sediments were significantly higher than in the previous unit. We did not observe pronounced changes in gamma density or organic matter with respect to older sediments. The uppermost unit (Unit 3, 108 - 0 cm depth; 1340 cal yr BP - present) was characterized by dark olive brown to dark brown gyttja. Sediment accumulation rates, gamma density and carbonate content were relatively high at the bottom of the unit and gradually decreased throughout the section. The organic matter profile showed the opposite trend, with lower values at the bottom and high values towards the top, suggesting an increase in lake productivity.

Lithologies from the cores obtained at L. el Trébol, L. Huala Hué, L. Padre Laguna, L. Cóndor and L. Mosquito are not described in detail in this study, as they have been published by Whitlock et al. (2006), Iglesias et al., (2012b; Chapter 3), Iglesias et al. (2012b; Chapter 3), Iglesias et al. (2012a; Chapter 2) and Whitlock et al., (2006),

respectively. Although the ages of the boundaries of the main lithological units vary among sites, sequential transitions in sediment type from glacial laminated clay to Holocene organic silt/fine detritus gyttja were observed in all cores (Fig. 4.3). The lithological change was associated with higher-than-before sedimentation rates, suggesting that increased lake productivity rather than erosion has been the main source of material to the lakes since the last glaciation.

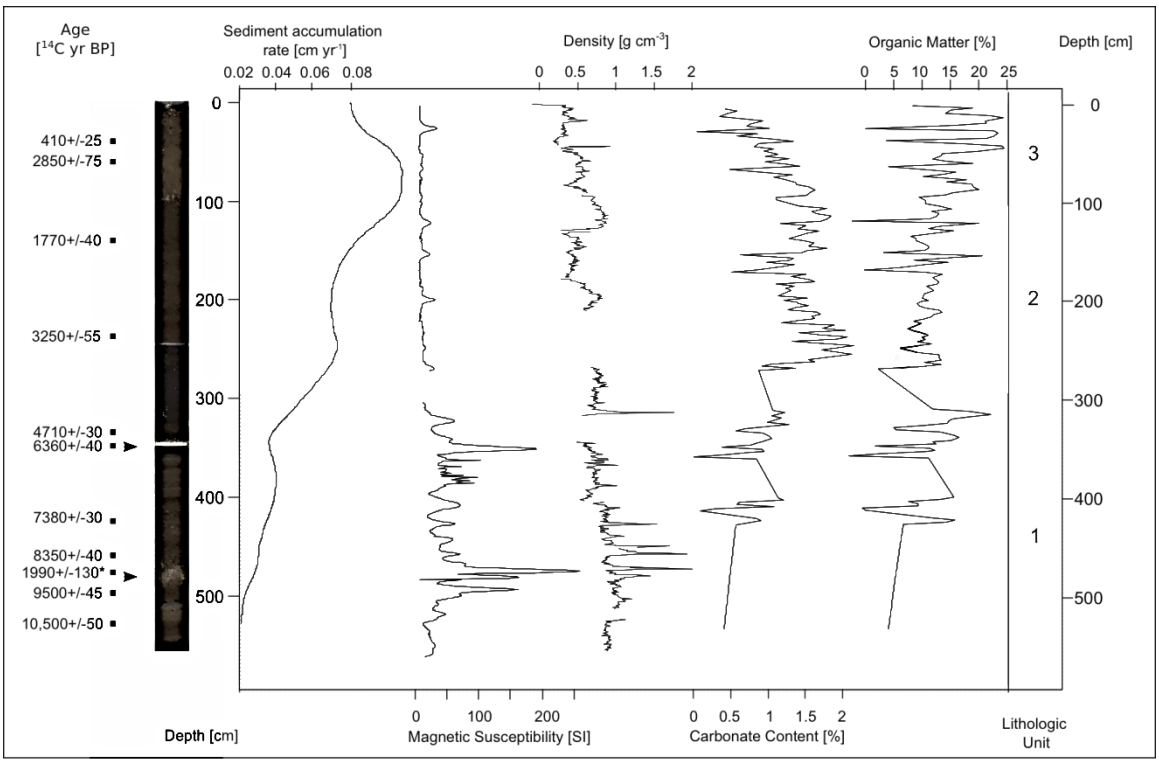


Figure 4.5: Lithology, sediment accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the TH09A core. Black triangles indicate the position of tephra layers and black squares represent radiocarbon years. Asterisks indicate dates that were not used in the chronology.

The Pollen and Charcoal Records

The charcoal and pollen stratigraphy was broadly similar among sites (Figs. 4.6, 4.7, 4.8 and 4.9). Changes in vegetation during the last 23,000 years are summarized in Figure 4.10. Cubic splines were used to smooth the forest and shurbland taxa time series and facilitate their comparison. Vegetation types (i.e., steppe, parkland, shurbland and forest) were defined following Markgraf and D'Antoni (1978) and Páez et al. (2001). Their modern pollen studies suggest that forest is characterized by percentages of arboreal pollen types (e.g., *Nothofagus dombeyi*-type, Cupressaceae, *Podocarpus*) > 70% and pollen influx > 8000 grains cm^{-3}. Shrubland is based on pollen percentages of shrub pollen types (e.g., *Berberis*, *Discaria*, *Maytenus*) > 4% and arboreal pollen types <70%. Parkland is inferred from arboreal pollen types >60% and pollen influx < 5000 grains cm^{3}. Steppe is characterized by Poaceae and steppe pollen types (e.g., *Acaena*, *Ephedra*, Chenopodiaceae) > 45%.

Based on shifts in dominant species abundance and trends in CHAR, and the inferred vegetation at each site, the vegetation and fire history of the study area was divided into four phases:

1. Late-glacial steppe (>16,000 cal yr BP). At L. el Trébol and L. La Zeta, sediments older than 16,000 cal yr BP were dominated by Poaceae (32 – 53% at L. el Trébol; 23 – 78%, at L. La Zeta), Asteraceae (<4% at L. el Trébol; <18% at L. La Zeta) and other shrubland and steppe taxa pollen (8 – 22% at L. el Trébol; 3 – 38% at L. La Zeta). *Nothofagus dombeyi*-type pollen was low (<55% at both sites). Comparison to modern samples indicates that these sites supported steppe vegetation (Páez et al., 2001).

PAR values were low, particularly at L. La Zeta, where they remained <12,000 grains cm^{-2} yr^{-1} throughout the period, suggesting sparse vegetation cover. Low CHAR (<0.03 particles cm^{-2} yr^{-1} at both sites) indicates that fire was not an important element of the system.

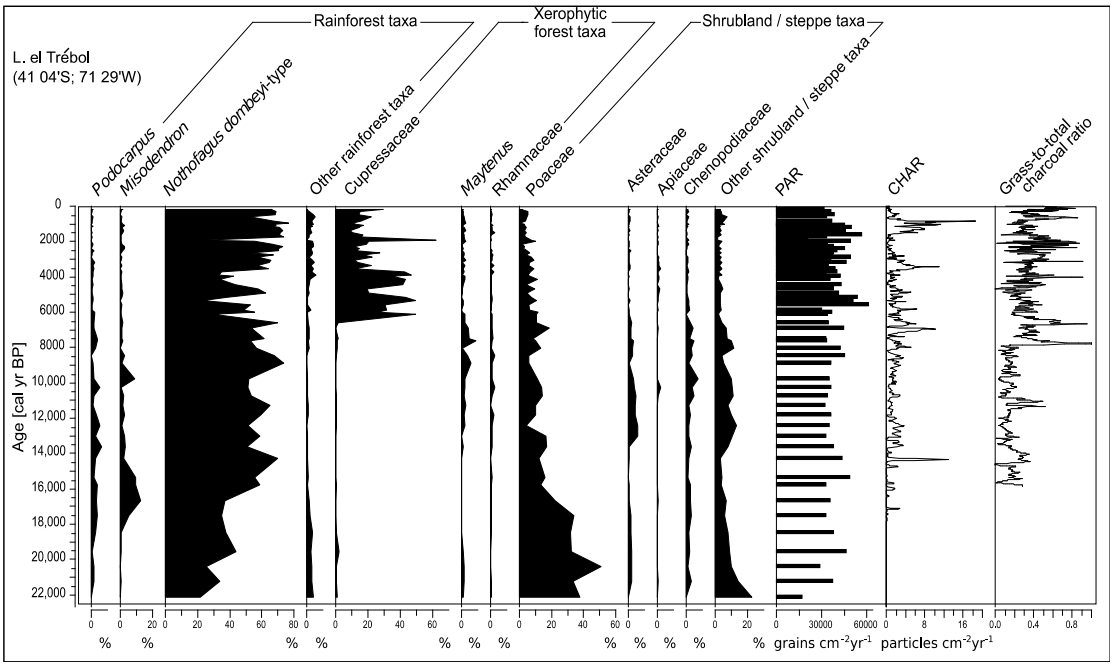


Figure 4.6: Selected pollen and charcoal data for L. el Trébol.

2. Late-glacial/early-Holocene parkland (ca. 16,000 - 8200 cal yr BP). At ca. 16,000 cal yr BP, percentages of *Nothofagus dombeyi*-type pollen increased from ca. 30% to >73% at both L. el Trébol and L. La Zeta and showed little variability thereafter, with the exception of the ca. 13,900 to 12,500 cal yr BP period at L. La Zeta, when it decreased to 31% and rapidly rose to 71%. Asteraceae (<3% at L. el Trébol; <5% at L. La Zeta), Chenopodiaceae (<2% at L. el Trébol; <3% at L. La Zeta) and other shrubland/steppe taxa (<14% at L. el Trébol; <6% at L. La Zeta), such as *Berberis*,

Escallonia and *Gevuina*, were abundant. Poaceae values were lower than before (<25% at both sites).

At L. Huala Hué, *Nothofagus dombeyi*-type and Asteraceae pollen decreased from 88 to 38% and 18 to 3% after 11, 125 cal yr BP, whereas Poaceae, Rhamnaceae, *Maytenus* and other shrubland and steppe taxa increased from 2 to 17%, 1 to 6%, 1 to 3.5%, and 2 to 6%, respectively. L. Cóndor and L. Mosquito featured pollen assemblages dominated by *N. dombeyi*-type (<69%), Rhamnaceae (<7%), Chenopodiaceae (<12%) and other shrubland and steppe taxa (<19%). *N. dombeyi* pollen-type fluctuated between 19 and 69% at L. Theobald, where Poaceae (<29%), Rhamnaceae (<19%) and other shurbland/steppe taxa (<17%; e.g., *Escallonia* and *Gevuina*) were also present. Modern pollen samples indicate that *Nothofagus*-dominated parkland (probably *N. antarctica*) prevailed in the L. el Trébol, L. Cóndor, L. Mosquito and L. La Zeta watersheds, and *Nothofagus* and Rhamnaceae dominated L. Huala Hué and L. Theobald (Markgraf and D'Antoni, 1978). PAR was low (<15,000 grains cm^{-2} yr^{-1} at all sites), suggesting that the ecosystem was colonized by woody species but vegetation cover was patchy. CHAR values increased to <20 particles cm^{-2} yr^{-1} at all sites, implying that biomass burning was higher than before. Grass-to-total charcoal ratios <0.4 indicate that fires burned predominantly woody fuels.

3. Middle Holocene shrubland (ca. 8200 - 4500 cal yr BP). *Nothofagus dombeyi*-type (<78% at all sites), Asteraceae (<3% at all sites) and Chenopodiaceae (<12% at all sites) pollen percentages and PAR (<15,000 grains cm^{-2} yr^{-1} at all sites) were similar to the previous assemblage. Cupressaceae pollen percentages rose at all sites, suggesting a

regional increase in *Austrocedrus* abundance. *Austrocedrus* influx data and percentage data indicate that, by 4500 cal yr BP, its geographic distribution was similar to present. Rhamnaceae and *Maytenus* pollen gradually decreased at all sites from <7% to <2% each, except at L. Zeta, where the opposite trend was observed (0 to 1.5%, and 1 to 4%,

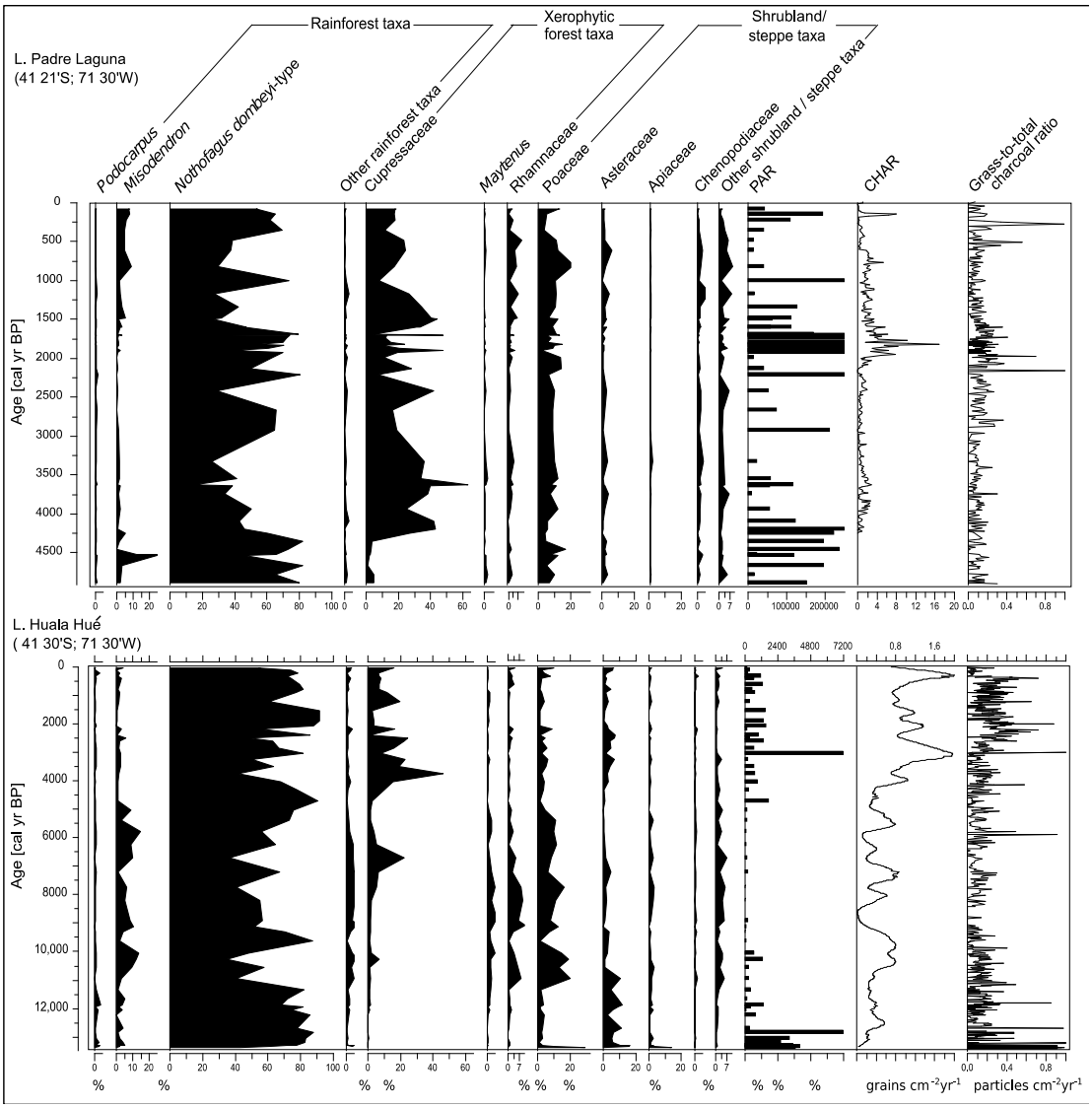


Figure 4.7: Selected pollen and charcoal data for a) L. Padre Laguna and b) L. Huala Hué.

respectively). Comparison with modern samples suggests shrubland vegetation grew at all sites (Markgraf and D'Antoni, 1978).

The fire regime was heterogeneous in the study area. At L. el Trébol, L. Huala Hué and L. Mosquito, CHAR values were similar to those observed in the previous period (CHAR <20 particles cm^{-2} yr^{-1}). At 7600 cal yr BP, grass-to-total charcoal ratio increased from 0.2 to 0.8 at L. el Trébol, suggesting that although biomass burning did not change significantly, grass fires were more prevalent. L. Cóndor (CHAR up to 4.1 particles cm^{-2} yr^{-1}), L. La Zeta (CHAR up to 14 particles cm^{-2} yr^{-1}) and L. Theobald (CHAR up to 0.8 particles cm^{-2} yr^{-1}) watersheds experienced increased biomass burning in the shrubland period as compared with fire activity during the previous open parkland period.

4. Late-Holocene *Nothofagus dombeyi-Austrocedrus chilensis* forest (ca. 4500 cal yr BP - present). After 4500 cal yr BP, pollen records indicate a general increase of *Nothofagus dombeyi*-type and Cupressaceae pollen (<58%; probably *A. chilensis;* Fig. 4.11) at expense of Poacaeae (<40%), Rhamnaceae (<15%) and other shrubland and steppe taxa (<10%). At L. el Trébol, L. Cóndor and L. Theobald, *N. dombeyi*–type pollen values increased from 20 to 74%, 45 to 64%, and 44 to 83%, respectively. L. Padre Laguna, L. Mosquito and L. La Zeta watersheds, on the other hand, showed pronounced variability in *Nothofagus* percentages, fluctuating between ~30 and 80%. Modern pollen samples suggest that mixed *Nothofagus-Austrocedrus* forest developed in the area during this period. The lower treeline was located east of L. Trébol, L. Huala Hué and L. Padre Laguna, and west of L. Cóndor, Mosquito, L. La Zeta and L. Theobald. The last four sites

were dominated by shrubland vegetation, as inferred from a comparison with modern pollen assemblages (Markgraf and D'Antoni, 1978; Páez et al., 2001).

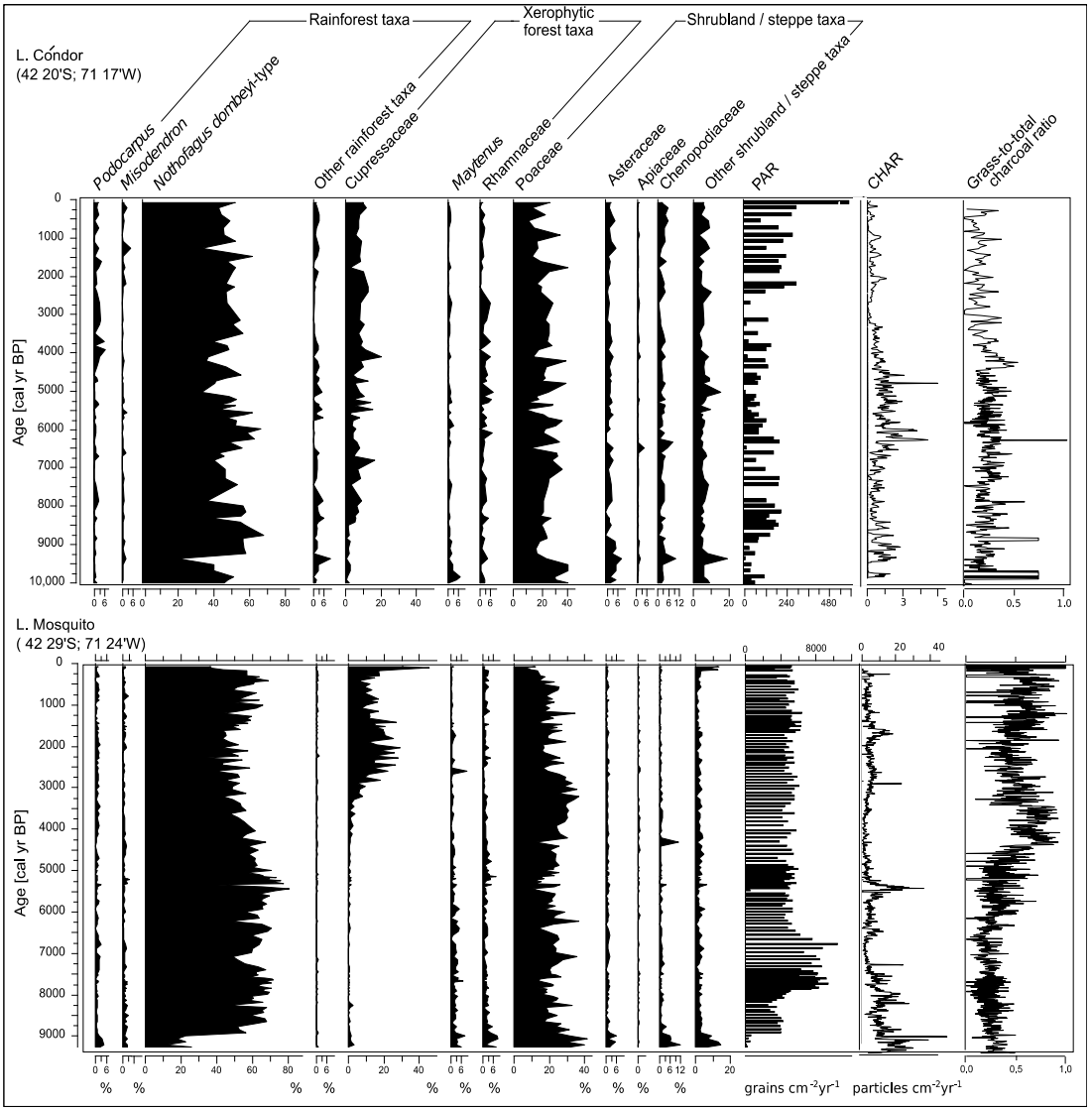


Figure 4.8: Selected pollen and charcoal data for a) L. Cóndor and b) L. Mosquito.

The Holocene expansion of *Austrocedrus*, inferred from the rise in Cupressaceae pollen percentages, was spatially and temporally variable. It expanded at the eastern limit of its range (i.e., L. Cóndor) as early as ca. 8000 cal yr BP (Cupressaceae <9%) but was

not a abundant at nearby at L. Mosquito until ca. 4000 cal yr BP, when Cupressaceae rose from 1 to 25%. After the regional expansion of *Austrocedrus* (Cupressaceae >4% at all sites), millennial-scale shifts between *N. dombeyi*-type and *Austrocedrus* pollen percentages were observed in all the pollen records.

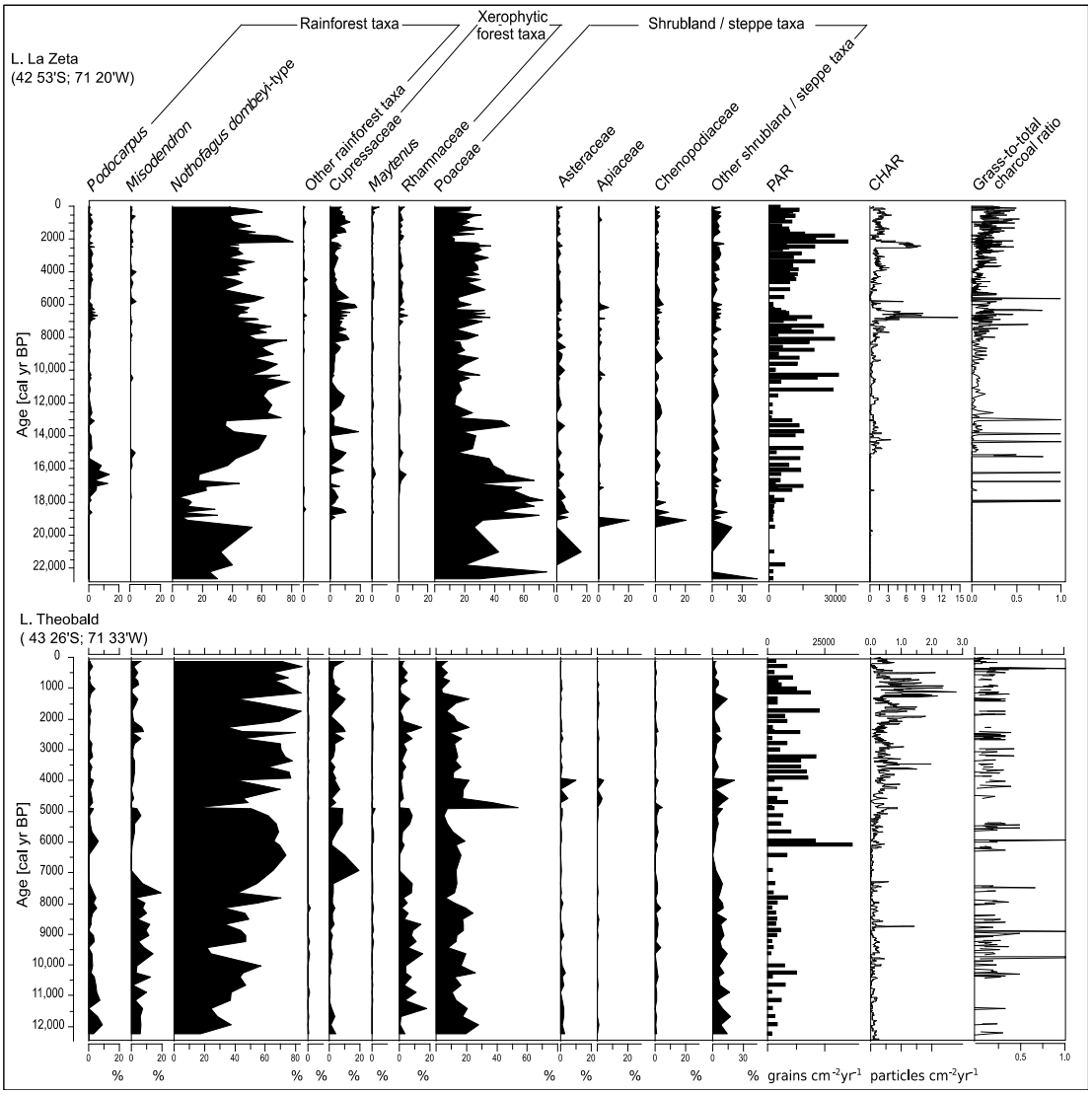


Figure 4.9: Selected pollen and charcoal data for a) La Zeta and b) L. Theobald.

During the late Holocene, total PAR reached its maximum values at all sites, suggesting the development of closed forest. Despite the fuel availability, fire regimes were spatially and temporally variable. Levels of biomass burning increased at L. Huala Hué (CHAR >0.3 particles cm^{-2} yr^{-1}), L. Mosquito (CHAR >2 particles cm^{-2} yr^{-1}) and L. Theobald (CHAR >0.4 particles cm^{-2} yr^{-1}) at the beginning of the period. At L. Huala Hué, a rise in the grass-to-total charcoal ratio to 0.8 units indicates that Poaceae (possibly *Chusquea*) burning increased at 2300 cal yr. A similar shift from wood-dominated fuels

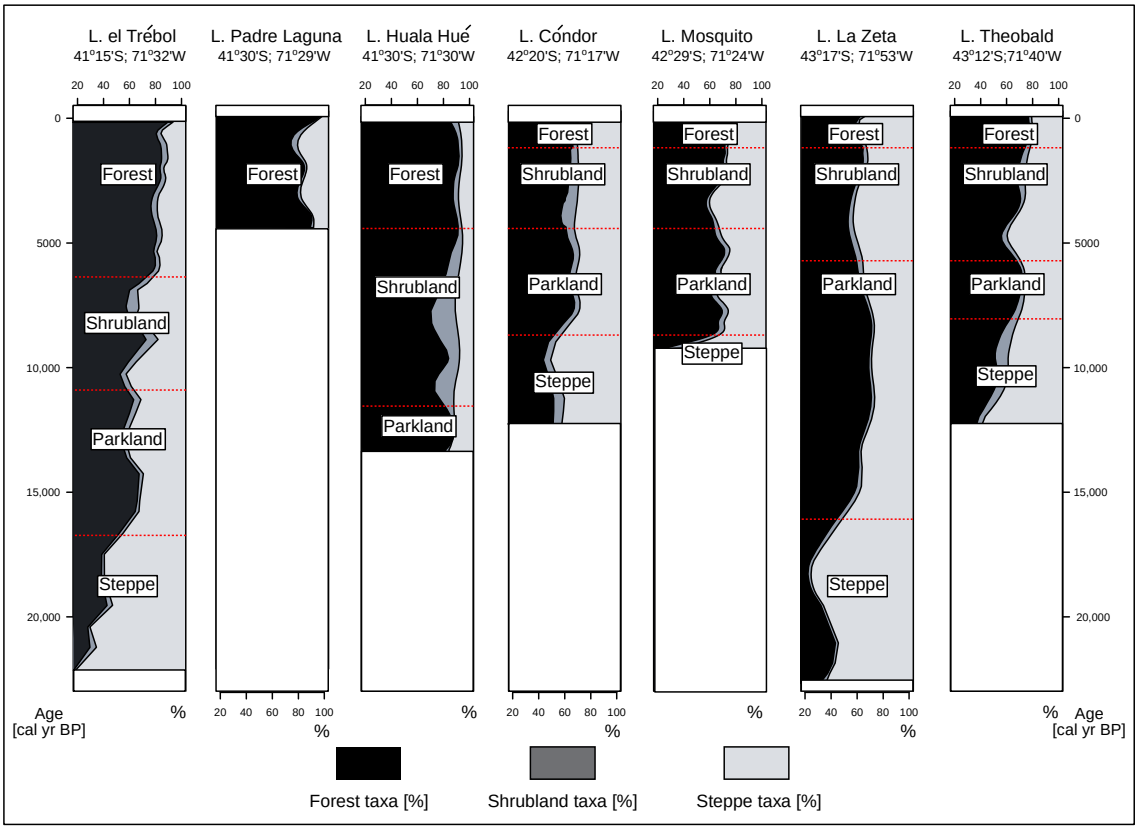


Figure 4.10: Relative proportion of forest, shrubland and steppe taxa as reconstructed from smoothed pollen percentages. The dashed lines show boundaries between pollen zones. Vegetation types are based on Markgraf and D'Antoni (1978) and Páez et al. (2001).

occurred at L. Mosquito at 4250 cal yr BP (grass-to-total charcoal ratio < 0.5) and at L. La Zeta (grass-to-total charcoal ratio < 1) at ca. 4000 cal yr BP. CHAR decreased at L Cóndor from 1.3 to 1 particles cm^{-2} yr^{-1} at 4500 cal yr BP, and the grass-to-total charcoal ratio (<0.3) was lower than before, suggesting a decrease in biomass burning and in particular, grass fires. CHAR levels showed little variation at L. el Trébol or L. Padre Laguna, indicating that biomass burning remained relatively high at those sites.

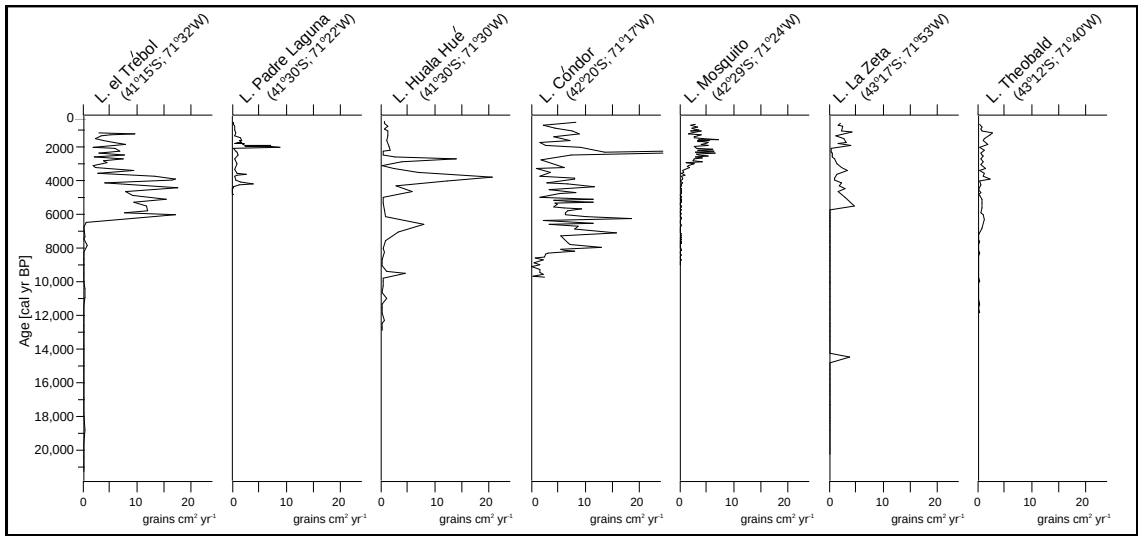


Figure 4.11: Cupressaceae pollen accumulation rates for L. el Trébol, L. Padre Laguna, L. Huala Hué, L. Cóndor, L. Mosquito and L. La Zeta and L. Theobald.

Time Series Analysis Results

Overall, ca. 23,000 years of data, encompassing 553 pollen samples and 5873 charcoal samples were used to construct regional composite records and estimate regional trends in vegetation and fire activity. In the case of the relative abundance of forest taxa as reconstructed from the counts of forest taxa pollen types (Forest $taxa_i$), a GAM [1] fitted by maximum likelihood that assumed Forest $taxa_i$ to be negative binomial-

distributed with mean μ_i x Terrestrial pollen sum_i^{-1} and variance μ_i x Terrestrial pollen sum_i^{-1} + (μ_i x Terrestrial pollen sum_i^{-1})^2/2.3 outperformed all the other models (Δ AIC>22; Table 4.3; Fig. 4.12):

[1] Forest $taxa_i = e^{(\alpha + f(Time)_{i\,4.2} + Site_i + \log(\text{Terrestrial pollen sum})_i^{-1} + \varepsilon_i)}$

where the i^{th} ratio of forest pollen types to terrestrial pollen sum in the time series was modeled as a smoothing function of the concatenated time series of all sites [$f(Time_i) = \sum_{j=i}^{n} s(Time_{ij})$; with n= total number of covariates, and $s(Time_{ij})$= smoothing function], and the nominal variable, $Site_i$. $\log(\text{Terrestrial pollen sum}^{-1})_i$ is the offset and ε_i, the residual error.

L. Padre Laguna was arbitrarily chosen by the model as the baseline site, which thus defines the base intercept, α. α was estimated to be 11.09 (standard error=0.15; z-val=72.85; $p<0.001$). The intercepts for the other sites (i.e., $Site_i$) were 11.79 (standard error=0.19; z-val=-3.77; p=3.54) for L. el Trébol, 11.55 (standard error=0.21; z-val=2.22; p=0.02) for L. Huala Hué, 11.51 (standard error=0.19; z-val=-2.21; p=0.02) for L. Cóndor, 10.91 (standard error=0.17; z-val=-1.07; p=0.28) for L. Mosquito, 10.83 (standard error=0.19; z-val=-1.36; p=0.57) for L. La Zeta and 10.97 (standard error=-0.57; z-val=-0.56; p=0.57) for L. Theobald. The model explained 55.5% of the deviance (i.e., quality of fit calculated as Deviance=2*[(maximized log likelihood of the model of interest) – (log likelihood of the saturated model)]).

The postglacial trend in regional biomass burning as inferred from charcoal data was best detected by a GAM [2] that assumed $Charcoal_i$ to be negative binomial-distributed with mean μ_i x Accumulation $rate_i$ and variance μ_i x Accumulation $rate_i$ + (μ_i

x Accumulation rate$_i$)^2/10.5. The GAM explained 59.4% of the deviance (Δ AIC>153; Table 4.3; Fig. 4.12):

[2] $\text{Charcoal}_i = e^{(\alpha + f(\text{Time})_{i\,19.9} + \log(\text{Accumulation rate})_i + \text{Site}_i + \varepsilon_i)}$

where the i^{th} Charcoal count per unit of accumulation rate is a function of time [$f(\text{Time}_i) = \sum_{j=i}^{n} s(\text{Time}_{ij})$; with n=total number of covariates, and $s(\text{Time}_{ij})$ is a smoothing function], $\log(\text{Accumulation rate})_i$ is the offset, and ε_i, is residual error.

The intercept for the baseline site (i.e., L. Padre Laguna), α, was estimated to be 6.05 (standard error=0.02; z-val=302; p<0.001). The interecepts for the remaining sites, Site_i, were 7.83 (standard error=0.02; z-val=74; p<0.001) for L. el Trébol, 6.15 (standard error=0.02; z-val=4.23; p<0.001) for L. Huala Hué, 6.95 (standard error=0.02; z-val= 34.56; p<0.001) for L. Cóndor, 5.00 (standard error=0.02; z-val=-47.19; p<0.001) for L. Mosquito, 7.11 (standard error=0.02; z-val=71.80; p<0.001) for L. La Zeta and 5.30 (standard error=0.02; z-val=-30.54; p<0.001) for L. Theobald. The results of both models are expressed on logarithmic scale.

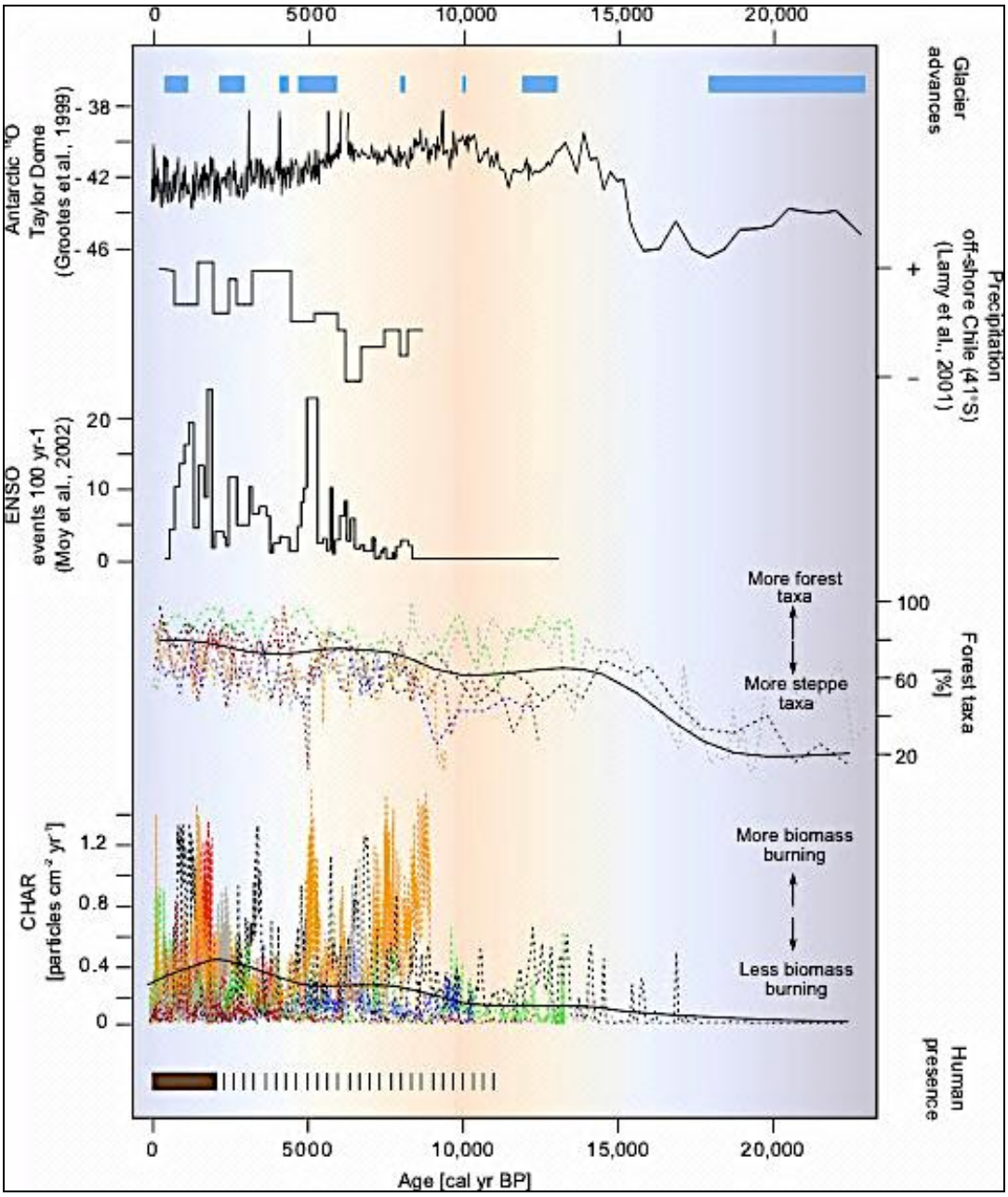


Figure 4.12: Glacier advances (Porter, 2000; Mayewski et al., 2004; Douglass et al., 2005), oxygen isotope ratios from Taylor Dome (Grootes et al., 1999), precipitation off-shore Chile at 41˚S (Lamy et al., 2001), ENSO (Moy et al., 2002), regional trends in forest taxa percentages and CHAR. Pollen percentages of forest taxa and CHAR time series for L. el Trébol (black), L. Padre Laguna (red), L. Huala Hué (green), L. Cóndor (blue), L. Mosquito (orange), L. La Zeta (gray) and L. Theobald (brown) are shown with dashed lines. Human numbers were sparse until ca. 2000 cal yr BP (vertical lines). The last 2000 years of high population density is shown with squares (Bellelli, 2007; Bellelli et al., 2003, Podesta et al., 2007; Fernandez et al., 2011).

Discussion

Vegetation and Fire History of the Forest/Steppe Ecotone

Visual comparison of the pollen and charcoal data with paleoclimate reconstructions suggest a close association between forest taxa abundance and biomass burning in northern Patagonia and temperature, as inferred from oxygen isotopes ratios from the Vostok ice core (Grootes et al., 1999); precipitation, as reconstructed from terrigenous sediments in a marine core collected off the coast of Chile (lat. 41˚S; Lamy et al., 2001); and a record of ENSO developed from a laminated sediment core retrieved from Laguna Pallcacocha (southern Ecuadorian Andes; Moy et al., 2003). These relations suggest that climate was the broad-scale driver of paleoenvironmental change along the Patagonian forest-steppe ecotone.

During the Last Glacial Maximum (LGM; ca. 23,000 – 19,000 cal yr BP), >500,000 km^3 of glacier ice volume extended along the Patagonian Andes between 38 and 55°S (Hulton et al., 2002). The Antarctic circumpolar current and the Southern Westerlies shifted equatorward by several degrees of latitude relative to their present position in response to a steepened pole-to-Equator temperature gradient. These changes in ocean and atmospheric circulation lowered sea-surface temperatures by ca. 6 °C along the Pacific coast (Lamy et al., 1999) and decreased precipitation throughout Patagonia (Markgraf et al., 1981). Such cold, dry and windy conditions, in addition to extensive glaciation, altered vegetation and led to the extirpation of several plant species over much of their current range. On the eastern flanks of the Andes, climate generalists survived in

unglaciated regions east of the ice sheets and periglacial areas, where open grass-dominated steppe was prevalent (Figs. 4.6, 4.9, a and 4.10).

Deglaciation began at ca. 17,500 cal yr BP (Hulton et al., 2002) and rapid glacial recession continued until ca. 13,000 cal yr BP. Although the Younger Dryas has not been recorded in South America (Glasser et al., 2004), glacier re-advance in northern Patagonia has been inferred from sediments from Lago Mascardi (Argentina; Ariztegui et al, 1997) and Lago Huelmo (Chile), suggesting that the late glacial/early Holocene transition was punctuated by a cold event known as Huelmo-Mascardi Cold Reversal (11,400 to 10,200 ^{14}C yr [ca. 13,300 to 11,870 cal yr BP]; Hajdas et al., 2003). This interpretation contrasts with data from marine cores off the coast of Chile (Lamy et al., 2004) and geomorphological studies south of lat. 41˚S (Andersen et al., 1995; Lowell et al, 1995) where evidence of glacier advances has not been found.

The late-glacial lithologies in our cores show a shift from inorganic clay with beds of magnetically enriched sediment to organic laminated clay (e.g., L. Huala Hué [Iglesias et al., 2012 b; Chapter 3], L. el Trébol [Whitlock et al., 2006]), suggesting that an initial period characterized by intermittent pulses of erosion and slope instability was followed by fluctuations of coarse- and fine-sediment deposition. This transition is consistent with sparsely vegetated periglacial landscapes that became more stabilized at 14,070 cal yr BP at L. el Trébol, at ca. 13,300 cal yr BP at L. Huala Hué, and at ca. 18,070 at L La Zeta (Fig. 4.3). L. Cóndor and L. Mosquito experienced an initial period of wetland development prior to lake formation, although at different times (Whitlock et al., 2006; Iglesias et al., 2012a; Chapter 2).

Vegetation changes during deglaciation have been attributed to a shift in dominance from year-long polar air masses during the glacial period to more humid Pacific air during the Holocene (Heusser, 2003). Along the transect, the vegetation was initially open at all latitudes and became progressively more forested. At L. el Trébol and L. La Zeta, percentages of *Nothofagus dombeyi*-type pollen increased from 30 to 65% at ca. 16,000 cal yr BP and showed little variability thereafter, possibly reflecting invasion of disturbance-resistant and disturbance-resilient species, including *Nothofagus antarctica*. Asteraceae, Chenopodiaceae, and initial establishment of a discrete forest/steppe ecotone along the transect. The northernmost sites that we studied (i.e., L el Trébol, L. Huala Hué) featured parkland vegetation as early as 16,000 cal yr BP and were located near the lower (eastern) margin of the forest/steppe boundary. In contrast, southern sites (i.e., L. Cóndor, L. Mosquito L. La Zeta and L. Theobald) supported steppe vegetation at this time, suggesting that the forest/steppe border lay farther west and at higher elevations south of lat. 41˚S. The increase of woody taxa, such as *Colletia*, *Discaria* and *Maytenus*, throughout the region after ca. 16,000 cal yr BP provided fuels, resulting in more biomass burning than in previous times (Figs. 4.6, 4.7, 4.8, 4.9 and 4.10). Subsequent vegetation development also shows similar latitudinal differences in that the changes occurred first in the northern sites (north of lat. 41˚S) and later in the southern ones (Fig. 4.10). This latitudinal gradient in vegetation response was probably driven by a precipitation regime characterized not only by a west-to-east gradient but also by decreasing north-to-south annual precipitation, similar to the present pattern in the study region.

All but one site in this study show no changes consistent with a Huelmo-Mascardi Cold Reversal, suggesting that either the magnitude of the environmental change was small relative to the fundamental niche of the dominant species or detection of environmental change at the time was constrained by the low diversity of pollen types (e.g., *Nothofagus dombeyi*-type, Poaceae). At L. La Zeta, a pronounced decline in *N. dombeyi*-type and PAR along with an expansion of disturbance- and/or cold-adapted taxa (e.g., Poaceae, Asteraceae) occurred between ca. 13,900 and 12,930 cal yr BP (Fig. 4.9, a). This inferred shift in vegetation composition may have been a response to cooling during the Huelmo-Mascardi Cold Reversal, but the local nature of the change suggests a non-climatic explanation.

The composition of the forest/steppe ecotone during the late-glacial/early-Holocene transition (ca. 13,000 to ca. 8,200 cal yr BP) was temporally and spatially heterogeneous and significantly different than at present. Although *Nothofagus* was the dominant tree at the forest/steppe boundary, pollen data suggest that shrubland and steppe taxa were abundant near L. el Trébol and L. Huala Hué after ca. 11,200 cal yr BP; in the L. Mosquito - L. Cóndor- L. La Zeta area after ca. 9200 cal yr BP; and in the L. Theobald watershed after ca. 11,000 cal yr BP. *Colletia*, *Discaria*, *Maytenus*, *Berberis*, and other shrubs probably constituted the woody component of the ecotone along with *Nothofagus*. As a result of the near-absence of *Austrocedrus* in the study area, the reconstructed *Nothofagus* and shrub-dominated vegetation has no analogs in the modern landscape or pollen rain (Markgraf et al., 1981; Páez et al., 2001). Genetic (Pastorino and Gallo, 2002) evidence supports our interpretation by implying that *Austrocedrus* populations

were likely small and restricted to areas near the steppe and possibly in intermountain valleys at lat. 41˚S (Fig. 4.12).

Latitudinal differences in the timing of the steppe-to-parkland/shrubland transition are attributed to decreasing north-to-south annual precipitation along the transect that affected the vegetation and fire regime. Woody species richness and abundance at present are controlled by water availability, as carbon fixation and resource allocation to woody and above-ground structures are limited by water stress (Schulze et al., 1996). Thus, differences in moisture variability would have allowed the northern watersheds (e.g., L. el Trébol and L. Huala Hué) to support shrub populations, while parkland grew in the southern ones (e.g., L. Cóndor, L. Mosquito, L. La Zeta and L. Theobald). Alternatively, burning at L. Cóndor, L. Mosquito, L. La Zeta and L. Theobald (CHAR<20 particles cm^{-2} yr^{-1} at the 3 sites) between 13,000 and 8200 cal yr BP (as opposed to L. el Trébol, L. Huala Hué and L. Theobald, where CHAR <3 particles cm^{-2} yr^{-1}) apparently precluded shrub recruitment in parkland-dominated ecosystems (Figs. 4.6, 4.7, 4.8, 4.9 and 4.10). Evidence from the pollen records shows that increases in shrub percentages are not concurrent with (nor immediately follow) shifts in CHAR or the grass-to-total charcoal ratio, suggesting that even though fire might have affected vegetation composition, low effective moisture was the most likely limiting factor of shrub expansion.

Cooler and/or effectively wetter conditions than before have been inferred from paleoenvironmental records throughout Patagonia during the middle Holocene (ca. 8200-4500 cal yr BP) and attributed to decreasing annual insolation and amplification of the seasonal cycle of insolation (Berger and Loutre, 1991). Lower annual insolation is likely

to have been coupled with lower-than-before winter and annual temperatures and strengthened Southern Westerlies, resulting in more precipitation throughout western Patagonia (Lamy et al., 1999; Fletcher and Moreno, 2011). Increased precipitation and decreased evaporation are consistent with evidence of higher-than-before lake levels north of lat. 40°S (Jenny et al., 2003; Bertrand et al., 2009), renewed mountain glaciation south of this latitude (Porter, 2000; Mayewski et al., 2004; Douglass et al., 2005), and sea-ice expansion in the Atlantic sector of the Southern Ocean (Lamy et al., 1999; Liu et al., 2003). Increased effective moisture also explain forest advances and reduced fire activity between lat. 40 and 50°S observed in high-resolution pollen and charcoal records from Argentina and Chile (Moreno, 2004; Mancini et al., 2005; Markgraf et al., 2007; Whitlock et al., 2007; Abarzua and Moreno, 2008; Wille and Schaebitz, 2009).

During the middle Holocene, the forest/steppe ecotone supported shrubland vegetation at L. el Treébol and L. Huala Hué, and parkland vegetation at the remaining sites and advanced eastward into steppe (Fig. 4.10). Biomass burning increased in most watersheds (i.e., L. el Trébol, L. La Zeta, L. Theobald) at ca. 8000 cal yr BP and remained high until present. Along with these environmental changes, a pronounced increase in *Austrocedrus* population size is inferred from a dramatic rise in Cupressaceae pollen percentages and accumulation rates along the transect (Fig 4.11). Comparison of pollen data reveals decreasing Cupressaceae pollen influx from east to west and north to south after ca. 8000 cal yr BP, with the highest values recorded at L. Cóndor and L. Huala Hué and the lowest at L. Theobald and L. Mosquito. This trend changed at ca. 4500 cal yr BP, when large *Austrocedrus* populations developed near L. el Trébol, L.

Huala Hué and L. Padre Laguna and *Austrocedrus*' geographic distribution became similar to present.

The resulting spatio-temporal pattern is consistent with an expansion of the taxon from glacial refugia in the steppe, possibly in the unglaciated terrain in the L. Cóndor area, and in the northern section of the study area (L. Huala Hué). Genetic evidence supports this interpretation, suggesting that *Austrocedrus* persisted east of its present distribution and at 41°S during the last glaciation. Low allelic variants detected in modern *Austrocedrus* populations are indicative of historical bottlenecks, possibly matching the evidence of significant small refugia. Moderate levels of heterozygosity also suggest rapid deglacial population growth (Pastorino and Gallo, 2002). Although pollen and genetic data support the existence of steppe glacial refugia and high *Austrocedrus* colonization rates during the Holocene, our results cannot identify the number of refugia nor their specific location. Our records indicate early-Holocene populations between 41°S and 42°S, but additional research is necessary to determine if other populations were present north of L. Nahuel Huapi.

The modern forest, co-dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*, developed at ca. 4500 cal yr BP (Figs. 4.10), probably in response to increased effective moisture. Wetter conditions are likely related to the northward shift and strengthening of the Southern Westerlies, as well as intensification of ENSO-related climate variability (Lamy et al., 2001; Markgraf et al., 2007). Lower treeline was located east of L. el Trébol, L. Padre Laguna and L. Huala Hué during the late Holocene. In contrast, L. Cóndor, Mosquito, L. La Zeta and L. Theobald supported shrubland

vegetation, while the forest margin lay at higher elevations to the west (Fig. 4.10). As a result, a pronounced eastward expansion of forest taxa in the northern part of the transect (e.g. L. el Trébol, L. Padre Laguna, L. Huala Hué) contrasts with the moderate advance of forest into steppe at the southern sites (e.g. L. Cóndor, L. Mosquito, L. La Zeta, L. Theobald).

Shrubland/steppe expanded at all sites between ca. 4000 and 2000 cal yr BP and decreased in abundance after 2000 cal yr BP (Fig. 10). These shifts in shrubland/steppe taxa distribution suggest that vegetation zones were geographically broader in the early late Holocene (4500 to 2000 cal yr BP) than they are at present and that the modern steep vegetation gradient was established after ca. 2000 cal yr BP. The contraction of steppe and shrubland probably reflects a steepening of the moisture gradient. During the last 2000 years, the forest/steppe boundary has been located as far east as any time during the Holocene (Fig. 4.10).

In addition to late-Holocene variability in vegetation distribution, millennial-scale fluctuations in *Austrocedrus* and *Nothofagus* population size have been observed at all sites (Figs. 4.6, 4.7, 4.8 and 4.9), likely driven by shifts in effective moisture and fire regime (Iglesias et al., 2012b; Chapter 3). Environmental heterogeneity, both temporal and spatial, has characterized the last ca. 4500 years in mid- and high-latitudes of the southern hemisphere, implying that humidity and ecosystem dynamics have been modulated by local biophysical factors as well as latitudinal shifts of the Southern Westerlies (Fletcher and Moreno, 2011).

Regional Trends in Vegetation and Fire at the Northern Patagonian Forest/Steppe Ecotone

Vegetation Dynamics along the Forest/Steppe Ecotone. Forest/grassland transitions around the world occur in areas of steep climate gradients, strong biotic interactions, and/or intense disturbance regimes. Recent studies suggest that at intermediate moisture levels, forest and grassland represent alternative stable states (Hirota et al., 2011; Staver et al., 2011). The salient properties that support trees or forbs, such as surface-energy balance, hydrology, erosion rates and nutrient cycling, are maintained by feedbacks between climate, vegetation and fire. Stability in ecology often refers to resilience in the vicinity of an equilibrium point in a deterministic system. Populations are in equilibrium when their growth rates are zero. Such equilibrium may be called stable if, after disturbance, growth rates eventually return to their steady-state values, either by dampening oscillations or monotonically (May, 1974). Our results suggest that millennial-scale forest/steppe ecotone dynamics in northern Patagonia are not stationary, as forest taxa have systematically grown and colonized landscapes previously dominated by steppe taxa. For this reason, steady-state models cannot be used to predict the long-term behavior of north Patagonian vegetation.

Both moisture availability and fire have been proposed to limit forest expansion into grasslands. Grasses are more efficient than trees at exploiting soil moisture and nutrients and obtaining water in the upper layers (Kitzberger, 2012). Therefore, forest/steppe ecotone dynamics are expected to depend on the amount and spatial distribution of soil moisture, and this, in turn, is determined by climate, soil properties

and land use. Support for the moisture-availability hypothesis comes from the African savannah and the Australian Northern Territories, where Bond (2008) found a strong positive correlation between mean annual precipitation and woody cover. Areas such as the transition from mixed forest to Great Plains prairie in central North America, on the other hand, exhibit sharp ecosystem boundaries despite their location along a gradual precipitation gradient. It has been proposed that North American prairie-forest border does not respond linearly to climate but rather the dynamics are governed by feedbacks involving vegetation and fire (Clark et al., 1996).

Long-term changes in vegetation composition in Patagonia have been attributed to large-scale changes in climate (Mancini et al. 2005; Markgraf et al., 2007). To test this assertion, we compared the regional trend in the position of the forest/steppe ecotone since the Last Glacial Maximum, as detected by a GAM fit to forest taxa pollen data, with independent paleoclimatic records (Fig. 4.12). Our results reveal synchronous shifts in vegetation, which are expressed as forest taxa percentages, and temperature and precipitation at millennial time scales, suggesting that forest cover was strongly determined by climate.

Very low percentages and PAR of forest species (Figs. 4.6, 4.7, 4.8, 4.9, 4.10) indicate that during the last glaciation, most forest taxa populations were small or, more likely, not present in the study area. Warming (Grootes et al., 1999) allowed a rapid expansion *Nothofagus* spp. and other trees. These species tracked favorable climate conditions into areas that were previously glaciated or in periglacial environments. Establishment of *Nothofagus* spp. (i.e., *N. dombeyi*, *N. antarctica* and *N. betuloides*) on

recent glacial deposits has been documented throughout Patagonia (Heusser, 1964; Pisano and Dimitri, 1973; Pisano, 1978; Rabassa et al., 1981). For example, Lawrence and Lawrence (1959) reported seedling establishment at the Río Manso glacier (lat. 41˚S) within two years of outwash deposition. Although joint colonization of bare sites by plants with nitrogen-fixating symbioses (e.g., *Gunnera chilensis*) is beneficial for tree development, *Nothofagus* seedlings do not require any site modifications by early colonizers (Veblen et al., 1989). These pioneering characteristics of the genus are likely to have contributed to the rapid establishment of parkland and development of the forest/steppe ecotone along the transect soon after deglaciation.

During the last 12,000 years, as annual insolation and temperatures decreased (Grootes et al., 1999), the Southern Westerlies gradually shifted to their present-day position and ENSO variability strengthened in the region. Evidence from marine records suggests that a northward shift of the Southern Westerlies in the middle to late Holocene resulted in increased precipitation in northern Patagonia (Lamy et al., 2001). In addition to this change in precipitation regime, the onset or strengthening of ENSO led to more variable precipitation and temperature during the growing season on interannual time scales (Moy et al., 2002). This long-term Holocene trend towards cooler, wetter and more variable climate conditions favored tree expansion at the expense of shrubland and grassland along the forest/steppe transect (Figs. 4.10 and 4.12). Tree-ring data and recent plant demographics at the forest/steppe border in northern Patagonia indicate that ecotone dynamics in recent centuries have been associated with spring-summer temperature and precipitation. For example, warm/dry conditions during the growing season in the 1980-

2000 AD period limited tree regeneration and led to massive tree mortality along the ecotone. In contrast, cool/wet times, such as the one from 1963 to 1979 AD, were associated with regional seedling establishment at the forest/steppe boundary (Villalba and Veblen, 1997). Similarly, sensitivity to moisture availability is likely a major control of the position of the ecotone also at millennial scales.

Although large-scale change in climate may explain the relative abundance of trees and grasses on millennial time scales, the composition of the ecotone at any time was governed by much shorter dynamics that cannot be attributed exclusively to one forcing. The Holocene expansion of *Austrocedrus* from glacial refugia (Fig. 4.11), for example, was possibly a response to the interplay between climate, vegetation and fire activity, such as is observed today. At present, seedling establishment at the lower treeline is sporadic and dependent on higher-than-average effective moisture (Veblen and Lorenz, 1987). The long-term Holocene trend towards higher effective moisture likely promoted *Austrocedrus* colonization on dry sites previously occupied by shrubland, allowing the expansion of the species from rocky outcrops near L. Cóndor (Iglesias et al., 2012a; Chapter 2) and Andean valleys at lat. 41˚S. Dendroecological data show that, except during exceptionally humid growing seasons, seedling establishment in open woodlands occurs exclusively under nurse shrubs (Kitzberger et al., 2000). Shrubs are shade-intolerant. For this reason, nurse plants usually die after they are overtopped by *Austrocedrus*, and shrublands do not co-occur with dense *Austrocedrus* stands (Veblen et al., 1992). The regional replacement of shrubs by *Austrocedrus* in the past also occurred

as a result of similar interspecific interactions superimposed on a long-term trend towards cooler and more humid (Figs. 4.6, 4.7, 4.8 and 4.9).

Fire dynamics explain some of the spatial differences in *Austrocedrus* abundance through time. Comparison of *Austrocedrus* pollen records and charcoal data suggests that increased biomass burning and/or fire intensity, as inferred from low grass-to-total charcoal ratios, limited tree abundance in a given location, even as populations were expanding regionally (Figs. 4.6, 4.7, 4.8, 4.9 and 4.11). These results are consistent with ecological and paleoecological data indicating that stand-replacing fires impede the establishment and survival of *Austrocedrus* seedlings even in climatically favorable sites (Whitlock et al., 2006; Amoroso et al., 2011; Iglesias et al., 2012a; Chapter 2; Markgraf et al., in review).

The expansion of *Austrocedrus* populations resulted in the formation of mixed *Nothofagus-Austrocedrus* forests during the late Holocene. These forests are located at the limits of the distribution of both species, and temporal shifts in dominance of one taxon over the other illustrate the hierarchical controls that govern vegetation change. Effective moisture was the main control of ecotone composition, as *Nothofagus* was more abundant during humid periods, and *Austrocedrus* establishment was favored by drier conditions (Iglesias et al., 2012b; Chapter 3). At intermediate-moisture levels, however, the lower forest supported both taxa, and fire became an important control of community composition, with intense infrequent fires facilitating *Nothofagus* regeneration and high frequency and low intensity fires supporting *Austrocedrus* (Iglesias et al., 2012b; Chapter 3). Transient responses to climate change are therefore difficult to predict due to

vegetation-fire feedbacks (Sankey et al., 2006), especially at present where changes in land use, livestock herbivory, and nonnative plant introductions affect fuel conditions and post-fire recruitment altering the timing and direction of environmental changes.

Changes in the Fire Regime since the Last Glacial Maximum. Generalized trends in fire activity (i.e., GAM results of CHAR levels expressed as charcoal accumulation rates) at the forest/steppe ecotone have increased since glacial times (Fig. 4.12). The long-term rise in biomass burning reflects shifts in fire regime driven by the pronounced changes in vegetation and climate in northern Patagonia. Superimposed on this long-term trend towards increased and more variable fire activity, millennial-scale periods of high biomass burning occurred between ca. 14,000 and 13,000, 9000 and 7000, and 3000 and 1900 cal yr BP.

During the last glaciation, the presence of extensive ice fields and sparsely vegetated periglacial environments limited fire occurrence in the study area. Higher-than-before CHAR is associated with rapid colonization after ca. 17,500 cal yr BP (Fig. 4.12), suggesting that woody parkland species burned occasionally during the late glacial/early Holocene transition. Although increased biomass was probably critical for fire spread, fire activity at the time was also favored by climatic conditions that increased the natural probability of ignition and decreased fuel moisture. Natural ignition in Patagonia is generally infrequent and associated with convective storms that increase lightning occurrence (Holtz et al., 2012). Large-scale climatic variations that promoted convection, in addition to late glacial/early Holocene widespread aridity, created conditions conducive for burning throughout the region (Huber et al., 2004; Whitlock et al., 2006).

Comparison of Holocene regional trends in fire activity and temperature (Grootes et al., 1999), precipitation (Lamy et al., 2001), and the position of the forest/steppe ecotone (Fig. 4.12) reveals that biomass burning was relatively low during warm/dry steppe-dominated landscapes in the early Holocene, and increased as more-humid-than-before conditions favored forest development and higher vegetation cover during the late Holocene. Such climate-vegetation-fire linkages suggest that Holocene fires were primarily limited by lack of horizontal fuel continuity. Vegetation influences fire regimes by affecting the size, abundance and spatial patterns of fuels across the landscape. The fine fuels of xeric environments desiccate quickly and readily burnable during the entire fire season. However, in these areas with extremely fire-conductive climate conditions, large proportions of bare ground preclude fires from spreading across the landscape (Parisien and Moritz, 2009). Holocene expansion of forest taxa into steppe increased vegetation productivity and provided biomass and fuel continuity, allowing more intense fire activity.

During the last ca. 2300 years, biomass burning decreased at the ecotone in spite of greater vegetation cover than at any time in the Holocene (Fig. 4.12). We propose that as forest taxa invaded the study area in the late Holocene, the fire regime shifted from fuel-limited to moisture-limited. Tree expansion into steppe provided sufficient fuels for fires to spread, but vegetation and soil moisture confined fire activity to prolonged drought events, when desiccation of coarse forest fuels created opportunities for fires to occur (Kitzberger et al., 1997). Millennial-scale oscillations in regional biomass burning are associated with long-term changes in ENSO frequency/intensity, with the late

Holocene maximum in fire activity immediately following the strengthening of ENSO at ca. 3000 cal yr BP (Moy et al., 2002; Fig. 4.12). This association suggests that regional patterns of fire are dependent, not only on changes in vegetation, but also on ENSO-driven climate variability.

ENSO is considered a primary driver of fire in northern Patagonia on decadal time-scales (Kitzberger et al., 1997), as well as an inter-hemispheric synchonizer of fire activity (Kitzberger et al., 2001). El Niño conditions induce positive anomalies in winter precipitation that enhance fine fuel production during the growing season. Widespread fires tend to follow the switching from El Niño to La Niña conditions, which favor desiccation of fuels accumulated in previous years (Kitzberger and Veblen, 1998). Increased fire activity and variability associated with the late Holocene onset/strengthening of ENSO are likely to have had significant effects on ecotone properties, by altering vegetation composition and distribution.

In addition to the Holocene long-term trend towards increased regional biomass burning followed by decreased fire activity after ca. 2300 cal yr BP, charcoal records show high spatio-temporal variability in fire occurrence at watershed scales (Figs. 4.6, 4.7, 4.8 and 4.9). This variability suggests that site conditions, such as vegetation, soil moisture and possibly human ignitions are likely to have influenced fire spread since glacial times. Thus, the interaction of large-scale (i.e., climate and position of the forest/steppe ecotone) and local biotic and abiotic controls of fire explains discrepancies in the occurrence of fires among sites (Parisien and Moritz, 2009).

Fire and Human Activity Along the Forest/Steppe Ecotone. Veblen and Lorenz (1999) proposed that frequent burning by aboriginal peoples in northern Patagonia was the main factor preventing *Austrocedrus* from occupying its entire climate space (i.e., its potential niche). Early explorers and missionaries mention fires set by indigenous peoples to hunt guanacos (*Lama guanicoe*) and rheas (*Rhea* spp.) at lower treeline (Musters, 1871; Cox, 1963), but there is no clear indication of fire as a tool to modify the landscape before European colonization and horse introduction (Fernandez et al., 2011). Archeological data from northern Patagonia indicate that humans were present north of the study area (Huenul Cave, lat. 36˚56'S; Barbena et al., 2010) and at L. el Trébol (Hadjuk et al., 2006) by ca. 10,600 cal yr. The low density of archeological findings and limited range of artifact types, however, suggest that the ecotone was not densely populated until ca. 2000 cal yr BP, when rapid population growth was recorded in the area (Bellelli, 2007; Bellelli et al., 2003; Podesta et al., 2007; Fernandez et al., 2011).

Fire activity inferred from the generalized CHAR trends from the GAM analysis is highest between 3000 and 1900 cal yr BP, peaking at ca. 2300 cal yr BP. Comparison of archaeological and charcoal data reveals that the late-Holocene maximum in fire activity occurred when human groups were still relatively small and decreased during the time of rapid population growth (ca. 2000 to present). The lack of synchrony between maximum fire activity and the onset of population expansion indicates that anthropogenic use of fire at regional scales, if any, was independent of population density. Nonetheless, it is also possible that the mismatch between archeological and charcoal data is a consequence of dating errors. For example, the beginning of the population rise may have

coincided with the peak in regional charcoal. This scenario implies that biomass burning decreased once larger human groups were established in the ecotonal region, either through increased landscape fragmentation or fire elimination. Further research and better-resolved chronologies are necessary to test this hypothesis.

Conclusions

The paleonevironmental history of the forest/steppe ecotone in northern Patagonia is characterized by strong climate-vegetation-fire linkages that reflect the pronounced changes in atmospheric circulation during last 23,000 cal yr BP. Cold, dry and windy conditions and extensive ice cover during the LGM (ca. 23,000 – 19,000 cal yr BP) limited vegetation to steppe-dominated unglaciated regions. Biomass burning was negligible until ca. 17,500 cal y BP, but it increased rapidly to peak at ca. 14,000 cal yr BP. Trees and shrubs colonized the study area at ca. 16,000 cal yr BP, probably favored by warmer wetter conditions brought about by a shift in dominance from year-long polar air masses to more humid Pacific air (Heusser, 2003). Disturbance-resistant and -resilient *Nothofagus antarctica*, as well as Asteraceae, Chenopodiaceae and other shrub population growth led to the development of parkland and the establishment of a well-developed forest/steppe ecotone in the region. The increase of woody taxa throughout the area provided fuel for more biomass burning than in previous times.

By ca. 8000 cal yr BP, increased precipitation throughout Patagonia promoted shrubland development along the transect and added complexity to the structure of the ecotone. The rise in vegetation productivity was paralleled by an increase in biomass burning, suggesting that the ecosystem was still fuel limited. The middle Holocene (ca.

8000 – 5000 cal yr BP) was characterized by eastward forest advances along the eastern flanks of the Patagonian Andes and pronounced *Austrocedrus* population growth. Increases in Cupressaceae pollen percentages and accumulation rates are consistent with a rapid postglacial expansion of *Austrocedrus* from unglaciated terrain in the L. Cóndor and L. Huala Hué areas. This finding is matched by modern genetic data which suggest that the conifer persisted east of its present distribution and at 41°S during the last glaciation. Moderate levels of heterozygosity in modern populations are consistent with a history of rapid population growth (Pastorino and Gallo, 2002).

The modern lower forest, co-dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*, developed at ca. 4500 cal yr BP. This vegetation probably established in the area in response to increased effective moisture, which independent records of climate change (e.g., Lamy et al., 1999; Lamy et al., 2001) ascribe to a northward shift and strengthening of the Southern Westerlies. Increased effective moisture also may be attributed to the intensification of ENSO-related interannual climate variability in the late Holocene (Moy et al. 2002).

Our results suggest that climate was the main driver of long-term dynamics at the forest/steppe ecotone, either through its direct effects on vegetation or its indirect effects on fire. Since glacial times, the position of the ecotone has been dependent on moisture availability driven by changes in the latitudinal position and strength of the Southern Westerlies, with more humid intervals allowing tree establishment and drier periods promoting steppe advances into the forest. Until ca. 2300 cal yr BP, fires were fuel-limited and therefore strongly controlled by climate-driven plant productivity and favored

by ENSO-related climate variability. During the last two millennia, nonetheless, forest taxa have advanced eastwards and, in spite of higher-than-before vegetation cover, biomass burning has decreased. We propose that at ca. 2300 cal yr, the ecosystem crossed a threshold in fuel availability and shifted from fuel- to moisture-limited, with fires being restricted to drier-than-average years that allow the desiccation of coarse forest fuels. Alternatively, increasing human populations may have eliminated natural fire occurrence in the last 2000 years.

At watershed scales, ecosystem dynamics were modulated by local biophysical factors in addition to changes in the water balance. Vegetation-fire feedbacks, in particular, were especially important at intermediate moisture levels. In the lower forest, for example, climate imposed physiological constraints that favored forest dominance by *Nothofagus* or *Austrocedrus*. At intermediate moisture levels, however, fire has been the main control of late-Holocene community composition with severe, infrequent stand-replacing fires facilitating *Nothofagus* regeneration and frequent, less intense fires supporting *Austrocedrus* (Iglesias et al., 2012b; Chapter 3). Our data suggest that, although stable-state models cannot be applied to non-stationary Holocene trends in vegetation composition, the position of lower treeline at watershed scales is largely dependent on fire activity. Open forest and steppe are alternate stable states at intermediate moisture levels. Our understanding of past vegetation-fire feedbacks supports the idea that transient responses to future climate change will be difficult to predict (Sankey et al., 2006). This vulnerability is especially heightened along ecotones where changes in land use, livestock herbivory, and nonnative plant introductions affect

fuel conditions and post-fire recruitment alter the timing and direction of environmental changes.

Fire ecology is an area of active research in Argentina that has provided important tools for management. Studies suggest that changes in land use, probability of human ignition and climate are very likely to have increased fire potential in Patagonia (Kitzberger and Veblen, 1998; Veblen et al., 2011). Although early explorers and missionaries reported fires set by aboriginal peoples (Cox, 1963; Musters, 1871), burning patterns that can be ascribed to human-set fires are not evident in northern Patagonia until European colonization in the 18th century. Comparison of archaeological and charcoal data reveals that the late-Holocene maximum in fire activity occurred when human groups were still relatively small (at ca. 2300 cal yr BP) and decreased during the time of rapid population growth (ca. 2000 to present). The mismatch between the beginning of population expansion and maximum fire activity suggests that anthropogenic use of fire at regional scales, if any, was either independent or inversely related to population density. This scenario implies that fire activity decreased once larger human groups were established in the ecotonal region, either through increased landscape fragmentation or fire elimination.

The prehistoric human-fire relationship contrasts with the influence that European settlement had on fire regimes. By increasing the probability of ignition through accidental and deliberate burning and converting large areas of native vegetation to fire-prone species, Europeans increased the present and future risk of fire in Patagonia (Veblen et al, 2011). The higher probability fire and its possible effects on native

vegetation need to be considered in future management plans and environmental policies, especially those related to plantation of flammable species, such as pines and eucalyptus, which are likely to further alter the fire regime.

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CHAPTER 5

CONCLUSIONS

In my dissertation, I examine climate-vegetation-fire linkages that have evolved in the north Patagonian forest/steppe ecotone over the last 23,000 years, covering the time span since the last glaciation. The study area is particularly sensitive to changes in effective moisture associated with the strength and latitudinal position of the Southern Westerlies and ENSO-related variability. Understanding the environmental history of the ecotone at different latitudes allows testing of multiple working hypotheses concerning the effects of large-scale changes in climate on local ecosystems and the regional development of the ecotone. In particular, the research undertaken in this dissertation aims to: (1) reconstruct the postglacial environmental history along the forest/steppe ecotone and estimate watershed- and regional-scale trends in vegetation and fire, including the relationship between the postglacial vegetation history of lower treeline and the biogeography of the keystone conifer species *Austrocedrus chilensis*; (2) examine climate-vegetation-fire linkages across scales to identify the relative importance of local-versus-regional drivers of Holocene ecological change and the role of past and present human activities in shaping the forest-steppe ecotone.

High-resolution pollen and charcoal records were analyzed from a transect of seven small lakes along the forest-steppe ecotone from lat. 41 to 43˚S to reconstruct the vegetation and fire history. New records were developed for five of the sites (i.e., Lago Huala Hué, Laguna Padre Laguna, Lago el Cóndor, Laguna La Zeta and Lago Theobald)

and added to previously published records from two of the sites (i.e., Laguna el Trébol and Lago Mosquito, Whitlock et al., 2006). Comparison of the reconstructed vegetation and fire history from these lakes with independent records of climate allows assessment of the natural variability of Patagonian ecosystems and their responses to changes in climate, providing a basis for evaluation of current and future environmental trends.

Postglacial Environmental History along the Forest/Steppe Ecotone

Pollen and high-resolution charcoal records suggest that the postglacial history of northern Patagonia is a response to pronounced large-scale changes in atmospheric circulation since ca. 23,000 cal yr BP. During the Last Glacial Maximum (ca. 23,000 – 19,000 cal yr BP), extensive glaciation and cold, dry and windy conditions supported steppe-dominated vegetation in unglaciated regions. In spite of the dry nature of the landscape, fires were rare until ca. 17,500 cal yr BP, probably because low fuel load and continuity limited fire spread.

Rapid deglaciation began at ca. 17,500 cal yr BP (Hulton et al., 2002). Along the transect, CHAR and woody taxa pollen percentages rose during the late-glacial/early-Holocene transition, suggesting that ice recession was coupled with a region-wide increase in fire activity, followed by the colonization of the study area by trees and shrubs. The ranges of disturbance-resistant and resilient taxa, such as *Nothofagus antarctica*, Asteraceae, Chenopodiaceae and other shrubs, expanded into the Patagonian foothills in response to rising temperatures and led to the establishment of parkland and development of the forest-steppe ecotone. Increased abundance of woody taxa throughout the area provided fuel for more biomass burning than in previous times.

The northernmost sites on the transect (i.e., L el Trébol, L. Huala Hué) featured parkland vegetation as early as 16,000 cal yr BP and were located near the lower (eastern) margin of the forest/steppe boundary. In contrast, southern sites (i.e., L. Cóndor, L. Mosquito L. La Zeta and L. Theobald) supported steppe vegetation at this time, suggesting that the forest/steppe border lay farther west and at higher elevations south of lat. 41˚S. Regional differences in the position of the forest/steppe ecotone were probably driven by the establishment of a precipitation regime characterized not only by a west-to-east gradient but also by decreasing north-to-south annual precipitation, similar to the present pattern in the study region. Subsequent vegetation development also shows similar latitudinal differences in that the changes occurred first in the northern sites (north of lat. 41˚S) and later in the southern ones.

Lithological boundaries identified in the cores are consistent with a transition from sparsely vegetated periglacial environments to parkland. A shift from inorganic clay with beds of magnetically enriched sediment to organic laminated clay at ca. 14,000 cal yr BP suggests that an initial period characterized by intermittent pulses of erosion and slope instability, was followed by fluctuations of coarse- and fine-sediment deposition occurring in more stabilized landscapes. L. Cóndor and L. Mosquito experienced an initial period of wetland development prior to lake formation, as evidenced by the presence of decomposed peat at the base of the sediment cores.

During the early Holocene (ca. 13,000 to ca. 8000 cal yr BP), higher-than-present annual and winter insolation and a weakening of the Southern Westerlies led to shrubland development. Climate conditions became progressively more humid after 11,200 cal yr

BP. At ca. 9000 cal yr BP, the expansion of *Nothofagus* and other forest taxa into steppe, as reconstructed from higher-than before pollen percentages, resulted in an eastward shift of the ecotone across the region. A rise in fire frequency and area burned paralleled this increase of vegetation productivity, suggesting that, in spite of higher-than-before vegetation cover, the system was still fuel limited.

The middle Holocene (ca. 8000 to 5000 cal yr BP) was characterized by climate-driven forest expansion along the eastern flanks of the Patagonian Andes. The eastward advance of the forest/steppe ecotone was associated with an increase in shrub taxa, most notably Rhamnaceae and *Maytenus*, as well as *Austrocedrus* population size. It is likely that *Austrocedrus* expansion was regionally driven by increased effective moisture, which allowed the establishment of seedlings in the steppe and broadening of its geographical distribution.

The modern forest, co-dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*, was established at ca. 5000 cal yr BP, probably in response to increased effective moisture. A northward shift and strengthening of the Southern Westerlies, as well as the intensification of ENSO-related climate variability, occurred at the time (Lamy et al., 2001; Moy et al., 2002), and it is likely that increase moisture and interannual variability in precipitation allowed trees to outcompete shrubland and steppe taxa. Shrubland/steppe expanded at all sites between ca. 4000 and 2000 cal yr BP and decreased in abundance after 2000 cal yr BP. These shifts in shrubland/steppe taxa distribution suggest that vegetation zones were geographically broader in the early late Holocene (4500 to 2000 cal yr BP) than they are at present and that the modern steep

vegetation gradient was established after ca. 2000 cal yr BP. During the last 2000 years, the forest/steppe boundary has been located as far east as any time during the Holocene.

Biogeography of *Austrocedrus chilensis*

Climate exerts a dominant control over the distribution of species by imposing physiological constraints on survival, growth, and reproduction (Williams et al, 2007). Depending upon the nature and magnitude of the environmental change relative to the fundamental niche, phenotypic plasticity, and genetic structure of a species population, populations can respond by tolerance (adaptation) or migration (Etherington, 1974; Hu et al., 2009). Populations respond by tolerance when the environmental change is small relative to the fundamental niche, provided that the population has sufficient phenotypic plasticity and/or genetic variability to accommodate the changed environment. Migration, or shift in the biogeographic distribution, occurs as a species colonizes new habitats in response to a changing environment. These local processes (i.e., toleration and migration) result in shifts in population densities that range from regional- to continental-scale latitudinal and longitudinal gradients (Mustin et al., 2009).

After the Last Glacial Maximum, the range of most tree taxa shifted as species expanded from their refugia to present habitats (Anderson et al., 2006). In this study, pollen influx data were used to test the hypothesis of the existence of an *Austrocedrus* glacial refugium in northern Patagonia. *Austrocedrus* is a keystone species along the forest/steppe ecotone whose present-day distribution was almost entirely glaciated during the Last Glacial Maximum. The data reveal decreasing Cupressaceae pollen influx from east to west before 8000 cal yr BP, with the highest values recorded at L. Cóndor and L.

Huala Hué, and the lowest at L. Theobald and L. Mosquito, This geographical pattern suggests the persistence of low-density populations in steppe-dominated landscapes in the L. Huala Hué and L. Cóndor areas, which expanded after ca. 8000 cal yr BP. Genetic data from modern populations support this interpretation (Pastorino and Gallo, 2002) by showing low allelic variants, which are indicative of historical bottlenecks and consistent with more than one small refugia.

Species range limits are often difficult to reconstruct from pollen data because of uncertainties associated with inferring the source area from low pollen levels or from taxa that produce pollen in great abundance (e.g., *Nothofagus dombeyi*-type). The presence of low amounts of pollen in a single core leaves unresolved whether the pollen came from a small local population or was transported from long-distance sources (Maher, 1963). In order to resolve this ambiguity, a network of sites along the transect was used to reconstruct spatial patterns of *Austrocedrus* during the Holocene. A pronounced increase in Cupressaceae PAR after ca. 8000 cal yr BP at all sites, along with decreasing PAR values from east to west and north to south suggests that *Austrocedrus* expanded from refugia located at lat. 41 and 42˚S, near the L. Huala Hué and L. Cóndor watersheds. This trend changed at ca. 4500 cal yr BP, when large *Austrocedrus* populations developed near L. el Trébol and L. Padre Laguna and *Austrocedrus*' geographic distribution became similar to present. The expansion of the population was probably a response to more humid conditions that allowed seedling establishment in steppe and hence a western expansion of its range.

Climate-Vegetation-Fire Linkages along the Forest/Steppe Ecotone

Vegetation Dynamics since the Last Glacial Maximum

The profound environmental changes that shaped the Quaternary also have left an imprint on modern biota through impacts on the distribution of species (Williams et al., 2007). The factors that influence vegetation distribution (e.g., climate, soil, herbivory) act at temporal scales that range from ecological to evolutionary. At ecological time-scales (i.e., $<10^5$ years), changes in tree population size and shifts in associations between taxa occur, whereas natural selection and speciation take place on longer evolutionary scales (i.e., $>10^5$ years, in the case of trees; Hamann and Wang, 2006). Because of the interplay among controls operating at different levels, a useful framework for addressing environment-biota relationships is that of a hierarchy of factors operating at different scales.

Turner et al. (2001) define a hierarchy, either spatial or temporal, as a system of interconnections wherein the higher levels of interconnections or processes that operate at one scale constrain lower ones to various degrees, implying that the relative importance of a given process is scale-dependent. For example, at continental scales, climate is the main driver of the present distribution of biomes. Further down the hierarchy, if conditions at higher levels are satisfied, biotic interactions, soil and disturbance regimes may become significant (Gavin and Hu, 2006).

Climate-vegetation-fire linkages can therefore be understood as a hierarchical system with factors operating at different temporal (Fig. 5.1). On millennial-time scales,

large-scale controls of climate, such as insolation and the latitudinal position of the Southern Westerlies, influence effective moisture and lead to changes in the position of vegetation associations like the forest/steppe ecotone. Shifts in vegetation boundaries result in changes in fuel load that favor or preclude biomass burning at regional scales. Precipitation variability at sub-millennial time scales induces shifts in plant community dominance. These shifts are usually associated with changes in fire frequency and intensity resulting from differences in fuel flammability. Changes in the fire regime, on the other hand, affect vegetation composition by altering the proportion of fire-resistant-to-fire-sensitive species. Finally, prehistoric peoples are likely to have shaped the environment by deliberate burning and fire elimination.

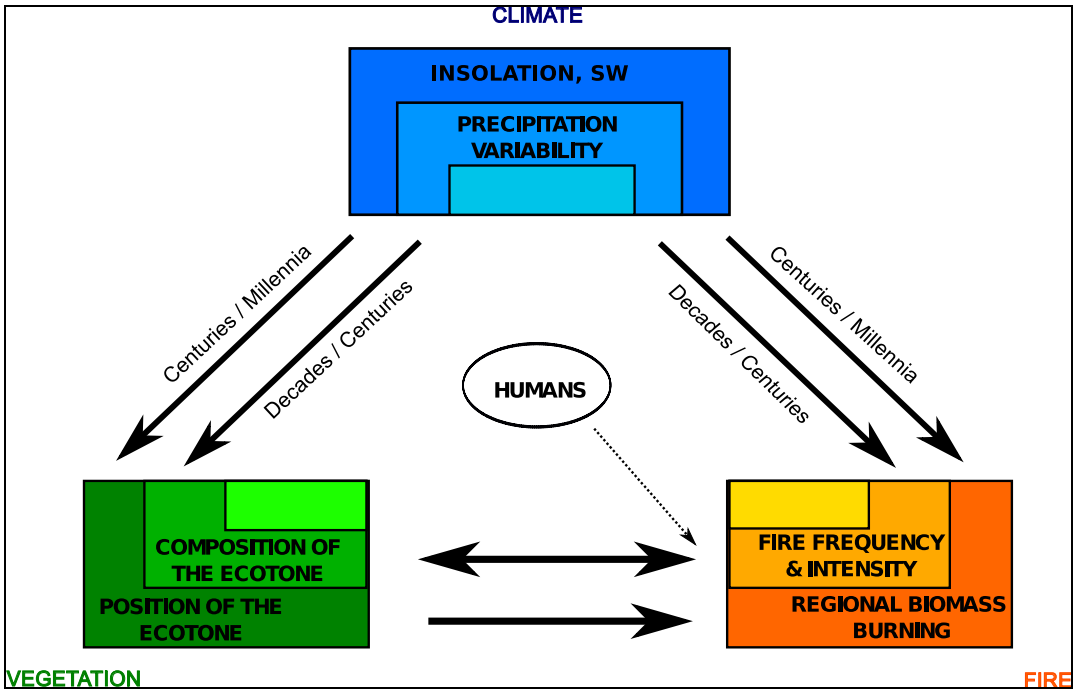


Figure 5.1: The hierarchy of climate-vegetation-fire linkages on decadal to millennial time scales.

Scale and scale-dependent properties are especially meaningful in paleoecology. In experimental ecology, relationships between environmental patterns and the processes that produce them are understood by controlling exogenous sources of variation and thus leaving the causal linkages exposed. The power of paleoecology, on the other hand, comes from the premise that consistent answers to ecological problems are found by eliminating the noise of site-specific variability (Jackson, 2004). For example, in order to understand regional trends in vegetation and fire and their drivers, trend detection techniques (i.e., GAMs) were applied to the pollen and charcoal records. This approach allowed long-term regional vegetation dynamics to be separated from the site-specific variability that result from edaphic controls, local drivers of disturbance including people, and analytical errors. The regional trend describes millennial-scale variability in the position of the forest/steppe ecotone and was compared with independent records of climate change from the region.

The regional reconstruction clearly shows the replacement of late-glacial steppe by parkland and shrubland in the early and mid-Holocene and the invasion of parkland and shrubland by forest species in last 5000 years. These dynamics closely match a long-term trend of increasing effective moisture that characterizes the Holocene. Such climate-vegetation association suggests that millennial-scale shifts in the regional position of the forest/steppe ecotone are dependent on variations in temperature and precipitation that affect moisture (Fig. 5.1). These variations are largely driven by insolation-mediated changes in the strength and latitudinal position of the Southern Westerlies. As a result, forest taxa expanded into steppe during more humid periods (e.g., 4000 cal yr BP -

present) and became locally extinct at the easternmost limits of their distribution in drier times (e.g., 6000 - 4000 cal yr BP).

In contrast to the location of the forest-steppe ecotone, the composition of the vegetation at watershed- and millennial-scales was not a direct response to climate but rather a consequence of the interaction between broad-scale climate and watershed-scale non-climatic conditions, such as topography, soil and fire. The relative importance of climate and non-climatic drivers apparently changed through time as critical thresholds in precipitation were reached. For example, comparison of pollen and charcoal data from two sites at lat. 41˚S (i.e., L. Padre Laguna and L. Huala Hué) and independent records of climate (Moy et al., 2002) indicates that centennial- to millennial-scale oscillations in the water balance resulted in multiple shifts between *Nothofagus* and *Austrocedrus* dominance during the last 5000 cal years. Humid periods allowed *Nothofagus* establishment at the lower treeline and drier times induced *Nothofagus* declines, thus favoring *Austrocedus* dominance. At intermediate moisture levels, however, fire was the primary control of community composition, with infrequent stand-replacing fires facilitating *Nothofagus* regeneration and frequent fires supporting *Austrocedrus*. Thus, at intermediate moisture levels, *Nothofagus*- and *Austrocedrus*-dominated forests constitute alternate stable states, and ecosystem dynamics are modulated by vegetation-fire feedbacks (Fig. 5.1). This finding is not unlike that of Staver et al. (2011) who suggested that fire determines the relative abundance of grassland and forest across present-day forest-steppe ecotones around the world.

Changes in the Fire Regime since the Last Glacial Maximum

Successful spread of fires requires a combination of low fuel moisture, high fuel accumulation and continuity, and suitable fire weather (Agee, 1993). Fuel characteristics are, in turn, determined by interactions between short-term weather conditions and long-term climatically driven vegetation productivity and flammability (Christensen, 1993). Such climate-vegetation-fire linkages operating at multiple spatiotemporal scales result in complex ecosystem dynamics that are often altered by human-mediated landscape modification (Fig. 5.1).

Large-scale changes in climate, such as those inferred for the last 23,000 cal yr BP, modified the composition and structure of fuels through shifts in vegetation in northern Patagonia. Fires at the forest/steppe ecotone, as inferred from regional trends in CHAR, increased until ca. 2300 cal yr BP, reflecting the expansion of woody species. Biomass burning was relatively low during warm/dry steppe-dominated landscapes in the late-glacial and early Holocene, and increased as more humid conditions favored forest development and higher vegetation cover during the last 10,000 years. Such climate-vegetation-fire linkages suggest that Holocene fires at regional scales were primarily limited by reduced fuel availability.

During the last ca. 2300 years, levels of biomass burning have decreased along the ecotone in spite of greater vegetation cover than at any time in the Holocene. While tree expansion into steppe provided sufficient fuels for fires to spread, conditions must have been generally too moist to support widespread burning at this time. Thus, the late

Holocene is characterized by a shift from fuel- to moisture-limited fire regimes along the forest/steppe ecotone.

Although increased biomass was a critical driver of past fire activity prior to 2300 cal yr BP, climatic conditions affecting fuel moisture and the natural probability of ignition were also important. For example, rapid colonization of the ecotone was critical for fire occurrence and probably explains the increase in regional CHAR during the late-glacial/early-Holocene transition. Fire then was likely favored by arid conditions as a result of weakened or more southerly Westerlies (Whitlock et al., 2006) as well as a higher probability of ignition associated with convective storms (Huber et al., 2004).

The onset/strengthening of ENSO after ca. 5000 cal yr BP (Moy et a., 2002) also had a profound effect on fire regimes. El Niño conditions induce positive anomalies in winter precipitation that enhance fine fuel production during the growing season. Dendroecological studies indicate that widespread fires tend to follow the switching from El Niño to La Niña conditions, which favor desiccation of fuels accumulated in previous years (Kitzberger and Veblen, 1998). Charcoal records show an increase in regional biomass burning after 5000 cal yr BP, which peaked at times of high ENSO activity (i.e., ca. 3000 - 1900 cal yr BP). This relationship implies that ENSO is likely to have altered the distribution and size of fire-prone ecosystems at millennial scales. The results of this study therefore indicate that climate was the main agent of pre-European ecological change at the forest-steppe ecotone, either by its direct effects on vegetation or its indirect effects on fire (Fig. 5.1).

The long-term Holocene long-term trend towards increased regional biomass burning beginning at ca. 10,000 cal yr BP and peaking at ca. 2300 cal yr BP was followed by decreased fire activity to the present day. In addition to this trend, the charcoal records along the transect show high spatio-temporal variability in fire frequency and intensity at watershed- and decadal- to centennial-scales throughout the period. This geographical variability suggests that site conditions, such as vegetation composition, soil moisture and possibly human ignitions, are likely to have influenced fire spread. Thus, the interaction of large-scale (i.e., climate and position of the forest/steppe ecotone) and local biotic and abiotic controls of fire explains discrepancies in the occurrence of fires among sites (Parisien and Moritz, 2009).

Currently, humans are a primary driver of change at forest-steppe ecotones around the world (Sankey et al., 2006) but understanding the prehistoric role of anthropogenic burning in shaping the forest-steppe border is problematic. In northern Patagonia, early explorers and missionaries reported fires set by aboriginal peoples associated with hunting practices (Cox, 1963; Musters, 1871). However, there is no clear indication of fire as a tool to modify the landscape before European colonization and horse introduction (Fernandez et al., 2011). Charcoal data indicate that regional biomass burning was highest between 3000 and 1900 cal yr BP and peaked at ca. 2300 cal yr BP, when human groups were still relatively small (Bellelli, 2007; Bellelli et al., 2003; Podesta et al., 2007; Fernandez et al., 2011). Decreased fire activity after 2000 cal yr BP coincides with the time of rapid population growth and occupation of the forest/steppe border. The mismatch between the beginning of population expansion and maximum fire

activity suggests that anthropogenic use of fire at regional scales, if any, was either independent or inversely related to population density. This scenario implies that fire activity decreased once larger human groups were established in the ecotonal region, either through increased landscape fragmentation or fire elimination. Further research and better-resolved chronologies are necessary to test this hypothesis.

Final Remarks

This study supports the hypothesis that long-term vegetation dynamics in northern Patagonia are driven by changes in regional climate (Mancini et al. 2005; Markgraf et al., 2007). Shifts in the reconstructed position and composition of the ecotone are associated with millennial-scale variability in effective moisture. Vegetation at watershed scales, however, does not respond linearly to climate but rather to the interplay between climate, fire and other local conditions, such as topography and soil type (Fig. 5.1).

Previous work by Veblen and Lorenz (1998) indicates that frequent burning by aboriginal peoples was an important factor preventing *Austrocedrus* from occupying its entire climate space. Although it is possible that pre-European human-ignited fires altered the landscape at watershed-scales, the co-occurrence of decreased regional biomass burning and higher human population densities/more intense use of the ecotone suggests that regional climate-vegetation-fire linkages in northern Patagonia evolved with limited human intervention. It is therefore likely that intense modern and future use of the ecotone will have a profound impact on ecosystem dynamics.

Accidental human ignitions as well as practices associated with European settlement (e.g., logging, introduction of non-native species, agroforestry, deliberate

burning), for example, have already increased the probability of fire in otherwise ignition-limited systems (Holtz et al., 2012). In addition, the introduction of livestock and conversion of large areas of native vegetation to plantations of non-native fire-prone species, such as pines and eucalypts, constitutes an increase of flammable fuel (Veblen et al., 2011). In addition, changes in fuel structure and composition threaten the regeneration of fire-sensitive species like *Austrocedrus* (Kitzberger et al., 2012). Paleoecological data provide a basis for evaluating present-day ecosystem dynamics in order to develop suitable strategies for sustainable management of the ecotone and allow a better assessment of the consequences of present and future changes in climate and land-use practices.

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