



## Postglacial history of the Patagonian forest/steppe ecotone (41–43°S)



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### ABSTRACT

Patagonian vegetation has dramatically changed in composition and distribution over the last 23,000 years. Although the vegetation history has been inferred from individual pollen records, the regional patterns and drivers of vegetation development are poorly understood. High resolution pollen and charcoal data from eleven sites located along the eastern flanks of the Patagonian Andes (41–43°S) were examined to reconstruct the Lateglacial and Holocene vegetation and fire history of steppe/forest ecotone and separate the relative influence of climatic versus non-climatic factors in shaping the patterns of ecological change. Pollen data indicate that, as the Lateglacial climate became progressively wetter, the initial steppe vegetation was replaced by open forest of *Nothofagus* in the Lateglacial and early Holocene periods, and by closed forest in the late Holocene. Fire activity was lowest during the Lateglacial/early-Holocene transition and gradually increased through the Holocene. Prior to ca 5000 cal yr BP, the conifer *Austrocedrus chilensis* possibly persisted in isolated populations along the eastern boundary of its modern distribution. Cooler/more humid conditions after ca 5000 cal yr BP allowed the development of the modern mixed *Nothofagus*–*Austrocedrus* forest. The paleoenvironmental record points to the sensitivity of the forest/steppe ecotone in the past, not only to climate but also to complex environmental feedbacks that amplified the effects of climate change.

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## 1. Introduction

Along the eastern Patagonian Andes, a sharp boundary separates North Patagonian forest, co-dominated by the evergreen broad-leaved species *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*, from low-elevation steppe. This ecotone is among the sharpest in the world and expected to undergo rapid and pronounced shifts in position and composition in response to future climate as well as land-use change (Kitzberger, 2012). As the dynamics of the ecotone shift, so too will surface energy and water balances, disturbance regimes, erosion rates, and nutrient cycling (Jobbágy et al., 1996; Kitzberger et al., 1997; Villalba and Veblen, 1997; Veblen et al., 2003; Kitzberger et al., 2005; Iglesias et al., 2012a). These changes in environmental properties are likely to affect not only regional biodiversity but also a wide range of

ecosystem processes and services, including carbon storage, forage production, water supply and quality, crop pollination, and outdoor recreation (Kupfer and Cairns, 1996).

The vegetation history of northern Patagonia has been reconstructed from individual pollen records. Nonetheless, in the absence of synthetic analysis, the broad latitudinal and longitudinal patterns of vegetation change are not well known. As a consequence, our understanding of the ecological response to climate variations ranging from multi-millennial to interannual time scales is poorly understood for the dry forest to steppe transition. In this study, we (1) reconstruct the Lateglacial and Holocene vegetation and fire history of the steppe/forest ecotone along the eastern flanks of the Andes from 41 to 43°S; (2) discuss the relative influence of climatic versus non-climatic drivers in shaping the patterns of ecological change; and (3) describe the Holocene history of an important conifer, *A. chilensis* Florin et Boutelje. Our study is based on lithologic, pollen and high-resolution charcoal data from nine published and two new sites located along the dry forest margin on the eastern slopes of the Andes in northern Patagonia.

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## 2. Study area

### 2.1. Climate

At present, 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 50–70% of the time in the eastern plains of Argentina (Prohaska, 1976). The latitudinal position of the Southern Westerlies is governed by the strength of the southeastern Pacific subtropical high-pressure system and a subpolar low-pressure trough centered along the Antarctic Circle (Mayr et al., 2005). These atmospheric circulation features 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 northward migration of the jet stream to subtropical latitudes (30°S; Paruelo and Lauenroth, 1998; Berman et al., 2013).

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, and 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 eastern flanks of the Andes produces adiabatic warming of the air masses and very dry conditions in eastern Patagonia (Paruelo and Lauenroth, 1998). Interannual and decadal climate variability in Patagonia is related to tropospheric forcing of mid-latitude sea-surface temperatures, pressure anomalies resulting from the fluctuations in strength and position of the polar vortex and the subtropical high, and the indirect effects of coupled ocean-atmosphere phenomena rooted in the tropical Pacific (Miller, 1976), such as El Niño Southern Oscillation (ENSO). 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).

### 2.2. Vegetation

Present-day vegetation is arrayed along the west-to-east gradient in effective moisture. East of the Andes between lat. 40 and 43°S, the steep decline in precipitation is associated with a well-defined transition from rainforests to xerophytic forests to steppe (Hajek and di Castri, 1975; Jobbágy et al., 1996). This transition is also influenced by a shift 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) and nutrient-poor desert soils (i.e., Aridisols, <500 mm annual precipitation) in the east (Mazzarino et al., 1998). Above 1500 m elevation, slopes are dominated by rainforests of *Nothofagus pumilio* Krass. *Fitzroya cupressoides* Johnst. and *Nothofagus 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).

At elevations between 1500 and 1000 m, 40-to-50-m tall *N. dombeyi* Mirb. dominates the humid forests, with *Saxegothaea*

*conspicua* and *Laurelia philippiana* Looser. in the understory. 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 integririma* 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, *A. chilensis* and *N. dombeyi* form extensive co-dominant stands. In these forests, a large number of arboreal (e.g., *Lomatia hirsuta* Diels ex Macbr.) and shrubby species (e.g., *Berberis darwinii* Hook., *Baccharis* L., *Nothofagus antarctica* Oerst.) occur together, and bamboos (*Chusquea argentina* Kunth and *Chusquea culeou* Desvaux.) form extensive stands. *N. antarctica* is a disturbance-resistant and -resilient tree or shrub that grows in dense thickets. Although it may occur in patches intermixed with other *Nothofagus* species, it is usually found on poorer/drier/shallower soils on steep slopes and along the forest/steppe ecotone, as well as in recently disturbed watersheds (Veblen et al., 1996). The herbaceous flora of the mixed forests, represented by *Calceolaria* L., *Viola* L. and *Blechnum* L., is rich, especially in open areas.

Under more xeric conditions to the east, *Austrocedrus* forms pure stands and then open woodlands co-dominated by sclerophyllous shrubs and small trees (e.g., *Berberis* L., *Maytenus* Molina, *Diostea juncea* Gill. et Hook. and *Embothrium coccineum* J.R. Forst. et G. Forst; Seibert, 1982). Marginal *Austrocedrus* populations are characterized by scattered poorly developed trees on rocky outcrops in the steppe in areas where mean precipitation may be as low as 500 mm annually (Dezzotti and Sancholuz, 1991; Ezcurra and Brion, 2005). 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. Lake-shores support *Carex* L., *Scirpus* L. and *Blechnum penna-marina* L. (Roig, 1998; Lara et al., 1999), as well as introduced *Salix* L., *Populus* L. and *Typha latifolia* L.

### 2.3. Study sites

Laguna La Zeta (42.89°S; 71.35°W; 774 m elev.; 675 cm water depth) and the wetland on its north margin are situated on a bench, west and above the city of Esquel (mean annual temperature = 9 °C; mean annual precipitation = 560 mm; Cordón et al., 1993; Table 1; Fig. 1). Two 40–60 m high moraine arcs lie south of the lake, which is periodically drained by the Arroyo Seco. Whereas geomorphologic studies indicate that the region was glaciated several times during the Pleistocene (Garleff, 1977), the origin of the lake is probably associated with a late-Pleistocene ice recession from the southwestern slopes of Cordón de Esquel (Schaebitz, 1994). Rapid melting created a prominent shoreline above the lake that dates to ca 18,000 cal yr BP. The site is located at the present-day forest/steppe border. Anthropogenic disturbance has been intense since the establishment of the town of Esquel, mostly associated with ranching, agroforestry, and burning. Currently, extensive plantations of non-native pines occur in the watershed.

Lago Theobald (43.48°S; 71.58°W; 678 m elev.; 488 cm water depth; Table 1; Fig. 1) lies within a late-Pleistocene glacial scour depression north of the town of Corcovado (mean annual temperature = 9 °C; mean annual precipitation = ca 530 mm; Servicio Meteorológico Nacional, 2012). Present vegetation is a mixture of *Nothofagus*, *Austrocedrus* and steppe taxa, although fires in the last decade have killed approximately 50% of the trees. Today the area is intensively grazed by sheep.

These records build on paleoecological data from nine sites located along a ca 275 km north–south transect in the foothills of

**Table 1**  
Study site information.

Site	Position	Elevation [m]	Water depth [cm]	Publications
M. Aguado	40.97°S; 71.93°W	930	NA	Markgraf and Bianchi, 1999
L. Escondido	41.05°S; 71.45°W	890	NA	Jackson, 1996
L. el Trébol	41.15°S; 71.32°W	977	1050	Whitlock et al., 2006
L. Mascardi	41.31°S; 73°W	1060	3000	Bianchi and Ariztegui, 2012
L. Padre Laguna	41.38°S; 71.32°W	1280	735	Iglesias et al., 2012a
L. Huala Hué	41.51°S; 71.58°W	849	864	Iglesias et al., 2012a
L. Cóndor	42.35°S; 71.29°W	818	850	Iglesias et al., 2012b
L. Mosquito	42.49°S; 71.39°W	551	800	Whitlock et al., 2006; Iglesias et al., 2012b
M. Serrucho	41.76°S; 71.42°W	995	NA	Markgraf et al., 2013
L. La Zeta	42.89°S; 71.35°W	774	675	This manuscript
L. Theobald	43.48°S; 71.58°W	678	488	This manuscript

the eastern Patagonian Andes at or near the forest/steppe boundary (Table 1; Fig. 1). Mallín Aguado (a bog on the northeast side of Lago Nahuel Huapi; 40.97°S; 71.93°W; 930 m elev.; Markgraf and Bianchi, 1999) lies in open *Austrocedrus* woodland on outwash surfaces east of (outside) late-Pleistocene moraines. Lago Escondido (41.05°S; 71.45°W; 890 m elev.; Jackson, 1996) and Laguna el Trébol (41.15°S; 71.32°W; 977 m elev.; Whitlock et al., 2006) are located in *N. dombeyi*–*Austrocedrus* forest, west of the city of San Carlos de Bariloche. L. Escondido lies west of (within) a late-Pleistocene moraine complex, and L. el Trébol is located in a depression created by meltwater spillways and glacio-fluvial deposits (Flint and Fidalgo, 1964, 1968; Bianchi et al., 1997).

Lago Mascardi (41.31°S; 73°W; 1060 m elev.; Bianchi and Ariztegui, 2012), Laguna Padre Laguna (41.38°S; 71.32°W; 1280 m

elev.; Iglesias et al., 2012a) and Lago Huala Hué (41.51°S, 71.58°W; 849 m elev.; Iglesias et al., 2012a) are located in the drainage of the Río Manso within Nahuel Huapi National Park, and surrounded by *N. dombeyi*–*Austrocedrus* forest. L. Mascardi is a large glacial lake fed by meltwater from Cerro Tronador glaciers. L. Padre Laguna is dammed by a broad postglacial alluvial fan (Iglesias et al., 2012a) 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).

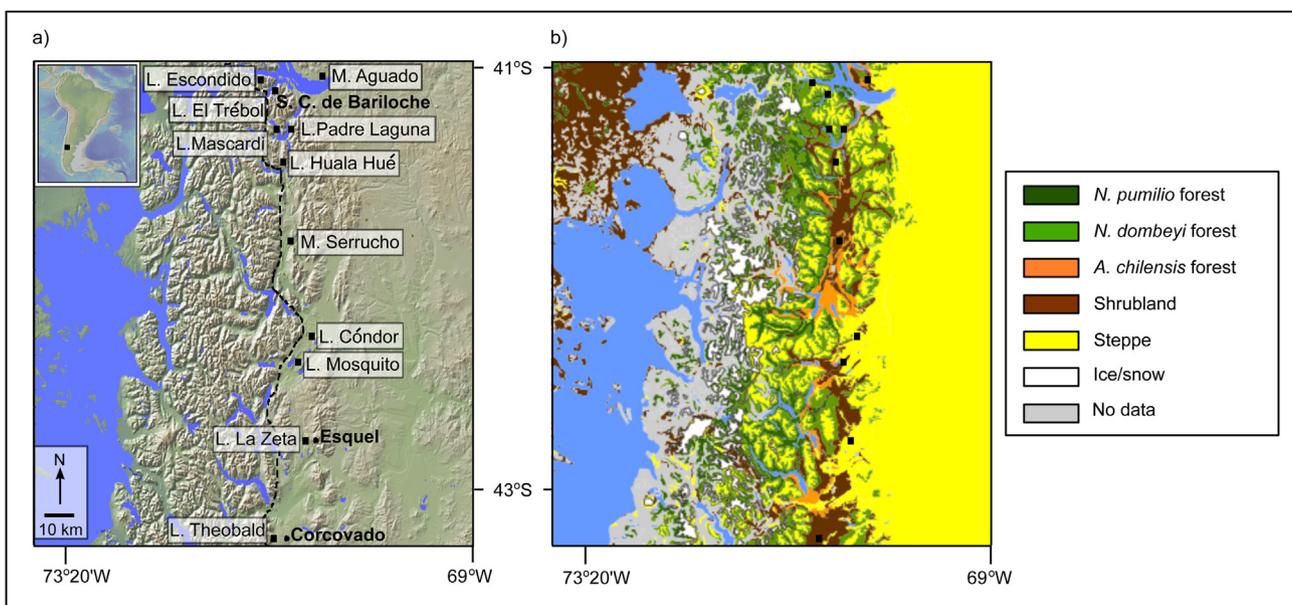
Mallín Serrucho (41.76°S; 71.42°W; 995 m elev.; Markgraf et al., 2013) is a Cyperaceae/*Empetrum nigrum* wetland located in a depression on the southwest slope of Cordón Serrucho Norte, ca 20 km northeast of the town of El Bolsón. Stands of *N. antarctica*, *Pilgerodendron uviferum* and *F. cupressoides* occur on the edges of the wetland, and the surrounding slopes support mixed *N. dombeyi*–*Austrocedrus* forest. Recent fires have favored the expansion of shrubs such as *N. antarctica* and *E. coccineum* into the formerly dense forest.

Lago Cóndor (42.35°S; 71.29°W; 818 m elev.; Iglesias et al., 2012b) and Lago Mosquito (also known as Lago Pellegrini; 42.49°S; 71.39°W; 551 m elev.; Whitlock et al., 2006; Iglesias et al., 2012b) are located 5 and 22 km northeast of the town of Cholila, respectively. The lakes lie close to late-Pleistocene terminal moraines, but the origin of the western site, L. Mosquito, is related to Holocene alluvial fans that dammed westward-flowing streams. The lakes are located within the transition zone from *Austrocedrus* woodland to steppe, and the landscape that surrounds them is heavily grazed by sheep and used for agriculture.

### 3. Methods

#### 3.1. Field and laboratory methods for L. La Zeta and L. Theobald

A modified Livingstone piston sampler was used to collect sediment cores from an anchored floating platform in L. La Zeta and L. Theobald lakes, and from the surface of La Zeta wetland. Cores were extruded in the field and shipped to LacCore Facility, University of Minnesota, for lithologic characterization. In the laboratory, cores were split longitudinally into a working half and an



**Fig. 1.** a) Study area and location of M. Aguado, L. Escondido, L. el Trébol, L. Mascardi, L. Padre Laguna, M. Serrucho, L. Huala Hué, L. Cóndor, L. Mosquito, L. La Zeta and L. Theobald. The dashed line shows the border between Argentina and Chile. b) Main vegetation types in the region (modified from Lara et al., 1999).

archive. The working half was described, photographed and analyzed. The archival core and other materials are stored at the Paleocology Laboratory at Montana State University.

Description of the lithology follows Schnurrenberger et al. (2003) and color specification is based on the Munsell system. 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 allocthonous sediment input from erosion and volcanic eruptions (Gedye et al., 2000). Gamma density ( $\text{kg cm}^{-3}$ ), 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  $\text{cm}^3$  samples taken at 1.5-cm intervals (Dean, 1974).

Pollen, charcoal, and bulk sediment were submitted for AMS radiocarbon dating (Table 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 were constructed with smoothing splines and a repeated sampling of point estimates approach (2000 iterations) that allows each date to influence the age model through the probability density function of the calibrated age (Fig. 2). The final age–depth models were based on the weighted mean of all runs (Blaauw, 2010).

Charcoal analysis was performed on 2-cm<sup>3</sup> volume samples taken at contiguous 0.5-cm intervals, following the methodology outlined by Whitlock and Larsen (2001) to reconstruct local fire

history. The material was wet-screened through a 125-mm-mesh sieve, and charcoal particles were identified under a stereomicroscope. Grass and wood charcoal were tallied separately. In order to override the effects of changing sedimentation rates, charcoal counts were converted to charcoal accumulation rates (CHAR; particles  $\text{cm}^{-2} \text{yr}^{-1}$ ; 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  $\text{cm}^3$  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  $\text{cm}^{-2} \text{yr}^{-1}$ ), which were interpreted as a general measure of plant abundance. Pollen identification was based on a reference collection and published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978) and performed at 400× and 1000× magnification. In all cases, counts exceeded 300 terrestrial pollen grains. Terrestrial pollen percentages were based on the sum of trees, shrubs and herbs, and plotted using C2 program (Juggins, 2007).

*N. dombeyi*-type pollen includes *N. dombeyi*, *N. pumilio*, and *N. antarctica*. Cupressaceae pollen is attributed largely to *Austrocedrus*, although rainforest cupressaceous taxa (*Fitzroya*, *Pilgerodendron*) may have been long-distance contributors. Rhamnaceae pollen is likely to come from species of the genera *Discaria* and/or *Colletia*. Minor pollen contributors are grouped into two ecological units: 'Other rainforest taxa' (e.g., *Hydrangea*, *Saxegothea*, *Gaultheria*); and 'Other shrubland/steppe taxa' (e.g., *Berberis*, *Acaena*, *Ephedra*).

### 3.2. Data synthesis

In order to evaluate the differences in vegetation development among sites, pollen percentage data from the eleven records were

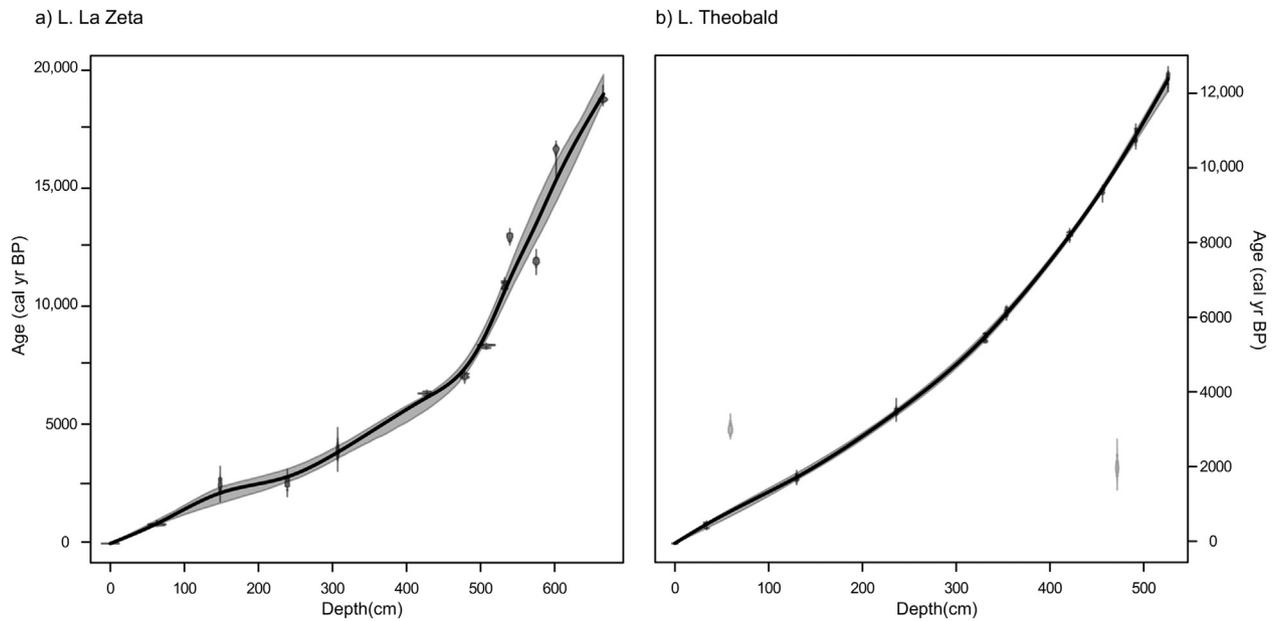
**Table 2**  
Radiocarbon and calibrated radiocarbon dates from La Zeta and Lago Theobald.

Core	Depth [cm]	Adjusted midpoint depth [cm] <sup>a</sup>	Lab no.	Material	<sup>14</sup> C yr BP	Corrected <sup>14</sup> C yr error	Median probability age [cal yr BP] <sup>b</sup>
<b>La Zeta lake</b>							
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	10,713
MLZ09A	185–185.5	171.25	85987	Pollen	11,050	60	12,940
MLZ09A	220.5–221	206.75	87552	Pollen	10,200	55	11,901
MLZ09A	251–251.5	233.75	85988	Pollen	13,450	45	16,636
MLZ09A	314.5–315	297.25	85989	Pollen	15,600	65	18,763
<b>Theobald lake</b>							
TH09A	0–0.05	0.5	n/a	Inferred	0		–59
TH09A	34–34.5	34.25	89039	Pollen	410	25	452
TH09A <sup>c</sup>	58.5–59	58.75	86923	Pollen	2850	75	2911
TH09A	130–130.5	130.25	86826	Pollen	1170	40	1624
TH09A	236–236.5	236.25	86828	Pollen	3250	55	3420
TH09A	331–331.5	331.25	86792	Pollen	4710	30	5404
TH09A	354–354.5	354.25	88953	Pollen	5360	40	6085
TH09A	421–421.5	421.25	86697	Pollen	7380	30	8114
TH09A	456–456.5	456.25	88955	Pollen	8350	40	9308
TH09A <sup>c</sup>	471–471.5	471.25	86930	Charcoal	1990	130	1883
TH09A	493.5–494	492.25	88957	Pollen	9500	45	10,680
TH09A	528–528.5	526.25	86696	Pollen	10,500	50	12,273

<sup>a</sup> Adjusted depths were used to calculate the age–depth model. Only true depths are referred to in text.

<sup>b</sup> Calibrated ages were based on CALIB 6.0 (Stuiver et al., 2005; <http://radiocarbon.pa.qub.ac.uk/calib/calib.html>).

<sup>c</sup> Not included in the chronologies.



**Fig. 2.** Age–depth models for a) L. La Zeta and b) L. Theobald. 95% confidence intervals are shown in gray. The distributions of the calibrated radiocarbon ages used to develop the models are shown in black, and dates that were not included in the models are indicated in gray.

grouped according to their ecological affinities into ‘*N. dombeyi* forest’, ‘Cupressaceae’, ‘Shrubland’ and ‘Steppe’ (Lara et al., 1999) and expressed as a function of latitude and time. Spatio-temporal patterns were further explored with isopoll maps. Isopolls were based on the median pollen percentage for each group (i.e., ‘*N. dombeyi* forest’, ‘Cupressaceae’, ‘Shrubland’ and ‘Steppe’) calculated at each site for the periods >15,000 cal yr BP; 15,000–10,000 cal yr BP; 10,000–5000 cal yr BP and 5000 cal yr BP – present. Bivariate interpolation onto a grid for irregularly spaced data was applied to the values calculated at each site to construct maps (Akima, 1978). For reference, modern isopolls, defined as the median pollen percentage for the <200 cal yr BP period, are also provided.

Instantaneous rates of forest taxa pollen percentage change, calculated as  $\lim_{\Delta t \rightarrow 0} \frac{\Delta \text{Forest taxa pollen percentage}}{\Delta \text{Time}}$ , were used as a proxy of forest vegetation variability at centennial scales. Calculation of the absolute value of the first derivative of the forest taxa time series (i.e., the difference in forest taxa pollen percentages between consecutive pollen samples divided by the difference in age between both samples) allowed us to infer the magnitude of vegetation change per year. Rates of change are shown with box-plots for the periods >15,000 cal yr BP, 15,000–10,000 cal yr BP, 10,000–5000 cal yr BP and 5000 cal yr BP – present. Unless indicated otherwise, all plots and analyses were performed in R (R Core Team, 2012).

## 4. Results

### 4.1. Chronology

Nine pollen samples and three charcoal samples from the L. La Zeta site were submitted for AMS radiocarbon dating analysis (Table 2). Four samples came from the lake core LZ09A and eight samples were obtained from the wetland core MLZ09A. A preliminary model was developed by independently modeling age as a function of depth in each core. In both cores, a distinctive white pumiceous tephra unit was observed, yielding an age of  $5200 \pm 300$  and  $5350 \pm 200$  cal yr BP, respectively. Although no tephrochronological studies were performed, the similarity in the physical properties of the ash, in addition to the overlap between

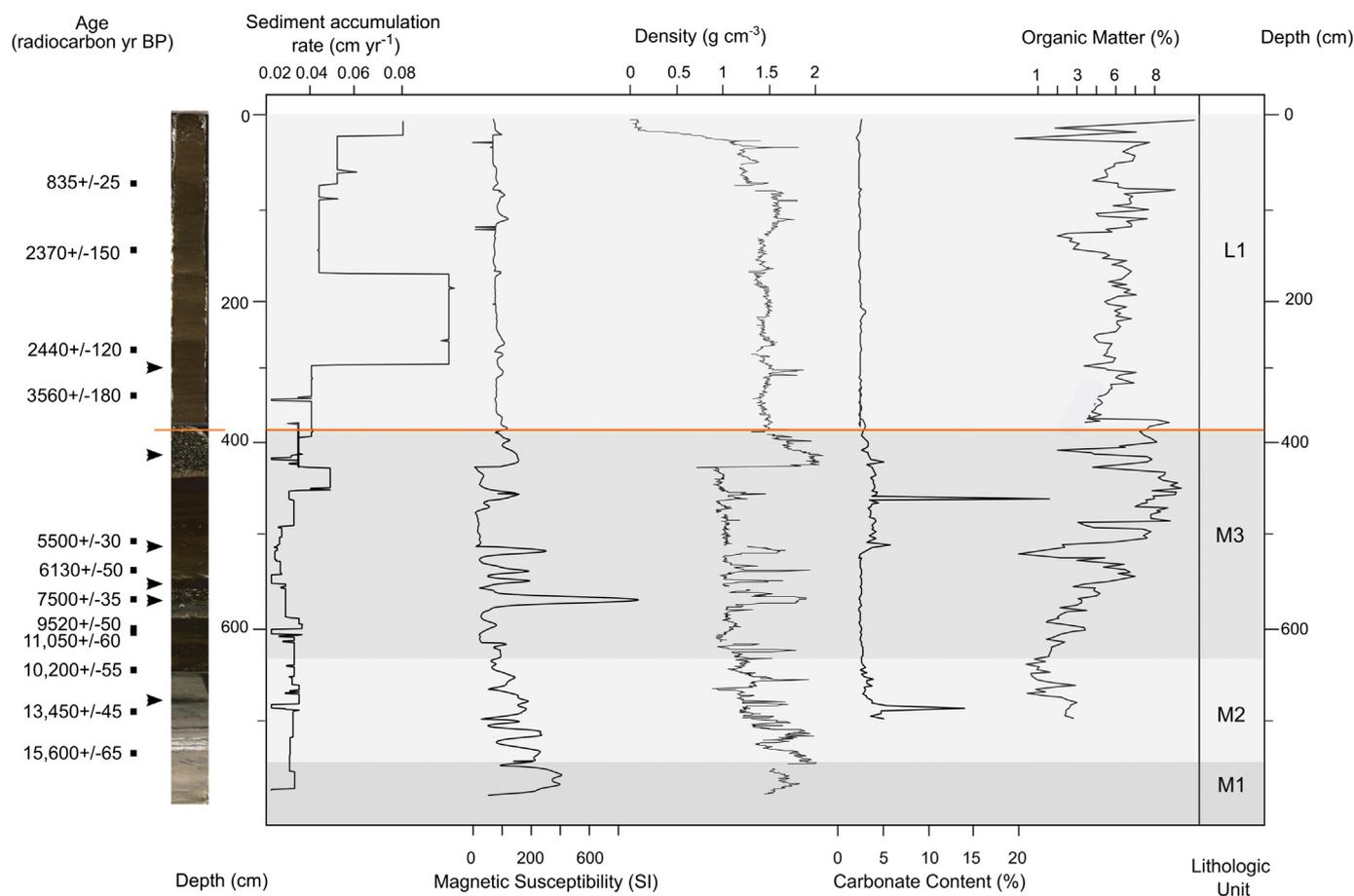
the confidence intervals for their ages suggested that they represent the same volcanic event. The final age–depth model was developed by Monte Carlo fitting smoothing splines through the probability distribution of all calibrated ages, and using this tephra as the point of correlation between cores. We developed five alternative chronologies at L. La Zeta based on AMS radiocarbon dates taken from the lake and wetland cores by applying different degrees of smoothing. The preferred chronology allowed for changes in sedimentation rates across different lithologies (Fig. 2a), although it did not significantly differ from models fitted independently to the LZ09A and MLZ09A cores. Hereafter, we refer to the combined lake and wetland record as “L. La Zeta.”

At L. Theobald, ten pollen samples and one charcoal sample from the TH09A core were submitted for AMS dating (Table 2). 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 to 471–471.5 cm depth was discarded as too young. We assumed that it had been contaminated with modern carbon during coring or sampling. All the models passed through the 95% confidence interval of the  $^{14}\text{C}$  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. 2b).

Chronologies from M. Aguado, L. Escondido, L. el Trébol, L. Mascardi, L. Huala Hué, L. Padre Laguna, L. Cóndor, L. Mosquito and M. Serrucho were published by Markgraf and Bianchi (1999), Jackson (1996), Whitlock et al. (2006), Bianchi and Ariztegui (2012), Iglesias et al. (2012a), Iglesias et al. (2012b), Whitlock et al. (2006) and Markgraf et al. (2013), respectively. Comparison of the chronologies from all sites suggests that sedimentation rates were variable among lakes. Nonetheless, a trend from low sedimentation rates during the Lateglacial/early-Holocene transition to higher deposition in the late Holocene was observed at all sites.

### 4.2. Lithology

At L. La Zeta, three lithological units were identified in the wetland core MLZ09A (Fig. 3). Unit M1 (763–725.5 cm depth) was



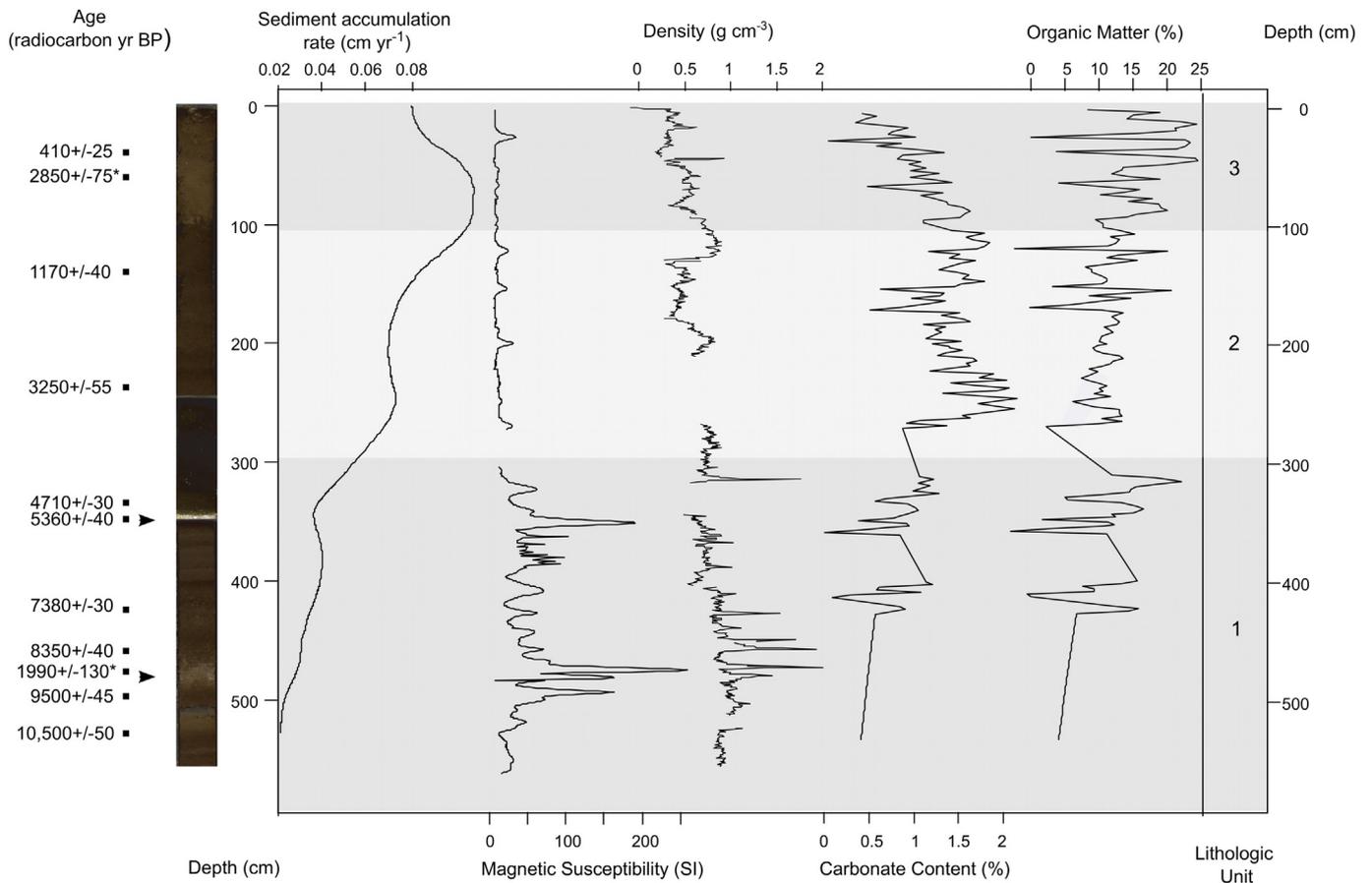
**Fig. 3.** Lithology, sediment accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the LZL09 (lake) and MLZ09A (wetland) cores. The correlation point (pumiceous tephra) between the two cores is shown with a dashed line. Black triangles indicate the position of tephra layers and black squares represent radiocarbon dates.

composed of clay and sand beds. Extrapolation of the chronology suggests that this unit was deposited between 22,870 and 21,550 cal yr BP. However, the basal age is poorly constrained and geomorphological evidence indicates that it may be too old (Schaebitz, 1994). High bulk density and magnetic susceptibility suggest that this interval was characterized by abundant allochthonous input possibly associated with poorly developed soils and sparse vegetation cover. Unit M1 was overlain by a laminated inorganic clay unit (Unit M2; 725.5–640 cm depth; >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, implying decreased allochthonous input and changes in sediment source. At 640 cm depth, a diffuse contact marked the beginning of the uppermost gyttja unit (Unit M3, 640–370 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 515 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 increase in organic matter content and sedimentation rates, possibly reflecting lower lake levels and the imminent establishment of the modern wetland. Nineteen ash layers were identified in the core, and are likely deposited after past eruptions of Chaitén, Corcovado,

Michinmahuida and other volcanoes in the Andean Southern Volcanic Zone (Naranjo and Stern, 2004; G. Villarosa, pers. communication, 2009).

The sediments in L. La Zeta LZ09A consisted of fine-detritus gyttja and three ash layers (Unit L1; 370–0 cm depth; 5930 cal yr BP-present; Fig. 3). The magnetic susceptibility and gamma density as well as carbonate and organic matter content of the sediments showed little variability throughout the core. As noted above, 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 TH09B was composed of fine-detritus gyttja (Fig. 4). The basal unit (Unit 1, 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 content was highly variable. Unit 1 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. Gamma density or organic matter did not change significantly from values in the basal unit. 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 and gradually decreased throughout the unit. 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.



**Fig. 4.** 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.

Lithologies from the cores obtained at M. Aguado, L. Escondido, L. el Trébol, L. Mascardi, L. Huala Hué, L. Padre Laguna, L. Cóndor, L. Mosquito and M. Serrucho were described by Markgraf and Bianchi (1999), Jackson (1996), Whitlock et al. (2006), Bianchi and Ariztegui (2012), Iglesias et al. (2012a) Iglesias et al. (2012b), Whitlock et al. (2006) and Markgraf et al. (2013), respectively. Although the ages of the lithologic boundaries vary among sites, sequential transitions in sediment type from inorganic laminated clay to organic silt/fine detritus gyttja were observed in all cores. The lithological change to more organic sediments was associated with higher-than-before sedimentation rates, suggesting that increased lake productivity rather than allochthonous clastic inputs have been the main source of material to the lakes in the last ca 5000 years.

#### 4.3. Pollen and charcoal records

Vegetation types (e.g., steppe, shrubland forest) were defined following Markgraf et al. (2002) and Páez et al. (2001). Their modern pollen studies suggest that forest is characterized by percentages of arboreal pollen types (e.g., *N. dombeyi*-type, Cupressaceae, *Podocarpus*) >70% and pollen influx >8000 grains  $\text{cm}^{-3}$ . Open forest is inferred from arboreal pollen types >60% and pollen influx <5000 grains  $\text{cm}^{-3}$ . Shrubland is characterized by pollen percentages of shrub pollen types (e.g., *Berberis*, *Discaria*, *Maytenus*) >4% and arboreal pollen types <70%; and steppe, by Poaceae and steppe pollen types (e.g., *Acaena*, *Ephedra*, *Chenopodiaceae*) >45%. The resulting pollen and charcoal stratigraphy was broadly similar among sites (Figs. 5–7). Based on inferred shifts in dominant

species abundance at each site, the vegetation and fire history of the study area was divided into four phases (Figs. 6–8).

##### 4.3.1. Lateglacial steppe (>15,000 cal yr BP)

At L. La Zeta, sediments older than 15,000 cal yr BP were dominated by Poaceae and other steppe taxa (<83%). Similarly, Poaceae and other steppe taxa pollen percentages from L. el Trébol, L. Mascardi, M. Serrucho were high and oscillated between 50 and 80%. Trace Cupressaceae pollen was observed at all sites. Comparison to modern pollen samples indicates that these four watersheds supported steppe vegetation, and low PAR values suggest sparse vegetation cover. Negligible CHAR at L. La Zeta (0.01 particles  $\text{cm}^{-2} \text{yr}^{-1}$ , on average) and very low CHAR at the remaining sites (<0.03 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) indicate that fire was not an important feature of the ecosystem. At ca 16,500 cal yr BP, *N. dombeyi*-type and other forest taxa pollen increased from about 40 to >60% at L. Mascardi. Based on comparison with modern pollen studies, the relatively high percentages of arboreal pollen likely came from isolated patches or distant sources of *Nothofagus* (Markgraf et al., 2002; Bianchi and Ariztegui, 2012).

##### 4.3.2. Lateglacial/early-Holocene open forest (ca 15,000–10,000 cal yr BP)

At ca 15,000 cal yr BP, percentages of *N. dombeyi*-type pollen increased up to ca 75% at L. La Zeta at the expense of steppe taxa. The same increase occurred at M. Aguado, L. el Trébol and M. Serrucho. Asteraceae, *Chenopodiaceae* and other shrubland/steppe taxa were abundant at all sites. Pollen percentages remained

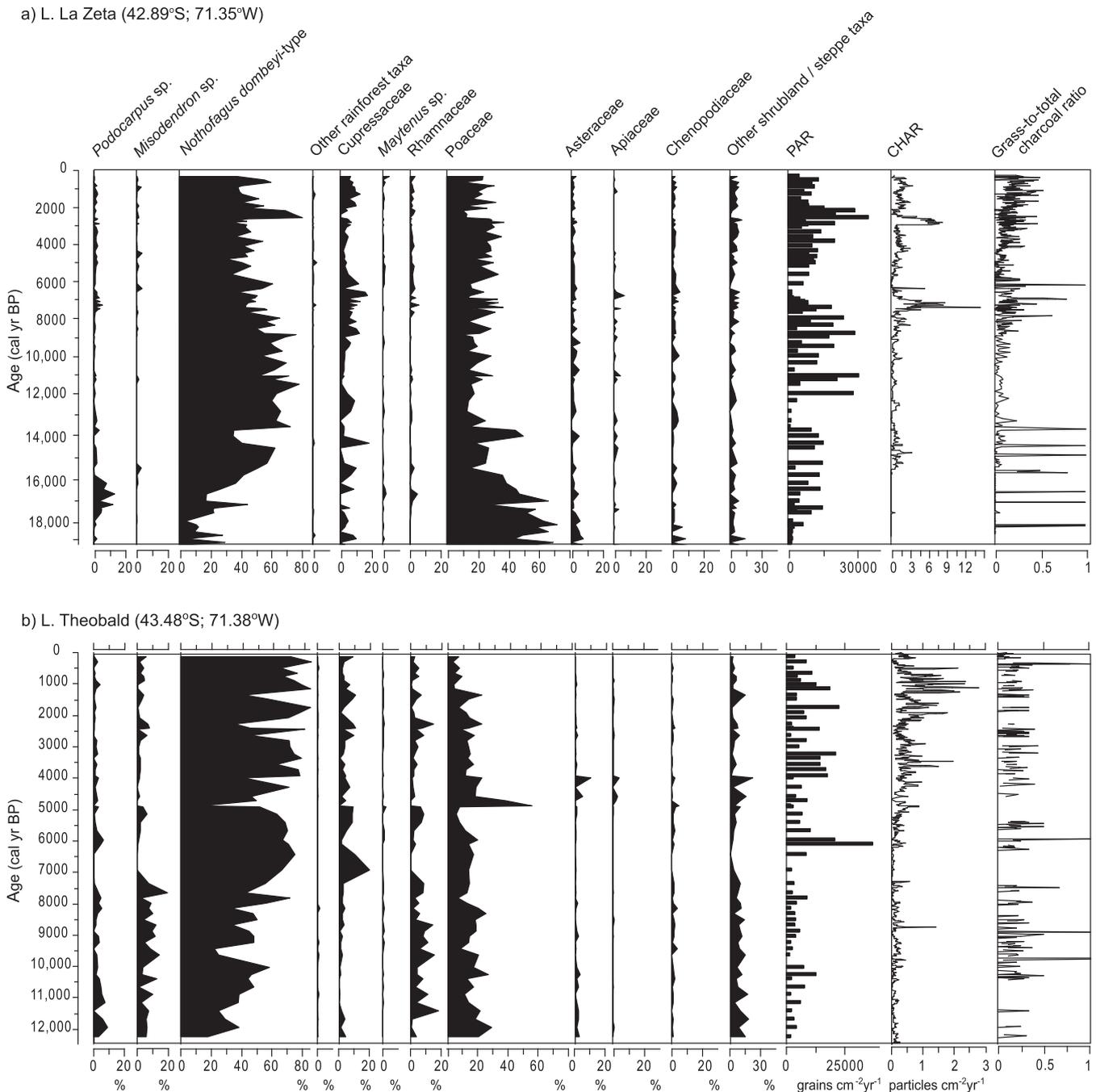


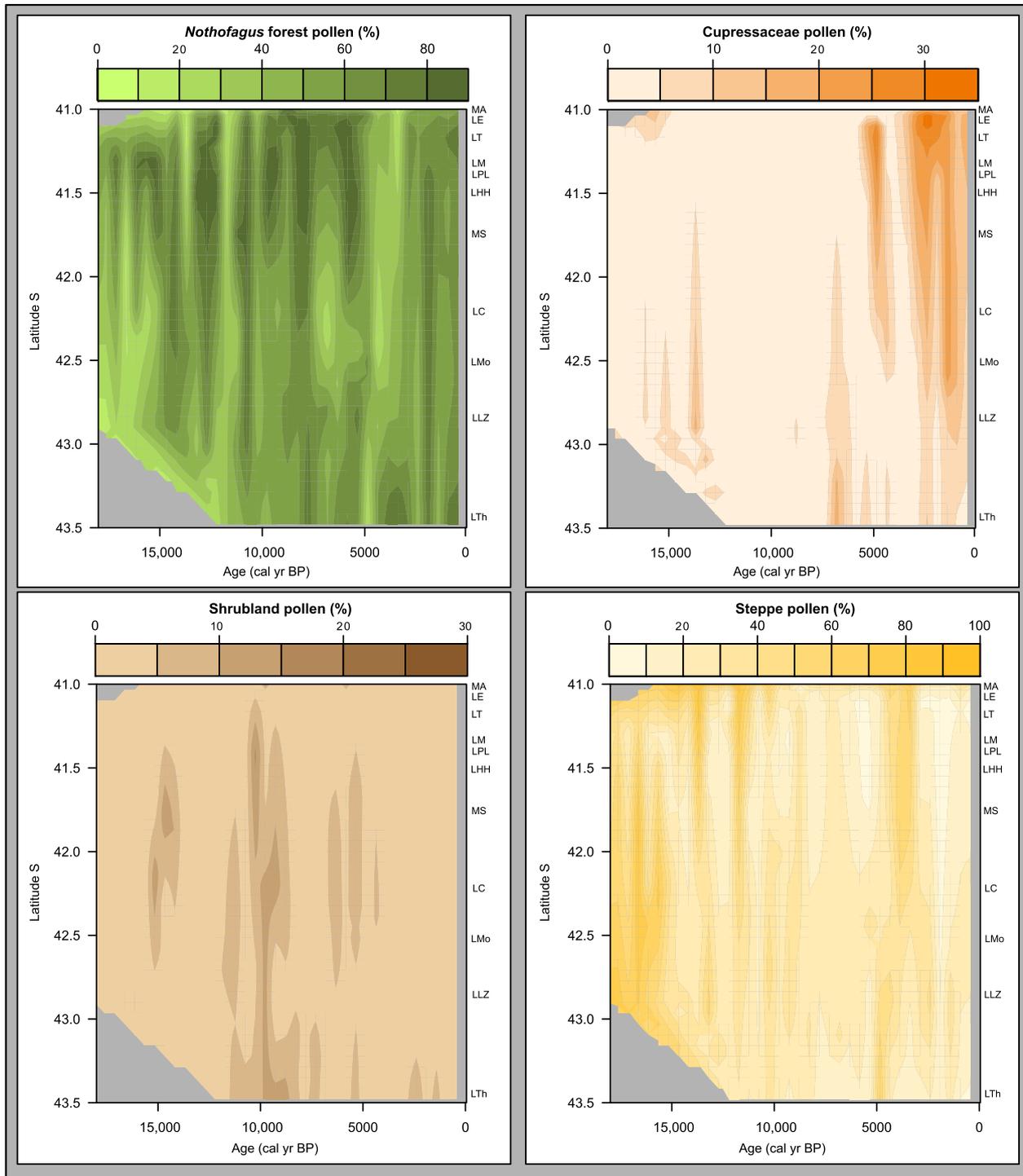
Fig. 5. Selected pollen and charcoal data for a) La Zeta, and b) L. Theobald.

similar to those in the previous zone at L. Mascardi, and forest pollen percentages oscillated between 65 and 80% at L. Escondido. At ca 13,900 cal yr BP, *Nothofagus* pollen decreased to 31% at L. La Zeta and rapidly rose to 71% at 12,500 cal yr BP. Conversely, pollen data showed little variability at M. Aguado, L. Escondido, L. el Trébol, and M. Serrucho throughout the Lateglacial/early-Holocene transition.

At L. Huala Hué, *N. dombeyi*-type pollen decreased from 88 to 38% at 11,125 cal yr BP, whereas shrubland and steppe taxa increased from 2 to 6% in both cases. 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 fluctuated

between 19 and 69% at L. Theobald, and Poaceae (<29%), Rhamnaceae (<19%) and other shrubland/steppe taxa (<17%; e.g., *Escalonia* and *Gevuina*) were also present.

Comparison with modern pollen samples suggests that open forest dominated by *Nothofagus* prevailed in the M. Aguado, L. el Trébol, L. Mascadi, L. Cóndor, L. Mosquito and L. La Zeta watersheds. *Nothofagus* and shrubland taxa dominated L. Huala Hué, M. Serrucho and L. Theobald (Markgraf et al., 2001). PAR was low (<15,000 grains cm<sup>-2</sup> yr<sup>-1</sup> at all sites), implying patchy vegetation cover. CHAR increased to <20 particles cm<sup>-2</sup> yr<sup>-1</sup> at all sites, indicating that biomass burning was higher than before. Grass-to-total charcoal ratios were <0.4, and it is likely that the shrub component was the source of the woody fuels.



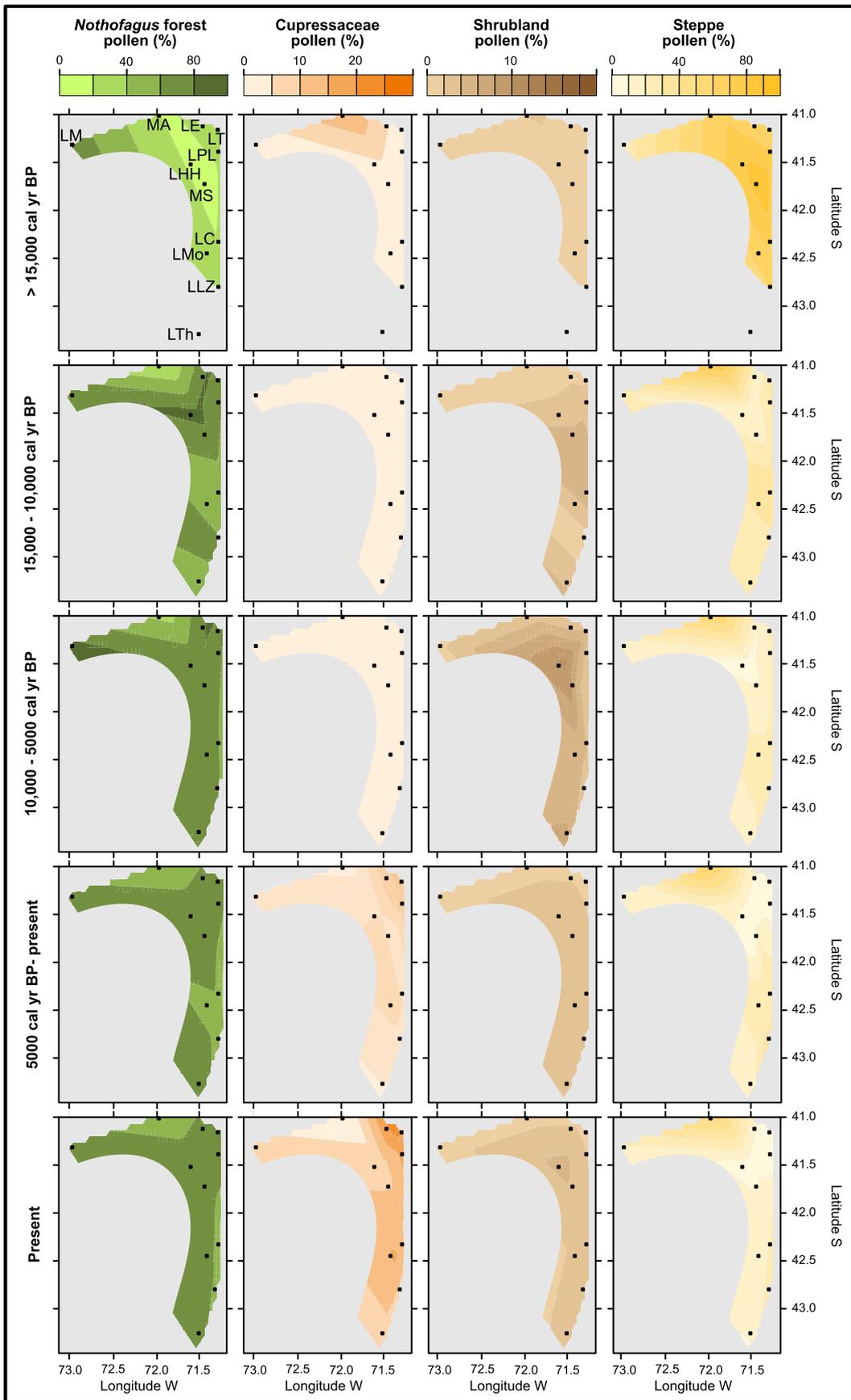
**Fig. 6.** Spatio-temporal patterns of vegetation change as reconstructed from bivariate interpolation of pollen percentages onto a grid defined by latitude and time (Akima, 1978). The panels show *Nothofagus* forest (e.g., *Nothofagus-dombeyi* [the dominant pollen type in the assemblage], *Saxegothaea*, *Laurelia*, *Hydrangea*, *Lomatia*), Cupressaceae (attributed to *Austrocedrus*, although it could also be *Fitzroya* or *Pilgerodendron*), shrubland (e.g., *Maytenus*, *Berberis*, *Rhamnaceae*) and steppe (e.g., *Mulinum*, *Poaceae*) taxa pollen percentages. The latitude of the sites employed in the analysis is shown on the right of each panel (MA = M. Aguado, LE = L. Escondido, LT = L. el Trébol, LM = L. Mascardi, LPL = L. Padre Laguna, LHH = L. Huala Hué, MS = M. Serrucho, LC = L. Cóndor, LMo = L. Mosquito, LLZ = L. La Zeta and LTh = L. Theobald).

#### 4.3.3. Early Holocene shrubland (ca 10,000–5000 cal yr BP)

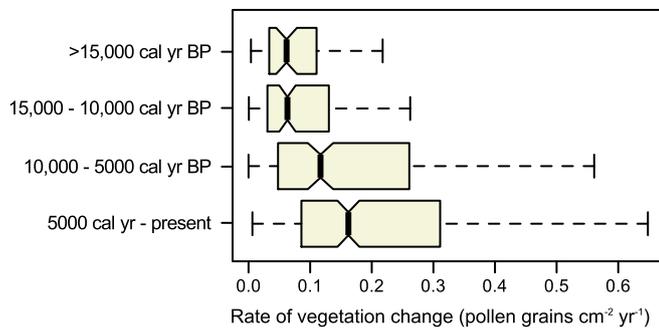
*N. dombeyi*-type (<78% at all sites), Asteraceae (<3% at all sites) and Chenopodiaceae (<12% at all sites) pollen percentages and PAR (<15,000 grains  $\text{cm}^{-2} \text{yr}^{-1}$  at all sites) were similar to those of the previous period. Cupressaceae pollen percentages rose at all sites, suggesting a regional increase in *Austrocedrus*. *Rhamnaceae* and *Maytenus* pollen gradually decreased at all sites from <7 to <2%

each, except at L. La Zeta, where the opposite trend was observed (and increase from 0 to 1.5%, and 1 to 4%, respectively). Comparison with modern samples suggests that shrubland vegetation grew at all sites (Markgraf et al., 2002).

The fire history was variable among sites. At L. el Trébol, L. Huala Hué and L. Mosquito, CHAR values were similar to those of the previous period (CHAR <20 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ). At 7600 cal yr BP, grass-



**Fig. 7.** Isopoll (i.e., lines connecting points of equal pollen percentages) maps for the periods >15,000 cal yr BP; 15,000 – 10,000 cal yr BP; 10,000–5,000 cal yr BP; 5,000 cal yr BP – present, as constructed by applying bivariate interpolation onto a grid for irregularly spaced data to the median pollen percentages calculated for each period at every site (Akima, 1978). For reference, modern isopolls, defined as the median pollen percentage for the <200 cal yr BP period, are also provided.



**Fig. 8.** Forest taxa rates of change (i.e., magnitude of change in forest taxa percentages per year) for the periods >15,000 cal yr BP; 15,000 – 10,000 cal yr BP; 10,000–5000 cal yr BP; and 5000 cal yr BP – present. The boxplots show the median (i.e., band inside the box), first and third quartiles (lower and upper values defining the box) and lowest and highest (i.e., whiskers) rates of change for each period. Note that non-overlapping notches (i.e., narrowing of the box around the median) provide evidence that the rates of change differ between groups (Chambers et al., 1983).

to-total charcoal ratio increased from 0.2 to 0.8 at L. el Trébol. The CHAR levels and composition suggest that fire activity did not change significantly from previous high levels but that grass fires were more prevalent. M. Serrucho (CHAR up to 16 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ), L. Cóndor (CHAR up to 4.1 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ), L. La Zeta (CHAR up to 14 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) and L. Theobald (CHAR up to 0.8 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) watersheds experienced more fires in the shrubland period as compared with fire activity during the previous open forest period.

#### 4.3.4. Late-Holocene *N. dombeyi*–*A. chilensis* forest (ca 4500 cal yr BP–present)

After 5000 cal yr BP, pollen records from M. Aguado, L. el Trébol, L. Mascardi, L. Padre Laguna, L. Huala Hué, M. Serrucho and L. Mosquito indicate a pronounced increase of *N. dombeyi*-type and/or Cupressaceae (up to 89 and 60%, respectively) at the expense of Poaceae (<40%), Rhamnaceae (<15%) and other shrubland and steppe taxa (<10%). At L. Cóndor, L. La Zeta and L. Theobald, *N. dombeyi*-type pollen values increased from 20 to 74%, 45 to 64%, and 44 to 83%, respectively. Close comparison with modern pollen samples from western Patagonia suggests that present-day mixed *Nothofagus*–*Austrocedrus* forest developed during this period (Markgraf et al., 2002). Except at L. Mosquito, shrub pollen percentages (e.g., *Colletia*, *Discaria*, *Berberis*) decreased at all sites at ca 3000 cal yr BP (to <10%), especially in the north.

During the late Holocene, total and arboreal PAR reached high values at all sites, suggesting the development of closed forest. Despite abundant woody fuels, fire regimes were spatially and temporally variable. Levels of biomass burning increased at L. Huala Hué (CHAR >0.3 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ), L. Mosquito (CHAR >2 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) and L. Theobald (CHAR >0.4 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) at the beginning of the period and at M. Serrucho at ca 3000 cal yr BP. At L. Huala Hué, a rise in the grass-to-total charcoal ratio to 0.8 units at 2300 cal yr BP indicates increased burning of Poaceae (possibly *Chusquea*). A similar shift from wood-dominated to grass fuels occurred at L. Mosquito at 4250 cal yr BP (grass-to-total charcoal ratio from <0.5 to 0.9) and at L. La Zeta (grass-to-total charcoal ratio 0.2–0.5) at ca 4000 cal yr BP. In contrast, CHAR decreased at L. Cóndor from 1.3 to 1 particles  $\text{cm}^{-2} \text{yr}^{-1}$  at 4500 cal yr BP, and the grass-to-total charcoal ratio (<0.3) was lower than before, suggesting less biomass burning and in particular, fewer grass fires. CHAR levels showed little variation at L. el Trébol or L. Padre Laguna, indicating that biomass burning remained relatively high and unchanged from early-Holocene levels.

## 5. Discussion

### 5.1. Environmental history of the forest/steppe ecotone

#### 5.1.1. Lateglacial period (>ca 15,000 cal yr BP)

During the Last Glacial Maximum (LGM; ca 23,000–19,000 cal yr BP), 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 approximately 6 °C along the Pacific coast (Lamy et al., 1999) and decreased precipitation throughout Patagonia (Markgraf et al., 2007). 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 former range (Barreda et al., 2007).

Regional deglaciation began at ca 18,000 cal yr BP (Hulton et al., 2002) and rapid glacial recession continued until ca 13,000 cal yr BP. Spatiotemporal analysis of pollen data suggests that climate generalists survived in unglaciated regions, where open grass-dominated steppe was prevalent (steppe taxa pollen > 50%; Fig. 6). At L. Zeta, for example, steppe was dominated by Poaceae, Asteraceae and sparse spiny shrubs such as *Mulinum* (Fig. 5a). Although arboreal pollen percentages were low prior to ca 15,000 cal yr BP (<35%; Fig. 6), the isopoll maps show a west-to-east decline in forest taxa pollen (Fig. 7) that argues for the early presence of trees west of the study area and even local forest patches in some watersheds (i.e., M. Serrucho; Markgraf et al., 2013). Rates of vegetation change were low (median rate of change < 0.1%  $\text{yr}^{-1}$ ; Fig. 8) either because the dominant steppe taxa were (and are) relatively insensitive to short-term changes in climate and physical conditions or the sampling resolution was too low to capture short-term vegetation responses. There is no evidence of fires at this time, probably as a consequence of sparse vegetation cover and limited ignitions.

#### 5.1.2. Lateglacial/early-Holocene transition (ca 15,000–10,000 cal yr BP)

The Lateglacial/early-Holocene transition was characterized by gradually wetter conditions associated with a shift in dominance from year-round polar air masses during the glacial period to more humid Pacific air masses in the Holocene (Heusser, 2003). Pronounced reorganization of the landscape at this time can be inferred from changes in the lithology of the sediment cores. A shift from magnetically enriched inorganic clay to organic laminated clay at L. el Trébol (Whitlock et al., 2006), L. Mascardi (Aritztegui et al., 1997) and L. Huala Hué (Iglesias et al., 2012a) suggests that an initial period of high meltwater input and slope instability was followed by one of greater lacustrine productivity and more stabilized slopes. This change is consistent with sparsely vegetated periglacial landscapes that became more stabilized at ca 18,000 cal yr BP at L. La Zeta (Fig. 4), 16,500 cal yr BP at M. Serrucho (Markgraf et al., 2013); 14,070 cal yr BP at L. el Trébol (Whitlock et al., 2006), and ca 13,300 cal yr BP at L. Huala Hué (Iglesias et al., 2012a). In contrast to fluctuations in lithology and limnobiota, forest pollen percentages at this time do not provide evidence of high-frequency variability in vegetation composition (median rate of change < 0.1%  $\text{yr}^{-1}$ ; Fig. 8).

After ca 15,000 cal yr BP, percentages of *N. dombeyi*-type pollen rose to 75% at L. el Trébol, M. Serrucho and L. La Zeta, likely reflecting the invasion of *N. dombeyi* and *N. antarctica*. *Nothofagus* expansion, which would have been favored by increasing moisture levels, was asynchronous, occurring as early as ca 16,500 at L. Mascardi and not until ca 14,000 at L. el Trébol (Figs. 6 and 8;

Whitlock et al., 2006; Markgraf et al., 2013). At L. Zeta, in particular, the pronounced increase in *Nothofagus* occurred at expense of Poaceae (Fig. 5a).

Spatiotemporal analysis of pollen data reveals pronounced regional low frequency variations in forest taxa pollen percentages (oscillating between 15 and 75%; Fig. 6) at expense of steppe species (10–50%) between 15,000 and 10,000 cal yr BP, suggesting millennial-scale fluctuations in the dominance of open forest versus steppe taxa. The variability was more pronounced north of lat. 42°S than south of that latitude, as evidenced by the contrast between the dramatic increase in forest taxa from 15 to 80% at ca 13,000 cal yr BP followed by a drop to 10% at the northernmost sites, and more moderate shifts in the south of the study area (forest taxa between 20 and 50%; Fig. 6).

The expansion of *Nothofagus* was followed by an increase in other woody species. Shrubs became abundant near L. el Trébol, L. Mascardi and L. Huala Hué after ca 11,200 cal yr BP; in the vicinity of L. Mosquito – L. Cóndor and L. La Zeta after ca 9200 cal yr BP; and in the L. Theobald watershed after ca 11,000 cal yr BP. Thus, *Colletia*, *Discaria*, *Maytenus*, *Berberis* and other shrubs constituted either a woody component of open *Nothofagus* forest at that time or a discrete shrubland zone east of closed *Nothofagus* forest.

The increase of woody taxa throughout the region provided fuels, resulting in more biomass burning than in previous times, as indicated by increased charcoal accumulation rates at most sites (e.g., Fig. 6; Whitlock et al., 2006). Nonetheless, changes in forest or shrub pollen percentages were not concurrent with (nor did they immediately follow) shifts in CHAR or the grass-to-total charcoal ratio (Fig. 6, Whitlock et al., 2006; Iglesias et al., 2012a,b; Markgraf et al., 2013). This lack of synchrony between the pollen and charcoal data suggests that even though changes in the fire regime may have altered local vegetation composition, this transformation did not significantly affect the dominant species. Instead, differences in effective moisture along with watershed-scale edaphic and topographic variability may explain the heterogeneous vegetation pattern.

A cooling event has been recorded in northern Patagonia and identified as the Huelmo-Mascardi Cold Reversal (11,400–10,200 <sup>14</sup>C yr [ca 13,300–11,870 cal yr BP], Hajdas et al., 2003). At L. Mascardi, declining populations of *N. dombeyi* between ca 13,700 and 11,800 cal yr BP have been attributed to the effects of low temperatures in vegetation establishment and development (Bianchi and Ariztegui, 2012). In contrast, data from marine cores off the coast of Chile (Lamy et al., 2004) and geomorphologic studies south of lat. 41°S (Andersen et al., 1995; Lowell et al., 1995) offer no evidence of cooling or glacier advances at this time. Similarly, the majority of sites in this study show no vegetation change during Huelmo-Mascardi Cold Reversal suggesting that 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., *N. dombeyi*-type, Poaceae). An exception in the pollen records is a pronounced decline in *N. dombeyi*-type pollen at L. La Zeta between ca 13,900 and 12,930 cal yr BP (Fig. 5a), where the loss of trees is coupled with a rise in disturbance and cold-resistant taxa such as Poaceae and Asteraceae. Thus, only two sites, L. Mascardi and L. La Zeta, show vegetation changes consistent with cooling during the Huelmo-Mascardi Cold Reversal. The absence of wider response argues that the fluctuations in forest were local or nonclimatic in origin.

### 5.1.3. Early Holocene (ca 10,000–5000 cal yr BP)

Progressively cooler and/or effectively wetter climate conditions have been inferred from paleoenvironmental records throughout Patagonia during the early Holocene and attributed to decreasing

annual insolation and amplification of the seasonal cycle of insolation (Berger and Loutre, 1991). Lower annual insolation was likely coupled with strengthened Southern Westerlies, resulting in more effective moisture throughout western Patagonia (Lamy et al., 1999; Fletcher and Moreno, 2011). Increased effective moisture is consistent with evidence of higher-than-before lake levels north of lat. 40°S (Jenny et al., 2003; Bertrand et al., 2008), 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).

Isopoll maps show that, between ca 10,000 and 5000 cal yr BP, a well-defined west-to-east vegetation gradient developed in northwestern Patagonia. Closed *Nothofagus* forests grew in L. Mascardi (the westernmost site; Bianchi and Ariztegui, 2012; Fig. 7). Further east (i.e., L. Escondido, L. el Trébol, L. Huala Hué and M. Serrucho and L. Theobald), closed forests transitioned to open forests and shrubland of *Colletia*, *Berberis* and *Discaria*. For example, *N. dombeyi*-type (<80%), Poaceae (<30%), *Misodendron* (<20%), *Maytenus* (<20%) and other shrubs (<25%) dominate the early-Holocene pollen record from L. Theobald. The great abundance of *Misodendron*, a semiparasite that grows on *Nothofagus*, suggests that *N. dombeyi* and/or *N. antarctica* were present in the watershed, and low PAR (<12,000 grains cm<sup>-2</sup> yr<sup>-1</sup>) is indicative of low vegetation cover (Fig. 5b). At the easternmost sites (i.e., L. Mosquito, L. Cóndor and L. La Zeta), steppe taxa were well represented in the pollen records (Fig. 6). At L. La Zeta, in particular, high pollen percentages of Poaceae (<50%) and shrubland/steppe taxa (<15%), along with PAR values similar to those observed during glacial times are consistent with open grass and shrub dominated vegetation (Fig. 5a).

Early-Holocene vegetation dynamics mainly involved millennial-scale trade-offs between trees and shrubs. For example, bivariate interpolation of pollen data shows that, at latitude 42°S, shrubs expanded at expense of trees between ca 10,000 and 8000 cal yr BP, ca 7000 and 6300 cal yr BP, and ca 6000 and 5500 cal yr BP, and declined at ca 8000–7000 cal yr BP and ca 6300–6000 cal yr BP (Fig. 6). Large-magnitude short-term fluctuations (i.e., centennial-scale) in vegetation composition are also inferred for the period (median rate of change = 0.13% yr<sup>-1</sup>; Fig. 8), and associated with increased magnetic susceptibility at most sites (i.e., L. La Zeta, Fig. 3; L. Theobald, Fig. 4; L. Huala Hué and L. Cóndor, Iglesias et al., 2012a,b, respectively; M. Serrucho, Markgraf et al., 2013). Changes in vegetation composition along with pulses of erosion may result from multi-decadal shifts in effective moisture.

Biomass burning increased in most watersheds prior to ca 8000 cal yr BP and remained relatively high until present. Variable moisture availability would have led to fluctuations between periods of fuel accumulation and desiccation, conditions conducive to fire in modern ecosystems (Whitlock et al., 2010). Additionally, fires were probably facilitated by the rapid fuel recovery, flammability and vertical continuity provided by the abundant shrubs growing in the area (Mermoz et al., 2005).

### 5.1.4. Late Holocene (ca 5000 cal yr BP-present)

During the last ca 5000 cal yr BP, precipitation increased in northern Patagonia, likely as a response to the continued northward shift/strengthening of the Southern Westerlies, as well as the strengthening of ENSO-related climate variability (Lamy et al., 2004; Markgraf et al., 2007, 2013). Along the study transect, higher effective moisture promoted the development of the modern vegetation, including the expansion of *A. chilensis* (Fig. 6). Forests co-dominated by *N. dombeyi* and *Austrocedrus* developed at L. Mascardi (at ca 5690 cal yr BP; Bianchi and Ariztegui, 2012), L. el Trébol (at ca 5800 cal yr BP; Whitlock et al., 2006), L. Padre Laguna

(at ca 3900 cal yr BP; Iglesias et al., 2012a), L. Huala Hué (at ca 4900 cal yr BP; Iglesias et al., 2012a), M. Serrucho (at ca 3000 cal yr BP; Markgraf et al., 2013) and L. Theobald (at ca 4100 cal yr BP; Fig. 5b) in the late Holocene. As a result, the ecotone was located as far east in recent millennia as any time during the last 15,000 cal yr BP. At L. Theobald, the highest average PAR of the record ( $>15,000$  grains  $\text{cm}^{-2}$   $\text{yr}^{-1}$ ) suggests that vegetation productivity was higher than at any other time in the Holocene (Fig. 5b). The forests were more open towards the east (i.e., L. Cónдор, L. Mosquito and L. La Zeta), where the pollen data registered abundant shrub taxa, including *Berberis*, *Maytenus* and *Rhamnaceae* (Iglesias et al., 2012b; Figs. 5a, 6 and 7).

Mixed *Nothofagus/Austrocedrus* forests are located at the limits of the modern distribution of both species (Roig, 1998) and are thus very sensitive to changes in environmental conditions. Bivariate plots of *Nothofagus*-forest and Cupressaceae pollen data show submillennial shifts in dominance of one taxon over the other during the late Holocene (Fig. 6). For example at L. La Zeta, *Nothofagus* was the dominant tree between ca 2300 and 1800 cal yr BP ( $<80\%$ ), whereas *Austrocedrus* populations was more abundant during the 1800–300 cal yr BP period (Fig. 5a). Analysis of two closely spaced sites (i.e., L. Padre Laguna and L. Huala Hué) reveals that *Nothofagus* was more abundant during humid periods (i.e., ca 4900–3860 and 2120–1650 cal yr BP), and *Austrocedrus* establishment was favored by drier conditions (i.e., ca 3860–2850 and 1350–450 cal yr BP; Iglesias et al., 2012a). At intermediate-moisture levels, both taxa were abundant in the pollen record and fire became an important control of forest composition, with periods of infrequent stand-replacing fires favoring *Nothofagus* (i.e., 2850–2120 cal yr BP), and high frequency surface fires supporting *Austrocedrus* (i.e., 1650–1350 cal yr BP).

Very high rates of environmental change are inferred for the last 5000 years. In this respect, the late Holocene featured the largest short-term fluctuations in forest taxa abundance since the Last Glacial Maximum (Fig. 8). A similar signal has also been noted for sites on the western side of the Andes (P. Moreno, pers. communication). Short-term fluctuations in vegetation composition may have resulted from increased climate variability brought about with the strengthening of ENSO (Moy et al., 2002). It is also possible that new disturbance regimes and/or biotic interactions (e.g., facilitation, competition) associated with the expansion of *Austrocedrus* and establishment of mixed forests favored more variable vegetation dynamics.

## 5.2. Holocene history of *A. chilensis*

Today, *Austrocedrus* occupies narrow longitudinal bands along the western and eastern flanks of the Patagonian Andes. Conspicuous forests are located between latitude 34 and 45°S in Chile (northwest populations), and less extensive forests occur on the Argentine slopes of the Andes (eastern populations) from latitude 39 and 43°S (Pastorino et al., 2006). Most of the modern distribution of the species lies in areas that were glaciated during the Last Glacial Maximum, and several studies have tried to identify possible glacial refugia based on paleoecologic and modern genetic evidence (Pastorino and Gallo, 2002; Whitlock et al., 2006; Arana et al., 2010; Markgraf et al., 2013).

Species range limits are often difficult to reconstruct from pollen data because 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; Tzedakis et al., 2002; McLachlan and Clark, 2004; Brubaker et al., 2005). The case of Cupressaceae in Patagonia is particularly problematic because the family comprises three genera whose pollen cannot be differentiated (i.e., *Fitzroya*, *Pilgerodendron* and

*Austrocedrus*). In spite of these limitations, comparison of genetic data and pollen records from a network of sites and helps better understand the biogeography of *Austrocedrus*.

After the Last Glacial Maximum (ca 23,000 cal yr BP), the range of most temperate tree taxa shifted throughout the world as species expanded from their refugia to present habitats (Stewart et al., 2010). On the east side of the Andes, it has been proposed that, during glacial times, *Austrocedrus* populations persisted either north (T. Kitzberger, pers. communication) or in several refugia east of their modern distribution (Pastorino and Gallo, 2002). The Holocene trend towards more humid conditions and more developed soils allowed the species to expand to its current range.

Isopoll maps show trace amounts of Cupressaceae pollen at all study sites during the Lateglacial and early-Holocene periods (with the exception of L. Padre Laguna, whose record only spans the late Holocene), with slight east-to-west pattern in percentage abundance (Fig. 7). We hypothesize that low percentages of Cupressaceae in the Lateglacial period could be from any of the three Patagonian species of Cupressaceae: *Austrocedrus*, from populations in dry areas east of the glacial margins, *Fitzroya* forests in unglaciated valleys west of the Andes (Bianchi and Ariztegui, 2012) and/or *Pilgerodendron* populations growing in unglaciated mountains to the east of the Andean front (Markgraf et al., 2013). Although long-distance transport of pollen grains is possible, the prevailing westerly winds and limited pollen dispersal capabilities of Cupressaceae (Pastorino and Gallo, 2002) suggest that pollen was likely produced by populations growing near the study lakes. The higher pollen abundance in the easternmost sites (Fig. 7) therefore argues for LGM survival or early postglacial colonization of *Austrocedrus* along the Andean front.

Holocene spread of *Austrocedrus*, inferred from the pronounced middle and late Holocene rise in Cupressaceae percentages, was spatially and temporally variable. The species expanded at the eastern limit of its distribution (i.e., L. Cónдор, L. La Zeta) as early as ca 8000 cal yr BP but was not abundant at L. Mosquito, located ca 20 km west of L. Cónдор until ca 4000 cal yr BP (Fig. 6). Thus, the pollen data imply slow expansion and the possibility that *Austrocedrus* populations may have persisted for millennia east of the study region.

The pollen interpretation supports modern genetic studies that hypothesize that *Austrocedrus* persisted in several glacial refugia (Pastorino and Gallo, 2002), with only a few becoming centers of dispersal and colonization (Gallo et al., 2008). Contrasting genetic population structures within the modern *Austrocedrus* range indicate that trees in the northwest of the distribution represent a single deme (population) with low genetic differentiation and high admixture levels. In contrast, modern trees that grow in isolated steppe populations are genetically heterogeneous with low levels of admixture, restricted gene flow isolation by distance (Arana et al., 2010).

Differences in the genetic structure of the northwestern and eastern populations of *Austrocedrus* may reflect a long-term interplay between disturbance and local climate conditions. The more humid sites (i.e., L. Mascardi, L. el Trébol, L. Huala Hué) featured rapid population growth between 8000 and 6000 cal yr BP, as evidenced by pollen percentage increases of up to 28% in 100 years. Conversely, *Austrocedrus* geographical expansion at the easternmost sites (i.e., L. Mosquito, L. La Zeta) was probably limited by low seedling establishment under the drier conditions of the steppe, coupled with limited westward seed and pollen dispersal due to strong westerly winds.

Spatiotemporal analysis of palynological data also indicates that early development of large *Austrocedrus* populations near L. Escondido at ca 6000 cal yr BP, L. el Trébol at ca 5000 cal yr BP and L. Padre Laguna at ca 4000 cal yr BP (Figs. 6 and 7) was followed by pronounced population growth at M. Aguado, L. Mascardi and L.

Mosquito at ca 2700 cal yr BP. Thus, the present-day geographic distribution of *Austrocedrus* was established only in the last few millennia. Additional pollen records north of the study transect, new techniques including ancient DNA, and improved understanding of modern pollen-vegetation relationships is needed to further resolve the migration history of this keystone species.

## 6. Conclusions

The environmental history of the Patagonian forest/steppe region from 41 to 43°S is reconstructed from pollen, high-resolution charcoal data, and other lithologic information from 11 lake and wetland cores. These records point to the importance of climate as well as the location of glacial refugia and site-specific biophysical conditions in shaping the vegetation history of the ecotone. During the LGM (ca >15,000 cal yr BP), cold dry and windy conditions supported open steppe communities in periglacial areas, and low percentages of *Nothofagus* and Cupressaceae pollen indicate the possible persistence of patches of trees in the region. Fires were rare and likely limited by fuel discontinuity and climate at this time.

Trees and shrubs colonized deglaciated substrates during the Lateglacial/early Holocene transition (ca 15,000–10,000 cal yr BP), favored by warmer wetter conditions brought about by a shift in dominance from year-round polar air masses to more humid Pacific air (Heusser, 2003). *Nothofagus* expansion in the area was asynchronous, occurring as early as ca 16,500 at L. Mascardi and not until ca 14,000 at L. el Trébol. The rise of *Nothofagus* was followed by an increase of Rhamnaceae, Asteraceae and Chenopodiaceae, leading to the establishment of open forest and enabling more fire activity than in previous times. Between 15,000 and 10,000 cal yr BP, the forest/steppe boundary advanced eastwards and retreated in millennial-scale cycles. Although changes in the fire regime may have altered local vegetation composition, comparison of pollen and charcoal data suggest that fire did not significantly affect populations of the dominant species. Instead, watershed-scale biophysical variability may explain the temporal differences in ecosystem evolution.

During the early Holocene (ca 10,000 and 5000 cal yr BP), a well-defined west-to-east vegetation gradient developed in northern Patagonia. Closed *Nothofagus* forests grew in the west and transitioned eastwards first to open forests and shrubland, and then steppe. Vegetation dynamics mainly involved trade-offs between trees and shrubs at both millennial- and centennial-scales that were likely brought about by shifts in water availability. The rise in vegetation productivity at the ecotone was paralleled by an increase in fire activity.

The modern lower elevation forest, co-dominated by *N. dombeyi* and *A. chilensis*, developed at ca 5000 cal yr BP, probably in response to increased effective moisture ascribed to a northward shift and strengthening of the Southern Westerlies, and greater interannual climate variability (e.g., Lamy et al., 1999, 2004; Moy et al. 2002). The late-Holocene vegetation history illustrates the interaction between broad-scale climate and site-specific factors. Comparison of two closely spaced sites shows that humid periods enabled *Nothofagus* expansion and drier times supported *Austrocedrus* dominance. At intermediate moisture levels, fire was apparently the primary control of species dominance, with infrequent stand-replacing fires facilitating *Nothofagus* regeneration and frequent fires supporting *Austrocedrus* (Iglesias et al., 2012a). In this sense, the paleoecological records reinforce modern studies in showing that a multivariate set of biophysical conditions, including weather/climate, soil, and disturbance, shape forest/steppe ecotone dynamics (Veblen et al., 2011; Kitzberger, 2012). In the past as well as the present, the relative importance of these drivers changes as critical thresholds in climate and disturbance are reached.

At present, *Austrocedrus* seedling establishment at lower tree-line is sporadic, dependent on years of higher-than-average effective moisture and low fire intensity (Veblen and Lorenz, 1988; Villalba, 1995). Thus, projected changes in climate toward drier summers and more fires constitute a risk to the viability of *Austrocedrus*. The postglacial history of the species suggests the possibility that isolated peripheral populations persisted *in situ* in the steppe during glacial and early-Holocene times, and that population growth was fast when the climate was suitable. Nonetheless, reconstructing the migration history of *Austrocedrus* remains limited by our inability to identify specific refugia.

In closing, it is important to note that the Patagonian forest/steppe ecotone is currently undergoing a dramatic transformation as a result of changes in climate, land-use and fire (Veblen et al., 2011). These changes are altering not only vegetation composition but also a wide range of ecosystem processes and services including carbon storage, forage production, water supply and quality, crop pollination, and outdoor recreation (Kupfer and Cairns, 1996). The paleoenvironmental record points to the sensitivity of this ecotone in the past, by revealing shifting vegetation dynamics as a consequence of climate change and the amplifying effects of fire. These feedbacks are likely to be critical as we move into the future and need to be considered in management and mitigation plans.

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