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Postglacial vegetation, climate, and fire history along the east side of the Andes (lat 41–42.5°S), Argentina

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Abstract

The history of the low-elevation forest and forest-steppe ecotone on the east side of the Andes is revealed in pollen and charcoal records obtained from mid-latitude lakes. Prior to 15,000 cal yr BP, the vegetation was characterized by steppe vegetation with isolated stands of *Nothofagus*. The climate was generally dry, and the sparse vegetation apparently lacked sufficient fuels to burn extensively. After 15,000 cal yr BP, a mixture of *Nothofagus* forest and shrubland/steppe developed. Fire activity increased between 13,250 and 11,400 cal yr BP, contemporaneous with a regionally defined cold dry period (Huelmo/Mascardi Cold Reversal). The early-Holocene period was characterized by an open *Nothofagus* forest/shrubland mosaic, and fire frequency was high in dry sites and low in wet sites; the data suggest a sharp decrease in moisture eastward from the Andes. A shift to a surface-fire regime occurred at 7500 cal yr BP at the wet site and at 4400 cal yr BP at the dry site, preceding the expansion of *Austrocedrus* by 1000–1500 yr. The spread of *Austrocedrus* is explained by a shift towards a cooler and wetter climate in the middle and late Holocene. The change to a surface-fire regime is consistent with increased interannual climate variability and the onset or strengthening of ENSO. The present-day mixed forest dominated by *Nothofagus* and *Austrocedrus* was established in the last few millennia.
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Keywords: Late-glacial and Holocene; Vegetation history; Fire history; Northern patagonia environmental history; Argentina; Charcoal analysis

Introduction

In recent decades, considerable attention has focused on southern hemisphere climate variations and their timing with respect to those in the northern hemisphere (e.g., Markgraf, 2001). In the mid-latitudes of southern South America, late-Quaternary paleoclimate information comes primarily from vegetation and climate reconstructions based on pollen data (e.g., Villagrán et al., 1996; Markgraf et al., 2002; Heusser, 2003; Moreno, 2004). Fire is an important component of the modern forest ecosystem (e.g. Kitzberger and Veblen, 2003), but detailed studies of past fire activity have only recently become a focus of paleoenvironmental research in this region. Previous low-resolution charcoal studies have shown long-term changes in fire frequency (Markgraf and Anderson, 1994; Moreno, 2000; Heusser, 2003; Haberle and Bennett, 2004), but high-resolution studies that would reveal the links between climate change and local ecosystem response are still missing. The eastern flanks of the Andes are of particular interest because of the strong west-to-east gradients in climate, vegetation, and fire regimes at present. Mean annual precipitation decreases from 3000 mm in rainforests in the Andes to <500 mm only 80 km to the east in steppe (New et al., 2002). Present-day fire regimes concomitantly change from infrequent stand-replacement fires in humid forests to frequent surface fires in steppe/shrubland (Veblen et al., 2003).

To increase our understanding of the mid-latitude fire–climate–vegetation interactions of northern Patagonia, we describe two well-dated postglacial pollen and charcoal records

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from lakes on the Argentine side of the Andes (Fig. 1). Laguna el Trébol (lat. 41.07°S, long. 71.49°W, 758 m elevation, 10.50-m coring water depth), located south of Lago Nahuel Huapi near San Carlos de Bariloche, is surrounded by closed forest dominated by *Nothofagus dombeyi* and lesser amounts of *Austrocedrus chilensis*. Previous studies have described lithologic, magnetic, limnologic and pollen data from the late-glacial and early-Holocene sediments of L. el Trébol at a coarse temporal resolution (Bianchi et al., 1999; Valencio et al., 1985) and archeological studies identify the presence of Pleistocene megafauna and early human occupation near its shores (Villarosa et al., in press). The second site, Lago Mosquito (also known as Lago Pelligrini) (lat. 42.50°S, long. 71.40°W, 556 m elevation, 8-m coring water depth) is located 150 km to the south, near the town of Cholila. It lies within the transition from open *Austrocedrus* woodland to shrubland and steppe farther east. L. Mosquito lies close to the terminal Pleistocene moraines, but its origin is related to Holocene alluvial fans that dammed westward flowing streams and created the lake upvalley. Our objective in studying these sites and comparing them with other records from the region was to (1) reconstruct the environmental history along the transition from closed dry forest to steppe vegetation at mid-latitudes in the eastern Andes; (2) identify the role of fire in maintaining the vegetation gradient during different periods; and (3) use the paleoecological data to infer aspects of long-term climate change and short-term climate variability.

Methods

Sediment cores were taken with a modified Livingstone piston sampler from a floating, anchored platform. The cores were collected from the center of the basin at L. el Trébol, and in the western side of L. Mosquito. Multiple overlapping cores were taken to ensure the continuity of the stratigraphy and obtain enough material for multiple analyses. Cores were extruded in the field and wrapped in cellophane and aluminum foil and transported back to the laboratory for refrigeration and sampling. In the laboratory, cores were split longitudinally, and charcoal and terrestrial plant macrofossils were extracted and submitted for radiocarbon age determinations. Cores were correlated by lithostratigraphy, including the presence of prominent tephra layers. A series of AMS radiocarbon dates at each site was used to develop age-versus-depth relations and calculate sediment deposition time (yr cm^{-1}).

Pollen was analyzed at 4- to 10-cm intervals, and samples were prepared with standard procedures (Bennett and Willis, 2001). A tracer of *Lycopodium* was added to each sample to calculate pollen concentration (grains cm^{-3}). At least 300 pollen grains were counted for most levels. Terrestrial pollen

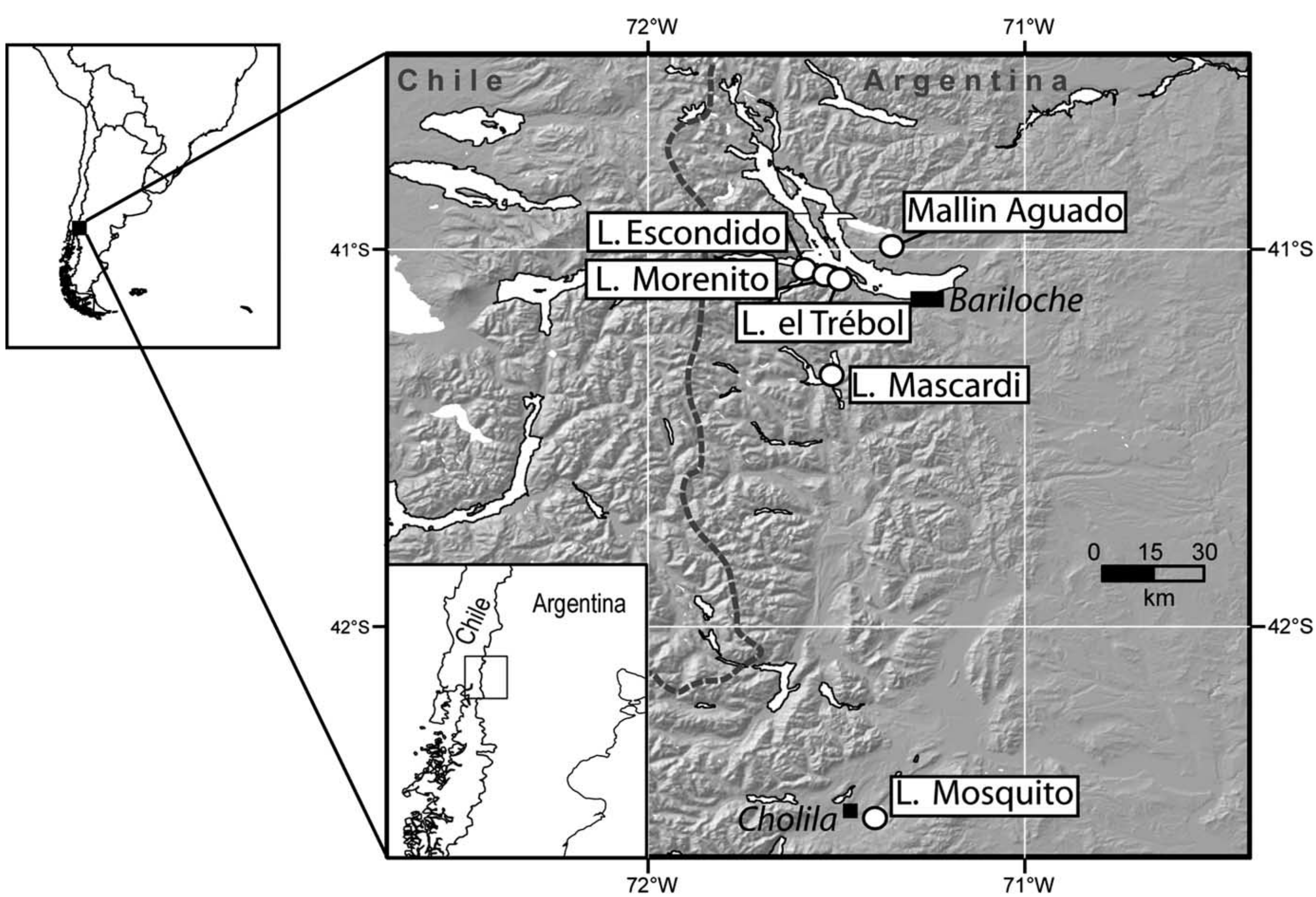

Figure 1. Location of sites discussed in text.

percentages were calculated based on a sum of terrestrial pollen and spores. Percentages of aquatic and wetland taxa were based on a denominator of total pollen and spores. Total pollen accumulation rates or influx (PAR, pollen grains cm^{-2} yr^{-1}) were determined by dividing pollen concentration by the deposition time (yr cm^{-1}) for each sample.

For this study, only the dominant pollen types are shown, and identifications were based on published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978). *Nothofagus dombeyi*-type pollen includes *N. dombeyi* and *N. pumilio* (closed-forest trees) and also *N. antarctica*, a small tree/shrub that grows on poor soils, bogs and at high and low elevations (Veblen et al., 2003). Cupressaceae pollen is attributed largely to *Austrocedrus chilensis* (an open-forest tree), although rainforest taxa (*Fitzroya cupressoides, Pilgerodendron uviferum*) may also have been long-distance contributors. Other taxa shown on pollen diagram were assigned to (mesic) closed forest, (dry) open forest, steppe/shrubland, and wetland, based on modern affinities of the likely pollen contributors. "Other steppe/shrubland herbs" in the L. Mosquito record include pollen of Asteraceae Mutisieae, Asteraceae Liguliflorae, Solanaceae, Apiaceae, *Acaena*, Caryophyllaceae, *Galium*, and other herbs. This pollen category was important in the oldest samples (up to 14%).

Charcoal analysis followed procedures outlined by Whitlock and Larsen (2001), which focus on the examination of macroscopic charcoal particles (>125 μm in size) to reconstruct local fire history. Sediment samples of known volume were taken from contiguous 1-cm intervals of the cores and washed through a 125-μm mesh screen. Charcoal particles in the residue were tallied, and counts were converted to charcoal concentration (particles cm^{-3}). Grass cuticle charcoal was counted separately from wood particulate charcoal. Charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) at constant (10-yr) intervals were calculated by interpolating charcoal concentrations (particles cm^{-3}) to annual values (to preserve the total charcoal abundance), averaging these values over 10-yr intervals, and dividing them by the deposition time (yr cm^{-1}) of each interval. The resulting time series were logarithmically transformed (for variance stabilization) and decomposed into background and peaks components (using CHAPS software, P. Bartlein, unpublished) using the approach of Long et al. (1998) (see Results for information on the decomposition parameters).

Magnetic susceptibility was measured on the L. Mosquito core to help identify intervals with high levels of ferromagnetic minerals. Such intervals may be associated with runoff from adjacent slopes or from deposition of volcanic ash (Gedye et al., 2000). For this analysis, samples of 8 cm^3 volume were taken from contiguous 1-cm intervals and placed in plastic vials. Magnetic susceptibility was recorded in electromagnetic units (emu) with a Sapphire Instruments cup-coil sensor. Prior analysis of sediment magnetism for L. el Trébol (Valencio et al., 1985; Irurzun et al., 2006) is not discussed here.

Lithology and Chronology

The L. el Trébol lithology was divided into three units: a basal section of inorganic clay with laminations (7.43–5.20 m depth), a middle unit of organic clay (5.20–4.43 m depth), and an upper section of fine-detritus gyttja with several tephra layers (4.43–0 m depth). Most tephra units are attributed to past eruptions of Puyehue and nearby volcanoes west of the site (Villarosa et al., in press). The lithologic changes reflect the stabilization of the landscape at the end of the Pleistocene and increased organic production of a small lake in the Holocene. These landscape changes were recorded by increased levels of organic matter, nutrients, biogenic silica, pigments, and chironomids described by Bianchi et al. (1999).

The L. Mosquito lithology was composed of two units: a basal unit of laminated silty organic clay below 14.21 m depth, overlain by a faintly laminated, fine-detritus gyttja unit with a few tephra layers. A thick tephra layer was noted at 8.66–8.54 m depth and several small tephra units were registered by high magnetic susceptibility. The lower unit suggests the existence of a seasonally flooded wetland during the initial damming of the basin before a shift to lake conditions.

Information on the radiocarbon chronology at both sites is presented in Table 1. Wherever possible, plant macrofossils and charcoal were used for age determinations, but at L. Mosquito, macrofossils were scarce and bulk sediment was submitted for AMS dating. The age of the bulk-sediment samples was similar to that of charcoal particles at three levels and supported the inclusion of the bulk-sediment ages in the chronology. Tephra layers >1 cm thick at L. el Trébol and >2 cm thick at L. Mosquito are assumed to have been deposited rapidly, and these thicknesses were subtracted from core depths to create the "adjusted depths" necessary to develop an age model. Adjusted depths and true depths are presented in Table 1, but only true depths are referred to in the discussion and shown on the figures.

Radiocarbon ages were converted to calendar years based on CALIB 5.0 (Stuiver et al., 2005). Relationships between age and adjusted depth were described with high-order polynomial regressions to avoid abrupt (and artificial) changes in sedimentation rate (Table 1). The base of the L. el Trébol core at 6.45-m depth had an extrapolated age of 24,750 cal yr BP, below the oldest AMS radiocarbon sample. This basal age is probably older than the true age, based on our understanding of the deglacial history of the region (Tatur et al., 2002), and was not considered in the interpretation. The sample from the L. Mosquito core at 15.03-m depth was 9400 cal yr BP. The sedimentation rates at L. el Trébol yielded deposition times of 12 to 53 yr/cm in the Holocene (<11,000 cal yr BP) and up to 104 yr/cm in the late-glacial period, and at L. Mosquito deposition times ranged between 4 and 8.5 yr/cm.

The pollen and charcoal records

Pollen

The pollen records were divided into local zones based on constrained cluster analysis (CONISS; Grimm, 1987).

Table 1
Chronology information for study sites

Core	Depth (m)	Adjusted Midpoint depth (m)[a]	Lab no.	Material	^{14}C yr BP	cal yr BP[b]	Median probability age (cal yr BP)[b]
Laguna El Trébol							
Tre02B	0	0	n/a	inferred	0	−52	−52
Tre02B	0.52	0.47	AA57044	charcoal	1224+71	985–1033, 1049–1173	1094
Tre02A	1.25–1.26	1.185	AA59576	sediment	1836+36	1620–1673, 1687–1740, 1757–1778	1703
Tre02A	1.59–1.60	1.43	AA59577	sediment	2241+36	2134–2184, 2196–2206, 2232–2306	2221
Tre02B	2.41	2.24	AA57045	charcoal	2990+80	2967–3211	3097
Tre02A	2.95–2.96	2.735	AA59578	sediment	4001+40	4296–4330, 4350–4374, 4378–4441	4391
Tre02A	3.31–3.32	3.075	AA59579	sediment	4516+41	4967–5016, 5032–5072, 5107–5128, 5166–5277	5120
Tre02B	3.55	3.30	AA57046	charcoal	5120+150	5615–5628, 5643–5940, 5974–5982	5815
Tre02B	3.91	3.62	AA57047	charcoal	5630+100	6282–6473	6372
Tre02B	4.45	4.13	AA57048	charcoal	7271+75	7961–8057, 8089–8112, 8116–8156	8040
Tre02A	4.52–4.53	4.205	AA59580	sediment	7641+48	8353–8423	8393
Tre02A	5.00–5.01	4.685	AA59582	sediment	10040+59	11397–11705, 11664–11705	11551
Tre02A	5.22–5.23	4.865	AA59581	sediment	10313+57	11995–12188, 12200–12237, 12320–12344	12131
Tre02B	5.42–5.43	5.035	AA54517	twig/charcoal	10733+67	12737–12839	12785
Tre02A	5.50–5.51	5.115	AA59583	sediment	11695+62	13454–13630	13548
Tre02A	5.86–5.87	5.385	AA59584	sediment	12,865+68	15041–15313	15192
Age (cal yr BP) = $119.69\times$adj depth$^3 - 487.64\times$adj depth$^2 + 2010.6\times$adj depth $- 52$							
Lago Mosquito							
Mos03A	0	0	n/a	inferred	0	−53	−53
Mos03A	0.45–0.46	0.455	AA58860	sediment	654+33	554–569, 593–635	606
Mos03A	1.05–1.06	1.055	AA58861	sediment	577+32	523–552	540
Mos03A	2.45–2.46	2.455	AA58862	sediment	1600+33	1386–1422, 1432–1442, 1460–1515	1444
Mos03A	3.085	3.085	AA58874	charcoal	1610+150	1304–1574, 1579–1605	1471
Mos03A	3.08–3.09	3.085	AA58863	sediment	1818+34	1612–1719	1670
Mos03A	3.49–3.50	3.495	AA58864	sediment	2066+34	1900–1912, 1921–1997	1961
Mos03A	3.49	3.49	AA58875	charcoal	2300+130	2006–2023, 2038–2362	2245
Mos03A	4.20–4.21	4.205	AA58865	sediment	2421+34	2340–2368, 2387–2457	2405
Mos03A	4.915	4.915	AA58876	charcoal	2699+76	2620–2631, 2709–2861	2762
Mos03A	4.91–4.92	4.915	AA58866	sediment	2859+35	2856–2955	2906
Mos03A	6.15–6.16	6.155	AA58867	sediment	3711+37	3904–3995, 4038–4077	3978
Mos03A	7.40–7.41	7.405	AA59431	sediment	4495+40	4961–5068, 5109–5123, 5169–5172, 5181–5274	5051
Mos03A	8.25–8.26	8.255	AA58868	sediment	4629+40	5070–5108, 5124–5167, 5175–5176, 5276–5322, 5418–5441	5237
Mos03A	9.25–9.26	9.135	AA58869	sediment	5038+39	5648–5748, 5831–5843	5710
Mos03A	10.25–10.26	10.135	AA58870	sediment	5714+47	6351–6367, 6396–6497	6441
Mos03A	11.25–11.26	11.135	AA58871	sediment	6499+43	7324–7402, 7408–7421	7362
Mos03A	12.08–12.09	11.965	AA58872	sediment	6892+45	7611–7704	7668
Mos03A	13.08–13.09	12.965	AA58873	sediment	7218+51	7937–8021	7983
Mos03C	14.82	14.70	AA58903	wood	8200+47	9007–9134, 9185–9186	9091
Age (cal yr BP) = $0.0559\times$adj depth$^5 - 1.961\times$adj depth$^4 + 22.266\times$adj depth$^3 - 85.536\times$adj depth$^2 + 687.08\times$adj depth $- 53$							

[a] Adjusted depths (adj depths) were used to calculate the age-depth model. They represent adjustments in the depth of the core after subtracting the depths of tephra layers >1 cm thick. This was done on the assumption that tephra layers were deposited very rapidly. Only true depths are referred to in text.
[b] Based on CALIB 5.0 (Stuiver et al., 2005; http://radiocarbon.pa.qub.ac.uk/calib/calib.html). Southern hemisphere calibration used for dates <11,000 cal yr BP). Median probability age was used to develop regression equations.

L. el Trébol

Zone Tre-1 (6.34–5.86 m depth; >15,360 cal yr BP) contains high percentages of Poaceae (up to 50%), low percentages (<10%) of open forest taxa (e.g., *Gaultheria, Maytenus*, Rhamnaceae and Cupressaceae) and low percentages (<10%) of other steppe taxa (e.g., Asteraceae Tubuliflorae, Chenopodiineae, and *Plantago*). *Nothofagus dombeyi*-type contributed 20–38% of the pollen. These relatively low percentages occur in modern pollen spectra from open communities where

Nothofagus is uncommon (Paez et al., 2001; Markgraf et al., 2002). Pollen of other forest taxa (<5% each) include Myrtaceae, *Podocarpus* (probably *P. nubigena*), *Saxegothaea*, and *Hydrangea*. These taxa grow in the rainforest at present; such low abundances are found in modern pollen samples from steppe regions (Markgraf et al., 2002) and attributed to long-distance transport from wetter areas to the west. *Gunnera* and Cyperaceae pollen (<10% each) indicate the presence of wet habitat. PAR (<1000 grains cm^{-2} yr^{-1}) in this zone are unreliable given age model extrapolations. The overall assemblage suggests steppe vegetation with patches of *Nothofagus* in protected habitats.

Zone Tre-2 (5.89–5.11 m depth; 15,360–11,380 cal yr BP) features an abrupt rise in *Nothofagus dombeyi*-type (up to 60%) and decreases in Poaceae (to 15%) and Asteraceae Tubuliflorae (to <2%). Based on modern pollen studies, abundant pollen (up to 13%) of the epiphytic *Misodendrum* implies an open canopy, and small amounts of *Podocarpus* and *Hydrangea* (<5%) suggest the presence of rainforest to the west (Markgraf et al., 2002). *Pediastrum* and *Botryococcus* are higher than before and suggest increased limnologic production. During this period, the L. el Trébol area featured a sparse *Nothofagus* forest (probably *N. dombeyi* and/or *N. antarctica*) and grassy areas.

Zone Tre-3 (11,380–5880 cal yr BP) has high values of *Nothofagus dombeyi*-type (up to 60%) and percentages of open forest taxa (e.g., *Maytenus* and Rhamnaceae), and steppe/shrubland herb taxa (e.g., Asteraceae Tubuliflorae and Chenopodiineae) are higher than before. Poaceae percentages (<17%) decline from the previous zone. *Misodendrum*, *Podocarpus*, and *Hydrangea* occur in persistent but low values. PAR increased >1000 grains cm^{-2} yr^{-1} after 8000 cal yr BP and remain high for the rest of the record. *Pediastrum* and *Botryococcus* show marked fluctuations suggestive of changes in water depth or lake production (Komárek and Jankovská, 2001). The pollen assemblage suggests an open *Nothofagus* forest with a shrub understory.

Zone Tre-4 (3.68–2.49 m depth; 5880–3500 cal yr BP) has decreased *Nothofagus dombeyi*-type percentages (26–53%) and high Cupressaceae percentages (to 49%). Pollen of Myrtaceae, *Podocarpus*, *Saxegothaea*, and open forest elements (e.g., *Maytenus* and Rhamnaceae) drop to trace percentages (<2%). Poaceae values continue to decline, and *Pediastrum* and *Botryococcus* are poorly represented. High values of Cupressaceae are attributed to *Austrocedrus chilensis*, which expanded in the Nahuel Huapi region during the middle Holocene (Markgraf, 1984; Markgraf and Bianchi, 1999). At L. el Trébol, this conifer probably grew in a mixed *Nothofagus* forest.

Zone Tre-5 (2.49–0.00 m depth; 3500 cal yr BP to present) features increased *Nothofagus dombeyi*-type percentages (to 73%), decreased Cupressaceae values (to <30%) and very low Poaceae (to 0.3%). Aquatic taxa were poorly represented in this zone. The slightly increased contribution of rainforest elements (e.g., Myrtaceae, *Saxegothaea*, and *Podocarpus*) probably indicates an expansion of rainforest farther west (Markgraf et al., 2002). Highest PAR values for the entire record are reached between 2500 and 1000 cal yr BP. This assemblage indicates establishment of the present-day mixed forest dominated by *Nothofagus* and lesser amounts of *Austrocedrus*. The record lacks a pollen signal of European activity in recent centuries that has been noted in less forested sites (Markgraf and Bianchi, 1999).

L. Mosquito

Zone Mos-1 (15.03–14.65 m depth; >9060 cal yr BP) has high percentages of steppe/shrubland herb taxa, including Poaceae, *Ephedra*, Asteraceae Tubuliflorae, and Chenopodiineae and open forest/shrubland taxa, including *Maytenus* and Rhamnaceae. *Nothofagus dombeyi*-type is present in relatively low amounts (<20%), and traces of *Podocarpus* and *Hydrangea* (<5%) pollen are probably from sources to the west. *Polypodium*-type fern spores and Cyperaceae and Juncaceae pollen are present in high percentages and suggest wetland conditions that are consistent with organic silty clay sediments of this interval. PAR of <1000 grains cm^{-2} yr^{-1} imply a sparsely vegetated landscape or poor pollen preservation. Based on a comparison with modern pollen samples (Paez et al., 2001; Markgraf et al., 2002), the vegetation featured steppe and shrubland with isolated forest elements.

Zone Mos-2 (14.65–6.45 cm depth; 9060–4030 cal yr BP) registers a sharp increase in *Nothofagus dombeyi*-type (up to 70%), fluctuating percentages of Poaceae (between 10 and 35%), and decreases in the pollen of steppe and shrubland taxa. Open forest taxa (e.g., Rhamnaceae and *Maytenus*) are present in the record in significant amounts (up to 10% each). PAR values rise to >2000 grains cm^{-2} yr^{-1} and remain high for the rest of the record. *Pediastrum* percentages are high between 8300 and 5700 cal BP; Cyperaceae and *Botryococcus* are low at the beginning of this zone and increase at the top of the zone. The pollen assemblage implies an open *Nothofagus* forest and significant areas of steppe and shrubland. Increased *Pediastrum* suggests shallow or warmer water than before (Komárek and Jankovská, 2001).

Zone Mos-3 (6.45–4.55 m depth: 4030–2670 cal yr BP) is divided into subzones Mos-3a (6.45–5.45 m depth; 4030–3290 cal yr BP) and Mos-3b (5.45–4.55 m depth: 3290–2670 cal yr BP). Subzone Mos-3a features decreasing percentages of *Nothofagus dombeyi*-type (from 60 to 50%), sharply rising percentages of Poaceae (to 30%), and slight increases in Cupressaceae percentages. Zone Mos-3b has moderate percentages of *Nothofagus dombeyi*-type (between 50 and 43%), increasing Cupressaceae percentages (up to 17%), and high Poaceae values (from 26 to 37%). The zone marks the beginning of the *Austrocedrus* expansion into open *Nothofagus* forests.

Zone Mos-4 (4.55–2.15 m depth: 2670–1380 cal yr BP) contains moderate values of *Nothofagus dombeyi*-type (<50%) and high values of Cupressaceae (up to 28%). Open forest taxa (e.g., *Maytenus* and Rhamnaceae) continue to be present in low values, and Poaceae percentages decrease from the previous zone (from 15 to 25%). The assemblage resembles modern samples from open *Nothofagus dombeyi*-*Austrocedrus* forest, where elements of steppe and grassland are also present (Paez et al., 2001; Markgraf et al., 2002).

Zone Mos-5 (2.15–0.425 m depth; 1378–225 cal yr BP) shows increased *Nothofagus dombeyi*-type percentages (to 63%) from the previous zone, and decreased values of Cupressaceae pollen (from 26 to 6%). Poaceae values fluctuate (up to 30%) and decrease at the top of the zone (to 13%). The pollen data suggest a shift towards a *Nothofagus* forest with less *Austrocedrus* than before.

Zone Mos-6 (0.425–0.00 m depth; 210 cal yr BP to present) shows a sharp decrease in *Nothofagus dombeyi*-type and an increase in Cupressaceae percentages. *Rumex* (*R. acetosella*-type), and *Pinus* (not shown) are present in small amounts. This zone records the effects of agriculture, forest clearance, and forestry related to European settlement. Apparently, logging of *Nothofagus* species increased the relative contribution of *Austrocedrus* in the pollen record.

Charcoal

The charcoal from L. el Trébol was examined for the last ca. 16,000 yr, the period when the chronology was reasonably secure. At L. Mosquito, the entire record, spanning ca. 9400 yr, was examined, and the high sedimentation rate at this site provided a very high-resolution reconstruction of past fire activity. Our charcoal analysis methods are based on the conceptual model of Long et al. (1998), which describes high-resolution macroscopic charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) as consisting of two main components: (1) a slowly varying "background" component that reflects long-term changes in fuel characteristics, regional fire, and/or secondary charcoal deposition, and (2) a "peaks" component that primarily reflects local fire events and noise. Several features of the background and peaks components were examined in reconstructing the fire history.

Background variations (particles cm^{-2} yr^{-1}) were identified in the CHAR by smoothing the CHAR time series with a locally weighted moving average using the tri-cube weight function. A smoothing-window width of 500 yr was used because it captured the general trends in the data (Long et al., 1998). Larger window-widths were considered, but they tended to oversmooth the data, while smaller window widths do the reverse; each of these alternatives yielded unrealistic results. Moderate variations in the window width (400 to 600 yr) did not substantially affect the results (see Whitlock and Larsen, 2001). The background CHAR trends at L. el Trébol show a shift from low CHAR in the early record (<1 particles cm^{-2} yr^{-1}) to high values of up to 3.5 particles cm^{-2} yr^{-1} at 880 cal yr BP. Periods of high background CHAR occur at 13,250–13,000, 12,500–11,400, 6800–6050, 3550–3000, and 1450–600 cal yr BP.

CHAR values are nearly twice as high at L. Mosquito as at L. el Trébol, which might reflect site differences in fire regime, fuel conditions, sedimentation rate, and local charcoal delivery. At L. Mosquito, background CHAR decrease from a high level of 16.9 particles cm^{-2} yr^{-1} at 9130 cal yr BP to a low value of 2.6 particles cm^{-2} yr^{-1} at 3770 cal yr BP. This local minimum is followed by a modest increase to 4.2 particles cm^{-2} yr^{-1} at 500 cal yr BP, after which values decline to <1 particles cm^{-2} yr^{-1}.

Fire episodes ("charcoal peaks"), defined by charcoal influx values that exceed background CHAR by a prescribed threshold, are interpreted as one or more fire events that occur during the time span of the charcoal peak (Long et al., 1998). In this study, a threshold of 1.01 times the background level (in log units) was conservatively chosen for both records, because it detected charcoal peaks in short-core records from these sites that matched documented fires in the 1860s, 1940s, and 1960s (T. Kitzberger, personal communication, 2005).

Fire-episode magnitude (particles cm^{-2}) is the total areal density of particles that comprise a peak (i.e., "peak magnitude"). The size of the peak provides information on the intensity or size of the fire (a function of both vegetation and climate) and the nature of charcoal delivery to the lake (a function of watershed and lake characteristics) (Whitlock and Millspaugh, 1996; Gardner and Whitlock, 2001). At L. el Trébol, large peaks occur before 11,000 and after 3500 cal yr BP. In general, peaks are larger (>250 particles cm^{-2}) at L. Mosquito before 6600 cal yr BP and after 2000 cal yr BP.

Fire-episode frequency (number of fire episodes/year) is a graphical representation of the smooth trends in the fire-episode data, obtained by smoothing the binary peak-frequency time series using a locally weighted mean with a 2000-yr window width. At L. el Trébol, fewer than five fire episodes/1000s occur prior to 10,000 cal yr BP, between five and ten fire episodes/1000 yr occur between 9540 and 3770 cal yr BP, and fire frequency reaches a maximum of 13 episodes/1000 yr at 1800 cal yr BP. Frequency decreases to nine fire episodes/1000 yr at 930 cal yr BP and rises to 11 fire episodes/1000 yr in recent centuries. At L. Mosquito, fire-episode frequency is highest between 6580 and 1590 cal yr BP, reaching 20 fire episodes/1000 yr, and decreases to 8 episodes/1000 yr in recent centuries. The fire-episode frequency at L. Mosquito is nearly twice as high as at L. el Trébol, except in the last 2000 yr, when frequencies are fairly similar. The difference in frequency values between sites is partly a function of the higher sedimentation rate at L. Mosquito, but this difference does not overwhelm the "signal" provided by the temporal variations in fire-event frequency at the individual sites.

Fire-free interval (years between individual fires) is the length of time between adjacent charcoal peaks and is an alternative, unsmoothed presentation of the fire-episode frequency data. It provides fire-history information similar to that from shorter composite tree-ring studies and facilitates comparison of the two records on submillennial time scales. At L. el Trébol, fire-free intervals are >400 yr before 10,000 cal yr BP and shorten after that. Fire-free intervals are variable (between 30 and 310 yr) in the last 6300 cal yr BP. At L. Mosquito, fire-free intervals are always short, ranging from 20 to 130 yr prior to 6550 cal yr BP, between 20 and 100 yr from 6550 to 3740 cal yr BP, and from 3210 to 1600 cal yr BP. The last 1600 yr feature longer fire-free intervals (>210 yr).

Grass charcoal/Total charcoal ratio describes the percent of burned grass cuticles relative to the total charcoal count (i.e., sum of grass and wood charcoal particles). By providing information on what component of the vegetation was burning, this ratio helps differentiate among low-severity surface fires that largely burn grass and herbs, mixed-severity fires that burn both surface cover and woody plants in a patchy manner, and high-severity stand-destroying crown fires (Veblen et al., 1992). At L. el Trébol, this ratio is low (<30%; more wood charcoal) prior to 7300 cal yr BP, but as high as 100% from 7400 to 6100 cal yr BP (more grass charcoal). It decreases to <40% for the period from 6100 to 3000 cal BP, when Cupressaceae pollen percentages are high, and is highly variable from 3000 cal yr BP to present, with noticeable grass charcoal peaks at ca. 2000 cal yr BP and in the last millennium. At L. Mosquito, the ratio is low (more wood charcoal) before 4550 cal yr BP. It is consistently high between 4550 and 3450 cal yr BP (more grass charcoal) and then drops somewhat during the rise in Cupressaceae pollen. Ratio values are high from 1500 to 500 cal yr BP, decline briefly and increase to the present.

Discussion

The environmental history of the east side of the Andes is inferred from the data at L. el Trébol (Figs. 2 and 4), L. Mosquito (Figs. 3 and 5), and existing published records (Fig. 6). Records from Lago Morenito (Markgraf, 1984), Lago Escondido (Jackson, 1996; Bianchi, 2000), and Laguna el Trébol lie south of Lago Nahuel Huapi at elevations of 750–780 m in mixed *Nothofagus dombeyi-Austrocedrus chilensis* forest. Mallin Aguado at 840 m elevation (Markgraf and Bianchi, 1999) is located in open *Nothofagus dombeyi-Austrocedrus* forest on the north side of L. Nahuel Huapi, and L. Mosquito (556 m elevation) is 150 km south of these sites in *Austrocedrus* woodland. L. el Trebol and L. Mosquito have high-resolution charcoal data, and M. Aguado has a lower-resolution microscopic charcoal profile.

Late-glacial period, >15,000 cal yr BP

The earliest late-glacial vegetation was dominated by Poaceae, Asteraceae Tubuliflorae, and other herbaceous taxa. Tree taxa, including *Nothofagus dombeyi* and/or *N. antarctica*, *Austrocedrus chilensis*, *Maytenus boaria*, and rainforest elements (*Podocarpus*, *Saxegothaea*, and *Hydrangea*) were present in trace amounts and probably grew in sheltered sites in the deep Andean valleys (Pastorino and Gallo, 2002; Markgraf et al., 1995). The presence of Cyperaceae and shallow-water diatoms in M. Aguado (Markgraf and Bianchi, 1999) and L. Morenito (Markgraf, 1984) suggests that these sites were wetlands or shallow lakes at this time. Early late-glacial pollen assemblages resemble present-day samples from north Patagonian steppe (Paez et al., 2001), which implies a drier and possibly colder climate than today (Markgraf et al., 2002).

Late-glacial period, ca. 15,000–11,400 cal yr BP

The establishment of an open woodland occurred at 15,000 cal yr BP at L. el Trébol, 14,600 cal yr BP at M. Aguado, 13,600 cal yr BP at L. Morenito, and 13,080 cal yr BP at L. Escondido (Fig. 6A). The differences in timing may reflect an expansion of patchy forest cover controlled by edaphic conditions or the poor dating control on site chronologies. The greater abundance of forest taxa implies generally warmer and somewhat moister conditions than before. Additional subtle changes in climate have been described at individual sites. For example, small fluctuations between Poaceae and *Nothofagus dombeyi*-type pollen at M. Aguado have been attributed to alternating dry and wet intervals. Increased percentages of Poaceae (at the expense of other herbaceous taxa) at the same site have been attributed to wetter conditions after 16,000 cal yr BP (Markgraf and Bianchi, 1999). Lower chlorophyll and organic content at L. el Trébol at ca. 13,400 cal yr BP has been interpreted as evidence of a brief cool period (Tatur et al., 2002).

To the south of L. Nahuel Huapi, cores from L. Mascardi feature shifts in sediment size and organic carbon that have been used to infer relatively warm conditions prior to ca. 14,500 cal yr BP, followed by cool dry conditions that intensified between 13,300 to 11,700 cal yr BP [=11,500–10,150 ^{14}C yr BP]. This period has been termed the Huelmo/Mascardi Cold Reversal based on the Mascardi record and concurrent pollen changes in L. Huelmo in the Chilean Lake District (Ariztegui et al., 1997; Hajdas et al., 2003), and the chronologies at those sites are good enough to suggest that these variations are not a South American expression of the Younger Dryas interval. CHAR values at L. el Trébol are higher than before between 13,250 and 13,000 cal yr BP and between 12,500 and 11,400 cal yr BP, generally concurrent with the Huelmo/Mascardi Cold Reversal. Microscopic charcoal levels from sites in the Chilean Lake District also increase after 13,000 cal yr BP (Hajdas et al., 2003; Moreno and León, 2003). Apparently, the end of the late-glacial period was arid enough and had sufficient fuel levels to support fire.

Late-glacial/early Holocene transition and early Holocene, ca. 11,400–6000 cal yr BP

Pollen records of L. Morenito, M. Aguado, L. el Trébol, and L. Escondido suggest development of open *Nothofagus dombeyi* forest during the transition to the Holocene (Fig. 6B). L. Morenito registers an open *Nothofagus* forest, with *Weinmannia* at ca. 9000 cal yr BP and a brief appearance of *Eucryphia* at 7000 cal yr BP. The latter two trees grow in early-successional forests at present and are prominent in early-Holocene pollen records of the Chilean Lake District (Villagrán et al., 1996; Moreno, 2004; Abarzúa et al., 2004). Pollen data from M. Aguado contain shrub and steppe elements with some evidence of *Nothofagus* forest between 9700 and 4800 cal yr BP, as did the L. Mosquito record (Fig. 4), after ca. 9400 cal yr BP.

The high-resolution charcoal records at L. el Trébol (Fig. 4) and L. Mosquito (Fig. 5) shed more light on this period. At L. el Trébol, mostly woody vegetation was burning (i.e., low grass/total charcoal ratio), and the fire-episode frequency was initially low but increased after 10,000 cal yr BP. A few long fire-free intervals (>450 yr) were noted at L. el Trébol after 10,000 cal yr BP, but generally fire-free intervals were short. Fire-episode magnitude was relatively low between 11,500 and 8000 cal yr BP, suggesting small or low-intensity burns. At L. Mosquito,

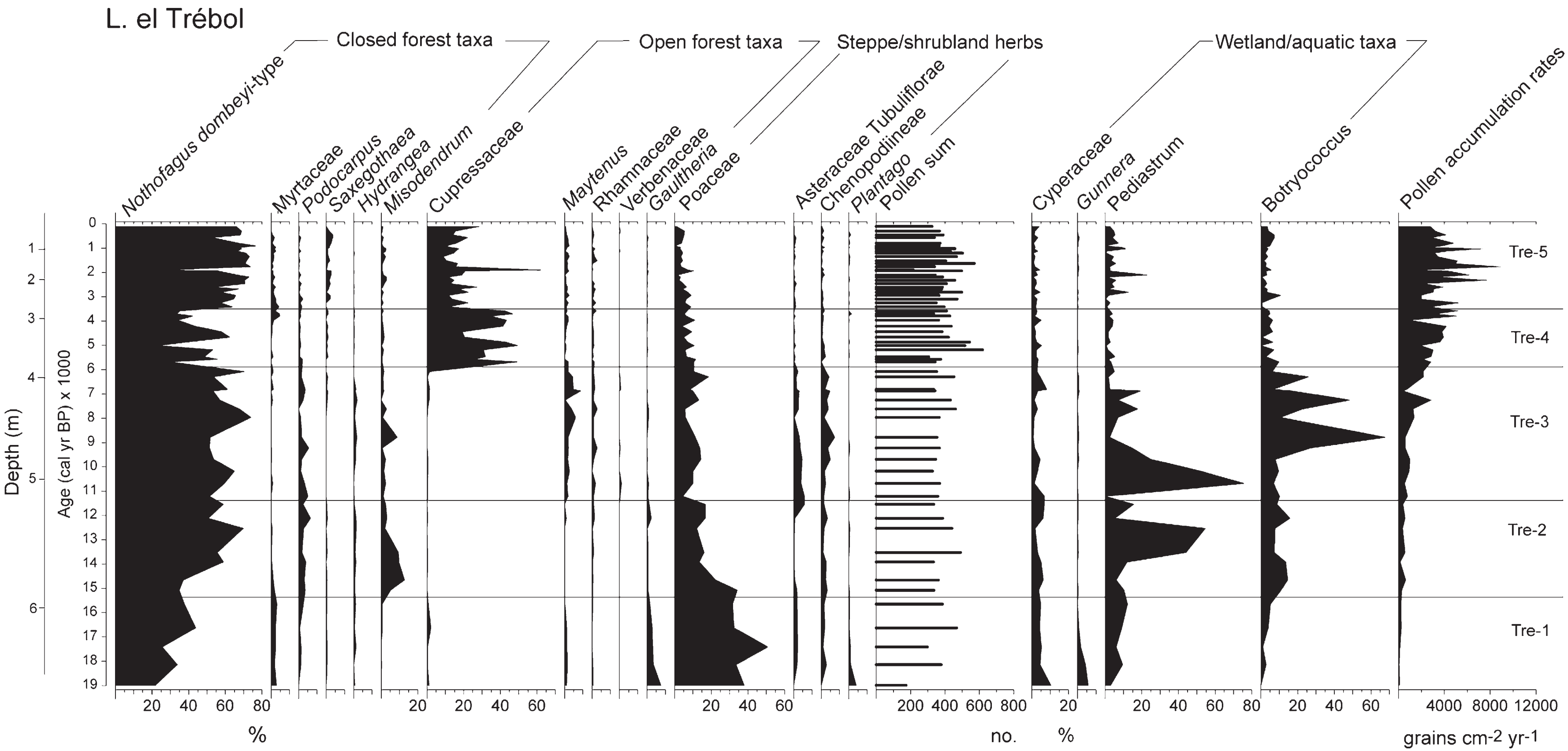

Figure 2. Selected pollen percentages and total pollen accumulation rates for L. el Trébol. True depths are shown.

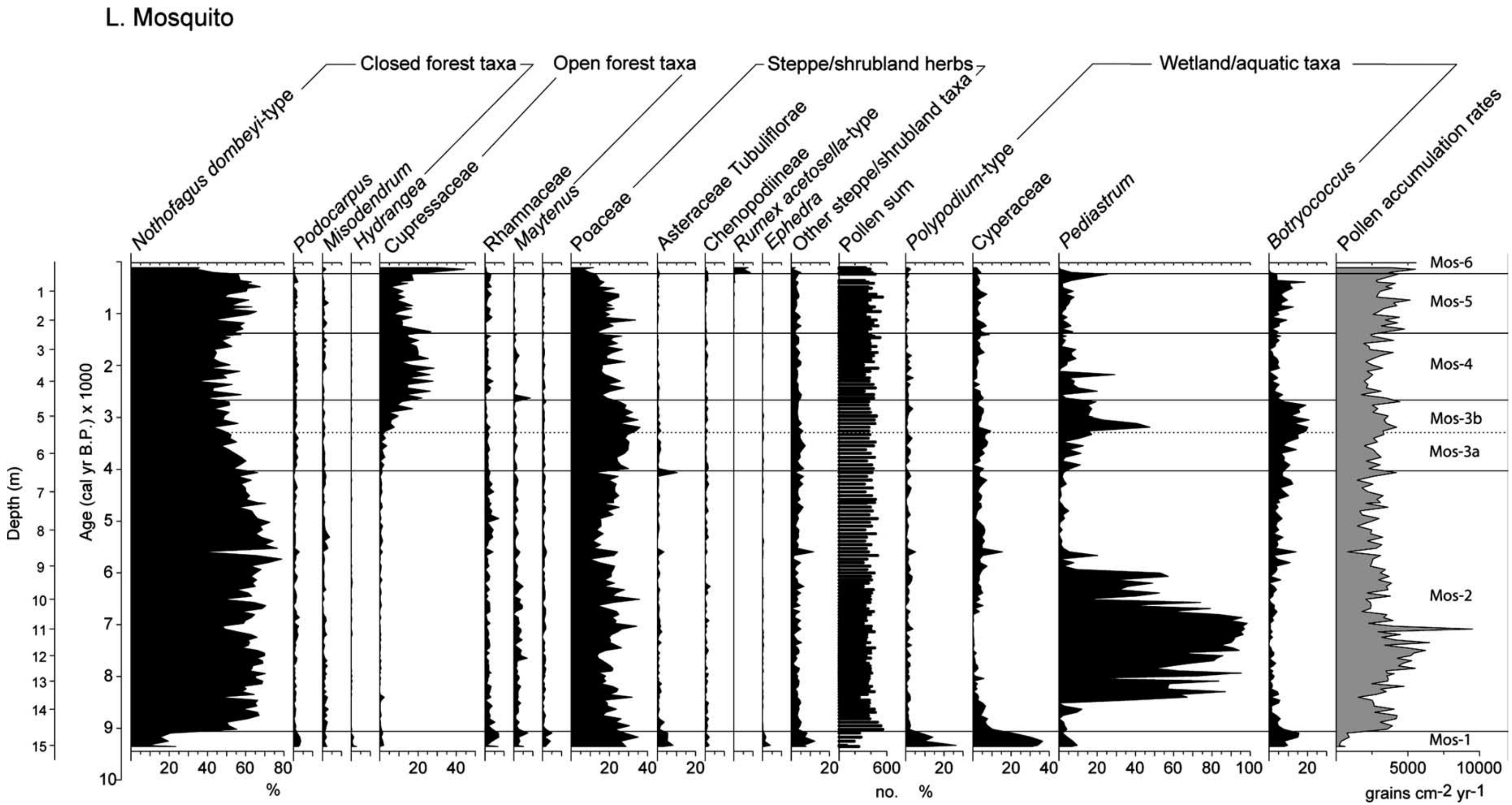

Figure 3. Selected pollen percentages and total pollen accumulation rates for L. Mosquito. True depths are shown.

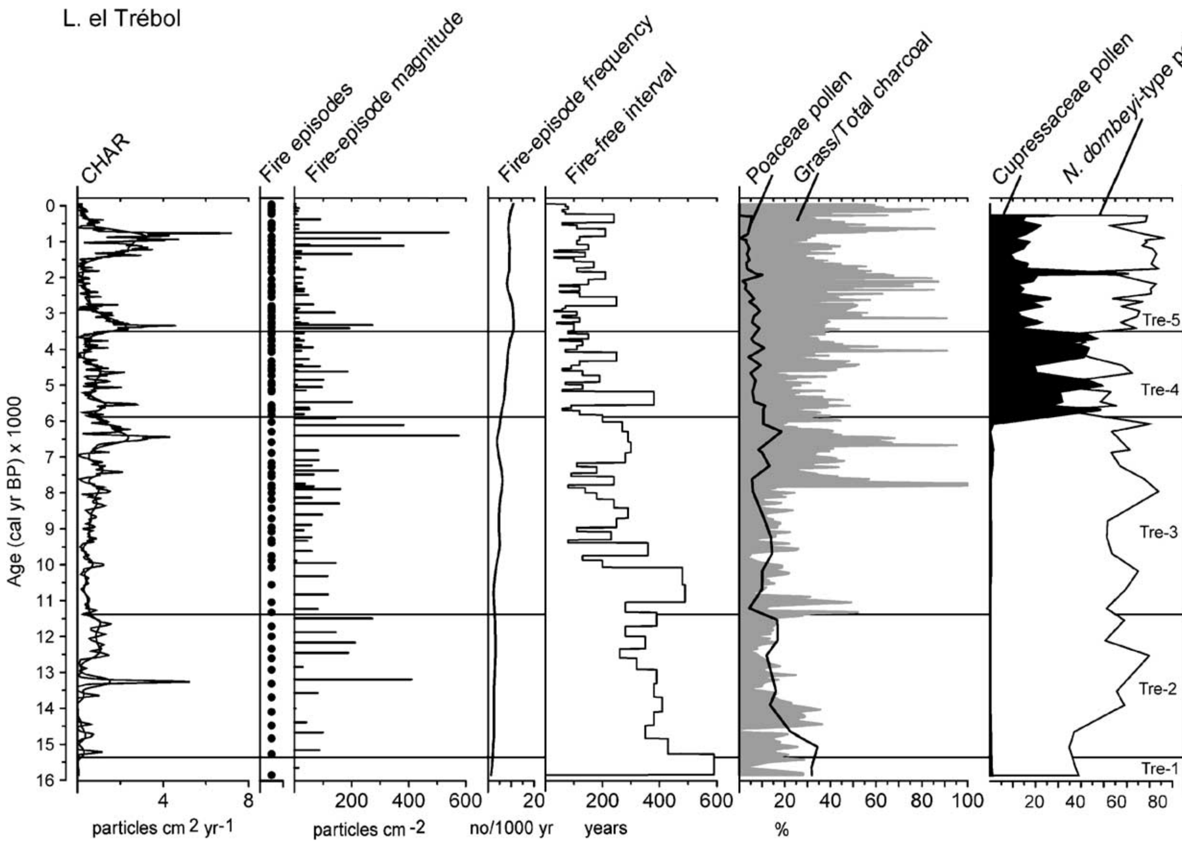

Figure 4. Fire history information based on charcoal data and pollen from L. el Trébol (see text for discussion). Charcoal accumulation rates (CHAR) provide the basic data for the fire history reconstruction. Superimposed on the CHAR is a smoothed line (i.e., the background component) that describes the general trend in the data. Fire episodes are the charcoal peaks that lie above the background values, using a 1.01 threshold ratio. Fire-episode magnitude is the areal density of the peaks above the background. Note that fire episodes are plotted at the beginning of a charcoal peak, whereas fire-episode magnitude is plotted at the end of a charcoal peak. Fire-episode frequency shows the temporal trends in the distribution of the fire-episode peaks, using a 2000-yr smoother. The fire-free interval is the years between individual fire-episodes. The grass/total charcoal ratio is calculated as the number of grass charcoal particles divided by the sum of grass and wood charcoal particles for each sample. Pollen percentages of Poaceae, *Nothofagus dombeyi*-type and Cupressaceae (cf. *Austrocedrus*) from Figure 2 are also shown for comparison.

charcoal abundance (CHAR) was high prior to 8500 cal yr BP and declined sharply with the increase of *Nothofagus dombeyi*-type after 8500 cal yr BP. Fire-episode magnitude was initially high but declined after 7300 cal yr BP. Fire-episode frequency increased gradually after 9000 cal yr BP, and woody fuels at L. Mosquito, as at L. el Trébol, were a major source of charcoal.

Open *Nothofagus* forest, supporting substantial amounts of steppe and shrubland elements, was widespread in the eastern foothills of the Andes at the end of the late-glacial period and in the early Holocene. This vegetation suggests drier conditions than at present. L. el Trébol registered low CHAR and fire-episode frequency, whereas M. Aguado and L. Mosquito show relatively high charcoal values. The charcoal data at L. Mosquito, in particular, indicate large (or severe) fires (i.e., high fire-episode magnitudes) during this period.

Early-Holocene aridity is documented throughout southern South America. Pollen and charcoal records from the Chilean Lake District (Moreno, 2004) to Tierra del Fuego (Huber et al., 2004) suggest more open vegetation and higher-than-present fire activity. Early-Holocene paleoclimate model simulations feature warm, relative dry winters and cool summers (Whitlock et al., 2001), and weakened westerly flow apparently reduced effective moisture in the mid- and high latitudes.

The last 6000 yr

The expansion of *Austrocedrus* in the Nahuel Huapi region began in the middle Holocene, but the timing from site to site was variable, and it occurred several centuries earlier in wet sites than in dry ones. *Austrocedrus* increased abruptly at L. el Trébol and L. Morenito at ca. 6000 cal yr BP. The rise was more gradual at L. Escondido, beginning at ca. 5500 cal yr BP, and it occurred at 6400 cal yr BP at M. Aguado (Fig. 6C). At L. Mosquito, *Austrocedrus* increased at 3300 cal yr BP and rose dramatically after 2700 cal yr BP. The shift at all sites came at the expense of *Nothofagus* rather than of steppe/shrubland elements (Fig. 6D).

The expansion of *Austrocedrus* was preceded by a change in fire regime from stand-replacing events that burned woody vegetation to a regime of more frequent and probably smaller surface fires. At L. el Trebol, this shift is evidenced by an abrupt increase in the grass/total charcoal ratio and increased fire-episode frequency at 7500 cal yr BP, approximately 1500 yr before the *Austrocedrus* rise. A shift to a surface-fire regime also occurred at L. Mosquito, but later, at 4400 cal yr BP. As at L. el Trébol, the change in fire regime precedes the *Austrocedrus* rise by 1100 cal yr. When *Austrocedrus* pollen is

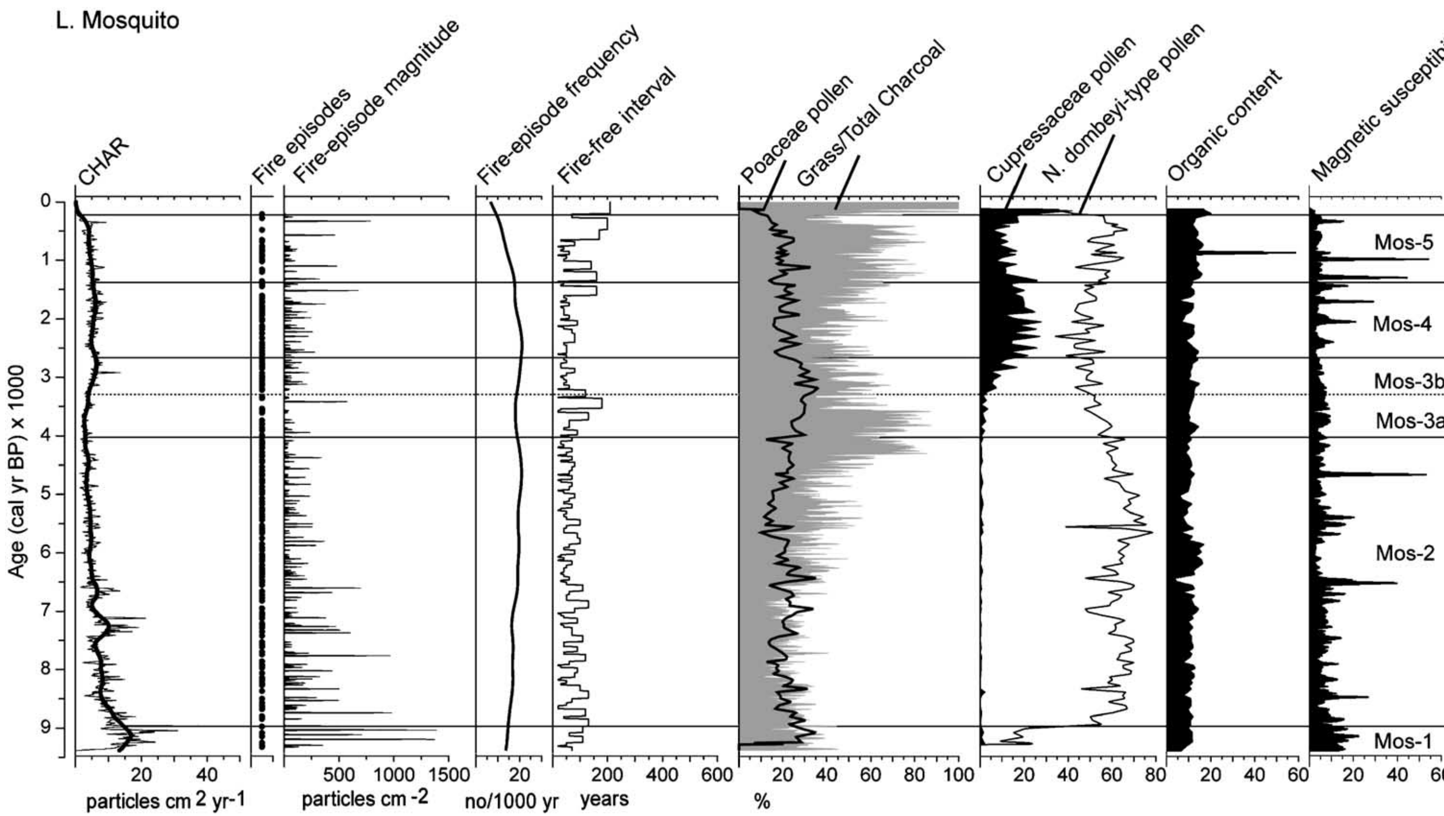

Figure 5. Fire history information based on charcoal and pollen data from L. Mosquito. See Figure 4 caption and text for explanation. Pollen data are from Figure 3.

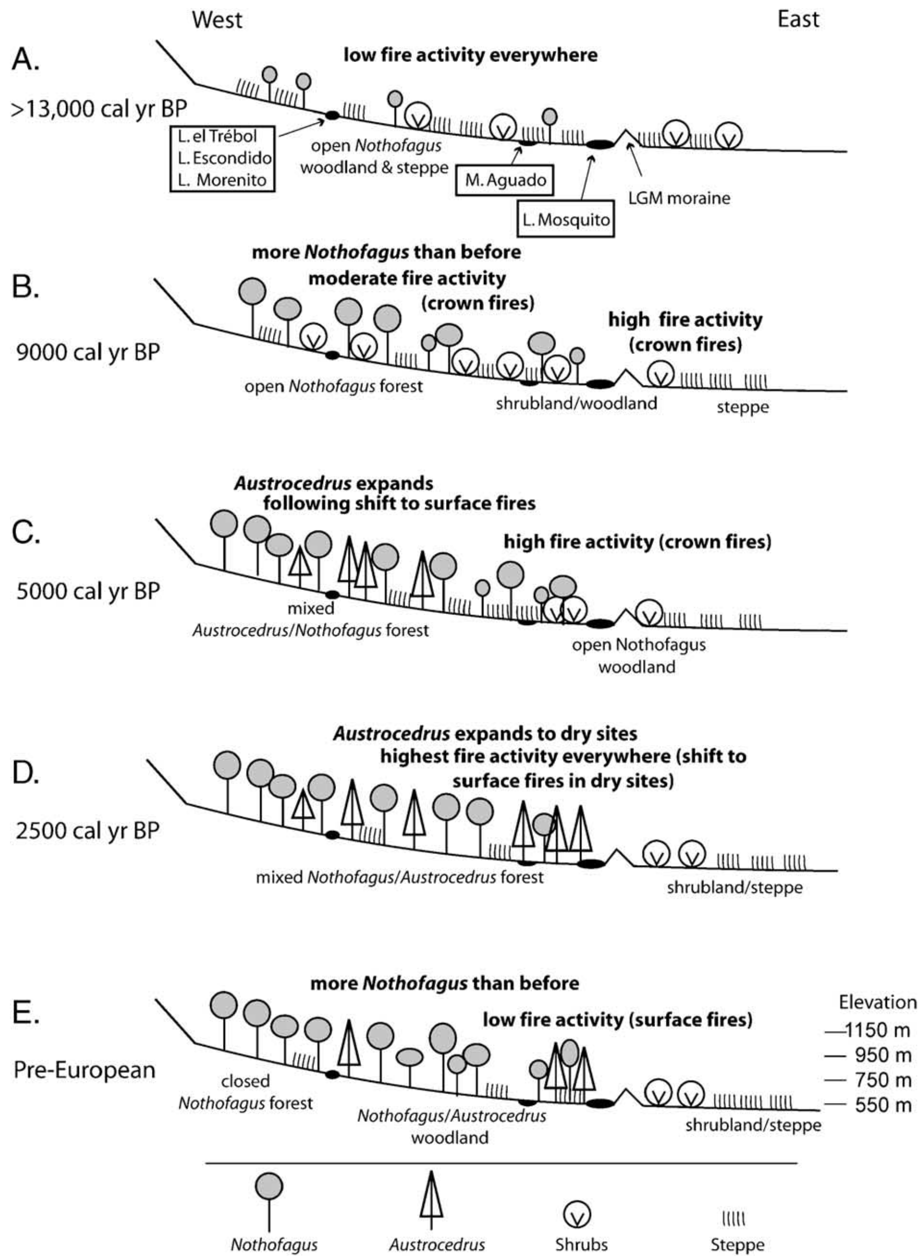

Figure 6. Schematic vegetation reconstruction of the east side of the Andes based on the data presented here and published records from nearby sites.

best represented in each site, the grass/total charcoal ratio decreases somewhat and fire-episode magnitude becomes more variable. This association suggests establishment of a mixed-severity fire regime that burned grassy areas, shrubland, and *Austrocedrus*. Although the source of grass pollen and charcoal was not identified, it could be from bamboo *Chusquea sp.*, which sprouts vigorously after fire in *N. dombeyi* forest (Kitzberger and Veblen, 1999).

Long-term variations in climate partly explain the changes in vegetation. Dendroecological studies indicate that spring and early summer precipitation is critical for present-day expansion of *Austrocedrus* into steppe and shrubland communities (Villalba and Veblen, 1997); increased growing season precipitation also likely contributed to its expansion in the middle Holocene. Other paleoclimatic studies indicate that the westerlies became stronger after 6000 cal yr BP, allowing an eastward spread of forest in the Andes (see Mancini et al., 2005; Grimm et al., 2001; Markgraf, 1993), as well as an increase in Valdivian rainforest taxa west of the Andes (Moreno, 2004; Abarzúa et al., 2004; Heusser, 2003; Villagrán et al., 1996). Our records suggest that the middle-Holocene moisture gradient was apparently steep enough to preclude the eastward expansion of *Austrocedrus* to dry sites like L. Mosquito, and the ecotone between forest, shrubland, and steppe lay west of its present position (Fig. 6C). *Austrocedrus* reached its present limit only in the last few millennia following a shift to wetter conditions and more-frequent surface fires. Superimposed on these long-term climate trends towards wetter conditions was an increase in interannual variability or greater monsoonal circulation necessary to support a surface-fire regime (Kitzberger and Veblen, 2003). For example, this combination explains the gradual decrease in grass pollen at L. el Trébol as a result of wetter conditions and forest closure, coupled with increased grass charcoal as a result of interannual variability and frequent surface fires. Increased short-term climate variability has been noted in many South American records after 6000 cal yr BP (Moy et al., 2002; Rodbell et al., 1999; McGlone et al., 1992) and is attributed to the onset (Markgraf and Diaz, 2000) or increased importance (Rodó and Rodriguez-Arias, 2004) of ENSO variability.

Changes in the last two millennia include a decrease in *Austrocedrus* and increase in *Nothofagus* at L. Escondido, M. Aguado, and L. Mosquito and suggest even wetter conditions than before (Figs. 6D and E). At L. el Trébol, CHAR declines between 3300 to 2000 cal yr BP and returns to high values between 1500 and 500 cal yr BP. The last 2000 yr at this site featured variable fire-episode magnitude, high fire frequency, and short fire-free intervals. High grass charcoal indicates that forest openings were burning. At L. Mosquito, CHAR was high between 1500 and 500 cal yr BP and declined in the last 500 yr to values similar to those at L. el Trébol. As in the previous period, seasonal, interannual, or interdecadal drought was apparently sufficient to support surface fires in the face of a cooler, effectively wetter climate.

European influence is registered between 200 and 600 yr at most sites in this region. Arrival of the European colonists to this region occurred after 1850s (Kitzberger and Veblen, 1997), although Europeans and native peoples may have affected fire regimes before this period (Huber and Markgraf, 2003). A decline of *Nothofagus dombeyi*-type pollen in the last 200–400 yr is accompanied by the appearance of non-native taxa. European settlement was initially associated with large fires for forest clearance and intensive livestock grazing (Veblen et al., 1992). In wet sites, fire created and maintained forest openings, as evidenced by the charcoal data at L. el Trébol, tree-ring data, and historic records (Kitzberger et al., 1997). The charcoal records also indicate decreasing fire frequency in recent centuries, which implies that fuel build-up, cumulative land-use impacts, and severe drought account for the severe fire events of the last few decades (Veblen et al., 2003).

Concluding remarks

Pollen and high-resolution charcoal records considered together greatly enhance our understanding of climate variability and its impact on past ecosystems, as well as the complex relationships between climate, vegetation, and fire regimes. Changes in vegetation, determined from the pollen data, show the influence of long-term shifts in climate that allow species ranges to expand, new communities to establish, and ecotones to develop. On millennial time scales, the pollen record registers the expansion of *Nothofagus* as a result of increased moisture and warming at the end of the glacial period. The data also suggest that continuing aridity in the early Holocene maintained open forests at both wet and dry sites along the eastern Andes. Early-Holocene fire records suggest that the west-to-east gradient in moisture was relatively steep, allowing for higher fire frequencies in drier sites. The expansion of *Austrocedrus* after 6000 cal yr BP occurred as long-term climate conditions shifted towards wetter summers. The expansion, however, was diachronous, occurring several millennia earlier at wet sites than at dry sites. With increasing effective moisture, the forests became more closed leading to the development of the present-day mixed *Nothofagus-Austrocedrus* forest.

Charcoal data supplement this reconstruction by providing information on the nature of past fire regimes and the climate conditions that dictate the fire season (Kitzberger and Veblen, 2003). In wet and dry sites, the *Austrocedrus* rise is preceded by a remarkable shift in the local fire regime towards frequent surface fires. This fire regime was likely driven by an increase in climate variability and/or an increase in convective storms, and it helped enable the subsequent *Austrocedrus* expansion. The data thus suggest that climate created a disturbance regime that conditioned the change in vegetation. The results of this study attest to the importance of interannual (or interdecadal) climate variability, shifts in seasonality, and long-term trends in climate in shaping the environmental history along the east side of the Andes and the importance of climate-driven fire regimes as a proximal control of vegetation change.

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