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Climate and local controls of long-term vegetation dynamics in northern Patagonia (Lat 41°S)

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ABSTRACT

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

Introduction

Paleoenvironmental records from the mid-latitudes (38–42°S) show a trend from early-Holocene aridity towards more humid and variable conditions during the late Holocene (e.g., Markgraf et al., 2008; Fletcher and Moreno, 2011). These long-term climate changes are attributed to variations in seasonal and annual insolation (Whitlock et al., 2007), the location and strength of the Southern Westerlies (Lamy et al., 2001), and the late-Holocene onset and/or strengthening of El Niño Southern Oscillation (ENSO; Moy et al., 2002). Plant populations responded to regional climate variations by altering their range and density, which, in turn, resulted in shifts in vegetation composition and structure. For example, the late-glacial steppe that was widespread along the eastside of the Andes was gradually colonized by shrub and tree taxa in response to rising temperature and humidity (Markgraf et al., 2007). The early Holocene was characterized by higher-than-present annual and winter insolation and weakened Southern Westerlies, and the eastern flanks of the Andes supported open, fire-adapted woodland. Present-day *Nothofagus* and *Austrocedrus* forests developed ca. 5000 cal yr BP (Whitlock et al., 2006; Bianchi and Ariztegui, 2012; Iglesias et al., in press), during a time of declining annual insolation and the onset or strengthening of ENSO.

Although long-term vegetation dynamics of the eastern Andes are relatively clear, our understanding of the proximal and distal mechanisms that produce them is limited. In Patagonia, modern plant communities are distributed along a steep west-to-east precipitation gradient, suggesting that climate exerts a significant control over the regional-scale variability in vegetation composition. However, historical studies suggest that natural and anthropogenic disturbances amplify or override the effects of climate on ecosystem processes (Mermoz et al., 2005). At the Patagonian forest–steppe ecotone, for example, decades of fire suppression have allowed fire-sensitive *Austrocedrus* to expand eastwards into steppe in spite of the relative stability of the climate (Veblen and Markgraf, 1989). This expansion indicates that patterns in ecological communities are determined by a variety of drivers and mechanisms, operating over a range of spatio-temporal scales (Levin, 1992). Understanding ecosystem dynamics requires disentangling regional drivers from more local feedbacks involving vegetation, fire and human activities.

We present high-resolution pollen and charcoal records from two small low-elevation lakes located in close proximity in the eastern slopes of the Patagonian Andes at the forest–steppe ecotone (Laguna Huala Hué, lat 41°30′24″S, long 71°30′32″W, 849 m elevation; and Laguna Padre Laguna, lat 41°21′34″S, long 71°30′29″W, 1280 m elevation). Our objectives are (1) to reconstruct the postglacial environmental history at the

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lower forest border; and (2) to compare these data with those from nearby sites to identify the relative importance of local and regional drivers of late-Holocene ecological change (Huber et al., 2004). The last 5000 years are of special interest because modern climates and plant communities were established in the late Holocene (Moy et al., 2002; Whitlock et al., 2006) and provide an opportunity to examine fire–climate interactions across multiple temporal and spatial scales.

Study area

The study sites are located in the drainage of the Río Manso, south of Volcán Tronador (Figure 1). Most of the large lakes in the Río Manso drainage are dammed by recessional moraines from eastward-flowing late-Pleistocene glaciers. L. Huala Hué, however, is blocked on its east side by a prominent glacial deltaic complex associated with late-Pleistocene meltwater from ice complexes from the north (Caldenius, 1932). L. Padre Laguna, located 15 km south of L. Huala Hué, is dammed by a broad postglacial alluvial fan.

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

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

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

Methods

A modified Livingston piston sampler was used to take a 731-cm-long core (HH08B) along the west margin of L. Huala Hué, and a 397-cm-long core from the center of L. Padre Laguna (LCar08B). Core segments were wrapped in plastic wrap and aluminum foil and transported to LacCore Facility, University of Minnesota, for lithologic characterization. High-resolution magnetic susceptibility (SI) was measured at 0.5-cm contiguous intervals in the core to assess changes in inorganic allochthonous sediment input (Gedye et al., 2000). Gamma density (kg cm^{-3}), measured at 1-cm contiguous intervals, was used as an indicator of lithology and porosity changes. Organic and carbonate contents (% dry weight) were determined from weight loss after ignition at 550° and 900°C of 1-cm^3 samples taken at 1.5-cm intervals (Dean, 1974).

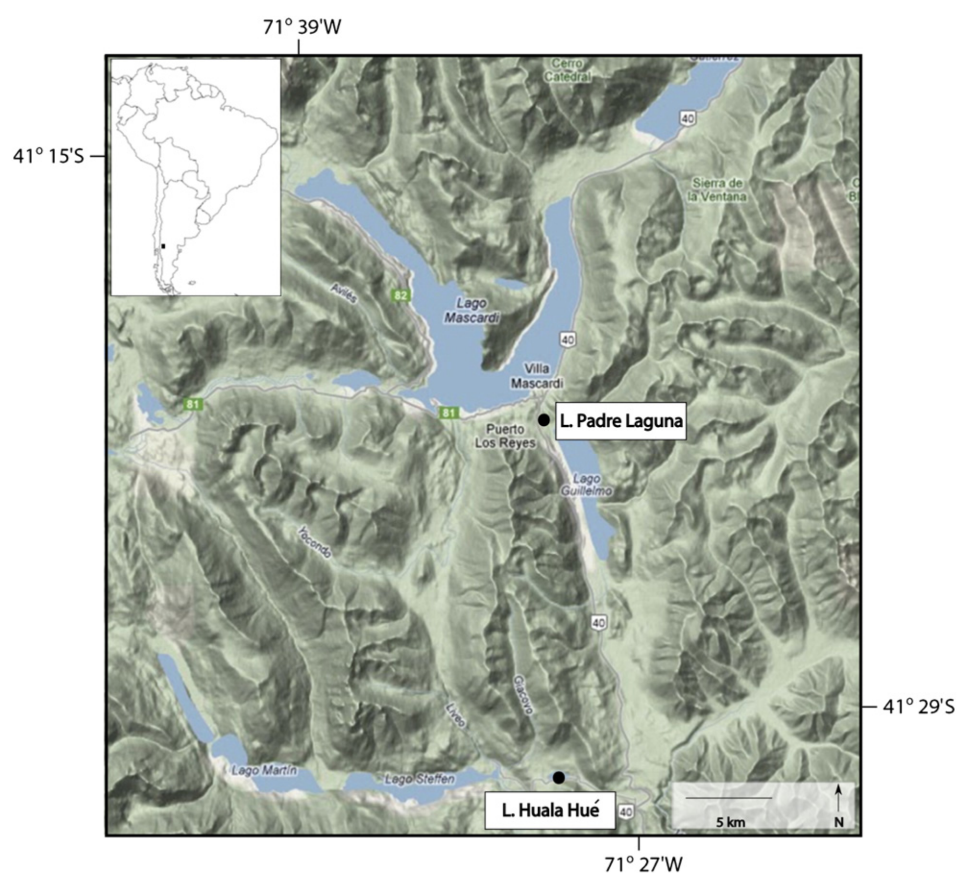

Figure 1. Location of L. Huala Hué and L. Padre Laguna.

Table 1
Radiocarbon and calibrated radiocarbon dates from L. Huala Hué and L. Padre Laguna.

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

Adjusted depths were used to calculate the age–depth models. Only true depths are referred to in text.
[a] Not included in the chronologies.
[b] Calibrated ages were based on CALIB 6.0 (Stuiver and Reimer, 1993; http://radiocarbon.pa.qub.ac.uk/calib/calib.html).

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

For this study, only the dominant pollen types are discussed. *N. dombeyi*-type pollen includes *N. dombeyi*, *N. pumilio*, and *N. antarctica*. Cupressaceae pollen is attributed largely to *A. chilensis*, although rainforest taxa (*Fitzroya*, *Pilgerodendron*) may have been long-distance contributors. Other taxa were grouped into ecological units: Rainforest taxa (e.g. *Gaulteria*, *Hydrangea*, *Podocarpus*, *Saxegothaea*); shrubland (e.g. *Schinus*, Rhamnaceae, *Berberis*, *Lomatia*, *Maytenus*); steppe (e.g. *Acaena*, *Ephedra*, Chenopodiaceae); and riparian and aquatic taxa (*Caltha*, Cyperaceae, *Myriophyllum*).

In order to provide a local signal of fire, large charcoal particles (>125 μm in diameter) were extracted from 2-cm^3 samples at contiguous 0.5-cm intervals with standard sieving methods (Whitlock and Larsen, 2001). Grass and wood charcoal particles were tallied separately. A grass-to-total charcoal ratio was used to infer the relative contribution of grass and woody fuels to total biomass burned. Charcoal time series were interpolated to the median resolution of the cores (15 yr for L. Huala Hué; 12 yr for L. Padre Laguna). Charcoal concentrations and deposition times were calculated and converted to charcoal accumulation rates (CHAR, particles cm^{-2} yr^{-1}). Smoothing techniques (a locally weighted 1000-yr median in the L. Huala Hué record; 750-yr locally weighted scatterplot smoother (LOWESS) robust to outliers in the L. Padre Laguna record) were used to separate the long-term trends (i.e., background CHAR) in the time series from the positive residuals (i.e., charcoal peaks). The latter are inferred to represent fire episodes (i.e., one or more fires occurring during the time span of the peak; Higuera et al., 2009). Fire-episode frequency was calculated in 1000-yr windows. The suitability of the records for fire-episode identification was assessed with the signal-to-noise index (SNI) proposed by Kelly et al. (2011). At both sites, 1000-yr bandwidths were used to calculate the SNI. Except for the periods 6240–6020 (2.6<SNI<2.9) and 3620–2720 cal yr BP (0.19<SNI<2.9) at L. Huala Hué, and 1200–700 cal yr BP (0.7<SNI<3) at L. Padre Laguna, the SNI (3<SNI<51) was well above the value expected from records without a signal.

Chronologies were developed from a series of AMS dates (Table 1), which were calibrated using CALIB 6.0.1 (Stuiver et al., 1993). For modeling purposes, depths were adjusted by removing volcanic ashes

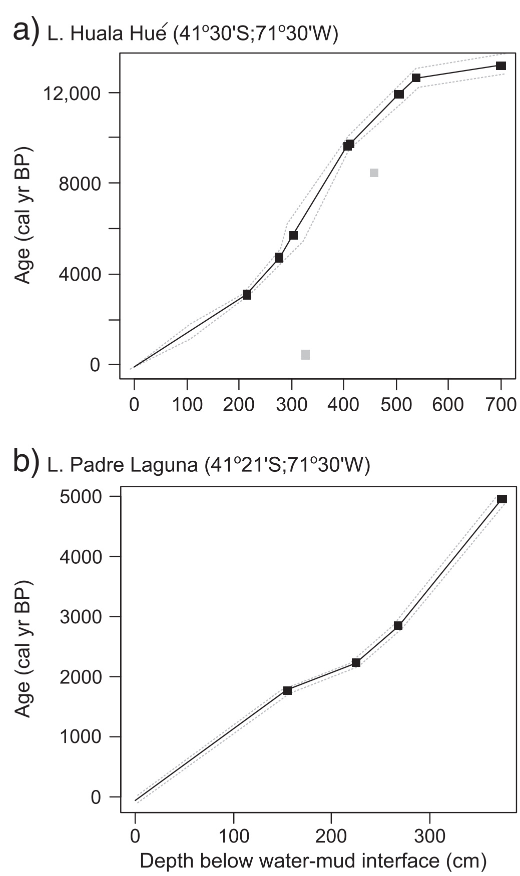

Figure 2. Age–depth model for a) L. Huala Hué (41°30′S; 71°30′W) and b) L. Padre Laguna (41°21′S; 71°30′W). 95% confidence intervals are shown in gray. Black squares are calibrated radiocarbon ages used to develop the models, and gray squares are dates that are ages that were not included in the models.

>1 cm in thickness on the assumption that these tephra layers were deposited in a negligible span of time. Age–depth models (Figure 2) were constructed with a cubic smoothing spline and bootstrap approach (2000 iterations) that allowed each date to influence the age model through the probability density function of the calibrated age (Higuera et al., 2009). All depths hereafter are given in true core measurements, not adjusted depths. Unless indicated otherwise, analyses were performed with R (R Development Core Team, 2010).

Results

Lithology

L. Huala Hué

Four lithological units were identified in the HH08B core (Figure 3). The basal unit (Unit 1; 731–628.5 cm depth; 13,500–13,300 cal yr BP) was composed of clay with gray and dark gray beds. High bulk density and sedimentation rates suggest that this period featured abundant allochthonous input and poorly developed soils. The magnetic susceptibility profile shows overall high values and variability, with high values associated with dark gray beds and low values with lighter beds. These data suggest periodic changes in sediment source and likely short-term fluctuations in sediment accumulation rates.

Unit 1 was overlain by an organic clay unit (Unit 2; 628.5–570 cm depth; 13,300–12,700 cal yr BP), which represents a transition from dark grayish brown to dark olive brown clay. This trend reflects a gradual increase in organic matter and decrease in carbonate content in the sediment, indicating increased lake productivity. Decreasing sediment accumulation rates, bulk density and magnetic susceptibility are consistent with decreased allochthonous input into the lake. At 570 cm depth, a sharp contact marks the transition to the overlying gyttja unit (Unit 3, 570–62 cm depth; 12,700–630 cal yr BP). The gyttja unit was characterized by relatively stable sedimentation rates and organic matter content and variable magnetic susceptibility and gamma density. Based on changes in color, magnetic susceptibility and gamma density, seven subunits were identified in Unit 3. The uppermost unit (Unit 4, 62–0 cm depth; 630 cal yr BP–present) consisted of low-density decomposed sedge peat. Eleven volcanic ashes were present and preliminary geochemical data suggest they are from eruptions of Puyehue and Chaitén volcanoes.

L. Padre Laguna

LCar08B core sediments consisted of homogenous fine-detritus gyttja and thirteen volcanic ashes (Figure 4). Carbonate and organic matter content showed little variability throughout the core. Seven lithological subunits were identified based on color and sedimentation rate changes, variability in the magnetic susceptibility profile, and gamma density.

Pollen and charcoal records

L. Huala Hué (Figure 5)

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

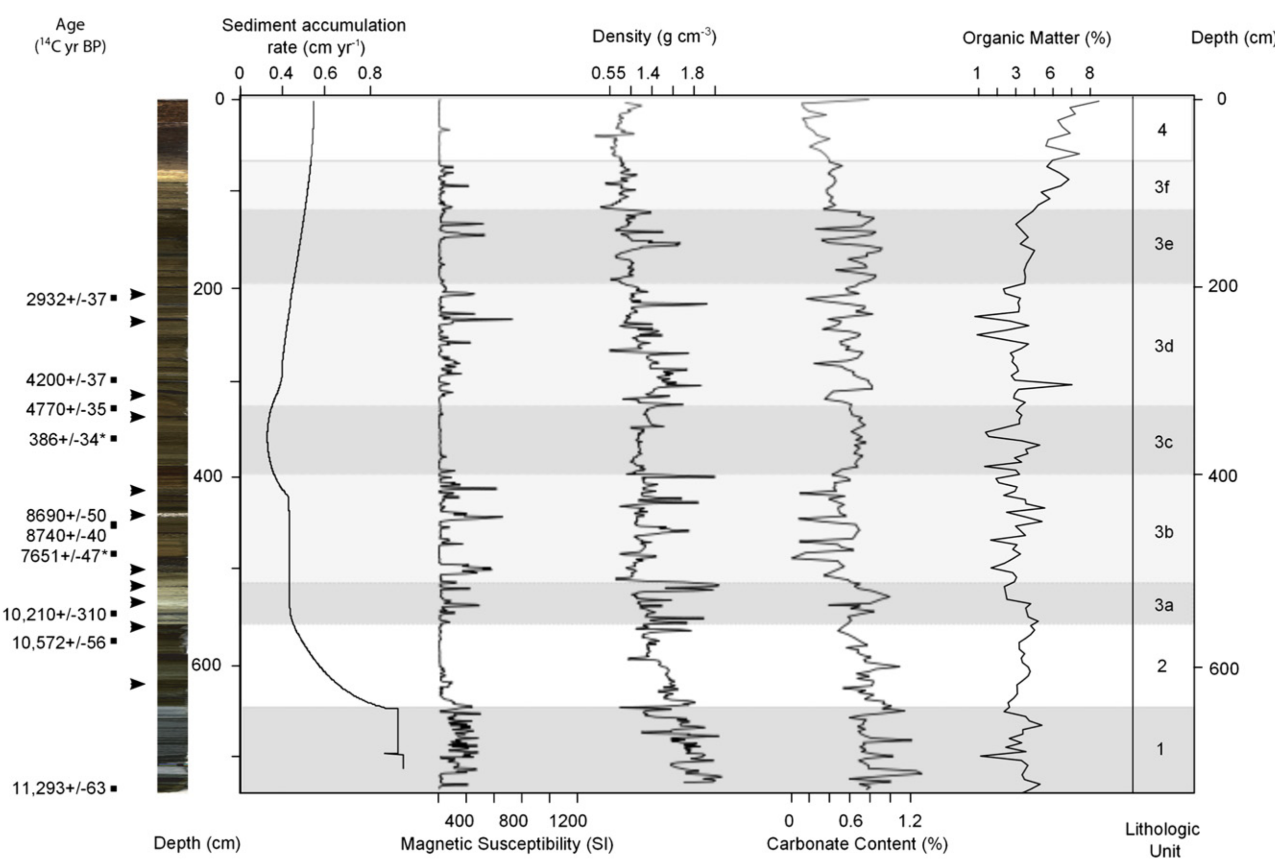

Figure 3. Lithology, sediment-accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the HH08B core. Black triangles indicate the position of tephra layers and black squares represent radiocarbon years. Asterisks indicate dates that were not used in the chronology.

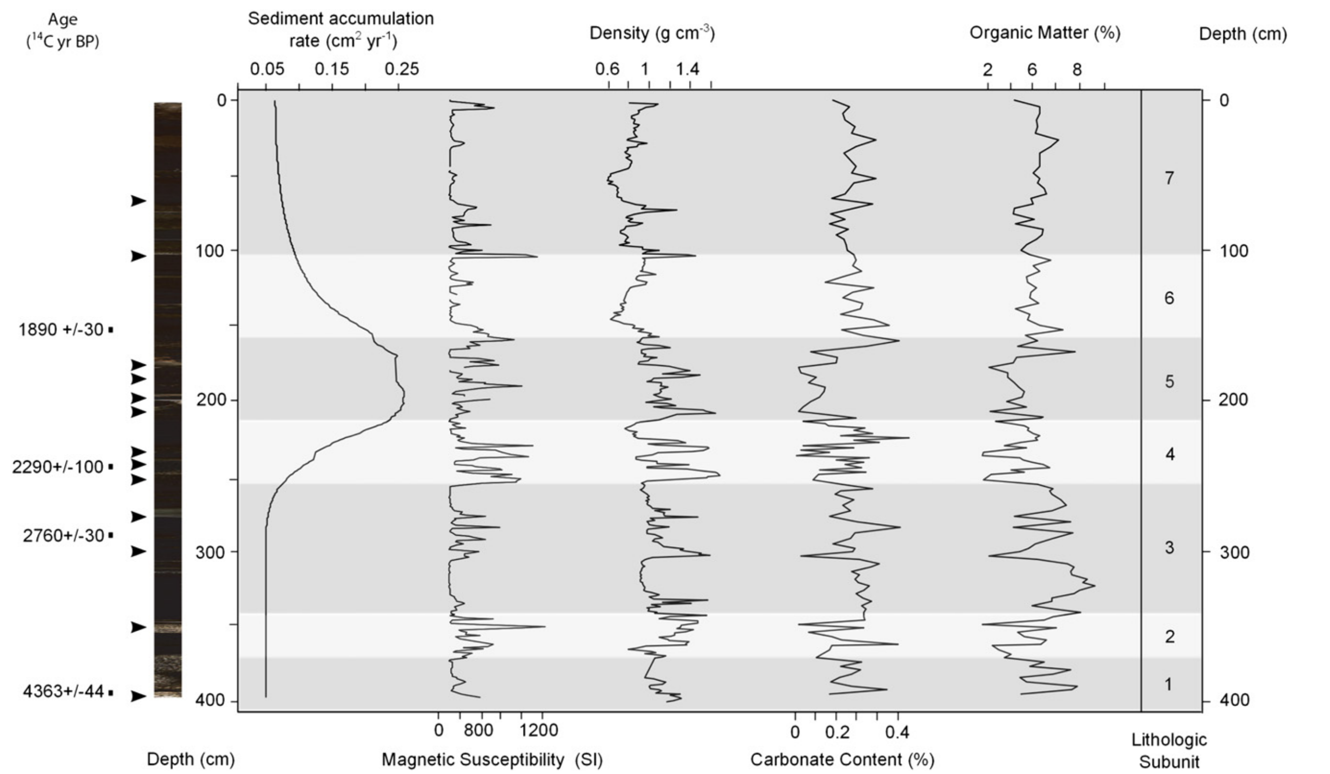

Figure 4. Lithology, sediment-accumulation rate, magnetic susceptibility, gamma density and loss-on-ignition data for the LCar08B core. Black triangles indicate the position of tephra layers and black squares are radiocarbon years.

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

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

Zone HH-3 (284–250 cm depth; 4900–3860 cal yr BP). Rainforest elements, *Misodendrum*, and shrubland and steppe taxa declined in this zone. *N.-dombeyi*-type was high at the bottom of the zone (83%) and decreased to 41% at the top. Cupressaceae — presumably *Austrocedrus* — pollen increased from 3 to 32%. PAR values rose to 1280 grains cm^{-2} yr^{-1}, suggesting an increase in vegetation productivity. The pollen assemblage compares most closely with modern samples from the *Nothofagus* forest. CHAR remained <1.5 particles cm^{-2} yr^{-1}. Fire frequency and the levels of grass-to-total charcoal were initially low and gradually increased to >4 episodes 1000 yr^{-1} and a grass-to-total charcoal ratio of 0.25 at the top of the zone, indicates a shift towards more frequent burning of open vegetation than before.

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

Zone HH-5 (165–117 cm depth; 2120–1350 cal yr BP). *N. dombeyi*-type percentages reached maximum values (90%), whereas humid forest taxa, *Misodendrum*, Cupressaceae, shrubland taxa, and Poaceae were poorly represented. PAR increased to 1200 grains cm^{-2} yr^{-1}, suggesting high vegetation productivity. CHAR values oscillated between 0 and 4.41 particles cm^{-2} yr^{-1}, and the grass-to-total charcoal ratio steadily declined from 0.49 to 0.19. Fire frequency increased to highest values at 2000 cal yr BP (<7 episodes 1000 yr^{-1}) and decreased thereafter to 4 episodes 1000 yr^{-1}, suggesting a transition from frequent grass fires to less frequent woody fires. Comparisons with modern pollen studies indicate a shift in forest dominance from *Austrocedrus* to *Nothofagus* (Paez et al., 2001).

Zone HH-6 (117–0 cm depth; 1350 cal yr BP to present). *N. dombeyi*-type decreased, and Cupressaceae and humid forest taxa increased to 8 and 9%, respectively. Shrubland and steppe taxa, and Asteraceae also became more abundant (10, 8 and 2.5%, respectively). PAR values were initially high (920 grains cm^{-2} yr^{-1}) and decreased to <140 particles cm^{-2} yr^{-1} towards the top of the zone, suggesting that the forest became less productive. After 450 cal yr BP, CHAR values rose and showed prominent peaks, including a value of 7 particles

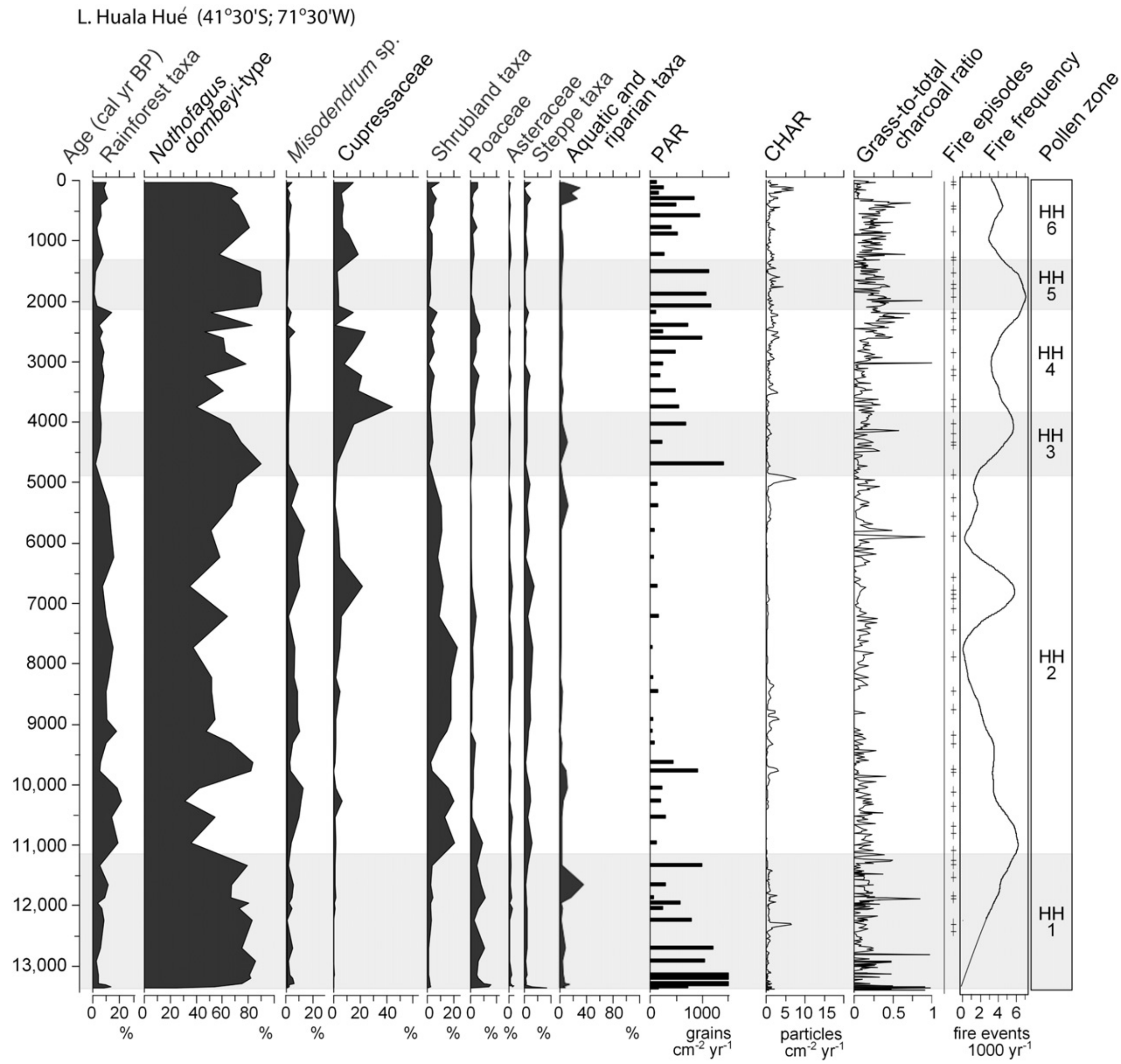

Figure 5. Selected pollen and charcoal data for L. Huala Hué.

cm^{-2} yr^{-1} at 15 cm depth, that corresponds with a large forest fire event in the watershed at AD 1761 (Veblen et al., 1999). Fire frequency steadily declined to 3.8 episodes 1000 yr^{-1}, and grass-to-total charcoal ratio, which reached 0.80 at the bottom of the zone, decreased to 0 towards the top, indicating a notable shift from surface to crown fires in recent times. The zone marks the establishment of open *Nothofagus–Austrocedrus* forest, and an infrequent but stand-replacing fire regime.

L. Padre Laguna (Figure 6)

Zone PL-1 (397–339 cm; 4910–3860 cal yr BP). *N. dombeyi*-type was the dominant pollen taxa in the assemblage (up to 80%). Rainforest taxa and *Misodendrum* oscillated between 5 and 7%, except at 4522 cal yr BP (352 cm depth), when they both peaked, reaching values >25%. Shrubland and steppe taxa as well as Poaceae did not exceed 12% of the total pollen sum. PAR was generally high and variable, fluctuating between 40 and 400 grains cm^{-2} yr^{-1}. CHAR and fire-episode frequency were initially low (>1 particles cm^{-2} yr^{-1}, 0 fire episodes 1000 yr^{-1}) and increased to 2.5 particles cm^{-2} yr^{-1} and ca.1.8 fire episodes 1000 yr^{-1} at the end of the zone. Grass charcoal was poorly represented (grass-total-charcoal ratio<0.23). Pollen and charcoal data suggest a *Nothofagus* forest where fires were infrequent but severe enough to burn predominantly woody vegetation dominated the watershed.

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

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

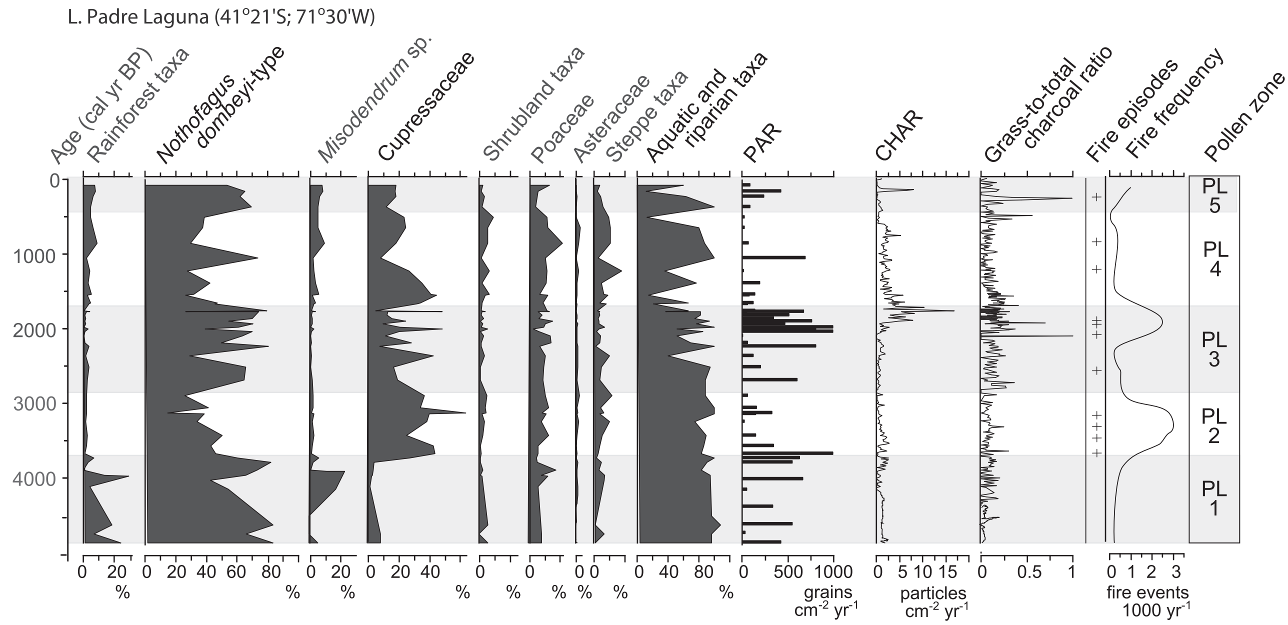

Figure 6. Selected pollen and charcoal data for L. Padre Laguna.

establishment of the *Nothofagus–Austrocedrus* forest and a shift in the fire regime from woody to grass fires at 2100 cal yr BP (246.5 cm depth).

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

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

Discussion

Regional vegetation and fire history

Late-glacial/early Holocene transition (13,500–11,200 cal yr BP)

The L. Huala Hué record begins at ca.13,500 cal yr BP following ice recession from the Río Manso valley. Initially, glacial clay was deposited in the basin in a quasi-periodic fashion, reflecting fluctuations in inorganic clastic sediment possibly related to changes in glacial meltwater input. The inorganic sediment contribution to the lake decreased after ca.13,300 cal yr BP and the system became increasingly more productive. This trend towards a more stable system was reversed between 12,700 and 11,200 cal yr BP, when laminations of carbonate-rich silt were periodically deposited in the lake. The lithological change suggests that the late-glacial/early-Holocene transition was characterized by pronounced fluctuations in sedimentation, a finding that is consistent with independent evidence of climatic variability at this time throughout Patagonia (Ariztegui et al., 1997; Hajdas et al., 2003; Moreno and León, 2003).

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

Fires were initially rare but became more frequent by 11,200 cal yr BP, occurring approximately every 200 yr and burning grassland and woody vegetation. Pollen data provide no evidence of increasing fuel biomass or changes in fuel composition to explain the increased fire activity, suggesting that it was related to increased ignition and decreased effective moisture. Widespread burning has been recorded throughout Patagonia during the late-glacial/early Holocene transition. Although human activity may explain the shift in the fire regime, it is likely that increased lightning occurrence associated with more frequent convective storms (Huber et al., 2004) and drier conditions (Whitlock et al., 2006) created conditions conducive for burning throughout the region.

Early and middle Holocene (11,200–4900 cal yr BP)

Between 11,200 and 4900 cal yr BP, the L. Huala Hué record suggests establishment of a shrubland dominated by Rhamnaceae, *Nothofagus* (presumably *N. antarctica*) and steppe taxa. Local fire frequency was high at the beginning of the period (5.5 episodes 1000 yr^{-1}) and decreased as vegetation cover became more discontinuous. Low CHAR indicates that regional biomass burning was limited except between 10,100–8500 and 5700–4700 cal yr BP. Periods of higher CHAR coincide with short-term fluctuations between inorganic and organic sediment deposition (lithological units 3b and d), which suggest intermittent pulses of erosion and deposition. Higher-than-average CHAR and episodes of erosion at these times may have been a consequence of multi-decadal variations in effective moisture that resulted in periods of fuel accumulation followed by periods of fuel desiccation, conditions conducive to fire in present-day fuel-limited ecosystems (Whitlock et al., 2010). It is also possible however, that some of the charcoal was secondarily introduced into the lake through erosion.

Increasing effective moisture is implied by the expansion of woody species (e.g., Rhamnaceae, *Maytenus*, *Schinus*) at ca. 11,200 cal yr BP. Shrubland establishment at L. Huala Hué corresponds in time with an eastward shift of the forest–steppe ecotone on the eastern flanks of the Andes (Iglesias et al., in press); an expansion of Valdivian forest taxa and an increase in disturbance-adapted species (e.g., *Eucryphia*, *Weinmannia*) in the mid-latitudes of Chile (Moreno and León, 2003; Abarzúa and Moreno, 2008); and higher-than-before lake levels at lat 40°S, on the western flanks of the Andes (Bertrand et al., 2008). Whitlock et al. (2006) attribute widespread fire activity in southern Patagonia (south of lat 42°S) during the early Holocene to a southward or weakening of the Southern Westerlies, related to higher-than-present annual and winter insolation. Conditions became cooler and/or effectively wetter from 11,200 to 5000 cal yr BP probably as a result of decreasing annual and winter insolation and a strengthening of the Southern Westerlies at mid-latitudes. Superimposed on this long-term trend, millennial-scale shifts in the position of the Southern Westerlies led to oscillations in moisture, vegetation and fire not only in Patagonia but throughout the mid- and high latitudes of the Southern Hemisphere (Huber et al., 2004; Fletcher and Moreno, 2011).

Late Holocene (4900 cal yr BP to present)

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

The development of the forest after 5000 cal yr BP was accompanied by millennial-scale shifts in forest species dominance (i.e., *Nothofagus* and *Austrocedrus*) and fire activity at L. Huala Hué and L. Padre Laguna (Figure 7). Between 4900 and 3860 cal yr BP, a closed *Nothofagus* forest was present in both watersheds, and fires became more frequent towards the end of the period (up to 4 fire episodes 1000 yr^{-1} at L. Huala Hué, and 2.8 fire episodes 1000 yr^{-1} at L. Padre Laguna) (Figures 5, 6). *Austrocedrus* abundance increased substantially at 3860 cal yr BP, leading to the development of open *Austrocedrus* forest, and local fire frequency (>3 fire episodes 1000 yr^{-1} at L. Huala Hué and 2.8 fire episodes 1000 yr^{-1} at L. Padre Laguna) as well as regional biomass burning (CHAR>3 particles cm^{-2} yr^{-1}at both sites) were higher than before. The expansion of *Austrocedrus* and concurrent increases in fire activity point to a strong climatic control and, in particular, to decreased effective moisture during the growing season (Villalba et al., 2003).

At 2850 cal yr BP, fires became more frequent and less severe at L. Huala Hué (up to 6.5 fire episodes 1000 yr^{-1}) and burned predominantly Poaceae (grass-to-total charcoal ratio of 0.65). Although the fire regime did not change significantly at L. Padre Laguna at this time, vegetation shifted to a *Nothofagus*-dominated forest. *Nothofagus* replaced *Austrocedrus* as the local dominant tree at L. Huala Hué at 2120 cal yr BP, when vegetation productivity (inferred from high PAR) and grass fuels (grass-to-total charcoal ratio<0.98) reached their maximum. Based on comparisons with modern fire regimes (Kitzberger et al., 1997), it is reasonable to assume that the abundance of grass charcoal particles associated with *Nothofagus*-dominated pollen assemblages

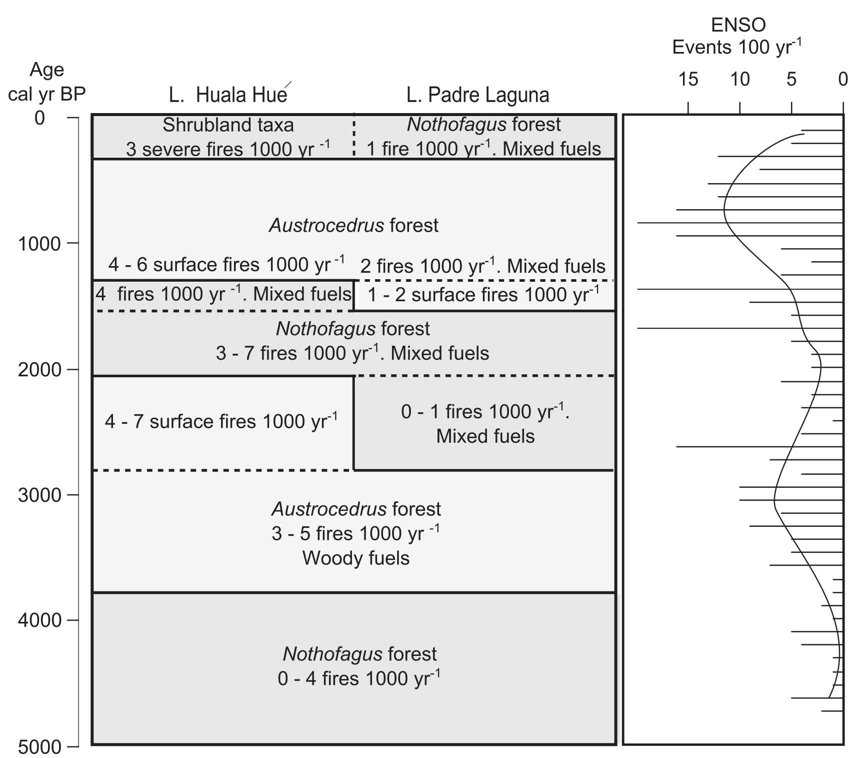

Figure 7. Late-Holocene vegetation and fire at L. Huala Hué and L. Padre Laguna and ENSO event frequency. Note that the y-axis is inverted. Modified from Moy et al. (2002).

originated from fires in bamboo stands (*Chusquea* sp.), widespread in disturbed *Nothofagus* forests, rather than grasslands. The persistence of grass charcoal and high fire frequency until 1650 cal yr BP suggests that short-term climatic variability (i.e., interannual or interdecadal) created conditions suitable for bamboo burning despite the generally wet character of the forest.

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

Paleoenvironmental records from the mid- and high latitudes of the Southern Hemisphere reveal increased millennial- to decadal-scale variability during the late Holocene (Fletcher and Moreno, 2011). Our data suggest oscillations between humid periods (4900–3800 cal yr BP and 2850–1350 cal yr BP) and dry periods (3800–2850 cal yr BP and 1350–450 cal yr BP). A similar pattern is inferred from nearby sites on the eastern flanks of the Andes (Whitlock et al., 2006; Iglesias et al., in press). Comparison of our records with an ENSO reconstruction (Moy et al., 2002) reveals that drier (more humid) periods are concurrent with intensified (decreased) ENSO activity (Figure 7). For example, whereas *Nothofagus* forest is dominant during periods with few ENSO events (i.e., 4900–3800 cal yr BP; 2100–1650 cal yr BP), *Austrocedrus* expands during times of active ENSO (i.e., 3800–2850 cal yr BP; 1350–450 cal yr BP). Mixed forests occur during the transitions between high and low ENSO activity periods (2850–2100 cal yr BP; 1650–1350 cal yr BP) (Figure 7).

This association suggests that ENSO variability accounts for some of the late-Holocene vegetation and fire history shifts in northwestern Patagonia. The positive (negative) phase of ENSO has been linked to decreased (increased) spring and summer precipitation and high (low) annual temperatures as a result of a strengthened (weakened) southeastern Pacific subtropical high-pressure system and southward (northward) shift in the position of the Southern Westerlies (Montecinos and Aceituno, 2003). These atmospheric teleconnections are also influenced by fluctuations in the strength and position of the polar vortex (Cash et al., 2005) but to a degree that is not well understood.

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

Distal and proximal controls of late-Holocene vegetation history

The relative importance of local non-climatic versus regional climate controls of vegetation and fire activity is often ascribed to the scale of observation, be it a reconstruction from a single site or a regional pattern inferred from multiple sites (e.g., Huber et al., 2004; Williams et al., 2007). Paleoecological studies suggest that local controls can confound the direct effects of climate, and the importance of distal and proximal controls on vegetation can alternate through time (i.e. Cwynar, 1987; Gavin et al., 2006). Our results support this assertion, by showing the significant role of fire in shaping the vegetation during the last 5000 yr in creating vegetation changes that climate alone cannot explain.

In the late Holocene at L. Huala Hué and L. Padre Laguna, humid periods are associated with *Nothofagus* forest expansion, and drier times have promoted *Austrocedrus* dominance (Figures 7 and 8). The ecological niches of *Austrocedrus* and *Nothofagus* partly overlap along west-to-east moisture gradient, with the former dominating drier environments and the latter prevailing under more humid conditions. At the extremes of the moisture gradient, climate imposes physiological constraints that favor one taxa or the other. Xerophytic adaptations such as reduced leaf surface and thick cuticle make *Austrocedrus* more resistant to water stress than *N. dombeyi*. As a result, climatic conditions that cause *Nothofagus* drought-induced mortality may not have consequences for *Austrocedrus* (Manion, 1981). *N. dombeyi*, on the other hand, is widely distributed along the humid slopes of the eastern Andes. High growth rates under open conditions, effective seed dispersion and longevity enables regeneration of *Nothofagus* in recently disturbed areas, and once established, it can persist for centuries and outcompete *Austrocedrus* (Veblen and Markgraf, 1989).

At intermediate moisture levels, where the niches of *Nothofagus* and *Austrocedrus* overlap, vegetation is characterized by mixed forests. The relative importance of either species in this situation depends upon the characteristics of the fire regime (Staver et al., 2011), which in turn is driven by climate–fuel interactions. Pollmann and Veblen (2004) suggest that *N. dombeyi* dominates the landscape after coarse-scale disturbances, such as large stand-replacing fires that occur every few centuries. This hypothesis is consistent with our data, which suggest severe fires during periods when *Nothofagus* was most abundant (i.e., 2800–2100 cal yr BP at L. Padre Laguna and 1650–1360 cal yr BP at L. Huala Hué). The dominance of *Austrocedrus*, on the other hand, is impeded by large-scale disturbance events (Amoroso et al., in press), but small surface fires promote regeneration of seedlings at the expense of *Nothofagus* and understory bamboos. This observation matches paleoecological data for a fire return interval of 180–300 yr when *Austrocedrus* dominated the forest (i.e., 2800–2100 cal yr BP at L. Huala Hué and 1650–1360 cal yr BP at L. Padre Laguna). Thus, climate variability has been the main driver of late Holocene vegetation change, but interactions between available moisture, disturbance regime, and species biology have been crucial in shaping the mosaic of vegetation at lower treeline.

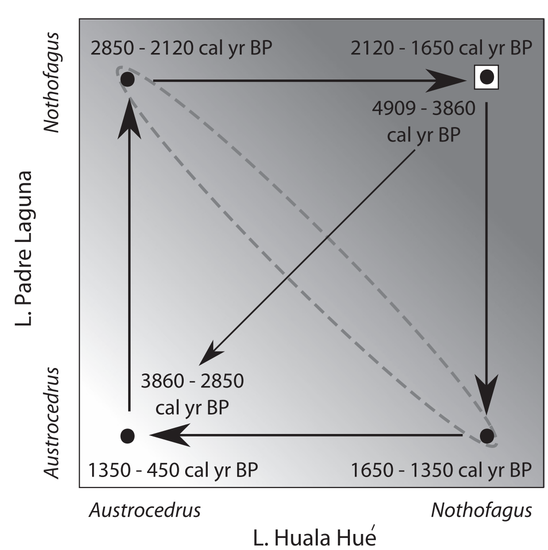

Figure 8. Late Holocene vegetation shifts in forest dominance at L. Huala Hué and L. Padre Laguna relative to effective moisture. The white square shows the beginning of the trajectory (4909 cal yr BP) towards modern communities. The white (dark gray) shade indicates drier (more humid) periods. At intermediate moisture levels (outlined with a dashed oval), either *Austrocedrus* or *Nothofagus* can dominate the ecosystem.

Conclusions

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

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

Short-term oscillations in humidity have resulted in alterations of forest types and shifts in fire regime in the last 5000 yr. *Nothofagus* expanded during humid periods and *Austrocedrus*-dominated forest prevailed during drier times. At intermediate moisture levels, both taxa co-existed and changes in the size, severity and frequency of fire explains differences in the relative abundance of species between the sites. Our results therefore provide further evidence that vegetation change is not simply a linear response to climate but rather a consequence of the combined effects of climate and disturbance, whose relative importance changes as critical thresholds are reached.

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