17,000 years of vegetation, fire and climate change in the eastern foothills of the Andes (lat. 44°S)

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Abstract

Paleoenvironmental records from Patagonia reveal the importance of latitude, longitude and elevation in shaping the response of vegetation to climate change. We examined the vegetation, fire and watershed history from two sites at lat. 44°S, as inferred from pollen, charcoal and lithologic data. These reconstructions were compared with independent paleoenvironmental records to better understand ecosystem dynamics along the southeastern Andes (lat. 41-50°S). Our results show that at lat. 44°S, late-glacial heath-steppe was colonized by trees at ~14,200 cal yr BP and forests became more closed at 11,500 cal yr BP. Differences in forest cover between the two sites are attributed to elevation-dependent disparities in humidity and fire. North of lat. 44°S, increasing precipitation favored initial forest development at 16,500 cal yr BP, while dry conditions restricted tree expansion in the south until 7000 cal yr BP. The time-transgressive pattern is attributed to a gradual southward shift in the Southern Westerlies resulting from deglaciation and increasing annual insolation. Present-day vegetation developed at all latitudes during the middle to late Holocene, when the core of the Southern Westerlies reached its modern position (50°S). Asynchronous forest expansions north and south of lat. 45°S between 5000 and 3000 cal yr BP are ascribed to centennial cycles of contraction and expansion of the Southern Westerlies, which led to seasonal variations in precipitation at the core and northern border of the wind belt. Synchronous oscillations in tree abundance along the eastern Andes prevailed during the last 3000 years. Decreased forest cover at all latitudes between 2500 and 1500 cal yr BP is concurrent with La Nina-like conditions and high solar irradiance. These climate drivers likely decreased effective moisture and favored fires at all latitudes.

Keywords

Climate history; vegetation history; fire history; Southern Westerlies; postglacial; Patagonia

1. Introduction

Reconstruction of past environmental conditions allows the identification of the drivers of long-term landscape evolution and ecosystem variability. Paleoenvironmental records from southern South America reveal the importance of latitude, longitude and elevation in shaping the response of vegetation to late-Quaternary climate change (e.g., Iglesias et al., 2014; Moreno et al., 2012). For example, east of the Andes, pollen records south of lat. 45°S, show that low-elevation forest densities did not reach present-day levels until ca. 7000 cal yr BP (Huber et al., 2004; Markgraf et al., 2007; Markgraf and Huber, 2010), whereas at sites north of lat. 43°S, low-elevation forest density was established in late-glacial times, and forest composition changed with the appearance of a shrubland zone in the early Holocene and the arrival of *Austrocedrus* in the middle and late Holocene (Whitlock et al., 2006; Bianchi and Ariztegui, 2012; Iglesias et al. 2012a; Markgraf et al. 2013). Past vegetation dynamics in this northern region were related to climate-driven changes in fire and the interaction of the large-scale controls of climate on local biotic and abiotic conditions (Iglesias and Whitlock, 2014).

Although the environmental history of the Patagonian Andes is relatively well understood north of lat. 43°S and south of 45°S, information on long-term ecosystem dynamics in the intervening latitudes (lat. 43-44.5°S) is limited to two paleoecological reconstructions from wet sites in Chile (Haberle and Bennett, 2004), and no data from the east side of the Andes are yet available. As a result, it is not known whether the north-south climate and vegetation transition zone was sharp or diffuse and stable or dynamic through time. In this study, we describe the vegetation and fire history from two sites at lat. 44°S, located along the modern forest-steppe border. The pollen, charcoal and lithologic records from these sites are compared with published records at higher and lower latitudes to better understand the environmental history and long-

term vegetation dynamics of southern South America. We suggest that (1) spatial variations along the latitudinal transect were driven by the combined effects of changes in available moisture, disturbance and species biology; and (2) the relative importance of these factors changed through time as critical climate thresholds were reached (e.g., Veblen et al., 2011; Iglesias et al., 2012; Kitzberger et al., 2012). A spatially diffuse pattern, with no abrupt transitions would therefore be associated with a large-scale driver, such as climate. Conversely, a sharp latitudinal transition could be attributed either to contrasting climate conditions north and south of the study sites or to local environmental feedbacks related to disturbance, soil or biotic interactions. These local factors would have amplified or hampered the direct effects of climate in shaping vegetation composition and distribution.

2. Methods

2.1. Study area

Lago Los Niños (44.01°S, 71.29°W; elevation 1015 m) and Laguna La Pava (44.28°S; 71.31°W, elevation 731 m) are located 30.5 km apart in southwestern Chubut Province, Argentina (Fig. 1). Both lakes lie close to late-Pleistocene terminal moraines in glacially scoured terrain (Caldenius, 1932). At Lago Vintter (43°87'S, 71 33'W; elevation 1300 m) just north of L. Los Niños, mean temperatures range from 2°C in winter (July) to 14°C in summer (January (1950-2010 AD; Servicio Meteorológico Nacional, 2015). Similar temperatures have been recorded in the town of Río Pico, east of L. La Pava.

Precipitation is associated with Pacific cyclones that migrate eastwards along the path of the Southern Westerlies. Uplift of low-level winds over the western flanks of the Andes produces orographic precipitation in the Chilean Andes (4000 mm yr⁻¹) which, combined with

adiabatic warming of the air masses, leads to increasingly drier conditions east of the Andean crest (680 mm yr⁻¹ at Lago Vintter and 650 mm yr⁻¹ in Río Pico; 1950-2010 AD; Servicio Meteorológico Nacional, 2015). Precipitation levels at this latitude are highest in late fall and winter, and lowest in summer. Weather station data at Río Pico from 1950 to 2010 AD, for example, record maximum precipitation in May (monthly average of 101 mm) and minimum values in January (monthly average of 22 mm). Precipitation variability is largely explained by changes in the strength and position of the Southern Westerlies and the southeastern Pacific Subtropical High Pressure system and their influence on storm tracks. The large-scale circulation features are influenced by variations in the latitudinal temperature gradient and affected by the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO; Fogt and Bromwich, 2006).

Present-day vegetation at L. Los Niños and L. La Pava is composed of a mosaic of forest and steppe. A broad zone of *Nothofagus antarctica* shrubs comprises the upper treeline at about 1300 m elevation. *Nothofagus pumilio* is the dominant tree of the forest, but its abundance has been much reduced as a result of 19th and 20th century land clearance, fire and recent livestock grazing. *N. antarctica* and *Escallonia* grow on wetlands surrounding the lakes and also in zones of disturbance. The area around L. La Pava features extensive bare rock outcrops and supports a more open forest mosaic than at L. Los Niños. Trees become sparser in progressively drier settings to the east. Lower treeline is characterized by a mosaic of woody taxa (e.g., *N. pumilio*, *N. antarctica*, *Schinus*, *Berberis*, Ericaceae) and grassland (dominantly *Festuca*). Farther east is grass-shrub steppe, which is characterized by a matrix of bare soil and xerophytic taxa, including cushion shrubs (e.g., *Mulinum*, *Adesmia*), tussock grasses (e.g., *Stipa*, *Poa*) and herbs (e.g., Asteraceae).

2.2. Field and laboratory methods

A modified Livingstone piston corer was used to take sediment cores from the center of L. Los Niños (LNL09D) and L. La Pava (LP09A). Due to short recovery of the LNL09D core, we collected two additional cores (ML09A and MLN09B) from the fen located at the northwest margin of the lake. All sediment cores were wrapped in plastic wrap and aluminum foil and transported to LacCore Facility, University of Minnesota, where they were split into a working half and an archive, described and photographed. Weight loss after ignition at 550° and 900°C of 1 cm³ samples was undertaken at 1.5-cm intervals and used to estimate the organic and carbonate content of the sediment, respectively (Dean, 1974). Magnetic susceptibility (SI) was measured at 1-cm contiguous intervals in LNL09D, MLN09A and MLN09B cores to assess changes in allochthonous sediment input (Gedye et al., 2000) and aid in the correlation of the cores. Fractional porosity and resistivity (Ohm m⁻¹) were used as indicators of lithology changes in LNL09D and MLN09B cores. All cores were subsampled and archived at the Montana State University Paleoecology Laboratory.

Chronologies were developed from a series of AMS radiocarbon dates obtained from samples of non-calcareous sediment and calibrated with the ShCal13 Southern Hemisphere calibration curve (Hogg et al., 2013; Table 1). Age-depth models were constructed by explicitly combining the probability distribution of each calibrated date and prior expectations about the sediment accumulation rate and its variability through time (Bacon 2.2; Blaauw and Christen, 2011; Table 2; Fig. 2). On the assumption that tephra layers were deposited in a very short span of time, core depths were adjusted by removing ash layers ≥1 cm in thickness prior to the development of the chronologies. These adjusted depths were employed in the development of the age model, but true depths (i.e., including tephra units) are used to describe the results.

Pollen preparation followed standard techniques, treating 1-cm⁻³ sediment samples from cores LP09A and LNL09D (38 to 118 cm depth) and MLN09A (102 to 789 cm depth) at 5- and 10-cm intervals with hydrochloric and hydrofluoric acids and acetolysis and mounting the residues in glycerine (Faegri and Iversen, 1989). Over 70 pollen types were identified at 500 and 1250x magnification with counts ranging between 200 and 400 grains per sample. Terrestrial pollen percentages were calculated based on the total sum of trees, shrubs and herbs. Excluded from the terrestrial sum were fern allies (Polypodiaceae, *Lycopodium*, *Hymenophyllum*), fen taxa (Cyperaceae, *Escallonia*) and aquatic taxa (*Isoetes*, *Botryococcus*, *Pediastrum*, *Myriophyllum*, *Typha*). *Azorella* was also excluded from the pollen sum because its values were highly erratic and related to local disturbance.

Pollen taxa were plotted as a function of time (cal yr BP) with Tilia 2.0.38. *Nothofagus dombeyi*-type is largely attributed to *N. pumilio* and *N. antarctica*; *Misodendrum* is a mistletoe, parasitic on *Nothofagus*. ‘Other rainforest taxa’ includes pollen from *Hydrangea*, *Eucryphia*/*Caldcluvia*-type, Myrtaceae, *Weinmannia*, *Coriaria*, *Drimys*, *Pseudopanax*, *Desfontainea* and *Azara*. *Schinus*, *Lomatia*-type, *Embothrium*, *Ribes*, Verbenaceae, Rhamnaceae, *Berberis* and *Ephedra* are grouped into the ecological unit ‘Other shrubs’. ‘Other steppe herbs’ includes *Armeria*, Caryophyllaceae (*Stellaria*-type), Amaranthaceae subfam. Chenopodioideae, *Gomphrena*, Calyceraceae (*Boopis*-type), *Oreopulus*, *Ovidia*, Solanaceae, *Muhlenbeckia*-type, *Phacelia*, *Viviana*); and ‘Wetland taxa’ corresponds to Ranunculaceae, Brassicaceae, *Gentiana*, *Valeriana*, *Gunnera*, Lamiaceae, *Primula farinosa*-type, *Sisyrinchium*. The diagrams were zoned by visual inspection to aid in the description of the stratigraphic changes.

We explored regional spatial and temporal patterns in vegetation with modified isopoll maps. Given that our interest is the latitudinal evolution of vegetation, standard isopoll maps (i.e., line figures showing sites with the same amount of a given pollen type as a function of latitude and longitude) were modified to display arboreal pollen percentages from 12 published sites at/near the forest/steppe ecotone (including L. Los Niños and L. La Pava; Table 3) as a function of time and latitude. Arboreal pollen was calculated as the sum of all arboreal pollen percentages and minmax-transformed to account for differences in longitude among sites. The modified isopoll map was developed by interpolating the transformed arboreal pollen percentages at each site to a grid defined by time and latitude (Akima, 1978).

Microscopic charcoal particles were tallied as a routine part of the pollen analysis. The number of particles <100 microns in diameter (labeled 'Microscopic charcoal') was calculated as a percentage of the terrestrial pollen sum. These charcoal data are interpreted as a general record of fire activity through time, with no indication of source area or other fire characteristics (Whitlock and Larsen, 2001).

In order to obtain a local high-resolution fire reconstruction, charcoal particles >125 microns in diameter (i.e., macroscopic charcoal) were extracted from contiguous 1-cm thick samples in the MLN09B and LP09D cores following the sieving methods of Whitlock and Larsen (2001). Macroscopic charcoal concentrations were converted to charcoal accumulation rates (CHAR; particles $\text{cm}^{-2} \text{yr}^{-1}$) and interpolated to their median temporal resolution. A locally weighted scatterplot smoother (LOWESS) was used to separate the slowly varying long-term trends in CHAR (i.e., background CHAR) from the high-frequency component of the time series (i.e., positive residuals of the model; Higuera et al., 2009). Gaussian mixed models were fit to the positive residuals of the model at 1000-year windows in order to locally identify exceptionally

large CHAR values. Values that exceeded the 95th percentile (i.e., charcoal peaks) were tested for significance with a Poisson distribution and interpreted as local fire episodes (i.e., fire events occurring within the time span of the peak). Local fire episodes were summarized as fire-episode frequency (fire episodes 1000 years⁻¹). Unless indicated otherwise, all analyses and figures were performed with R programming language (R Core team, 2015).

3. Results

3.1 Chronology

3.1.1. L. Los Niños

Two radiocarbon dates were employed in the development of the age-depth model from the lake core LN09D, while the chronologies for fen cores MLN09A and MLN09B were based on six and eight radiocarbon dates, respectively (Tables 1 and 2). In all cases, the age-adjusted depth relationship was relatively linear (Fig. 2), resulting from quite stable sedimentation rates ranging from 0.0045 to 0.0070 cm² yr⁻¹ in the lake core and from 0.035 to 0.075 cm² yr⁻¹ in both cores from the bog (Figs. 3 and 4). Interpretation of LN09D core was limited by the slow sediment accumulation rates and large uncertainties in the estimated sediment age. Our analysis mainly focused on the fen cores MLN09A and MLN09B, which have basal ages of 17,560±90 and 17,720±100 cal yr BP.

3.1.2. L. La Pava

The chronology of L. La Pava was based on seven radiocarbon dates from the core LP09B (Tables 1 and 2). The age-depth relationship resembled an exponential model with lower

sedimentation rates on the top of the core (0-170 cm adjusted depth; $0.03\text{-}0.045\text{ cm}^2\text{ yr}^{-1}$) and faster accumulation towards the bottom ($0.045\text{-}0.085\text{ cm}^2\text{ yr}^{-1}$; Figs. 2 and 6). The high temporal resolution of the sediment and overall reduced uncertainties of the model make of this core an excellent repository of environmental change. The basal age is estimated to be $14,230\pm 70$ cal yr BP.

3.1. Lithology

3.1.1. L. Los Niños fen cores: MLN09A and MLN09B.

Five lithologic units were identified in the MLN09B fen core (Fig. 3a). The basal unit (Unit 1: 842-824 cm depth; 17,720-17,350 cal yr BP) was composed of inorganic dark gray clay. High magnetic susceptibility suggests that sediments represent a period of allochthonous deposition into the lake. Unit 1 was overlain by olive-brown laminated medium-detritus gyttja (Unit 2: 824-576 cm depth; 17,350-12,150 cal yr BP). A pronounced decline in magnetic susceptibility at the base of Unit 2 was probably the result of lower allochthonous input and rising lake production. The laminations as well as the high variability in sediment resistivity and porosity in Unit 2 point to periodic changes between organic and inorganic sediment sources. Dark fine-detritus gyttja and significantly lower resistivity characterized Unit 3 (576-463 cm depth; 12,150-8220 cal yr BP), likely due to increased lake production at the beginning of the Holocene. Unit 4 (463-200 cm depth; 8220-2450 cal yr BP) featured subunits of decomposed sedge peat alternating with diatomaceous fine-detritus gyttja. Between 200 and 210 cm depth was a pumiceous tephra layer that displayed the highest magnetic susceptibility of the core, as well as very low sediment resistivity and fractional porosity. The overlying unit (Unit 5: 200-0 cm depth; 2450 cal yr BP to present) consisted of peat. Correlation between the two cores was

based on alignment of the radiocarbon chronologies that were developed independently. Additional volcanic ash layers were identified in the MLN09B core at 740-741 and 832-835 cm depth (removed in the age-adjusted depth model). The same lithological units (Fig. 3b) and ash layers were observed in the MLN09A core, also taken from the fen surface.

3.1.2. L. Los Niños lake core: LNL09D

LNL09D was divided into three lithologic units (Fig. 4). Unit 1 (140-128 cm depth; 22,510-20,380 cal yr BP) consisted of grayish brown gyttja with peat layers, which appeared as peaks in the organic content of the sediment. A decrease in sedimentation rate marks the transition to Unit 2 (128-45 cm depth; 20,380-10,410 cm depth). This section featured light brown gyttja with laminations and highly variable sediment porosity, resistivity, organic matter and carbonate content, suggesting an unstable depositional environment. The uppermost unit (Unit 3: 45-0 cm depth; 10,410-(-59) cal yr BP) was characterized by relatively stable values of magnetic susceptibility, resistivity and organic matter content. All these parameters, however, had extreme values between 20 and 33 cm depth, where we identified a pumiceous tephra layer. Additional ash layers were observed at 0-1.5, 73-74.2, 80-81, and 118-136.7 cm depth, and removed to develop the age-adjusted depth model. The uppermost ash layer likely comes from the 2008 explosive eruption of Volcán Chaitén.

3.1.3. L. La Pava core: LP09A

Two lithologic units were observed in LP09A (Fig. 5). Sediments from 480 to 461 cm depth (Unit 1: 14,230-13,900 cal yr BP) were composed of grayish brown clay featuring high magnetic susceptibility. Unit 2 (461-0 cm depth; 13,900-(-59) cal yr BP) was characterized by fine-detritus gyttja and an upward trend towards decreased magnetic susceptibility and higher

organic content, consistent with increased lake productivity. A sharp increase in carbonate content was observed at 160 cm depth (2460 cal yr BP). Tephra layers were present at depths of 120-127, 177-181, 248-250, 263-265, 351-352, 357-358 cm; these units were removed in the development of the age-adjusted depth model.

3.2. Pollen and charcoal records

Records from L. Los Niños (Fig. 6) and L. La Pava (Fig. 7) show a comparable history of vegetation development. Pollen was preserved in sufficient quantity in the MLN09A core to a depth of 752 cm in the 842 cm long core. The extrapolated depth of the bottommost pollen sample is $16,800 \pm 270$ cal yr BP. In the LP09A core, pollen preservation was good to 443 cm depth in the 480 cm long core, and the basal pollen sample had an extrapolated age of $13,300 \pm 70$ cal yr BP.

3.2.1. L. Los Niños

The L. Los Niños record was divided into seven pollen zones. Zone LN-1 (752-665 cm-depth; 17,000-15,500 cal yr BP) was dominated by non-arboreal taxa, such as Poaceae, Asteraceae, Ericaceae (mostly *Empetrum*) and steppe and wetland herbs in percentages between 10 and 20%. Pollen of steppe taxa, including *Acaena*, *Koenigia*, *Plantago*, *Ovidia* and *Azorella*, suggest areas of disturbance and bare ground. *Nothofagus dombeyi*-type was found at levels between 10 and 20%, consistent with the presence of trees, at low densities, in the region. High amounts of shallow-water algae (e.g., *Pediastrum*, *Botryococcus*) indicate a productive lake. Very low CHAR (<0.1 particles $\text{cm}^{-2} \text{yr}^{-1}$; Fig. 8) and low values of microscopic charcoal imply that fires were negligible at both the watershed and regional scales. The environment resembled a present-day heath-steppe as found in southeastern Patagonia (Mancini, 2007). In such settings,

267 *Empetrum rubrum*-dominated communities occur as heathland, often growing on south-facing
268 slopes within the moister Magellanic grass-dominated steppe (Collantes et al., 1999).

269 Zone LN-2 (665-595 cm-depth; 15,500-14,200 cal yr BP) continued to be dominated by
270 non-arboreal taxa. Poaceae increased from 20 to 40%, as did Asteraceae (up to 20%). Ericaceae
271 decreased from 20% to <5%, and *Nothofagus dombeyi*-type declined to between 5 and 10%.
272 Wetland taxa persisted at similar values as before. Increased Asteraceae and Poaceae percentages
273 imply denser and more mesic grass-dominated steppe vegetation. Macroscopic and microscopic
274 charcoal values were similar to those of the previous zone, implying no significant changes in
275 fire regime.

276 Zone LN-3 (595-560 cm-depth; 14,200-13,400 cal yr BP). *Nothofagus dombeyi*-type
277 percentages increased to 60%, somewhat less than present-day values but significantly more than
278 before. Ericaceae increased to over 10%, while Poaceae, Asteraceae and other steppe herbs
279 decreased. Disturbance indicators, including *Acaena*, *Azorella*, *Koenigia* and *Plantago*, declined.
280 This assemblage suggests conditions comparable to lower treeline in southern Patagonia
281 (Mancini et al., 2012). Microscopic and macroscopic charcoal values did not change from those
282 of the previous zone.

283 Zone LN-4 (560-471 cm-depth; 13,400-11,500 cal yr BP). *Nothofagus dombeyi*-type
284 percentages substantially decreased to between 50 and 40%, Ericaceae values persisted at 10%,
285 and Poaceae and Asteraceae values increased to 30 and 10%, respectively. *Podocarpus*
286 abundance rose to between 10 and 20%. Apparently, the forest became more open than before,
287 which resulted in increased proportions of *Podocarpus* pollen, which was likely transported

288 long-distance from rainforests to the west. Increasing levels of CHAR and high values of
289 microscopic charcoal point to rising levels of biomass burning during this period.

290 Zone LN-5 (471-280 cm-depth; 11,500-5800 cal yr BP). *Nothofagus dombeyi*-type
291 increased to 80%, while pollen of rainforest taxa and Poaceae decreased each to <10%. Overall,
292 the forest became more closed than before, with arboreal pollen values similar to those of the
293 present. Rising levels of *Isoetes* suggest higher lake levels, consistent with effectively wetter
294 conditions. CHAR gradually declined to reach a local minimum at ca. 8500 cal yr BP (<0.1
295 particles cm⁻² yr⁻¹), increased between 8500 and 7000 cal yr BP (to <0.7 particles cm⁻² yr⁻¹) and
296 declined afterwards. This pattern suggests that fire activity, particularly fire size, oscillated on
297 millennial time scales.

298 Zone LN-6 (280-65 cm-depth; 5800-800 cal yr BP). Although *Nothofagus dombeyi*-type
299 continued to dominate the zone (80%), high percentages of *Azorella* and *Escallonia* in several
300 levels provide evidence of intermittent disturbance. Cyperaceae percentages increased, while
301 aquatic taxa decreased, indicating markedly lower lake levels than before. Several periods of
302 high microscopic charcoal, with a peak at 3000 cal yr BP, and high and variable macroscopic
303 charcoal values suggest that fires were common. The maximum fire-episode frequency was
304 reached between 5000 and 3000 cal yr BP (2 to 2.6 fire episodes 1000 yr⁻¹).

305 Zone LN-7 (65-30 cm-depth; 800-100 cal yr BP). *Nothofagus dombeyi*-type pollen
306 remained high (80%) and Poaceae decreased to <5%. High levels of *Azorella* are consistent with
307 intervals of disturbance, especially at the onset of the zone. Higher-than-before amounts of
308 *Isoetes* indicate a deepening of the lake. No pollen of European invasive plants (e.g., *Rumex*,
309 *Ambrosia*) was found suggesting that the last century of European land-use was not preserved in

the core. The absence of the most recent assemblage is not surprising given the low sedimentation rates in the lake core. The macroscopic and microscopic charcoal data from the lake core lack the temporal resolution to reconstruct the fire history of this zone.

3.2.2. L. La Pava

The record from L. La Pava was divided in four zones. In Zone LP-1 (430-398 cm depth; 13,200-11,500 cal yr BP), *Nothofagus dombeyi*-type pollen gradually increased from initial values of 20 to 70% at the top of zone. Woodland shrub taxa, Ericaceae, disturbance taxa (e.g., *Plantago*, *Acaena*) and other steppe taxa, and Poaceae steadily decreased within the zone. *Pediastrum* and fern allies were present, indicating low water levels. CHAR displayed a trend similar to that of *Nothofagus dombeyi*-type, reaching values up to 0.18 particles cm⁻² yr⁻¹ at the top of the zone (Fig. 8). Comparison with modern pollen samples (Mancini et al., 2012) suggests an initial period of heath-steppe that was gradually replaced by forest.

Zone LP-2 (398-342 cm depth; 11,500-8700 cal yr BP). *Nothofagus dombeyi*-type values fluctuated between 50 and 70%, and *Misodendrum* pollen in low but steady amounts confirms the local presence of *Nothofagus*. *Podocarpus* was present throughout this zone between 5 and 10%. Poaceae values fluctuated between 5 and 10%, suggesting millennial oscillations between closed and open forest. Changes in the abundance of *Pediastrum* and especially *Isoetes* indicate greater fluctuations in water levels than before, providing evidence of variable precipitation/evaporation. Specifically, *Pediastrum* species are generally abundant in shallow, warmer waters (Komarek and Jankovska, 2001), while *Isoetes* is found in cooler and acidic waters (Pietsch, 1991). Microscopic charcoal had high values, especially after 11,000 cal yr BP. Macroscopic CHAR levels did not change significantly from previous low values. Evidence of

high fire-episode frequency associated with fluctuating non-arboreal pollen percentages suggests that fires helped maintain a mosaic of forest and grassland.

Zone LP-3 (342-178 cm depth; 8700-3000 cal yr BP). *Nothofagus dombeyi*-type pollen was dominant, reaching percentages of 85%, indicating a period of stable, closed forest. Long-distance *Podocarpus* pollen accounted for <5% of the terrestrial pollen. These pollen percentages are comparable to those from present-day *Nothofagus pumilio* forests on the eastern side of the Andes (Mancini et al., 2012). Macroscopic charcoal data indicate that local fires gradually increased to a maximum postglacial level at 5500 cal yr BP (3.1 fire episodes in 1000 years) and decreased thereafter. Increased amounts of *Isoetes* suggest a deepened or less productive lake consistent with increased precipitation.

Zone LP-4 (178-8 cm depth; 3000-50 cal yr BP). *Nothofagus dombeyi*-type continued to have high, albeit slightly fluctuating levels (80-94%). Spores of aquatic taxa, especially *Isoetes*, are abundant, indicating relatively high water levels. The high and fluctuating levels of macroscopic and microscopic charcoal along with increased fire-episode frequency after 2800 cal yr BP (to 2.4 fire events 1000 years⁻¹) suggest that fires were of varying size and magnitude but occurred regularly.

4. Discussion

4.1. Paleoenvironmental history of L. Los Niños and L. La Pava

The early postglacial environment prior to 14,300 cal yr BP was largely treeless and dominated by heath-steppe taxa characteristic of open ground and disturbance. The sparse

vegetation cover is consistent with unstable slopes, poor soil development, and low lake productivity suggested by high magnetic susceptibility, variable sediment porosity, resistivity, organic matter and carbonate content. Fires were virtually absent at this time, likely due to the discontinuous fuel cover and/or low probability of ignition. The environment would have resembled the present-day heath-steppe found today in wind-swept regions of south Patagonia (Mancini, 2007). Based on modern climate-vegetation comparisons, about 200 mm of annual precipitation would have been necessary to support these plant communities (Mancini et al., 2012).

Between 14,300 and 13,200 cal yr BP, the L. Los Niños record documents the establishment of open forest, and vegetation comparable to present-day steppe/forest ecotone (i.e., lower treeline). A shift in vegetation towards a more open landscape and effectively drier conditions between 13,200 and 11,500 cal yr BP is evidenced by the decline in pollen percentages of *Nothofagus* and rise in those of steppe taxa and distant rainforest taxa. Decreased moisture availability would have precluded seedling establishment, allowing the expansion of light-demanding non-arboreal taxa. Charcoal data do not reveal any changes in the fire regime in association with this steppe advance. The L. La Pava record began at 13,200 cal yr BP, and pollen data suggest slowly increasing forest cover with no evidence of a dry interval prior to 11,500 cal yr BP. The charcoal record, however, indicates a prominent fire period between 12,800 and 11,500 cal yr BP, consistent with aridity.

After 11,500 cal yr BP, *Nothofagus* forest, likely composed primarily of *N. pumilio* with some *N. antarctica*, developed at both sites. Pollen data suggest that the forest was as closed as it was at the time of European settlement and that early-Holocene moisture levels were similar to those at present. Rising lake levels are evidenced by high percentages of aquatic taxa and

increasingly more organic sediments at both sites. The onset of effectively wetter conditions than before would explain the reconstructed vegetation and lake-level changes.

Despite the similarities, forest cover at L. Los Niños was apparently denser or more extensive than that at L. La Pava. Heterogeneous tree abundance may be explained by the different elevations of the two sites. L. Los Niños, located at 1050 m elevation, is about 400 m higher than L. La Pava and has better developed soils at present. Due to the orographic effects of the Andes on atmospheric circulation, it is likely that precipitation was higher at L. Los Niños than at L. La Pava, favoring greater tree establishment at the higher site. Additionally, the charcoal data suggest more frequent fires in the more open low-elevation L. La Pava watershed. Biophysical feedbacks associated with effectively drier conditions, poor soils and frequent burning at L. La Pava would have limited seedling survival and helped maintain more open vegetation than at L. Los Niños.

At 8500 cal yr BP, the charcoal record indicates a near-absent fire activity at both sites. At L. La Pava, the absence of fires occurred concurrently with the development of dense *Nothofagus* forests. Forest expansion coupled with reduced fire activity during the Early Holocene has been registered on both sides of the Patagonian Andes and attributed to the onset of cooler and/or effectively wetter conditions than before (e.g., Moreno, 2004; Markgraf et al., 2007; Whitlock et al., 2007; Abarzúa and Moreno, 2008; Wille and Schäbitz, 2009). These climate conditions also supported the Neoglacial advance of mountain glaciers in the mid-latitudes of South America (Porter, 2000; Douglass et al., 2005).

Between 5800 and 3000 cal yr BP, the charcoal time series reveal a sharp increase in fire frequency at both sites. This shift in the fire regime was likely a response to increased interannual climate variability (Moy et al., 2002), and possibly to rising human populations in some watersheds. In the absence of archeological data, separating the influence of people and climate on increased fire activity is not feasible. Pollen data from L. Los Niños suggest that disturbance-adapted taxa (e.g., *Azorella*, *Escallonia*) colonized the watershed but no sign of vegetation change is evident at L. La Pava. It is possible that fires at L. La Pava were not sufficiently intense to kill old *Nothofagus* trees or restrict seedling establishment (e.g., Behling and Pillar, 2007). Alternatively, fires could have favored the expansion of fire-resistant and resilient *N. antarctica* at expense of *N. pumilio*. Deciding between these explanations is not currently possible, given the inability to differentiate the pollen of the two *Nothofagus* species.

During the last 3000 years, L. Los Niños and L. La Pava watersheds were dominated by *Nothofagus* forests, which were likely favored by higher moisture availability. The abundance of palynomorphs from aquatic taxa at L. La Pava suggests higher lake levels than before, and this evidence as well as a rise in carbonate content in the sediments is consistent with increased effective moisture. A similar rise in carbonate deposition in sediment records from Torres del Paine National Park (51°S; 72°W) has been associated with enhanced contribution of alkaline groundwater as a result of increased precipitation or aquifer recharge at the onset of Neoglaciation (Larson et al., 2008).

High levels of microscopic charcoal at both sites indicate increased burning in the region in the last 3000 years. The macroscopic charcoal data from L. La Pava also suggest that, at the local scale, fire episodes were frequent and of large magnitude after 3000 cal yr BP. This late-Holocene increase in fire activity is noted at many sites in southern Patagonia and attributed to

greater climate variability with the strengthening of ENSO and/or to more anthropogenic burning associated with the increase in human populations (e.g., Haberle and Bennett, 2004; Whitlock et al. 2007; Moreno et al., 2009; Villa-Martínez and Moreno, 2009). Given that this increase occurs across a moisture gradient from extremely wet forests in the Chonos Archipelago of Chile (Haberle and Bennett, 2004) to our sites along the forest-steppe border, increases in interannual or interdecadal variability seem to be the primary explanation.

4.2. Paleoenvironmental history of the eastern flanks of the Andes

Paleoclimate model simulations suggest that the Southern Westerlies were located at about lat. 41°S during the late-glacial period and were substantially weaker than at present as a result of a steepened Pole-to-Equator temperature and pressure gradients (Rojas et al., 2008). These large-scale features are associated with low annual insolation (Alder & Hostetler, 2015) and low sea-surface temperatures along the Chilean coast (ca. 6°C lower than at present; Lamy et al., 1999). The northward position in storm-track position and general weakening of the Southern Westerlies would have led to drier-than-present conditions in both summer and winter throughout Patagonia. A substantial number of pollen records are available along the eastern foothills of the Andes between lat. 41 and 52°S to validate the model output (Laguna Huala Hué: Iglesias et al., 2012a; Laguna Zeta, Lago Theobald: Iglesias et al., 2014; Cordón Serrucho: Markgraf et al., 2013; Lago Pollux: Markgraf et al., 2007; Cerro Frias, La Tercera: Sottile et al., 2011; Brazo Sur: Wille and Schäbitz, 2009; Rio Rubens: Huber et al., 2004; Markgraf & Huber, 2010; Lago Cardiel: Markgraf et al., 2003; L. Guanaco: Moreno et al., 2009; Potrok Aike: Wille et al., 2007). These records indicate that treeless conditions and bare-ground steppe vegetation

characterized the landscape after deglaciation as early as 18,000 cal yr BP (Glasser et al., 2006). East of the Andes, conditions were likely too dry to support forest cover, and the lack of fuel availability and continuity along with limited natural ignition led to a near-absence of fires.

North of lat. 43°S, *Nothofagus* pollen percentages rose during the late-glacial period at L. el Trébol, Cordón Serrucho, and L. La Zeta, reflecting the expansion of *N. dombeyi* and/or *N. antarctica* populations (Fig. 9). Forest development is generally attributed to an increase in effective moisture but the timing of forest expansion was asynchronous with no clear latitudinal pattern. Pollen data suggest the presence of an open *Nothofagus* forest at 16,500 cal yr BP at L. Mascardi (lat. 41°S, Bianchi and Ariztegui, 2012), at 15,000 cal yr BP at Cordón Serrucho (lat. 41°46'S, Markgraf et al., 2013) and not until 14,000 cal yr BP at L. el Trébol (lat. 41°S, Whitlock et al., 2006). Asynchronous forest expansion could have been caused by the specific location of glacial refugia, which were likely small and dispersed (Premoli et al. 2012), and/or differences in microclimate or soil characteristics (e.g., Iglesias et al., 2012).

In contrast to relatively early forest establishment east of the Andes in the northern latitudes, south of lat. 45°S, *Nothofagus* was present in low amounts in many late-glacial records by 14,000 cal yr BP but did not reach present-day percentages until after 7000 cal yr BP (Fig. 9; Huber et al., 2004). By 16,000 cal yr BP, grass-dominated steppe expanded at sites south of lat. 45°S, and cores from southern Patagonia register repeated isotope fluctuations as well as oscillations between heath (e.g., *Empetrum*) and disturbance taxa (e.g., *Koenigia*, *Plantago*) versus grass and wetland taxa. These isotope and pollen oscillations in the southern sites imply overall low but largely variable levels of effective moisture between 16,000 and 12,000 cal yr BP (Pendall et al., 2001; Markgraf and Huber, 2010).

At lat. 44°S, *Nothofagus* forests established at L. Los Niños at 14,200 cal yr BP and

closed forests dominated both L. Los Niños and L. La Pava by 11,500 cal yr BP, representing an intermediate situation between the northern and southern response. West of the Andes, the Chonos Archipelago (44°S; 73°W) was ice-free by 16,000 cal yr BP (Denton et al., 1999). Recently deglaciated landscapes were rapidly colonized by heath, and *Nothofagus-Pilgerodendron-Podocarpus* forests were present in the area by 14,200 cal yr BP (Haberle and Bennett, 2004). The synchronous expansion of mesophytic vegetation at lat. 44°S west and east of the Andes suggests that the change was driven by a large-scale increase in effective moisture.

Some pollen records from northern Patagonia with sufficient temporal resolution register a cold dry reversal towards the end of the late-glacial period. Based on pollen and lithologic changes at two sites at lat. 41°S, Hajdas et al. (2003), defined the period between ca. 13,300 and 11,870 cal yr BP as the Huelmo-Mascardi Cold Reversal. Independent proxies at other sites, including diatoms, chironomids and stable isotopes, suggest that the late-glacial/early Holocene transition was characterized by pronounced environmental fluctuations, but the timing of these fluctuations is asynchronous from site to site (Pendall et al., 2001; Huber et al., 2004; Wille et al., 2007; Massaferro et al., 2009; Markgraf and Huber, 2010; Iglesias et al., 2012a). At L. La Zeta (latitude 43°S), for example, a dramatic decline in *Nothofagus* pollen and rise in Poaceae and Asteraceae occurred between 13,900 and 12,930 cal yr BP (Iglesias et al., 2014). At L. Mascardi (latitude 41°S), a comparable change took place between 13,300 and 11,870 cal yr BP (Bianchi and Ariztegui, 2012), whereas no significant shifts in plant communities were observed at nearby L. el Trébol (Whitlock et al., 2006), L. Huala Hué (Iglesias et al., 2012a) or Cordón Serrucho (Markgraf et al., 2013). The heterogeneous environmental response suggests that either detection of these environmental fluctuations was constrained by the sensitivity of the proxy records (e.g., the relatively low pollen diversity) or the magnitude of the environmental changes

was small relative to the fundamental niche of the dominant species.

The early establishment of *Nothofagus* forests in northern Patagonia as compared to the later forest expansion in the south likely reflects shifts in the location and/or intensity of westerly storm tracks (Fletcher and Moreno, 2011). Model simulations suggest that storm tracks lay at lat. 41°S and were weaker than at present in the late-glacial period. As a result, moisture levels were sufficient for early forest establishment in the northern latitudes of the transect, but not in the south. Increased winter cyclone density (i.e., storm activity) and forest establishment at lat. 44°S occurred at ca. 14,300 cal yr BP, after forest expansion in the north. This time-transgressive pattern was likely driven by the poleward migration of the Southern Westerlies (Toggweiler, 2009) and progressively fewer polar air mass incursions (Heusser, 2003) associated with increasing annual insolation. During the period, steppe vegetation is recorded in all records south of lat. 45°S and fire frequency was high (Huber et al., 2010). By 10,000 cal yr BP, the Southern Westerlies were probably south of their present position or weakened (Fletcher and Moreno, 2011; Moreno et al., 2011), leading to dry conditions at all latitudes.

North of lat. 43°S, the development of *Nothofagus* forests was accompanied by an expansion of shrubs, suggesting that woody taxa including Rhamnaceae, *Maytenus* and *Berberis* constituted either the understory of the *Nothofagus* forest or more likely, a discrete shrubland at the eastern edge of the forest (Whitlock et al., 2006; Iglesias et al., 2012a; Iglesias et al., 2012b). Regionally, high macroscopic charcoal levels indicate that fires were promoted by increasing woody biomass accumulation and amplified by higher-than-present winter and annual insolation. Both factors would have led to an earlier onset of the fire season (Iglesias and Whitlock, 2014). Fires were associated with fluctuations in the relative abundance of shrubs and trees at all sites (Huber et al., 2004; Whitlock et al., 2007; Holz et al., 2011).

At lat. 44°S, L. Los Niños had lower fire activity than at L. Pava, and the difference is attributed to its higher elevation and slightly cooler setting. This same difference in fire activity occurred between L. Mosquito and L. Trébol (Whitlock et al., 2006) and L. Mosquito and L. Cóndor (Iglesias et al., 2012b) in northern Patagonia as a result of west-to-east moisture differences. A similar pattern was also observed in Tierra del Fuego at lat. 54°S, with higher levels of burning at high-elevation Paso Garibaldi than at the more-maritime Harberton site (Markgraf and Huber, 2010). This spatial heterogeneity reinforces the idea that subtle variability in moisture, arising from elevational position or east-west location, has a profound effect on biomass accumulation, fuel flammability, and probably ignition. These factors ultimately create different fire regimes and plant communities in close proximity.

Comparison of the charcoal records indicate that fire activity remained relatively high until between 8000 and 5000 cal yr BP at L. La Pava and other sites to the south (lat. 45 to 52°S; Huber et al., 2004). Fire activity was low at L. Los Niños between 11,000 and 8000 cal yr BP, and increased to reach a local maximum at 7000 cal yr BP. High fire activity in the early and middle Holocene is also characteristic of the Chonos Archipelago (44°S; 73°W, Haberle and Bennett, 2004), where it likely promoted the establishment of *Tepualia* and *Weinmannia* as important disturbance-adapted elements of the forest.

Changes in vegetation composition in the early Holocene have also been registered north and south of lat. 44°S. Oscillations in vegetation composition at Vega Ñandú (51°S, 72°S; Villamartín and Moreno, 2007) were possibly driven by climate variability and/or fire. Similarly, paleoenvironmental records from northern Patagonia suggest trade-offs between trees and shrubs occurring on millennial time scales as early as 10,000 cal yr BP. Pollen data from seven sites between lat. 41° and 43°S, for example, reveal that shrubs expanded at expense of trees between

ca. 10,000-8000 cal yr BP, ca. 7000-6300 cal yr BP, and ca. 6000-5500 cal yr BP, whereas trees were dominant at ca. 8000-7000 and 6300-6000 cal yr BP (Iglesias et al., 2014). Vegetation fluctuations on centennial time-scales have also been inferred for the early to middle Holocene and associated with periods of erosion at L. Huala Hué (Iglesias et al., 2012a), L. Cóndor (Iglesias et al., 2012b), Cordón Serrucho (Markgraf et al., 2013), L. La Zeta and L. Theobald (Iglesias et al., 2014).

A different paleoenvironmental history has been described from Lago Cardiel (lat. 49°S), located in the plains east of the Andes. There, an increase in moisture from ca. 8000 to 6000 cal yr BP has been inferred from rapidly rising lake levels (Markgraf et al., 2003; Gilli et al., 2005a; Markgraf and Huber, 2010), which would have been caused by an intensified easterly precipitation regime. Present-day precipitation occurs east of the Andes when the westerly winds are weak and allow Atlantic moisture to reach the Patagonian plains (Schneider et al., 2003; Garreaud et al., 2013; Agosta et al., 2015). Thus, weakened Southern Westerlies in the early Holocene (as reconstructed from records from throughout the Southern Hemisphere; e.g., McGlone and Meurk, 2000; Anselmetti et al., 2009; Waldmann et al., 2010; Moreno et al., 2011) were likely associated with dry conditions in the Patagonian Andes and increased humidity in the plains.

By the middle Holocene, the establishment of *Nothofagus* forests south of lat. 45°S is consistent with increased precipitation in the southern latitudes (Fig. 9). Climate models suggest that the core of the Southern Westerlies reached its present position (lat. 50°S) at this time as a result of a stronger pole-to-Equator pressure gradient than before and a southward migration in the position of the southeastern Pacific Subtropical High Pressure system (Wagner et al., 2007). Paleoenvironmental records from lat. 55°S validate these results (e.g., Björk et al., 2012).

Increasing summer insolation and decreasing winter insolation in the middle and late Holocene led to stronger storm tracks than before (Gilli et al., 2005b). A strengthening of the Southern Westerlies at this time is supported by pollen-based reconstructions of effective moisture on Annkov Island (54°S; Strother et al., 2015) and Torres del Paine (51°S; 71°W; Moreno et al., 2009). Increasing seasonality was associated with interannual variability in sea-surface temperatures and the latitudinal pressure gradient. The Southern Westerlies responded to these seasonal changes by contracting in summer and expanding in winter (Gilli et al., 2005; Lamy et al., 2010). Stronger and variable Southern Westerlies brought greater moisture to southern Patagonia year-round and more moisture north of lat. 45°S in winter (Garreaud et al., 2013).

North of lat. 43°S, higher-than-before effective moisture in the middle and late Holocene promoted an expansion of *Austrocedrus chilensis* and the establishment of the modern mixed forest (Whitlock et al., 2007; Iglesias et al., 2012a and b). Superimposed on this trend towards increased effective moisture, high frequency climate variability has been inferred from paleoenvironmental records from lat. 41 to 55°S. Our results show increased fire activity at both L. Los Niños and L. La Pava after ca. 6000 cal yr BP (Fig. 8). In the modern forest-steppe ecotone, widespread fires tend to follow the switching from wet to dry conditions, given that high effective moisture allows fuel build and desiccation takes place at drier times (Kitzberger et al., 2001). High fire activity at lat. 44°S is thus consistent with increased climate variability.

Centennial-scale oscillations in tree abundance at occurred at all latitudes during the late Holocene (Fig. 9). Between 5000 and 3000 cal yr BP, advances of lower treeline in northern Patagonia are concurrent with reduced tree cover at the southern sites (e.g., 4500-3500 cal yr BP) and vice versa (e.g., 5000-4500; and 3500-3000 cal yr BP). Asynchronous forest expansions may

be explained by latitudinal and seasonal differences in the position of storm tracks from 5000-3000 cal yr BP, which would have led to north-south differences in tree cover along the transect. These out-of-phase oscillations are consistent with centennial-scale cycles of meridional expansions and contractions of the westerly belt (Lamy et al., 2010). A strong northern margin of the Southern Westerlies in winter would have brought precipitation to northern Patagonia at 4500-3500 cal yr BP and the associated weaker core would have resulted in drier conditions in the south. Conversely, the summer-like position of the Southern Westerlies at 5000-4500 and 3500-3000 cal yr BP would explain increased precipitation at lat. 50-55°S and drier conditions in the north.

Synchronous oscillations in the abundance of forest taxa along the latitudinal transect are characteristic of the last 3000 years (Fig. 9). A vegetation reconstruction from the western flanks of the Andes (Laguna Cipreses, 51°S; Moreno et al., 2014) suggests that this period featured 250-year oscillations between cold/wet and warm/dry conditions, which have been attributed to the negative and positive phases of the Southern Annular Mode (SAM). A similar periodicity has been noted in pollen data from the Falkland Islands, where variability in westerly intensity has been ascribed to oscillations in solar irradiance, namely the effects of the de Vries/Suess solar cycle (Turney et al. 2016). Although our data lack the temporal resolution to register these high-frequency changes, our results show peaks in tree abundance throughout the eastern flanks of the Andes at ca. 2800 and 1100 cal yr BP and minimum densities at 2100 cal yr BP. Reduced forest cover from ca. 2500 to 1500 cal yr BP is coeval with La Niña-like conditions in the Pacific Ocean (Moy et al., 2002) and with high solar irradiance (Turney et al., 2016). A tree-ring reconstruction from Tasmania (Cook et al., 1999) suggests that, in the southern hemisphere, higher solar output at the time led to increased summer temperatures (Lüdecke et al., 2015). It is

thus possible that decreased forest cover along the eastern flanks of the Andes was driven by (a) reduced precipitation resulting from weakened Southern Westerlies associated with La Niña-like conditions; and/or (b) lower effective moisture as a consequence of increased evapotranspiration during the warm growing season. SAM is likely to have contributed to climate dynamics during the late Holocene but our data do not allow the detection of its influence on terrestrial systems. Although growing human populations in some watersheds (e.g., Belleli et al., 2003; Podestá et al., 2007; Méndez and Reyes, 2008) could have altered the probability of ignition and the distribution of fuel, a climate forcing seems to be sufficient to explain the vegetation changes observed at the time, especially at the regional scale (e.g., Iglesias and Whitlock, 2014). Archeological data and modeling efforts would help assess the role (if any) of humans in altering pre-European climate-vegetation-fire linkages.

5. Conclusions

Paleoecological data from L. Los Niños and L. La Pava allow the reconstruction of the climate, vegetation and fire history at lat. 44°S and provide an important piece of information for understanding the environmental dynamics on the east side of the Andes from lat. 41 to 52°S. Late-glacial landscapes throughout Patagonia were dry and dominated by heath and steppe taxa. Pollen records from lat. 41 to 44°S show a step-wise evolution from treeless conditions to *Nothofagus* forest in the late-glacial/early Holocene transition. This development was likely favored by increased moisture levels, but the timing was asynchronous, occurring between 16,500 cal yr BP north of lat. 43°S and at 14,000 cal yr at lat. 44°S. The time-transgressive pattern of forestation represents a response to latitudinal shifts and/or changes in strength of the westerly storm tracks following regional ice recession. By 10,000 cal yr BP, the Southern Westerlies were located south of their present position or weakened, favoring drying and high

626 fire activity throughout the Patagonian Andes.

627 The establishment of *Nothofagus* forests south of lat. 45°S at ca. 7000 cal yr BP is
628 consistent with increased precipitation in the southern latitudes. Intensification of the Pacific
629 Subtropical High Pressure system at the time would have allowed the core of the Southern
630 Westerlies to reach its present position (lat. 50°S). Favored by higher effective moisture in the
631 Patagonian Andes, *Nothofagus* forests dominated the 41-52°S latitudinal band during the middle
632 Holocene.

633 Pollen data suggest that the development of modern vegetation, including the
634 establishment of *Austrocedrus* north of lat. 43°S and the advance of lower treeline south of this
635 latitude, took place during the late Holocene. High spatial and temporal variability throughout
636 Patagonia between 5000 and 3000 cal yr BP can be attributed to the onset of ENSO and/or to
637 centennial cycles of contraction and expansion of the Southern Westerlies. These cycles likely
638 resulted in climate conditions of opposite sign at the core (ca. lat. 50°S) and northern border (lat.
639 41°S) of the westerly belt.

640 Synchronous oscillations in the abundance of forest taxa along the eastern flanks of the
641 Andes are characteristic of the last 3000 years. Lower percentages of tree pollen at all latitudes
642 of the 41-52°S latitudinal band from ca. 2500 to 1500 cal yr BP are concurrent with La Niña-like
643 conditions in the Pacific Ocean and with high solar irradiance. It is thus possible that reduced
644 forest cover at the time was driven by (a) decreased precipitation resulting from weakened
645 Southern Westerlies associated with La Niña-like conditions; and/or (b) lower effective moisture
646 as a consequence of increased evapotranspiration during the warm growing season. The
647 influence of SAM or humans is not clearly evident in our records.

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Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

L. Los Niños
V. Markgraf, analyst

Figure 7

L. La Pava
V. Markgraf, analyst

Figure 8

Figure 9

Table 1: Radiocarbon and calibrated dates from L. Los Niños and L. La Pava

Core	Depth (cm)	Lab. no.	Material	Age (^{14}C yr BP)	Age error	Age (cal yr BP; 1 sigma range)
<i>L. Los Niños</i>						
MLN09A	245-246	OS-119277	Bulk sediment	4530	20	5049-5280
MLN09A	460-462	OS-116565	Bulk sediment	11,700	50	13,443-13,548
MLN09A	500-501	OS-119278	Bulk sediment	10,150	50	11,417-11,925
MLN09A	571-573	OS-116564	Bulk sediment	9510	55	10,587-11,053
MLN09A	609-610	OS-119279	Bulk sediment	12,400	70	14,166-14,569
MLN09A	742-743	OS-119280	Bulk sediment	13,500	85	16,057-16,322
MLN09B	36-37	OS-98580	Pollen	2880	25	2881-2980
MLN09B	245-246	OS-98579	Pollen	7200	35	7951-8006
MLN09B	252-253	OS-101100	Bulk sediment	5480	25	6211-6287
MLN09B	365-366	OS-98578	Pollen	10,400	45	12,052-12,389
MLN09B	457-458	OS-98577	Pollen	12,450	55	14,274-14,668
MLN09B	536-537	OS-98583	Pollen	13,500	70	16,074-16,304
MLN09B	550-551	OS-86766	Pollen	13,150	50	15,620-15,845
MLN09B	625-626	OS-98586	Pollen	14,450	75	17,440-17,677
LNL09D	93-94	OS-98584	Pollen	14,650	75	17,675-17,898
LNL09D	95-96	OS-101099	Bulk sediment	14,800	50	17,870-18,041
<i>L. La Pava</i>						
LP09B	54-55	OS-98585	Pollen	770	20	661-677
LP09B	182-183	OS-98587	Pollen	2690	25	2747-2776
LP09B	274-275	OS-98589	Pollen	5040	30	5658-5843
LP09B	315-316	OS-101101	Bulk sediment	6110	30	6864-6983
LP09B	392-393	OS-98590	Pollen	9340	55	10,404-10,581
LP09B	423-424	OS-110940	Pollen	10,600	50	12,434-12,638
LP09B	454-455	OS-98582	Pollen	12,700	65	14,925-15,198

Table 2: Parameters used in the age-depth models from L. Los Niños and L. La Pava

Core	Acc. mean	Acc. shape	Memory mean	Memory strength
<i>L. Los Niños</i>				
MLN09A	20	1.5	0.7	4
MLN09B	20	1.5	0.7	4
LNL09D	200	1.5	0.7	4
<i>L. La Pava</i>				
LP09A	20	1.5	0.5	2

Table 3: Sites discussed in this study

Site	Position	Elevation (m)	Publications
L. el Trébol	41.15°S; 71.32°W	977	Whitlock et al., 2006
L. Padre Laguna	41.38°S; 71.32°W	1280	Iglesias et al., 2012a
L. Huala Hué	41.51°S; 71.58°W	849	Iglesias et al., 2012a
L. Cóndor	42.35°S; 71.29°W	818	Iglesias et al., 2012b
L. Mosquito	42.49°S; 71.39°W	551	Iglesias et al., 2012b
L. La Zeta	42.89°S; 71.35°W	774	Iglesias et al., 2014
L. Theobald	43.48°S; 71.58°W	678	Iglesias et al., 2014
L. Los Niños	44.01°S; 71.29°W	1015	This manuscript
L. La Pava	44.28°S; 71.31°W	731	This manuscript
M. Pollux	45.68°S; 71.84°W	640	Markgraf et al., 2007
Río Rubens	52.08°S; 71.52°W	220	Huber et al., 2004
Haberton	54.53°S; 67.10°W	20	Markgraf, 1993

Figures

Figure 1: Study area and location of the sites discussed in this manuscript. The city of San Carlos de Bariloche and the town of Río Pico are also shown. The dashed line represents the international border between Argentina and Chile. ##Double column##

Figure 2: Age-depth model for a) L. Los Niños LNL09D core, b) L. Los Niños MLN09A core, c) L. Los Niños MLN09B core, and d) L. La Pava LP09A core. The red curve shows the weighted mean age for each depth. Dark and light gray lines depict the more likely age-depth models and 95% confidence intervals, respectively. Blue areas are the probability distributions of the calibrated dates. ##Double column##

Figure 3: Lithology, magnetic susceptibility and sediment accumulation rates for the L. Los Niños cores a) MLN09B and b) MLN09A. Radiocarbon dates, lithologic units and tephra layers (arrows) are indicated. Fractional sediment porosity and resistivity for MLN09B are also shown. ##Double column##

Figure 4: Lithology, magnetic susceptibility, fractional porosity, resistivity, carbonate content, organic matter and sediment accumulation rates for the L. Los Niños lake core LNL09D. Radiocarbon dates, lithologic units and tephra layers (arrows) are shown. ##Double column##

Figure 5: Lithology, magnetic susceptibility, carbonate content, organic matter and sediment accumulation rates for the L. La Pava core LP09A. Radiocarbon dates, lithologic units and tephra layers (arrows) are shown. ##Double column##

Figure 6: Pollen diagram for L. Los Niños core MLN09A; uppermost levels are from MLN09B. ##Double column##

Figure 7: Pollen diagram for L. La Pava LP09A core. ##Double column##

Figure 8: Macroscopic charcoal from L. Los Niños core MLN09B. CHAR and background CHAR are shown in black and red, respectively for a) L. Los Niños and c) L. La Pava. Fire events are represented with '+'. Statistically significant fire events are indicated in black. c and d) Fire event frequency for L. Los Niños and L. La Pava, respectively. ##1.5 column##

Figure 9: Modified isopoll map showing transformed arboreal pollen as a function of latitude and time. Darker shades represent higher minmax-transformed pollen percentages (unitless). The black squares mark the latitude of the sites used in the analysis (from north to south: L. El Trébol, L. Padre Laguna, L. Huala Hué, L. Cóndor, L. Mosquito, L. La Zeta, L. Theobald, L. Los Niños, L. La Pava, M. Pollux, Río Rubens, Haberton), and the arrows indicate forest establishment as proposed by the authors of the original publications. Cycles of contraction/expansion of the Southern Westerlies (SW), La Niña-like conditions and solar irradiance are based on independent proxies (i.e., Lamy et al., 2010; Moy et al., 2002; Turney et al., 2016; respectively). ##Single column##