JOURNAL OF QUATERNARY SCIENCE (2017) ISSN 0267-8179. DOI: 10.1002/jqs.2948

JQS Journal of Quaternary Science QRA Quaternary Research Association

Climate change and resilience of deciduous *Nothofagus* forests in central–east Chilean Patagonia over the last 3200 years

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Received 6 September 2016; Revised 6 February 2017; Accepted 28 February 2017

ABSTRACT: We examine the response of *Nothofagus* forests to climate change and disturbance regimes over the last 3200 years near Coyhaique (45°S), central–east Chilean Patagonia, using fine-resolution pollen and charcoal records from lake sediment cores. Closed-canopy deciduous *Nothofagus* forests have dominated the region with little variation until the arrival of Chilean–European settlers, suggesting a predominance of cool-temperate and wet conditions. Within this state we identify centennial-scale episodes of forest fragmentation, increase in littoral macrophytes and volcanic/paleofire disturbance between 2700 and 3000 cal a BP, 2200 and 2500 cal a BP and over the last ~250 years, which we interpret as intervals with negative hydrologic balance. Natural variability caused little impact on the physiognomy and composition of the vegetation in pre-European time, in contrast to the accelerated shift that started during the late 19th century associated with deforestation, homogenization and synchronization of ecosystem changes at the landscape level, and spread of exotic plant species brought by Chilean and European settlers during a warm/dry interval. The resilience of deciduous *Nothofagus* forests to natural disturbance regimes and climate change was exceeded by large-scale human disturbance since the late 19th century by fire, timber exploitation and livestock grazing. These disturbances caused an ecosystem shift towards artificial meadows and scrublands with frequent high-magnitude fires. Copyright © 2017 John Wiley & Sons, Ltd.

KEYWORDS: human disturbance; *Nothofagus* forests; paleofires; resilience; tephras.

Introduction

The most recent 3000 years, commonly referred to as the Late Holocene, provide an adequate interval to study centennial-scale fluctuations in global climate, including the most recent warming since the mid-19th century associated with globalization of the Industrial Revolution. The onset of this shift, which has been characterized by abundant instrumental and historical records, coincided with the end of an anomalously cold/wet interval termed the Little Ice Age, which took place between ~100 and 600 cal a BP (Osborn and Briffa, 2006). Historical and paleoclimate records from Europe and North America also indicate an interval of anomalously warm/dry conditions during mediaeval time (i.e. the Medieval Climate Anomaly, ~800–1100 cal a BP) (Osborn and Briffa, 2006), at times of relatively small-scale anthropogenic disturbance of the landscapes and atmospheric chemistry relative to the changes observed during the Anthropocene (Lewis and Maslin, 2015). Determining the geographical occurrence, magnitude and rapidity of these events could offer clues to elucidating the mechanisms involved in the generation/propagation of low-frequency (centennial-scale) anomalies, characterize their environmental consequences and assess the role of human activities in the context of natural climate variability. Little is known, however, about centennial-scale changes in temperature and precipitation regimes in the southern extra tropics during the most recent millennia, a vast sector characterized by a strong zonal atmospheric circulation pattern controlled by the southern westerly winds (SWWs) (Garreaud *et al.*, 2013).

South America is the only continuous continental landmass in the Southern Hemisphere that intersects the SWW in its entirety, straddling the critical climatic interface between mid to high latitudes, and thus is an important region for examining past changes in the SWW, their effects on land biota, and high-latitude coupled ocean–atmosphere processes. The SWW are the sole source of precipitation in the Pacific and Andean sectors of central Patagonia (Fig. 1), the amount of which exhibits a positive and significant correlation with low-level zonal wind intensity (Moy *et al.*, 2008; Garreaud *et al.*, 2013; Moreno *et al.*, 2014).

Sedimentary records from fast sediment-accumulating, small closed-basin lakes yield ideal material for developing time series of vegetation and fire-regime shifts, allowing detailed examination of past environmental changes at spatial scales of a few hectares to square kilometers surrounding the site, with time resolution ranging from decadal to millennial timescales. Pioneering studies on lake sediments from small closed-basin lakes in central–west Chilean Patagonia from Laguna Venus (45°32′S, 72°01′W) and Laguna Miranda (46°08′S, 73°26′W) examined the time evolution of vegetation and disturbance regimes in over the most recent millennia through analyses of sediment–water interface cores (Szeicz *et al.*, 1998; Haberle *et al.*, 2000). These studies stressed the role of paleofires, volcanism and soil chemistry as primary drivers of vegetation change in deciduous and evergreen *Nothofagus*-dominated forests. More recent studies in north-western (40°–43°S) (Jara and Moreno, 2012; Henríquez *et al.*, 2015; Moreno and Videla, 2016) and south-western Patagonia (50°–51°S) (Huber and Markgraf, 2003; Moreno *et al.*, 2009, 2014) have detected centennial-scale shifts in the native vegetation in response to natural climate variability and disturbance regimes (volcanism and paleofires) over the last three millennia, along with the establishment of artificial meadows and grasslands associated with the onset of Chilean and European disturbance. The centennial and

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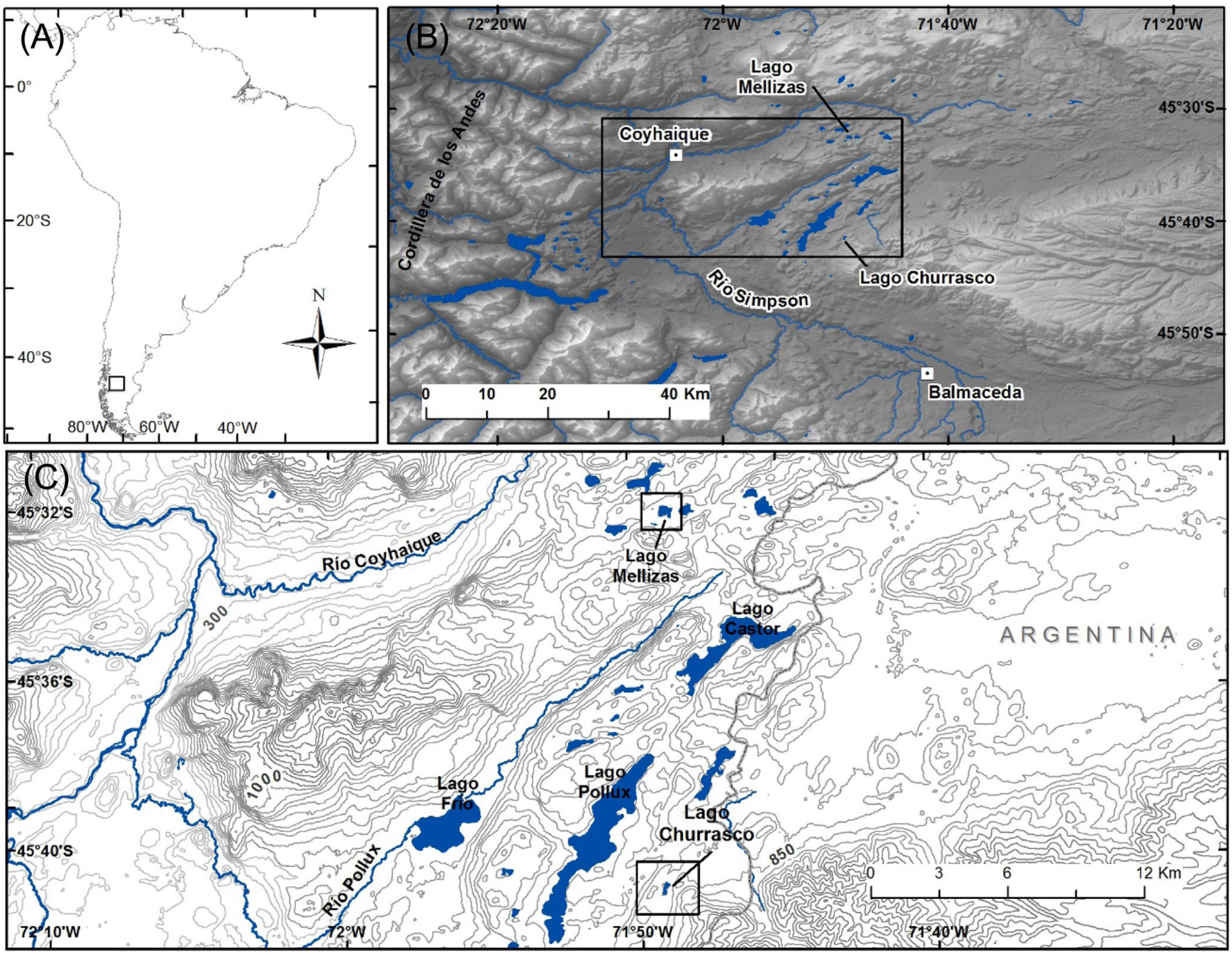

Figure 1. (A) Reference of map of South America showing the location of central–west Patagonia. (B) Digital elevation model of the study area. (C) Topographic map showing the location of Lago Churrasco and Lago Mellizas. Contour intervals are 50 m.

millennial-scale response of deciduous *Nothofagus* forests to natural (climate change, disturbance) and direct (vegetation disturbance) or indirect (atmospheric circulation changes) human perturbations near the forest–steppe ecotone of central Chilean Patagonia, however, has not been addressed in sufficient detail. Knowledge from this area will help to identify the timing, direction and magnitude of past changes in atmospheric circulation at regional and zonal scale in the southern mid-latitudes. Comparisons among detailed records located along a latitudinal gradient in SWW influence throughout Patagonia could help decipher whether the SWW changed their intensity, latitudinal position or seasonality at centennial timescales over the most recent millennia, and the varying degrees of influence on the composition, structure and dynamics of terrestrial and aquatic ecosystems.

We set out to examine the natural ranges of vegetation and climate variability over the last ~3000 years in the Coyhaique area of central Chilean Patagonia, detect the onset of Chilean–European disturbance of the landscape, and compare the magnitude and rapidity of human-set changes in reference to natural environmental change. For this we developed detailed pollen and charcoal records from lake sediment cores that include the water–sediment interface collected from Lago Churrasco (45°41′30.68″S, 71°49′13.12″W, 800 m a.s.l., 10.3 ha, radius <200 m) and Lago Mellizas (45°32′35.83″S, 71°48′49.08″W, 760 m a.s.l., 23.2 ha, radius ~300 m). These closed-basin lakes are located in sectors currently dominated by human-disturbed deciduous *Nothofagus pumilio* forests in the eastern Andean slopes of Central Chilean Patagonia.

Study area

The Aysén region of central–east Chilean Patagonia (44–48°S) is characterized by numerous islands, channels, fjords and archipelagos along its Pacific sector. These grade eastward into the rugged central Patagonian Andes with summits reaching up to 3000 m a.s.l., deep valleys and lakes of glacial origin, and active volcanoes such as Hudson, Macá, Cay, Mentolat and Melimoyu (Weller et al., 2015). Further to the east the landscape transitions into the back-arc extra-Andean plains and plateaus. The region is under the permanent influence of the SWW, which deliver abundant precipitation to sustain glaciers and icefields in the Andes and a suite of vegetation communities from the hyper-humid Pacific coast to semi-arid environments eastward. This remarkable contrast is induced by the uplift of moisture-laden westerly winds on the windward side of the Andes, causing intense orographic rains, and the subsidence and acceleration of moisture-deprived air masses passing the eastern Andean slopes ~250 km from the western coast. Orographic precipitation on the windward side of the Andes increases with altitude and overall SWW strength to produce extreme environmental and climatic gradients.

The intricate relief, climatic heterogeneities and disturbance regimes create a vast diversity of environments, which leads to zonation of the terrestrial vegetation along latitudinal, longitudinal and altitudinal gradients (Schmithüsen, 1956; Veblen *et al.*, 1996). The cool-temperate and hyper-humid Pacific coasts are dominated by Magellanic Moorland and evergreen North Patagonian rainforests, the former dominated by cushion bogs (*Donatia fascicularis*, *Astelia pumila*, *Gaimarda australis*, *Drosera uniflora*), the latter by the trees *Nothofagus betuloides*, *Drimys winteri*, species of the myrtle family (i.e. *Tepualia stipularis*, *Amomyrtus luma*, *Myrteola nummularia*), and the conifers *Podocarpus nubigena* and *Pilgerodendron uviferum*, among others. Further inland the evergreen forests transition into Subantarctic deciduous forests in response to cool-temperate and wet conditions with higher seasonality in temperature and precipitation. This vegetation unit is dominated by *Nothofagus pumilio* in cooler, higher elevation zones and by *Nothofagus antarctica* in the drier lowlands further east. Deciduous forests grade into the Patagonian Steppe east of the Andes in sectors strongly affected by the mountain rainshadow effect, with grasslands dominated by species of the Poaceae family (e.g. *Festuca pallescens* and *F. gracillima*), herbs (*Acaena splendens*) and scrubland (e.g. *Mulinum spinosum* and *Senecio filaginoides*).

Our study is based on sediment cores we collected from Lago Churrasco (LCh) and Lago Mellizas (LMe) to examine the tempo and mode of changes in deciduous *Nothofagus* forests in response to natural climate variability and changes in disturbance regimes (Chilean–Europeans, fire/paleofire, tephra inundation). The lakes are surrounded by relatively open, in some places fragmented *Nothofagus pumilio–N. antarctica* forests, with an understorey consisting of *Blechnum penna-marina*, *Viola reichei*, *Osmorhiza chilensis*, *Berberis serrato-dentata*, *B. microphylla*, *Acaena pinnatifida*, *A. pinnatifolia*, *Ribes* sp., *Calceolaria* sp., *Geranium* sp., *Chiliotrichum diffusum*, *Rumex acetosella*, *Phacelia secunda* and *Fragaria chiloensis*. The littoral zone in both lakes features *Myriophyllum*, *Potamogeton* and Cyperaceae that extend down to 2–3 m depth. LCh features a more extensive littoral zone dominated by macrophytes than LMe owing to its shallow depth (5 m water depth) and gentle slopes.

The Andean sector of central Patagonia (44–48°S) is one of the most recently colonized areas of southern South America. Initial Chilean–European discovery of the Coyhaique area started on February AD 1897 and was followed by the establishment of permanent settlers on September AD 1903 (Martinic, 2005). The process of colonization included intensive logging, brush and fire (between the years AD 1930 and 1950) for the generation of grasslands for livestock, leading to a 50% reduction in forest cover in this area (Veblen *et al.*, 1996; Otero, 2006; Armesto *et al.*, 2010). This characteristic allows examination of the natural ranges of variability in the vegetation, fire regimes and climate through detailed high-resolution fossil-pollen and charcoal records over the last millennia until the 20th century.

Materials and methods

We obtained lake sediment cores from LCh and LMe using a 7.5-cm-diameter water–sediment interface piston corer and a 5-cm-diameter Wright piston corer from an anchored platform at water depths of 4.8 and 7.4 m, respectively, after conducting a bathymetric survey of each site (Fig. 2). The water–sediment interface cores were sampled *in situ* at contiguous 1-cm-thick sections, then stored at 4 °C at the Quaternary Paleoecology Laboratory at the Universidad de Chile and subsequently subsampled for loss-on-ignition (LOI, 1 mL), pollen (1 mL) and macroscopic charcoal (2 mL) analyses, as well as ^{14}C- and ^{210}Pb-dating from 1-cm-thick sections. LOI and palynological processing were performed following standard protocols (Bengtsson and Enell, 1986; Faegri and Iversen, 1989; Heiri *et al.*, 2001). We lumped *Pinus*, *Plantago* and *Rumex acetosella* in the group 'non-natives', and acknowledge that these palynomorphs may include native herbs belonging to the same genus (multiple *Plantago* species) or family (Polygonaceae), not particularly abundant in the deciduous *Nothofagus* forests of central Patagonia. We counted at least 300 pollen grains of terrestrial origin in each palynological sample using a Zeiss Axioskop stereomicroscope at a magnification of 400× and 1000×. The LOI results are expressed as per cent weight loss (organic and carbonate per cent: LOI_{550} and LOI_{925}, respectively), dry siliciclastic density data (LOI_{925} ash), and the palynological results in pollen percentage diagrams. We normalized abundance of the selected terrestrial and aquatic indicator taxa to identify positive and negative anomalies along each time series and establish comparisons with data from other sites.

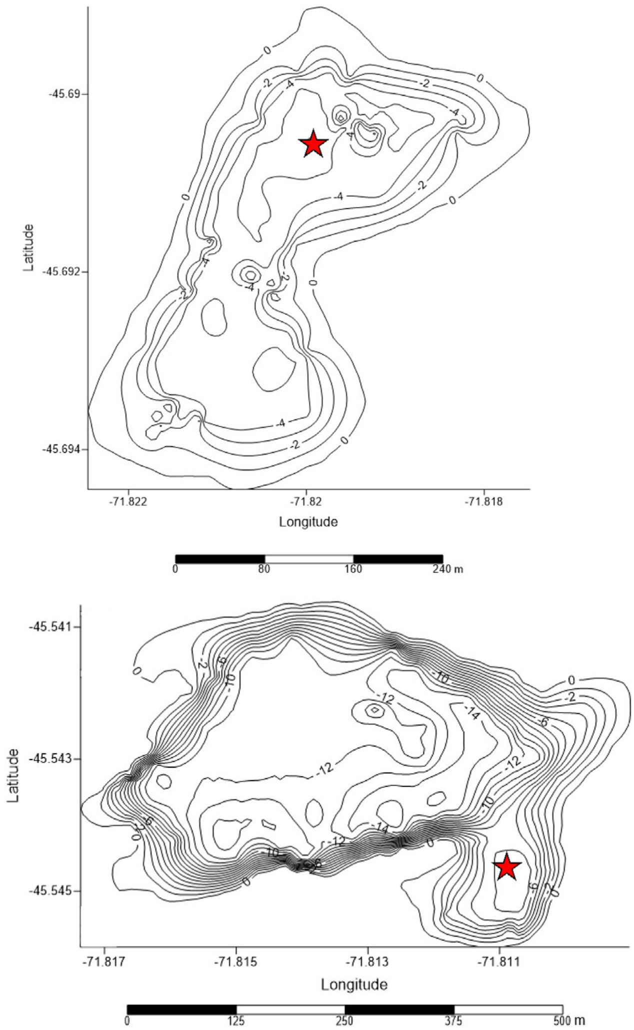

Figure 2. Bathymetric charts from Lago Churrasco (above) and Lago Mellizas (below) showing the coring sites. Contour lines are at 1 m intervals.

We tallied macroscopic charcoal particles from 2-mL sediment continuous contiguous samples throughout the cores and distinguished two size classes (>106 and >212 µm) under a Zeiss KL1500 LCD stereoscope, following careful sieving to avoid rupture of individual particles. The abundance of macroscopic charcoal is expressed in accumulation-rate units (particles cm^{-2}.year). We performed time-series analysis of the macroscopic charcoal particles to detect local fire events using the CharAnalysis software (Higuera *et al.*, 2009), through deconvolution of the peaks signal from slowly varying background abundance. For this, we interpolated samples at regular time windows (median time resolution of each charcoal series) and subtracted the background component using a lowess with a 1000-year window width, and calculated a locally defined threshold to identify charcoal peaks (99th percentile of a Gaussian distribution) which we interpret as local fire events.

We calibrated the radiocarbon dates using the SHCal13 calibration dataset included in CALIB 7.01 and developed Bayesian age models on the calibrated ^{14}C and ^{210}Pb dates using Bacon (Blaauw and Christen, 2011) to assign interpolated ages to all levels analyzed.

Results

We retrieved sediment cores from LCh (PC1107SC+PC1107AT1, spliced length: 151 cm) and from LMe (PC1106SC+PC1106AT1, spliced length: 178 cm) (Fig. 3) which consist of organic-rich lake mud devoid of carbonates (<4% LOI$_{925}$) and tephra layers at 25–26 (a), 51–52 (b), 60–61 (c), 65–66 (d), 80–82 (e), 87–92 (f), 107–112 (g), 123–128 (h) and 136–138 cm (i) in the LCh cores, and at 41–42 (1), 68–69 (2), 84–85 (3), 95–99 (4), 108–111 (5), 132–138 (6), 143–149 (7), 153–157 (8) and 168–171 cm (9) in the LMe cores (Fig. 4). Weller *et al.* (2015) studied the most conspicuous tephras in these cores and traced them to Volcán Hudson (clastic peaks: e, f, g, h, i, 5, 6, 7, 8, 9) and Volcán Mentolat (clastic peaks: d, 4); clastic peaks a, b, c, 1, 2 and 3 were not studied. We obtained 15 ^{210}Pb dates from each water–sediment interphase core which afford finite age estimates until AD 1870 (80 cal a BP) at 12–13 and 11–12 cm in LCh and LMe, respectively (Table 1), in addition to five (LCh) and seven (LMe) accelerator mass spectrometry (AMS) radiocarbon dates (Table 2). These data suggest undisturbed, continuous, high-sediment accumulation rates in both lakes since 3250 cal a BP. Based on these data we developed Bayesian age models (Fig. 5) using the Bacon package for R to assign interpolated ages for each level analyzed.

We analyzed the pollen (Figs 6 and 7), microscopic and macroscopic charcoal content (Fig. 8) of 116 (LCh) and 155 (LMe) samples with median time steps of 22 and 15 years between levels, respectively. We performed a CONISS ordination in each pollen record to aid in the description of the pollen stratigraphy. In the following paragraphs, we provide brief descriptions of these zones highlighting the mean per cent abundance of key taxa in parentheses.

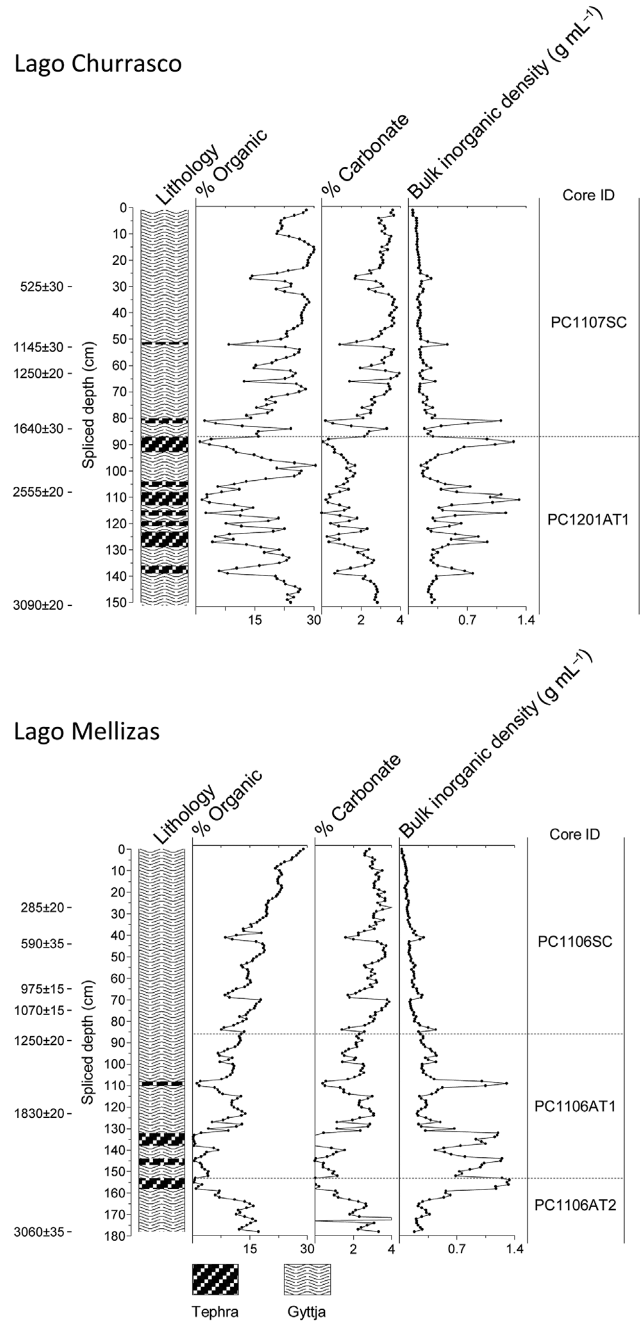

Figure 3. Stratigraphic column of cores PC1107SC and PC1201AT1 (Lago Churrasco) and PC1106SC, PC1106AT1 and PC1106AT2 (Lago Mellizas), along with corresponding ^{14}C dates and results of the loss-on-ignition analysis. Dashed horizontal lines represent core boundaries. We have omitted the ^{210}Pb dates because their values overlap each other at this scale.

Palynology of Lago Churrasco

Zone LCh-1 (107–151 cm, 2350–3200 cal a BP): *Nothofagus dombeyi* type (84.8%) dominates with *Misodendrum* (3%) and traces of *Podocarpus nubigena* (0.9%). Poaceae shows two increases from a background of ~8% following deposition of tephras. Other herbs and shrubs reach maximum abundances (<2%) of the record. Cyperaceae (3.2%) and the green microalga *Pediastrum* (40.8%) are most abundant during this zone.

Zone LCh-2 (70–104 cm, 1200–2120 cal a BP): *Nothofagus dombeyi* type persists with high values and little variation (87.5%), along with slight declines in *Podocarpus nubigena* (0.5%), Poaceae (6.9%) and Cyperaceae (2.1%), and a modest increment in *Misodendrum* (3.7%). *Pediastrum* (40.5%) starts a long-term declining trend during this zone.

Zone LCh-3 (13–67 cm, 60–1300 cal a BP): *Nothofagus dombeyi* type dominates with little variation (89.3%), while *Podocarpus nubigena*, Cyperaceae and *Isoetes* remain low, along with declines in *Misodendrum* (2.7%) and *Pediastrum* (from 3.7 to 2.7% and 40.5 to 26%, respectively). Traces (<1%) of Asteraceae and the exotic *Pinus* sp. appear during this zone.

Zone LCh-4 (0–12 cm, the last ~120 years): *Nothofagus dombeyi* type exhibits a ~20% decline in the initial 75 years, contemporaneous with a compensatory increase in Poaceae. The *Nothofagus* decline was preceded by a sustained long-term decline in *Misodendrum*, *Podocarpus nubigena* and *Pediastrum*. Cyperaceae and *Isoetes* exhibit steady, but variable increases. Asteraceae subfam. Asteroideae and the exotic *Pinus* sp. persist in trace abundance during this zone. *Nothofagus*

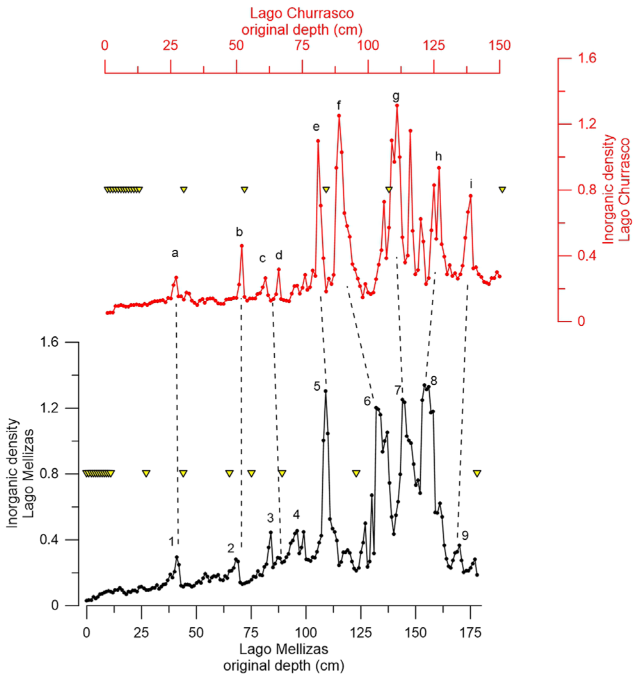

Figure 4. Detail of the siliciclastic density data of the spliced records from Lago Churrasco and Lago Mellizas. The triangles indicate the position of ^{210}Pb- and ^{14}C-dated levels. The letters and numbers provide an informal identification of conspicuous peaks in the siliciclastic density data that can be correlated (dashed lines) among both records. Most of these levels were analyzed and reported by Weller *et al.* (2015).

dombeyi type declines to 67%, its lowest abundance in the entire record, and the same applies to *Podocarpus nubigena* and *Pediastrum*. Abrupt increases are evident in *Misodendrum* (from 0 to 7.7%), Poaceae, Asteraceae subfam. Cichorioideae, Cyperaceae, *Isoetes*, *Potamogeton* and *Myriophyllum*, along with the exotic *Pinus* sp., *Plantago* and *Rumex*.

Palynology of Lago Mellizas

Zone LMe-1 (148–177 cm; 2400–3200 cal a BP): *Nothofagus dombeyi* type (90.8%) dominates the record with Poaceae (3.5%), *Misodendrum* (2.4%) and *Podocarpus nubigena* (1.6%). *Pediastrum* remains abundant (63.1%) while Cyperaceae and *Myriophyllum* exhibit very low abundance (<0.1%).

Zone LMe-2 (88–142 cm; 1100–2300 cal a BP): *Nothofagus dombeyi* type persists with high values and little variation (93.7%), *Podocarpus nubigena* and *Misodendrum* maintain their abundance of the previous zone, while Poaceae decreases slightly (2.3%) relative to the previous zone. *Pediastrum* declines abruptly to ~30% and increases values >60% near the end of this zone.

Zone LMe-3 (15–87 cm; 110–1100 cal a BP): *Nothofagus dombeyi* remains abundant (94.2%) along with Poaceae (2.2%), while *Podocarpus nubigena* and *Pediastrum* decline slightly. *Misodendrum* (1.9%) shows a long-term and variable decline, which culminates with values approaching zero. Near the end of this zone *Pediastrum* exhibits an abrupt decline from 78 to 20%, while other aquatic taxa (Cyperaceae, *Myriophyllum*) remain invariant.

Zone LMe-4 (0–14 cm; the last ~140 years): *Nothofagus dombeyi* type declines from 96 to 56%, along with modest increases in Poaceae (11.6%) and other herbs (1.2%). *Misodendrum* (3%) shows a sudden increase that led to multiple peaks and troughs that define a variable, relatively high-abundance interval. Exotic taxa appear and reach their maxima during this zone: *Pinus* (12.5%), *Plantago* (2%), Asteraceae subfam. Cichorioideae (0.7%) and *Rumex* (15%). Among the aquatic taxa and ferns, Cyperaceae (4.1%), *Myriophyllum* (1.8%) and *Blechnum* (1.6%) attain their maxima and *Pediastrum* increases substantially from minimum values to > 50%.

Table 1. ^{210}Pb dates from cores PC1107SC (Lago Churrasco) and PC1106SC (Lago Mellizas).

MyCore Sc.	Core ID	Depth (cm)	^{210}Pb (Bq g^{-1})	Age (AD)	Age (cal a BP)	1σ error
271	PC1106SC	0	0.071	2011	−61	0
272	PC1106SC	1	0.083	2009	−59	0
273	PC1106SC	2	0.073	2005	−55	1
274	PC1106SC	3	0.071	2003	−53	1
275	PC1106SC	4	0.078	1999	−49	2
276	PC1106SC	5	0.070	1994	−44	2
277	PC1106SC	6	0.068	1985	−35	4
278	PC1106SC	7	0.077	1977	−27	4
279	PC1106SC	8	0.048	1958	−8	12
280	PC1106SC	9	0.039	1948	2	19
281	PC1106SC	10	0.030	1938	12	43
282	PC1106SC	11	0.029	1924	26	62
311	PC1107SC	0	0.065	2011	−61	0
312	PC1107SC	1	0.069	2007	−57	0
313	PC1107SC	2	0.047	2003	−53	1
314	PC1107SC	3	0.031	1998	−48	2
315	PC1107SC	4	0.030	1995	−45	3
316	PC1107SC	5	0.047	1991	−41	2
317	PC1107SC	6	0.036	1984	−34	4
318	PC1107SC	7	0.048	1976	−26	5
319	PC1107SC	8	0.036	1960	−10	8
320	PC1107SC	9	0.020	1939	11	17
321	PC1107SC	10	0.017	1921	29	22
322	PC1107SC	11	0.012	1898	52	50
323	PC1107SC	12	0.009	1870	80	121

Table 2. AMS radiocarbon dates and calibrated ages from Lago Churrasco (PC1107SC, PC1201AT1) and Lago Mellizas (PC1106SC, PC1106AT1). Radiocarbon ages were calibrated using CALIB 7.01.

	Lab. code	Sample code	Depth (cm)	Age (^{14}C a BP)	1σ error	Age (cal a BP)	2σ range
Lago Churrasco	UCIAMS-122947	SC1107SC _29	30	525	30	550	492–654
Lago Churrasco	CAMS-158525	SC1107SC_52	53	1145	30	1065	934–1228
Lago Churrasco	CAMS-158300	SC1107SC_83	84	1640	30	1539	1399–1697
Lago Churrasco	UCIAMS-145956	PC1201AT1_35	108	2555	20	2648	2491–2757
Lago Churrasco	UCIAMS-145957	PC1201AT1_77	151	3090	20	3295	3182–3385
Lago Mellizas	UCIAMS-133063	PC1106SC_27	27	285	20	300	155–435
Lago Mellizas	CAMS-159616	PC1106SC_44	44	590	35	550	510–630
Lago Mellizas	UCIAMS-133064	PC1106SC_65	65	975	15	860	798–904
Lago Mellizas	UCIAMS-133065	PC1106SC_75	75	1070	15	940	920–960
Lago Mellizas	UCIAMS-122979	PC1106AT1_34	89	1250	20	1120	1070–1180
Lago Mellizas	UCIAMS-122980	PC1106AT1_68	123	1830	20	1720	1615–1810
Lago Mellizas	CAMS-159610	PC1106AT2_25	178	3060	35	3210	3070–3340

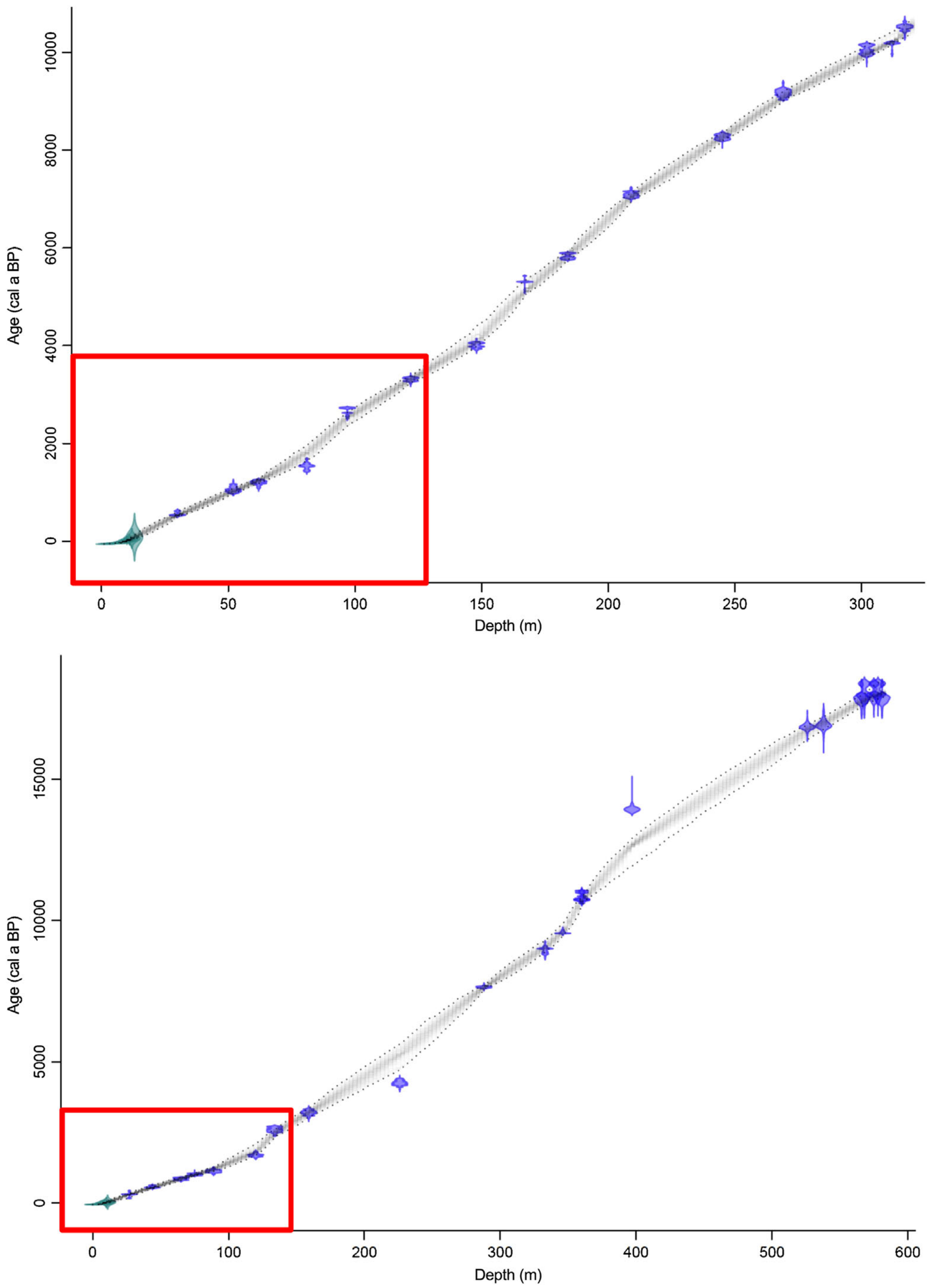

Figure 5. Bayesian age models from cores PC1107SC–PC1201 AT1 (Lago Churrasco, above) and PC1106SC–PC1106AT1 (Lago Mellizas, below). The red boxes encompass the depth and age range discussed in this paper. The blue zones denote the probability distribution of the calibrated radiocarbon dates. The gray zone denotes the 95% confidence interval of the age model.

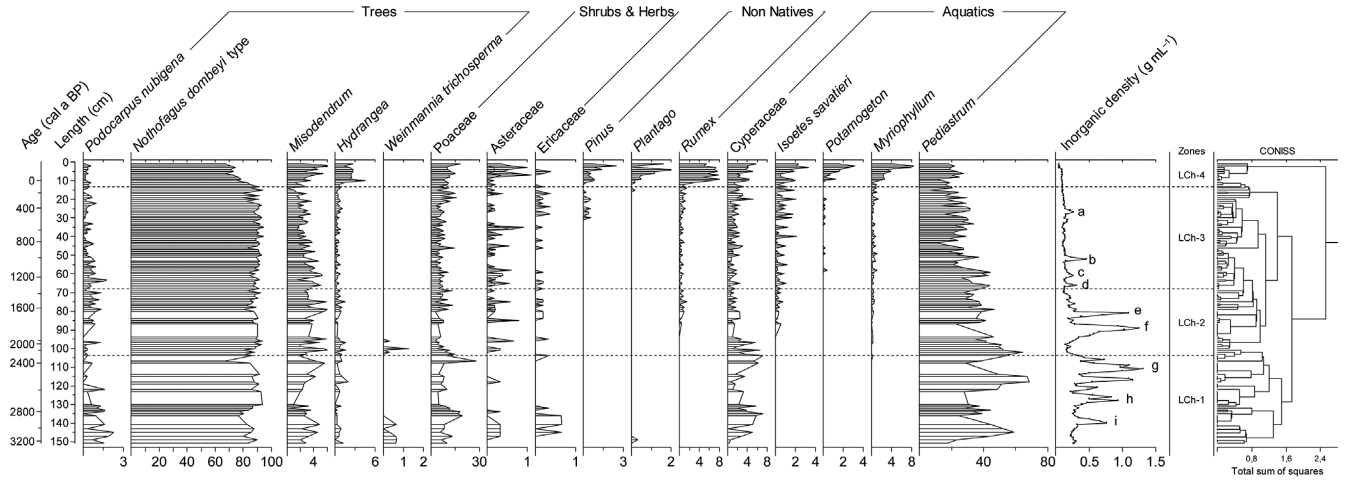

Figure 6. Percentage pollen diagram of selected taxa from Lago Churrasco. The dashed horizontal lines indicate major changes in pollen stratigraphy as indicated by a CONISS ordination. The solid horizontal lines represent palynological levels analyzed. The curve on the right shows the siliciclastic density data and peak tephra layers.

Charcoal

Macroscopic charcoal records show low charcoal accumulation rate (CHAR) before 100 cal a BP with a predominance of discrete low-magnitude increases in the LCh and LMe records. In addition, the LMe record shows five large-magnitude increases over the same interval with two distinct very large-magnitude peaks at 2600 and 3000 cal a BP. Both sites show major increases in CHAR since 100 cal a BP that led to maxima during the second half of the 20th century. Time-series analysis reveals statistically significant CHAR peaks (8 and 15 in LCh and LMe, respectively) that we interpret as local fire events, the frequency of which is minimal between 2000 and 3200 and 250 and 750 cal a BP and maximal between 750 and 1500 cal a BP and over the last 150 years (Fig. 8).

Discussion

A median abundance of *Nothofagus* of 88% throughout the LCh and LMe records (Figs 6 and 7) suggests a dominance of closed-canopy *Nothofagus* forests over the last 3200 years. These percentages approach the highest abundance of this palynomorph in surface samples from modern deciduous Subantarctic forests (Quintana, 2009). The conifer *Podocarpus nubigena* is present in trace percentages ($\leq$2%) in both sites, with slight increases between 1100–1600 and 2600–3200 cal a BP in the LCh record. Because this tree species is currently absent from the studied lakes, we interpret its palynological signal as representing long-distance transport from evergreen Subantarctic rainforest communities located upwind along the channels, fjords and the Pacific coast located 80–210 km westward. Species of the genus *Nothofagus* also produce large quantities of pollen grains susceptible to long-distance transport (Heusser, 1989), raising the possibility that local variations in forest density and continuity near LCh and LMe might be overprinted by an extra-local or regional signal, in particular in the larger lake (LMe). The mistletoe *Misodendrum* (a specific hemiparasite on *Nothofagus* species), however, is present throughout the record with relatively low values and modest increments during the last ~140 years. The incidence of parasitism by *Misodendrum* is limited by the density of *Nothofagus* populations and the luminosity levels within those populations, being minimal at low densities of its host, maximal at intermediate levels (woodland, discontinuous

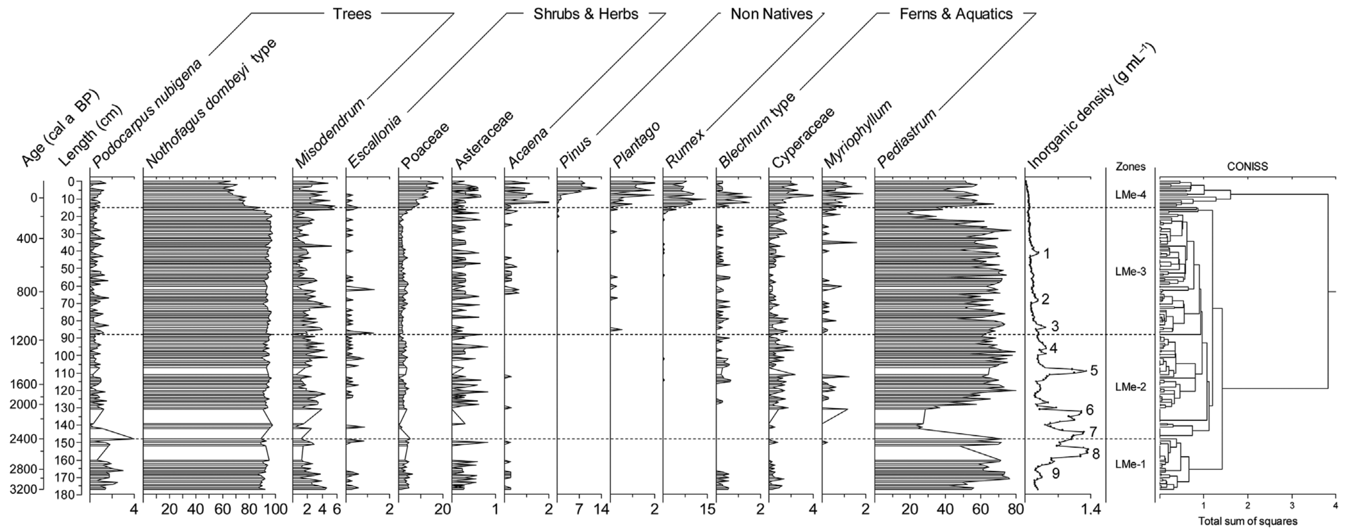

Figure 7. Percentage pollen diagram of selected taxa from Lago Mellizas. The dashed horizontal lines indicate major changes in pollen stratigraphy as indicated by a CONISS ordination. The solid horizontal lines represent palynological levels analyzed. The curve on the right shows the siliciclastic density data and peak tephra layers.

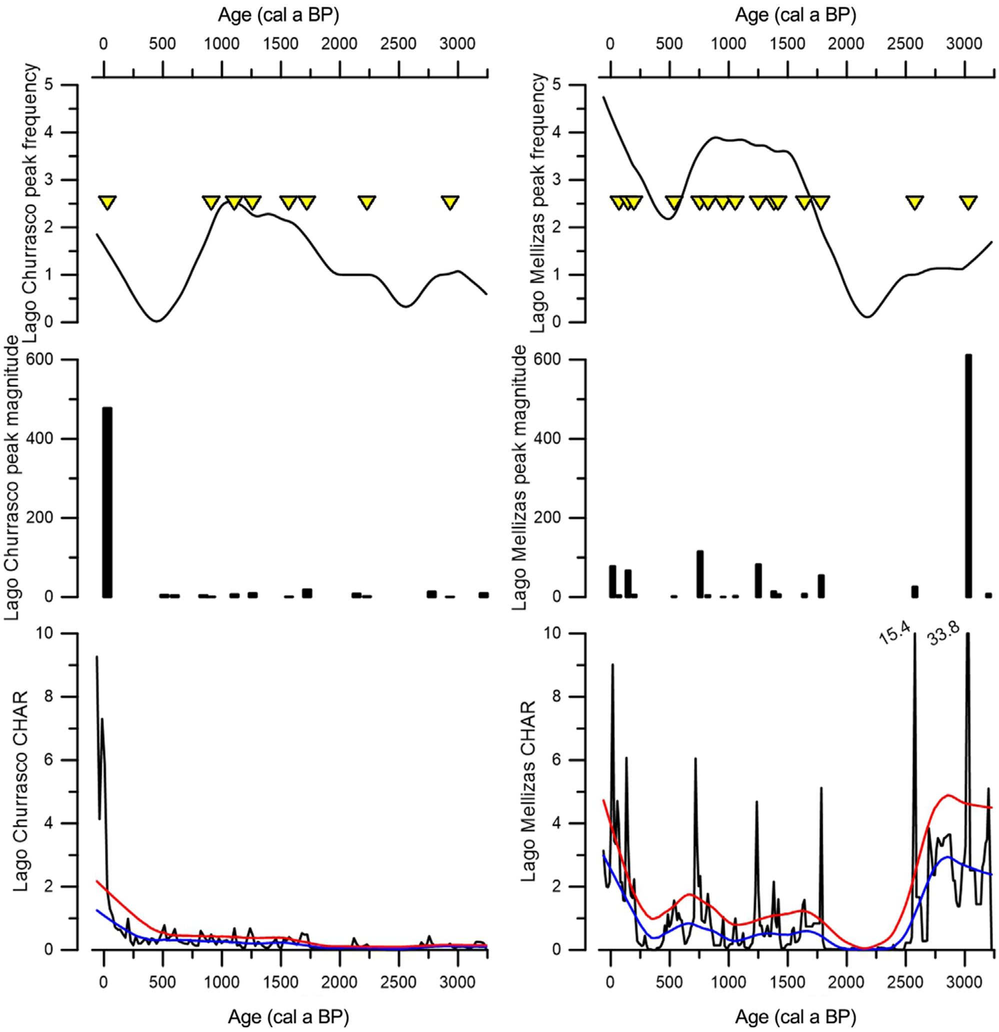

Figure 8. Macroscopic charcoal accumulation rates from the Lago Churrasco and Lago Mellizas sites, along with results of the CharAnalysis (statistically significant charcoal peaks shown as triangles, peak magnitude as vertical bars, and frequency of fires per 500 years).

forests), and declining towards closed-canopy forests (Soler *et al.*, 2014). Our findings attest to the local occurrence of *Nothofagus* forests in the periphery of LCh and LMe, the predominance of low-luminosity levels in that forested landscape and the lack of radical changes in forest continuity during the pre-Chilean/European portion of the records.

The pollen record from LCh shows low abundance of the littoral Cyperaceae with discrete increases between 2200–2500 and 2700–3000 cal a BP. We also observe increases in *Myriophyllum* and small increments in Cyperaceae in both sites over the last ~250 years, accompanied by *Isoetes* and *Potamogeton* in the case of LCh. These results suggest that high lake levels kept the littoral rim of vascular macrophytes away from the lake's center over much of the record, except during centripetal shifts in littoral environments. The magnitude of these changes is larger in LCh than in LMe (18 versus 4% range, respectively), reflecting a higher sensitivity of the smaller (10.3 versus 23.2 ha, respectively), shallower lake (4.8 versus 7.4 m water depth at the coring site, respectively) to centennial-scale lake regressive phases in response to changes in hydrologic balance.

Forest dominance persisted until the late 19th century, when *Nothofagus* declined substantially (25 and 40% decreases in LCh and LMe, respectively) along with increases of herbs, littoral macrophytes, charcoal and subsequent increments in exotic plants ('non-natives' in Figs 6, 7 and 9) introduced by Euro-Chilean settlers. This interval features increases in *Misodendrum*, suggesting an increase in light availability in the forested landscape by fragmentation and exacerbated edge effects. We interpret the late 19th century change as a shift from closed-canopy forests to patchy woodlands/scrublands interspersed with open ground dominated by native and exotic herbs. The timing, character and stratigraphic association of this transformation suggest that fires set by Chilean–European settlers triggered an unprecedented decline in forest cover and rapid conversion to pasturelands and scrubland. We note that *Rumex* and *Plantago* are present in low abundance during the last two millennia; this background palynological signal may represent the presence of native species of these genera in pre-Chilean/European time or, alternatively, field or laboratory contamination with modern material.

The LCh and LMe records show nine volcanic ash layers, attesting to explosive volcanic activity originating from Volcán Hudson and Volcán Mentolat over the last 3200 years (Figs 3, 4, 6 and 7). Ash fallout can potentially lead to edaphic changes, massive defoliation, canopy gaps and understorey burials, generating favorable conditions for tree recruitment and increases in fast-growth, shade-intolerant pioneer species. We note, however, that *Nothofagus* forests located east of Coyhaique were capable of absorbing natural disturbances without changing their mean state, highlighting their resilience to climate change and disturbance agents since 3200 cal a BP (Fig. 9). This resilience can be explained

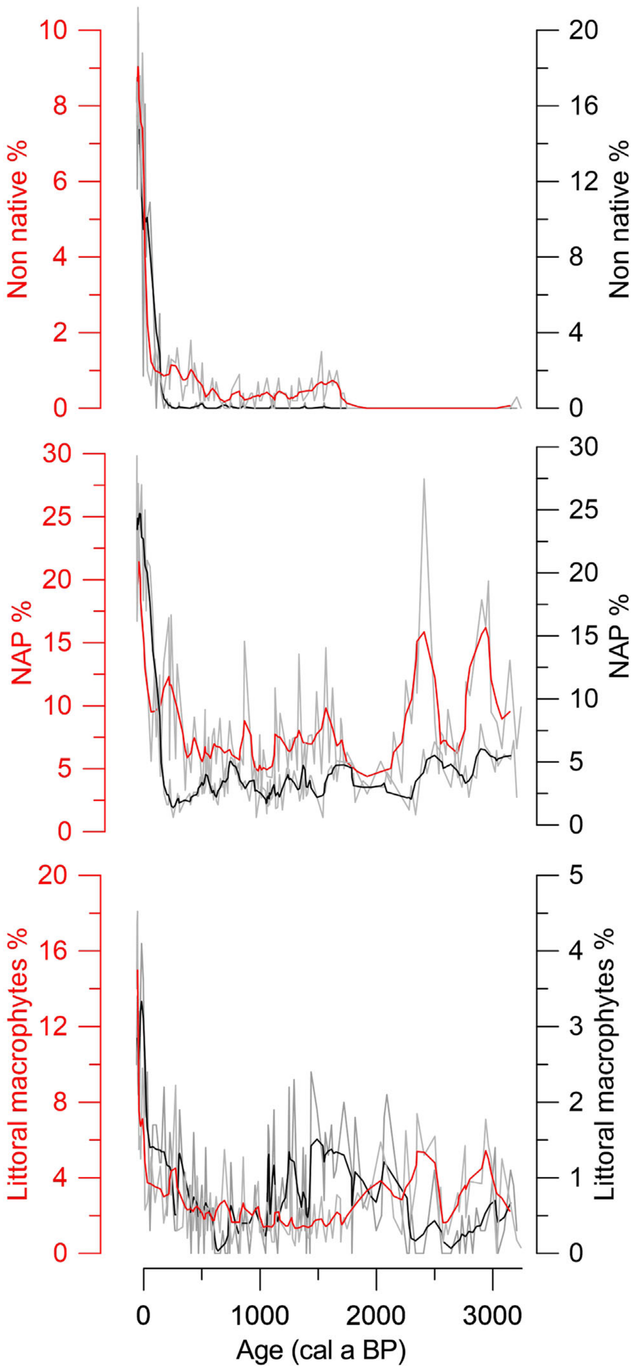

Figure 9. Selected palynological variables from the Lago Churrasco and Lago Mellizas records expressed as a function of age. The gray line represents the raw values of each variable, and the thick lines are weighted running means through each record (red: LCh, black: LMe). NAP, non-arboreal pollen.

by (i) the broad tolerance range of the dominant tree species (*N. pumilio*, *N. antarctica*) to temperature and precipitation gradients in southern South America; (ii) the depauperate species richness of these forest communities, limiting our ability to detect compositional changes through palynological records; and (iii) the relatively low magnitude and frequency of natural disturbance agents. We posit that the magnitude and ubiquity of Chilean–European disturbance in this sector of central Patagonia exceeded the resilience of deciduous *Nothofagus* forests to natural disturbance, thus eliciting an ecosystem shift towards an alternative state consisting of artificial meadows, scrublands and exotic tree plantations.

The LCh record shows centennial-scale increases in Poaceae and Cyperaceae in stratigraphic association with thick tephras deposited during the interval 2400–3000 cal a BP (Figs 3, 4, 6 and 7), suggesting transient responses of the herbaceous vegetation to volcanic disturbance. The LMe record does not record those changes; instead, it features prominent paleofires at 2600 and 3000 cal a BP (Fig. 8). These constitute the largest-magnitude local fires during the last 3200 years in both records, suggesting that negative hydrologic balance at that time favored the desiccation of coarse fuels and occurrence of severe fires near LMe.

We observe an interval with frequent local fires in both records between 750 and 1500 cal a BP; in the case of LCh this interval features low-magnitude events, while in LMe we find low- and intermediate-magnitude events (Fig. 8). Closed-canopy *Nothofagus* forests remained unaltered during this frequent-fire interval. Large-magnitude fires associated with Chilean and European settlers since the late 19th century terminated the dominance of dense *Nothofagus* forests in both sites, and constitute the main driver of physiognomic change in the vegetation in the eastern Andean slopes of central Patagonia over the last 3200 years. This change is coeval with the rise in littoral macrophytes discussed above, indicating that large-scale disturbance by Euro-Chilean since the end of the 19th century coincided with a regressive lake-level phase in both sites.

We now assess the similarities and differences of the LCh and LMe records in an effort to identify regional patterns and their possible cause.

- Both records show a continuous dominance of closed-canopy deciduous *Nothofagus* forests in the region since 3200 cal a BP, increases of aquatic macrophytes during the 18th century, deforestation and large-magnitude fires during the late 19th century, followed by spread of exotic plants shortly after (Figs 6, 7 and 9). This coherent behavior suggests that cool-temperate and humid conditions, characteristic of the region where this forest community occurs, have persisted in the region, followed by a regressive lake-level change driven by negative hydrologic balance starting in the 18th century. These conditions set the stage for the arrival of Euro-Chileans to the Coyhaique area and the beginning of large-scale disturbance by fire, which promoted a replacement of closed-canopy forests by woodlands/scrublands interspersed with pine plantations and meadows containing natural and introduced herbs.
- Both records show nine tephras since 3200 cal a BP (Figs 3 and 4) which correspond with minimal variations in the percentage arboreal pollen (Figs 6 and 7), suggesting that *Nothofagus* forests are highly resilient to ash fallout associated with explosive volcanism in central–east Chilean Patagonia.
- Both records show similar trends in local fire frequency with a low occurrence between 250–750 and before 2000 cal a BP, and higher frequency during the last 150 years and between 750 and 1500 cal a BP (Fig. 8). This coherence indicates a uniform fire regime across the region, which we interpret as a reflection of climate change. Higher fire frequencies suggest intervals with lower-than-average precipitation regime, particularly during the summer months (Holz and Veblen, 2012). These conditions allow the desiccation of coarse fuels which, according to the pollen records, were abundant and laterally/temporarily continuous throughout the landscape. These results indicate that *Nothofagus* forests are highly resilient to natural fire regimes in central–east Chilean Patagonia (Figs 6 and 7).

- We detect differential responses of terrestrial and aquatic herbs among sites during the oldest portion of the record (2400–3000 cal a BP) (Fig. 9). We attribute these divergences to differences in the sensitivity and capability of integrating regional and extra-local palynological signals in LCh and LMe. By virtue of being a smaller, shallower closed-basin lake, LCh maximizes local palynological signals and allows detection of low-magnitude changes in past vegetation and climate. Increases in Poaceae and Cyperaceae between 2200–2500 and 2700–3000 cal a BP in LCh post-date the deposition of thick tephras (Figs 6 and 9), suggesting disturbance by ash fallout associated with explosive volcanism.

Our preferred interpretation for the divergent behavior of the LCh and LMe pollen records during the interval 2400–3000 cal a BP is that centennial-scale changes in hydroclimate were insufficient in magnitude to trigger uniform responses in closed-basin lacustrine environments of various sizes, depths and bathymetries in the Coyhaique area. We also note that terrestrial and aquatic vegetation remained unaltered during other episodes of volcanic ash deposition and increased fire frequency over the last 2400 years in the LCh record (with the exception of changes attributable to Euro-Chilean disturbance). This stratigraphic contrast suggests that the interaction of volcanic disturbance and negative anomalies in hydrologic balance, evinced by variations in Cyperaceae in LCh, drove an increase in terrestrial herbs between 2200–2500 and 2700–300 cal a BP.

Regional implications

Few pollen records from central–west Patagonia have examined in detail the vegetation, fire regime and climate changes over the most recent millennia; notable exceptions are the Laguna (L.) Fácil (Szeicz *et al.*, 2003), L. Venus (Szeicz *et al.*, 1998) and L. Miranda (Haberle *et al.*, 2000) records (Fig. 1). L. Fácil, located in the Chonos Archipelago ~225 km north-west of Coyhaique, shows a dominance of evergreen *Nothofagus* forest (>40%) since 3200 cal a BP with a conspicuous increase in the conifer *Pilgerodendron* following paleofires at ~600 cal a BP. L. Venus, situated ~25 km north-west of L. Churrasco and ~15 km west of L. Mellizas, shows a dominance of deciduous *Nothofagus* forest (>70%) since 1600 cal a BP and a persistent decline at the beginning of the 20th century coeval with increases in fire and introduced weeds (*Rumex*, *Plantago*) (Szeicz *et al.*, 1998). The L. Miranda site, located 125 km south-west of Coyhaique, also shows a dominance of evergreen *Nothofagus* forest (>55%) during the last 2100 years and a conspicuous increase in *Pilgerodendron* at 200 cal a BP, changes that Haberle *et al.* (2000) interpreted as precipitation and lake-level lowering. It is difficult to assess the similarities/differences in timing, direction and character of vegetation response to climate and disturbance agents among records, considering the environmental heterogeneities, dating uncertainties and the possibility of site-specific changes. Notwithstanding these difficulties, the records show relatively wet conditions starting at ~600 cal a BP, a subsequent shift towards relatively dry conditions starting at ~200 cal a BP and a major change associated with Euro-Chilean disturbance since the late 19th century. Pollen and macroscopic charcoal records from Mallín Pollux (Markgraf *et al.*, 2007), a fen located ~1.6 km east of LCh, show similar changes over the last ~3000 years, lending support to our findings.

A recent study from L. Cipreses (Moreno *et al.*, 2014), located in south-western Patagonia ~625 km south of LCh and LMe, found a dominance of mixed evergreen–deciduous *Nothofagus* forests (>85% arboreal pollen) during the last three millennia and identified discrete, ~200-year warm/dry intervals with forest opening, decline in lake levels, paleofires and diversification of the forest understorey (2700–3000 [CC5], 2200–2400 [CC4], 1500–1600 [CC3], 800–1000 [CC2] cal a BP and over the last 150 years CC1) (Moreno *et al.*, 2014) (Fig. 10). Three of these events (CC1, CC4, CC5)

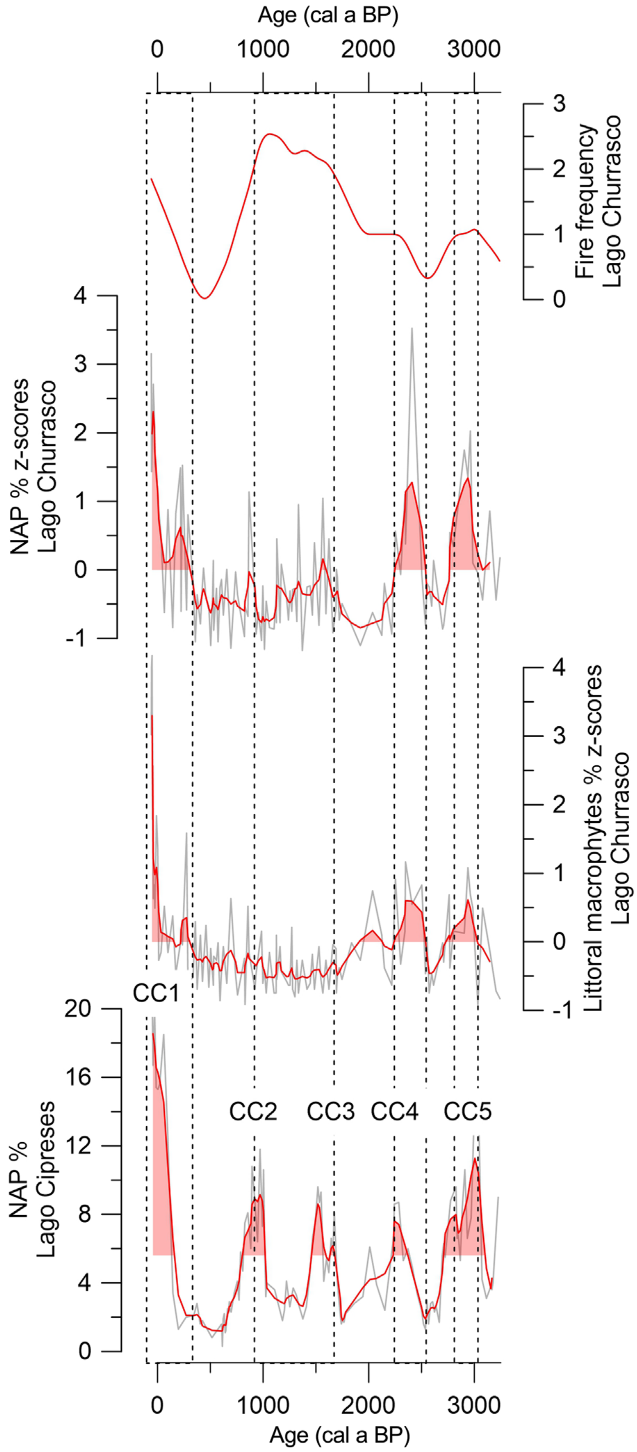

Figure 10. Selected palynological variables from the Lago Churrasco record shown as normalized *z*-score values relative to the mean of the entire record expressed as a function of age. NAP, non-arboreal pollen. The gray line represents the raw values of each variable, while the red line is a weighted running mean through each record. The red filled pattern highlights the positive anomalies in the weighted running mean. The lower curve is the NAP record from Lago Cipreses. The dashed vertical lines indicate intervals interpreted as negative hydrologic balance phases in the LCh record.

overlap in timing and direction with negative hydrologic balance episodes in the LCh record, raising the possibility of a broad central and southern Patagonian paleoclimate signal. We note that the interval with frequent fires between 750 and 1500 cal a BP in LCh and LMe encompasses the CC2 and CC3 events and the intervening cold/wet phase in L. Cipreses (Fig. 10). Altogether, these results suggest diminished SWW influence during distinct centennial-scale episodes in western Patagonia between 45°S and 51°S over the last 3200 years.

Summary and conclusions

The LCh and LMe records reveal a detailed picture of terrestrial and aquatic ecosystem change over the last 3200 years in a forested sector of central–east Chilean Patagonia. Within this interval we detect a continuous dominance of dense *Nothofagus* forests until the late 19th century, because of large-scale disturbance by Euro-Chilean settlers through the intensive use of fire. This event took place in the context of negative hydrologic balance, judging from the synchronous rise in macrophyte abundance in both sites starting in the 18th century. Climate change and stratigraphically detectable natural disturbance regimes (wildfires, deposition of volcanic ashes) did not alter the persistence of dense *Nothofagus* forests, suggesting they are highly resilient ecosystems. This resilience was surpassed by fire, timber exploitation and livestock grazing, concomitant with the spread of non-native invasive plants (*Rumex*, *Pinus* and *Plantago*) in response to large-scale land use changes.

We interpret a slight opening of the forest canopy, lake-level lowering and large-magnitude paleofires to between 2200–2500 and 2700–3000 cal a BP. Fire frequency reached its maximum between 750 and 1500 cal a BP and during the last 250 years. We interpret these intervals as showing lowered hydrologic balance, probably caused by centennial-scale reduction in SWW influence at 45°S.

Disturbance set by Chileans and Europeans since the late 19th century caused a shift in *Nothofagus* forests towards an alternative state consisting of artificial meadows, scrublands and exotic tree plantations with frequent large-magnitude fires. This shift caused a nearly synchronous homogenization of the landscape, aided by the introduction of livestock and industrial forestry.

Acknowledgments. This research was funded by Fondecyt #1121141, 1151469, ICM grants P05-002 and NC120066, CONICYT USA2013-0035 and Fondap 15110009. We thank C. Miranda, M. Kaplan, and W. Henriquez for providing field assistance and C. Miranda for drafting figure 1.

Abbreviations. LCh, Lago Churrasco; LMe, Lago Mellizas; LOI, loss-on-ignition; SWW, southern westerly winds.

References

Armesto JJ, Manuschevich D, Mora A *et al.* 2010. From the Holocene to the Anthropocene: a historical framework for land cover change in southwestern South America in the past 15, 000 years. *Land Use Policy* **27**: 148–160 [DOI: 10.1016/j.landusepol.2009.07.006].

Bengtsson L, Enell M. 1986. Chemical analysis. In *Handbook of Palaeoecology and Palaeohydrology*, Berglund BE (ed.). John Wiley & Sons: Chichester; 423–451.

Blaauw M, Christen JA. 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* **6**: 457–474 [DOI: 10.1214/ba/1339616472].

Faegri K, Iversen J. 1989. *Textbook of Pollen Analysis*. John Wiley & Sons: Chichester.

Garreaud R, Lopez P, Minvielle M *et al.* 2013. Large-scale control on the Patagonian climate. *Journal of Climate* **26**: 215–230 [DOI: 10.1175/JCLI-D-12-00001.1].

Haberle S, Szeicz JM, Bennett KD. 2000. Late Holocene vegetation dynamics and lake geochemistry at Laguna Miranda, XI Región, Chile. *Revista Chilena de Historia Natural* **73**: 655–669.

Heiri O, Lotter AF, Lemcke G. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* **25**: 101–110 [DOI: 10.1023/A:1008119611481].

Henríquez WI, Moreno PI, Alloway BV *et al.* 2015. Vegetation and climate change, fire-regime shifts and volcanic disturbance in Chiloé Continental (43°S) during the last 10, 000 years. *Quaternary Science Reviews* **123**: 158–167 [DOI: 10.1016/j.quascirev.2015.06.017].

Heusser CJ. 1989. Late Quaternary Vegetation and Climate of Southern Tierra del Fuego. *Quaternary Research* **31**: 396–406 [DOI: 10.1016/0033-5894(89)90047-1].

Higuera PE, Brubaker LB, Anderson PM *et al.* 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* **79**: 201–219 [DOI: 10.1890/07-2019.1].

Holz A, Veblen TT. 2012. Wildfire activity in rainforests in western Patagonia linked to the Southern Annular Mode. *International Journal of Wildland Fire* **21**: 114–126 [DOI: 10.1071/WF10121].

Huber UM, Markgraf V. 2003. Holocene fire frequency and climate change at Rio Rubens Bog, southern Patagonia. In *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*, Veblen TT, Baker W, Montenegro G, Swetnam TW (eds). Springer: New York.

Jara IA, Moreno PI. 2012. Temperate rainforest response to climate change and disturbance agents in northwestern Patagonia (41°S) over the last 2600 years. *Quaternary Research* **77**: 235–244 [DOI: 10.1016/j.yqres.2011.11.011].

Lewis SL, Maslin MA. 2015. Defining the Anthropocene. *Nature* **519**: 171–180 [DOI: 10.1038/nature14258] [PubMed: 25762280].

Markgraf V, Whitlock C, Haberle S. 2007. Vegetation and fire history during the last 18, 000 cal yr B.P. in Southern Patagonia: Mallín Pollux, Coyhaique, Province Aisén (45°41′30″S, 71°50′30″W, 640 m elevation). *Palaeogeography, Palaeoclimatology, Palaeoecology* **254**: 492–507 [DOI: 10.1016/j.palaeo.2007.07.008].

Martinic M. 2005. *De la trapananda al Aysén: Una mirada reflexiva sobre el acontecer de la región de Aysén, desde la prehistoria hasta nuestros días*. Pehuén Editores Limitada: Santiago, Chile.

Moreno PI, François JP, Villa-Martínez RP *et al.* 2009. Millennial-scale variability in Southern Hemisphere westerly wind activity over the last 5000 years in SW Patagonia. *Quaternary Science Reviews* **28**: 25–38 [DOI: 10.1016/j.quascirev.2008.10.009].

Moreno PI, Videla J. 2016. Centennial and millennial-scale hydroclimate changes in northwestern Patagonia since 16, 000 yr BP. *Quaternary Science Reviews* **149**: 326–337 [DOI: 10.1016/j.quascirev.2016.08.008].

Moreno PI, Vilanova I, Villa-Martínez R *et al.* 2014. Southern Annular Mode-like changes in southwestern Patagonia at centennial timescales over the last three millennia. *Nature Communications* **5**: 4375 [DOI: 10.1038/ncomms5375] [PubMed: 25007832].

Moy CM, Dunbar RB, Moreno PI *et al.* 2008. Isotopic evidence for hydrologic change related to the westerlies in SW Patagonia, Chile, during the last millennium. *Quaternary Science Reviews* **27**: 1335–1349 [DOI: 10.1016/j.quascirev.2008.03.006].

Osborn TJ, Briffa KR. 2006. The spatial extent of 20th-century warmth in the context of the past 1200 years. *Science* **311**: 841–844 [DOI: 10.1126/science.1120514] [PubMed: 16469924].

Otero L. 2006. *La huella del fuego. Historia de los bosques nativos y cambios en el paisaje del sur de Chile*. Pehuén Editores: Santiago, Chile.

Quintana FA. 2009. *Paleoambientes del extremo sur de Santa Cruz: análisis polínico de sedimentos lacustres del Cuaternario Tardío, Doctoral Thesis, Facultad de Ciencias Exactas y Naturales*. Universidad Nacional de Mar del Plata, Mar del Plata.

Schmithüsen J. 1956. Die raumliche Ordnung der chilenischen Vegetation. *Bonner Geographische Abhandlungen* **17**: 1–86.

Soler R, Martínez Pastur G, Lencinas MV *et al.* 2014. Variable retention management influences biomass of *Misodendrum* and

Usnea in Nothofagus pumilio southern Patagonian forests. *New Zealand Journal of Botany* **52**: 224–235 [DOI: 10.1080/0028825X.2013.846918].

Szeicz JM, Haberle SG, Bennett KD. 2003. Dynamics of North Patagonian rainforests from fine-resolution pollen, charcoal and tree-ring analysis, Chonos Archipelago, Southern Chile. *Austral Ecology* **28**: 413–422 [DOI: 10.1046/j.1442-9993.2003.01299.x].

Szeicz JM, Zeeb BA, Bennett KD *et al.* 1998. High-resolution paleoecological analysis of recent disturbance in a southern Chilean Nothofagus forest. *Journal of Paleolimnology* **20**: 235–252 [DOI: 10.1023/A:1007950905200].

Veblen TT, Donoso C, Kitzberger T *et al.* 1996. Ecology of the southern Chilean and Argentinian Nothofagus forests. In *The Ecology and Biogeography of Nothofagus Forests*, Veblen TT, Hill RS, Read J (eds). Yale University Press: New Haven; 293–353.

Weller DJ, Miranda CG, Moreno PI *et al.* 2015. Tephrochronology of the southernmost Andean Southern Volcanic Zone, Chile. *Bulletin of Volcanology* **77**: 1–24.