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

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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.

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 paleoclimatic 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
The 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–west 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, 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. graciliflora), herbs (Acaena splendens) and scrubland (e.g. Malinium spinosum and Senecio filagooides).

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 repeatedly open, in some places fragmented Nothofagus pumilio–N. antarctica forests, with an understory consisting of Blechnum penna-manna, 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 (Martínic, 2005). The process of colonization included intensive logging, brush and fire (between the years AD 1930 and 1950) for the generation of grasslands and 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 Paleocology 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 14C- and 210Pb-dating from 1-cm-thick samples. 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 ‘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: LOL50 and LOL95, respectively), dry siliclastic density data (LOD95, 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.

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...
Bayesian age models on the calibrated 14C and 210Pb dates calibration dataset included in CALIB 7.01 and developed by 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 14C and 210Pb 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% LOI925) 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 210Pb 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.

**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. *Asteridaeae* and the exotic *Pinus* sp. persist in trace abundance during this zone. *Nothofagus*
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 /C24 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.** 210Pb dates from cores PC1107SC (Lago Churrasco) and PC1106SC (Lago Mellizas).

<table>
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<tr>
<th>MyCore Sc.</th>
<th>Core ID</th>
<th>Depth (cm)</th>
<th>210Pb (Bq g⁻¹)</th>
<th>Age (AD)</th>
<th>Age (cal a BP)</th>
<th>1σ error</th>
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<td>0.071</td>
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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.

<table>
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<th>Lab. code</th>
<th>Sample code</th>
<th>Depth (cm)</th>
<th>Age ($^{14}$C a BP)</th>
<th>1σ error</th>
<th>Age (cal a BP)</th>
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Figure 5. Bayesian age models from cores PC1107SC–PC1201AT1 (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.

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 (<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 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.

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.
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 understory 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...
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 2700–3000 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 understory (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)
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 surmounted 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 paleo-fires 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.

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

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