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Vegetation and climate change, fire-regime shifts and volcanic disturbance in Chiloé Continental (43°S) during the last 10,000 years

W.I. Henríquez [a, *], P.I. Moreno [a], B.V. Alloway [b], G. Villarosa [c]

[a] Department of Ecological Sciences and Millennium Institute of Ecology and Biodiversity, Universidad de Chile, Santiago 7750000, Chile
[b] School of Geography, Environment and Earth Sciences, Victoria University of Wellington, Wellington 6140, New Zealand
[c] Instituto de Investigación en Biodiversidad y Medioambiente, CONICET-Universidad Nacional del Comahue, Bariloche 8300, Argentina

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A B S T R A C T

Disentangling the roles of paleofires and explosive volcanism from climatic drivers of past vegetation change is a subject insufficiently addressed in the paleoecological literature. The coastal region of the Chiloé Continental sector of northwestern Patagonia is ideal in this regard considering its proximity to active eruptive centers and the possibility of establishing comparisons with more distal, upwind sites where volcanic influence is minimal. Here we present a fine-resolution pollen and macroscopic charcoal record from Lago Teo with the aim of documenting the local vegetation and climate history, and assessing the role of disturbance regimes as drivers of vegetation change during the last ~10,000 years.

The Lago Teo record shows a conspicuous warm/dry interval between ~7500 and 10,000 cal yrs BP followed by a cooling trend and increase in precipitation that has persisted until the present, in agreement with previous studies in the region and interpretations of past southern westerly wind activity at multi-millennial scales. The presence of 26 tephras throughout the record allows examination of the relationship between explosive volcanism and vegetation change under contrasting climatic states of the Holocene. We found consistent statistically significant increases in *Tepualia stipularis* after tephra deposition over the last 10,000 years, in *Eucryphia/Caldcluvia* between 7500 and 10,000 cal yrs BP and in *Hydrangea* over the last 7500 years. Our results indicate a primary role of climate change as driver of long-term vegetation change and as a modulator of vegetation responses to volcanic disturbance at multidecadal and centennial timescales.

1. Introduction

Chiloé Continental, southern Chile, is an important sector to examine the interplay between vegetation, climate change, paleofires and the effects of explosive volcanism on terrestrial ecosystems (Fig. 1). Numerous paleoecological studies have been conducted in northwestern Patagonia but few have examined the effects of explosive volcanism on the structure, composition and dynamics of vegetation and fire regime-shifts at multi-decadal scales through a time continuum since local deglaciation (Jara and Moreno, 2014). Some studies in the region have identified millennial and multi-millennial-scale changes in temperature and precipitation of westerly origin since the last glacial maximum (Moreno and León, 2003; Pesce and Moreno, 2014), thus offering the opportunity to analyze potential climate-dependent responses of the rainforest vegetation and fire regimes to tephra deposition in the vicinity of active volcanic centers.

Recent eruptions at Volcán Chaitén (VC, 42°50′12.02″S, 72°39′5.52″W) and the Puyehue-Cordón Caulle (PCC, 40°35′5.06″S, 72°6′52.68″W) complex in 2008 and 2011, respectively, and the ongoing eruption of Volcán Calbuco (41°19′56.19″S, 72°36′42.22″W) have caused immediate social and economic impact on Chilean and Argentinean territory. These recent events have raised considerable awareness in the local inhabitants, Chilean and Argentinian authorities and the scientific community about the recurrence of rhyolitic eruptions (VC and PCC), a potentially devastating type of explosive volcanism, from putative dormant or inactive centers as well as their broad impacts on human activities and terrestrial ecosystems. Recent studies have detected a more active explosive eruptive history at VC than originally thought, raising the estimate of 1 or 2 events since 10,500 yr BP (Naranjo and Stern, 2004) to 6 events since 9750 cal yrs BP

* Corresponding author.
E-mail address: willybgo@ug.uchile.cl (W.I. Henríquez).

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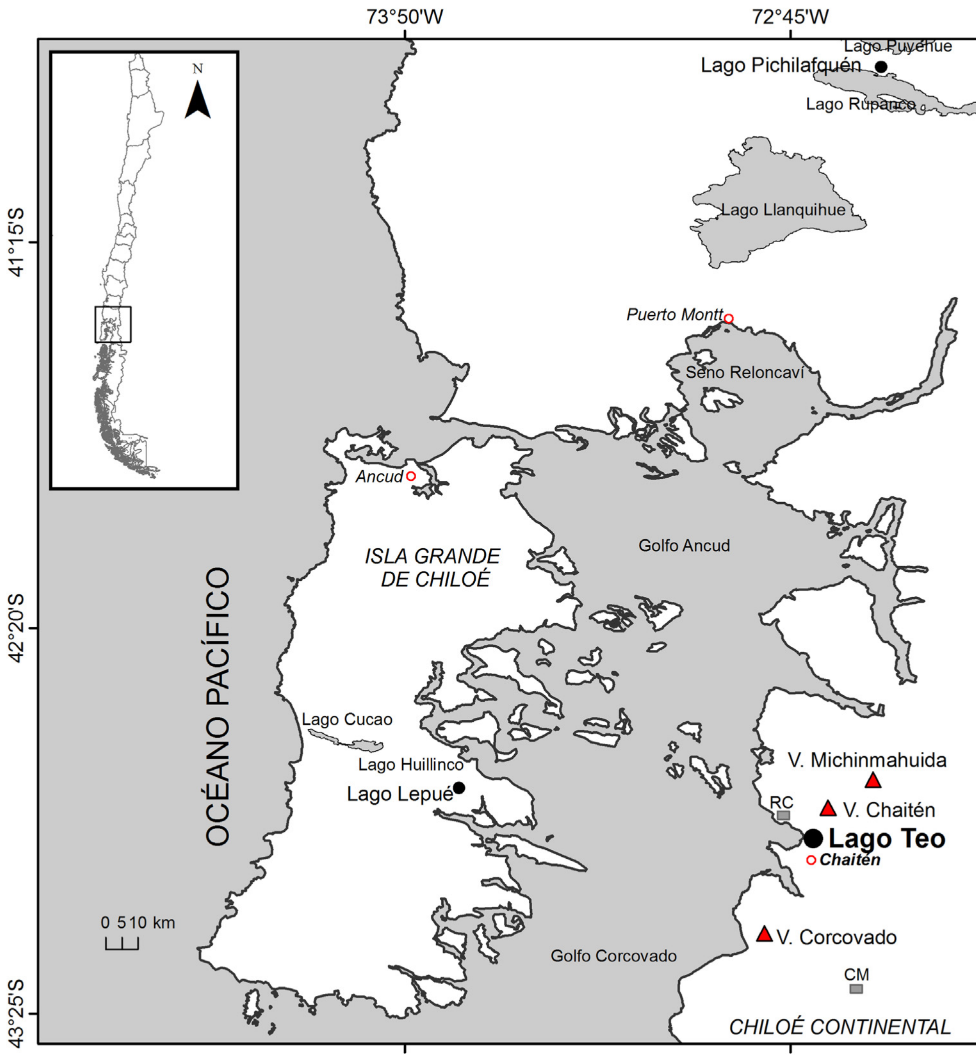

Fig. 1. Map of the study area indicating the name and location of pollen records from the Chilean Lake District discussed in this paper, our study site Lago Teo, and several geographic landmarks and volcanoes. Also shown are the location of the Cuesta Moraga (CM) and the road cut (RC) sites studied by Heusser et al. (1992).

(Amigo et al., 2013; Lara et al., 2013; Watt et al., 2013). Previous estimates were based on whole-rock geochemistry from the soil-forming environments, constrained by limited radiocarbon dating of key horizons. More recently we reported a continuous lake sediment record from Lago Teo, a small closed-basin lake located in the immediate vicinity of Chaitén township and volcano, that contains 26 tephras and spans uninterrupted the last 10,000 years (Moreno et al., 2015). This precisely dated record features 10 tephras derived from VC, including the 2008 eruption, 10 from the Michinmahuida Volcanic Complex (MVC) and 6 from as yet unknown eruptive sources (Moreno et al., 2015). The high frequency of volcanic activity and relatively high sediment-accumulation rates from Lago Teo motivated us to study the effects of volcanic disturbance on past vegetation and fire regime shifts at multi-decadal and centennial timescales under different climatic states during the Holocene.

In this study we present fine-resolution pollen and macroscopic charcoal records from sediment cores retrieved from Lago Teo (42°54′S, 72° 42′W, 45 masl, Fig. 1) to examine vegetation, fire and past climate change and their relationship to the record of explosive volcanism over the last 10,000 years. Lago Teo is located 7 km from Volcán Chaitén, ~24 km from Volcán Michinmahuida and ~33 km from Volcán Corcovado-Yanteles (Fig. 1). This situation is ideal for assessing the role of climate and volcanism as drivers of past vegetation and fire-regime changes during the Holocene, through analysis of the stratigraphic association of key changes in the paleoecological records and tephra layers within the same core. The Lago Teo data enabled us to address the following questions: i) What was the timing and direction of vegetation change in Chiloé Continental during the last 10,000 years?; ii) Did these changes occur in a gradual or abrupt manner? iii) How did the southern westerly winds vary through the Holocene? and iv) Did explosive volcanism alter the composition/structure/dynamics of the local vegetation and fire regimes at multidecadal/centennial timescales?

2. Study area

The Chilean Lake District (Fig. 1) features the Valle Longitudinal, a north-to-south trending tectonic depression bounded by Cordillera de la Costa and Cordillera de los Andes. Further south this landscape gives way to the Seno Reloncaví seaway, Golfo Ancud and Golfo Corcovado (Fig. 1) as a result of tectonic subsidence of the Valle Longitudinal. In this setting we find several fjords, channels and the Chilotan archipelago which consists of a myriad of small islands, islets and Isla Grande de Chiloé (Fig. 1), the largest and westernmost island of the archipelago. The adjacent Andean sector is locally known as Chiloé Continental and extends from 42°S to 44°S, and within its geographical confines we find several volcanic centers along the Southern Andean Volcanic Zone as a result of the subduction of the Nazca Plate underneath the South American Plate (Stern, 2004). The volcanic centers are associated with the Liquiñe-Ofqui fault zone (Cembrano et al., 1996), a major north–south fault system that extends 200 km from 38°S to 47°S (Cembrano and Lara, 2009).

The climate of the Chilean Lake District is temperate and wet with a precipitation minimum during the summer months. Metereological data from the Puerto Montt (41°26′S, 73°07′W, 90 masl), Ancud (41°54′S, 73°48′W, 116 masl) and Chaitén (42°55′S, 72°43′W, 3 masl) stations show annual precipitation values of 1900, 2840, and 3470 mm/year, respectively. Mean annual temperature in Puerto Montt reaches 10 °C (14.3°–6.5 °C: mean monthly temperature in January and July), in Ancud is 11.1 °C (15°–7.5 °C), and in Chaitén 11 °C (14°–8 °C).

Regional precipitation is delivered by storms embedded in the southern westerly winds (SWW), as revealed by a positive correlation between zonal wind speeds at 850 hPa and local precipitation measured in weather stations throughout western Patagonia (Garreaud, 2007; Moy et al., 2008). This correlation extends over a broad portion of the southern mid-latitudes implying that local precipitation in the study area is a good indicator of the position and strength of the SWW at a zonal scale. Climate variability associated to El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) impacts the precipitation of northwestern Patagonia as reflected by negative correlations with precipitation anomalies during the summer months (Montecinos and Aceituno, 2003). Moreover, positive summer temperature anomalies are positively correlated with SAM at regional scale (Villalba et al., 2012), and tree ring-data along western Patagonia reveal that natural fire activity is associated with positive departures of the SAM (Holz and Veblen, 2012).

Temperate rainforests dominate the region from sea level up to the treeline, located at ~1200 m a.s.l. The low to mid-elevation sectors of Chiloé Continental feature a transition from Valdivian to North Patagonian rainforest communities, attesting for large-scale latitudinal gradients in temperature, precipitation and summer moisture stress in the region (Heusser et al., 1999, 1981; Páez et al., 1994; Schmithüsen, 1956).

Valdivian rainforests are dominated by *Eucryphia cordifolia*, *Caldcluvia paniculata*, *Aextoxicon punctatum*, *Weinmannia trichospera*, along with *Nothofagus dombeyi*, Proteaceae (*Embothrium coccineum*, *L. ferruginea*, *Gevuina avellana*), Myrtaceae (*Myrceugenia planipes*, *Luma apiculata*) and the vine *Hydrangea serratifolia*. The North Patagonian rainforests are dominated by *N. dombeyi*, along with *Weinmannia trichosperma*, *Drimys winteri*, Myrtaceae (*Amomyrtus luma*) and conifers *Podocarpus nubigena*, *Saxegothaea conspicua*, *Fitzroya cupressoides* and *Pilgerodendron uviferum*. Although these forests share many species, the presence of key diagnostic species enables their distinction in palynological records. The palynomorph *E. cordifolia*/*C. paniculata* is a characteristic component of Valdivian rainforest communities which today dominate the warm lowland sectors of Valle Longitudinal and the foothills of Cordillera de los Andes in northwestern Patagonia, where relatively high temperatures and summer precipitation declines are most pronounced. North Patagonian rainforests can be distinguished in pollen records by the absence of *E. cordifolia*/*C. paniculata*, the presence of the cold-resistant hygrophilous conifers of the family Podocarpaceae (*P. nubigena*, *S. conspicua*) and Cupressaceae (*F. cupressoides* and *P. uviferum*), along with numerous other trees, epiphytes and vines.

Volcanic disturbance is an important influence on the composition, structure and dynamics of the rainforest vegetation in the vicinity of active volcanic centers. A recent example of this influence is the eruption of VC (Fig. 1) on May 2008 in Chiloé Continental (Lara, 2009), one of the largest explosive eruptions to have occurred in Patagonia since the 1990s (Major and Lara, 2013). The large volume of ash released (≤0.5–1.0 km^3) (Alfano et al., 2011; Watt et al., 2009) and pyroclastic flows produced severe damage on the native vegetation surrounding the volcano (Major and Lara, 2013; Swanson et al., 2013), including the burning and scorching of trees and forest floor, breakage of tree trunks and branches, complete to partial leaf defoliation, as well as abrasion of epiphytes and bark (Alfano et al., 2011; Major and Lara, 2013; Major et al., 2013; Watt et al., 2009).

Ecological studies have shown that rapid-growth, shade-intolerant, opportunistic rainforest species commonly occupy high-luminosity gaps or edges generated by disturbance, in otherwise continuous closed-canopy forests (Donoso, 2006; Gonzalez et al., 2002; Veblen et al., 1981). Fossil pollen records from northwestern Patagonia commonly feature plant taxa (palynomorphs) having those ecological attributes, among them are several species of the genus *Nothofagus*, along with the trees *W. trichosperma, Eucryphia/Caldcluvia, T. stipularis*, *D. winteri*,, shrubs such as *E. coccineum, Fuchsia magellanica, Escallonia* spp., bamboo species of the genus *Chusquea*, the giant herb *Gunnera tinctorea*, and ferns such as *Lophosoria quadripinnata, Blechnum* spp. Although several studies in the Chilean Lake District in southern Chile have reported on the historical and postglacial eruptive history and its effects on the local vegetation, there is a virtual absence of detailed stratigraphic records and chronologies near the Andean Range that monitor the effects of explosive volcanism on the vegetation composition, structure and dynamics over the past ~10,000 years.

3. Materials and methods

We retrieved sediment cores from the deepest part of Lago Teo (5.5 m water depth) from an anchored coring rig equipped with a 7.5-cm diameter aluminum casing tube, using a 5-cm diameter Wright piston corer and a 7.5-cm diameter sediment-water interface piston corer with a transparent plastic chamber. The former were sent intact to the laboratory of Quaternary Paleoecology, Facultad de Ciencias Universidad de Chile, wrapped in plastic foil and kept in a walk-cooler at 5 °C; the latter was sampled and bagged in the field at intervals of 1-cm thickness and then stored at 5 °C.

We characterized the stratigraphy, chronology and geochemistry of the Lago Teo record through textural descriptions, digital X radiographs, loss-on-ignition (LOI) analysis (Heiri et al., 2001), AMS dating of bulk sediment samples, and Electron Microprobe analysis of glass shards from each tephra layer. Details on these procedures and development of the age model can be found in Moreno et al. (2015).

We developed palynological and macroscopic charcoal records from continuous/contiguous 1-cc samples obtained from 1-cm thick intervals throughout the sediment cores, avoiding the tephra levels. The samples for palynological analysis were processed following a standard procedure that included 10% KOH, sieving with a 120-μm mesh, 40% HF and acetolysis (Faegri and Iversen, 1989). We added tablets with exotic *Lycopodium* spores to calculate the concentration (particles*cm^{-3}) and accumulation rate (particles*cm^{-2}*year^{-1}) of microscopic charcoal particles from each level (Fig. 2). The concentrates were mounted in methyl-silicone 2000 cs and analyzed with a binocular transmission microscope at 400× magnification. We counted a minimum of 300 pollen grains from trees, shrubs and herbs (terrestrial pollen) for each level. The percentage of each terrestrial taxon was calculated in reference to this sum. The percentages of aquatic and

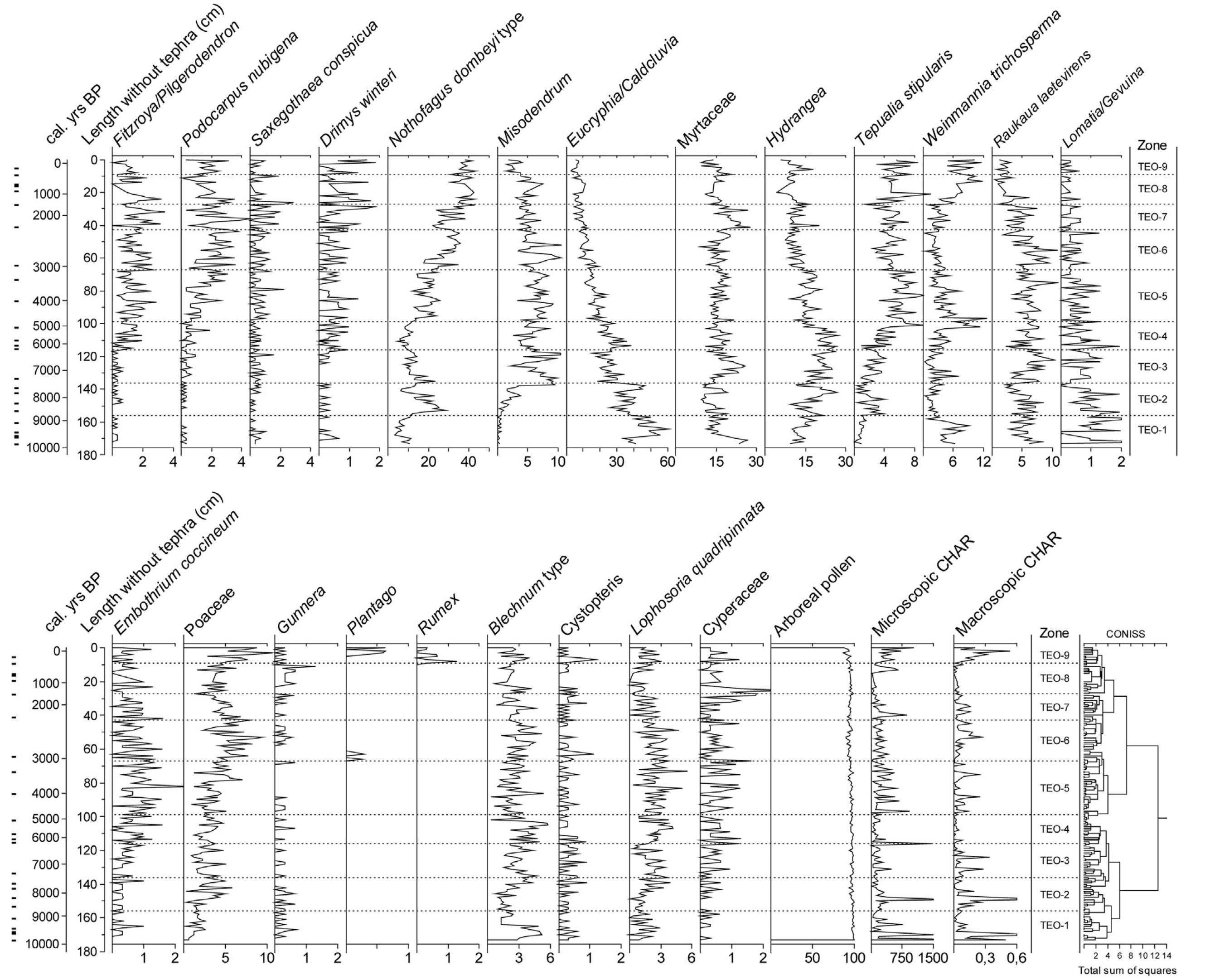

Fig. 2. Pollen percentage diagram and charcoal record from Lago Teo. The X axes represent abundance (%) of each taxa, the primary Y axis shows the core length without tephra, the secondary Y axis shows the age model in calendar years before present (cal. yrs BP). Microscopic and macroscopic charcoal are expressed as accumulation rate (particles*cm^{-2}*year^{-1}). The dashed horizontal lines represent pollen zone boundaries, the cluster analysis on the far right was constructed using a stratigraphically constrained cluster analysis. The short horizontal lines on the left indicate the position of each tephra.

pteridophytes were calculated in reference to hierarchically superior sums named Total pollen (terrestrial + aquatic pollen) and Total Pollen and Spores (total pollen + Pteridophyta), respectively. The results are presented in percentage pollen diagrams made with the Tilia program version 2.0.4 (Fig. 2).

The identification of palynomorphs was based on reference samples available in the laboratory of Quaternary Paleoecology of Universidad de Chile, as well as published descriptions and keys (Heusser, 1971; Villagrán, 1980). Most palynomorphs were identified to the family or genus level; in some cases it was possible to determine their identity to the level of species (*P.nubigena*, *S. conspicua*, *D. winteri*, *T. stipularis*, *W. trichosperma*, *Raukaua laetevirens*). The palynomorph *N. dombeyi* type includes the species *N. dombeyi*, *Nothofagus betuloides*, *Nothofagus pumulio*, *Nothofagus antarctica*, *Nothofagus alessandri*, *N. leonii* and *Nothofagus nitida*, *Fitzroya/Pilgerodendron* includes the cupressaceaous conifers *F. cupressoides* and *P. uviferum*, *Eucryphia/Caldcluvia* includes the species *E. cordifolia and C. paniculata*.

We performed a stratigraphically constrained cluster (Fig. 2) analysis on all terrestrial pollen taxa having abundance ≥2%, followed by recalculation of sums and percentages, to aid in the identification of pollen assemblage zones.

We tallied all microscopic charcoal particles (<120 μm) found on the pollen slides along with the exotic *Lycopodium* spores counts, these data are expressed as microscopic Charcoal Accumulation Rates (CHAR = particles*cm^{-2}*year^{-1}). We also counted all macroscopic charcoal particles from 2-cc sediment samples retrieved from 1-cm thick, continuous-contiguous sections throughout the cores. The procedure involves deffloculation in 10% KOH, careful sieving through 106 and 212 μm-diameter meshes to avoid breakage of individual charcoal particles visual inspection on a ZEISS KL 1500 LCD stereoscope at 10× magnification. These results are expressed as macroscopic CHAR. We performed time-series analysis of the macroscopic charcoal data 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 that purpose, we interpolated samples at the median time step between charcoal levels and subtracted the background component using a lowess robust to outliers smoother with a 1000-yr window width, and calculated locally defined thresholds through the time series to identify statistically significant charcoal peaks (99th percentile of a Gaussian distribution), which we interpret as local fire events.

We conducted Superposed Epoch Analyses (Prager and Hoenig, 1992) on selected plant taxa and macroscopic CHAR with the aim of detecting consistent statistically significant changes in the vegetation and paleofires in response to explosive volcanism. We analyzed the responses of the trees *Eucryphia/Caldcluvia*, *W. trichosperma*, *N. dombeyi* type, *T. stipularis*, Myrtaceae, *R. laetevirens*, the vine *Hydrangea*, the herb Poaceae and the ferns *Blechnum* type and *L. quadripinnata* given their constant presence in the pollen record and their modern ecological responses to disturbance (Jara and Moreno, 2014). We defined each tephra as a putative forcing event and assigned them a time zero (key event). Tephras temporarily spaced at less than 150 years were considered as single Volcanic Triggering Events (VTE). We then analyzed the variation of each taxon 50, 100 and 150 years before and after each VTE. We adjusted the data by removing the mean to every individual value at each temporal window (Genries et al., 2009). Because an extreme event could have a disproportionate effect over all the data series, we normalized by dividing all the values for each window series by its absolute maximum value (Adams et al., 2003).

4. Results

The stratigraphy, x-radiographs, LOI data and radiocarbon chronology of the Lago Teo record suggest undisturbed, continuous deposition of organic mud in a small closed-basin lake since ~10,000 cal yrs BP (Moreno et al., 2015; see Supplementary Figure 1 and 2, and Supplementary Table 1). The record includes 26 tephras, each represents fallout from individual eruptive events originating from VC, MVC and other unknown distal sources (UDS) (Supplementary Table 2).

The pollen record from Lago Teo consists of 169 levels we divided in 9 zones to facilitate description and discussion (Fig. 2). Table 1 summarizes these zones indicating the 3 or 5 most abundant pollen taxa of each zone in decreasing order. Here follows brief descriptions of each pollen zone indicating the stratigraphic and chronologic range, and the mean abundance of important taxa in parenthesis.

Zone Teo-1 (153–173 cm; 8800–10,000 cal yrs BP) is dominated by *Eucryphia/Caldcluvia* (47%), along with Myrtaceae (17%), *Hydrangea* (13%), *N. dombeyi* type (7%), *R. laetevirens* (6%) and *W. trichosperma* (5%). This zone stars with an increase in *Eucryphia/Caldcluvia*, and decrease in Myrtaceae and *W. trichosperma*. *R. laetevirens* (5%) and Poaceae (2%) show fluctuations throughout the whole zone between 3–8% and 1–3%, respectively. *T. stipularis* (1%) and *Hydrangea* show a sustained increase in their abundance.

Zone Teo-2 (137–157 cm; 7600–8800 cal yrs BP) is dominated by *Eucryphia/Caldcluvia* (37%), *N. dombeyi* type (17%) and *Hydrangea* (18%). This zone begins with a rapid decrease in *Eucryphia/Caldcluvia* (from 50 to 25%), along with an abrupt increase in *N. dombeyi* type (from 11 to 28%) and in *T. stipularis* (from 2 to 4 %). Sustained increases are evident in *Hydrangea* (18%) and *Misodendrum* (2%), *Blechnum* (2%) and *L. quadripinnata* (2%).

Zone Teo-3 (117–137 cm; 6300–7600 cal yrs BP) shows a marked decline in *Eucryphia/Caldcluvia* (from 41 to 18%, mean 25%), along with increases in Myrtaceae (18%), *T. stipularis* (3%) and *R. laetevirens* (7%). *T. stipularis* (3%) exhibits an increase with fluctuations between 1 and 4%, meanwhile *Misodendrum* (7%) shows a conspicuous increases and decrease in its abundance and *N. dombeyi* type (13%) present a smooth decrease. A noteworthy aspect is the appearance and increase the conifers *Fitzroya/Pilgerodendron* (<1%), *P. nubigena* (<1%) and *S. conspicua* (<1%).

Zone Teo-4 (100–117 cm; 4800–6300 cal yrs BP) begins with an increase in *Eucryphia/Caldcluvia* (27%) followed by its decrease until the end of this zone. The overall abundance of *Hydrangea* (22%), Myrtaceae (16%) and *R. laetevirens* (6%) remains stationary with variations between 14 and 27%, 10–20% and 2–8%, respectively. *T. stipularis* (4%) increases with fluctuations between 1 and 5% through most of this zone and increases abruptly toward the end of this zone (from 5 to 9%) in concert with *W. trichosperma* (from 5 to 11%; mean 5%). *N. dombeyi* type (10%), *Fitzroya/Pilgerodendron* (1%) and *L. quadripinnata* show slight increases.

Zone Teo-5 (68–100 cm; 3200–4800 cal yrs BP) is co-dominated by *N. dombeyi* type (19%), *Eucryphia/Caldcluvia* (17%) and Myrtaceae (16%). *W. trichosperma* (4%) decreases abruptly at the beginning of this zone from 13 to 3%, while *P. nubigena* (1%), *Fitzroya/Pilgerodendron* (1%) increase with fluctuations along this zone, and *S. conspicua* exhibits a slight rise.

Zone Teo-6 (44–68 cm; 2300–3200 cal yrs BP) characterized by a sustained increase in *N. dombeyi* type (30%) and declining trend in Myrtaceae (16%), *Eucryphia/Caldcluvia* (12%), *Hydrangea* (11%) and *Misodendrum* (6%). The conifers *Fitzroya/Pilgerodendron* (2%) and *P. nubigena* (3%) reach their peak abundance in the record.

Zone Teo-7 (28–44 cm; 1600–2300 cal yrs BP) starts with an abrupt decrease in *N. dombeyi* type (from 31 to 22%), and a rise in Myrtaceae (21%). *Eucryphia/Caldcluvia* (9%) and Poaceae (5%) and *Misodendrum* (5%) show a decreasing trend, while *Hydrangea* (12%) shows no variation. *Eucryphia/Caldcluvia* maintains its decreasing trend in this zone, while *Fitzroya/Pilgerodendron* (~2%) and *P. nubigena* (2%) and *S. conspicua* (1%) show conspicuous increases and decreases in their abundance.

Zone Teo-8 (10–28 cm; 500–1600 cal yrs BP) is dominated by *N. dombeyi* type (38%) along Myrtaceae (15%) and *Hydrangea* (10%), along with *Eucryphia/Caldcluvia* (8%) and *W. trichosperma* (7%). Myrtaceae and *Hydrangea* decline as *W. trichosperma* increases until the end of this zone. *Eucryphia/Caldcluvia* shows variations between 4 and 11% in its abundance.

Zone Teo-9 (0–10 cm; present-500 cal yrs BP) is dominated by *N. dombeyi* type (37%), Myrtaceae (15%), *Hydrangea* (11%), *W. trichosperma* (8%), Poaceae (7%), *Eucryphia/Caldcluvia* (6%) and *Tepualia stipulari* s(6%). *Rumex* (<1%) and *Plantago* (<1%) appear during this zone and remain in trace abundance.

Table 1
Summary of the pollen zones from Lago Teo, indicating their age range and dominant taxa in descending order of abundance.

Age range (cal. yrs BP)	Zone	Dominant taxa
0–500	TEO-9	*Nothofagus*, Myrtaceae, *Hydrangea*, *Weinmannia*
500–1600	TEO-8	*Nothofagus*, Myrtaceae, *Hydrangea*,*Eucryphia/Caldcluvia*, *Weinmannia*
1600–2300	TEO-7	*Nothofagus*, Myrtaceae, *Hydrangea*,*Eucryphia/Caldcluvia*, Poaceae
2300–3200	TEO-6	*Nothofagus*, Myrtaceae, *Eucryphia/Caldcluvia*
3200–4800	TEO-5	*Nothofagus*, *Eucryphia/Caldcluvia*, Myrtaceae
4800–6300	TEO-4	*Eucryphia/Caldcluvia*, *Hydrangea*, Myrtaceae, *Nothofagus*, *Raukaua*
6300–7600	TEO-3	*Eucryphia/Caldcluvia*, *Hydrangea*, Myrtaceae, *Nothofagus*, *Misodendrum*
7600–8800	TEO-2	*Eucryphia/Caldcluvia*, *Nothofagus*, *Hydrangea*
8800–10,000	TEO-1	*Eucryphia/Caldcluvia*, Myrtaceae, *Hydrangea*

We developed microscopic and macroscopic charcoal records from 169 contiguous levels to characterize regional and local fire occurrence, respectively (Fig. 2). Microscopic and macroscopic CHAR show similar stratigraphies throughout the record. Microscopic CHAR are high between 9710–9850 and 8250–8500 cal yrs BP (pollen zone Teo-1 and Teo-2), along with discrete low-magnitude increases at 7260 and 6230 cal yrs BP (Teo-3), a series of pulses between 2160 and 4700 cal yrs BP (Teo-5 and Teo-6) and an increase over the last 570 years (Teo-8 and Teo-9). Macroscopic CHAR shows high values between 9710–9850 and 8250–8500 cal yrs BP (Teo-1 and Teo-2), multiple discrete pulses between 2600 and 7330 cal yrs BP (Teo-3, Teo-4, Teo-5 and Teo-6) and an increase during the last 500 years (Teo-9). Time-series analysis of the macroscopic charcoal record with CharAnalysis shows variation in frequency and magnitude of local fire peaks during the last 10,000 years. We identify 12 statistically significant fire peaks through the record, with magnitudes that vary from 1 to 12 particles*cm^{-2}*$peak^{-1}$ (Fig. 3). We observe lower frequency of fire events occurred between 7000 and 9000, 5000–6000 and 1000–4000 cal yrs BP, and high frequency of fire events between 6000–7000 and 4000–5000 cal yrs BP and over the last 1000 years (Fig. 3).

The Superposed Epoch Analysis (SEA) reveals time-dependent vegetation changes in reference to explosive volcanic events near Lago Teo. According to SEA *T. stipularis* shows consistent statistically significant increases between 100 and 150 years (95% confidence level: CL) after VTEs during the last 10,000 years; *Eucryphia/Caldcluvia*, on the other hand, shows consistent increases (0–50 years, 90% CL, n = 16) over the same time frame. *N. dombeyi* type, *W. trichosperma*, *Hydrangea*, Poaceae, Myrtaceae, *R. laetevirens*, *Blechnum* type, *L. quadripinnata* and macroscopic charcoal do not show consistent or statistically significant changes to the deposition of tephras (Fig. 4 and Supplement Figure 3). We explored the possibility that the responses of these taxa might have been modulated by the mean multi-millennial climate phases recognized in the region between 7500 and 10,000 cal yrs BP (warm/dry) and since 7500 cal yrs BP (cool/moist, see discussion section). Between 7500 and 10,000 cal yrs BP we detect prominent declines in *T. stipularis* (0–50 years, CL = 90%), significant increases in *Eucryphia/Caldcluvia* (50–100 years, CL = 95%), and consistent increments in Poaceae (0–50 years, 90% CL) after 6 VTEs (Fig. 4). Also, since 7500 cal yrs BP we detect consistent increments in *Eucryphia/Caldcluvia* (0–50 years, 90% CL), and significant increases in *Hydrangea* (0–50 years, 95% CL) (Fig. 4) after 12 VTEs. When analyzing responses to different volcanic sources, SEA detects consistent statistically significant increases in *W. trichosperma* (100–150 years, 95% CL, n = 5) after VTEs originating from VC, consistent increments in *Lophosoria* (0–50 years, 90% CL), and declines in Myrtaceae (50–100 years, 90% CL), Also, significant increases in *Hydrangea* (0–50 years, 95% CL, n = 7) after VTEs originating from MVC (Fig. 5), and lack of consistent significant response in all other taxa irrespective of tephra source (Fig. 5 and Supplement Figure 4).

We also conducted SEA on the same taxa to evaluate the role of local fires as agents of local vegetation change. The analysis reveals lack of consistent responses for all taxa over the last 10,000 years and under different climatic scenarios (results not shown).

5. Discussion

The pollen record from Lago Teo indicates dominance of closed-canopy, broad-leaved evergreen temperate rainforests in the lowlands of Chiloé Continental since 10,000 cal yrs BP, with little physiognomic variation (mean of arboreal pollen = 96 ± 2%). The palynology features preeminence of the Valdivian rainforest tree *Eucryphia/Caldcluvia* between 4800 and 10,000 cal yrs BP (pollen zones Teo-1, 2, 3, and 4), along with Myrtaceae, low abundance of *N. dombeyi* type and *T. stipularis*, and discrete increases in Poaceae and *Blechnum*. The palynology then shifts gradually to dominance of *N. dombeyi* type for the remainder of the record, along with other rainforest trees (Myrtaceae, *R. laetevirens*), shrubs (*E. coccineum*), herbs (Poaceae), vines (*Hydrangea*), ferns (*Blechnum* and

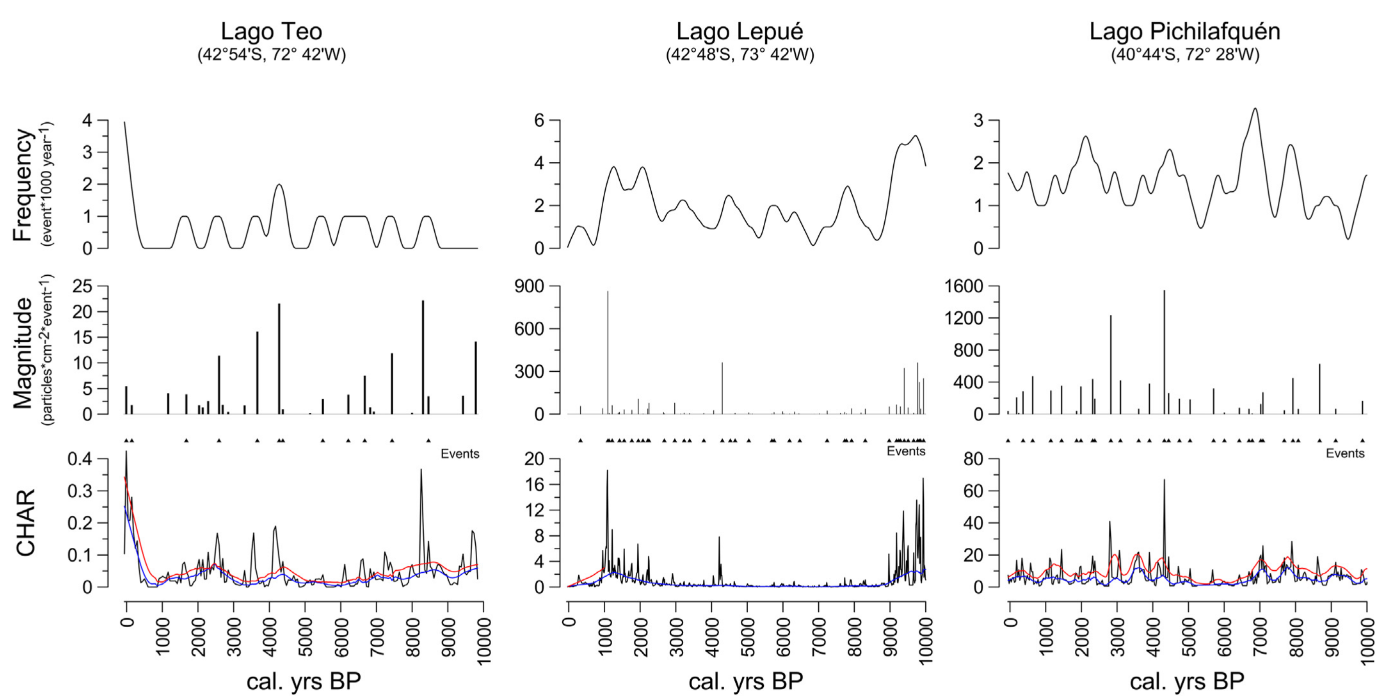

Fig. 3. Time series analyses on the Lago Teo, L. Lepué and L. Pichilafquén macroscopic charcoal records. The diagrams include CHAR, magnitude, frequency and statistically significant charcoal peaks detected by CharAnalysis. Each interpolate CHAR series is shown with the locally defined thresholds for charcoal peaks (red line) and background CHAR (blue line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

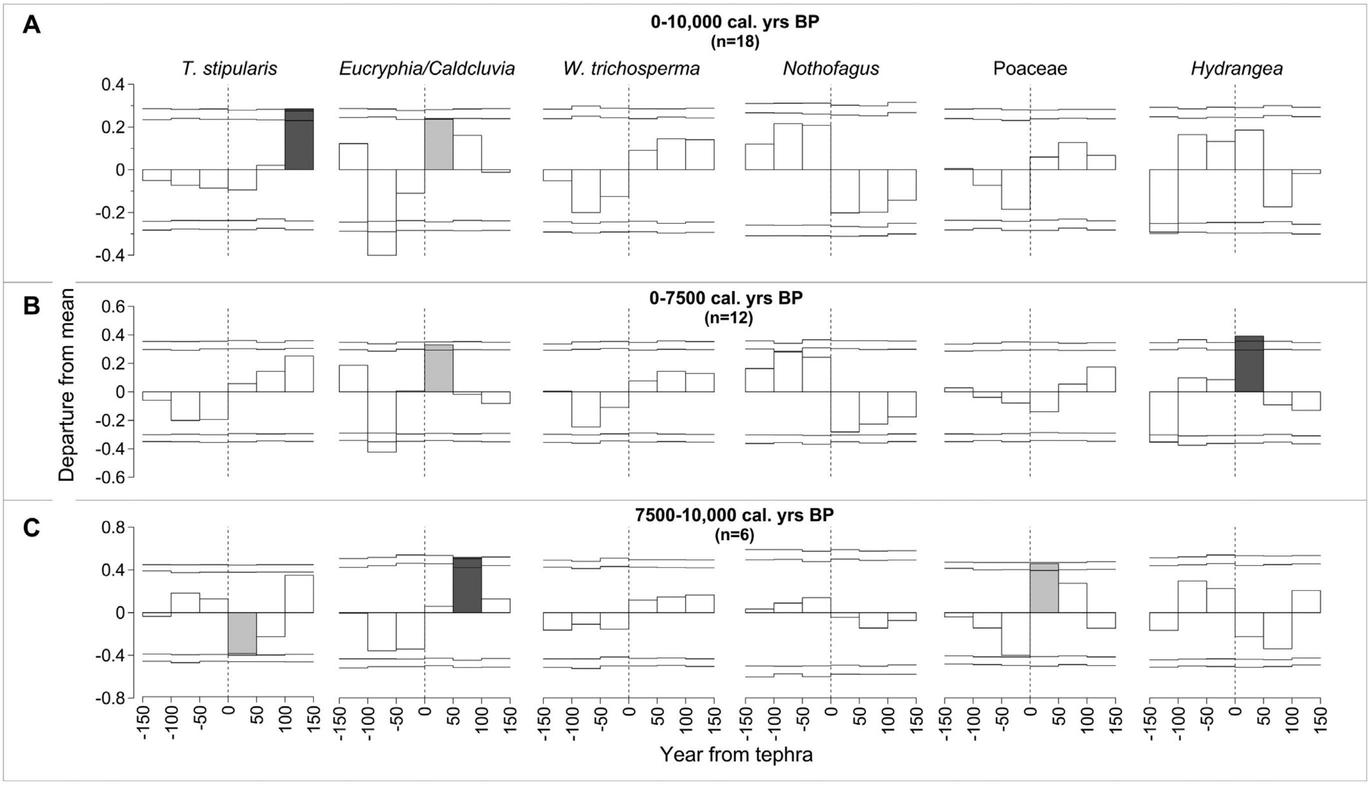

Fig. 4. Superposed Epoch Analysis applied toselected pollen taxa from Lago Teo in three different time ranges: A) the last 10,000 years, B) warm/dry interval between 7500 and 10,000 cal yrs BP, C) cool/humid interval between 0 and 7500 cal yrs BP. The years 0 indicated the VTEs (vertical dash lines). The 95% and 90% confidence level (horizontal lines) were calculated with Monte Carlo randomization using 5000 iterations. Significant changes (95% CL) are represented as dark grey rectangle, strong changes (90% CL) as soft grey rectangle.

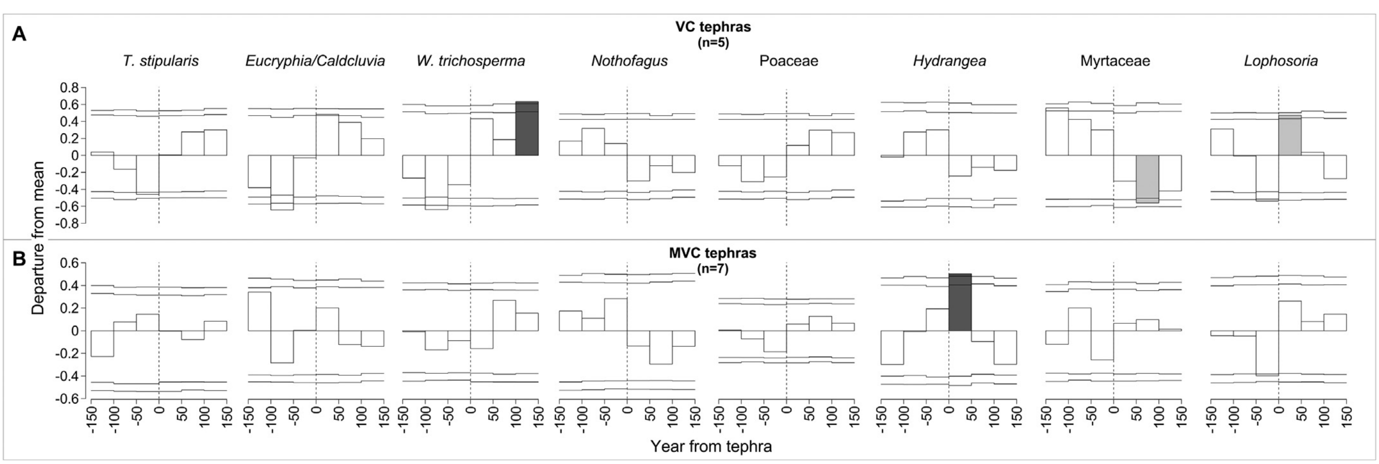

Fig. 5. Superposed Epoch Analysis applied to selected pollen taxa from Lago Teo in reference to tephras derived from A) Volcán Chaitén and B) Volcán Michinmahuida. The year 0 indicate the VTEs (vertical dash lines). The 95% and 90% confidence level (horizontal lines) were calculated with Monte Carlo randomization using 5000 iterations. Consistent increment is represented (90% CL) as soft grey rectangle.

L. quadripinnata), the hygrophilous *T. stipularis*, *D. winteri* and cold-resistant North Patagonian conifers (*Fitzroya*/*Pilgerodendron*, *P. nubigena* and *S. conspicua*). This transition started at ~7600 cal yrs BP (Teo-3) and proceeded in a gradual manner until ~4800 cal yrs BP, overprinted by centennial-scale variations.

Eucryphia/Caldcluvia includes the species *E. cordifolia* and *C. paniculata*, the former is a thermophilous drought-resistant tree characteristic of the Valdivian rainforest, which develops in the lowlands and upslope until 300 masl on the western flank of the Andes at 42°S (Heusser, 1981; Heusser et al., 1999; Páez et al., 1994; Schmithüsen, 1956). Species of the palynomorph *N. dombeyi* type, on the other hand, are present along all vegetation zones along the altitudinal and climatic gradient and co-occur with North Patagonian conifers in sectors located above 450 masl in areas with higher orographic precipitation and lower temperatures (Heusser, 1981; Heusser et al., 1999; Páez et al., 1994; Schmithüsen, 1956). Therefore, the pollen record from Lago Teo suggests an increase in the dominance of the North Patagonian rainforest at the expense of

Valdivian rainforest communities starting at 7600 cal yrs BP, aspect we interpret as a multi-millennial trend toward cooler and wetter conditions.

N. dombeyi type and *W. trichosperma* increase and reach their maxima during the last 1600 years (Teo-8 and Teo-9), along with declines in *Fitzroya/Pilgerodendron*, *P. nubigena*, *S. conspicua* and the lowest abundance of *Eucryphia/Caldcluvia*. In this context we observe conspicuous increases in Poaceae and the appearance of *Rumex* and *Plantago* shortly after ~389 cal yrs BP (313–473 cal yrs BP confidence interval), defining an interval of modest forest opening and onset of disturbance of European origin. *Rumex* and *Plantago* are exotic herbs introduced in the region at the onset of Spanish settlement, which started at AD 1888 in the Chiloé Continental area (Martinić, 2004). This divergence in timing can be attributed to the lack of firm chronologic constraints in the upper 10 cm of the Lago Teo record.

5.1. Disturbance paleoecology

The Lago Teo record demonstrates that explosive volcanism has been a frequent phenomenon in the Chaitén sector of the southern Andes during the last 10,000 years (Moreno et al., 2015). Our results indicate an average recurrence of ~400 years between eruptive events with a background of at least 1 explosive eruption per thousand-year bin and peak frequency of events between 9000 and 10,000 cal yrs BP and during the last 1000 years (Fig. 6). This constant supply of tephric material allows examining time and climate-dependent responses of the vegetation and fire regimes to volcanic influence since 10,000 cal yrs BP. SEA allowed detection of consistent statistically significant increases in *T. stipularis* within 100–150 years following all VTEs (n = 18) over the last 10,000 years (Fig. 4). The character of this response, however, is dependent upon the background paleoclimate state as suggested by consistent, though statistically non-significant (CL = 90%), declines of this species within 0–50 years after VTEs during the warm/dry multi-millenial interval between 7500 and 10,000 cal yrs BP, and a trend toward consistent non-significant (CL = 90%) increases over the cold/wet phase characteristic of the last 7500 years (Fig. 4). The tree *T. stipularis* commonly forms dense thickets in waterlogged substrates, with individuals growing partly submerged along the lake margins; thus the results of SEA suggest that forest openings associated to volcanic disturbance favored the establishment of *T. stipularis* over the last 10,000 years in sectors with impeded drainage in the vicinity of Lago Teo during extended cool/moist conditions. A different behavior is evident in *Eucryphia/Caldcluvia,* which exhibits consistent statistically significant increases within 50–100 years after VTE between 7500 and 10,000 cal yrs BP, and consistent non-significant (CL = 90%) increases over the last 7500 years (Fig. 4). These results suggest that *Eucryphia/Caldcluvia* dominated forest gaps originated from volcanic disturbance during the warm/dry multi-millennial phase between 7500 and 10,000 cal yrs BP, along with consistent, though statistically non-significant (CL = 90%) increases in bamboo species of the family Poaceae following tephra deposition (Fig. 4). Quite a different response in evident over the cool/wet multi-millennial phase over the last 7500 years during which the vine *Hydrangea* shows consistent, statistically significant increases and *Eucryphia/Caldcluvia* shows strong, though non-significant (CL = 90%) increases after tephra deposition.

SEA reveals persistent, though statistically non-significant (CL = 90%) declines in *N. dombeyi* type in relation to all VTEs over the last 10,000 years, a particularly strong pattern since 7500 cal yrs BP (Fig. 4). This lack of statistical significance, however, must be taken with caution considering that species of the genus *Nothofagus* produce large quantities of pollen which are carried over long distances by the prevailing westerly winds. Thus, local declines in this taxon might be compensated by the advection of extra-local *Nothofagus* pollen grains into Lago Teo masking genuine, potentially significant local declines driven by local volcanic disturbance.

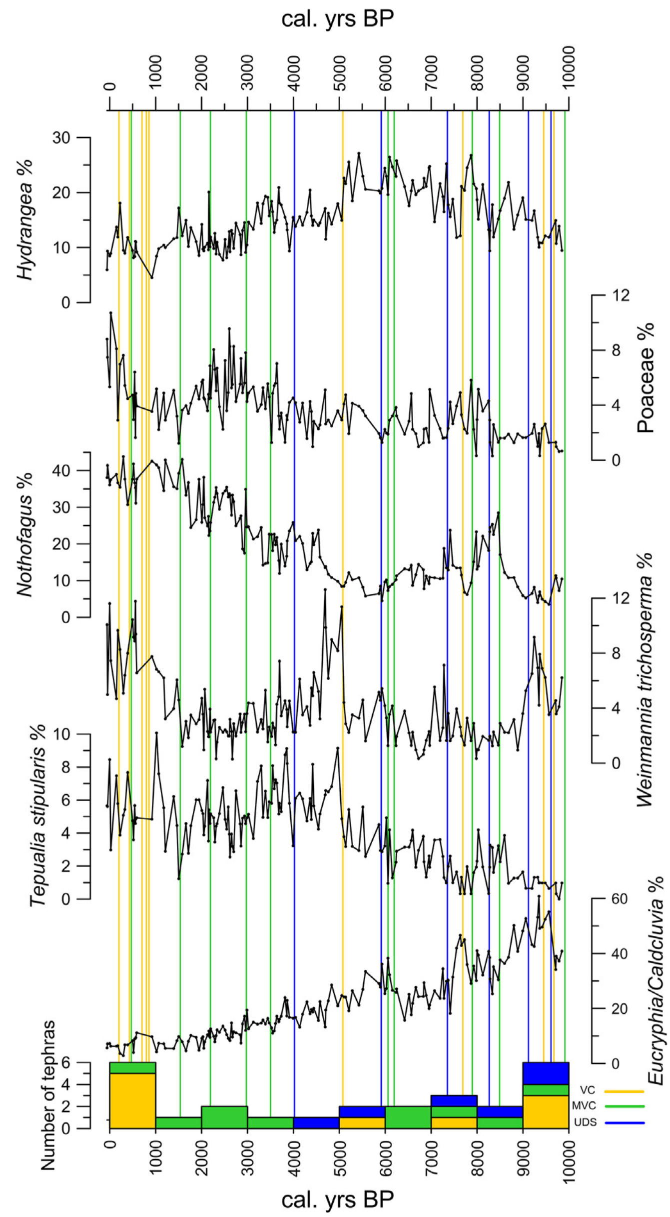

Fig. 6. Summary diagram of selected pollen taxa, CHAR and tephras from Lago Teo (vertical lines). The X-axis indicates the age model in cal. yrs BP. Yellow filling in the histogram and vertical lines represent tephras derived from Volcán Chaitén (VC), green filling in the histogram and vertical lines represent tephras from the Michinmahuida Volcanic Complex (MVC), and blue filling in the histogram and vertical lines represent all other tephras of unknown distal source (UDS) (Moreno et al., 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We also explored the influence of tephra origin (VTEs originating from VC [n = 5] and MVC [n = 7]) on the same taxa and found lack of consistent statistically significant changes (95% CL) over the last 10,000 years (Fig. 5 and Supplementary Figure 4) except in *W. trichosperma* and *Hydrangea*. The tree *W. trichosperma* shows consistent statistically significant increases 100–150 years after the deposition of tephras originating from VC (CL = 95% n = 5), while the vine *Hydrangea* shows consistent statistically significant increases 0–50 years after the deposition of tephras originating from MVC (n = 7). Also, we detected in *Lophosoria* a trend toward consistent increases 0–50 years and consistent decrease in Myrtaceae 50–100 years after the deposition of tephras originating from VC (CL = 90% n = 5). These results demonstrate a positive response of vegetation to disturbance by explosive volcanism originating from nearby VC and an abundance increase of this vine species after events from MVC.

The effect of tephra thickness on vegetation change is evident in *Hydrangea* (rapid decline) and *W. trichosperma* (rapid increase) associated to the deposition of a 31-cm thick pyroclastic layer originating from VC at ~ 5000 cal yrs BP (LTT-12, VTE-9). Another thick layer from VC deposited at ~7700 cal yrs BP (LTT-17 VTE-13, 48-cm thick) precedes notable declines in *Hydrangea* and *Eucryphia/Caldcluvia*, along with increases in *N. dombeyi* type and *T. stipularis*. Multiple closely spaced tephras antedate major increases in *Hydrangea*, Poaceae and *W. trichosperma* (LTT-4, 5 and 6 [VTE-3] originating from VC between ~600 and 850 cal yrs BP), and increases in *Eucryphia/Caldcluvia* and *W. trichosperma* (LTT-25, 24, 23 and 22 [VTE-18] originating from VC (except LLT-24) between ~9450 and 9700 cal yrs BP.

5.2. Regional comparisons and implications

Vegetation and fire-history records from the Chilean Lake District have identified multi-millennial and millennial-scale fluctuations in temperature and precipitation during and since the last glaciation (Abarzúa and Moreno, 2008; Jara and Moreno, 2014; Montade et al., 2012; Moreno, 2004; Pesce and Moreno, 2014). The lack of detailed studies on pre-Andean sectors of the Chiloé Continental area, however, has resulted in an important gap in our knowledge about the regional vegetation, fire-regime and climate history in an area of northwestern Patagonia having several active volcanic centers. Notable exceptions are studies carried out by Heusser et al.,(1992), who published pollen records from Cuesta Moraga (CM, 43°25 S, 72°23 W, 700 masl) and a road cut (RC, 42°54 S, 72° 44 W, 60 masl) (Fig. 1) near Chaitén township.

At multi-millennial timescale the Lago Teo record replicates the pollen-based paleoclimate inferences from the mainland (Moreno, 2004; Moreno and León, 2003), Isla Grande de Chiloé (Abarzúa and Moreno, 2008; Pesce and Moreno, 2014) and a marine pollen record obtained from Seno Reloncaví (Montade et al., 2012) in northwestern Patagonia, all of which indicate weaker SWW influence at regional scale at the beginning of the Holocene and an intensification starting at ~ 7500 cal yrs BP. The transition at ~7500 cal yrs BP appears to have been a gradual phenomenom from a Valdivian to a North Patagonian rainforest assemblage. We note that the Cuesta Moraga pollen record, also located in Chiloé Continental (Heusser et al., 1992), shows a conspicuous increment in Cyperaceae between ~8800 and 11,500 cal yrs BP, attesting for the establishment of a minerogenic bog which then shifted to an ombrotrophic bog, probably representing a local response to increased precipitation of westerly origin over the last 7500 years.

Comparison of the vegetation and fire histories from Lago Teo (LT) with similar records from Lago Lepué (LL, 42°48′S, 73° 42′W) (Pesce and Moreno, 2014) and Lago Pichilafquén (LP, 40°44′S, 72° 28′W) (Jara and Moreno, 2014) (Fig. 1) reveals interesting similarities and differences: (i) all sites were dominated by temperate, evergreen broad-leaved rainforests over the last 10,000 years, suggesting similar temperature and precipitation conditions at regional scale; (ii) all sites show evidence of explosive volcanism, the recurrence of which (iii) varies among sites with maximum frequency in the Andean foothills (LP and LT with 21 and 26 distinct tephras, respectively) and minimum in the westernmost (upwind) site (LL with 2 distinct tephras); (iv) a west-to-east (LL vs. LT) and north-to-south (LP vs. LT) decline in fire frequency and magnitude (Fig. 3), (v) consistent significant association between VTE and local fires in LP and the opposite in LT (with 16 and 18 VTE respectively). This pattern suggests that climate and vegetation changes in this temperate, maritime, hyperhumid sector of Chiloé Continental were not conducive for persistent long-term shifts in fire regime since 10,000 cal yrs BP. (vi) *Eucryphia/Caldcluvia* remains abundant in the (northern) LP record between 2700 and 7500 cal yrs BP, whereas the LL and LT records show steady multi-millennial gradual declines until the present, also (vii) *Eucryphia/Caldcluvia* shows consistent significant association with VTE over the last 10,000 years in LP, whereas in the LT record this relationship is strong over the same interval and only becomes significant between 7500 and 10,000 cal yrs BP, suggesting a climate-modulated relationship between volcanic disturbance and the spread of fast-growth thermophilous trees in in the vicinity to active volcanic centers in northwestern Patagonia.

6. Conclusions

The pollen record from Lago Teo shows multi-millennial dominance of Valdivian rainforest between 7500 and 10,000 cal yrs BP, followed by a gradual replacement by North Patagonian rainforests over the last ~7500 years in the Andean foothills of Chiloé Continental. Aspects of this transition can be explained by a multi-millennial cooling trend concomitant with a shift from weaker-than-present SWW during the early Holocene to stronger SWW since 7500 cal yrs BP (Moreno, 2004).

The tephrostratigraphy of Lago Teo shows 26 airfall deposits which precede conspicuous changes in the fossil pollen record. We found consistent statistically significant declines in *T. stipularis* and increases in *Eucryphia/Caldcluvia* following the deposition of tephras between 7500 and 10,000 cal yrs BP, and increases in *T. stipularis* over the last 10,000 years. We also observe consistent and significant increases in *Hydrangea* after the deposition of tephras between 0 and 7500 cal yrs BP and after tephras originating from the Michinmahuida Volcanic Center, and consistent significant increases in *W. trichosperma* after tephras originating from the Volcán Chaitén. Thick tephras also precede major vegetation changes, however, the paucity of these events prevents us from drawing firm conclusions. In sum, our results suggest that explosive volcanism has influenced the structure and composition of the temperate rainforests of Chiloé Continental over the last 10,000 years, and that the response of different opportunistic tree species is modulated by the mean climate state.

We identify high paleofire activity between 8250 and 9850 cal yrs BP and during the last 520 years, and lack of consistent statistical significance association between tephra deposition and local fire. This sporadic nature of local fire close to Lago Teo contrasts with the multi-millennial pattern at regional scale (Power et al., 2008; Whitlock et al., 2007), suggesting that climate and vegetation changes in this hyperhumid sector of Chiloé Continental were not conducive for persistent long-term shifts in fire regime during the last 10,000 years and that explosive volcanism did not influence fire regimes near Lago Teo during the Holocene.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2015.06.017.

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