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Holocene changes in forest composition in northern Patagonia responded to climate with little impact of disturbance

Valentina Álvarez-Barra [a, b, *], Thomas Giesecke [a, c], Sonia L. Fontana [d, e]

[a] Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Science, Georg-August-Universität Göttingen, Wilhelm-Weber-Str. 2a, 37073, Göttingen, Germany
[b] Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Moraleda 16, 5951601, Coyhaique, Chile
[c] Palaeoecology, Department of Physical Geography, Faculty of Geosciences, Utrecht University, P.O. Box 80115, TC, 3508, Utrecht, the Netherlands
[d] Cátedra de Palinología, Facultad de Ciencias Naturales y Museo, UNLP, Calle 64 n◦3, 1900, La Plata, Argentina
[e] Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Büsgenweg 1a, 37077, Göttingen, Germany

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ABSTRACT

Postglacial climate change and changing disturbance regimes have shaped the vegetation composition in the forest-steppe ecotone in northern Patagonia (Argentina and Chile; lat. 40°–lat. 43°S). Several investigations between 41° and 43°S document shifts in the position of the forest-steppe ecotone and the population expansion of the cypress *Austrocedrus chilensis*, while little is known about the vegetation dynamic of *Nothofagus alpina* and *Nothofagus obliqua* within the Lácar basin. With the aim to contribute to this respect, the sediments of a small lake within a dense *Nothofagus* forest, in the Lanín National Park were collected and analysed in high resolution for pollen charcoal and sediment composition. Additionally, this work assessed the role of natural disturbance on vegetation composition. Results document the environmental history for the last 11,600 years. The record indicates high fire activity during the early Holocene, associated with dry conditions and the presence of a diverse *Nothofagus* shrubland. The middle Holocene starts with increased percentage of Cupressaceae pollen (up to 15%) which drops following the dominance of *Nothofagus* associated with wet conditions and low fire frequency. The late Holocene is marked by the rise in the abundance of *N. obliqua* and *N. alpina*, documenting the spread and increased importance of these trees within the Lácar basin during the last two millennia. A statistically significant effect of ash deposition on overall vegetation composition could not be detected, while *Hydrangea* and *Lomatia hirsuta* seem to benefit from ash fall. Fire affected stands of *A. chilensis* and *N. obliqua*/*N. alpina*, but climate was likely the dominant factor controlling average vegetation composition. Recent anthropogenic disturbance is noticeable by the presence of introduced taxa *Rumex*, *Plantago* and *Pinus*, and by the decrease in the percentage of *Nothofagus obliqua*-type, associated to extensive timber activities around the Lácar basin.

1. Introduction

Understanding the function and the dynamic of forest communities on decadal to centennial timescales is an important prerequisite for implementing adequate management strategies, because long-term perspectives on landscape dynamics and cycles allow to set feasible goals for guiding resource managers (Davies et al., 2014; Froyd and Willis, 2008; Wingard et al., 2017). Pollen and charcoal from lake sediments allow for the reconstruction of ecosystem dynamics and offer insights into how climate and disturbance regimes changed in the past (Bartlein et al., 2011; Harrison et al., 2009). Disentangling the effect of different drivers of ecosystem dynamics at millennial and centennial scales, such as disturbance regimes and climate change is an important requirement to understand past vegetation development and therefore, to reconstruct past climate change. Both of these overall objectives motivate palaeoecological research in northern Patagonian Argentina, within the climatically sensitive forest-steppe ecotone, which is subject to frequent disturbances by forest fires and volcanic ash deposition.

* Corresponding author. Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Science, Georg-August-Universität Göttingen, Wilhelm-Weber-Str. 2a, 37073, Göttingen, Germany.
E-mail address: valentina.alvarez@biologie.uni-goettingen.de (V. Álvarez-Barra).

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Past and present climate variability in Patagonia is mainly controlled by the Southern Westerlies (SW) (Fletcher and Moreno, 2011; Garreaud, 2009; Mansilla et al., 2016; Rojas et al., 2009). Westerly airflow is blocked by the north-to-south orientation of the Andes, resulting in enhanced precipitation on the windward slopes of the Andes and a rain shadow to its lee (Viale and Garreaud, 2015). This phenomenon results in the sharp west-east precipitation gradient, determining the location of the forest-steppe ecotone, which is interpreted as a proxy for millennial-scale changes in climate, as it is documented in several investigations of the east Andes (Iglesias et al., 2011, 2014; Whitlock et al., 2006). Some of these studies are situated near the steppe within or near woodlands dominated by *Austrocedrus* between 42° and 43°S (e.g. Lake Cóndor, L. Mosquito; Iglesias et al., 2011), while other are located within a mixed *Nothofagus-Austrocedrus* forest between 41° and 42°S (e.g. Lake Moreno, L. El Trébol, L. Mascardi; Whitlock et al., 2006). Nevertheless, little information is available from areas further north, east of the Andes between 39° and 40°S, within the main geographical distribution of *Nothofagus alpina* and *N. obliqua* in Argentina (Sabatier et al., 2011).

In addition to climate, disturbance regimes such as volcanic eruptions and fire, together with anthropogenic impact also play an important role in shaping landscape patterns and vegetation composition (Jentsch et al., 2002; Johnstone et al., 2016). In forest ecosystems, disturbance creates patchiness, spatial and temporal heterogeneity, and alters successional pathways (Jentsch et al., 2002). For instance, repeated disturbance events can affect regeneration patterns and consequently change species composition (Van der Maarel, 1996). Moreover, disturbance also alters site productivity and resource availability, affecting colonization and growth of plants (Jentsch et al., 2002). Additionally, the effects of a disturbance event depend on the state of the community prior to the disturbance as well as on biotic and physical factors (White and Pickett, 1985).

Among natural phenomena, fire has been by far the most studied disturbance agent in Patagonia and its role in the past and the present is crucial (Holz et al., 2017). The investigations conducted in the region suggest that the magnitude and frequency of fire events throughout the Holocene are linked to changes in temperature and effective moisture (Moreno et al., 2018a), influencing moisture and biomass available for ignition and fire spread. Historical fire dynamics have been analysed using tree-ring records and sedimentary records from lakes and bogs (e.g. Holz et al., 2012; Moreno et al., 2018b; Whitlock et al., 2007). Fire patterns during the Holocene east of the Andes (41°–44°S) are synthesized by Nanavati et al. (2019), suggesting increased levels of charcoal during the early Holocene; a decrease in fire activity during the middle Holocene associated with increased moisture; and intermediate fire activity during the late Holocene in northern Patagonia. Nevertheless, different patterns in fire regime during the Holocene are also documented in other records in Patagonia. For example, Mallín Fontanito (44°S; Nanavati et al., 2019) shows low levels of charcoal during the early and middle Holocene, and increased values throughout the late Holocene. On the other hand, the record from Lake Shaman (44°S; de Porras et al., 2012) shows a period of high fire activity during the middle Holocene. Likely, dissimilarities in the fire history might be the result of differences in vegetation type at the landscape level.

Another major disturbance agent in northern Patagonian Argentina is the impact of volcanic ash deposition on the vegetation. Along the Andes, between 35° and 55°S, several active volcanoes are present (Fontijn et al., 2014). Recent eruptions in the region allowed investigation *in situ* of the short- and long-term impact of these events in *Nothofagus* forest. For example, after the Puyehue-Cordón Caulle eruption (2011), the evergreen tree *Nothofagus dombeyi* experienced higher mortality in comparison with the deciduous tree *Nothofagus pumilio*, due to abrasion and mechanical damage because of thick ash deposit on the foliage (Swanson et al., 2016). In the case of the Chaitén eruption (2008–2009), Swanson et al. (2013) indicate that coarse tephra abraded foliage from tree canopy over an area of 50 km^2 while fine tephra accumulating in tree crowns led to breaking branches over an area of 480 km^2. Holocene eruptions and their influence on vegetation dynamics are documented in records located on the western side of the Andes. Henríquez et al. (2021) suggest that explosive volcanism accounts for the rise in the evergreen trees *Eucryphia/Caldcluvia* at ~6800 cal yr BP (Lake Fonk, 40°S). Likewise, Jara and Moreno (2012) associate major increases in *Eucryphia/Caldcluvia* trees with tephra fall (Lake Pichilafquén, 41°S). In contrast, Jara et al. (2019) document that changes in the Southern Westerlies (SW) were the dominant driver of vegetation change rather than disturbance (Lago Espejo, 43°S) Studies on the impact of ash deposition on vegetation have been conducted also east of the main mountain chain (Álvarez-Barra et al., 2020; Moreno-González, 2020), showing negligible impact of ash deposition on the vegetation composition.

Despite numerous palaeoecological studies in northern Patagonian Argentina, few records capture the past abundance of the deciduous *Nothofagus alpina* and *Nothofagus obliqua*. These species co-exist within the Lácar basin (40°09′57.78″S, 71°29′22.96″W), the major centre of distribution of both trees in Argentina (Sabatier et al., 2011). Hitherto, the investigations have focussed on aspects such as genetic characterization and phylogeography (Acosta and Premoli, 2010; Azpilicueta et al., 2009; Marchelli et al., 1998, 2007; Paredes, 2003; Vergara, 2011; Vergara et al., 2013), as well as hybridization between the species (Azpilicueta et al., 2016; Donoso et al., 1990; Marchelli and Gallo, 2004). Studies also examined the spatial growth patterns (Donoso, 1988; Donoso et al., 1993; Echeverría and Lara, 2004; Puntieri et al., 2006; Sabatier et al., 2011) and site index models to quantify the productivity of a determined area with silvicultural purposes (Attis et al., 2015; Trincado et al., 2002). Unfortunately, few palynological records show the *Nothofagus obliqua* pollen type, which comprises pollen grains from *N. obliqua* and *N. alpina* (Álvarez-Barra et al., 2020; Markgraf et al., 2009; Nanavati et al., 2020), and yet, little is reported on their Holocene history within their distribution range in northern Patagonian Argentina.

The aim of the present work is to reconstruct the past vegetation dynamics and fire regime within a dense mixed evergreen/deciduous *Nothofagus* forest at the eastern slope of the Andes, from a lacustrine sediment core recovered from Lake Vizcacha (40°12′S; 71°30′W; 1095 m a.s.l.; 2.5 m depth), located at 2 km south of the Lácar basin, within the Lanín National Park, Argentina. Additionally, this work assesses the influence of fire and volcanic ash deposition on vegetation composition through multivariate statistical analyses and discuss the possible anthropogenic effects on vegetation patterns.

2. Modern environmental setting

2.1. Climate and vegetation

The climate in the Lanín National Park (LNP) is warm-temperate. Mean winter and summer temperatures are 4.1 °C and 20.1 °C respectively (Administración de Parques Nacionales, 2012). Due to the rain shadow effect induced by the Andes (Garreaud, 2009), the precipitation decreases from 3000 mm per year to < 600 mm in just 50 km in a west-east gradient in this region. The territory of the LNP is located on ancient volcanic rocks, mainly characterized by basaltic plateaux (Iriondo, 1989). Quaternary glaciations have played a role in shaping the modern topography creating moraines and the characteristic lakes of this region (Coronato et al., 2004; Glasser et al., 2008). The lakes present in the LNP exhibit an elongated shape-oriented west-east (Diaz et al., 2000).

The vegetation in this region is principally composed by *Nothofagus* species. At low and middle altitudes (~600–1000 m a.s.l.) *N. dombeyi* dominates, especially on more humid sites such as slopes with western aspects and along bodies of water (Administración de Parques Nacionales, 2012). Between 650 and 800 m a.s.l. *N. obliqua* occurs on slopes with a northeastern aspect. *N. alpina* can be found between 950 and 1150 m a.s.l. and can form pure stands. Usually, it is present on slopes with northwestern aspects (Sabatier et al., 2011). At highest altitudes (>1000 m a.s.l.) *N. pumilio* becomes the dominating tree and forms the treeline. *N. antarctica* is a disturbance-tolerant species and capable of inhabiting marginal landscapes. Most of the *Nothofagus* species present in the study area are colonized by the epiphyte, *Misodendrum*. Other epiphytes present in the study area include the fern *Polypodium feuillei*, *Tristerix corymbosus* (Loranthaceae), and *Lepidoceras kingii* (Eremolepidaceae). The evergreen liana, *Hydrangea serratifolia*, infest several tree species in the region (Jimenez-Castillo and Lusk, 2009). The understory is composed by the bamboo *Chusquea culeou*, *Drimys winteri*, *Aristotelia chilensis*, *Maytenus* sp., *Berberis microphylla*, *Embothrium coccineum* and *Lomatia hirsuta* (Conticello et al., 1996). Towards the east, following the decrease in precipitation, *N. antarctica* occurs together with *Austrocedrus chilensis*, *Maytenus boaria*, and *Schinus patagonicus*. However, at the border with the steppe, only scattered individuals of *Austrocedrus chilensis* occur (Veblen et al., 1995). The steppe is characterized by elements such as Poaceae, Asteraceae, Amaranthaceae, *Discaria*, *Acaena*, *Eryngium*, among others.

2.2. Site description

Lake Vizcacha (40°12′S; 71°30′W; 1095 m a.s.l.; Fig. 1) is located 14 km southwest of San Martín de los Andes (Province Neuquén). It is a small lake with a depth of 2.5 m within a larger peat filled depression in the saddle between the adjacent mountains (Fig. 1). *Potamogeton* forms a ring within the lake. The shrubs of *Escallonia virgata* and *Berberis microphylla* encircle the lake. *Sphagnum* mosses occur beside the lake, while the rest of the wetland is dominated by Cyperaceae. *Nothofagus*, is present around Lake Vizcacha with five species: *N. antarctica*, *N. dombeyi*, *N. pumilio*, and *N. alpina*. The understory is mainly dominated by the bamboo *Chusquea culeou* and *Drimys winteri.*

3. Material and methods

Two overlapping parallel cores were retrieved from Lake Vizcacha in January 2017, using a modified square-rod piston corer (Wright, 1967). The sediment-water interface was collected using a gravity corer and subsampled in the field as 1-cm thick slices, stored in plastic bags. In the laboratory the cores were described and combined into a 580-cm-long sediment sequence. The connection between the gravity and longer core was determined by comparing the percentage of *Pinus* pollen. The core contained more than 20 tephra layers ranging from a few centimetres to half a meter. Loss on ignition at 500 °C (Heiri et al., 2001) was analysed from 175 samples. The lithological description based on textural characteristic was combined with the results from the loss-on-ignition analysis to define lithological units.

Terrestrial macrofossils for radiocarbon dating were not encountered in several test samples and 10 bulk sediment samples were carefully selected and submitted for radiocarbon dating. For the construction of an age model, we subtracted tephra layers with a thickness >1 cm as they represent discreet sedimentation events. In addition to the results from radiocarbon analysis and the top sample we used the appearance of *Pinus* pollen as an indication of anthropogenic land-use around 1970 ± 10 (Moreno-González et al., 2020). The age-depth model was constructed using Bacon (Blaauw and Christen, 2011). Radiocarbon dates were calibrated with SHCal13.14C (Hogg et al., 2020).

Pollen samples of 0.5 cm^3 were taken every 2 cm, avoiding tephra sections. Before and after major tephra layers the sampling was carried out at an interval of 1 cm. Processing of samples for pollen analysis was conducted following Bennett and Willis (2001), including hydrofluoric acid and acetolysis. Samples with coarse particles were sieved at 120 μm. High pollen producing *Nothofagus* trees are dominating the forest in the region. To reduce the uncertainty in estimating the frequency of less abundant pollen types (Birks and Birks, 1980) a minimum of 500 pollen grains were counted. Aquatic pollen and spore taxa were excluded from the main pollen sum and were calculated separately based on the total pollen sum (terrestrial pollen plus spores). Cyperaceae pollen was included in the group of aquatics as the site was a peatland at times with Cyperaceae pollen being locally produced. *Pediastrum* and *Botryococcus* were counted with the aim to infer changes in the aquatic system. Also other non-pollen palynomorphs were identified in order to add detail on changes in the local site conditions. Percentages of non-pollen palynomorphs were expressed based on the sum of terrestrial pollen. Pollen identification was guided by pollen atlas (Heusser, 1971; Markgraf and D'Antoni, 1978) and reference material held at the Department of Palynology and Climate Dynamics of the University of Göttingen. Non-pollen palynomorph identification was aided by descriptions collected at http://nonpollenpalynomorphs.tsu.ru/.

To reconstruct the past fire regime, macroscopic charcoal particles were counted in 1 cm^3 samples contiguously along the core at 1-cm intervals avoiding tephra layers wider than 1 cm. The samples were processed according to the methodology by Stevenson and Haberle (2005). Particles >125 μm were counted under a binocular dissecting microscope (Whitlock and Anderson, 2003). Raw charcoal counts were transformed to charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) based on the above described age model and analysed using the software CharAnalysis (Higuera et al., 2009). The record was interpolated to the median sample resolution (yr $sample^{-1}$) of the record (31 years). Low-frequency CHAR (charcoal background) was estimated using a lowess smoother with a 500-years window. Fire Frequency and Fire-Return-Intervals (FRI) were analysed over 1500-yr time window following Higuera et al. (2010) and Moreno-González et al. (2021). Charcoal peaks were calculated as a ratio while the threshold was locally defined and noise distribution was determined by a Gaussian mixture model.

Tephra layers in the cores document ash fall on the vegetation with potentially negative or positive effects on different species. Assuming that influence of the tephra deposition on the vegetation would decay linearly with time we use the distance of each sample to the prior tephra layer as an indicator of impact. We also explore an exponential decay with time of the influence that the tephra deposition had (Lotter and Birks, 1993). Here we also consider the magnitude of the disturbance as indicated by the tephra thickness (Moreno-González, 2020):

$$\exp x^{-\alpha t}$$

where x is the thickness of a tephra in cm, α is the decay coefficient (0.5 as suggested by Lotter and Birks, 1993) and t is the distance of each sample to the prior tephra layer in cm. Both indexes were used as an environmental variable in the RDA with the descriptive name

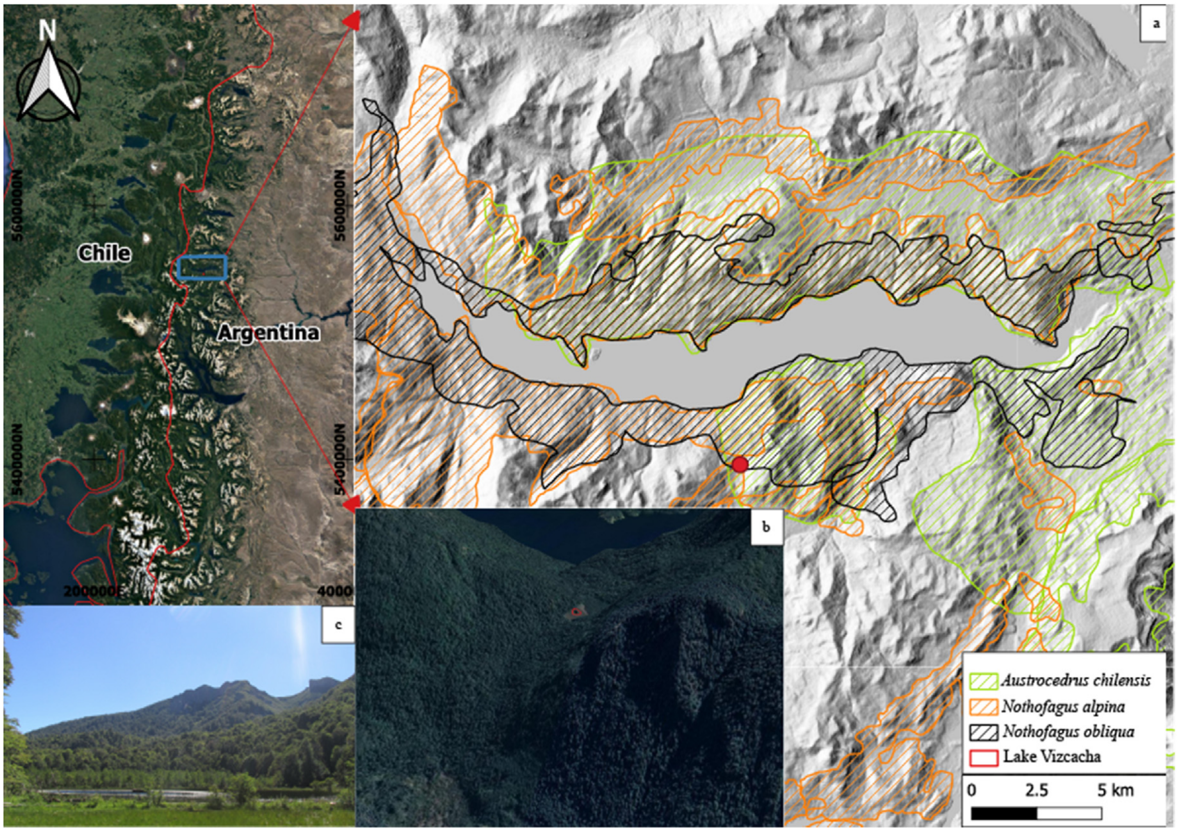

Fig. 1. a) Map with the location of the study site referred in this study (red circle), and the current distribution of *N. alpina*, *N. obliqua*, and *A. chilensis* around Lake Lácar basin based on Sabatier et al. (2011); Dezzotti and Sancholuz (1991); Administración de Parques Nacionales (2012). b) topography around Lake Vizcacha taken from @Google Earth. c) photography of Lake Vizcacha taken during fieldwork. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

distance and decay respectively.

The pollen diagram and associated constrained cluster analysis (CONISS) were constructed using Tilia 2.0.4 (Grimm, 2004). A summary diagram with supplementary information was created using C2 (Juggins, 2003). Principal Component Analysis (PCA) and Redundancy Analysis (RDA) were performed with CANOCO 5.0 (ter Braak and Šmilauer, 2012) with square root transformation of percentage data in order to suppress the influence of dominant taxa. The ordinations were conducted with the aim to visualize patterns in the pollen data and explore the response to environmental variables.

The vegetation response to fire regime on selected taxa was assessed by fitting response models using indices characterizing the fire regime as well as using Pearson correlation between charcoal and pollen counts. A Generalized Additive Model (GAM) was fitted in CANOCO 5.0 (ter Braak and Šmilauer, 2012) to visualize the response of selected taxa (*Nothofagus obliqua*-type, Cupressaceae, and Poaceae) to changes in the fire regime. The final model was smoothed at 2 degrees of freedom, assuming a Gaussian response distribution. The performance of the model was assessed by the Akaike Information Criterion (AIC) using the number of model degrees of freedom (Hastie and Tibshirani, 1990; Šmilauer and LepŠ, 2014). The direct influence of fire on the vegetation is often evaluated using cross correlation analysis (e.g. Tinner et al., 1999) requiring contiguous sampling of pollen and charcoal. While charcoal was analysed contiguously pollen was not, making it necessary to reduce the number of charcoal samples or combine them to carry out Pearson correlation analysis. We resampled the charcoal data to match the pollen samples in three different ways: i) using only the charcoal concentration in the same depth as the pollen sample; ii) using the charcoal concentration in the previous cm of the pollen sample; iii) combining the charcoal concentration in the same depth and in the previous cm of the pollen sample. These three sets of pollen concentrations were compared to pollen percentages and pollen concentration. We use these different combinations of the charcoal samples to overcome the limitation of discontinuously analysed samples for pollen. Pollen concentrations were tested to evaluate the contribution of the closure effect of percentage data due to the high pollen production of *Nothofagus dombeyi*.

4. Results

4.1. Chronology and sedimentology

The nine radiocarbon age determinations (Fig. 2, Table 1) are in stratigraphic order and the younger five dates follow a near linear trend when plotted against age. Dates at 679 and 761 cm depth have overlapping calibrated age ranges, which could indicate a rapid sediment accumulation between their position at depth. As there was no indication of a rapid sedimentation rate between these dates one of them should be an outlier, but the dated material gave no indication which. Assuming a gradual sedimentation rate for the entire core, by using a narrow range for the variation of the mean sedimentation rate in 'rbacon', the date at 679 cm depth fell outside the confidence limit for the assigned ages. This age model is not causing spuriously high pollen accumulation rates, which would occur when including the dates at 679 and 761 cm depth in a linear interpolation. Extrapolating the sediment accumulation to the base of the sequence results in a basal age of 11,600 cal yr BP for

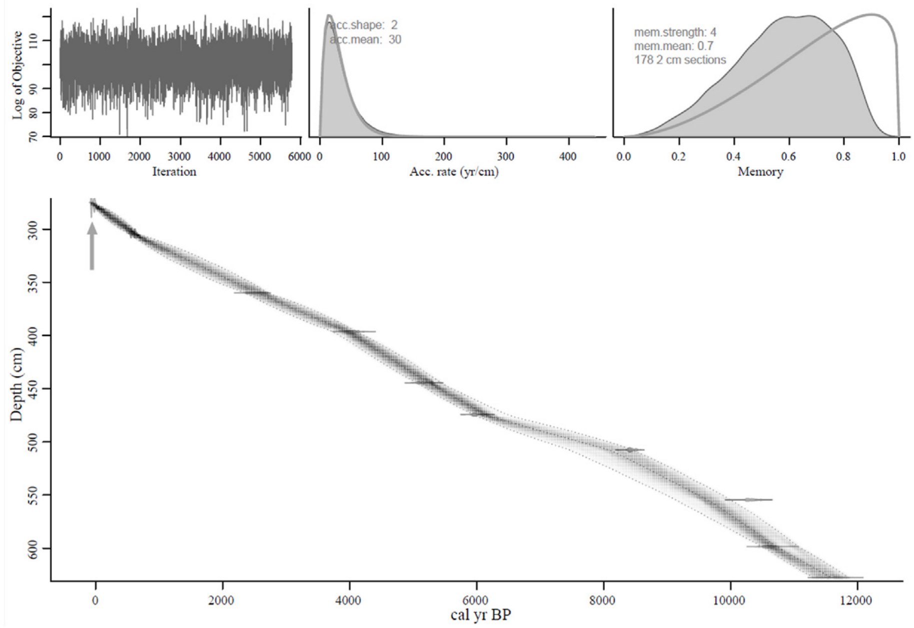

Fig. 2. Age-depth model of Vizcacha record. The probability distribution of the nine calibrated ages for each radiocarbon dates is represented in horizontal grey lines. Calendar ages are indicated with an arrow. The dotted line in the middle of the grey shadow indicates the median probability age of the age model. Grey shadow represents 95% confidence interval.

Table 1
Chronological control points.

Lab. code	ID sample	Material type	^{14}C age	±	Adjusted depth (cm)	Assigned age	Age (cal yr BP)	2σ range (cal yr BP)
	Cp 1	Core top			274	2017		
	Cp 2	Introduction of *Pinus* in the region			279	1970 ± 10		
UBA 39236	306–306.5 cm depth	Bulk sediment	630	20	304		615	548–649
UBA 39235	444–444.5 cm depth	Bulk sediment	2496	27	360		2594	2384–2712
Poz-122533	494–494.5 cm depth	Bulk sediment	3745	30	396.5		3981	3754–4107
Poz-115934	551–551.5 cm depth	Bulk sediment	4580	30	441.5		5161	4979–5351
Poz- 122534	582–582.5 cm depth	Bulk sediment	5270	35	474.5		6161	5970–6472
UBA 39233	633–633.5 cm depth	Bulk sediment	7670	39	505.5		8113	7467–8380
Poz-122536	679–679.5 cm depth	Bulk sediment	9180	50	554.5		9666	9202–10010
UBA 39234	761–761.5 cm depth	Bulk sediment	9412	36	598.5		10,676	10,528–11065
UBA 29235	856–856.5 cm depth	Bulk sediment	10,120	50	627.5		11,612	11,374–11949

the sequence.

A description of the sediment composition is presented in Table 2 together with the results from the loss-on-ignition analysis. A total of 26 tephra layers of different thicknesses were identified. Some of these layers are composed of angular sand-sized grains or distinguishable pumice particles up to 10 mm length. Two peat sections were identified, characterized by the presence of plant remains. Brownish-gyttja with varying organic matter content

Table 2
Sediment description. Depths are given as original core depth relative to the water level of the lake.

Depth (cm)	Age (cal yr BP)	Sediment characteristics
275–375	Present–1900	Brownish gyttja section with alternating greyish layers of volcanic ash and a 5-cm thick peat-muddy layer. LOI values between 1 and 50%
376–437	1900–2300	Occurrence of a 40-cm thick tephra layer with varying particle size and colour from dark to light grey. A clayey-gyttja section exhibit 20–30% of organic matter content.
438–634	2300–8100	Thick layers of brownish gyttja separated by several tephra layers and a thin layer of gyttja mixed with ash. LOI varies between 5 and 60%.
635–682	8100–9600	Peat with remains of Cyperaceae/Poaceae leaves, mixed with *Sphagnum* fragments, dicot leaves, and embedded large pieces of wood. LOI ranging between 60 and 80%.
683–715	9600–10,400	Brownish gyttja section. LOI values fluctuate between 10 and 40%.
716–813	10,400–10,800	Two major greyish tephra layers with different particle sizes (31 and 52 cm thick) separated by a thin gyttja layer characterize this section.
814–856	10,800–11,600	Consolidated peat with remains of Cyperaceae/Poaceae leaves, mixed with *Sphagnum* fragments, dicot leaves, and embedded large pieces of wood. LOI fluctuates between 50 and 90% organic matter, separated by a 14-cm thick layer of pumice ash.

makes up more than half of the core depths.

4.2. The pollen record

The pollen diagram is dominated by *Nothofagus dombeyi*-type representing *N. antarctica*, *N. dombeyi* and *N. pumilio* occurring in the area around the lake at different elevations. We interpret that most of the Cupressaceae pollen likely originates from *Austrocedrus chilensis*, as the modern distributions in Argentina of *Fitzroya cupressoides* and *Pilgerodendron uviferum* also producing this pollen type lies more than hundred kilometers to the south (Kitzberger et al., 2000; Rovere et al., 2002). Nevertheless, as *Fitzroya* and *Pilgerodendron* occur also in areas west of the Andes, the contribution of these species into the Cupressaceae pollen cannot be dismissed. The summary pollen diagram (Fig. 4) shows the main types of pollen, spores, and non-pollen palynomorphs with a short description of the main changes provided in Table 3. Pollen assemblage zones were divided based on visual recognition of the major changes in the record, guided by the constrained cluster analysis (CONISS). In total five different zones were determined, with a subdivision of zones VIZ-2 and VIZ-3 based on increases in Cupressaceae 10,700–9900 (VIZ-2a) cal yr BP and 8000–7300 cal yr BP (VIZ-3a). Some of the larger changes in pollen composition indicated by the CONISS dendrogram coincide with changes in sediment composition.

Cyperaceae pollen is high at the beginning of the record (zone VIZ-1, 11,600–10,800 cal yr BP) and decline in zone VIZ-2 (10,800–9900 cal yr BP), where Poaceae and *Myriophyllum* show an abrupt increase. Zone VIZ-2b (9800–8100 cal yr BP) is marked by a decline in the percentage of Poaceae and a slight increase in Cyperaceae. Zone VIZ-3a is characterized by an increase in Cupressaceae (15%). This zone marks the onset of the rise in the algae *Botryococccus*. *Nothofagus obliqua*-type pollen occur with values between 1 and 2% throughout zone VIZ-3b (7200–2300 cal yr BP) and the pollen type rises to co-dominant abundances at the onset of zone VIZ-4 (2200–300 cal yr BP). The last zone (VIZ-5, 300 cal yr BP to Present) is featured by a slight increase in non-pollen palynomorphs percentages such as *Glomus* and *Pediastrum*, and by the presence of human indicator taxa (*Plantago*, *Rumex*, and *Pinus*).

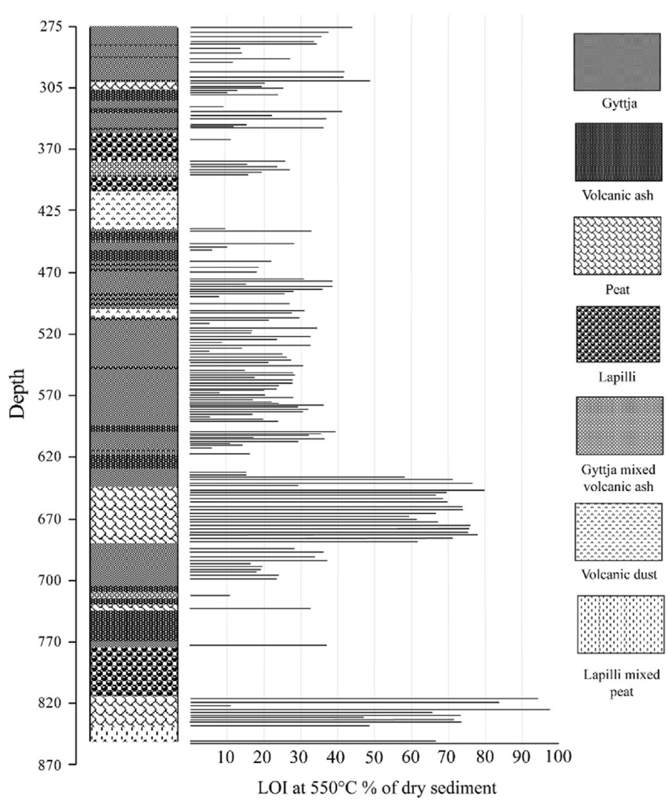

Fig. 3. Lithology and loss-on-ignition (LOI) results of the Lake Vizcacha core. Loss-on-ignition was analysed only on peat and gyttja sections excluding sediment dominated by tephra. Y-axis indicates original core depths.

4.3. The fire record

The fire recorded in Lake Vizcacha shows pronounced changes over the course of the Holocene (Fig. 5). The pollen zonation was applied to the fire record for comparison with the inferred vegetation changes. Throughout the record, the signal-to-noise index (SNI) is > 3, indicating that the charcoal peak signal obtained from the time series analysis is well separated from noise (Kelly et al., 2011). Nevertheless, values < 3 occur intermittently between 9800 and 9100 cal yr BP, 7000–6300 cal yr BP, and 3600–2600 cal yr BP.

The record begins with high CHAR values until ~8300 cal yr BP. In this interval the fires are of high frequency (6–8 fires 1500 yr^{-1}), suggesting high fire activity at the beginning of the Holocene. Additionally, during this period, 13 fire episodes (charcoal peaks) were detected with their magnitudes. Noticeable is the low values of CHAR during VIZ-3a (8000–7300 cal yr BP) corresponding to the increased percentages in Cupressaceae. Several high magnitude fires were detected during the period 7300 to 2300 cal yr BP (VIZ-3b). The number of fire episodes, fire magnitude and fire frequency are low during the period from 2300 cal yr BP to 500 cal yr BP. A single charcoal peak indicating one high magnitude fire is detected in the youngest section zone VIZ-5.

4.4. Numerical analyses of data

The PCA ordination (Fig. 6) shows the main compositional trends in pollen data, which have a gradient of 1.7 SD units long, suggesting little variation within data assemblages. The samples scores gradually changing with time, without clearly separating distinct groups. The symbols of the sample scores in the PCA biplot are indicating their affiliation to a pollen zone and together with the species scores of the 15 taxa with highest variance assist in the interpretation of the data. The first axis may represent (from the left to the right) a time axis between older and younger samples, following the long-term development of *Nothofagus obliqua* and *N. alpina* populations. The second axis captures the changing abundance of Poaceae pollen, while Cupressaceae and *Nothofagus dombeyi*-type result as opposing vectors characterizing samples in the first and third quadrant respectively. Group VIZ-1 is dominated by *Nothofagus dombeyi* and VIZ-2 by Poaceae. Samples from both clusters are characterized by *Discaria*, Amaranthaceae, *Gaultheria*, and Asteraceae. subf. Asteroideae. These taxa are rare in VIZ-3 and the position of the sample scores are scattered depending on the abundance of *Nothofagus dombeyi* versus Cupressaceae. VIZ-4 is characterized by *Eucryphia*, *Misodendrum*, *Saxegothaea conspicua*, and *Nothofagus obliqua*, while samples from zone VIZ-5 are set apart by their presence of introduced taxa *Plantago*.

The redundancy analysis (RDA) was performed with the aim to visualize the relationships between samples and species with the environmental variables and to test which environmental variable explains variation in the pollen proportions. Taken together, the explanatory variables account for 9.4% of the variation, suggesting low contribution of the environmental variables tested on data variability. Nevertheless, CHAR, Distance and fire frequency

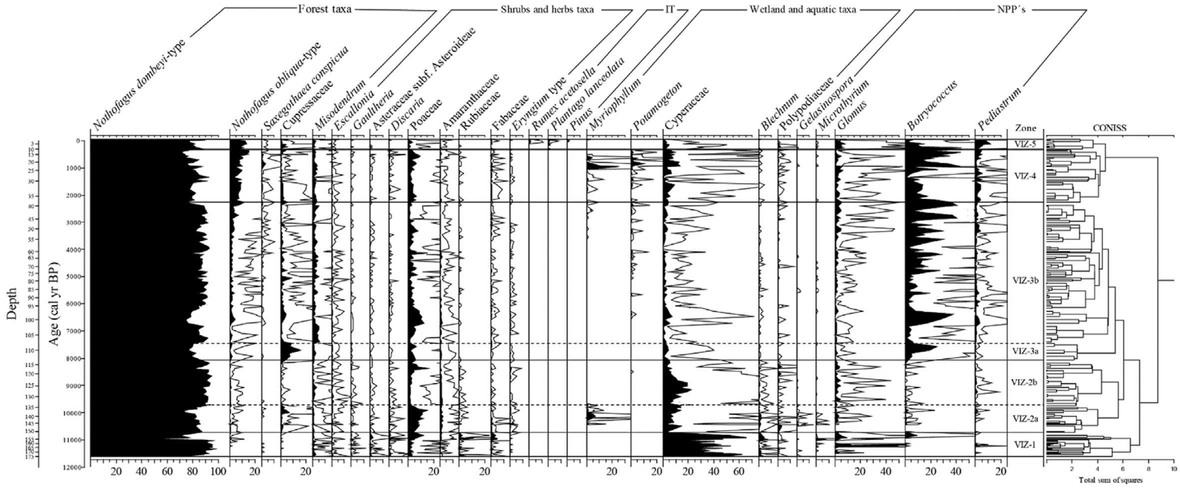

Fig. 4. Percentage diagram showing selected taxa including pollen, spores and NPP's for Lake Vizcacha. A 10 × exaggeration (black line) was used to visualize less abundant taxa. IT = introduced taxa.

Table 3
Vegetation history of Vizcacha record.

Zone	Age (cal yr BP)	Characteristic taxa	Observations and Interpretations	Characteristic NPP's and Interpretations
VIZ-5	300–Present	*Nothofagus dombeyi*-type, *Nothofagus obliqua*-type, Poaceae, *Rumex*, *Plantago*,	Human activities close to the lake.	*Glomus*, *Pediastrum*. Lake eutrophication by human activities
VIZ-4	2300–300	*Nothofagus dombeyi*-type, *Nothofagus obliqua*-type, Poaceae, *Myriophyllum*, *Potamogeton*.	Establishment of *Nothofagus alpina/obliqua* around the Lácar basin	*Glomus*, *Botryococcus*, *Pediastrum*. Soil erosion and lake eutrophication
VIZ-3b	7300–2300	*Misodendrum*, *Escallonia*, *Potamogeton*,	Dominance of mixed *Nothofagus* species forest.	*Botryococcus*, *Pediastrum*. Changes in water depth and/or lake production.
VIZ-3a	8100–7300	Cupressaceae	Uphill expansion of *Austrocedrus* on north-facing slopes of the Lácar basin	*Botryococcus*. Changes in water depth.
VIZ-2b	9800–8100	*Misodendrum*, Cyperaceae.	*Nothofagus dombeyi*-type forest dominance	*Glomus*, *Pediastrum*. Soil erosion
VIZ-2a	10,800–9900	Cupressaceae, Poaceae, *Myriophyllum*	Higher-than-before vegetation cover. Open *Nothofagus* forest dominance.	*Gelasinospora*, *Microthyrium*. Local fires, wood decomposition.
VIZ-1	11,600–10,800	*Discaria*, Rubiaceae, Cyperaceae	Deteriorated pollen grains. Low PAR and pollen from shrubs and herbs plants suggesting open *Nothofagus* shrubland.	*Microthyrium*, *Glomus*. Wetland desiccation, soil erosion.

(Table 4) have a statistically significant effect on vegetation composition ($p < 0.05$) (see Table 5).

The variable CHAR has the highest explanatory power and this variable points in the opposite direction to *Nothofagus obliqua*-type indicating that the parent tree thrived in periods of low severity fires. In this sense, the variable fire frequency points also in opposite direction to *Nothofagus obliqua*-type, supporting the interpretation that *N. obliqua* and *N. alpina* trees prosper under infrequent fire events. *Nothofagus alpina* and *N. obliqua* have moderately thick bark and resprout after being burned (Veblen et al., 2003), which may occur under low fire activity. Also, tephra deposition has a small but significant effect on the vegetation, with the linear decrease of tephra influence (Distance) explaining 3.0% of the variance in pollen proportions. The variable Distance shows a positive correlation with *Lomatia hirsuta* (tall shrub) and *Hydrangea* (vine) indicating that these pollen types are more common away from tephra layers.

Fitting generalized additive models (GAM) using the environmental parameters as predictors visualizes the response of individual taxa rather than the full assemblage as in the RDA. Also here there is a statistically significant influence of fire on the abundance of *Nothofagus obliqua*-type, when examining fire frequency (fires 1500 yr^{-1}) and CHAR (pieces cm^{-2} yr^{-1}). Moderate fire frequency is associated with the highest percentages in Cupressaceae.

In addition to the derived parameters describing the different aspects of the fire regime a direct correlation comparison was conducted by resampling the charcoal data to match the available pollen samples. In these Pearson correlations, pollen concentrations were tested alongside pollen percentages as large fires may result in an overall reduction in the pollen production in the years after charcoal in the sample before the pollen sample. Negative correlations are found for percentage and concentration values of *Nothofagus obliqua*-type as well as for Cupressaceae, with the highest correlations when considering the charcoal concentration from the same depth as the pollen sample plus the charcoal concentration in the sample before. No significant correlation could be found for Poaceae, while the epiphyte *Misodendrum* shows the strongest negative correlation when compared to the charcoal in the sample before the pollen sample.

5. Discussion

5.1. Environmental reconstruction

5.1.1. Early Holocene (11,600–8100 cal yr BP)

The results demonstrate marked changes in the environment

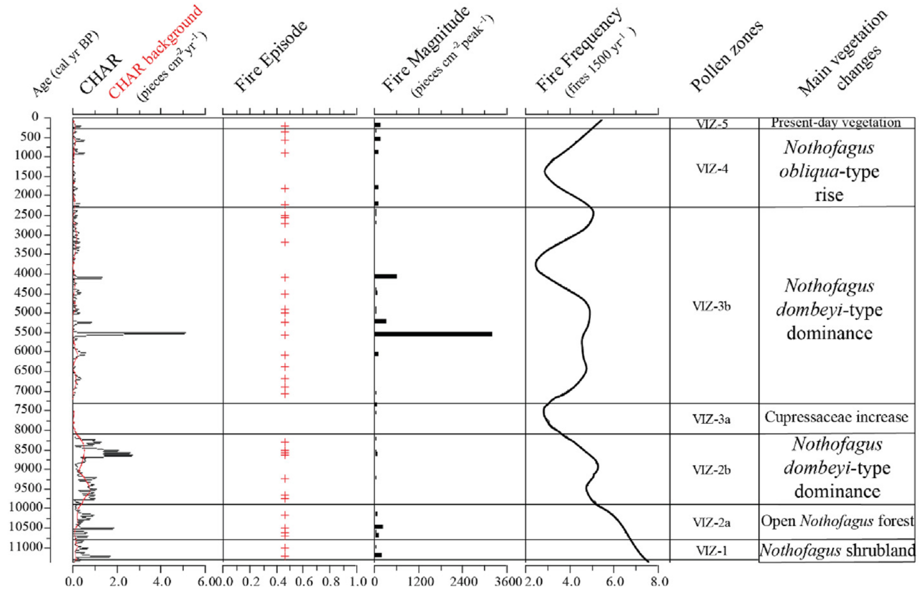

Fig. 5. Holocene fire characteristic reconstructed from Vizcacha. Charcoal accumulation rates (CHAR), fire episodes, fire magnitude, and fire frequency, and their units are indicated. Pollen zones are included for comparison.

around Lake Vizcacha during the Holocene. Lake Vizcacha is a closed basin, whose main source of water is precipitation and surface runoff from the surrounding slopes, but without a stream entering. At 11,600 cal yr BP a Cyperaceae-dominated wetland covered the basin. The water level was low enough for the growth of shrubs, such as *Escallonia* and *Gaultheria*. Elements used as indicators of dry environments such as Asteraceae, Amaranthaceae, Fabaceae, and *Discaria* (Iglesias et al., 2016; Markgraf et al., 2002) also occurred during this period. Nonetheless, given the accumulation of organic matter in this section, the wetland was likely intermittently flooded allowing for the accumulation of organic matter (Segnini et al., 2010). The presence of the fungus *Microthyrium* corroborates the interpretation of a peatland (van Geel, 1978) that occasionally dried out (Mancini, 2009). Also the poor pollen preservation in the peat section indicates episodically lowered water tables causing oxidation of pollen (Havinga, 1967).

The period between 11,600 cal yr BP and 10,800 cal yr BP features high percentages of *Nothofagus dombeyi*-type pollen. However, pollen concentration and accumulation rate (PAR) in zone VIZ-1 (Fig. 9) are the lowest for the entire record. Pollen preservation in the samples from this interval is very poor and several samples were counted to obtain the minimum pollen sum (500 grains). Therefore, the environmental deposition at that time might hide the actual pollen flux signal to the basin. Under this scenario, we suggest that likely a *Nothofagus* shrubland dominated the basin, accompanied by shrubs and herbs elements such as *Gaultheria*, Asteraceae, *Discaria*, Rubiaceae and Fabaceae. Modern and fossil pollen records along an environmental gradient in northern Patagonia (40.5°–44°S), synthetized by Iglesias et al. (2016) indicate that high values in *N. dombeyi*-type percentage represent forested areas, probably *N. pumilio* or *N. dombeyi*. Nevertheless, as it is not possible to determine species level, we infer that *N. pumilio* and *N. antarctica* were the major contributors to the *Nothofagus* pollen signal. The latter tolerates a wide range of disturbed and marginal environments and occurs in boggy areas (Amigo and Rodríguez, 2011; Donoso, 2013). Alternating gyttja and peat horizons (interpreted as wet and dry conditions respectively), characterized the early Holocene in our record, which support the interpretation of changes in water fluctuation in the basin, environmental conditions that *N. antarctica* can tolerate.

Dry conditions during the early Holocene are reported in palaeoecological studies in southern South America. West of the Andes, Abarzúa (2013) and Abarzúa et al. (2014) concluded that the high percentages of *Nothofagus obliqua*-type, *Eucryphia/Caldcluvia* and *Weinmannia trichosperma* indicate a warming pulse during this period. Moreover, high amounts of charcoal particles in these cores also point to dry climatic conditions during this period. In addition, paleoclimatic reconstruction of sea surface temperatures (SST) at middle latitudes of southern South America (Kaiser et al., 2005) also documents warmer-than-today climate during the early Holocene.

The abrupt decline in the percentage of Cyperaceae after 10,800 cal yr BP coupled with the appearance of the aquatic plant *Myriophyllum* suggest an increase in precipitation which allowed the development of a shallow lake (zone VIZ-2a). This is supported by the shift in sedimentology, from peat to gyttja. Pollen concentration and PAR increase in comparison with the prior zone, suggesting an increase in vegetation cover compared to the previous period. The time between 10,800 and 9800 cal yr BP is marked by the highest percentages of Poaceae. Increased Poaceae percentages are also observed in sites further south from Lake Vizcacha, east of the Andes, such as Mallín Fontanito (10,400–7000 cal yr BP; 44°S, 71°W; Nanavati et al., 2019), and Lake Cóndor and Lake Mosquito (>9150 and >9060 cal yr BP respectively; 42°S, 71°W; Iglesias et al., 2011). The slight increase observed in the percentage of Cupressaceae might be the result of this inferred increase in precipitation likely during the growing season, favouring the growth of *Austrocedrus chilensis* (Iglesias et al., 2011).

Towards the end of the early Holocene (9900–8100 cal yr BP; Fig. 4, zone VIZ-2b), a second peat section documents the renewed reduction in the water table with the development of the wetland once again. A *Nothofagus* forest dominated the landscape around Lake Vizcacha, despite the inferred dry climate. The abrupt decline in the percentage of Poaceae might be the result of the spread of *Nothofagus* trees into sites that were previously dominated by grasses, and the dominance of Cyperaceae over Poaceae in areas before covered by water. This is supported by the decline in Poaceae PAR values during this period (Fig. 9, from 16,000 to < 4000 grains

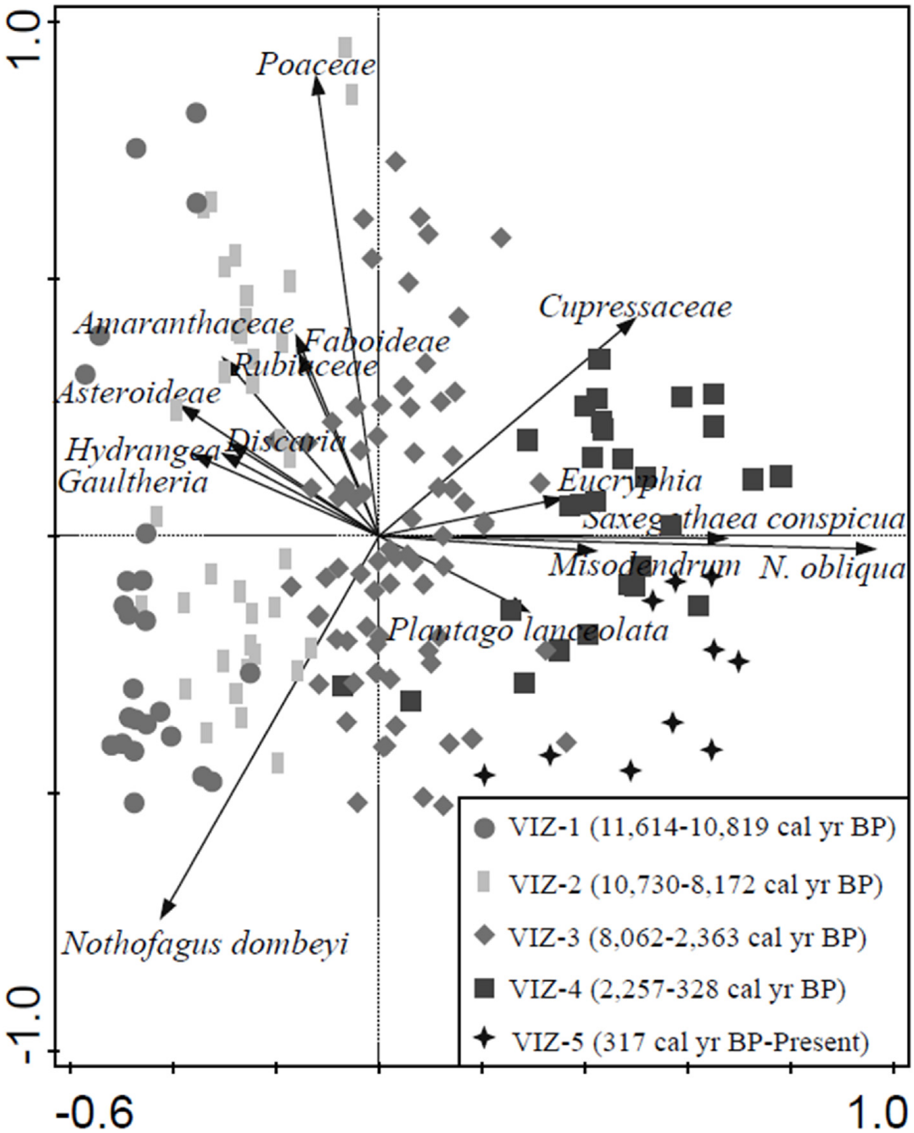

Fig. 6. PCA scatterplot of samples and selected taxa of Lake Vizcacha. Sample affiliation to pollen zones is shown by different symbols (see the panel at the right-bottom of the PCA). Notice that subzones VIZ-2a, b and VIZ-3a, b are combined as VIZ-2 and VIZ-3.

Table 4
Simple effect derived from the RDA.

Variable	Explains %	Pseudo-F	*P* (adjusted)
CHAR	4.1	7.3	0.01
Distance of each sample to the prior tephra layer (linear decrease of tephra influence)	3.0	5.3	0.01
Fire frequency	2.0	3.4	0.03
Exponential decrease of tephra influence (Decay)	0.4	0.7	1.
Fire magnitude	0.3	0.5	1.

cm^{-2} yr^{-1}); since PAR is applied for estimating past plant abundances independently for each species (Giesecke and Fontana, 2008; Seppä and Hicks, 2006).

5.1.2. *Middle Holocene (8100–4200 cal yr BP)*

The high percentage of Cupressaceae pollen between 8000–7300 cal yr BP (7–15%), represents the most important vegetation shift documented for the middle Holocene. The pollen, most likely originated from *Austrocedrus chilensis*, currently growing on north-facing slopes around Lake Lácar, a few hundred meters north of Lake Vizcacha, as well as in the transition to the steppe, about 20 km to the east of the lake. A middle to late Holocene increase in the percentage of Cupressaceae is a common feature in pollen diagrams between 41° and 43°S and attributed to a regional expansion of *Austrocedrus* triggered by an increase in effective moisture (Iglesias and Whitlock, 2014). However, the period with high Cupressaceae pollen at Lake Vizcacha differs from the patterns in other sites to the south where the increase in the pollen type is sustained and occurs later (around 6000 cal. BP at Laguna El Trébol, and ~3200 cal yr BP at Lake Mosquito, Whitlock

Table 5
Pearson correlation coefficient (r) and *p*-values summary results for selected taxa. Different significance levels represented as *: *No significant (0.09–0.9), ** Significant (0.0001–0.05), *** Strongly significant (<0.0001).

Taxa	Concentration sample		Percentage sample		Concentration sample before		Percentage sample before		Concentration sample + before		Percentage sample + before	
	p	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r
N. dombeyi	*	−0.08	**	0.28	**	−0.30	*	0.14	**	−0.21	**	0.25
N. obliqua	***	−0.29	***	−0.34	***	−0.40	***	−0.32	***	−0.40	***	−0.39
Cupresacceae	**	−0.22	**	−0.22	**	−0.22	**	−0.20	**	−0.27	**	−0.27
Misodendrum	*	−0.18	**	−0.26	***	−0.32	**	−0.26	**	−0.25	**	−0.27
Poaceae	*	0.03	*	0.05	*	0.00	**	0.17	*	−0.02	*	0.09

et al., 2006). *Austrocedrus* has a restricted pollen dispersal and percentages above 10% therefore indicate the presence of a population of this cypress near a site or the dominance of the tree in the wider area (Markgraf et al., 1981). As the period of high percentages of Cupressaceae is brief, ecological interpretations may be not accurate. Nevertheless, this signal might somehow reflect the dominance of *Austrocedrus* population on north-facing slopes of Lake Lácar between 8300 and 7300 cal yr BP, as the modern signal of this cypress in the uppermost sample of our record is <5%, which captures the present-day pollen signal from *Austrocedrus*.

After 7300 cal yr BP, a decline in the percentage of Cupressaceae is associated to the rise in the abundance of *Nothofagus dombeyi* pollen type, which from here on maintains values above the 83% mean. This shift is also documented by the absolute pollen counts and cannot be ascribed to an artefact percentage due to the low pollen production/dispersal from Cupressaceae pollen. A rise in the abundance of *Nothofagus dombeyi*-type during the middle Holocene is also reported throughout the region by Iglesias et al. (2014), Markgraf et al. (2002), Nanavati et al. (2019) and Whitlock et al. (2006). Additionally, Markgraf et al. (2002) document a decline in *Eucryphia/Caldcluvia* and steppe elements. They attribute these changes to a regional increase in summer precipitation and to a decline in summer and winter temperatures during the middle Holocene. In this respect, the variation in the abundance of aquatic taxa at Lake Vizcacha is worth noticing. *Potamogeton* is interpreted in pollen records as indicator of water table fluctuations in lakes since this aquatic plant occur under moderate water depth (Van den Berg et al., 1999). For instance, Ashworth et al. (1991) interpret the presence of *Potamogeton* and hydrophilid beetles remains as indicators of shallow water table in bogs. Similarly, Fletcher and Moreno (2012) interpret cool and wet conditions due to low CHAR values and increased *N. dombeyi*-type and *Potamogeton* values. In our record, *Potamogeton* appears at 6400 cal yr BP and its presence from here onwards is intermittent, suggesting seasonal fluctuation in the water table of the lake, associated possibly to inter-annual precipitation variability triggered by ENSO (Montecinos and Aceituno, 2003; Fletcher and Moreno, 2012). *Botryococcus* and *Pediastrum* are species typical of eutrophic lakes (Jankovská and Komárek, 2000) and stagnant water (Echeverría et al., 2014; Markgraf et al., 2009; Moreno et al., 2009; Whitlock et al., 2006) and their fluctuating abundances in the Lake Vizcacha record, suggest variations in water depth due to oscillations in precipitation from 8000 cal yr BP onwards, altering the water table of the lake and therefore, modifying the shallow conditions suitable for the development of *Pediastrum* and *Botryococcus*. The continued occurrence of lake sediment (gyttja) documents the presence of a permanent lake and, therefore, constant water input and wetter conditions compared to the early Holocene. This assumption is supported by Moreno et al. (2010), who suggest a strengthening of the SW, which is associated with glacier advances, indicating cooler temperatures and/or increased precipitation after 7800 cal yr BP.

The observed increase in the abundance of *Glomus* during the middle Holocene may be indicating soil erosion in the catchment area (Musotto et al., 2012), which may be due to increased runoff after high precipitation events (Cook, 2009). Precipitation in our study area is ruled by the SW, which brings moisture from the Pacific, being intercepted by the Andes triggering orographic precipitation (Garreaud et al., 2013). Moreover, El Niño Southern Oscillation (ENSO) is also an important factor influencing seasonal variability in precipitation (Montecinos and Aceituno, 2003). Paleoclimatic reconstruction of ENSO activity in the region suggests strong ENSO activity (above normal average precipitation) after ~7000 cal yr BP (Moy et al., 2002). At the latitude of our study site (40°S), the La Niña (El Niño) phase of ENSO is associated with wet (dry) conditions in summer (Montecinos and Aceituno, 2003). This event might have triggered frequent sediment flux into the Lake Vizcacha, explaining the presence of *Glomus*, a spore associated with eroded soils (van Geel et al., 1995). This interpretation is also supported by the low values of organic content between 8100–2300 cal yr BP (Fig. 3, Table 2) associated to increased runoff. On the other hand, the low but persistent presence of *Nothofagus obliqua*-type could be indicating a trend towards increasing summer temperatures.

The middle Holocene features a moderate rise in the percentage of *Misodendrum* in comparison with the prior zone (Fig. 4, zone VIZ-3b). The genus *Misodendrum* comprises 8 species (Tercero-Bucardo and Rovere, 2010) that infest specifically *Nothofagus* species along their entire distribution range (33–56°S). Around lake Vizcacha *Nothofagus pumilio*, *N. antarctica*, and *N. dombeyi* host mainly *Misodendrum punctulatum* (Tercero-Bucardo and Rovere, 2010). Iglesias et al. (2016) suggest that percentages of *Nothofagus dombeyi*-type > 67 and *Misodendrum* < 1.5 may indicate a *Nothofagus dombeyi* zone. In the record from Lake Vizcacha, *Misodendrum* present values between 3 and 5% from ~7300 to ~6800 cal yr BP and drops up to <2% after 6800 cal yr BP. These changes probably may suggest changes in the dominance between *Nothofagus dombeyi* (evergreen) and *N. pumilio* (deciduous) populations around the Lake Vizcacha, as suggested by Iglesias et al. (2016).

5.1.3. Late Holocene (4200 cal yr BP to present)

After ~ 4200 cal yr BP (zone VIZ-3b and VIZ-4), *Nothofagus obliqua*-type starts to increase, which relates to both deciduous *Nothofagus alpina* and *Nothofagus obliqua*, that nowadays occur around the Lácar basin. The major population of both deciduous species in Argentina are located within the Lácar basin (Donoso, 2013; Sabatier et al., 2011). As the pollen morphology of both trees are undistinguishable from one another, precise determinations on the main contributor of the signal captured in the pollen diagram is difficult. Moreover, hybridization between these species is documented in several studies (Azpilicueta et al., 2016; Donoso et al., 1990; Marchelli and Gallo, 2004). Nevertheless, their ecological significance in palynological records allows interpreting that its presence is associated with warmer temperatures (Abarzúa et al., 2014; Heusser et al., 2006; Villagrán, 1980). In this respect, the expansion of *Nothofagus obliqua*-type forest during the late Holocene marks the establishment of both *Nothofagus alpina* and *Nothofagus obliqua* around the Lácar basin, being the main vegetational change observed at this site. The same pattern of expansion of *Nothofagus obliqua*-type was observed by Álvarez-Barra et al. (2020) in two lakes, Bruja (at ~2000 cal yr BP) and Avutarda (at ~1500 cal yr BP) located at 4 km and 13 km south of Lake Vizcacha respectively. These results document that the expansion of populations and the spread of the trees was not a local event, but a regional process. Towards the north, Markgraf et al. (2009) reported a rise in the abundance of *Nothofagus obliqua*-type at 5300 cal yr BP in the record from Mallín Vaca Lauquen (36°S), suggesting that this event marks the establishment of the modern climate regime (winter rain/summer drought) in the region.

The vegetation change during the late Holocene at Vizcacha is also characterized by a decline in Cupressaceae and Poaceae and several fluctuations in the abundance of aquatic taxa. A maximum in the percentage of *Myriophyllum* and *Potamogeton* occur around 900 cal yr BP associated with low abundances of *Glomus* indicating a dry phase. This is followed by a disappearance of shallow-water plants concomitant with an increase in *Glomus* indicating a shift to higher lake levels and increased precipitation at the border to VIZ-5, ~300 cal yr BP. Despite that ENSO activity became less frequent during the last millennia (Moy et al., 2002), moist conditions in the region have been documented for this period (Flantua et al., 2016; Nanavati et al., 2020). On the other hand, SST decrease gradually throughout the middle and late Holocene (Kaiser et al., 2005).

The last zone (VIZ-5, last ~300 cal yr BP) includes samples documenting human activities close to Lake Vizcacha. This is inferred by the presence of the introduced taxa *Rumex*, *Plantago*, and *Pinus*. *Plantago* and *Rumex* have been used worldwide to determine woodland replacement by farmland and pasture (Behre, 1981; Brun, 2011; Deza-Araujo et al., 2020; Iglesias et al., 2016; Li et al., 2008). In Argentina *Pinus* monoculture constitute one of the major human disturbances at expenses of native species (Huber et al., 2008; Moreno-González et al., 2020; Rehfeldt and Gallo, 2001; Trentini et al., 2017). Regarding this point, the Lácar basin is located within the Lanín National Park, created in 1937 (Administración de Parques Nacionales, 2012), therefore, any human activity related to introduction of exotic species and conversion of forest into farmland is illegal since then. Prior to the creation of the National Park, historical documents report the extensive extraction of *Nothofagus alpina* and *Nothofagus obliqua* around the Lácar basin due to the high-quality of its wood for building (Attis et al., 2015). Moreover, several sawmills were present in the area (Secretaría de Turismo y Desarrollo Económico, 2021). A corresponding decline in the abundance of *Nothofagus obliqua*-type is visible at Vizcacha, which might reflect the reduction in the populations of both deciduous trees. This decline occurs with the appearance of *Plantago* and with a slight increase in *Glomus* and *Pediastrum*. The extensive clear-cutting might have contributed to the erosion and eutrophication processes in Lake Vizcacha, together with low-scale animal husbandry, explaining the increase in *Pediastrum*.

5.2. Disturbance regimes and their effects on the local vegetation dynamics nearby Lake Vizcacha

5.2.1. Tephra deposition

Twenty-six tephra horizons of different thicknesses were identified in the core from Vizcacha. Their presence along the entire core is an indicator of the constant volcanic activity in the region during the Holocene (Fig. 3). Explosive Holocene eruptions in the segment of the Andean Central and Southern Volcanic Zone are documented in Fontijn et al. (2014), Naranjo and Stern (2004), and Naranjo et al. (2017). Given the frequent deposition of ash, one would expect some influence of ash deposition on the vegetation as it has been documented in studies on modern responses of vegetation to volcanic eruptions in the region (Chaitén eruption: Swanson et al., 2013; Cordón Caulle eruption: Swanson et al., 2016) The RDA results (Fig. 7) indicate no statistically significant effect of ash deposition for the variable decay, which represents an exponential decrease of the influence of ash deposition on vegetation composition with time. Nevertheless, according to the *p*-value, the variable distance (linear decrease of the influence of ash deposition) indicates a significant influence of this variable on vegetation composition (Table 4). As it is shown in Fig. 7, the variable distance is positively correlated with *Lomatia hirsuta* and *Hydrangea*. This relationship may indicate an increase of both taxa during longer periods without ash deposition. *Lomatia hirsuta* is a shrub common in open woodlands near the tree limit towards the steppe. *Hydrangea* is a vine characteristic of the forest in this region (Jimenez-Castillo and Lusk, 2009), being abundant in the shaded understory of mature forest, although its richness is similar in treefall gaps, secondary forest, and old-growth forest (Gianoli et al., 2010). Increases in the abundance of *Hydrangea* after tephra deposition are reported by Henríquez et al. (2015) in Lago Teo (Chiloé Island, 43°S). In contrast, Jara and Moreno (2014) describe an abrupt decline of this vine after tephra deposition in Lago Pichilafquen (40°S). These differences may be due to the season during which the disturbance event occurred. The season of ash deposition may also determine the impact on the foliage of the deciduous trees *Nothofagus pumilio* and *Nothofagus antarctica* (Swanson et al., 2013). The pollen concentration of *Nothofagus dombeyi*-type, which includes the deciduous *N. pumilio*, and *N. antarctica* as well as the evergreen *N. dombeyi*, shows a random pattern when comparing the samples

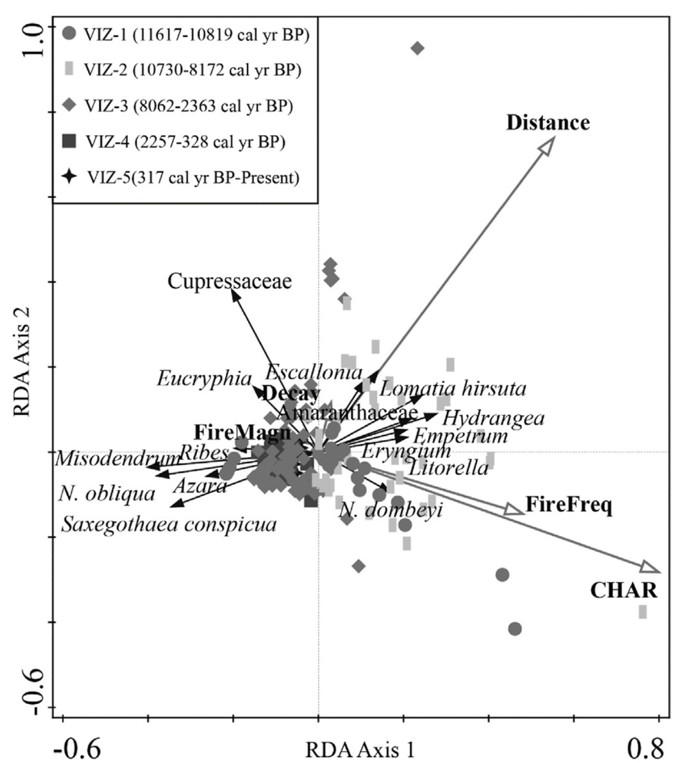

Fig. 7. Redundancy analysis (RDA) biplot of samples/species/environmental variables of Lake Vizcacha. The RDA shows the 15 best fitting species indicated by the ordination analysis. Environmental variables: CHAR, fire frequency, fire magnitude, Distance, Decay. Notice that subzones VIZ-2a, b and VIZ-3a, b are combined as VIZ-2 and VIZ-3.

before and after the tephra deposition. Although our results show a negligible or almost null response of *Nothofagus dombeyi*-type after tephra fall, several studies demonstrate the significance of disturbance events in the dynamics of the *Nothofagus* forest in southern South America at short and long-term (Dickson et al., 2020; González et al., 2014; Montiel et al., 2016; Swanson et al., 2016; Veblen et al., 1977, 1996).

Overall, the deposition of tephra layers might not have triggered substantive changes in the local vegetation around Lake Vizcacha. Moreover, the vegetation response to ash deposition seems to be somewhat random, probably as a result of certain conditions like the season of eruption, the age of the species, and their biological adaptation to disturbance. On the other hand, millennial and/or sub-millennial climatic variations interact with disturbance events and may be the true cause of a response, while disturbance acts as a trigger for the change (Dickson et al., 2020).

5.2.2. Fire

The presence of macrocharcoal particles along the Vizcacha core attests to the local occurrence of fire. The results obtained from the time series analysis presented in Fig. 5 suggest an early Holocene characterized by high-to-moderate fire activity under dry conditions, associated with warmer-than-today climate during the early Holocene (Kaiser et al., 2005). This pattern is also observed by Iglesias and Whitlock (2014) in sites located between 41° and 43°S in Argentina and along the western Andes, between 40° and 44°S (Markgraf et al., 2007; Moreno and Videla, 2016; Moreno et al., 2018b). This moisture deficit promoted dry fuel and allowing the spread of fire. The interpretation of the local occurrence of fires is supported by the presence of *Gelasinospora*, a fungal spore that develops in charred organic material (van Geel and Aptroot, 2006).

The highest percentages of Poaceae are associated with high fire frequency (5–8 fires 1500 yr^{-1}), as it is shown in Fig. 8. However, the analysis indicates no statistically significant influence of fire frequency on the abundance of Poaceae. Grass pollen maxima occur in the early Holocene between 10,700 and 9900 and at 8300, and during the middle Holocene between 6700 and 6200 cal yr BP. All these periods correspond with shallow to deep water levels of Lake Vizcacha respectively. While the middle Holocene is characterized by increased summer precipitations at mid latitudes (Whitlock et al., 2007) the early Holocene featured a widespread warming (Kaiser et al., 2005; Lamy et al., 2015). Wet intervals during the early Holocene might be caused millennial-scale shifts in the position and strength of the SW (Fletcher and Moreno, 2011; Iglesias et al., 2012). Years with high moisture availability during the growing season would lead to high biomass production of grasses (Markgraf et al., 2007; Whitlock et al., 2001), which where the main fuel according to the charcoal deposited in the lake.

The middle Holocene fire regime starts with low fire frequency (<2 fires 1500 $year^{-1}$) between 8000 and 7300 cal yr, which might be explained by the wet conditions inferred for this period (Iglesias and Whitlock, 2014), increasing fuel moisture, decreasing fire probability. Null-to-low fire activity between 8000–7000 cal yr BP is also documented further south in Lake Shaman (44°S, de Porras et al., 2012) and Mallín Fontanito (44°S, Nanavati et al., 2019). In addition to high effective moisture, PAR values in Lake Vizcacha are low during this interval, suggesting low fuel biomass, adding another variable that might explain the low fire activity during this interval. This period is characterized by an increase in Cupressaceae. Short- and long-term studies demonstrate the importance of fire in the dynamic of *Austrocedrus* in the region (Donoso, 2013; Veblen et al., 1995). As we discussed before, the brief increase in Cupressaceae (attributed mostly to *A. chilensis*) may reflect the dominance of *Austrocedrus* population on north-facing slopes of Lake Lácar. GAM results (Fig. 8) show statistically significant influence of moderate fire frequency (4–6 fires 1500 yr^{-1}) on the abundance of Cupressaceae pollen. Likely, surface fires coupled with effectively wet conditions, favoured the settlement of *Austrocedrus* individuals on north-facing slopes of Lake Lácar. Notwithstanding, correlations between fire dynamics and plant abundance also could be the product of both fire-caused disturbance as well as fuel-fire dynamics. Overall, during the middle Holocene, *Nothofagus dombeyi*-type forest dominated the landscape, associated with wetter conditions. The increased biomass with low fire frequency resulted in high magnitude fires, as it is detected at ~5500 cal yr BP.

Cupressaceae and *Nothofagus obliqua*-type show a high negative correlation between charcoal and pollen abundance (Fig. 8) suggesting that both trees thrive under low-to-moderate fire frequency with low biomass burned, i.e. surface fires. A comparison of photographs taken between 1896 and 1985 Veblen and Lorenz (1988) compared changes in *Austrocedrus chilensis* populations around Lake Lácar, documenting a development from sparse woodland to dense *Austrocedrus chilensis* forest and increased density of *Nothofagus obliqua* and *Nothofagus dombeyi* on south facing slopes, changes attributed to forest burning, whose causes might be both natural and anthropogenic.

Nothofagus alpina and *Nothofagus obliqua,* become abundant during the Late Holocene, and both species possesses a relatively thick bark (Donoso, 2013) and exhibit active resprouting after being cut or burned (Veblen et al., 1996). Individuals of *Nothofagus obliqua* were observed in relatively open sites with evidence of fire (scars fires) indicating the ability of this tree to survive surface fires (Veblen et al., 2003). *Nothofagus alpina* and *Nothofagus dombeyi* coexist in the Lácar basin, at high elevation areas and south-facing slopes together with *Azara*, *Lomatia*, and *Maytenus* trees and here, fires are usually stand replacing (Veblen et al., 2003). Our results show that since 1500 cal yr BP onwards *Nothofagus obliqua*-type abundance increased continuously associated with the occurrence of low fire frequency (1–4 fires 1500 yr^{-1}) attesting for the capacity of these trees of tolerating surface fires.

For the last 1500 cal yr BP, a continuous increase in fire occurrence is documented in our record. Low CHAR values during this period suggest low severity, small and/or distant fires (*sensu* Nanavati et al., 2020). Many studies suggest the anthropogenic source of fire ignition in Patagonia during the Holocene (Heusser, 1994; Holz and Veblen, 2011; Holz et al., 2016), and in the XIX century, the combined role of fire ignition by indigenous people and European settlers in north Patagonia is well documented (Rothkugel, 1916). Pérez et al. (2016) reconstructed human demographic patterns in Patagonia during the late Pleistocene and Holocene based on radiocarbon dates and molecular data. The authors suggest that a remarkable acceleration in population size occurred after 7000–5000 cal yr BP, reaching its maximum at 1000 cal yr BP. In our study region, at least 36 archaeological sites around the Lácar basin attest to the presence of indigenous communities (Pérez, 2016), and there is evidence of the use of *Chusquea culeou* for shelter and fuel (Pérez and Aguirre, 2013). On the other hand, Prieto et al. (2011) describe that during the displacement of indigenous communities, they set fire at intervals to mark their path and for hunting guanacos (*Lama guanicoe*, Camelidae). Depending on wind direction, these fires could become more extensive and even dangerous to the hunters, combusting wider areas. Despite the archaeological evidence nearby the Lácar basin of human occupation before the European arrival in the region (Pérez and Aguirre, 2013; Pérez et al., 2016), we consider that both human and climate where an important factor influencing fire for the last millennia. Undoubtedly, shifts in seasonality and interannual/interdecadal climatic variability play an important role in driving fire regimes at the east of the Andes (Whitlock et al., 2006).

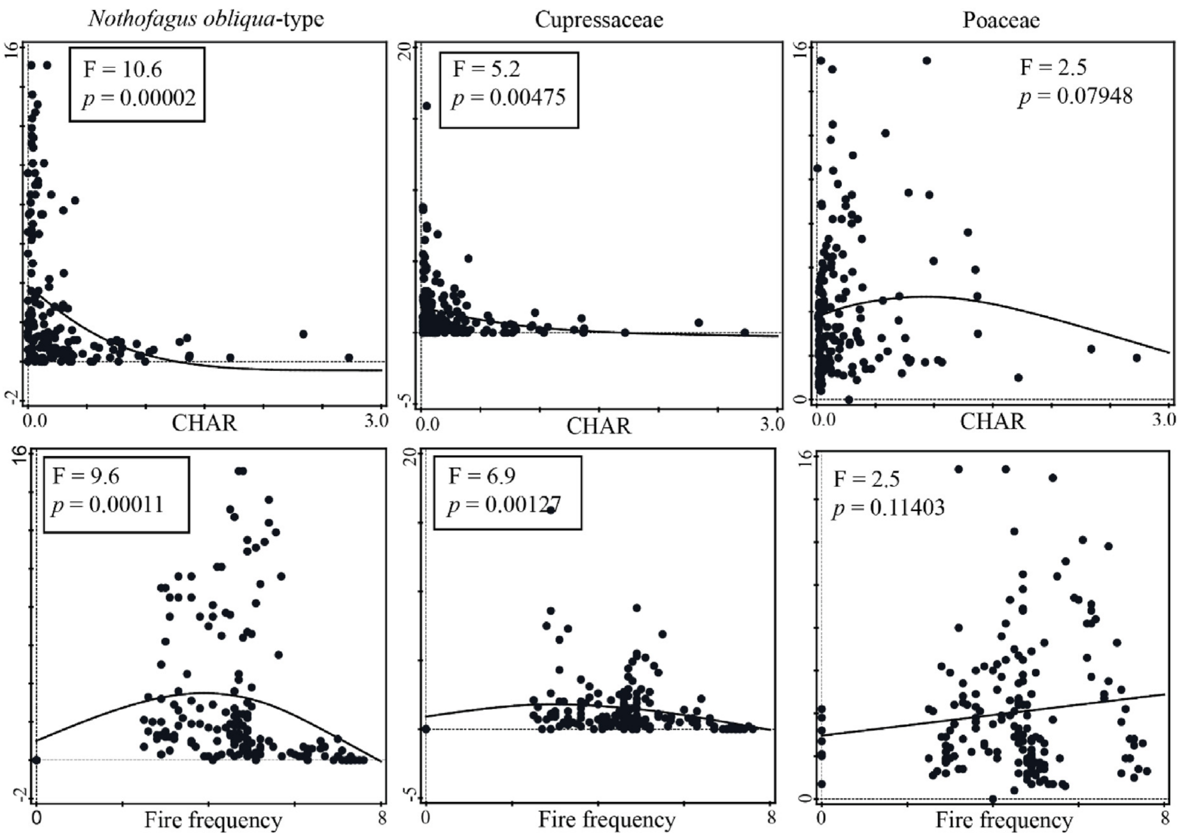

Fig. 8. Generalized additive models (GAMs) for the effect of fire descriptors (X-axis, *sensu* White and Pickett, 1985) on the percentage of selected taxa (Y-axis). Statistically significant results are highlighted with a rectangle.

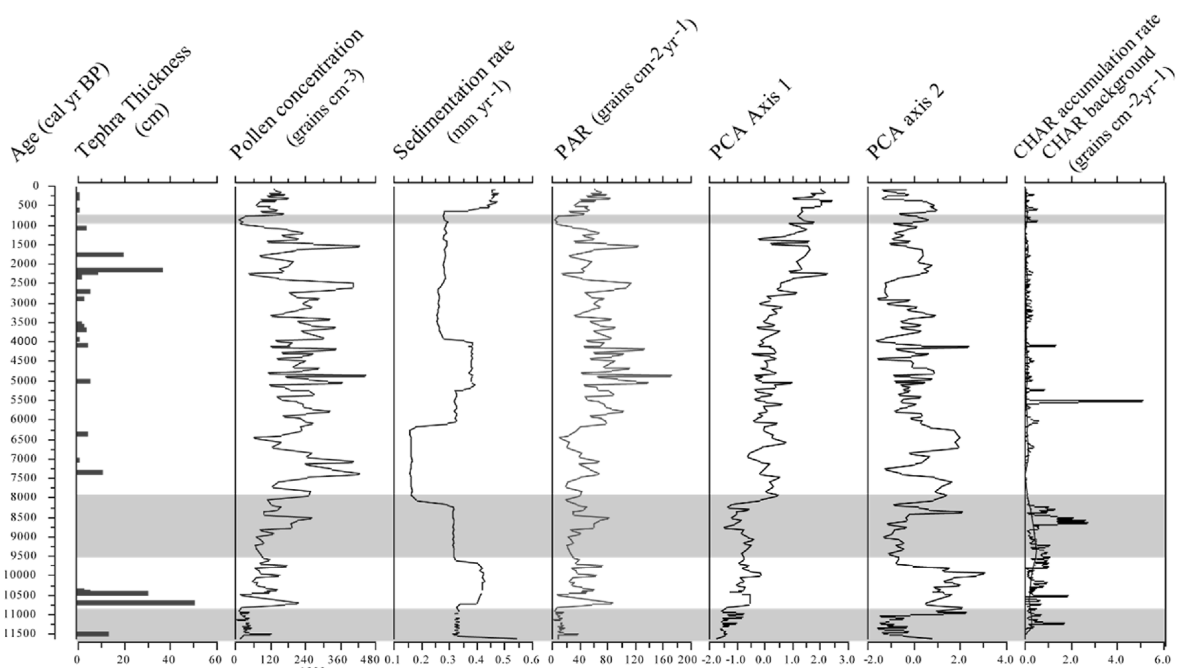

Fig. 9. Summary diagram with the main result obtained from Vizcacha record. Peat sections are highlighted in grey.

Moreover, the rise in the abundance in the percentage of *Nothofagus obliqua*-type, attests to warmer conditions in the region during the last two millennia, enhancing dry fuel and fire ignition, as it is evidenced on tree-ring records from the region (Lara et al., 2020) indicating a trend towards warmer conditions during the last millennia, and also, evidenced by the less expansive Patagonian glacier advances in comparison with the middle Holocene (Kaplan et al., 2016).

6. Conclusions

The pollen record from Lake Vizcacha documents the last 11,600 years of vegetation history and disturbance regimes. The early Holocene is characterized by overall dry conditions, with a landscape dominated by a *Nothofagus* shrubland (likely *Nothofagus antarctica* and *N. pumilio*) accompanied by shrub elements such as *Discaria*, *Gaultheria* and Asteraceae. During this time wet intervals are also observed as increases in the percentage of Cupressaceae (likely *A. chilensis*) and Poaceae. Frequent fires occur during this period. The rise in the percentage of Cupressaceae pollen marks the main vegetational change towards the forest composition during the middle Holocene. Humid conditions benefited the expansion of a dense *Nothofagus* forest. Fires decrease in frequency. The increased abundance of *Nothofagus obliqua*-type during the late Holocene represents the most noticeable change in vegetation composition at this site. Fire frequency increased slight for the last 1500 years.

The comparison of tephra to the vegetation history suggests that *Lomatia hirsuta* and *Hydrangea* benefit with time after ash deposition. The effect of ash deposition on *Nothofagus* species is not clear since the results show a random pattern when comparing the percentages before and after the tephra layer. Overall, the deposition of tephra layers might not have triggered substantive changes in the local vegetation recorded in lake Vizcacha. Fires may affect stands of *A. chilensis* and *N. obliqua/N. alpina*, but climate is likely the dominant factor controlling average vegetation composition. Indigenous people inhabiting the Lácar basin before the arrival of the European settlers in the region will have used fire. Nevertheless, climate is likely the main control influencing fire for the last millennia.

Data availability

The raw pollen and microcharcoal counting are available in PANGAEA Data Archiving and Publication under the following link https://doi.pangaea.de/10.1594/PANGAEA.936378.

Author contributions

Valentina Álvarez-Barra: Conceptualization, Data curation, Investigation, Methodology, Visualization, Formal analysis, Writing – original draft, Writing – review & editing. **Thomas Giesecke:** Conceptualization, Methodology, Visualization, Validation, Writing – review & editing. **Sonia L. Fontana:** Conceptualization, Writing – review & editing, Funding acquisition, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests that could have appeared to influence the work reported in this paper.

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