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Fire and vegetation dynamics of endangered *Araucaria araucana* communities in the forest-steppe ecotone of northern Patagonia

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ABSTRACT

Recent changes of the fire regime in northern Patagonia may have reduced populations of *Araucaria araucana*, which is listed as an endangered species. Although *Araucaria* does not depend on fire to persist, natural fires are part of the ecosystem and *Araucaria* withstands moderate fires. To understand recent and long-term vegetation patterns and processes that help in conservation tasks, we reconstructed the vegetation and fire history of the forest-steppe ecotone over the last 9 kyr based on a well-dated sediment core obtained from Lake Relem in northern Patagonia. Before 4.5 ka, pollen content indicates that steppe vegetation dominated the landscape. Pollen composition after 4.5 ka suggests that steppe was gradually replaced by scrublands and woodlands. The highest amount of *Nothofagus* woodland cover was reconstructed for the last 2.5 kyr. A continuous record of macro-charcoal particles indicates 20 fire events of low magnitude, with more frequent fires between 6 and 2.5 ka. Changes in vegetation composition were partly related to fire frequency changes, while the magnitude of fire events had no detectable influence on the vegetation. Pollen from the endangered *Araucaria* documents that the species was widespread around Lake Relem between 8 and 6 ka, decreasing abruptly ~6 ka, and slightly increasing up to the present. Results do not show a change in the fire regime due to the Euro-American colonization. The long-term trend of this *Araucaria* population does not show the decline observed elsewhere.

1. Introduction

Change in fire regime due to climate and land-use change might be altering vegetation structure and composition of the forest-steppe ecotone in Patagonia (Mundo et al., 2014). Although fire is a natural component in the Patagonian Andes ecosystems (e.g., Whitlock et al., 2007), there is still concern that fire regime change may be threatening the conservation status of particular plants. Increasing trends of fire frequency and severity during the last decades (Gonzalez et al., 2018) have led to discussions on the stability of the vegetation boundaries and the persistence of endangered species in the ecotone. The fire regime in northern Patagonia might have started during the Euro-American colonization in the late 19th century when about 25% of the forested areas close to the steppe were burned (Rothkugel, 1916). Grasses and shrubs recolonised these areas shortly after fires set by the Euro-Americans, which led to the interpretation of a progressive expansion of the steppe vegetation toward the forest due to aridification (Kalela, 1941). Later, Veblen and Lorenz (1988) realized that some of those burned areas were subsequently colonized by trees, arguing that the precipitation was not decreasing during the last century. Veblen and Markgraf (1988) interpreted that the vegetation composition and structure was mainly associated to humans setting fires while tree species recolonized the area as a result of decreased fire frequency. However, recent studies indicate a significant decrease in precipitation over the last century (Villalba et al., 2012), whilst repeated fires may have driven the vegetation to a dominance of pyrophytic shrubs (Kitzberger et al., 2016). Current vegetation patterns of the forest-steppe ecotone are the results of historical complex interaction between climate, human land use change and fire disturbance (Kitzberger, 2012; Whitlock et al., 2007). To understand the role of fire disturbance on vegetation dynamics, the stability of the ecotone boundaries, and the persistence of endangered species in the ecotone in Patagonia, it is necessary to take a

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long-term perspective in investigating natural variability.

The current location of the forest-steppe ecotone in northern Patagonia has shifted from its past distribution (Iglesias et al., 2014). Today, Patagonia's forests are mostly distributed in mountains above 600 m elevation (Roig, 1998), an area covered by ice before 15 ka (Hulton et al., 2002). During the transition from the Late-Glacial to the Holocene, pollen records suggest a progressive replacement of steppe vegetation by an open forest of *Nothofagus* (Iglesias et al., 2014). As the temperature increased during the Early and Mid-Holocene (Lamy et al., 2002), occurrence of the *Nothofagus dombeyi* pollen type indicates an expansion of the forest in northern Patagonia (e.g., Iglesias et al., 2014; Whitlock et al., 2006). In Patagonia, the *Nothofagus dombeyi*-type pollen abundance through the Holocene expanded firstly in northern Patagonia and stayed high until the Late-Holocene (Nanavati et al., 2019). Yet, the Late-Holocene in northern Patagonia (~41° S) is also characterized by a spread of *Austrocedrus chilensis*, likely due to an increase in fire frequency that created today's mixed forest (Whitlock et al., 2006; Iglesias et al., 2012). In the region of *Araucaria araucana* forest in northern Patagonia, ecosystems might followed similar patterns, however, the main drivers and the pace of changes in the forest-steppe ecotone are not well known.

Although, past changes in the forest-steppe ecotone are mostly influenced by climate, fire disturbances that occurred throughout the Holocene might have played an important role for the vegetation composition (e.g. Whitlock et al., 2007; Iglesias et al., 2018). During the Holocene, the pace of fire along the Patagonian forest-steppe ecotone is clearly variable (Nanavati et al., 2019). Studies have focused on climatic drivers, such as the intensification of Southern Westerly Winds (SWWs) and the onset of El-Niño-Southern-Oscillation (ENSO) (e.g., Fletcher and Moreno, 2012a), but also lightning strikes (Holz et al., 2012; Whitlock et al., 2007) or indigenous people (Veblen and Markgraf, 1988) might have played a role. While SWWs and ENSO may account for dry periods allowing the expansion of fires, lightning and humans were the most likely mechanisms to spark a fire. Although the factors causing past fires need to be better understood, it is generally accepted that the spread of fire is spatially and temporally limited by fuel biomass availability and climatic factors, that could be modified by human actions such as increasing fuel biomass or suppressing fire (Whitlock et al., 2015). For instance, along the northern Patagonian forest-steppe ecotone, a fire starting in the grasslands and scrublands is normally suppressed when reaching the forest due to more humid conditions beneath the tree canopy (Mermoz et al., 2009). In addition, due to increasing extensions of non-native pine plantations, the fuel biomass has increased, therefore the risk of more severe fire is increasing too (Taylor et al., 2017). Understanding the causes that trigger past and present fire, and the role that fires have had on the vegetation dynamics or the shifts of the ecotone, may help in the conservation of endangered species in Patagonia, for example *Araucaria araucana*.

Araucaria araucana (hereafter *Araucaria*) has a limited and fragmented distribution in the Patagonian Andes (~390 km^2; Premoli et al., 2013), occurring in the mountains principally above 1000 m a.s.l. (Gonzalez et al., 2006). *Araucaria* is classified as an endangered species because of a sharp reduction of almost 50% of its area of occupancy caused by intense selective logging and land-use change (Gonzalez et al., 2006; Premoli et al., 2013). Further concerns include the lack of regeneration for about 100 years in northern and eastern areas of its distribution (Roig et al., 2014), perhaps caused by an overconsumption of the seeds by humans, birds and mice, and goats grazing the seedlings (Gonzalez et al., 2006). Moreover, a decreasing trend in precipitation during the last centuries might have resulted in the reduction of the tree-ring growth across the *Araucaria* distribution (e.g., Muñoz et al., 2014), and recent human settlement might be changing the fire regime from infrequent catastrophic events to more frequent fires (Armesto et al., 2009). For instance, fires have burned ~600,000 ha in the last decade in central-south Chile, where the *Araucaria* region was one of the most affected (Gonzalez et al., 2018). Also, a mega-drought in 2010–2015 greater than any in the last 1000 years (Garreaud et al., 2017) may have facilitated the spread of fire and increased lightning-strikes (Gonzalez et al., 2018; Mariani et al., 2018). The current conservation status of *Araucaria* is the sum of many factors, but the predicted trend of increasing fire suggests that *Araucaria* is under serious risk. *Araucaria* shows adaptations to resist low and medium intensity fire disturbances, such as a thick bark, protected terminal buds and re-sprouting of shoots (e.g., Burns, 1991; Gonzalez et al., 2006; Veblen, 1982). The authors even suggest that the persistence of *Araucaria* as a dominant tree is related to fire disturbances, where *Araucaria* would regenerate abundantly after fire events resulting in a new cohort. Palaeoecological records are valuable tools that help understanding long-term population trajectories and responses to disturbance events, and by providing a baseline that can help in anticipating future trends in the face of the ongoing global change, i.e. assessing vulnerable species responses to current shifts in fire regime toward more frequent and severe fires (Froyd and Willis, 2008).

The Holocene vegetation dynamics of the *Araucaria* forest at the steppe ecotone are poorly known. *Araucaria* pollen abundance was found to be decreasing over the last 1.5 ka Lake San Pedro, ~38°S (Fletcher and Moreno, 2012b). However, during the last 3 ka, Mallín Paso del Arco (~38°S) shows a slight increase in the *Araucaria* pollen abundance (Heusser et al., 1988) as well as the record from Lake Cilantro (Dickson et al., 2020). While at the southern end of the *Araucaria* distribution, Mallín Río Malleo (~39°S), the pollen abundance did not change (Heusser et al., 1988). Over the last 300 years approximately, Moreno-Gonzalez et al. (2020) suggest that in some areas of the *Araucaria* forest, the vegetation did not change significantly during the time of Euro-American colonization (1850–1900 CE), but rather during the most recent decades, due to the arrival of extensive pine plantations. Thus, it remains an open question, whether *Araucaria*'s populations are declining on a millennial scale, since when and for which reasons. Here we provide a case study based on palaeoecological information over 8 millennia documenting the vegetation, fire regime and the trend in *Araucaria* populations. The main goals of this study were: 1) to reconstruct the local vegetation and fire history in the *Araucaria* region, and 2) to assess the role of the fire regime on the vegetation composition and spatial shifts of the ecotone. Addressing the current concern on the conservation status and future predictions, we aim to contribute to discussions by looking at *Araucaria*'s historical range of variability.

2. Study area

The study area is located in the current forest-steppe ecotone, in northern Argentinean Patagonia. Lake Relem is shallow (~2.5 m depth), small (~1 ha), without river inflow, and located in 38°58′39.64“S; 71° 4′51.13”W, at 1268 m a.s.l. (Fig. 1). At this latitude, the weather in the Andes Mountains is strongly influenced by low-level atmospheric flow that transports moist air masses on the South Westerly Wind (SWW) from the Pacific Ocean to the continent (Garreaud, 2009). The high altitude of the Andes at this latitude (>2000 m a.s.l.) creates a sharp rain-shadow effect with the storm tracks and westerly winds arriving from the Pacific Ocean and discharging most of the precipitation on the western slopes (Garreaud, 2009; Mundo et al., 2013). Although the study area is located in the current northernmost area of the SWW belt, the position of SWW varies at multiple time-scales, from intra-annual to millennia-scale. The climate is temperate with monthly average temperatures above freezing and a marked precipitation minimum during the austral summer (DJF) (Luebert and Pliscoff, 2006). Inter-annual precipitation regime is influenced by ENSO, which during positive phase increases the precipitation above average (Garreaud, 2009). On the eastern slopes of the Andes around 39°S regional precipitation on average is 200 mm, decreasing from 2500 mm or more at 1600 m a.s.l. (Bianchi et al., 2016; Paruelo et al., 1998), while annual mean temperature ranges between 12 °C to 8 °C at high altitudes, and increases up to 16 °C in the surrounding of Lake Relem (Bianchi et al., 2016). During

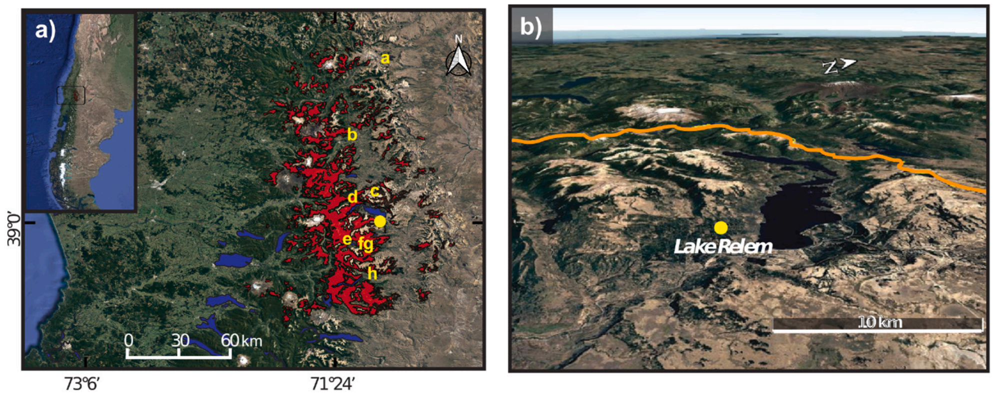

Fig. 1. Study area. a) Present-day distribution of *Araucaria araucana* (red polygons) located in northern Patagonia. The yellow circle indicates the location of Lake Relem, and the letters (a-h) indicate sites where other palaeoecological studies within the *Araucaria* region have been undertaken (see Table 2 for details). Notice the steep transition from forested areas (greenish pixels) toward the steppe (brownish pixels) on both sides of the Andes Mountain. b) Close-up of Lake Relem showing the surrounding topography and its position regarding current forest-steppe ecotone eastward of the Andes. The border between Chile (west) and Argentina (east) is marked by the orange line. Base map obtained from Google (2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the last 100 years, a 20–40% decrease in rainfall was observed (Garreaud et al., 2017). Lightning strikes are common in the Patagonian Andes, with ~2 lightning event per km^2 year^{-1} (WWLLN 2017), although 10-fold lower than in tropical and subtropical areas (Garreaud et al., 2014). The uprising of the moist air masses on the windward of the Andes, followed by the rain discharge, alters the electric charge of the clouds and eventually creates lightning storms, mainly during dry summers (Garreaud et al., 2014).

Close to 25% of the forest was burned in northern Patagonia during the Euro-American colonization (1880–1920 CE) (Rothkugel, 1916). The study of fire in *Araucaria* tree-rings evidenced an increase in fire frequency during the Euro-American colonization compared with previous 300 years (Mundo et al., 2013; and González et al., 2005). Although, periods of increasing frequency are clearly related to humans, climate conditions have also played an important role. For example, periods of negative phases of ENSO are correlated with fire events (e.g. Mundo et al., 2013) and low precipitation (Garreaud, 2009). Apparently, lightning strikes are more frequent during ENSO (Mariani et al., 2018). However, less than 5% of fires occurred in the last decades were produced by natural causes (Gonzalez et al., 2018).

The interaction between climate, topography and the disturbance regime in the ecotone promotes a variety of plant associations, creating a complex landscape (Kitzberger, 2012). In the area near Lake Relem (Fig. 1b) we observed *Araucaria* growing in different plant associations: (1) Dense, multilayer forest with dominance of *Nothofagus dombeyi*, and *N. pumilio,* associated with *Drimys andina, Berberis microphylla, Maytenus magellanica, Gaultheria mucronata, Escallonia virgata,* and *Desfontainia spinosa* in the understory. Under disturbed conditions, *Chusquea culeou* can form dense understory.; (2) mixed forest with *Austrocedrus chilensis* and/or *Nothofagus obliqua,* or open forest with dominance of deciduous *Nothofagus antarctica.* Common understory shrubs such as *Schinus patagonicus, Empetrum rubrum, Escallonia virgate, Maytenus disticha, G. mucronata,*and the herbs *Poa pratensis, Azorella caespitose, Galium antarcticum, Caltha appendiculata, Festuca pallescence, Acaena pinnatifida*; (3) scattered individuals of *Araucaria* without or scarce *N. antarctica* and *A. chilensis,* and broadly dominated by bunch grasses and shrubs like *Discaria* and *Colletia*. In the steppe, *Araucaria* is normally absent and the vegetation is characterized by herbs such as *Festuca pallescens, Cerastium arvense, Azorella caespitosa, Nassauvia abreviata, Poa spp., Elymus patagonicus, Quinchamalium chilense, Sencecio patagonius, Acaena pinnatifida, Adesmia longipes, Galium antarcticum*, and shrubs: *Discaria serratifolia, G. pumila, Baccharis magellanica, Mulinum spinosum, Colliguaja integerrima, Ephedra chilensis.*

3. Methodology

3.1. Chronology

The age of 7 samples was obtained by accelerator mass spectrometry (AMS) on bulk sediment submitted to the CHRONO Centre, Queen's University Belfast, UK (UBA) (Table 1). Radiocarbon dates were calibrated with SHCal13.14C (Hogg et al., 2020) and the post-bomb_SH1–2.14C for post-bomb dates (Hua et al., 2013). We also made use of a well-known volcanic eruption in the area, the Sollipulli-Alpehue dated in 2990 ± 0.09 BP (Table 1; Naranjo et al., 1993). The age-depth model was constructed using a smooth spline (0.1 smooth), with a 95% of confidence interval (1000 iterations). Calibration and age-depth model (Fig. 2) were conducted with Clam 2.2 (Blaauw, 2010).

3.2. Sediment and pollen analysis

Subsamples of 0.2 cm^3 were taken to obtain an estimation of the dry bulk density and organic content of the sediment, the samples were first dried at 105 °C for 24 h. and then burned at 550 °C for 4 h. (Heiri et al., 2001). A total of 176 pollen samples of 0.5 cm^3 were taken along the core, avoiding tephra layers. Pollen analysis was done following standard techniques (Bennett and Willis, 2001). The samples were not sieved. By adding *Lycopodium clavatum* tablets, we could estimate the pollen concentration, and the results were multiplied by the sedimentation rate to estimate the Pollen-Accumulation-Rate (PAR). Among other uses, PAR has been found as good proxy for reconstruction of past tree biomass (Seppä et al., 2009). Pollen was counted using a light microscope at 400-1000×. Pollen concentration was low, therefore a minimum of 400 terrestrial pollen grains were counted. The identification of pollen and spores was carried out with the atlases of Heusser (1971), Markgraf and D'Antoni (1978) and pollen references stored in the Department of Palynology and Climate Dynamics at Göttingen University. Pollen taxonomy follows modern plant distribution within the study area then linking the pollen types to this species and genera (Fontana and Bennett, 2012).

3.3. Macro-charcoal analysis

To reconstruct the fire history, we followed procedures proposed by Whitlock and Larsen (2001) to process the macro-charcoal particles in sedimentary records. Subsamples of one cubic centimetre were extracted contiguously every centimetre and sieved through a 125 μm mesh. Macro-charcoal particles were counted in a stereomicroscope. To calculate the Grass-to-total charcoal index, we identified charcoal morpho-types following a simplified classification of Enache and

Table 1
AMS Radiocarbon dates from sediment core obtained from Lake Relem, northern Patagonia. Bulk sediment were analysed in the CHRONO Centre, Queen's University Belfast, UK (UBA). Original depth considers the water column above the sediment, and the adjusted depth corresponds to the exclusion of tephra layers >0.5 cm from the original depth.

Lab. no.	Original depth (cm)	Adjusted depth (cm)	Age (^{14}C yr BP)	%pMC	Age (cal yr BP) (2σ)	probability (%)
UBA-29237	270–271	270–271		109.88 ± 0.34	−53.4–47	93
					−8.8–8.7	2
UBA-29238	277–278	277–278		100.37 ± 0.32	−7.4–5.9	95
UBA-29239	325–325.5	325–325.5	330 ± 24		295.9–340.5	28.8
					351.8– 451.3	66.2
UBA-29242	442–442.5	430–430.5	1949 ± 22		1750.9–1768.3	5.1
					1815.7–1916.8	89.9
So-A[a]	724	482	2990 ± 0.09		2847.1–3054.8	95
UBA-29243	848–848.5	576–576.5	4576 ± 26		5049.5–5193.5	61
					5211.7–5312.5	34
UBA-29244	930–930.5	637.5–638	6359 ± 30		7167.4–7313	95
UBA-23305	1004–1004.5	700–700.5	7994 ± 47		8641.1–8989.5	95

[a] So-A date corresponds to Sollipulli-Alpehue eruption (Naranjo et el., 1991). The age was assigned to the adjusted depth, just below the tephra (original depth, 724 cm).

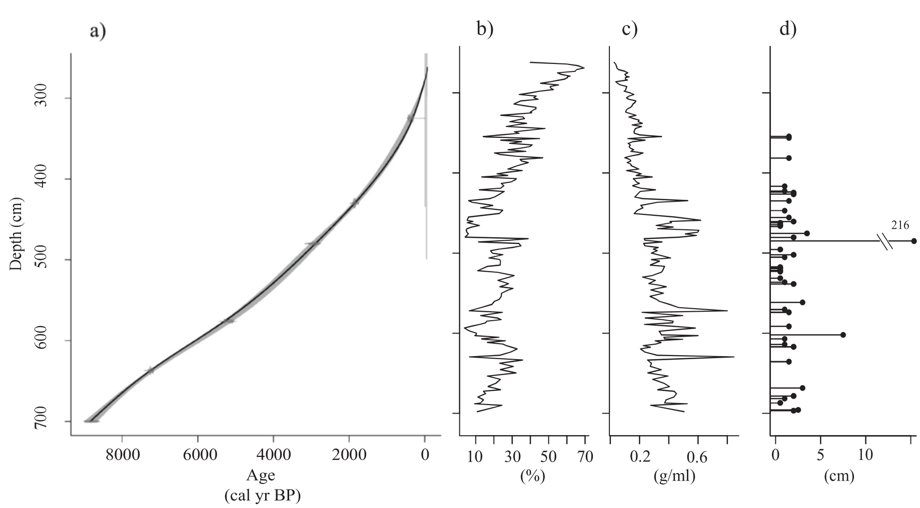

Fig. 2. a) Age-depth model; b) percentage of organic content loss after ignition (LOI); c) the dry bulk density; d) tephra thickness. All tephra layers >0.5 cm thick were excluded from the age-depth model.

Cumming (2006). Charcoal particles per sample were multiplied by sedimentation rate to obtain the charcoal accumulation rate (CHAR). This result was then interpolated to the median sampling interval and smoothed with Robust Lowess method for a 500-yr time window to estimate low-frequency CHAR ($C_{background}$). Row data were not transformed. To estimate high-frequency of macro-charcoal accumulation rate we used the ratio between CHAR and $C_{background}$ as suggested by Higuera et al. (2010) when CHAR data presents unequal average and variance. Peaks events (cPeak) were detected with a local threshold, modelled with a mean Gaussian cut-off at 90% confidence. Fire Frequency and Fire-Return-Intervals were analysed over 1500-yr time windows. Pre-treatment and analysis of macro-charcoal data were conducted with CharAnalysis v.1.1 (Higuera, 2009).

3.4. Data analysis

Selected taxa >1% abundance were plotted in the pollen-diagram for the manuscript. Aquatic plants were summed apart from the total of the terrestrial taxa. Pollen zones were defined by depth-constrained cluster analysis of the pollen samples, based on the Euclidian distance of all terrestrial taxa. Statistical significant zones were defined according to the broken stick model (Bennett, 1996). Compositional trends of the terrestrial taxa were explored through a Principal Component Analysis (PCA). The compositional turn-over was evaluated by Detrended Correspondence Analysis (DCA) (Ter Braak and Smilauer, 2012). For both PCA and DCA, the taxa abundance was square-root transformed and centred. Further, to assess the vegetation responses to fire regime, we constrained the compositional data against CHAR, Fire Frequency, Fire Return Interval, Peak events, and Fire-Magnitude. To assess the burn severity we followed partially the criteria proposed by Assal et al. (2018), where high tree mortality in a big area indicate a high severe fire. Since direct transfer function cannot be done, we mostly relied on abrupt changes in pollen percentage after a fire event. All analyses were conducted with RStudio v.3.3.1 (Rstudio Team, 2016), Vegan-package 2.4–2 (Oksanen et al., 2017), and Rioja-package (Juggins, 2015).

4. Results

4.1. Chronology and sedimentary process

The core had a total length of 743 cm, and 442 cm without tephra layers. The base of the core was dated to ~9000 cal yr BP (hereafter all dates correspond to cal yr BP). Using 7 radiocarbon dates and the published radiocarbon age of one tephra layer (Table 1), we obtained an age-depth model (Fig. 2a). Sedimentation rate was relatively constant between <0.1 to 0.2 cm yr^{-1}. Near the top of the core the sedimentation rate increased up to 0.5 cm yr^{-1}. Organic content in the sediment, expressed as the percentage of organic material lost after ignition (LOI %), showed a strong variation along the core, with an increasing trend from c. 500 cm depth to the top (Fig. 2b). Dry bulk density (Fig. 2c) mirrored LOI for most samples. Peaks in bulk density and drops in organic material are related to tephra layers (Fig. 2d), in particular after the Sollipulli-Alpehue eruption. In the core, 39 tephra layers more than 0.5 cm thickness were detected, most of them ranged in between 1 and 5 cm and one of ~200 cm thick (Fig. 2d).

4.2. Vegetation history

The general trend in vegetation composition over the last 9 kyr showed an overall vegetation transition from steppe grassland (Poaceae) to forest (*Nothofagus dombeyi*-type) (Fig. 3). The pollen of *N. dombeyi*-type in the study area is represented by three *Nothofagus* species*, N. dombeyi, N. pumilio* and *N. antarctica*, while Poaceae might represent over 100 species. Differentiation of pollen grain of the Poaceae family to lower taxonomic levels was not viable. DCA indicated a low compositional turnover for the whole period analysed (1.25 SD), however the cluster analysis differentiated five significant local pollen zones in the pollen diagram (Fig. 3 and 5a). The pollen diagram showed important taxa >1% abundance and were ordered following their weighted average. Between 9 and 4.5 ka the pollen assemblage was characterized by high abundances of *Mulinum*, Verbenaceae, Cyperaceae, Amaranthaceae and Poaceae (Fig. 3, pollen zone LR-1; Appendix 1). These taxa are typical of the modern steppe vegetation. Although the above mentioned taxa were present along the record, the relative abundance decreased toward the present (Fig. 3 from LR-2 to LR-5), but the PAR remain relatively stable (Appendix 1). Pollen from *Prumnopitis andina* was found sporadically in low percentage along the record, but it was more abundant between 9 and 4.5 ka (Fig. 3, pollen zone LR-1). Likely traces were indicative of long dispersal pollen or might represent scarcity of individuals nearby.

Araucaria pollen exhibited a maximum abundance between 8 and 6 ka (Fig. 3, LR-1, Appendix 1). From 8.2 ka the percentage of *Araucaria* pollen was increasing, but a small drop occurred about 7.4 ka. Later the pollen increased continuously up to 15% around 6.7 ka. Similar pollen percentages over consecutive samples suggested a relatively stable population near the lake for approximately 200 years before a drastic decay about 6.7 ka. This trend was also reflected in the *Araucaria* PAR reaching between 400 and 500 grains cm^2 $year^{-1}$ at around 6.7 ka (Appendix 1). After the steep decline, the pollen abundance persisted between 1 and 3% (Fig. 3, LR-2), increasing from 2 ka to the present (Fig. 3 LR-4 and 5; Appendix 1).

Pollen of *Schinus patagonicus* was found at low abundances, however, more frequent before 4.5 ka and from 4.5 ka to the present was less frequently found. *Nothofagus dombeyi*-type presented low percentage (40–45%) between 8.7 and 4.5 ka, suggesting the presence of dispersed patches with likely shrubby *N. antarctica*. Likely small patches of *Nothofagus* forest remained somewhere in protected hills westward of lake Relem (Fig. 1b), based on the continuing amount above 41% (cut-off to differentiate steppe from forest in Patagonia; Iglesias et al., 2017) of *Nothofagus dombeyi*-type, and the presence of pollen of vines species (e.g., *Muehlembeckia* and *Hydrangea*, Fig. 3). Between 4.5 and 3 ka approximately, *Nothofagus dombeyi*-type showed a stepwise abundance increases from 45% up to 60%. This increase in *Nothofagus dombeyi*-type around 4.5 ka mirrored a decline in Poaceae pollen indicating an expansion of the forest into the steppe. A notorious decline in *Nothofagus dombeyi*-type and Poaceae occurred around 3 ka, probably as consequence of the Sollipulli-Alpehue eruption. This eruption had a strong imprint on the vegetation (Fig. 3, pollen zone LR-3), an insight on the impacts of this eruption and others in the area is published elsewhere (Moreno-Gonzalez, 2020; Moreno-Gonzalez et al., 2020). In the fourth pollen zone (LR-4), during the last 2.5 ka the pollen percentage of *Nothofagus dombeyi*-type (Fig. 3) reached high proportions, ranging between 60 and 80%. The same trend was observed in the PAR (Appendix 1). Poaceae pollen in turn, remained at low percentage after 2.5 ka, with relatively constant PAR. The pollen abundance of Poaceae denoted the close proximity of the steppe and/or the presence of patches with open forest and shrubs. Pollen from *Araucaria*, *Nothofagus obliqua*-type, *Saxegothaea conspicua*, and *Austrocedrus chilensis* were slightly more abundant after 2.5 ka. During recent times, pollen from the non-native taxa characterized the topmost samples with significant increase of *Rumex acetosella* and *Pinus* together reaching up to 20% (Fig. 3, LR-5).

Most frequent aquatic taxa found were: *Myriophyllum, Potamogeton,* and *Sagittaria* (Fig. 3). Between 8 and 6 ka all aquatic taxa decreased the abundance with low and sporadic appearance. After 6 ka *Potamogeton* and *Sagittaria* increased again and remained relatively stable until present, but *Myriophyllum* was the dominant taxa between 6 and 2 ka. The fall of *Myriophyllum* after 2 ka and the quasi-continuous presence of *Potamogeton* might indicate a strong change within the lake level and water condition up until the present.

4.3. Fire history

Fire history was reconstructed following the pollen zones. CHAR showed a variation over time, with periods of high accumulation (5–10 pieces cm^{-2} yr^{-1}) between 9 and 8 ka and 5.8–3 ka (Fig. 4a). The Grass-to-total charcoal index (Fig. 4b) indicated that grass was the main fuel combusted during the last 9 ka. The analysis detected 20 significant fires in the last 9 ka around Lake Relem (Fig. 4c). Although, peaks in the interpolated charcoal data were detected, some of them could not pass the threshold remaining insignificant. Of those significant peaks, most of them have a SNI close or higher than 3 (Fig. 4d) adding confidence to the results. Fire magnitude was normally <40 pieces cm^{-2} yr^{-1}, but one peak registered 520 pieces cm^{-2} yr^{-1}. The event occurred approximately 5.6 ka ago (Fig. 4e). Between 9 and 6 ka fires were fairly infrequent, with a single fire every 1.5 ka (Fig. 4f). Fires became more frequent between 6 and 2.5 ka, to the point where fire events occurred every 200 years.

Changes in the fire regime explained a small fraction of the variation in pollen proportions (7.1%). Fire Frequency and Fire Return Interval significantly explained some variation in pollen composition, while the fire event (peak events) and the magnitude of the event (peak Magnitude) had no significant relation with pollen abundance (Fig. 5b). The highest abundance of *Araucaria araucana* pollen occurred during a period when fire frequency was lowest (Fig. 5b). Conversely, *Ephedra, Nothofagus obliqua*-type and Caryophyllaceae were positively related to high Fire Frequency, given the abundance of these taxa increased during periods of greater Fire Frequency.

5. Discussion

5.1. Vegetation and fire dynamics at the ecotone

Nothofagus dombeyi-type and Poaceae pollen are the major components of the shifting forest-grasslands dynamic in Patagonia, and their changes in abundance show that the position of the forest-steppe ecotone has changed through the Holocene (Iglesias et al., 2014; Whitlock et al., 2006). As the ecotone is determined by the steep precipitation gradient from west to east, the increasing (decreasing) pollen abundance of *N. dombeyi*-type (Poaceae) is related to the expansion (contraction) of the forest in response to increasing (decreasing) precipitation throughout the Holocene. A compilation of pollen diagrams between 41 and 44° S in northern Patagonia (Nanavati et al., 2019) serves as a reference to interpret the local vegetation change. In these diagrams *N. dombeyi*-type shows a continuous decline from 11 until about 7.5 ka (Nanavati et al., 2019). Nevertheless, the high variability particularly around 7.5 ka suggests local changes rather than a regional trend. The authors showed that *N. dombeyi*-type increased about 7 ka, reaching a maximum around 5 ka, which is distinct from the increase in relative abundance of *N. dombeyi*-type at Lake Relem (~39° S) starting from 4.5 ka reached a maximum around 3 ka. Causes for the lag in *N. dombeyi*-type expansion at this latitude are not clear. Perhaps the influence of persistent arid condition during early and mid-Holocene

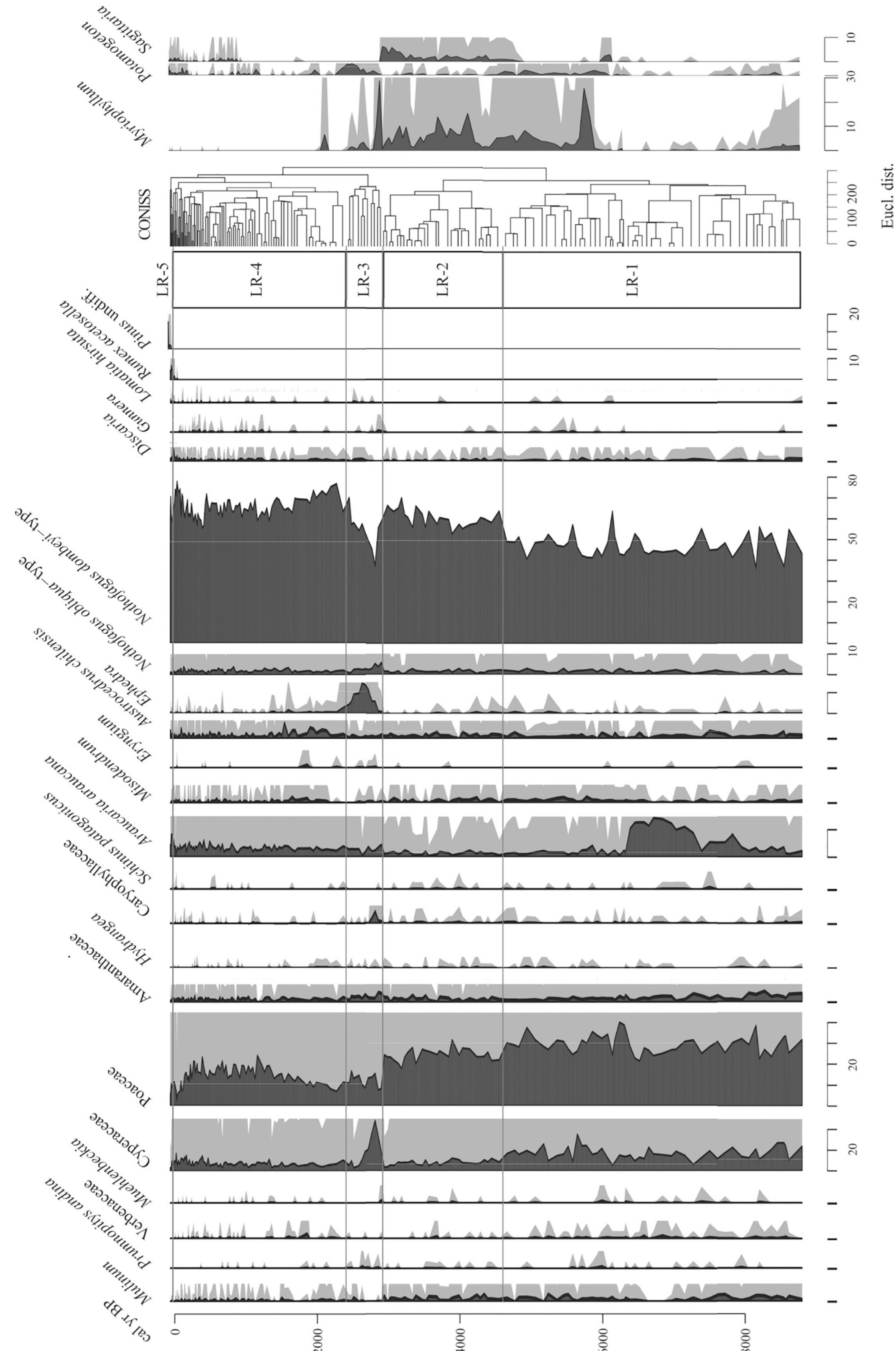

Fig. 3. Pollen diagram showing selected taxa. The order of the pollen taxa follows the weighted average, where highest abundances toward the bottom of the core (oldest samples) being placed in the left side of the diagram. The grey silhouette indicates magnification ×10. CONISS and pollen zones were calculated only with terrestrial pollen taxa. Aquatic pollen percentage were calculated based on terrestrial pollen sum.

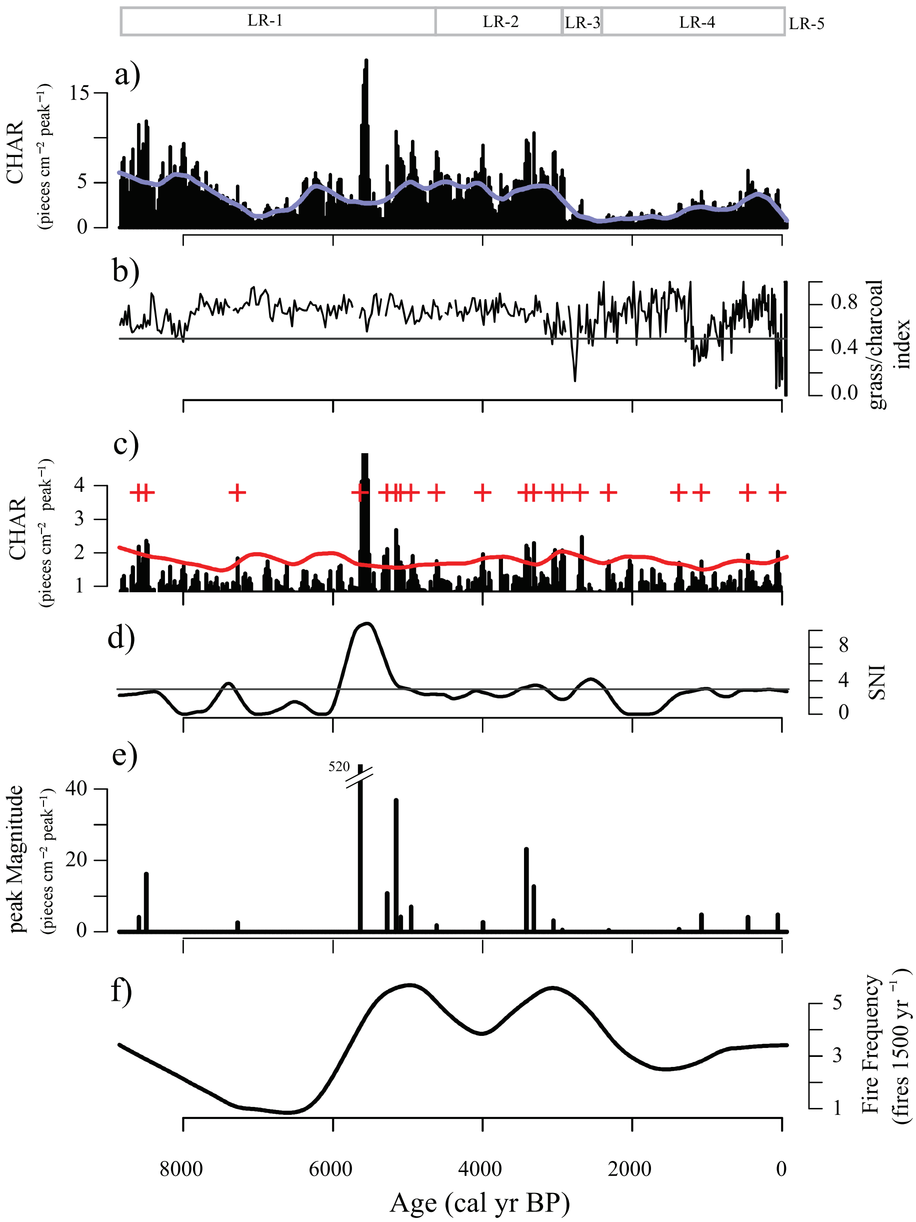

Fig. 4. Local fire history for Lake Relem reconstructed following pollen zones (small box above panels). a) Charcoal accumulation rate (CHAR) interpolated to 20 yr and $C_{background}$ defined by 500 yr trend with robust Lowess method (blue line). b) Grass-to-total charcoal index, threshold indicate values >0.5 with dominance of grass charcoal and < 0.5 dominance of wood charcoal particles. c) shows the peak magnitude (C_{peak}), obtained from the ratio between CHAR and $C_{background}$. Threshold defining C_{noise} (90%) for identification of the significant events (crosses); d) Local Signal-to-Noise Index (SNI), values ≥3 indicate consistent peak detection. e) peak magnitude of significant fires. f) fire frequency for time span of 1500 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Jenny et al., 2003) were likely sharper and enhanced north of 41° S. At Lake Relem current precipitation is lower than south of 41° S and characterized by drier summers than south of 41° S (Bianchi et al., 2016). Lake Relem is also at a higher altitude and more distant from the Andes mountain to the east than sites south of 41°S. This might limit the distribution and abundance of tree taxa such as *Nothofagus dombeyi*, *Nothofagus pumilio,* and *Austrocedrus chilensis*. From 5 ka to the present, *N. dombeyi*-type in the ecotone between 41 and 44° S decreased as *Austrocedrus chilensis* expanded, likely caused by climatic changes occurring, concomitant to an increase in fire activity that formed a mixed forest with *Nothofagus dombeyi* and *Austrocedrus chilensis*. This might have not displaced the position of the forest-steppe ecotone since Poaceae does not show a significant long-term increase (Iglesias et al., 2014). Conversely, around Lake Relem no other pollen taxa than *N. dombeyi*-type increased its abundance, which indicates a change in the location of the forest-steppe ecotone. It seems that the shifts of the ecotone boundaries in the *Araucaria* region followed a distinct pattern compared to other areas in northern Patagonia and current boundaries may have established since ~4.5 ka. Also, vegetation in Relem changed after the increase in fire frequency as we discuss below.

The fire history in Relem shows that fire frequency (Fig. 4e) increased when precipitation rose about 6 ka (Jenny et al., 2003; Lamy et al., 2001)L, while fire frequency was low during the driest period. Relatively low PAR of tree taxa before 6 ka suggest low fuel biomass and from 6 ka to the present PAR increased gradually. Increasing precipitation should have resulted in increased vegetation cover (biomass), but increasing ENSO event frequency from 6 ka to the present added more variability to weather conditions (Moy et al., 2002). Nowadays, negative ENSO at this latitude is related to the dry periods (Garreaud, 2009). In addition, ENSO-events cause an increase in the number of lightning-strikes that can be linked to fire ignition (Mariani et al., 2018). Yet, in recent decades, fires caused by lightning accounted for less than 5%, as most fires were caused by humans (Gonzalez et al., 2018). Perhaps, frequent fires between 6 and 4.5 ka negatively affected the grassland, while increasing moisture availability might have caused the development of *N. dombeyi* and *N. pumilio* in the hills west of Relem (Fig. 1b). In turn, fire regime and the interaction between climate and vegetation differed over the last 2.5 kyr compared to the previous period of 6–4.5 ka. During the last 2.5 k, the precipitation tends to be relatively stable (Jenny et al. 2003; Lamy et al., 2001), but higher than previous periods.

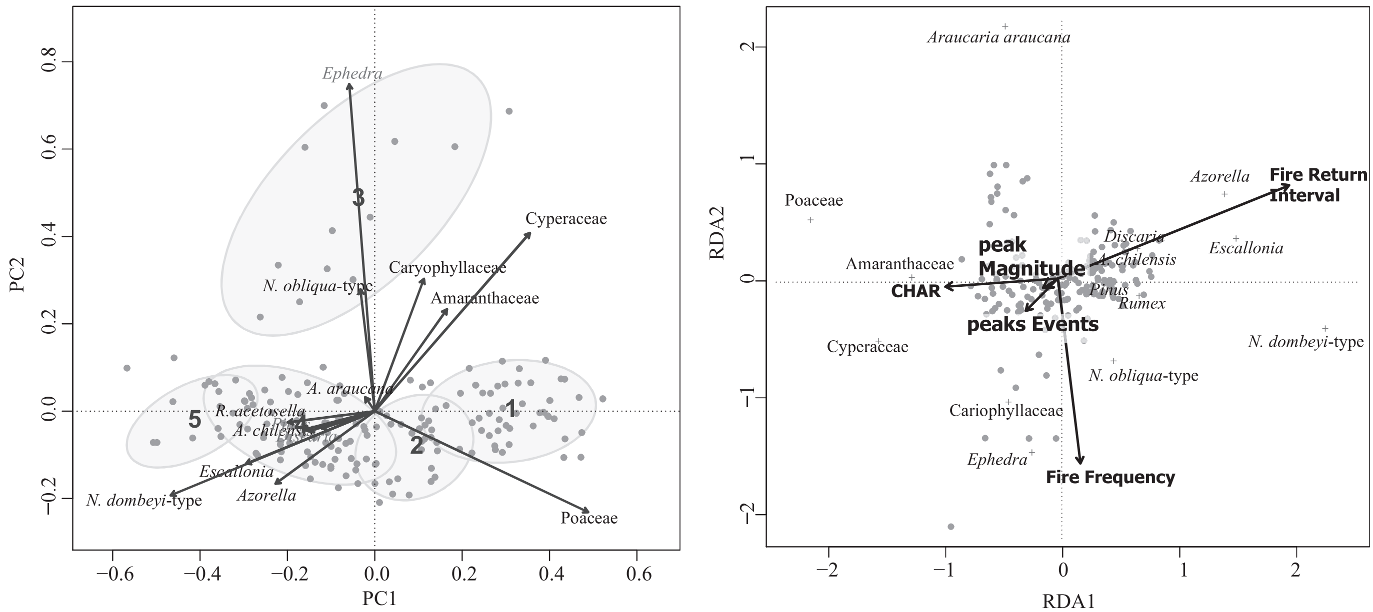

Fig. 5. Ordination diagrams, only the most abundant taxa are plotted. a) Results of the Principal Component Analysis for pollen data. Ellipses group samples regarding to the significant local pollen zones as result of cluster analysis. b) Constrained pollen data by parameters of fire regime, Charcoal accumulation rate (CHAR, $P = 0.001$), fire event (peak Events, $P = 0.331$), the peak Magnitude ($P = 0.27$), Fire Frequency ($P = 0.001$) and Fire Return Interval ($P = 0.001$).

The results show that *Nothofagus dombeyi*-type remained stable too, but fire frequency decreased. ENSO events became less frequent during the last 1.2 ka (Moy et al., 2002), and likely lightning storms could have decreased too, which would have decreased the absence of significant fires. Alternatively, the recurrence of lightning did not result in fires because of a predominant moist condition; also because the forest at the ecotone acted as fire-break (Mermoz et al., 2009; Morales et al., 2015).

Contrary to expectation, the role of humans set fires in the area, (e.g., Veblen and Markgraf, 1988) may be less important than hypothesized. Along the Holocene indigenous people were dispersedly settled in the *Araucaria* region, although sporadically and with long hiatuses especially during the mid-Holocene (Barberena et al., 2015b; Perez et al., 2016). There are scarce archeological sites until ~4 ka suggesting they probably inhabited east of Andes in non-forested areas (Barberena et al., 2015b). The artifacts found so far in those archeological sites show they were hunter-gatherers until the European colonization, and the selective use of rocks and of wood material suggest that manufacturing of artifact was not well developed and integrated in their activities (Barberena et al., 2015a). In Relem, the low Fire Frequency coincides with the highest indigenous population before the arrival of Spaniards (Perez et al., 2016). However, high fire frequency occurred when population in the surroundings of Relem was low. Whether indigenous people managed the forest and set fires to keep stands of Araucaria (Aagesen, 2004) is unclear. Apparently, indigenous activities in the area were probably not the principal cause of fire ignition during the Holocene.

In more recent history, indigenous and Euro-Americans caused fires are well documented. The Euro-American colonization between 1850 and 1900 CE burned approximately 25% of the forest on the eastern flank of the Andes of northern Patagonia (Rothkugel, 1916). For the same period dendrochronological evidence recorded an increase in fire occurrence across the *Araucaria* region (González et al., 2005; Mundo et al., 2013). Contrary to expectations, our analysis recorded a single macro-charcoal peak for this period (1895 CE) showing that the surroundings of Relem were burned without a change in fire frequency. Perhaps the increase in macro-charcoal accumulation (Fig. 4a) for the last 200 years represents the burning of several distant areas during colonization. The analysis of macro-charcoal in Relem also indicates that the magnitude of the 1895 fire event was similar or smaller than others registered in the history (Fig. 4e). This event seems to be even smaller than other records throughout Patagonia, but composed of mostly non-grass material (Fig. 4b). The results show that this event had a minor effect on dominant taxa, with *Nothofagus dombeyi*-type (Poaceae) showing a small decrease (increase) for a brief time before recovering previous abundance. Furthermore, the results do not reflect the increasing fire frequency and more severe fires during the last decade as response of the ongoing mega-drought (Garreaud et al., 2017; Gonzalez et al., 2018). Likely, because of the time resolution macro-charcoal records provide, it might not directly transfer to short-term ecological processes, as dendroecological records do. Therefore, it is difficult to anticipate future trends in fire regime and the effects it could have to the *Araucaria* forest.

The vegetation around Lake Relem shows a stronger response to changes in fire frequency, while fire events and their magnitude have little or no importance (Fig. 5b). *Nothofagus* species resprout vigorously within a decade after severe disturbance (González et al., 2005; Veblen, 1982). Vegetation in the mixed *Nothofagus-Austrocedrus* forest (around 41°S), may change from forest to shrubs dominance in response to repeated fire disturbances (Kitzberger et al., 2016; Paritsis et al., 2015). The authors observed that following repeated fires during the 20th century stands were re-colonized by pyrophytic shrubs species (e.g. *Discaria, Berberis, Ephedra*) creating a mosaic of vegetation among primarily forest dominance at the landscape level. In our results, *Ephedra* is well related with high fire frequency, while *Discaria* is associated with fire free periods (Fig. 5b). The results presented here suggest that vegetation in *Nothofagus-Araucaria* forest can resist light fire disturbances without changing the composition at the landscape level and recover pre-disturbance values relatively fast. If forests stands have changed recently to an alternative stable state, and if fires have altered the location of the ecotoneis unclear. The results from Lake Relem do not show that high fire frequency promoted the expansion of the forest, but it seems that the surrounding landscape has been a patchy landscape rather than pure forest or grassland steppe for significant periods.

5.2. The role of fire in the natural variability of Araucaria dynamics

The role of fire in the *Araucaria* dynamics is complex when comparing different fire regime parameters such as magnitude and return interval. The development of *Araucaria* was independent of fire events and only slight changes can be visually attributed to past fire events (Fig. 6). Charcoal accumulation rate in Patagonia is commonly considered as an indicator of fire activity, however we found no effect on *Araucaria* (Fig. 5b). On the other hand, we expected that fire events would have a negative effect on abundance, but neither the events, nor their magnitude showed effect on *Araucaria* pollen (Fig. 5b). This is likely due to low fuel biomass in the past, as suggested by PAR, that might caused mostly superficial fires of low intensity. The increase in Fire Frequency since 6.2 ka might have produced a decrease in the abundance of *Araucaria* around Relem, below the overall average. Contrarily, periods free of fire coincide with higher than average abundance (Fig. 6). While the ability to resist and/or recover low-to-medium fire intensity agrees with proposed models from Burns (1991), the negative responses to more frequent fires contradicts the idea that *Araucaria* benefits from fires (e.g. (Kershaw and Wagstaff, 2001). As we discussed above, long-term fire records should be cautiously compared to short-term ecological process before implementing conservation strategies.

The rise and fall of *Araucaria* between 8 and 6.2 ka (Fig. 6a) is also documented in Lake Torta ~20 km south of Relem (Fontana and Giesecke, 2017) and in Lake Cilantro (Dickson et al., 2020), but two other sites in the Lake Torta valley do not show the same pattern (Fontana and Giesecke, 2017; Moreno et al., 2018). In modern pollen rain, *Araucaria* can reach up to 23% nearby Relem around Paso Los Arcos (Paez et al., 2001). Vegetation cover in this area is low, composed of scarce grasses and the near absence of shrubby *N. antarctica,* while *Araucaria* is the only tree, forming groups of dense woodland. The origin of the rise in pollen and its persistence is unknown, but it coincides with a long period of low precipitation (Lamy et al., 2001; Jenny et al., 2003), and a long period free of fires, perhaps providing an advantage over *Nothofagus* species. *Araucaria* perhaps has been present in the area since the Last-Glacial period (Marchelli et al., 2010), although no published records can confirm its presence during the Post-Glacial. Maybe the established populations of *Araucaria* before 8 ka expanded into the area in response to a local fire about 8 ka (Fig. 6b). Likely the lack of shrubs competition and the absence of subsequent fires burning young individuals may have allowed establishment and expansion. Seedlings of *Araucaria* tend to be

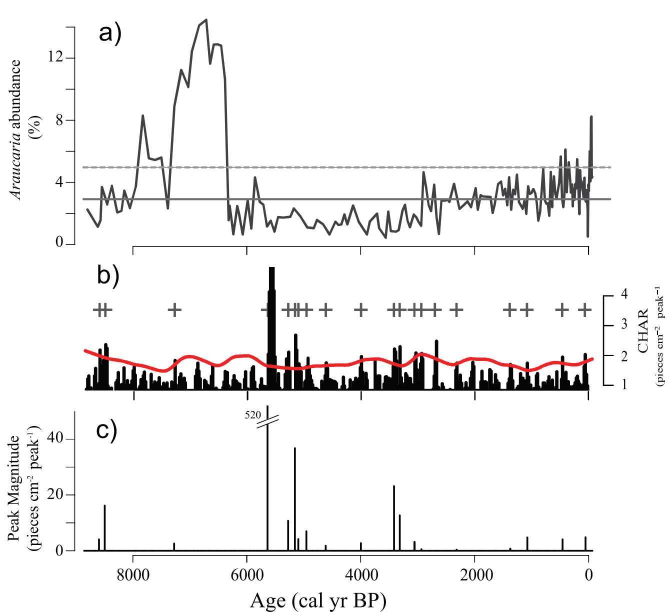

Fig. 6. a) Long-term variation of *Araucaria araucana* pollen abundance (~8.5 ka), horizontal lines reference the mean abundance for the last 50-yrs (5%, dotted line) and for the whole period (3%, continuous line). b) Occurrence of fire events (cross) along the history detected from Charcoal accumulation rate (CHAR). Line shows charcoal background for determination of peaks as Fig. 4 c c) shows the magnitude of these events as indicated in Fig. 4e.

abundant under canopy and can cause continuous regeneration with multi-age stands (Gonzalez et al., 2006; Roig et al., 2014). Later, at 6.2 ka, after prolonged dry period (Lamy et al., 2001; Jenny et al., 2003), the *Araucaria* population around Relem may have weakened, with many individuals dying and registering a decrease in the pollen load. Since there is no significant fire peak around 6.2 ka, the decrease in *Araucaria* pollen is not related to fire, nor volcanism (Moreno-Gonzalez et al., 2020), another explanation could be a catastrophic disease, as it is affecting nowadays several populations across its distribution. Alternatively, high abundance of *Araucaria* during 8 to 6 ka might have played a role in suppressing fire. The thick bark (5–20 cm) of mature *Araucaria* trees is resistant to fire, and their crown is hardly reached with surficial fire of low intensity (Burns, 1991). So far, it is not clear if *Araucaria* decreases due to an increase in fire frequency, or if fire frequency increased because of disappearance of *Araucaria*. This period could shed light on the current task of conservation facing the massive unknown disease affecting several populations, which could be understood from a past-analogue.

Current ecological patterns, i.e. the fragmentation of *Araucaria* or decreasing population, are the result of historical processes. The relative abundance of *Araucaria* around Relem during the last 50 years is slightly higher than the overall mean abundance by about 3% (Fig. 6a, dotted line). This is probably the result of the logging ban and the creation of protected areas, but also because of more localized logging and reduced land-use before 1950 CE (Moreno-Gonzalez et al., 2020). High resolution of pollen and macro-charcoal depict a sudden drop in abundance related to a fire event dated to 1895 CE, during colonization (Fig. 6a, b). However, the pollen drop was relatively small and recovered shortly thereafter. This event was of low-magnitude and burned principally grasses, suggesting that the event was not severe for *Araucaria*. The response of *Araucaria* pollen documents the taxon's sensibility to fire disturbance, the resistance of mature individuals to low and medium intensity fire disturbances (Burns, 1991) and for a quick recovery.

To observe tendencies in the decrease and fragmentation of *Araucaria,* we need to search for records longer than 100 years, though (Table 2). For instance, a comparison of 6 short records for the last 200 years did not found a common significant decrease. Instead, moist *Araucaria* sites show small declining trends, while other sites under mesic to xeric conditions display a slight increase, still others do not show any trend (Moreno-Gonzalez et al., 2020). Heusser et al. (1988), showed in the Mallín Paso del Arco (c. 12 km north of Lake Relem) *Araucaria* tends to increase since over the last 2 kyr, but decrease in the last 2 uppermost samples (Heusser et al., 1988). The same authors showed that in Mallín Río Malleo (c. 75 km south-west of Relem) there is no change for the same period. In Mallín Miraflores (c. 38 km north-west of Relem), although the record has a low sample resolution, the pollen abundance of *Araucaria* increases from 3 ka to the present (Rondanelli-Reyes, 2000). Furthermore, Fletcher and Moreno (2012b), in Lake Sn Pedro (c. 64 km north-west of Relem) observed a continuous decrease from 1.5 ka to the present. In addition, two other recent records show that *Araucaria* reached low abundance between 6 and 3 ka, but then increasing toward the present (Dickson et al., 2020); (Nanavati et al., 2020). Therefore, contrary to the belief that the species is decreasing overall, the comparison shows that there is not a general decrease of *Araucaria* and the natural variability seems to be site dependent. Perhaps the most relevant current risk to the stability of *Araucaria* are the *Pinus* plantations. The impact of these plantations to the vegetation includes the *Pinus* regeneration in non-vegetated areas, homogenization of the landscape (García et al., 2018; Moreno-Gonzalez et al., 2020), and an increased risk of severe fires (Taylor et al., 2017). Based on the review presented, it seems that pine is perhaps pressing *Araucaria* forest-steppe ecotone out of the natural range of historical variability, especially during dry periods with low burning biomass.

Table 2
Palaeoecologial records within the current *Araucaria araucana* region discussed in the text. Letters correspond to the sites referenced in Fig. 1.

Site name	Coord. Location	Altitude (m asl)	Generalized trends in *Araucaria* pollen abundance	Authors
a) Laguna Portezuelo	37.9° S; 71.0° W	1730	Sporadic, low abundance (11–3 ka), then increasing up to the present.	Nanavati et al. (2020)
b) Lago San Pedro	38.4° S; 71.3	910	Continuous decreasing for the last 1.5 kyr	Fletcher and Moreno (2012b)
c) Mallín Paso del Arco	38.9° S; 71.1° W	1200	Although age reversal, pollen records showed an increasing trend for the last 2.5 ka	Heusser et al. (1988)
d) Lago Cilantro	38.86° S; 71.28° W	1400	High abundance about 9–6 ka, and low abundance between 6 and 3 ka. Although top samples are not well constrained, the last 3 ka *Araucaria* shows more abundance than previous period	Dickson et al. (2020)
e) Lago Torta	39.1° S; 71.3° W	1065	High abundance between 8.5 and 6 ka. From 6 ka until ~1 ka *Araucaria* shows continuous low abundance, and later shows a step increase toward the present.	Fontana and Giesecke (2017)[a]
f) Mallín Piedra pintada	39.1° S; 71.2° W	1100	Long record of 14 ka. *Araucaria* shows low abundance across the record without a trend	Moreno et al. (2018)[a]
g) Lago Tonkol	39.1° S; 71.1° W	~1040	Continuous low abundance along the record, without a trend	Fontana and Giesecke (2017)[a]
h) Mallín Río Malleo			Very low abundance and sporadic appearance without a clear trend	Heusser et al. (1988)

[a] Unpublished records, but presented in conferences.

6. Conclusions

The pollen record from Lake Relem shows that steppe vegetation dominated between 9 and 4.5 ka and changed gradually for about 1.5 ka toward woodland and scrubland vegetation. From 3 ka to the present, *Nothofagus dombeyi*-type became more abundant, yet the range of variability suggests that the forest was never fully developed near Lake Relem. Perhaps it was a patchy landscape less fragmented than today.

We found that fire events were ubiquitous for the last 9 ka, however are seemingly stochastic and normally not severe. Fire in the study area has been rather infrequent and variable, with long periods free of ignition events. Also, the severity of fire was low and the vegetation could resist and/or recover shortly after events. Published climatic reconstructions suggest some relationship with the reconstructed fire and vegetation presented here, but the underlying mechanism triggering fire in the past, such as drought, humans, and lightning, are not conclusive. In the study area, only a single fire event was captured during the Euro-American colonization. Therefore the evidence does not support that the fire regime has changed over the last centuries, nor during the last decades. Also, the magnitude of this one event was not higher than other past events.

The rise of pollen abundance of *Araucaria* (between 7 and 6 ka) may be indicative of a fairly dense population near Lake Relem, a pattern observed in few other sites so far. In absence of fire evidence, the decrease of the *Araucaria* population around Relem was likely due to a disease. The comparison of published pollen records does not show a common large-scale population decrease, but a local pattern. Notwithstanding, further studies are needed to assess the historical range of populations variability. The recent expansion of *Pinus* plantations is a novel disturbance in the region that could increase the risk of *Araucaria* persistence.

Declaration of Competing Interest

None.

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Appendix A

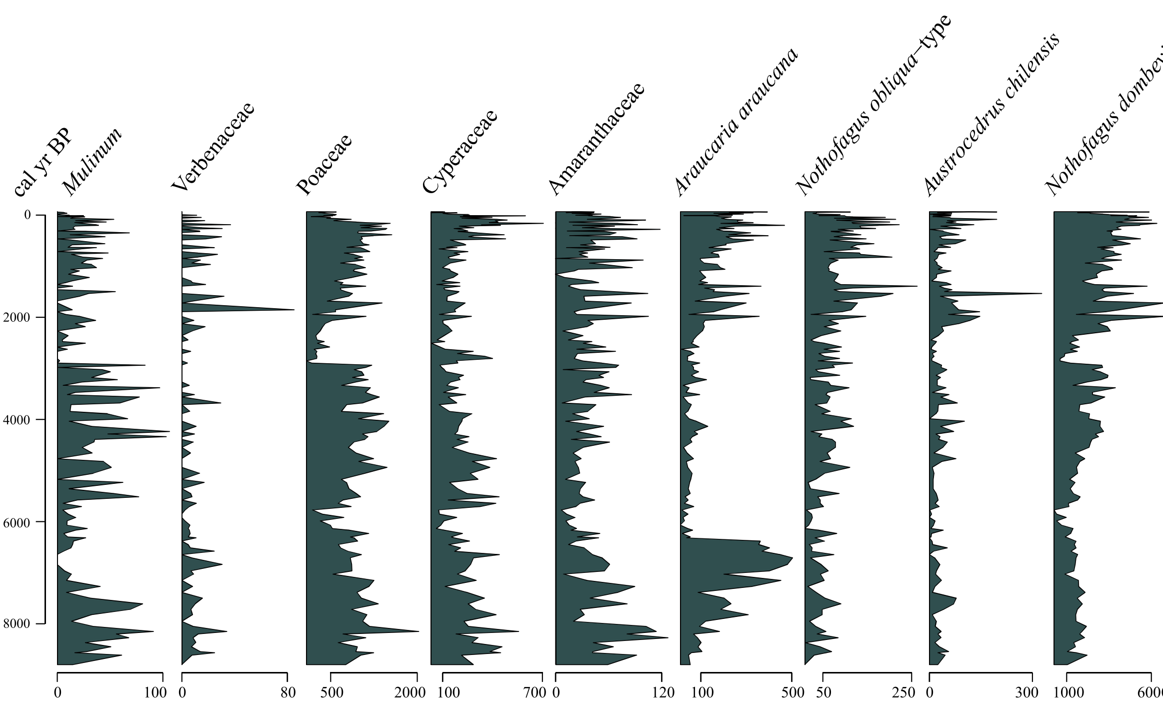

Fig. A1. Pollen accumulation rate (grains cm^{-2} yr^{-1}) of selected taxa along the record. Taxa are ordered regarding their weighted average. Note different x-scale for readability of the diagram.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110276.

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