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Article type : Research Paper

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Title: Centennial and millennial-scale dynamics in *Araucaria-Nothofagus* forests in the southern Andes

Running title: Conifer-beech forest response to ashfall

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Acknowledgements

M.S.F. was funded by Fondecyt 3110180 and the Institute of Ecology and Biodiversity, Chile, and P.I.M by Fondecyt 1191435, and the Millennium Science Initiative of the Ministry of Economy, Development and Tourism, grant Núcleo Paleoclima. Our appreciation goes to Oscar Pesce, William Henríquez, and Lucía Gonzalorena for help in the field.

Aim: To assess the relative roles of long-term (millennial-scale) climatic change, fire, and volcanic disturbance on the dynamics of *Araucaria-Nothofagus* forests of south-central Chile. Through this analysis we provide insight into how these iconic ecosystems may respond to future ashfall events under anticipated changes to climate and burning regimes.

Location: Lago Cilantro is a small lake located in south-central Chile (38°51'36.72S, 71°17'14.52 W, 1400 masl), proximal to several active volcanos within the Southern Volcanic Zone of the Andes Mountain range.

Methods: We developed a continuous 8700-year long pollen and charcoal record from Lago Cilantro. We compared these results with proxies of regional climatic change and used a combination of Principal Component Analysis and Superposed Epoch Analysis to test the relationship between tephra deposition and pollen composition.

Results: We detect a shift in dominance from *Araucaria araucana* to *Nothofagus* species between ~8.7 and ~5.5 ka (ka = 1000 years before present-1950 CE), in concert with increasing regional precipitation and decreasing local-scale fire activity. A reversal in this trend occurred after ~4 ka, contemporaneous with a reduction in regional precipitation. Centennial-scale increases in *Araucaria araucana* from ~0.2-0.9 ka, ~5.2-4.2 ka and ~8.6-7 ka are associated with reductions in fire-return intervals. We found 25 tephra layers in this record; tephra >2 cm thickness are associated with short-term (<100 year) compositional shifts in the pollen spectra, while a single large (255 cm) tephra at ~3 ka is associated with a substantial reduction in *Nothofagus* and no change in *Araucaria*.

Main Conclusions: Climate change drove millennial-scale shifts in *Araucaria-Nothofagus* forests and fire regimes near Lago Cilantro. A shortening of the fire-return-interval is

associated with an increase in the importance of *Araucaria*, supporting the notion that recurrent fires are required to allow this tree species to compete with *Nothofagus*. Tephra deposition triggered short-term compositional responses in this system that appears to be overwhelmed by climate and fire at longer-timescales. *Araucaria araucana* can survive and potentially outcompete *Nothofagus* following the deposition of very thick tephra, thanks to its thick bark and tall canopy (>15 m).

Keywords: *Araucaria araucana*, climate, fire, *Nothofagus dombeyi*, *Nothofagus pumilio*, palaeoecology, south-central Chile, tephra, volcanism

Introduction

Long-term vegetation dynamics are driven by a range of factors that include history, climate, disturbance, soil type and hydrology (Attiwill, 1994). In the absence of a negating factor, vegetation develops toward a dynamic equilibrium with climate (Webb, 1986). Factors such as disturbance, soil type and hydrology can potentially cause a disequilibrium between vegetation and climate (Attiwill, 1994). Disturbances are of particular interest as they are often stochastic, short-lived and have severe consequences for ecosystem dynamics and functioning (Folke et al., 2004). Much attention has focused on the impact and role of disturbances such as fire events on vegetation dynamics (Burns, 1993; Bowman, 2000; Bond et al., 2005; Bowman et al., 2011), whereas the impact of volcanic disturbance on vegetation, while often catastrophic and highly unpredictable, has received comparatively less attention (Tognetti et al., 2012). Here we use palaeoecological data to examine the contribution of climate, fire, and explosive volcanism on vegetation dynamics in a temperate forest system in south-central Chile over the last ~8700 years.

Fire is a key driver of ecosystem dynamics, with an estimated doubling of global forest cover in the absence of fire (Bond et al., 2005). The effects of fire vary among species, with factors such as physiology and regeneration strategy (e.g. resprouting versus obligate seeding) governing the response of terrestrial vegetation to fire disturbance (Scott et al., 2013). Fire regimes, i.e. the intensity, spatial and temporal structure of fires, vary in response to changes in climate, fuel and ignition types (Scott et al., 2013) and the regeneration dynamics of vegetation communities are often fine-tuned to, and can even dictate, specific fire regimes

(Bond & Midgley, 1995; Murphy et al., 2013). Volcanic disturbance, on the other hand, is an entirely exogenous and stochastic disturbance type that can significantly impact vegetation dynamics (Hennessy et al., 2005; Allen & Huntley, 2018). Outside of the immediate area of volcanic eruptions, where lava and pyroclastic flow significantly impact vegetation, volcanic ash fall (tephra) associated with explosive volcanism exerts the most spatially extensive physical impact on vegetation systems. The impact of tephra on vegetation systems can be extensive (>600 km from volcanic source) (Marti & Folch, 2005) and includes burial, defoliation, altered hydrology (Foster et al., 1998; Jara & Moreno, 2012) and exposure to toxic foliar and soil contaminants (Tognetti et al., 2012). Studies on long-term (centennial to millennial-scale) responses of vegetation dynamics indicate that repeated disturbance from tephra can result in a long-term decoupling of vegetation from climate (Jara & Moreno, 2012) and the emergence of alternate successional trajectories (Wilmshurst & McGlone, 1996). The specific response of vegetation systems to tephra deposition can vary significantly, however, depending on the vegetation type and species composition, and the thickness of the ash layer (Allen & Huntley, 2018).

The iconic *Araucaria-Nothofagus* forests of southern Andes Cordillera are a fire-adapted forest type that persists within one of the highest densities of active explosive volcanoes on Earth (Veblen, 1982). *A. araucana* is a long-lived tree (>1000 years) that has thick insulating bark and absence of foliage below the canopy (>15 m), traits that afford this species resistance to fire. In contrast, *Nothofagus* species (principally *N. pumilio* and *N. dombeyi*) are short-lived obligate seeders that rapidly regenerate from seed post-fire. Considerable attention has focussed on short-term (~300 years) response of these forests to fire (Gajardo, 1980; Veblen, 1982; Burns, 1993; Finckh & Paulsch, 1995; Rondanelli-Reyes, 2000; Gonzalez, Veblen & Sibold, 2005; Fajardo & Gonzalez, 2009; González & Veblen, 2009; Paulino, Godoy & Boeckx, 2009; Gonzalez, Veblen & Sibold, 2010; Muñoz et al., 2014), yet only one study has investigated the longer term (supra-centennial) role of fire in this community (Heusser et al., 1988). This has led to divergent views about the long-term ecological role of fire in this system, with some contending that *A. araucana* out-lives and dominates over *Nothofagus* in the absence of fire (Fajardo & Gonzalez, 2009), while others argue that continued successful *A. araucana* recruitment is dependent on *Nothofagus* canopy gaps created by fires (Burns, 1991; Gonzalez et al., 2010). From the scant evidence for the role of tephra deposition on *Araucaria-Nothofagus* forests dynamics (Veblen, 1982; Urrutia et al., 2007), it is likely that the traits that protect *A. araucana* from fire also convey protection from this kind of disturbance (Veblen, 1982). Indeed, *A. araucaria* trees have been observed surviving burial by tephra between 0.5-1 m thick (Veblen, 1982) and the overall dominance of andisols under *Araucaria-Nothofagus* forests suggest an ability of this ecosystem to survive in the presence of repeated volcanic disturbance (Veblen, 1982).

Here we use palaeoecological data to assess the centennial to millennial-scale response of an *A. araucana-Nothofagus pumilio* forest to changes in climate, fire activity and explosive volcanic events over the last ~8700 years, to elucidate the factors governing long-term ecosystem dynamics in this system. We hypothesise that millennial-scale fire activity in this forest community will be modulated by long-term climatic change and we anticipate that this has driven changes in the relative dominance of *A. araucana* and *Nothofagus*. Further, we hypothesise that the morphological traits of thick bark, significant height and the concentration of foliage in the crown of *A. araucana* (hereon *Araucaria*) will convey a resistance to disturbance by thick tephra deposits, thus, conferring a competitive advantage for this conifer over smaller and more susceptible angiosperm species, such as *Nothofagus*.

Study area

Our study focusses on Lago Cilantro in south-central Chile (38°51'36.72S, 71°17'14.52 W, 1400 masl), a small 8.4 m-deep flow-through lake located close to the Chile-Argentina border, proximal to active volcanic centres. The site lies within the fallout zone of a known thick (2-3 m) tephra deposited ~3000 years ago sourced from Volcán Sollipulli (Naranjo et al., 1993) (Fig. 1).

The lake is surrounded by *Araucaria* forest with a floristically simple understorey dominated by *N. pumilio* and *Chusquea culeao*. The climate is highly seasonal, with an average annual rainfall at Paso Icalma (1390 masl) of 1077 mm (maximum in June of 176 mm; minimum in November of 40 mm). January is the warmest month, with an average temperature range of 30°C and 7°C, while July temperatures range between -3°C and -7°C. Lago Cilantro lies downwind of several active stratovolcanoes (Llaima, Lonquimay, Tolhuaca, and Sollipulli)

(Fontijn et al., 2014). The most proximal of these is Volcán Sollipulli, the source of a large-scale eruption event at ~3 ka that deposited the Alpehué Tephra, which blanketed the landscape around Lago Cilantro with thicknesses between 2-3 metres (Fig. 1) (Naranjo et al., 1993).

Araucaria is a tall (up to 20 m) tree with large, poorly dispersed seeds, very thick insulating bark and a concentration of foliage at the crown, morphological traits that convey both poor dispersal and considerable protection from even high intensity fires (Finckh & Paulsch, 1995). This species is a shade-tolerant, long-lived (>1000 years) pioneering species considered to be an equilibrium strategist adapted to achieve a lasting dominance once established (Veblen, 1982). *Nothofagus* species in this forest system, on the other hand, are relatively short lived, shade-intolerant and are comprised of vigorous post-fire resprouters that produce sparse open canopies on xeric sites (*N. antarctica*) and obligate seeders that rapidly establish post-fire, producing very dense canopies on mesic sites (*N. pumilio and N.dombeyi*), such as at Lago Cilantro.

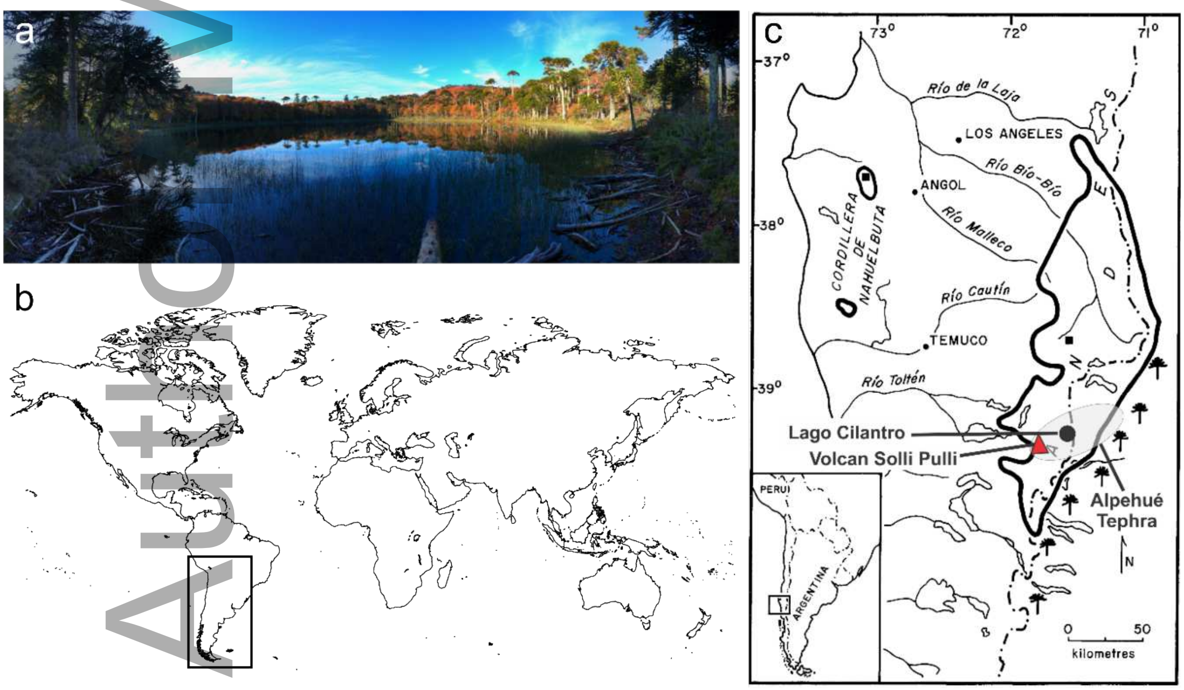

Figure 1. (a) A photo of Lago Cilantro; (b) Map of the world indicating the location of the study area represented in (c); (c) Map of the study area modified from Veblen (1982) showing the distribution of *Araucaria araucana* (black outline), the location of Lago Cilantro

(black circle), the location of Volcan Solli Pulli (red triangle) and the area covered by more than 1 m thick Alpehué Tephra (pale grey) (Naranjo et al., 1993).

Materials and Methods

We retrieved sediment cores from the deepest part of Lago Cilantro (8.4 m water depth) from an anchored coring rig equipped with a 7.5-cm diameter aluminium casing tube, using a 5-cm diameter Wright piston corer and a 7.5-cm diameter sediment-water interface piston corer with a transparent plastic chamber (Wright, 1991). We characterized the stratigraphy and chronology of the Lago Cilantro record through textural descriptions and loss-on-ignition (LOI) analysis (Heiri et al., 2001) (1-cm^3 sediment samples at continuous 1-cm intervals exposed to sequential burns at 550 °C for 2 h and 925 °C for 4 h), along with AMS radiocarbon dating of bulk sediment samples.

The reconstruction of chronologies was based on radiocarbon dating and age–depth modelling (Blaauw, 2010). Age-depth modelling of the radiocarbon ages (see Table 1) was performed in *rbacon* for *R* (Blaauw and Christen, 2011) (see Fig. 3 and Supplementary Information Fig. S2). Tephras were considered instantaneous depositions and were subtracted from the sediment depth prior to age-depth modelling. Tephras were detected via visual inspection and using the LOI data, with an inorganic content >97.5% selected as the threshold inorganic content indicating a tephra layer (see Supplementary Information Fig. S1). Radiocarbon dates were calibrated to calendar years before 1950 CE ('present') using Southern Hemisphere calibration curve SHCal13.14C (Hogg et al., 2013) prior to age-depth modelling.

We use sedimentary charcoal to reconstruct past fires and pollen for past vegetation change since ~8.7 ka. We developed palynomorph and macroscopic (>125 µm) charcoal records using standard techniques (Faegri & Iversen, 1989; Whitlock & Larsen, 2001). Palynomorphs were identified at 400× magnification and a minimum of 300 pollen grains from trees, shrubs and herbs (terrestrial pollen) was identified for each level. The percentage of each terrestrial taxon was calculated in reference to this sum, whereas the percentages of aquatics and pteridophytes were calculated in reference to the inclusion of these. We tallied all macroscopic charcoal particles from 2-cm^3 sediment samples retrieved from continuouscontiguous 1-cm intervals throughout the cores. The charcoal data were converted to accumulation rates (fragments cm^{-2} yr^{-1}) using the results of the age-depth modelling. We computed pollen accumulation rates using pollen concentrations (estimated via the addition of a marker spore (*Lycopodium* sp.) spike of known concentration) and the results of the age-depth model. Pollen accumulation rates have been shown to be linearly related to tree biomass in some forest systems (Matthias & Giesecke, 2014) and we use this metric as a broad indicator of trends in vegetation that are independent of the effects of the closed pollen sum on proportional data.

S-ANU#	d13C	±	F14C	±	14C age	±	Original core	Original depth (cm)	Tephra-free depth (cm)	Calibrated age range (yr BP) (2σ)	Median age (cal. yr BP)
50609	-28	1	0.8673	0.003	1143	30	MSF1203 SC1	35-36	35.5	937-1061	1044.5
50618	-30	1	0.8063	0.003	1729	36	MSF1203 SC1	43-44	43.5	1532-1701	1600
50610	-28	1	0.7047	0.002	2812	33	MSF1203 SC1	72-73	60.5	2779-2955	2927
50611	-24	1	0.6915	0.004	2963	49	MSF1203 AT1	43-44	61.5	2891-3214	3077
50612	-32	1	0.6751	0.002	3156	34	MSF1203 AT4	23-24	64.5	3216-3441	3299
50613	-30	1	0.5874	0.003	4274	40	MSF1203 AT4	66-67	99.5	4618-4867	4769
50614	-27	1	0.55	0.002	4803	38	MSF1203 AT4	87-88	116.5	5328-5591	5482
50615	-31	1	0.505	0.003	5489	45	MSF1203 AT5	24-25	129.5	6028-6392	6204
50616	-29	1	0.4513	0.003	6392	59	MSF1203 AT5	48-49	149.5	7170-7417	7232
50617	-31	1	0.3788	0.002	7798	42	MSF1203 AT5	90-91	170.5	8426-8604	8610

Table 1. Results of radiocarbon dating. Individual dates were calibrated to the southern hemisphere calibration curve (SHCal13) (Hogg et al. 2013) using *rbacon* software (Blaauw and Christen, 2011). Original depth refers to the initial depth measurements of each separate core. Tephra-free depth refers to the corrected depth of the composite core, following the removal of the tephra layers.

A cluster analysis constrained by depth (CONISS) was used to aid the division of the pollen record into pollen zones (Grimm, 1987), with a broken-stick model used to determine the number of significant zones (Bennett 1996). Principal component analysis (PCA) was used to summarise the main trends in the multivariate terrestrial pollen dataset using PCOrd (McCune & Mefford, 1999). The percent pollen data were square root transformed prior to running the PCA and the PCA was run on a variance/covariance matrix. Superposed Epoch Analysis (SEA) in *R v.3.0.3* (R Core Team, 2014) was used to identify consistent statistically significant relationships (p = 0.1) between tephra layers and selected pollen taxa and the first and second axes of the PCA (PCA1 and PCA2). This analysis assesses the significance of the departure from the mean of a time-series for a given set of key event years (in our case – tephras) (Lough & Fritts, 1987). SEA is a particularly useful statistical tool for detecting response signals in records with low signal-to-noise ratios (Adams et al. 2003) and where lag effects may be significant (Lough & Fritts, 1987). It has been applied to test for responses in regional temperatures (Lough & Fritts, 1987), El-Nino events (Adams et al., 2003), and global streamflow patterns (Iles & Hegerl, 2015) to volcanic forcing, and in vegetation systems to burning events (Fletcher et al., 2018; Dunnette et al., 2014). To satisfy the requirements of even age steps and stationarity for the SEA, the pollen data and PCA1 data were interpolated to 100-year age bins (the median age resolution of the record) and the time-series data were differenced to remove the effects of stationarity (Diggle, 1990) prior to running the SEA. Tephra events are instantaneous, allowing a clear definition of event years for the SEA analysis. The depth of the tephra was used to ascertain the age of the event using the interpolated ages from the age-depth model, with tephra ages assigned to the appropriate 100-year age bin. Prior to analysis, tephra events were binned into thickness categories (1-5): 1=1-2 cm; 2=3-4 cm; 3=4-6 cm; 4=6-8 cm; 5=>8 cm.

Results

We retrieved a sediment core from Lago Cilantro with a spliced length of 525 cm (cores MSF1203 SC1 and MSF1203AT1 through 5). The sediments were overwhelmingly inorganic (>80%) with discrete tephra layers. Tephra layers were detected visually and using the inorganic density data. Using this criterion we detected 24 tephra layers which we classified in to the five thickness categories: 1: n=13; 2: n=3; 3: n=3; 4: n=3; 5: n=2. We also found a 255-cm thick tephra between 51-321 cm sediment length, comprised of large (>4 cm) pumice fragments and dated to ~3 ka, potentially corresponding to the Alpehué Tephra described by Naranjo et al. (1993).

The results of the radiocarbon analyses are presented in Table 1 and show increasing sediment age with depth. The age model reveals a remarkably linear accumulation of sediment through time, with the record spanning the present (coring year: 2012 CE, -0.062 ka) to 8.67 ka (Fig. 3, see also Fig. S2).

We analysed macroscopic charcoal at 1-cm (~58 yr) intervals. Macroscopic charcoal content is low throughout the record (Figs. 2,7D) with intermittent, discrete charcoal peaks at 8.5, 8, 6.5, 6.2, 4.2 and 0.4 ka. We observe relatively high and declining charcoal accumulation rates (CHAR) between ~8.5 and ~4 ka, low or zero CHAR values between 4 and 2.3 ka, increased values between ~2.3 and ~0.4 ka, when CHAR values reach the highest for the entire record. CharAnalysis allowed the calculation of the fire-return interval (FRI) and fire frequency (charcoal peaks per millennia) (Fig. 2). The average FRI for the record was 350 years, with notable reductions in the FRI occurring between ~ 8.5 and ~7.5 ka (250 years), ~5 and ~4.5 ka (260 years) and between ~1 and ~0.25 ka (270 years), and maximum FRI occurring between ~7 and ~5.5 ka (360 years).

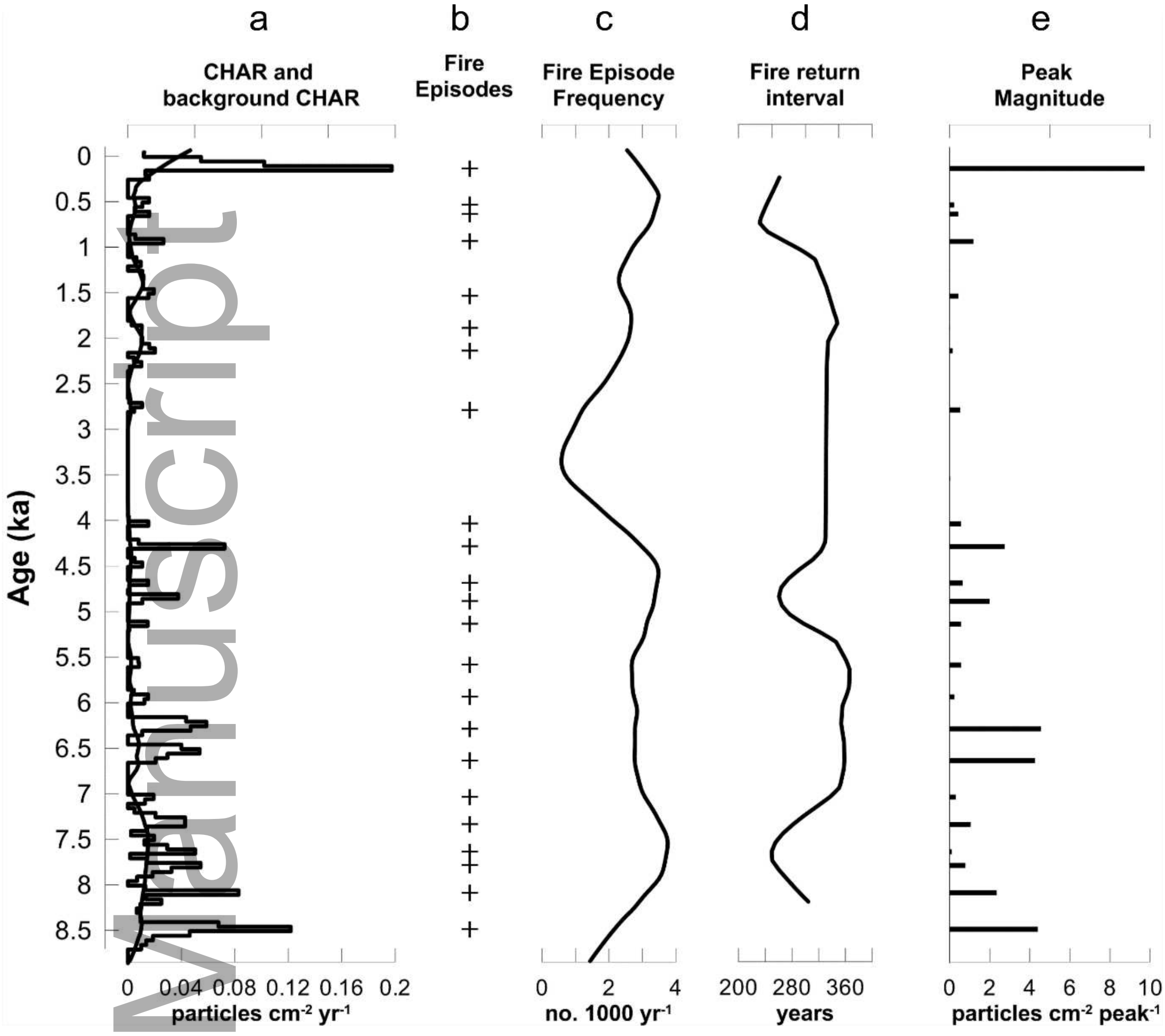

Figure 2. CHARanalysis results for the Lago Cilantro record showing (a) CHAR and CHAR background; (b) inferred fire events; (c) fire episode frequency; (d) Fire return interval; (e) charcoal peak magnitude.

A total of 115 pollen samples were analysed, with 36 terrestrial pollen types identified. The fossil pollen spectra were overwhelmingly dominated by *Nothofagus dombeyi* type (which includes *N. antarctica*, *N. pumilio* and *N. dombeyi*), with *Araucaria*, Poaceae and *Misodendrum* being important components. We identified 3 pollen zones with the aid of the CONISS cluster analysis and the following is a summary of the main trends (Fig. 3):

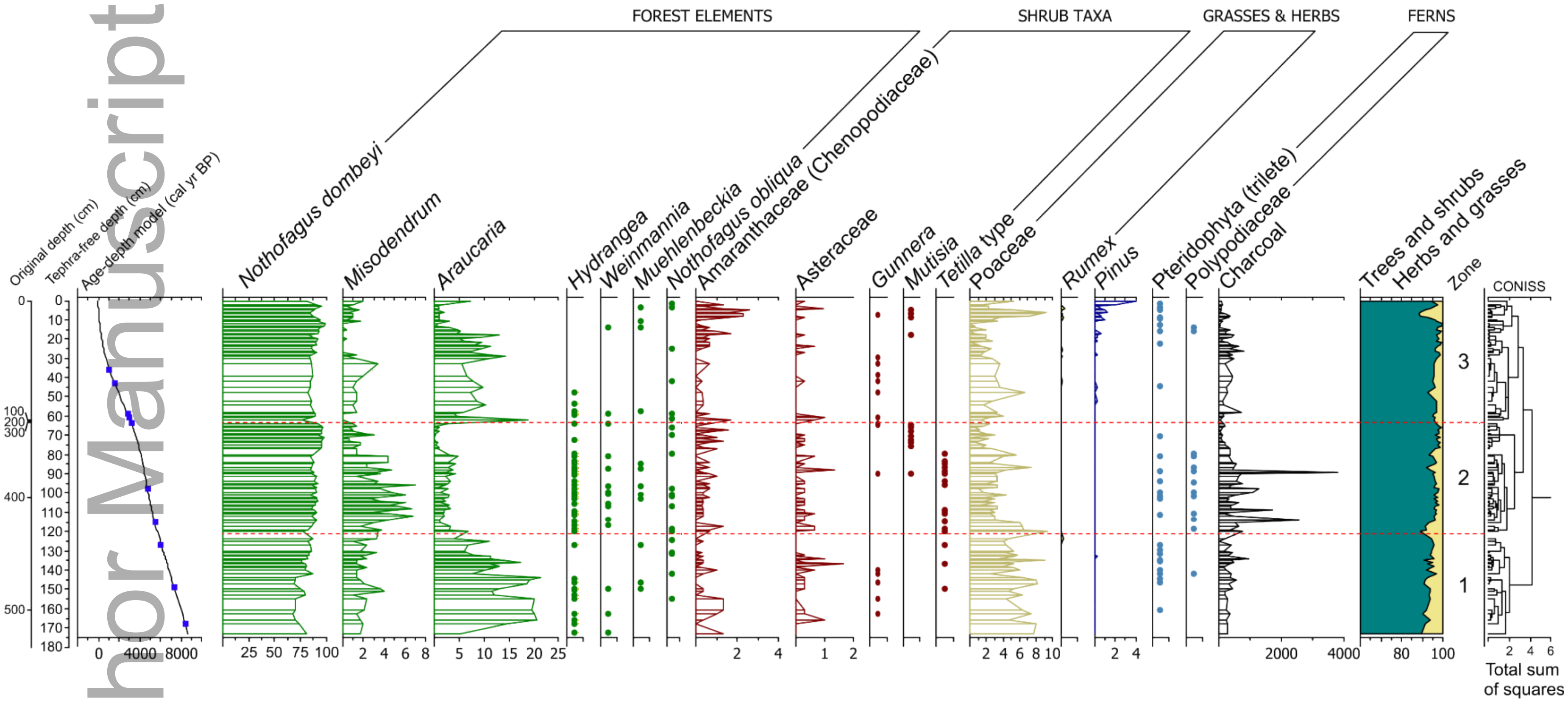

Figure 3. Percent pollen diagram showing trends in selected taxa through the Lago Cilantro pollen record, including the results of the CONISS cluster analysis and zonation of the pollen diagram. N.B. changes in x-scale. Modelled age-depth relationship presented on the left, with blue squares indicating radiocarbon-dated depths.

Zone 1 173-122 cm tephra-free depth (8.7-5.8 ka): Zone 1 is dominated by *N. dombeyi* type pollen (86%). *N. dombeyi* type fluctuates throughout the zone but never declines below 65%. There is a gradual increase to a peak of 86% at 6.8 ka and then a decrease to 70% as it transitions into zone two. *Araucaria* pollen initially increases sharply in this zone from 5% to 20% at 8.5 ka followed by a gradual decrease ending at 3% at the end of the zone.

Zone 2 122-63 cm tephra-free depth (5.8-3.2 ka): *N. dombeyi* type again dominates zone 2 maintaining a presence between 70% to 90% throughout this period. There is a general decrease in *Araucaria* pollen in this zone until it reaches 0 at 3.5 ka followed by a shallow increase to 4% at the transition into zone 3. Poaceae peaks at 9% at 5.8 ka which is then proceeded by a fluctuating decreasing trend ending at 3%.

Zone 3 63-0 cm tephra-free depth (3.2 ka – present): *N. dombeyi* type again dominates this zone. There is a minor depression across the transition between zone 2 to 3 to *N. dombeyi* type lowest presence of 70% following a shallow increase to 85%. *Araucaria* fluctuates in this zone after an initial increase in pollen to 20% at 3 ka and a sharp decrease down to 5%, there are three more preceding shallow peaks. From 0.5 ka there is a decreasing trend with frequent sharp short peaks ending at 7%.

To interrogate the apparent positive impact of the 255-cm thick tephra deposited at ~3 ka on *Araucaria* percentage data, we focus our analysis of pollen accumulation rates (PAR) on the millennia preceding this event (presumed to be the Alpehué Tephra) (4-2 ka) (Fig. 4). The full PAR record is provided in the Supplementary Information (Fig. S3). We observe a small increase in *Araucaria* PAR ~3.2 ka from minimum values between ca. 4-3.3 ka, prior to the deposition of the Alpehué Tephra. Importantly, we observe no immediate change in *Araucaria* PAR following the Alpehué Tephra (in contrast to the sharp peak evident in the *Araucaria* % data), with a sustained increase occurring between ca. 2.9-2 ka. *Nothofagus* PARs are variable between ca. 4-3 ka, with a sharp decline to almost zero values immediately following the Alpehué Tephra. This is followed by a rapid increase in *Nothofagus* PAR to peak values at ca. 2.7 ka, with a resumption of varying values toward ca. 2 ka.

The first two axes of the PCA capture 60.3% of the variance within the dataset (PCA1-40.9%; PCA-19.4%). Fig. 5 shows the PCA ordination biplot for the Lago Cilantro fossil samples, grouped according to CONISS zones. *Araucaria* shows strong positive correlation with PCA1 (r^2 = 0.96), and *Nothofagus* shows strong negative correlation with PCA1 (r^2 = 0.84). *Misodendrum* (a parasite of *Nothofagus* species) shows strong negative association with PCA2 (r^2 = 0.87). There is good agreement between the pollen zones and the clustering of samples within the ordination biplot. The PCA biplot reveals a shift from an *Araucaria* dominant ecosystem in zone 1, to a *Nothofagus* dominated system in zone 2, with a shift toward zone 3 marked by a decrease in *Misodendrum* and an increase in *Araucaria.*

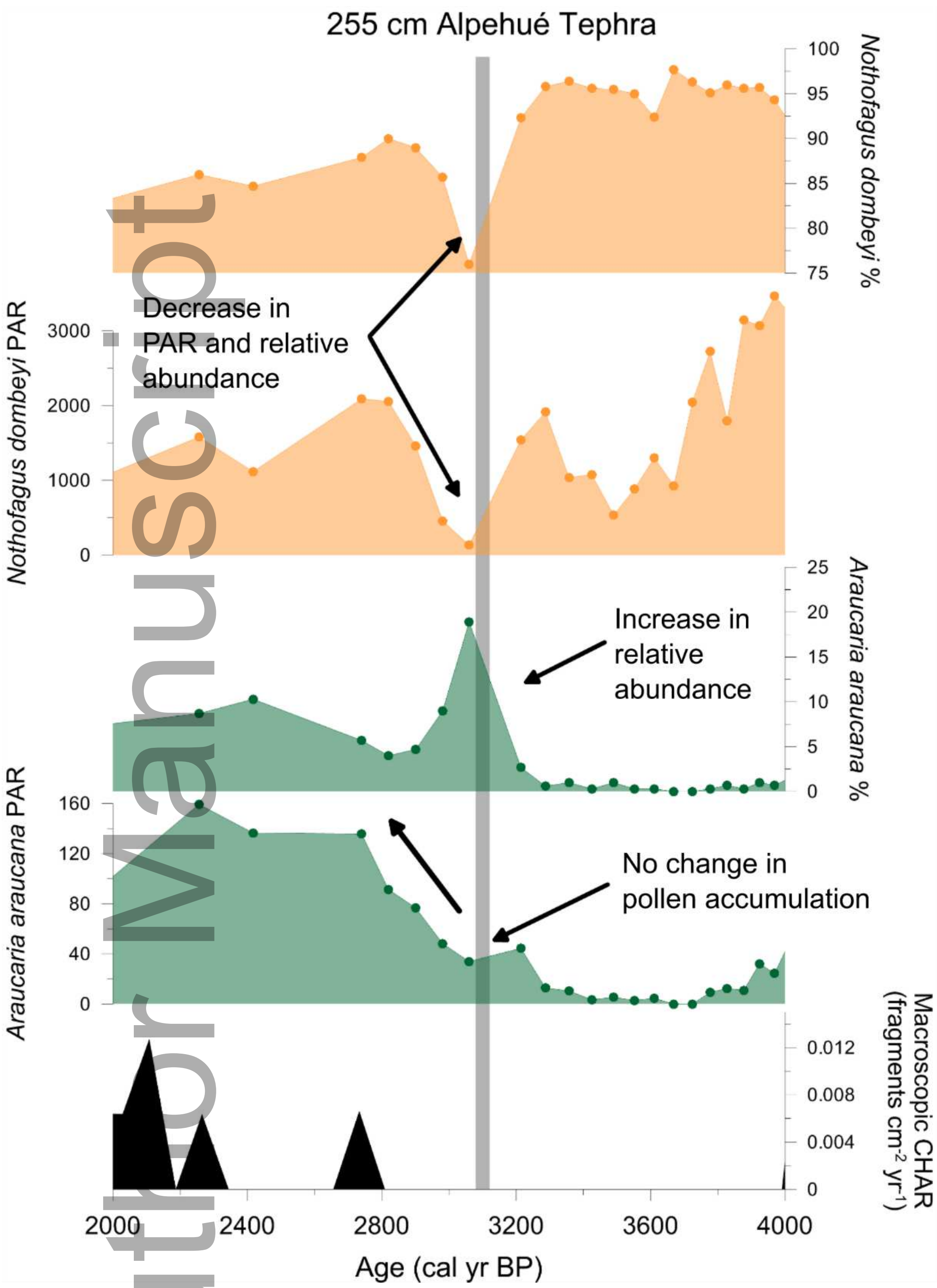

Figure 4. Summary plot of pollen accumulation rates (PAR) for *Araucaria* and *Nothofagus* between 4-2 ka plotted against relative values of these pollen taxa for the Lago Cilantro record. Macroscopic CHAR is also shown. The location of the Alpehue Tephra is indicated by the grey bar.

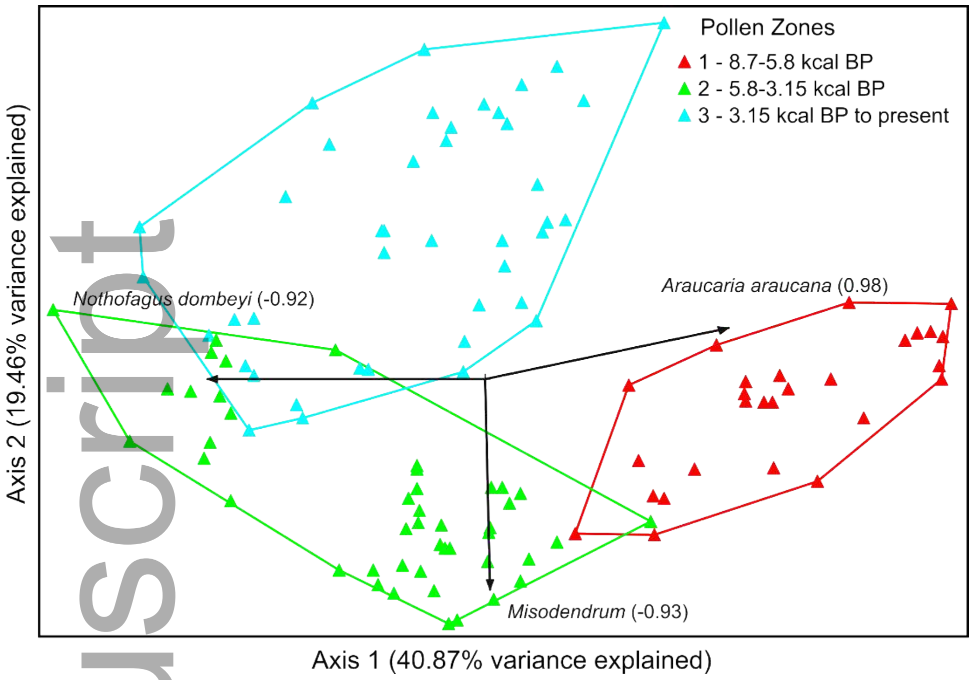

Figure 5. The PCA biplot, showing the position of fossil samples from the Lago Cilantro record in 2-dimensional ordination space. Samples are grouped as per the results of the CONISS cluster analysis. Values in parentheses indicate r^2 values between indicated taxa and PCA axes.

We ran the SEA between tephra events for selected pollen taxa, and PCA1 and PCA2 for all tephra size categories independently and for combinations in hierarchical clusters (Category 1-5; Category 2-5; etc.) (see supplementary information for the full results). The only significant relationship ($p = 0.1$) between tephra events and pollen composition was between Category 2-5 tephras (i.e. >2 cm thickness) and PCA1 at 0 lag (between 0-100 years) (Fig. 6, see also Supplementary Information (Fig. S4) for full results), indicating a significant shift in the pollen composition in the 100 years following the tephra event (i.e. a single sample unit). The absence of a significant relationship between individual pollen taxa and tephra in the SEA indicates that the effect of tephra deposits >2 cm thick are not uniform with respect to species specific effects, rather they affect the composition of pollen in a significant manner.

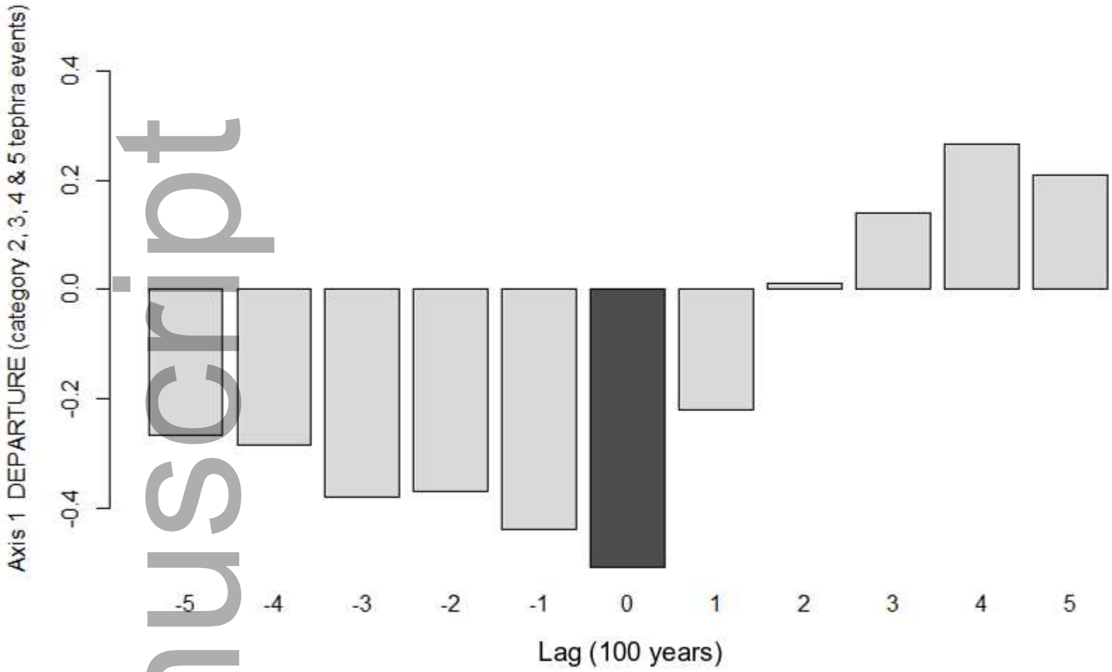

Figure 6. Results of the Superposed Epoch Analysis (SEA) for tephra events >2 cm (categories 2-5) and PCA1 from the Lago Cilantro record, showing a significant negative departure of PCA1 at 0-lag with tephra events >2 cm (i.e. 0-100 years following tephra deposition).

Discussion

Long-term climate-fire-vegetation dynamics

We observe a millennial-scale reduction in *Araucaria* at the expense of *Nothofagus* between ~8.7 and ~5.5 ka (Fig. 7B,E). This decline is concomitant with (1) a shift toward lower charcoal accumulation rates into Lago Cilantro and (2) a phase of decreasing regional charcoal influx in sediment cores across southern South America (>30°S) (Power et al., 2008) that reflects a millennial-scale increase in precipitation over the region (Fig. 7A) (Fletcher & Moreno, 2012). Our data suggest that a long-term increase in precipitation and a concomitant reduction in fire activity around Lago Cilantro favoured an increase in the relative abundance of *Nothofagus* species relative to *Araucaria*, culminating in the almost total exclusion of *Araucaria* in the absence of fire between ~4 and ~3.2 ka (Fig. 7B).

Modern ecological studies (Gonzalez et al., 2010) indicate that *N. pumilio* and *N. dombeyi* rapidly invade canopy gaps created by disturbance or treefall in mesic areas, limiting the opportunity for successful *Araucaria* recruitment, which requires canopy gaps created by relatively frequent moderate-intensity fires that leave live adult *Araucaria* trees as a seed source (Burns, 1991). Indeed, *N. pumilio* currently forms pure self-replacing stands within this forest system on mesic south-facing slopes where disturbance from moderate to high intensity fires is infrequent (Veblen, 1982; Burns, 1991). The close correspondence between decreased FRI (Fig. 7C) and increases in *Araucaria* around Lago Cilantro since ~8.5 ka (Fig. 7B), under both relatively mesic (~5.2-4.2 ka) and xeric (~8.3-7 ka) climate conditions inferred from the regional charcoal influx curve (Fig. 7A) highlights the importance of recurrent moderate frequency fires in the regeneration dynamics of *Araucaria-Nothofagus* forests (Veblen, 1982; Burns, 1993; Gonzalez et al., 2010). We, thus, support the model of Burns (1991), which depicts a dependency of *Araucaria* recruitment on recurrent fire in mesic *Araucaria-Nothofagus* forests such as those found in the Lago Cilantro region.

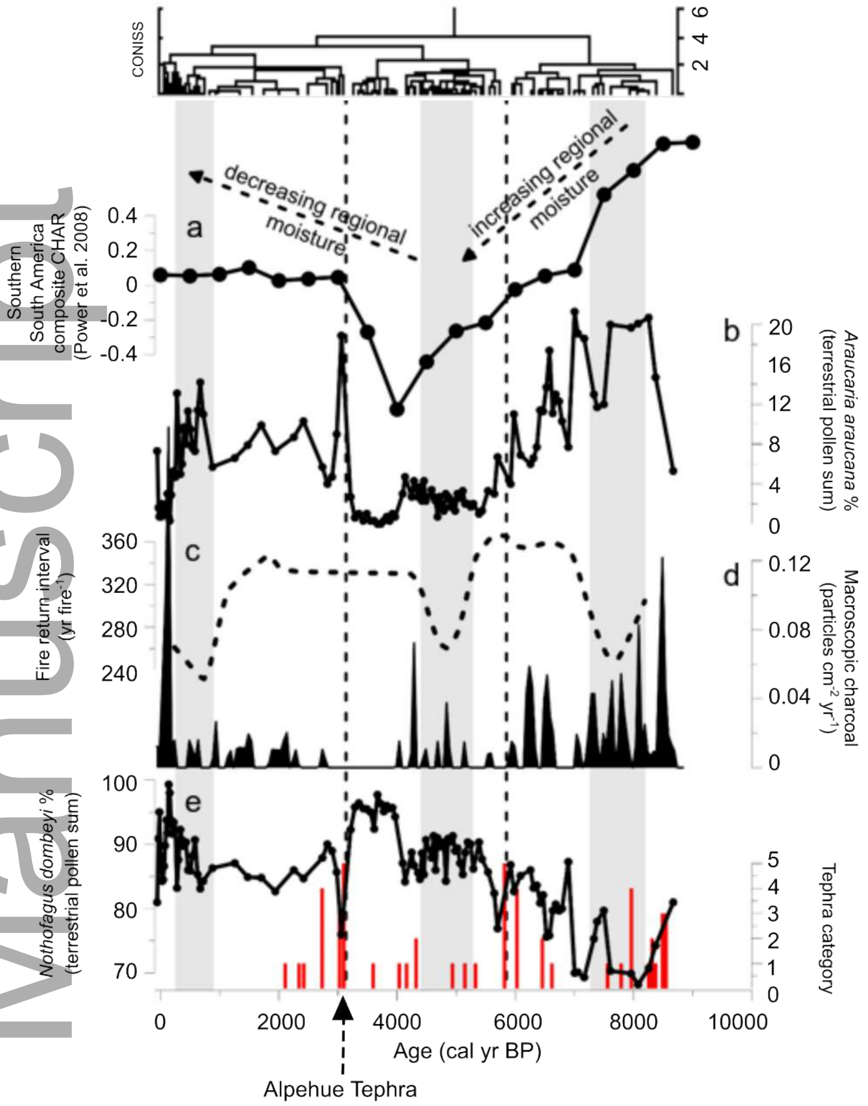

Figure 7. Summary plot showing (a) Regional southern South American charcoal influx (Power et al., 2008); (b) *Araucaria* pollen from Lago Cilantro; (c) fire return interval from Lago Cilantro; (d) macroscopic CHAR from Lago Cilantro; (e) *Nothofagus* pollen from Lago Cilantro; and (f) tephra events by category from Lago Cilantro.

The long-term role of volcanic ash-fall

We investigated the influence of volcanic ash-fall over *Araucaria-Nothofagus* ecosystem dynamics around Lago Cilantro over the past ~8700 years. We record a total of 24 tephra layers within the sedimentary sequence ranging from <1 to 255 cm in thickness. All but one of the tephras were <8 cm, indicating that the deposition of very thick tephras was rare at this site over the last ~8700 years. The SEA revealed a significant shift in the pollen spectra in the 100 years following tephras >2 cm in thickness (Fig. 6). This was manifest as a shift toward lower/higher relative values of *Araucaria*/*Nothofagus*. Our results are consistent with the study of Veblen (1982), who performed a detailed ecological analysis of *Araucaria-Nothofagus* forests that concluded that repeated small-scale disturbance from volcanic ashfall favours the relatively fast growing *Nothofagus* relative to *Araucaria*, a result that is consistent with our findings, and with long-term (palaeoecological) studies on the role of tephra of other forest types, both within southern South America (Jara & Moreno, 2012; Henríquez et al., 2015) and further afield (Wilmshurst & McGlone, 1996).

The work of Veblen (1982) also identified a competitive advantage for *Araucaria* following the deposition of thick ca. 100 cm volcanic deposits, conveyed by the same morphological characteristics that protect *Araucaria* from fire (thick bark and height). The 255 cm thick tephra we encountered was dated at ~3 ka, and this event likely represents the Alpehué Tephra from Volcan Sollipulli (21 km SE of Lago Cilantro), previously dated at ~2.9 ka (Naranjo et al., 1993) and recorded within the sediments of Lago Icalma (5 km north of Lago Cilantro) (Bertrand et al., 2008). Our data reveal a sharp increase/decrease in the proportion of *Araucaria*/*Nothofagus* pollen immediately following the presumed Alpehué Tephra. Importantly, calculation of pollen accumulation rates, which reveal trends in pollen taxa independent of the effects of a closed pollen sum, reveals two critical factors about the response of this system to the deposition of the 255 cm Alpehué Tephra: (1) that *Nothofagus* decreases immediately after this tephra; and (2) *Araucaria* remains unchanged and subsequently increases prior to the return of fire in the system (Fig. 4).

While we cannot constrain the source of the well-dispersed pollen from *Nothofagus*, the contemporaneity of the trends (large tephra followed immediately by a decline in *Nothofagus* PAR and no change in *Araucaria* PAR) is consistent with the survival of *Araucaria* through the Alpehué Tephra deposit and the destruction of the *Nothofagus* component of the forest vegetation. The subsequent increase in *Araucaria* PAR, then, likely reflects the successful recruitment of *Araucaria* in the absence of competition from *Nothofagus*, while the rapid increase in *Nothofagus* following the initial decline is consistent with the ability of

Nothofagus species to rapidly recolonise open areas of forest following disturbance (Veblen, 1982).

Conclusion

Our interpretation of ecosystem dynamics of *Araucaria-Nothofagus* forest from lake sediments in the south-central Andes Cordillera since ~8.7 ka represents the first study of its kind in this system. We propose a key role of fire activity and regional climatic change in the long-term dynamics of this system. We also report a positive response of *Araucaria* to reductions in the charcoal-inferred fire-return-interval (FRI) implying that *Araucaria* are favoured (relative to *Nothofagus*) by increased fire activity. Further, we identify a significant short-term (<100 years) influence of tephra events >2 cm in thickness over dynamics in *Araucaria-Nothofagus* forests, manifest as a shift in compositional trends. Finally, we observe a remarkable ability of *Araucaria* to survive and potentially capitalise on large-scale ash-fall events (255 cm), likely resulting from its thick bark and concentration of foliar material in the crown (which reaches heights of up to 20 m).

Data availability statement

Data used in this research will be made available for download at https://www.neotomadb.org/data following publication using the site name (Lago Cilantro and/or geographic coordinated provided in the text). The corresponding author can also be contacted for data access.

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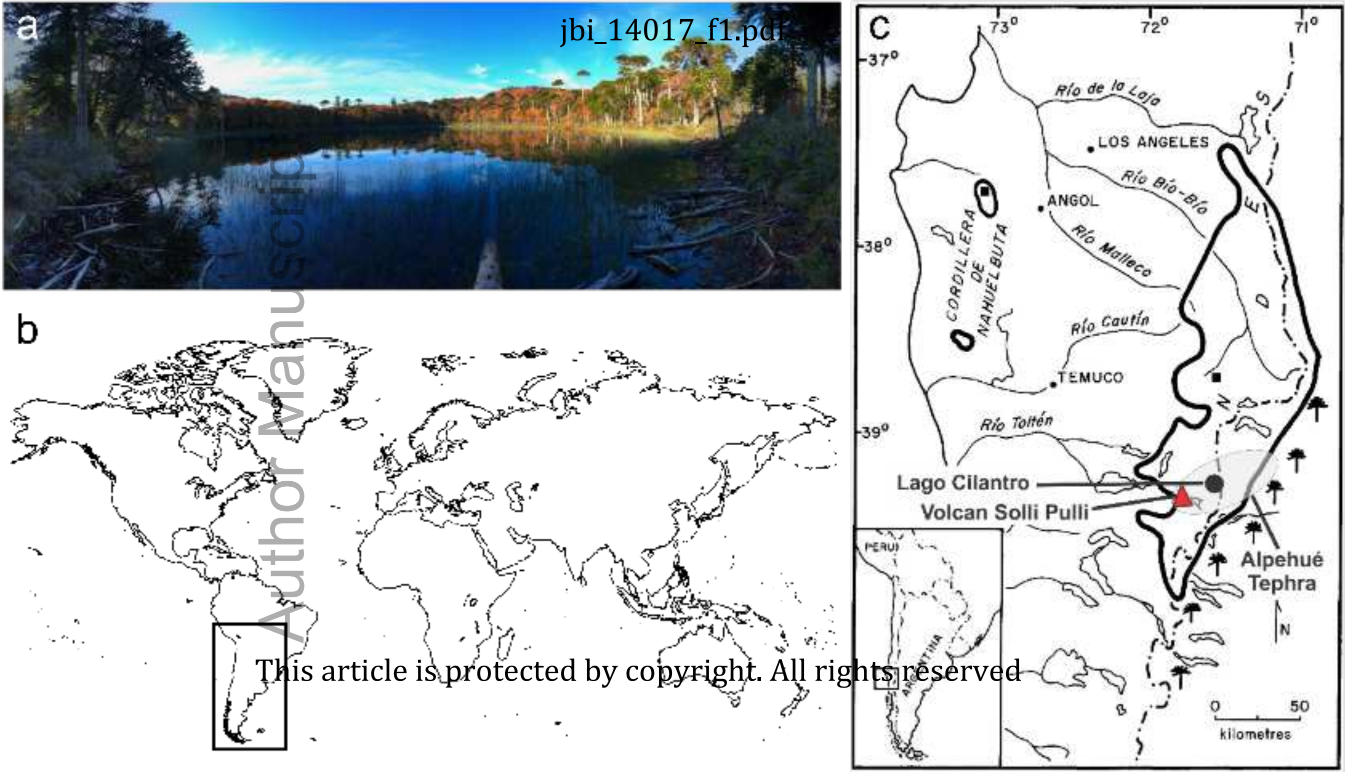
Biosketch:

B. Dickson is a palaeoecologist interested in understanding long-term vegetation dynamics in floristically diverse environments. She specialises in analysing palaeorecords preserved in speleothems and lacustrine sediments. She is currently completing her PhD research.

Author contributions: M.-S.F and B.D conceived ideas for this research; B.D. and M.-S.F collected and analysed data; M.-S.F. led the writing of the manuscript; T.L.H. contributed to manuscript writing, editing and supplementary data analysis; P.I.M. contributed to manuscript editing and the formation of the project.


a
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c
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39°
Río de la Laja
LOS ANGELES
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ANGOL
Río Malleco
CORDILLERA DE NAHUELBUTA
Río Cautín
TEMUCO
Río Toltén
A
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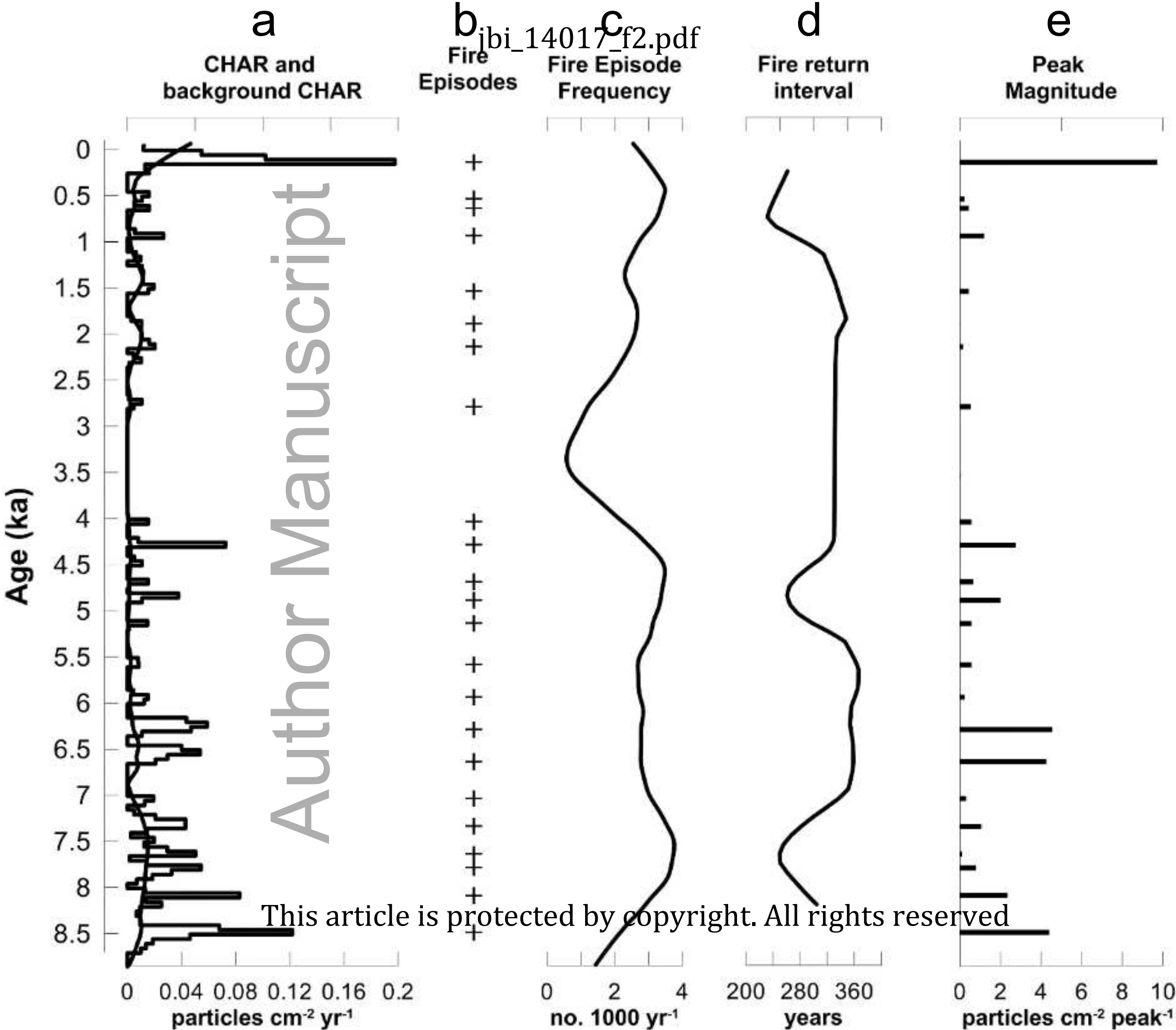
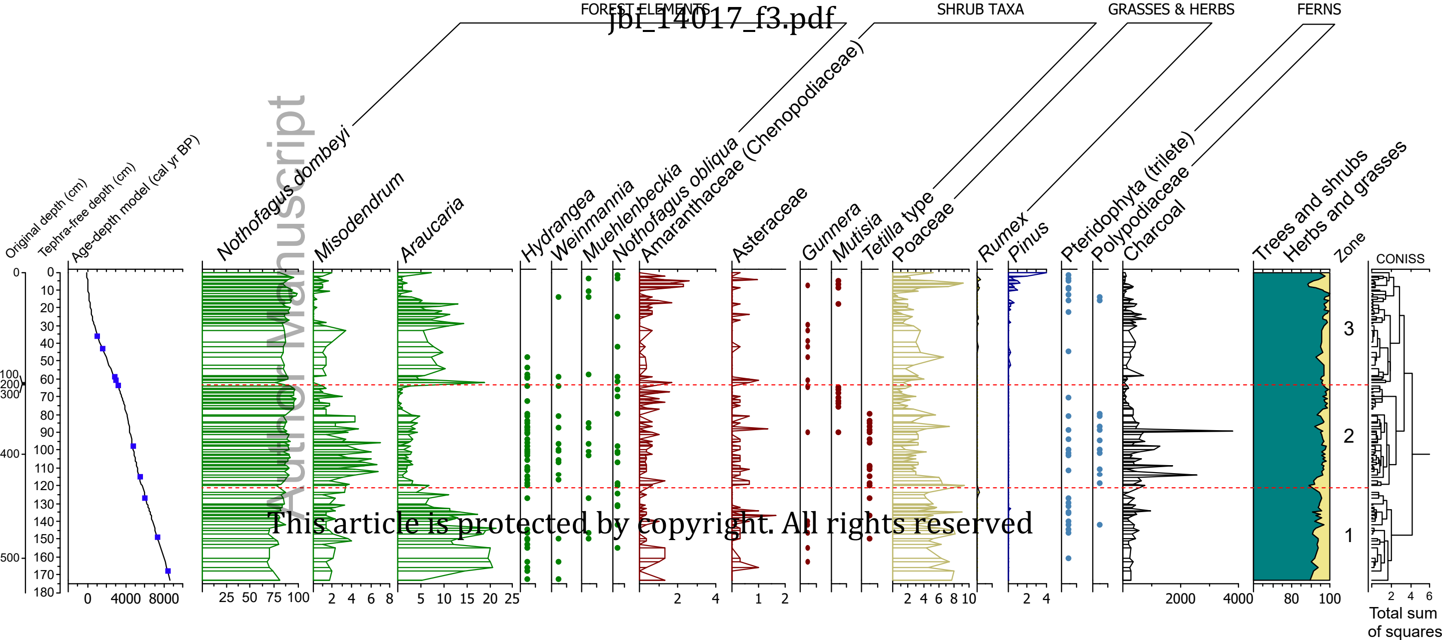

a
CHAR and background CHAR
b
Fire Episodes
c
Fire Episode Frequency
d
Fire return interval
e
Peak Magnitude
Age (ka)
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
8.5
0 0.04 0.08 0.12 0.16 0.2
particles cm-2 yr-1
0 2 4
no. 1000 yr-1
200 280 360
years
0 2 4 6 8 10
particles cm-2 peak-1


FOREST ELEMENTS
SHRUB TAXA
GRASSES & HERBS
FERNS
Original depth (cm)
Tephra-free depth (cm)
Age-depth model (cal yr BP)
Nothofagus dombeyi
Misodendrum
Araucaria
Hydrangea
Weinmannia
Muehlenbeckia
Nothofagus obliqua
Amaranthaceae (Chenopodiaceae)
Asteraceae
Gunnera
Mutisia
Tetilla type
Poaceae
Rumex
Pinus
Pteridophyta (trilete)
Polypodiaceae
Charcoal
Trees and shrubs
Herbs and grasses
Zone
CONISS
Total sum of squares
1
2
3

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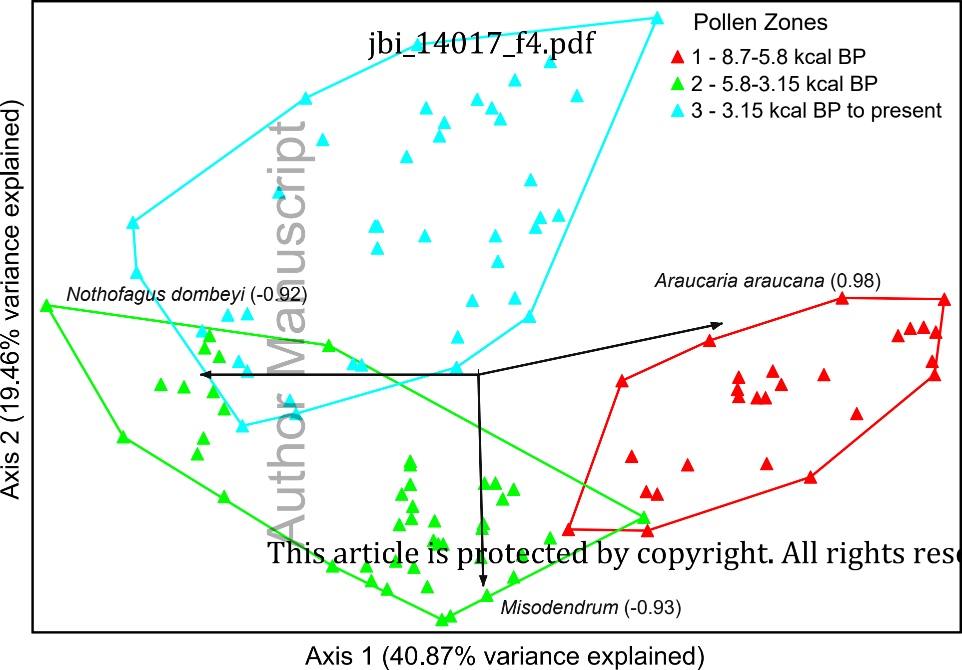
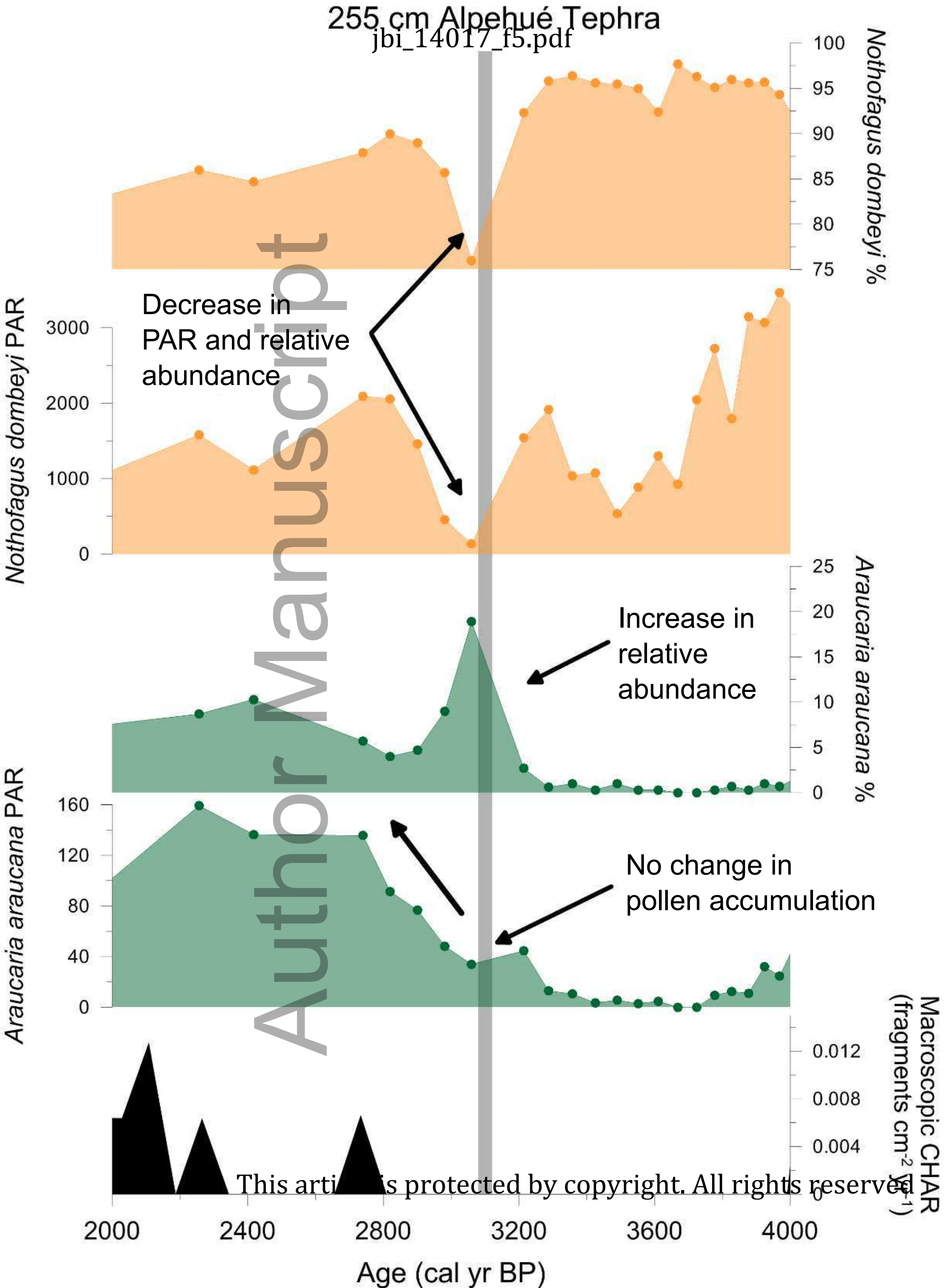
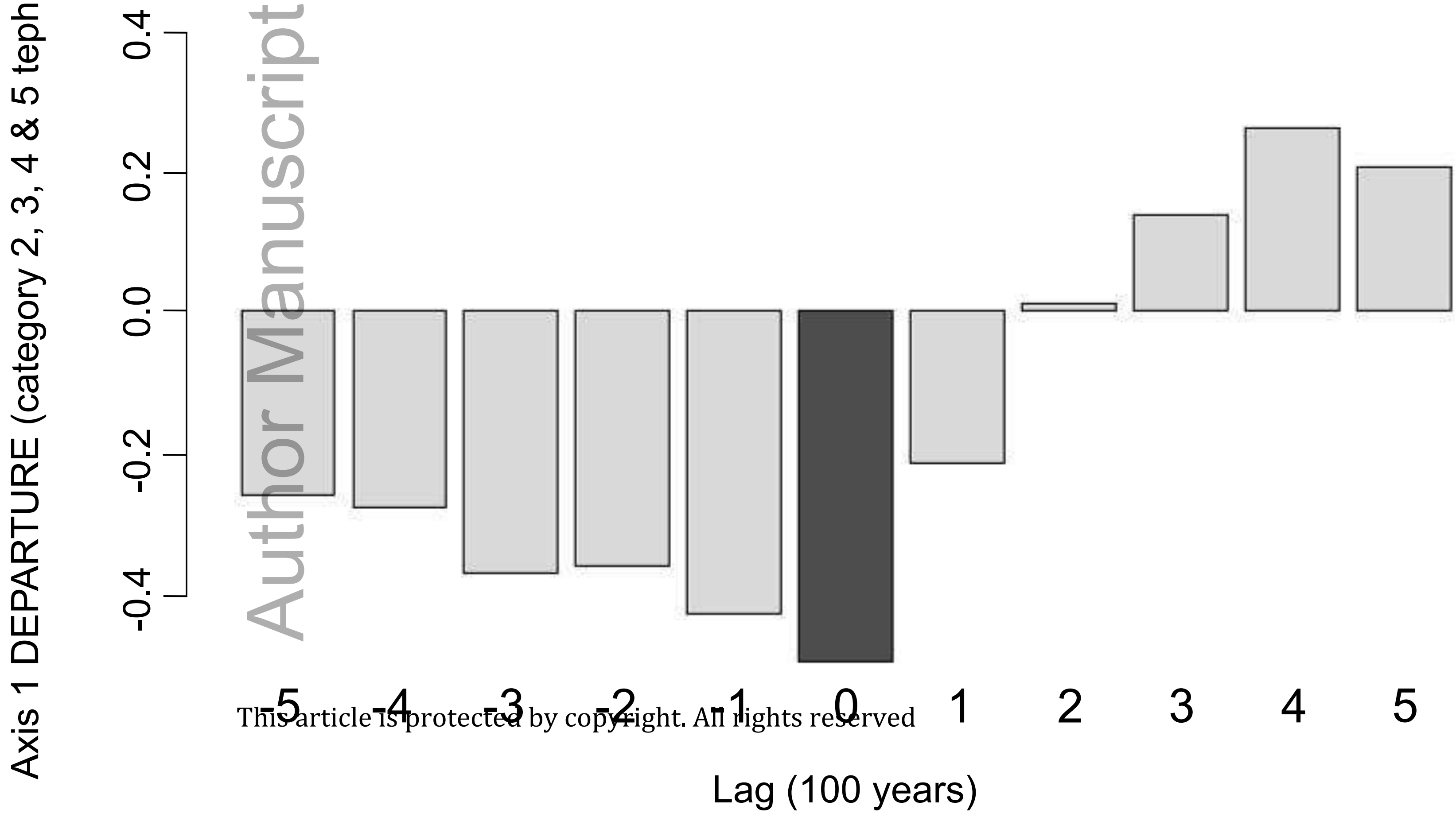



255 cm Alpehué Tephra
Nothofagus dombeyi %
100
95
90
85
80
75
Nothofagus dombeyi PAR
3000
2000
1000
0
Decrease in PAR and relative abundance
Araucaria araucana %
25
20
15
10
5
0
Increase in relative abundance
Araucaria araucana PAR
160
120
80
40
0
No change in pollen accumulation
Macroscopic CHAR (fragments cm^{-2} yr^{-1})
0.012
0.008
0.004
0
2000
2400
2800
3200
3600
4000
Age (cal yr BP)


Axis 1 DEPARTURE (category 2, 3, 4 & 5 tephra events)
0.4
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-2
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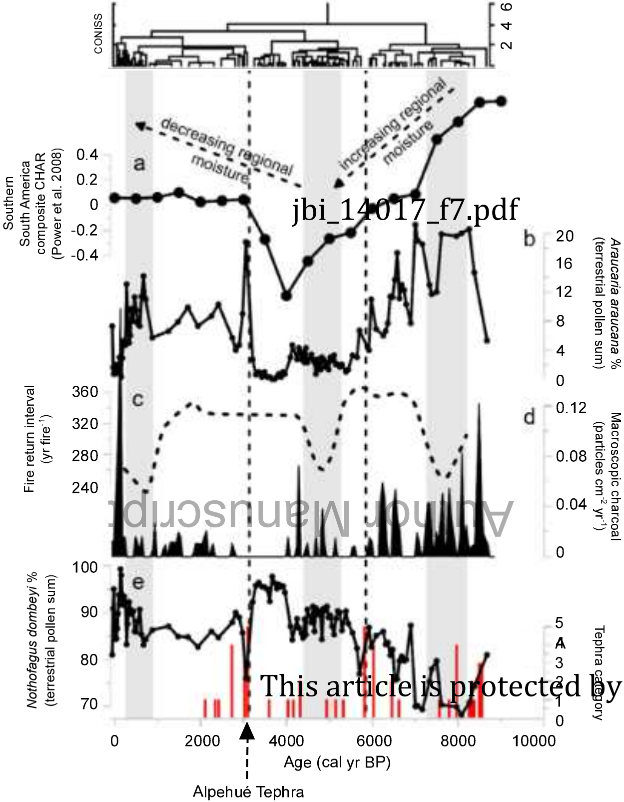
3
4
5
Lag (100 years)


CONISS
decreasing regional moisture
increasing regional moisture
Southern South America composite CHAR (Power et al. 2008)
Araucaria araucana % (terrestrial pollen sum)
Fire return interval (yr fire⁻¹)
Macroscopic charcoal (particles cm⁻² yr⁻¹)
Nothofagus dombeyi % (terrestrial pollen sum)
Tephra category
Age (cal yr BP)
Alpehué Tephra
a
b
c
d
e