# The effects of climate, natural disturbances, and human occupation on the rainforest boundary at the eastern foothills of Northern Patagonian Andes since the Late Glacial period

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## ARTICLE INFO

## ABSTRACT

Available studies on the vegetation development in Patagonia cluster along the forest-steppe ecotone, whilst little information is available from within the mountains. This study investigates shifts in the eastern boundary of rainforest taxa during the Late Glacial and Holocene periods. Continuous sections of highly organic sediments with several interbedded tephra layers were obtained at El Laguito del Morro Lake (41° 32′ 24.4″ S, 71° 47′ 50.0″ W), which were analyzed for pollen and macro charcoal. Additional macrofossil analysis was conducted to support the interpretations of pollen data and gain reliable material for radiocarbon dating. Fluctuations in regional precipitation were inferred from changes in the adjacent peatbog. The pollen record documents five distinct periods of forest diversity and structure. Late Glacial and early Holocene vegetation were characterized by a combination of *Podocarpus* and Cupressaceae pollen which has no modern analogue. Taxa in question became rare, and or gradually disappeared around 10,300 cal yr BP when *Nothofagus dombeyi* type pollen increases but fluctuates. With the overall decline of charcoal concentrations around 7500 cal. BP *Nothofagus dombeyi*-type pollen stabilizes and dominates the diagram. After the rise in charcoal concentrations around 4000 cal yr BP also the overall vegetation composition changes around 3600 cal yr BP, with the rise of Cupressaceae pollen attributed to *Austrocedrus chilensis* marking the establishment of the modern vegetation structure. The last stronger change in vegetation composition is characterized by the expansion of the shrub *Discaria* sp. 770 cal yr BP. Charcoal and pollen data show a clear link between changes in fire regime and vegetation composition, however, changes in climate were most likely the main driver for both. During the Late Glacial period, a rainforest developed under cool temperatures and high moisture. Severity of fires decreased during a cold reversal period from ca. 12,800 to 11,300 cal yr BP. During Early Holocene, increased seasonality, volcanism-derived disturbances, and low-frequency surficial fires, enhanced *Nothofagus dombeyi* forest establishment. The expansion of the mixed *Nothofagus dombeyi - Austrocedrus chilensis* forest occurred under increased precipitation variability and the increase of low severity fires related to the establishment of El Niño Southern Oscillation and the Southern Annular Mode during the Late Holocene. Scrub expansion occurred during historical times because of induced fires.

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## 1. Introduction

Patagonia represents one of the few areas on the planet where mid to high-latitude climate change can be studied in the southern hemisphere. The species composition in north Patagonian forests

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changes along a strong east-west precipitation gradient across the Andes from a temperate rainforest in the west to the Patagonian steppe in the east. This strong gradient and the availability of lakes and mires has made this region a focal area for studying past climate change by means of pollen analysis (e.g., Heusser, 1984; Iglesias et al., 2012a; Markgraf and Bianchi, 1999). The temperate forest of southern South America also attracted interest from forest ecologists investigating the effect of climate and disturbance on forest dynamics (Holz et al., 2012; Kitzberger, 2012; Paritsis et al., 2014; Veblen et al., 2016; Villalba, 1990). Large forest fires, volcanic eruptions and landslides often caused even-aged forest stands (Veblen and Ashton, 1978), and tree rings reveal the climate variability of the last few hundred years (Lara et al., 1999; Masiokas et al., 2010). These studies influenced palynological research and interpretations of Northern Patagonia forest history at millennial and sub-millennial scales.

Divergent results obtained from paleoecological records and glacial geoforms have been taken as proof of the timing and latitudinal displacements of the westerly winds since the Late Glacial Maximum. Consequently, paleoclimate features and their drivers were matters of long-lasting disagreements about the direction and timing of climatic events (Heusser et al., 1996; Markgraf, 1989; Markgraf, 1993a; Moreno et al., 2001). Different models of deglaciation have been proposed (Bianchi and Ariztegui, 2012; Hoganson and Ashworth, 1992; Heusser et al., 1996) The number of available palynological records at 39-43°S from Cordillera de la Costa in Chile to Patagonian "precordillera" in Argentina has steadily increased during the last fifty years although studies from within the mountains are rare (Sottile et al., 2018). In Argentina, pollen studies mainly focused on the forest-steppe ecotone, identifying fluctuations and displacements of forest and steppe communities along the sharp west-east precipitation gradient since the postglacial warming. In contrast, rainforest spots at the eastern Andean foothills have received little attention, and pollen studies from the boundary between per-humid and temperate locations are lacking. At the eastern Andean flank, disjoint rainforest locations with a lower plant richness are found in low sheltered valleys and mountain slopes where the average annual rainfall reaches 1500−3000 mm (Brion et al., 1988; Ezcurra and Brion, 2005). These sites represent the eastern limit of distribution of Andean rainforests, which form a dynamic boundary populated by pure *Nothofagus dombeyi* forests. Such boundary is mostly driven by shifts in precipitation variability and, to a lesser extent, by temperature, the latter governing moister availability during summers. The extent of these rainforest spots depend on water availability and therefore respond to changes in Pacific Ocean winds, which allows the tracing of long-term shift and intensity of the westerly wind belt. To understand the drivers and dynamics of the postglacial history of Patagonian forests, it is, therefore, necessary to add small sites with a local pollen source area from within the mountains, to complement the studies developed along the trans-Andean bioclimatic gradient between 40 and 42° S. The aim of this study is to discuss the long-term dynamics within the rainforest - *Nothofagus dombeyi* forest border with respect to climate variability, fire and volcanic disturbances since the Late Glacial Period. Undergoing such endeavour would mean closing the gap between available data from either side of the mountains. Consequently, this study may contribute to gaining a better understanding of the vegetation history along the entire west-east bioclimatic gradient by giving interpretations that may resolve the controversies concerning the effects of timing and latitudinal displacements of the westerly winds on Andean forests since the Late Glacial Maximum.

In addition, we aim to provide critical information in order to preserve this biome under a changing climate and provide a base for managing protected areas.

## 2. Regional setting

### 2.1. Present climate

The atmospheric circulation in Patagonia is strongly influenced by the westerly flow of subtropical and subpolar latitudes of the Southern Hemisphere (Garreaud et al., 2009). The Andes blocks the transport of humid air from the Pacific Ocean (Berman et al., 2012). In addition to the frontal precipitation, the uplift of low-level air over the western slope of the Andes produces orographic rainfall. Rain that takes place over the west slope of the Andes then crosses the mountains and falls on the eastern flank and adjacent areas (Hoffmann, 1975). Forced subsidence over the lee side produces arid conditions in Patagonian areas a few kilometres from the mountains (Garreaud et al., 2009; Jobbágy et al., 1995).

### 2.2. Present vegetation

Temperate rainforests extend along a narrow strip within the Andes, between 40 and 42°S hosting a high diversity of vascular plant species in southern South America. At the western Andean flank, moist air coming from the Pacific reduces the seasonal temperature amplitude, resulting in mild winters and cool summers. Here rainforests develop due to annual precipitation exceeding 2000 mm. The evergreen Valdivian rainforest, with an overwhelming floristic diversity with a total of 44 tree species, extends from the lowlands up to 400 m a.s.l. (Jara and Moreno, 2014). Between 400 and 900 m a.s.l., the evergreen North Patagonian rainforest is dominated by *Nothofagus dombeyi*, along with *Weinmannia trichosperma*, and several *Myrtaceae* species (Villagrán Moraga, 1980). Above 600 m a.s.l., *Nothofagus dombeyi* is accompanied by cold-resistant conifers such as *Podocarpus nubigenus*, *Fitzroya cupressoides*, and *Pilgerodendron uviferum,* (Villagrán Moraga, 1980; Villagrán and Hinojosa, 1997).

At the eastern Andean flank, small rainforest locations with a lower plant richness (15 tree species in situations where most moisture is present) are found in low sheltered valleys, with an average annual rainfall of 1500−3000 mm, accompanied by mild winters, and cool summers (Brion et al., 1988; Ezcurra and Brion, 2005). They represent the eastern boundary between the rainforests and *Nothofagus dombyi* forest, replaced to the east by mixed *Nothofagus dombeyi - Austrocedrus chilensis* forests and scrubs (matorral). Deciduous *Nothofagus pumilio* forest occurs above 1000 m, while alto-Andean vegetation prevails on the summits. East of the forest, *Pappostipa* and *Festuca* steppes occur at mean annual precipitation below 500 mm and extend into the Patagonian plains (Oyarzábal et al., 2018).

## 3. Site description

Laguito del Morro (41° 32′ 24.4″S - 71° 47′ 50.0″W) is a small lake with an open water surface of 240 m$^2$ and a 6 m-depth, situated at an elevation of 505 m within the Lower Río Manso valley near the Argentinean-Chilean border, approximately 60 m above the current river (Fig. 1). The Río Manso originates at the Manso glacier in Cerro Tronador, and discharges through the Río Puelo into the Seno de Reloncaví at the Pacific Ocean coast. Laguito del Morro is of glacial origin, fed by groundwater without an incoming stream. The lake is surrounded by peatbog and is partly overgrown by a floating mat of *Shpagnum magellanicum*. Peatbog spots are frequent in the Andean rainforest. The *Sphagnum* bog surrounding the lake is part of a peatbog-lake system located on glacial terraces above the river valley.

In these peatlands, *Sphagnum* mosses and vascular plant species such as sedges and ericoids co-occur with variating proportions
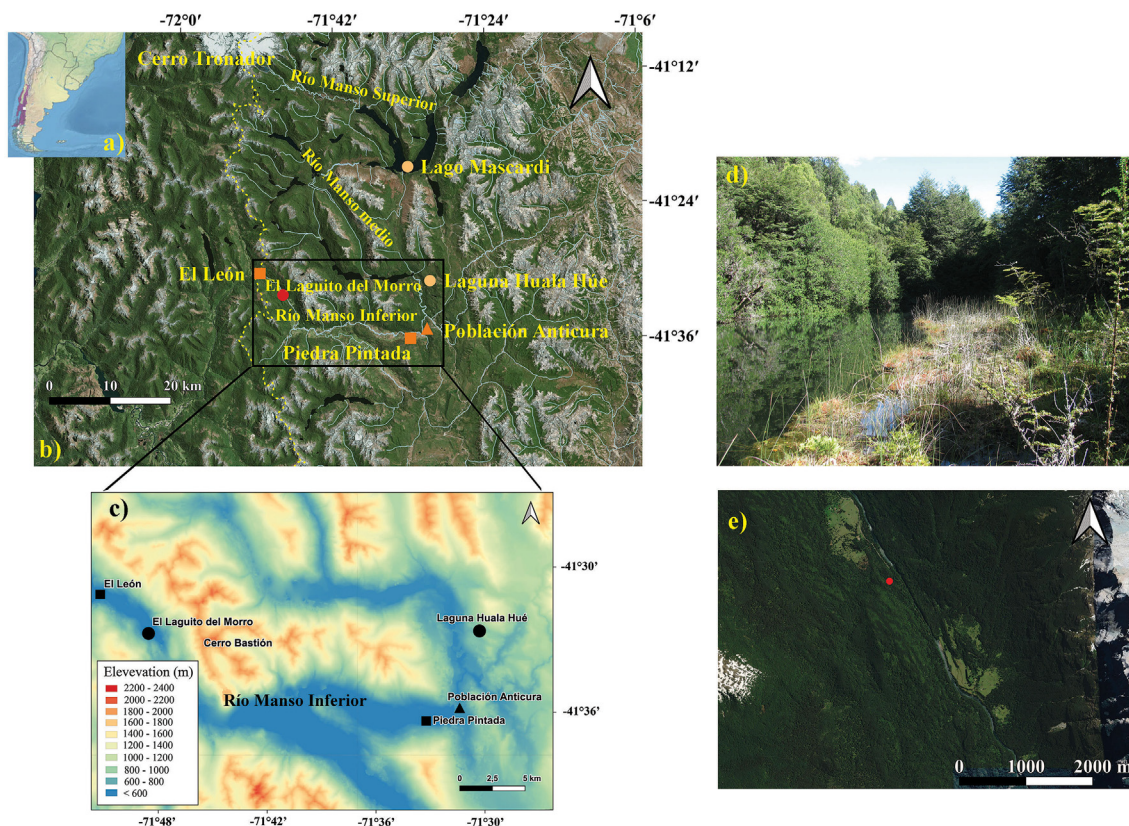
**Fig. 1.** a) rainforest distribution b) Study area of Laguito de Morro. (●) pollen sites, ( ▲ ) archaeological sites, (■) meteorological stations. c) hypsometric map d) photography of El Laguito del Morro e) site location (red dot) on a satellite image taken from Google Earth. 3.1 El Manso Valley Climate.

along the water table (WT) gradient. Changes in the position of the WT affect plant composition. According to experimental studies, *Sphagnum* growth is higher than vascular plant growth when the WT is high and vice versa (Breeuwer et al., 2009). Based on these findings, variations in the proportion of *Sphagnum* and vascular plants in the bog were taken in this study as changes in the water table level.

Climate station data is available from the nearby border post at Paso El León (41°30′29.18″ S - 71°50′39.31″ W, 350 m a.s.l.) (Tabla climática). The climate is of warm temperate (Cfb) without a dry season. The mean annual temperature is 10.1 °C, and the mean annual precipitation is 2300 mm (Kottek et al., 2006). At the meteorological station Piedra Pintada (41°36′17.05″S - 71°32′28.86″W, 486 m a.s.l.), located 30 km to the east, mean annual precipitation decreases to 1300 mm, with 75% of it falling during April−September (Autumn to Spring). At this station, the minimum and maximum monthly mean temperatures are −2 °C in July and 24 °C in February, respectively (Bustos, C., 1995).

### 3.1. El Manso Valley vegetation

The steep precipitation gradient is manifested by the sharp vegetation changes within the valley. From west to east, pockets of rainforest communities below 500 m a.s.l. change to *Nothofagus dombeyi* stands, mixed *Nothofagus dombeyi - Austrocedrus chilensis* forests and scrubby vegetation, dominated by *Lomatia hirsuta*. *Nothofagus antarctica* and *Schinus patagonicus* (matorral), alternate with farmland within the eastern, wider part of the Río Manso valley. The altitudinal vegetation gradient follows the regional vegetation pattern (Salguero and Sancholuz, 1989).

At Laguito del Morro, the vegetation is composed of *Nothofagus*

*dombeyi*, scattered trees of *Austrocedrus chilensis,* and *Fitzroya cupressoides,* with the latter representing remnants of larger populations, decimated during the 19th century (Armesto et al., 1995; Otero, 2006). The shrubs *Lomatia hirsuta* and *Discaria chacaye,* are found downhill from the lake, indicating forest disturbance. The hygrophilous tree M*yrceugenia exsucca,* with epiphytic ferns (Polypodiaceae), *Mitraria coccinea* and the bamboo *Chusquea culeou* grow at the edge of the peatbog bordering the lake. *Sphagnum magellanicum* alongside palustrine rush *Schoenoplectus califronicus* are dominant in the adjacent wetland. Shrubs such as *Escallonia virgata*, *Gaultheria pumila*, and ferns like *Austro-blechnum chilensis* and *Austro-blechnum penna-marina* also occur on the bog.

## 4. Material and methods

### 4.1. Core recovery and processing

Coring was conducted with a modified square rod piston corer (Wright, 1967) from a raft at a water depth of 4−6 m. Frequent tree trunks embedded within the sediment often caused coring to stop. Several parallel cores of different lengths were therefore collected. The results are based on the longest two sediment cores, Elamo 01 (10,25 m) and Elamo 07 (7.24 m). The cores provided continuous organic-rich sediment sections with tephra layers of different thicknesses, grain-sizes and colours. Several plant macrofossils with excellent preservation, and decomposed wood fragments were also found. Cores were described and sub-sampled for dating, pollen, charcoal analyses, and macrofossil identification. A total of 107 pollen samples were collected at 8 cm intervals.

### 4.2. Magnetic susceptibility and elaboration of the composite profile

Volume magnetic susceptibility (k) was measured at 0.5 cm intervals on longitudinally split core sections using a Bartington MS3 point sensor. To build a composite profile, the cores Elamo 01 and Elamo 07 were correlated based on characteristic susceptibility peaks and troughs by visual inspection. Some of the tie-lines used to connect core sequences are shown in Fig. 2. K logs were used to define lithostratigraphic correlation of core sequences. Elamo 01 was used as the master core, so the field-depth of Elamo 07 was modified to match the field-depth of Elamo 01. Between two tie-lines, the depth scale of Elamo 07 was adjusted using linear spacing.

### 4.3. Pollen and plant macrofossil analysis

$5-10$ cm$^3$ samples for macrofossil analysis were disaggregated in water and washed through a 0.25 mm mesh sieve (Birks, 2001). The plant remains were picked out under a binocular microscope and identified following Gandolfo and Romero (1992).

The preparation of pollen samples followed Bennett and Willis (2001) using Hydrofluoric Acid (HF) to eliminate the inorganic fraction. Exotic *Lycopodium* spores were added to calculate pollen concentrations (grains cm$^{-3}$), and pollen accumulation rates (PAR) (grains cm$^2$ yr $^{-1}$). Pollen counting was performed with a Nikon Eclipse 50i Microscope, at a final magnification of 1000×. Pollen and spore determination was aided by pollen atlases (Heusser, 1972; Markgraf and D'Antoni, 1978) and reference collection slides. Two different pollen types of Cupressacae can be identified in the Sub-Antarctic region. *Austrocedrus chilensis* and *Fitzroya/Pilgerodendron,* the latter being larger, with a thicker wall and fewer but larger verrucae (Abarzúa, personal communication). Pollen sums reached at least 300 pollen grains and fern spores, with the total pollen sum including peatbog taxa.

Infrequent pollen types were grouped according to their ecological affinities as: "other rainforest trees and shrubs" (*Raukaua laetevirens, Tristerix tetrandrus, Fucsia magellanica, Myoschylus*

oblongus, *Aextoxicum punctatum, Embothrium coccineum, Drimys winteri,* and Asclepiadaceae), "other understory herbs" (*Gunnera,* Urticaceae, Gentianaceae, *Oxalis,* Liliaceae, *Viola, Ribes, Galium, Berberis, Valeriana,* Gesneriaceae, Geraniaceae, *Glaux, Rubus* and Primulaceae), "Andean-steppe herbs" (Euphorbiaceae, Caryophyllaceae, *Acaena/Alchemilia, Quinchamalium,* and *Ephedra*), and "other mixed forest trees and scrubs" (*Maytenus* and *Schinus*). "Ferns" (Pteridopsida) include *Blechnum* sp., *Lophosoria quadripinnata,* Polypodiaceae, and undifferentiated spores. Constrained Cluster Analysis was used to aid in the zonation of the pollen diagram using CONISS (Grimm, 1987). Data were square root transformed, excluding rare taxa (<0.1%). Edwards and Cavalli-Sforza's chord distance was used as the dissimilarity coefficient.

Pollen percentages and accumulation rates (PAR) were calculated with TILIA 2.1.1. (Grimm, 1991−2018). Palynological richness, E (T$_{307}$), was calculated by rarefaction (Birks and Line, 1992) with PSIMPOLL 4.25 (Bennett, 2005). Modern pollen and vegetation samples from vegetation units, in the three sections of the Río Manso watershed, were used to provide analogues for the different vegetation types within the Río Manso watershed (Bianchi and Ariztegui, 2012; Pérez et al., 2017).

### 4.4. Charcoal analysis

In order to obtain a local high-resolution fire record, the cores were sampled contiguously. Samples of 1 cm$^3$ were soaked in a 25 cm$^3$ deflocculant solution (2% sodium hexametaphosphate) for 48 h and washed through both 125 and 250 μm mesh screens.

Charcoal particles were counted under a stereomicroscope with 40× magnification in gridded Petri dishes (Whitlock and Larsen, 2001). Grass cuticle charcoal was counted separately from wood charcoal. Individual cuticles and wood specimens were photographed with a scanning electron microscope at the facilities of Servicio de Microscopía Electrónica de Barrido at Museo Argentino de Ciencias Naturales. Cuticles were identified as belonging to *Chusquea culeou* (Fig. 3).

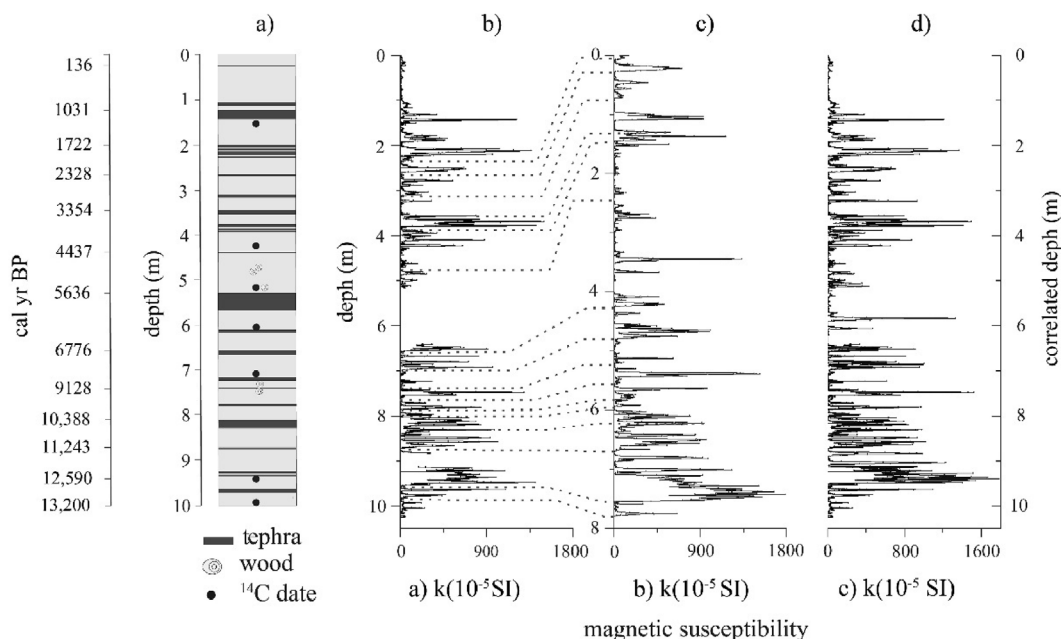Grass and wood charcoal particles were combined for numerical



**Fig. 2.** a) Lithology, b) magnetic susceptibility profile (MSP) of core ELAMO 01, c) MSP of core ELAMO 07, d) correlated and composite MSP from Laguito del Morro LMO master core.
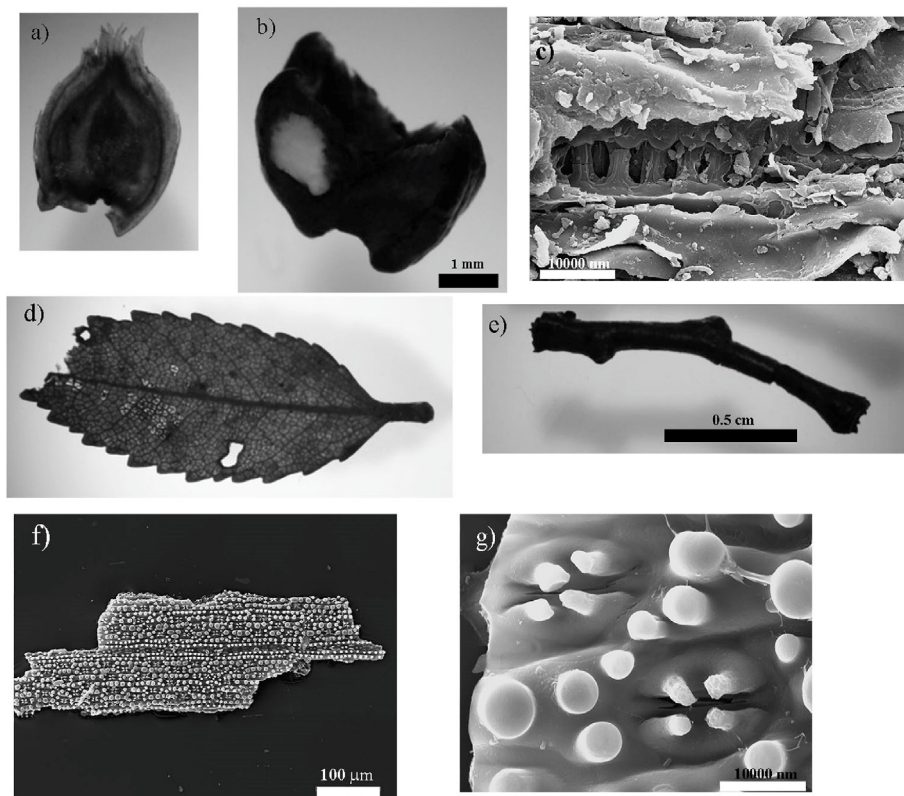
**Fig. 3.** Plant macrofossils found in sediment cores. a) *Nothofagus dombeyi* seed; b) *N. dombeyi* bud scale with resin secretion; c) SEM image of Cupressaceae wood fragment; d) leaf of *Nothoagus dombeyi*; e) young twig of *N. dombeyi*; f) SEM image of *Chusquea sp* charred epidermis; g) SEM image of *Chusquea culeou* leaf epidermis collected from the herbarium.

analysis using CharAnalysis (http://sites.google.com/site/charanalysis/, Higuera et al., 2009). Low-frequency variations in charcoal records were interpreted to reflect changes in secondary charcoal transport, and sediment mixing ($C_{back}$). We estimated $C_{back}$ using a 500-yr window by applying a moving median, which allowed the signal-to-noise index and the goodness-of-fit between the empirical and modelled noise distributions to be maximized (Higuera et al., 2009, 2010). The 99.9th percentile of the $C_{noise}$ distribution was chosen to estimate charcoal peaks (Higuera et al., 2008, 2009). Variations in fire frequency were assessed using a locally weighted regression with a 700-yr window. A severity index was computed as: (total grass charcoal particles cm$^{-3}$)/(total charcoal particles cm$^{-3}$ + 0.01). This index ranges from 0 (high severity) to 1 (low severity) (Sottile et al., 2018; Whitlock et al., 2006).

### 4.5. Dating and Chronology

Plant macrofossils with excellent preservation were submitted for dating to CHRONO Centre, Queens University Belfast. Radiocarbon ages were calibrated using the SHCal13 calibration curve for the Southern Hemisphere (Hogg et al., 2020). The overall age-depth relationship was established using Bayesian age modelling with the BACON (v. 2.2) R package (Blaauw and Christen, 2011) (Fig. 4). Accumulation rates were estimated at 10 cm resolution. Prior accumulations rates of 20 yr/cm were selected using a shape parameter k = 1.5. The mean prior memory was set to 0.7. The tephra layers were assumed to represent rapid deposition, and layers >1 cm thick were subtracted from the core depths prior to age modelling. Only true depths are referred to in the text. An age e.g. year of coring was added to 0 depth with an uncertainty of −60

to (−52) cal yr BP. Actual and adjusted depths are presented in Table 1.

### 4.6. Charcoal pollen comparisons

The effect of fire on local vegetation was assessed using correlation and ordination analysis. Both comparisons between charcoal and pollen samples required a resampling of the charcoal record to match the resolution of the pollen data. For the correlation analysis, charcoal concentrations were resampled in three ways: a) the charcoal sample matching the depth of the pollen sample; b) the charcoal sample coming from the cm prior the pollen sample; and c) the combination of a and b. Pearson's correlation was applied to compare the three sets of charcoal data with pollen proportions and pollen accumulation rates of selected taxa.

Principal component analysis (PCA) of pollen data was used to visually compare average charcoal accumulation rates passively fitted to the PCA. Here the aim was to characterize the general fire regime around the time the pollen sample was deposited. Therefore, a local regression smoother (loess) with a span of 0.1 was applied to the charcoal accumulation rate data, and respective values were collected for the locations of pollen samples. The PCA was run on the square root transformed pollen proportions using the covariance matrix. Only taxa with high variance were used for plotting. Redundancy analysis and additional significance test were carried out to explore the explanatory power of the variance in charcoal concentrations in explaining the pollen data. All analyses were run in R (R Core Team, 2022) using the Vegan package (Oksanen et al., 2022).
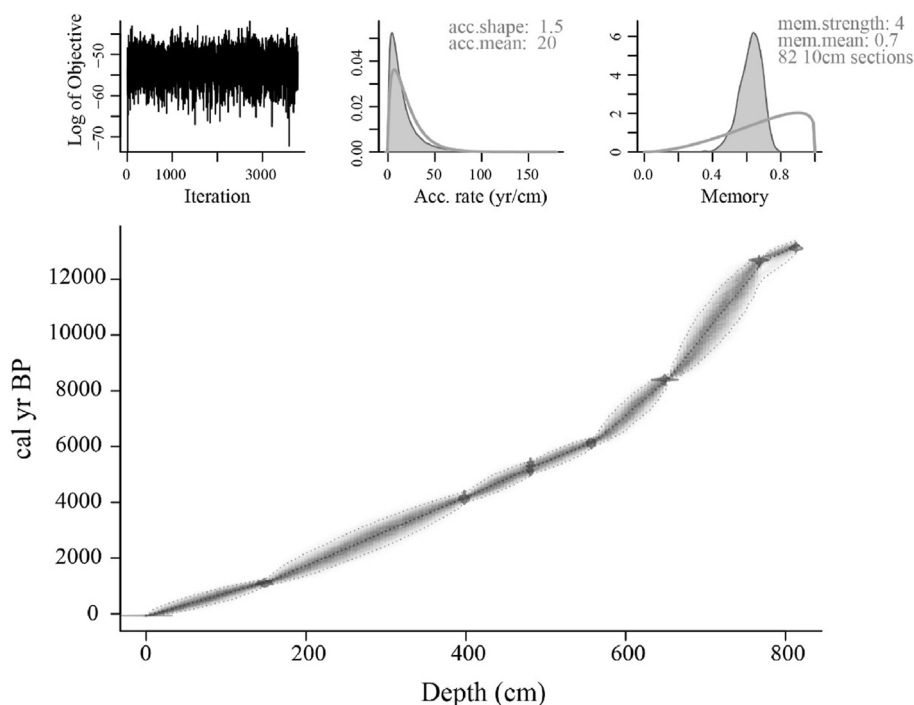
**Fig. 4.** Age-depth model for Laguito del Morro based on seven calibrated AMS radiocarbon dates using Bacon 2.2. The dotted areas are the probability distributions of the calibrated ages, and dark and light gray lines depict the more likely age-depth models and 95% confidence intervals. The central dotted line in the middle of the gray shadow shows the weighted mean age for each depth.

**Table 1**
Radiocarbon and calibrated radiocarbon dates from the core of Laguito del Morro. [a]Adjusted depths were used to calculate the age-depth model. They represent adjustments in the core depths after subtracting the depths of tephra layers >1 cm thick. [b]Based on BACON Southern Hemisphere calibration. [b]Based on BACON (v. 2.2) R package (Blaauw and Christen, 2011).

| Lab. ID | [a]Top depth (cm) | [a]Bottom depth (cm) | [14]C age | ± | [b]Cal.Yr. BP |
|---|---|---|---|---|---|
| NA | 0 | 1 | Inferred | NA | −60 to (−52) |
| UBA-26969 | 147 | 150 | 1229 | 25 | 1123 |
| UBA-26970 | 397 | 400 | 3816 | 35 | 4154 |
| UBA-29133 | 479 | 483 | 4628 | 53 | 5226 |
| UBA-26971 | 557 | 558 | 5386 | 42 | 6156 |
| UBA-26972 | 648 | 651 | 7648 | 33 | 8319 |
| UBA-20549 | 767 | 768 | 10,790 | 63 | 12,466 |
| UBA-29134 | 811 | 815 | 11,316 | 49 | 13,182 |

## 5. Results

### 5.1. Lithology and macrofossil finds

The lithology indicates the preservation of continuous sedimentation, disrupted by tephra deposition along the entire sedimentary record (Fig. 2). Several tephra layers, identified visually and by high magnetic susceptibility, were embedded in a dark brown organic-rich fine-detritus matrix that gradates into a brown gyttja towards the bottom of the core. A total of 16 tephra layers (>1 cm thickness) were observed along the core (Fig. 2). Tephra deposits in sediments are attributed to past eruptions of the Puyehue-Cordón del Caule (Daga et al., 2006; Villarosa et al., 2006).

Wood fragments >4 cm, recorded at 503 cm (field-depth) (ca. 4990 cal yr BP), 575 cm (ca. 5800 cal yr BP) and 745cm (field-depth) (ca. 9200 cal yr BP) were identified with SEM as Cupressaceae (Fig. 3). Abundant twigs, leaves, flowers, fruits and bud-scales of *Nothofagus. dombeyi* were found along the core, as well as fronds of *Blechnum* sp. and fruits of Myrtaceae. (Fig. 3).

### 5.2. Pollen and charcoal records

The percentage pollen diagram of Laguito del Morro is divided into five pollen zones which capture the different steps of vegetation development (Fig. 5). According to the broken stick model, only three of these zones are found to be statistically significant with the zone boundaries at around 351,5 and 705 cm. The oldest zone, LMO 1 (10,346−13,230 cal yr BP) is characterized by the combination of *Podocarpus* (2.6%), *Austrocedrus* (3.4%), and *Fitzroya/Pilgerodendron* (2.8%) with average values indicated in brackets. Compared to the rest of the core, the proportions of the dominating *Nothofagus dombeyi*-type (thereafter *Nothofagus*) are low during this zone, with an all-time minimum of 46% at around ca. 10,950 cal yr BP following a tephra layer of ca. 20 cm of thickness.

Fern spores reach the highest value (23%) at ca. 12,320 cal yr BP following a charcoal peak and attain values of 17% after the tephra layer mentioned above. The highest peak of scrub pollen (>19%) is concurrent with the minimum of *Nothofagus. Poaceae* frequently peak around 8% following char peaks or tephras. Pollen grains in Poaceae can seldom be distinguished under optical microscope.
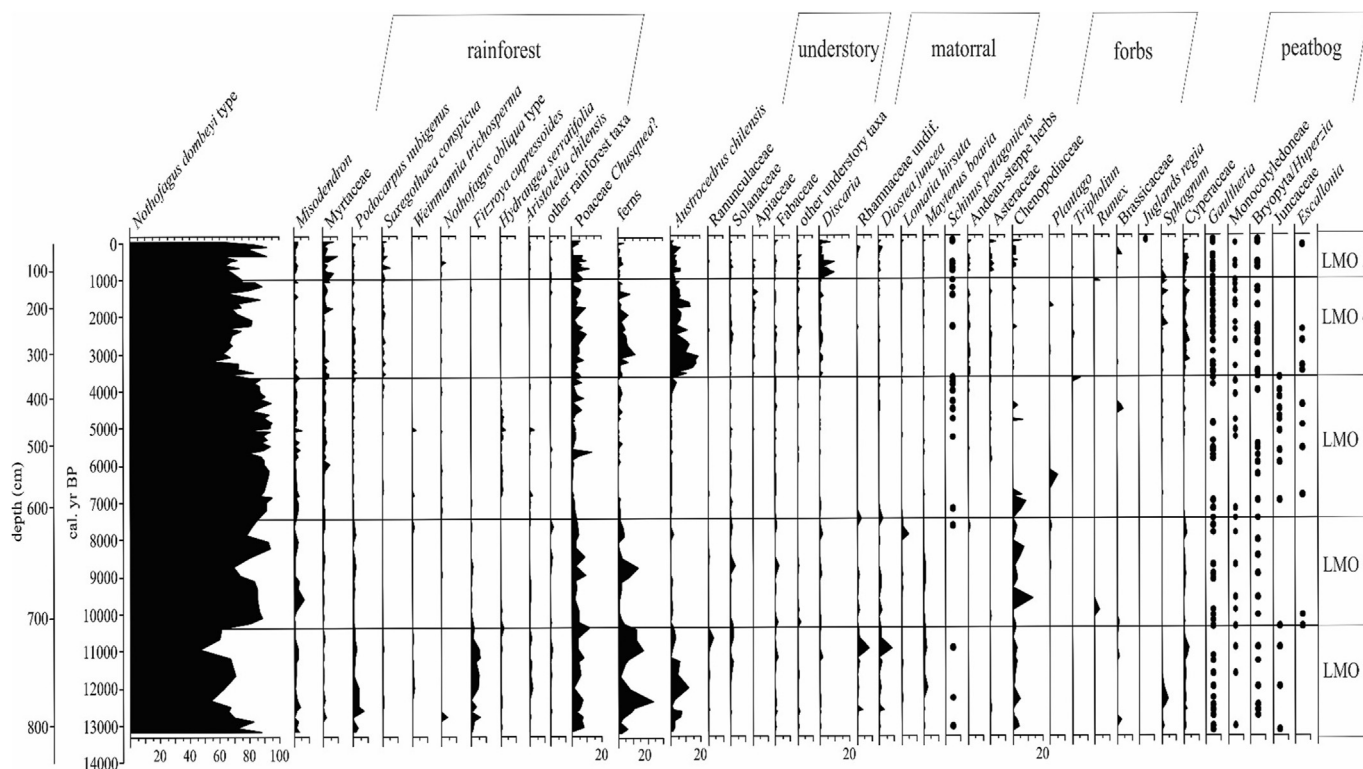
**Fig. 5.** Percentage diagram showing selected taxa including pollen and spores.

Grass pollen was mainly attributed to *Chusquea culeou* because of its abundance at the study site and the scarcity of other grasses growing in the watershed. Today, *Chusquea* species preponderates the understories of *N. dombeyi* temperate rain forests in south-central Chile (ca. 38–42°S), and the similar adjacent forests in southwestern Argentina (Veblen, 1982). *Sphagnum* spores increase to 4% at ca. 12,300 cal yr BP indicating the initial peat growth. *Nothofagus* increases (90%) at the onset of pollen zone LMO 2 (7471–10,346) whilst pollen from *Fitzroya/Pilgerodendron, Austrocedrus,* and *Podocarpus* become rare and disappear. Also, in this zone, peaks of Poaceae pollen and fern spores coincide with decreases of *Nothofagus dombeyi* below 80%, frequently following charcoal peaks.

Highest *Nothofagus* values above 80% characterize pollen zone LMO 3 (3636–7471 cal yr BP) without strong fluctuations. *Aristotelia, Weinmannia* and *Hydrangea* frequently occur in this zone with maximum values at different times. At the bottom, Poaceae values that fall below 3%, peak at 13% around 5660 cal yr BP, and are preceded by an 18 cm thick tephra marking the middle of this zone. *Poaceae* values decrease below 3% towards the top. Dominance in *Nothofagus* starts declining with fluctuations around 4700 cal yr BP towards the top of the zone. Low peatbog values are observed throughout this zone.

The major shift in forest composition occurs from zone LMO 3 to LMO 4 around 3500 cal yr BP, one characterized by the sharp increase of Cupressaceae pollen interpreted to represent *Austrocedrus chilensis. Poaceae* pollen and fern spores are abundant in LMO 4 (986–3636 cal yr BP) with peaks around 9% and 11% respectively. After maximum values above 15% during the first half of this zone, *Austrocedrus* percentages decline towards the top with values around 5%. *Myrtaceae* pollen increases towards the top and *Saxegothaea* pollen is regularly found, almost forming a continuous curve. *Podocarpus, Raukaua,* and *Fitzroya/Pilgerodendron* reappear, alongside an increment in understory herbs and *Asteraceae.*

*Poaceae* and ferns increase to around 7% and 9% at ca. 3636 and 1757 cal yr BP, following tephra layers. Also, *Sphagnum* spores reappear during this zone. *Discaria* characterizes the samples in the youngest pollen zone LMO 5 (986 cal yr BP- present). The rise of *Discaria* to an initial peak of 10% coincides with a decline in *Austrocedrus.* Rainforest elements such as *Saxegothaea, Podocarpus, Embotrium,* an increase in *Myrtaceae,* and pollen of *Hydrangea* and *Fucsia* (0.5%) are recorded. *Poaceae* remain high with peaks around 10% reaching 12% around ca. 768 cal yr BP following fires peaking. Pollen from the *Asteraceae* is frequent in this zone, with peaks above 3%. The six uppermost samples of this zone differ in composition, as *Nothofagus* increases with fires, with percentages fluctuating between 69 and 92%. Pollen from the exotic tree *Juglands regia* is found in the top sample. Cyperaceae increase (3%), while *Sphagnum* spores almost disappear.

Modern pollen samples characterizing different vegetation types in the region (Bianchi and Ariztegui, 2012) aid in interpreting this pollen diagram. Comparisons undergone suggest the presence of a pure *Nothofagus dombeyi* forest during pollen zone LMO 3, with *Nothofagus* pollen surpassing 90%. Mixed *Nothofagus dombeyi - Austrocedrus chilensis* forests in the region were represented by their pollen with *Nothofagus* between 49% and 80%, and *Cupressaceae* pollen ranging between 7% and 20% (Bianchi and Ariztegui, 2012). This composition corresponds to the pollen proportions in LMO 4. The combination of taxa in zone LMO 1 has no modern analogue in surface samples from Patagonia.

Pollen accumulation rates (PAR) from terrestrial pollen sum as well as pollen from bog plants both show high variability. *Nothofagus* has highest PAR in LMO 3 (13.699 grains cm$^{-2}$ yr$^{-1}$). *Fitzroya cupressoides* (178 grains cm$^{-2}$ yr$^{-1}$) and *Austrocedrus chilensis* (586 grains cm$^{-2}$ yr$^{-1}$) attain PAR maximum value in LMO 1 and LMO 4, respectively while *Discaria* (430 grains cm$^{-2}$ yr$^{-1}$) reaches PAR maximum value in LMO 5. The peatbog PAR values show peaks in LMO 1 and LMO 4.

Fires record from El Laguito del Morro (Fig. 7) shows distinct changes in fire regime through time. The high signal-to-noise index (SNI > 3) allows good separation of the noise from distinct peaks which show high level of confidence (Kelly et al., 2011). The sequence starts with elevated CHAR (values of up to 15.77 particles cm$^{-2}$ yr$^{-1}$), high fire frequency (7 fires 700 yr$^{-1}$), and high magnitude. During this period the severity index is low, indicating high-severity fires. Fire frequency decreases around 12,400 cal yr BP and stays low (~3 fires 700 yr$^{-1}$) until 8000 cal yr BP, with a total of 27 low magnitude fire episodes in 5400 yr. Between 8000 and 4300 cal yr BP (LMO2 and LMO3), the record is characterized by low CHAR values (~3 particles cm$^{-2}$ yr$^{-1}$) with an increasing trend of fire frequency (>6 fires 700 yr$^{-1}$). The severity index during this period is high, suggesting surficial fire events. Around 4300 cal yr BP, CHAR increases substantially, while the detected fire frequency decreases (3−5 fires 700 yr$^{-1}$). During this period, lasting until 1800 cal. BP, the fire magnitude remains low and the severity index decreases, suggesting a period with a lower frequency of severe fires. During the youngest 1800 years, the fire record has its highest CHAR values, with maxima of 25.9 particles cm$^{-2}$ yr$^{-1}$. Detected fire frequency increases up to six fires 700 yr$^{-1}$ and the severity index increases, suggesting surficial fires.

## 6. Numerical analyses

The overall gradient as obtained from the detrended correspondence analysis has a length of 1.28 standard deviation units. This relatively short gradient is best represented by a PCA ordination (Fig. 6). The two first components explain 47% of the overall variance and the biplot separates the samples with respect to their assigned pollen zone, except for LMO 4 and 5. The first axis represents the modern humidity gradient along the valley: from dense *Nothofagus dombeyi* forests to open woodlands characterized by *Austrocedrus chilensis*. Samples from the Late Glacial and early Holocene with *Fitzroya cupressoides* and *Podocarpus nubigenus*, which have no modern analogue in the region, are separated along the second axis.

The added surface indicates average CHAR values decline along the first axis, so that this vegetation gradient can also be interpreted to respond to fire. In a redundancy analysis, average CHAR explains 11% of the variability in the pollen data yielding a highly significant

model. The clear response of *Nothofagus dombeyi* and *Austrocedrus chilensis* to low and high overall charcoal accumulations is also seen in the correlation analysis (Table 2). In addition to *Nothofagus dombeyi*, also *Hydrangea* shows a negative correlation with charcoal concentration in the same and previous sample. A positive correlation to charcoal concentrations is visible for *Poaceae, Pteridopsida*, and *Discaria*, which is strongest when comparing the pollen to the charcoal in the previous sample. The positive correlation for *Austrocedrus chilensis* with charcoal is strongest when considering the same sample.

## 7. Discussion

### 7.1. Late Glacial vegetation development and climate drivers

There is little direct evidence of the distribution of trees during the Last Glacial Maximum (LGM), while the extent of glaciers is exceedingly well documented (e.g. Glasser et al., 2008). Additional constraints on where plants may have survived the LGM in Patagonia come from the modern distribution of genetic markers (e.g. Prémoli et al., 2003, 2004), indicating the persistence of trees on ice-free terrain between glacier tongues. Cold-resistant elements of the Sub-Antarctic Andean biomes (conifers and some *Nothofagus* species) might have survived on the ice-free western Andean flank between 40° and 43°S. Also, at the eastern Andean flank, pollen studies suggest the existence of tree populations in some ice-free terrains (Bianchi and Ariztegui, 2012; Markgraf, 1993b).

Genetic studies support these findings showing that cold-tolerant conifers such as *Fitzroya cupressoides, Podocarpus nubigenus,* and *Pilgerodendron uviferum,* exhibit high genetic diversity, suggesting that small populations remained isolated in multiple *refugia* in the Andes during the glacial period (Prémoli et al., 2003, 2004). Eastward from the mountain range, a mosaic of herb-shrub steppes, semi-desert spots, and forest patches developed under a dryer and cooler climate (Bianchi, 1999; Markgraf, 1983; Markgraf and Bianchi, 1999). Consequently, a west-east vegetation gradient, from evergreen forest to steppe may have occurred between 37° and 42°S over a very narrow range, likely disintegrated in patches (Bianchi and Ariztegui, 2012; Villagrán and Armesto, 1993).

Forest recolonization began during the Late Glacial (LG) at ca. 16,000 cal yr BP. North-Patagonian and Valdivian rainforests spots
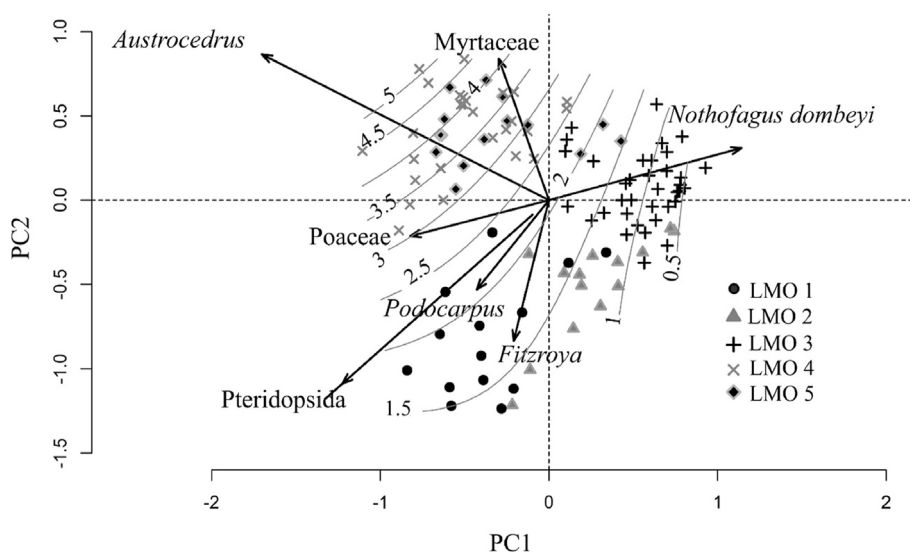


Fig. 6. PCA scatterplot of samples and selected taxa of Laguito del Morro. Sample affiliation to pollen zones is shown by different symbols at the right-bottom of the PCA. Average CHAR values obtained from the redundancy analysis are shown as isolines.
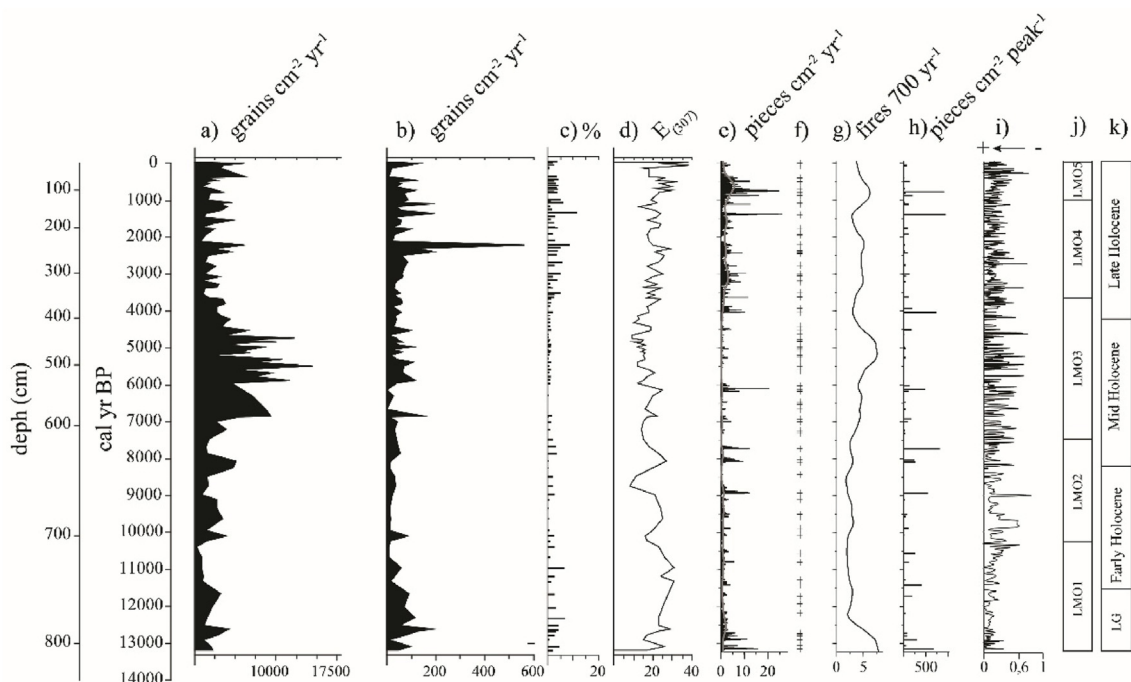
**Fig. 7.** Pollen and charcoal synthetic variables from Laguito del Morro record. a) total pollen accumulation rates (PAR), b) peatbog taxa accumulation rates, c) proportion of peatbog taxa in the total pollen sum, d) palynological richness, e) charcoal accumulation rates (CHAR), background CHAR (thin gray line), f) peaks plotted as "+" symbols, g) peaks magnitude, h) fire frequency, i) fire severity index, j) pollen zones, k) geological periods, Late Glacial (LG) Late Glacial.

**Table 2**
Pearson correlation coefficient (r) and p-values summary results for selected taxa.

| Taxa | Same sample | | Previous sample | | Sample + previous | |
|---|---|---|---|---|---|---|
| | p | r | p | r | p | r |
| *N. dombeyi* | 0.000129214 | −0.36 | 0.000132765 | −0.36 | 1.64649E-05 | −0.4 |
| *A. chilensis* | 0.005210947 | 0.27 | 0.245592916 | 0.11 | 0.02475238 | 0.22 |
| *Hydrangea* | 0.000198421 | −0.35 | 0.007012 | −0.26 | 0.00023436 | 0.35 |
| Poaceae | 0.038370922 | 0.20 | 0.011074 | 0.24 | 0.010616084 | 0.25 |
| Pteridopsida | 0.012731948 | 0.24 | 0.002808 | 0.29 | 0.002523761 | 0.29 |
| *Discaria* | 0.218621085 | 0.12 | 0.018258 | 0.23 | 0.037785284 | 0.2 |

first occupied the lowlands in the Lake District and Chiloé Island and expanded to slopes below 500 m a.s.l. at the eastern Andean flank (41-43° S) (Markgraf, 1983; Moreno, 2000; Villagrán and Armesto, 1993). The pollen record of Laguito del Morro documents that a diverse rainforest, with elements of the North-Patagonian and Valdivian rainforests, had already been established at ca. 13,200 cal yr BP in the valley of Río Manso Inferior. The dominant *Nothofagus dombeyi* formed the closed canopy stratum of the rainforest together with *Fitzroya cupressoides, Austrocedrus chilensis,* and *Podocarpus nubigenus.*

Several rainforest trees and shrubs grew in a lower canopy layer. Herbs such as hydrophilic *Gunnera* and Ranunculaceae grew in the understory. Ferns expanded after fires. A rush-sedge bog developed at the lake margin. Cooler than present temperatures may have been the prevailing climatic conditions. Climate elements may have occurred in no-analogue combinations causing the unique vegetation composition.

Between ca. 13,000−12,800 cal yr BP, the occurrence of high magnitude severe fires may have been caused by frequent lightning either produced by climatic conditions or volcanic eruptions. The presence of several tephra layers at the bottom of the core may account for intense volcanic activity at ca. 12,500 cal yr BP.

After 12,800 cal yr BP *Myrtaceae* increased, indicating moister

conditions. Between ca. 12,800 and 11,700 cal yr BP, populations of *Fitzroya. cupressoides, Austrocedrus chilensis* and *Podocarpus nubigenous* expanded with the decline in *Nothofagus dombeyi*. The increase of cold-resistant conifers suggests the occurrence of colder and humid conditions.

Pollen trends at Laguito del Morro are in accordance with the results found at Lake Mascardi and several pollen sites from the Lake District where cold periods were recorded (Huelmo Mascardi Cold reversal and Younger Dryas) (Hajdas et al., 2003; Heusser et al., 1996; Lowell et al., 1995). In the neighbouring basing of Río Manso Superior, changes in the forest composition were linked to a glacial advance associated with a cold reversal period, suggesting increasing moisture and decreasing temperature between ca. 13,000 and 11,500 cal yr BP (Ariztegui et al., 1997; Bianchi and Ariztegui, 2012; Hajdas et al., 2003). At Laguito del Morro, conifers declined during a rapid expansion of *Nothofagus dombeyi* after ca. 11,000 cal yr BP following a considerable tephra fall at ca. 11,300 cal yr BP. The frequency of highly severe fires decreased, suggesting a change in fire regime. During the cold reversal period fire regimes show differences along the west-east bioclimatic gradient. Severe fires are recorded at Pilauco, a pollen site in the Lake District (Pino et al., 2019). However, fire activity increases towards the end of this period at Canal de la Puntilla and Lago Melli

located in the Chilean Lake District (Abarzúa and Moreno, 2008; Moreno et al., 1999). In contrast, very low fire activity is observed in some locations in the eastern Andean foothills e.g. at Cordón Serrucho and La Zeta Lake between ca. 15,000 and 10,000 cal yrs BP (Iglesias and Whitlock, 2014; Markgraf et al., 2013).

Paleoclimate reconstructions suggest that during the LGM and the Late Glacial - Interglacial transition, southern South America was affected by changes in the south westerly winds (SWW) and in the position of the southern border of the semi-permanent Atlantic and Pacific anticyclones (Compagnucci, 2011). However, these are matters of long-lasting discussions, particularly regarding the cold reversal for the North Patagonian Andes (Bennett et al., 2000; Heusser, 1984; Lowell et al., 1995; Lamy et al., 1993a, 1999; Moreno et al., 2001). The cold episode, named Huelmo-Mascardi Cold Reversal (HMCR), occurred between ca. 13,700 and 11,000 cal yr BP, partially overlapping the Younger Dryas Period (YD) (Hajdas et al., 2003). Most of the evidence for vegetation changes responding to the cold episode comes from pollen records in the Chilean Lake District and Chiloé Island (Heusser et al., 1996; Moreno, 2000, 2004; Moreno et al., 1999, 2001; Moreno and León, 2003). The vast evidence found west of the Andes contrasts the scant evidence east of the mountains. In sites currently located at the mixed forest and forest-steppe ecotone, the cold reversal is not clearly evident in most available pollen records. A continuous warming trend is proposed based on Lago El Trébol, Lago Escondido, Lago Morenito, and Mallín Aguado pollen sites (Jackson, 1996; Markgraf, 1984; Markgraf and Bianchi, 1999; Whitlock et al., 2006). This remarkable difference between the extremes of the trans-Andean bioclimatic gradient poses the question of the causes of this asymmetry (Flantua et al., 2016).

Despite this sharp contrast, widespread burning has been recorded for the hyper-humid regions of the western Andes to eastern Patagonia during the Late Glacial transition into the Holocene (Álvarez-Barra et al., 2022). The weakening and migration of SWW is a proposed explanation for vegetation and fire regime changes at that time (Heusser, 2003; Villagrán, 1988; Whitlock et al., 2007). In eastern Patagonia seasonal moisture stress was most pronounced between ca. 12,500 and 9600 cal yr BP (Whitlock et al., 2006, 2007).

### 7.1.2. Holocene vegetation development and its climatic drivers

#### 7.1.2.1. Early Holocene period.
During the Early Holocene, the pure *Nothofagus. dombeyi* forest replaced the rainforest at the eastern Andean flank. Several rainforest taxa declined or disappeared between ca. 10,500 and 9000 cal yr BP. i. e *Hydrangea*, a thermophilous vine with low tolerance to fires. *Nothofagus dombeyi* gained space in the canopy, with increased temperature and precipitation variability. A less diverse understory coincides with more frequent swings in the peat bog water table, indicating oscillations in moisture. Under these climatic conditions, the fire regime changed from high severity fires to more frequent low severity fires. Fires were followed by highly competitive *Chusquea culeou* and ferns dominating the understory thanks to their rizome adaptations that allow them to resprout after fires.

The weakened influence and seasonal displacement of westerly winds between ca. 11,000 and 8000 cal yr BP are the proposed drivers for increased seasonality in precipitation (Fletcher and Moreno, 2012; Lamy et al., 2010; Villa-Martínez and Moreno, 2007).

At a regional scale, variations in the distribution of temperate rainforests indicate a minimum in the precipitation of westerly origin at the western Andean flank (40-43°S) (Abarzúa et al., 2004; Abarzúa and Moreno, 2008; Moreno, 2004). Evergreen *Nothofagus dombeyi* forest developed under decreased precipitation, increased temperature and seasonality at the eastern Andean flank during the Early -Holocene (Bianchi and Ariztegui, 2012; Markgraf, 1983). By

that time, maxima in temperature and fire activity were recorded throughout Northern Patagonia (Iglesias et al., 2018; Nanavati et al., 2019; Whitlock et al., 2007).

Widespread burning has been reconstructed for the hyper-humid regions of the western Andes to eastern Patagonia during Early Holocene. The weakening and migration of SWW is the proposed explanation for vegetation and fire regime changes based on evidence from multiproxy records from Northern Patagonia (Fletcher and Moreno, 2012; Heusser, 2003; Villagrán, 1988; Whitlock et al., 2007). However, despite the large number of reconstructions and models of Glacial and Holocene climates, the cause of changes in the SWW are still poorly understood (Compagnucci, 2011).

#### 7.1.2.2. Mid-Holocene period.
During most of the Mid-Holocene, *Nothofagus dombeyi* dominated the forest. The variable charcoal concentration has a high negative correlation to *Nothofagus dombeyi* indicating that this tree grows in periods of low fire activity (see Table 2 and Fig. 6). After ca. 7000 cal yr BP, the peatbog plant composition changed recurrently. *Sphagnum* was frequently absent from the bog indicating decreases in moisture. Contrastingly, the expansion of riparian *Myrceugenia exsuca* at the lake margin at ca. 5900 cal yr BP accounts for high water availability. Although highly flammable, the trees show post-fire regeneration capacity and vegetative propagation (Latsague Vidal et al., 2010). After ca. 7000 cal yr BP, fire frequency increased as dryer periods became more frequent, favouring the penetration of scrub into the forest at Laguito dell Morro.

The expansion of *Chusquea culeou* increased with low magnitude fires. Disturbance-adapted bamboo controlled the understory. Thick tephra layers enriched soils may have promoted its expansion, as has been shown in ecological studies (Veblen, 1982). The feedback between increased precipitation variability, tephra-enriched soils and large bamboo fuel production resulted in frequent low magnitude fires. Forest ecology studies indicate that once established, pure *Nothofagus dombeyi* forest can persist for centuries (Veblen et al., 2016). The phenology and ecology of *Chusquea culeou* provides insights for understanding the dynamics of this forest type. Where the forest has been disturbed, bamboo forms extensive thickets becoming an impediment to the regeneration of *Nothofagus dombeyi* (Veblen, 1982). Their shading effects and high litter production inhibit tree establishment and development (Veblen, 1982). *Nothofagus* recruitment is only successful when strong disturbances such as a high severity fire occur, and sufficient gaps are opened (Veblen, 1982).

A moderate increase in fire activity at the western Andean flank created a fine-scale mosaic of Valdivian and North Patagonian rainforest species at low-to mid-elevation between ca. 7000 and 3000 cal yr BP (Abarzúa and Moreno, 2008; Moreno, 2004). In contrast, a pure *Nothofagus dmbeyi* forest prevailed during a period of low fire activity and effectively wetter conditions on the eastern Andean flank (Iglesias et al., 2018; Markgraf et al., 2013; Nanavati et al., 2019). At the beginning of the Late Holocene, the mixed *Nothofagus dombeyi* - *Austrocedrus cilensis* forest expanded eastward into the land previously occupied by shrub-land and steppe, possibly caused by a shift to cooler and or more humid conditions (Iglesias et al., 2012).

Model simulations indicate stronger westerlies and increased seasonality over Patagonia during Mid-Holocene (Compagnucci, 2011), supporting paleoecological evidences. These models suggest that negative pressure anomalies increased with latitude during summer leading to stronger westerlies and increased seasonality over Patagonia (Compagnucci, 2011).

#### 7.1.2.3. Late Holocene period.
At Laguito del Morro, the initiation of

the Late Holocene shift in forest composition is marked by high severity fires at ca. 4000 cal yr BP. *Austrocedrus chilensis*, rainforest trees and scrubs expanded while *Nothofagus dombeyi* declined, creating a more open and diverse forest. A change in precipitation regime is consistent with this vegetation shift. Increased inter-annual variability with pronounced dry and humid years might also have contributed to the vegetation change. After ca. 3600 cal yr BP, a mixed *Nothofagus dombeyi - Austrocedrus chilensis* forest established while fire frequency decreased.

*Austrocedrus chilensis* quickly reached maximum abundance and consequently declined during the Late Holocene. Progressively, humid/dry phases became shorter and more frequent. During dry phases, forest gaps opened by low-severity fires favoured the rapid colonization of shrubs. During humid phases, *Austrocedrus chilensis* expanded east in the ecotone, probably with the help of nursing shrubs already established during previous dry spells as has been shown in ecological studies (Kitzberger et al., 2000). Scattered rainforest conifers survived under frequent fires and volcanic events between ca. 3600 and 2500 cal yr BP at Laguito del Morro. After ca. 2500 cal yr BP *Nothofagus dombeyi* forest re-established, and several rainforest plants developed. *Myrtaceae* and *Sphagnum magellanicum* grew at the lake margin, suggesting that the water table rose as precipitation increased. At ca. 1300 cal yr BP, after the highest severity fire episode ever recorded in the sediments of Laguito del Morro, scrub thickened, and disturbance-related forbs extended during a period of higher moisture. *Austrocedrus chilensis* started to decline as fires became more frequent. Competition dynamics between *Nothofagus dombeyi* and *Austrocedrus chilensis* are proposed to explain the alternation in the prevalence of one or the other tree under mesic conditions (Iglesias et al., 2012a).

Currently, the alternative dominance of either *Austrocedrus* or *Nothofagus* occurs along the west-to-east moisture gradient, with the former gaining drier environments and the latter prevailing under humid conditions (Iglesias et al., 2012a). However, under frequent and severe fires, both obligate-seeded *Nothofagus dombeyi* and *Austrocedrus chilensis* trees fail to re-establish, and several sites became dominated by scrub, best represented by species capable of regrowth after a fire, for instance, *Lomatia hirsuta*, *Schinus patagonicus*, *Diostea juncea*, and *Maytenus boaria* (Mermoz et al., 2005). After 3000 cal yr BP, intensified fire activity along the trans-Andean bioclimatic gradient has been associated with the increase in climate variability generated by ENSO (Abarzúa et al., 2004; Abarzúa and Moreno, 2008; Holz et al., 2012; Kitzberger et al., 1997; Villalba et al., 2003). In Northern Patagonia, pollen and charcoal data suggest that high moisture variability, mainly through its effects on fire occurrence, shaped the composition of the forest-steppe ecotone during the Late Holocene. Cooler/more humid conditions allowed the development of the mixed *Nothofagus dombeyi - Austrocedrus chilensis* forest that expanded eastward into the land previously occupied by woodland and steppe at the beginning of the late Holocene (Iglesias et al., 2012; Whitlock et al., 2006).

During the last two millennia, an invasion of *Nothofagus dombeyi* into *Austrocedrus chilensis* forest occurred along the forest-steppe ecotone. It was probably associated with a shift towards a cooler and wetter climate leeward from the Andes. (Iglesias and Whitlock, 2014; Jackson, 1996; Markgraf, 1983; Markgraf and Bianchi, 1999; Whitlock et al., 2006). During the last centuries, burning occurred at local scales asynchronically, triggered by increased climate variability, and anthropogenic disturbances on both sides of the Andes (41-47°S) (Iglesias and Whitlock, 2014; Iglesias et al., 2018; Nanavati et al., 2019; Whitlock et al., 2007).

Our results from Laguito del Morro suggest that at ca. 500_400 cal yr BP, a rich *Nothofagus dombeyi* forest, with scattered *Austrocedrus chilensis* and thermophilous rainforest taxa developed at Río Manso Inferior basin. The prevalence of vascular plants in the bog margin suggests dryer conditions. Low-severity fires enhanced scrub expansion into the forest at ca. 500_440 cal yr BP. Tree-ring reconstructions from Central Chile indicate significant temperature and precipitation departures related to an intense ENSO episode at the end of the fifteenth century (ca. 500 cal yr. BP) (Villalba, 1994; Villalba et al., 2003). Towards the top of the record (about the last four centuries), bamboos, ferns, and disturbance herbs expanded in the understory providing fuels for low severity fires at Río Manso Inferior.

*Astrocedrus chilensis* expanded while *Saxegothaea conspicua* and *Podocarpus nubigenus* declined. The sedges-bog reduced in size suggesting drier conditions. According to charcoal data from Lake Huala Hué, large fires occurred in Río Manso Medio in 1761 CE. At ca. 196_104 cal yr BP at Laguito del Morro, A*ustrocedrus chilensis* and scrub expanded under larger precipitation variability. Moisture continued to increase, favouring the re-establishment of low-diversity, *Nothofagus dombeyi* forest. Since the end of the nineteenth century, human activities have added disturbance pressure to forest ecosystems in the Manso Inferior valley. Massive forest destruction by fire and cutting started during the last decade of the nineteenth century. In 1899 CE, the first European settlers arrived at El Manso from Chile, according to historical chronicles (Caracotche et al., 2010). Over trails previously used by natives for trading cattle, a road was opened, facilitating the extraction of wood, mainly of *Fitzroya. cupressoides* and *Auatrocedrus chilensis*, and the forest clearance for pastures. Therefore, scrub expanded and diversified, mostly represented by *Discaria chacaye*, *Lomatia, hirsuta* and *Maytenus boaria*. Forbs e.g. *Rumex*, *Asteraceae Chicorioidea*, and *Plantago* appear in the understory under more frequent fires. Both wet and dry periods became shorter, suggesting the increase in sub-centennial climate variability up to the present and probably the occurrence of extreme climatic events. Scrub expanded while *Nothofagus dombeyi* forest decreased up to the present. Charcoal peaks detected at the top of the sediment record of El Laguito del Morro could be associated with high-magnitude fires during the first part of the twentieth century. For example, inhabitants of El Manso valley reported large fires in 1905 CE and 1912 CE (Caracotche et al., 2010).

Those changes in forest ecosystems occurred under a more variable climate during the Late Holocene. On a regional scale, the increase in frequency of dry periods characterizes the last four centuries in northern Patagonia (Villalba et al., 1998; Villalba et al., 2003). A steepened pole-to-equator thermal gradient at this time, would have driven stronger westerly winds, and a general increase in the intensity of atmospheric circulation (Moreno, 2020). El Niño/Southern Oscillation, the Southern Annular Mode, and the Pacific-South American oscillation modes have influenced the climate of Patagonia since the late Holocene (Compagnucci, 2011).

### 7.3. Forest occupation by native populations

Archaeological evidence from the Población Anticura site, accounts for the human presence in the Río Manso Inferior valley since the mid-Holocene (Fig. 1). Small but varied artefactual assemblages suggest short and probably seasonal staying in the search of food and raw materials for subsistence (Fernández et al., 2019). Human occupation reached its maximum after ca. 3500 cal yr BP (Bellelli et al., 2008; Podestá et al., 2008). However, archaeological studies do not present evidence of any kind of fire manipulation beyond dwelling locations (Fernández and Carballido Calatayud, 2015). Moreover, the site of Laguito del Morro does not show evidence of the presence of native populations since their first forest occupation in the valley (Giaché and Bianchi, 2018).

### 7.4. Forest decimation during the last centuries

The last centuries are characterized by human impact on ecosystems throughout southern Chile and Argentina (Markgraf, 1983; Veblen and Lorenz, 1988; Villagrán, 1988). At the end of the nineteenth century, European settlement began. The introduction of cattle triggered vegetation-fire feed-backs, producing irreversible changes in natural forests up to the present times (Kitzberger and Veblen, 1999; Speziale et al., 2010; Veblen et al., 2003).

The synergic effect of grazing and fires exerted profoundly impacted both the floristic composition and structure of a wide range of forest communities, generating optimal environmental conditions for the expansion of scrub and non-native forbs (Veblen et al., 1992). This successional process, presumed as "matorralización", implies a radical replacement of the arboreal community by scrub (also called transition forest or "matorral") (Raffaele et al., 2014).

The replacement of forest with scrub determines irreversible changes, triggering a positive feedback mechanism since scrub communities contribute to the occurrence of more frequent and more extensive fires (Kitzberger et al., 2012; Paritsis et al., 2014; Raffaele et al., 2007, 2011). Such vicious cycle can lead to a biodiversity decline at regional scales threatening ecological interactions (Fontúrbel et al., 2018). Biogeography may also be affected (Villagrán, 2018).

### 8. Conclusion

Our findings document the transformation of the rainforest-*Nothofagus dombeyi* forest boundary due to climate variability and disturbances since the Late Glacial period. Shifting Pacific Ocean winds are likely the main driver for the reconstructed changes in forest composition and fire regimes in the Río Inferior basing since the Late Glacial period.

During the Late Glacial Period *Nothofagus dombeyi,* North Patagonian Rainforest conifers and Valdivian shrubs formed a rainforest that grew around El Laguito del Morro under high-severity fires. Our findings show that similar climatic conditions prevailed at both flanks of the Andes during the Late Glacial under the strong influence of westerly winds. The rainforest conifers achieved their maximum development under colder conditions and reduced fire frequency during a cold reversal period (ca. 12,800−11,300) partially contemporary to Huelmo Mascardi and Younger Dryas periods, more extensively described west of the Andes.

During the Early Holocene the southward displacement of the westerly winds belt, weakened the supply of moist winds to the eastern Andean flank, increasing seasonality. Under reduced moisture, conifers disappeared from Laguito del Morro, and *Nothofagus dombeyi* forest replaced the rainforest. The gradual increase in temperature and volcanic activity generated optimal conditions for the development of the pure *Nothofagus dombeyi* forest during the Early and mid-Holocene. *Chusquea culeou* dominated the understory providing plenty of fuel for low-severity fires, becoming a key factor of forest dynamics. At long-term scales, the canopy structure of *Nothofagus dombeyi* forest was mainly shaped by precipitation variability and coarse-grain disturbances, e.g. large fires. At shorter time scales, the composition and structure of the understory were defined mainly by fine-grain disturbances, e.g. the opening of canopy gaps or tephra deposits.

During the Late Holocene, the increase in sub-centennial climate variability related to the establishment of ENSO and Annular modes induced the replacement of per-humid *Nothofagus dombeyi* forest by the mesic mixed *Nothofagus dombeyi − Austrocedrus chilensis* forest, and the concurrent increase in surficial fires.

During the last two centuries, increased climate variability and anthropogenic disturbances changed the structure and dynamics of forest ecosystems, inducing the occurrence of high-severity fires. According to historical documents extensive fires, logging, and change in land use since the beginning of the nineteenthth century caused major changes in vegetation cover and composition. Currently, ecological studies indicate that the replacement of different types of forest, either deciduous or evergreen, by scrub communities contributes to the occurrence of more frequent and more extensive fires. At a regional scale, this vicious circle leads to a biodiversity decline threatening ecological interactions and biogeographical connectivity.

### Authorship statement

María M. Bianchi: Conceptualization, Formal analysis, Investigation, Resources, Writing - Original Draft, Review and Editing, Project administration, and funding acquisition. Yamila Giaché: Formal analysis, Investigation, Writing - Original Draft, Reviewing and Editing. Alicia Irurzún: Formal analysis, Resources, Writing - Review and Editing. Claudia Gogorza: Formal analysis, Resources, Writing - Review and Editing. Sonia Fontana: Formal analysis, Resources. Thomas Gieseke: Formal analysis, Resources, Writing - Review & Editing.

### Declaration of competing interest

### Data availability

Data will be made available on request.

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