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The vulnerability of the *Nothofagus* forest-steppe ecotone to climate change: Palaeoecological evidence from Tierra del Fuego (~53°S)

Claudia A. Mansilla[a], Robert D. McCulloch[b,*], Flavia Morello[a]

[a] Universidad de Magallanes, Instituto de la Patagonia, Centro de Estudios del Hombre Austral, Av. Bulnes 01890, Punta Arenas, Chile
[b] Centro de Investigación en Ecosistemas de la Patagonia, Moraleda 16, Coyhaique, Chile

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ABSTRACT

A new Late glacial-Holocene palaeoenvironmental record from near Lago Lynch (53°54′S, 69°26′W), Tierra del Fuego is presented. The record was sampled from a mire located within the deciduous *Nothofagus* forest-steppe ecotone and pollen and spore analysis suggest a high degree of vulnerability of past vegetation to changes in effective moisture. AMS radiocarbon dating supplemented by the application of tephrochronology including the geochemical fingerprinting of six visible and cryptotephra layers provides robust age constraint. The Lago Lynch record commences at *c.*15.6 ka. The sequence of vegetation changes between *c.*15.6 and 14.4 ka reflect a gradual increase in temperature and humidity followed by a colder interval between *c.*14.4 and 13.3 ka, which is broadly coeval with the Antarctic Cold Reversal. After *c.*13.3 ka patches of *Nothofagus* forest appeared, suggesting more mesic-temperate conditions leading gradually to the establishment of an open-canopy *Nothofagus* forest by *c.*12.5 ka which marks the start of the Holocene. Moderate to strong effective moisture levels dominated during the early Holocene until *c.*11.0 ka, followed by a sustained period (*c.*11.0–6.5 ka) of drier climatic conditions, particularly two arid phases at *c.*10.5–10.0 ka and 8.5–6.5 ka. An eastwards expansion of the forest margin after *c.*6.5 ka at the site suggests a return to more humid conditions during the late Holocene. We argue that the periods of increased moisture and aridity inferred from Lago Lynch closely reflect the extent to which the southern westerly winds (SWWs) push eastwards to the drier regions of Fuego-Patagonia during the Holocene. The longitudinal variations in moisture are driven by the nature and timing of latitudinal shifts in the SWWs. More significantly the vulnerability of the forest-steppe ecotone to moisture changes amplifies the ecological impact of relatively small-scale shifts in the SWWs.

1. Introduction

Southern South America (SSA) plays a key role for palaeoenvironmental and climatic reconstructions at the regional, hemispheric and global scales. The presence of the Antarctic continent leads to stronger pressure gradients between the high latitudes and the subtropics of the southern hemisphere when compared to the northern hemisphere (Aceituno et al., 1993) which leads to higher wind speeds within the belt of southern westerly winds (SWWs, ~40–65°S). The southern Andes form an orographic obstacle to the SWWs leading to an abrupt change of climate across short distances that produces a dramatic west-east precipitation gradient, from > 6000 mm yr^{-1} in the west to < 300 mm yr^{-1} in the east (Schneider et al., 2003; Garreaud et al., 2013). This gradient is reflected in the vegetation patterns of the region (Pisano, 1977). The distribution of *Nothofagus* forest (southern beech) across Fuego-Patagonia (~53–55°S) is intrinsically linked to the precipitation gradient (Fig. 1). Eastward shifts of the forest-steppe ecotone are likely to indicate an increase in precipitation and correspondingly a westward shift of the forest-steppe ecotone indicates a decrease in precipitation.

In Fuego-Patagonia few continuous low elevation palynological records have described the responses of vegetation to climatic changes during the Late glacial (*c.*18,000–11,700 Cal yr BP) from mires (Heusser, 1989, 1993, 1998; Heusser et al., 2000; McCulloch and Davies, 2001; Fesq-Martin et al., 2004; Markgraf and Huber, 2010; Ponce et al., 2011; Borromei et al., 2016; Mansilla et al., 2016; Musotto et al., 2016a, 2016b) and from lakes (Fontana and Bennett, 2012). The early stages of deglaciation after *c.*17,000 Cal yr BP in the present central and south-eastern-drier sites appear to have been rapidly colonized and dominated by *Empetrum* heath-grassland with relatively colder and/or humid climatic conditions inferred (McCulloch and Davies, 2001; Mansilla et al., 2016; Musotto et al., 2016a, 2016b). In

* Corresponding author.
E-mail address: roberto.mcculloch@ciep.cl (R.D. McCulloch).

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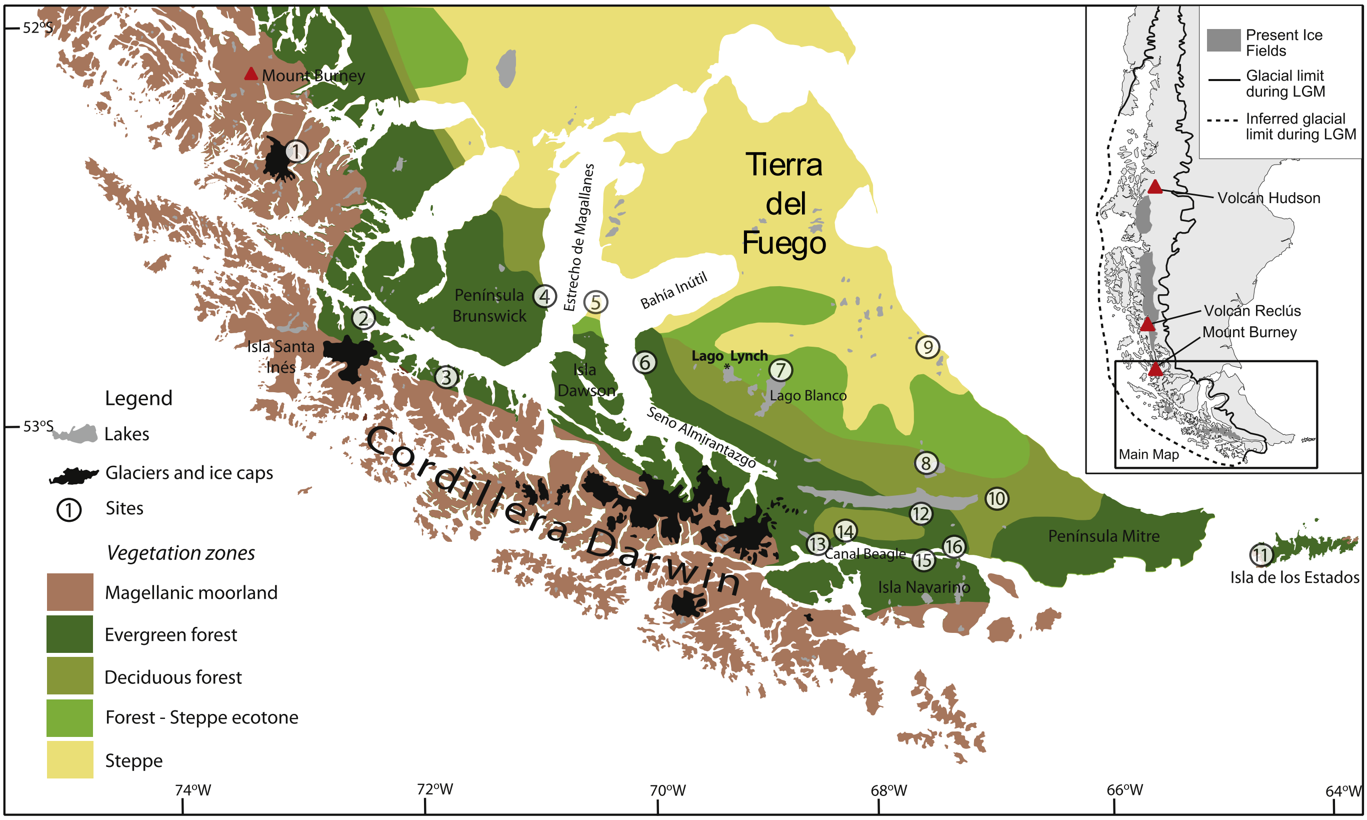

Fig. 1. Fuego-Patagonia and the principal vegetation zones (from Tuhkanen et al., 1989–1990). Sites mentioned in the text and indicated on the map are: * Lago Lynch core site; ① Gran Campo Nevado; ② Isla Santa Inés; ③ Isla Clarence; ④ Pto del Hambre; ⑤ Est. Esmeralda; ⑥ Punta Yartou; ⑦ Onamonte; ⑧ Lago Yehuin; ⑨ La Misión; ⑩ La Correntina; ⑪ Isla de los Estados; ⑫ Terra Australis; ⑬ Cañadon del Toro and Lapataia; ⑭ Valle Andorra, Ushuaia I, II and III; ⑮ Caleta Robalo and ⑯ Puerto Harberton (see Supplementary Information 1 for further details).

the western-wetter sites, the earliest vegetation was dominated by cold and more moisture-demanding taxa such as *Gunnera* and cushion bog (Magellanic moorland). Thus, the climatic conditions were likely to have been colder across the whole region and the west-east precipitation gradient already existed during the Late glacial (Fesq-Martin et al., 2004; Fontana and Bennett, 2012).

The early arrival, expansion and establishment of *Nothofagus* forest (interpreted from the proportions of *Nothofagus* pollen: ~2%, < 20% and > 20% (Total Land Pollen, TLP) respectively, Trivi de Mandri et al., 2006) varies at different latitudes/longitudes in Fuego-Patagonia. This coupled with a limited number of study sites in the region has hindered our understanding of the temporal and spatial patterns of vegetation changes during the Last glacial – interglacial transition (LGIT, *c.*16,000–8000 Cal yr BP). The extant palynological evidence from Tierra del Fuego suggests that after *c.*14,550 Cal yr BP, the early vegetation was followed by the expansion of grassland coinciding with the beginning of the Antarctic Cold Reversal (ACR, *c.*14,550–12,800 yr BP) (Lemieux-Dudon et al., 2010). By *c.*13,500 Cal yr BP, during the nadir of the ACR, the vegetation changed to a more mesic community, leading gradually to the spread of *Nothofagus* forest towards the end of the Late glacial. The early dates for the establishment of *Nothofagus* are located mainly along the Canal Beagle by *c.*13,500 Cal yr BP at Ushuaia I (54°47′S, 68°23′W) (Heusser, 1998) and by *c.*12,800 Cal yr BP at Puerto Harberton (54°53′S, 67°10′W) (Markgraf and Huber, 2010). In south-eastern Tierra del Fuego *Nothofagus* was established by *c.*13,500 Cal yr BP at Terra Australis (54°36′S, 67°46′W) (Musotto et al., 2016b), by *c.*13,000 Cal yr BP at La Correntina (54°33′S, 66°59′W) (Musotto et al., 2016a) and in the central part of Tierra del Fuego at Punta Yartou (53°51′S, 70°08′W) by *c.*12,900 Cal yr BP (Mansilla et al., 2016) (Fig. 1, Supplementary information). This pattern suggests that the climatic conditions favourable for the *first pulse* of establishment of *Nothofagus* forest occurred sometime between *c.* 13,500 and 12,800 Cal yr BP and that the forest probably expanded from refugia located in ice-free areas during the glaciation along Peninsula Mitre, in south-east Tierra del Fuego (Premoli et al., 2010; Mansilla et al., 2016) (Fig. 1). Thus, the earliest dates for the establishment of *Nothofagus* forest in Tierra del Fuego is likely to have happened during the nadir of the ACR in the present ecotone between *Nothofagus* evergreen forest and *Nothofagus* deciduous forest (Fig. 1), where the average precipitation is between ~1500 and 450 mm yr^{-1}. Pollen records along Estrecho de Magallanes such as Isla Dawson (Estancia Esmeralda II, 53°30′S, 70°35′W) and Peninsula Brunswick (Puerto del Hambre I, 53°36′S, 70°55′W) (McCulloch and Davies, 2001) and from sites located in the western-wetter area such as Gran campo Nevado (52°48′S, 72°35′W) (Fesq-Martin et al., 2004) and Isla Santa Inés (53°38′S, 72°25′W) (Fontana and Bennett, 2012) suggest no significant vegetation changes during the ACR.

During the early Holocene in Tierra del Fuego, a broadly synchronous *second pulse* of establishment of *Nothofagus* forest was recorded along Canal Beagle (~54°S) within the present *Nothofagus* evergreen and *Nothofagus* deciduous forest, by *c.*10,500–9900 Cal yr BP at Ushuaia II (54°47′S, 68°18′W) and III (54°48′S, 68°23′W) (Heusser, 1998), Cañadón del Toro (54°49′S, 68°27′W) (Borromei et al., 2016), Lapataia (54°51′S, 68°32′W) (Heusser, 1989), Puerto Harberton (Markgraf and Huber, 2010), Valle Andorra (54°45′S, 68°18′W) (Borromei, 1995) and in the far south-east at Isla de los Estados (54°50′S, 64°38′W) (Ponce et al., 2011). In north-western Fuego-Patagonia near the Gran Campo Nevado (GCN) *Nothofagus* was present continuously in high abundance under cold and relatively moist conditions during the Late glacial followed by a severe decline at *c.*11,200 Cal yr BP that was related to a re-advance of the GCN with a later expansion of *Nothofagus* forest (≤20% TLP), probably evergreen, after *c.*10,900 Cal yr BP (Fesq-Martin et al., 2004). On Isla Santa Inés cold-wet tolerant vegetation dominated until *c.*10,500 Cal yr BP after which *Nothofagus* forest became established along with the expansion of cushion plants in the area suggesting an increase in humidity (Fontana and Bennett, 2012). Finally, on Isla Clarence (54°12′S, 71°14′W) the *Nothofagus* forest was established later by *c.*9800 Cal yr BP (Markgraf, 1983) likely due to the persistence in many areas of the ice along the southern Andes. The timing and pattern of the establishment of *Nothofagus* forest during the early Holocene *c.*10,900–9800 Cal yr BP suggests a regional response to climatic amelioration within the wetter areas of Fuego-Patagonia.

There are also few palynological records from the drier central and eastern areas of Fuego-Patagonia (Markgraf, 1983; McCulloch and Davies, 2001; Heusser, 1993). The timing of the first establishment of *Nothofagus* forest was later within the areas presently dominated by *Nothofagus* evergreen forest and *Nothofagus* deciduous forest: by *c.*9500 Cal yr BP at Estancia Esmeralda II (McCulloch and Davies, 2001) and La Misión (53°30′S, 67°50′W) (Markgraf, 1983), *c.*9000 Cal yr BP at Lago Yehuin (54°20′S, 67°45′W) (Markgraf, 1983) and *c.*6000 Cal yr BP at Onamonte (53°54′S, 68°57′W) (Heusser, 1993). This pattern suggests that the favourable climatic conditions for the establishment of *Nothofagus* forest in the drier eastern areas occurred after *c.*9500 and as late as *c.*6000 Cal yr BP close to the present steppe boundary. This spread of forest more closely reflects the present longitudinal precipitation pattern, and shifts in the intensity and/or proximity of the SWWs driving from west to east, more than the initial latitudinal spread of forest during the *first pulse* of *Nothofagus* establishment at *c.*13,500–12,500 Cal yr BP. Unfortunately, most of the eastern-drier sites do not have robust dating control due to lower bio-productivity and poor preservation of organic material. This lack of dating control limits the level of detail at which we can see the vegetation responses to climate change in the drier areas of Fuego-Patagonia.

Here, we present a new continuous palynological reconstruction spanning the Late glacial to the late Holocene from near Lago Lynch (53°54′S, 69°26′W), on the margins of the *Nothofagus* deciduous forest-steppe ecotone in central Tierra del Fuego. We argue that the forest-steppe ecotone is more sensitive and so vulnerable to subtle longitudinal shifts in moisture which in turn will reflect latitudinal shifts in the SWWs, with focus on two key periods of the *Nothofagus* forest reorganisation in Tierra del Fuego: 1) the nadir of the ACR *c.*13,500–12,500 yr BP and, 2) the early Holocene (*c.*10,500–10,000 Cal yr BP). It is anticipated that this approach will advance our understanding of past forest dynamics and the nature and the timing of shifts in the SWWs and the influence of climate changes recorded in the Antarctic ice cores on the Fuego-Patagonian vegetation during the Late glacial.

2. Material and methods

2.1. Study area

The site is a mire near Lago Lynch (53°54′20″S, 69°26′19″W, altitude 165 m a.s.l.; Fig. 1). The mire is punctuated by a series of small lakes and ponds within a distinct arcuate moraine (~197 m a.s.l.). The surrounding glacial geomorphological landforms were probably formed during the Last Glacial Maximum, when the glaciers expanded from the Cordillera Darwin and flowed into the lowlands and fjords of Fuego-Patagonia, the larger marine embayment of Bahía Inútil and the Estrecho de Magallanes. Smaller glacier lobes pushed eastwards from Seno Almirantazgo and formed the ice scoured basins, including Lago Blanco and Lago Lynch. The mire site vegetation today is dominated by *Sphagnum magellanicum* and lesser proportions of *Tetroncium magellanicum* (Juncaceae). Cyperaceae, *Gaultheria antarctica* and *Empetrum rubrum* are occasionally present. The landscape around the mire is covered by primary and secondary *Nothofagus pumilio* deciduous forest. The vegetation assemblage is characteristic of a transitional forest-steppe ecotone where forest composition changes gradually from mixed evergreen-deciduous forest dominated by *Nothofagus betuloides* (western Tierra del Fuego) to the drier Fuego-Patagonia steppe (eastern Tierra del Fuego). The area has been extensively impacted by forestry enterprises for logging and extraction of wood from the 19th Century to the present. More recently beaver dam construction has increased the extent of wetlands and allowed the presence of *Drimys winteri* in areas where the canopy of *Nothofagus* forest is open. The local climate is continental with annual precipitation uniformly distributed throughout the year (~450 mm yr^{-1}). There is a relatively pronounced seasonal difference in temperature, with a mean temperature in January (austral summer) of ~9 °C and in July (austral winter) −3 °C (Tuhkanen et al., 1989–1990).

2.2. Sediment coring and laboratory methods

The mire was cored to an impenetrable base at 950 cm using a 50 cm long Russian corer with a 5.5 cm diameter (Jowsey, 1966). Unfortunately, the Russian corer was unable to securely sample very uncompact and unhumified *Sphagnum* peat between 550 cm and the surface. Each core section was stored in plastic guttering, sealed in polythene lay-flat tubing and stored at 4 °C prior to analysis. The organic matter content of the core was estimated by Loss on Ignition with samples combusted for 4 h at 550 °C (LOI_{550}).

Sub-samples of 1 cc were taken from the core at a resolution of between 8 cm and 4 cm and prepared for pollen analysis using a standard methodology (Moore et al., 1991). More mineral-rich samples were treated with Hydrofluoric acid (HF) 40%. Pollen, spores and algae were identified using an Olympus BX41 light microscope, at 400× magnification and a minimum of 300 total land pollen (TLP) were counted per sub-sample, excluding Cyperaceae, aquatics and spores. Known concentrations of *Lycopodium clavatum* spores were added to the samples to facilitate the estimation of the concentration of pollen, spores and algae (No. grains cm^{-3}) (Stockmarr, 1971). The concentration values and sediment accumulation rates (cm yr^{-1}) were used to calculate the total pollen accumulation rate (pollen influx, No. grains cm^{-2} yr^{-1}) and total charcoal accumulation rate (charcoal influx, No. particles cm^{-2} yr^{-1}). The charcoal particles were counted and measured alongside the pollen and were classified into two categories by size ≤ 100 μm (microscopic) and 100–180 μm (macroscopic) (Whitlock and Larsen, 2001).

Pollen and spores were identified with the aid of a reference collection at the University of Stirling supported by photographs of pollen and spores (Heusser, 1971; Villagrán, 1980; Wingenroth and Heusser, 1984; Moore et al., 1991). The palynological data was plotted using Tilia and Tilia-Graph software, version 2.0.41 (Grimm, 2011). Local pollen assemblage zones (LPAZs) were determined using the stratigraphically constrained incremental sum-of-squares cluster analysis (CONISS, Grimm, 1987). Further information about environmental conditions at the site was obtained through the hierarchical categorization of the state of preservation of each land pollen grain: normal, broken, crumpled, corroded and degraded (Havinga, 1964, 1984; Cushing, 1967; Tipping, 1987; McCulloch, 1994) (Fig. 2). Pollen grains are best preserved (i.e. normal) in wetter-acidic and anaerobic conditions found in peat and undisturbed lake sediments. Corroded and degraded pollen are considered to have been damaged by oxidation and the actions of bacteria and fungi (biochemical factors) operating under more aerobic conditions.

3. Results

3.1. Sediment stratigraphy

From 950 cm to 926 cm, the basal sediments consist of bluish-grey silts and clays including gravel sized clasts. Between 926 cm and 786 cm, the sediment is an organic-rich lacustrine-mud; the upper boundary at 786 cm (~80% LOI_{550}) marks the shift from lake to peat. The accumulation of peat continues to the top of the sampled core

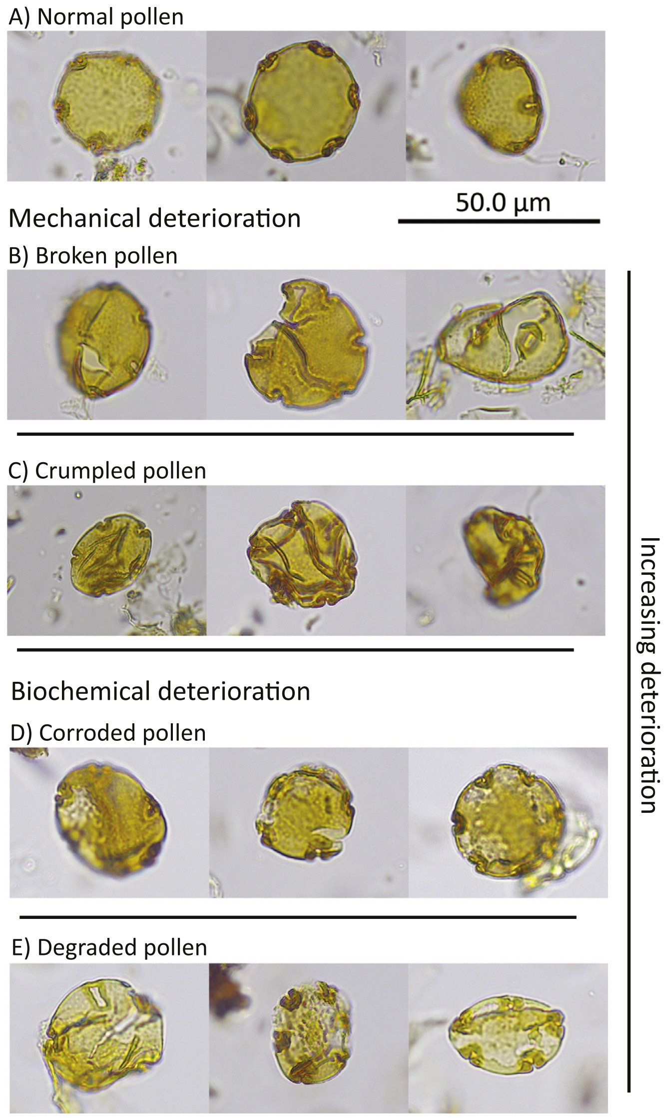

Fig. 2. Photomicrographs of *Nothofagus dombeyi* type pollen illustrating the hierarchical five categories of pollen preservation: A) normal; mechanical deterioration B) broken, C) crumpled; biochemical deterioration D) corroded and E) degraded.

(550 cm depth) characterized by medium humified mainly *Sphagnum magellanicum* peat (Fig. 3).

3.2. Tephrochronology

The sediment stratigraphy contains three visible tephra and three cryptotephra layers. The identification of the tephra layers was initially based on shard color and morphology and then confirmed using major element geochemical analysis. The tephra layers were separated from the organic matrix by acid digestion (Dugmore et al., 1992). The glass component of each tephra layer was geochemically analyzed (minimum of 10 glass shards) by the authors using the SX100 Cameca Electron Microprobe at the University of Edinburgh (Hunt and Hill, 1993; Hayward, 2011) (Fig. 4).

At 905 cm a 1 cm thick creamy-white silt sized rhyolitic tephra was geochemically linked to an eruption of Volcán Reclús (~51°S) within the Andean Austral Volcanic Zone (AVZ; ~49°–55°S) (Stern, 2008) and dated to 12,627 ± 48 ^{14}C yr BP (Sagredo et al., 2011). Tephra layers comprising greenish-brown platy glass shards of an andesitic source were identified at depths 749–750 cm (Ha cryptotephra), 669–674 cm (H1, visible 5 cm thick) and at 617–618 cm (Hb cryptotephra). All three layers have been geochemically linked to eruptions of Volcán Hudson (~46°S) within the Andean Southern Volcanic Zone (SVZ; ~33°–46°S). The Ha cryptotephra has been AMS radiocarbon dated to 9288 ± 44 ^{14}C yr BP (Mansilla et al., 2016). The H1 tephra layer has been dated to 7241 ± 23 ^{14}C yr BP (Stern et al., 2016). The age of the Hb cryptotephra layer has been estimated to *c.*6040 Cal yr BP by interpolation within the Lago Lynch age-depth model produced using the BACON program (Fig. 3). Two creamy-white highly-vesicular rhyolitic tephra layers have been identified at 742–743 cm (MB1 cryptotephra) and at 586–590 cm depth (MB2 visible 4 cm thick). These tephra layers have been geochemically linked to eruptions of Mt. Burney (~52°S) within the Andean Austral Volcanic Zone (AVZ; ~49°–55°S) (Stern, 2008). MB1 has been AMS radiocarbon dated to 8870 ± 35 ^{14}C yr BP (Mansilla et al., 2016) and MB2 has been dated to 3860 ± 50 ^{14}C yr BP (McCulloch, 1994).

3.3. Chronology

The chronology of the Lago Lynch record was constructed using five AMS ^{14}C dates from organic material and supplemented by the tephrochronology (Table 1). Bayesian age-depth modelling, using BACON 2.4 (Blaauw and Christen, 2011) and the SH13 calibration curve (Hogg et al., 2013), was used to construct an age-depth model (Fig. 3) and the weighted mean ages (WMA) were used to constrain the Cal yr BP axis for the pollen record. The resolution between pollen samples is centennial scale ≤ 150 yrs.

3.4. Pollen stratigraphy

Seven Local Pollen Assemblage Zones (LPAZs) have been defined in the Lago Lynch record (Fig. 5).

3.4.1. LPAZ LL-1 (926–905 cm, c.15,610–14,980 Cal yr BP)

The basal section is dominated by Ericaceae (~54%) and herbs such as Poaceae (~20%) and *Acaena* (~10%). Wetland-herbs, such as Ranunculaceae, *Gunnera* and *Caltha* are present at ~8%, ~2% and ~1% of TLP respectively. The aquatic *Myriophyllum* and freshwater algae *Pediastrum boryanum* are abundant at ~52% and ~58% respectively. During LPAZs LL-1, and LL-2 (*c.*15,690–12,710 Cal yr BP) the total pollen influx is moderately low, ~650 grains cm^{-2} yr^{-1}, and is principally made up of Ericaceae and the pollen is well-preserved overall (Normal ~ 62%) during this LPAZ.

3.4.2. LPAZ LL-2 (905–824 cm; c.14,980–12,760 Cal yr BP)

In sub-LPAZ LL-2a (905–884 cm; *c.*14,980–14,410 Cal yr BP) the pollen assemblage continues to be dominated by the same taxa as LPAZ LL-1. However, Ericaceae increases to ~66%, Poaceae slightly decreases to ~18% and *Acaena* also decreases to ~5%. Proportions of wetland herbs, *Ranunculaceae*, *Gunnera* and *Caltha*, decrease in this subzone to trace amounts while Apiaceae and Asteraceae (Subf. Asteroideae) both increase to ~3%. *Nothofagus dombeyi* type appears continuously in trace amounts. The aquatic taxa increase: *Myriophyllum* to ~70% and *Pediastrum* to ~67% but the proportion of normally preserved pollen decreases to ~47%.

Sub-LPAZ LL-2b (884–844 cm; *c.*14,410–13,300 Cal yr BP) is characterized by an increase in the abundance of Poaceae to ~33% and a corresponding decrease in Ericaceae to ~51%, while *Acaena,* Apiaceae and Asteraceae (Subf. Asteroideae) remain at 6%, 3% and 3% respectively. Ranunculaceae, *Gunnera* and *Caltha* increase slightly to ~2%. During this period *Nothofagus* is present continuously at ~1%. *Myriophyllum* gradually decreases from ~70% to ~15% and *Pediastrum* fluctuates widely from ~87% to ~17%. The total pollen influx decreases dramatically to ~360 grains cm^{-2} yr^{-1} and then rises to ~750 grains cm^{-2} yr^{-1}.

During sub-LPAZ LL–2c (844–824 cm; *c.*13,300–12,760 Cal yr BP)

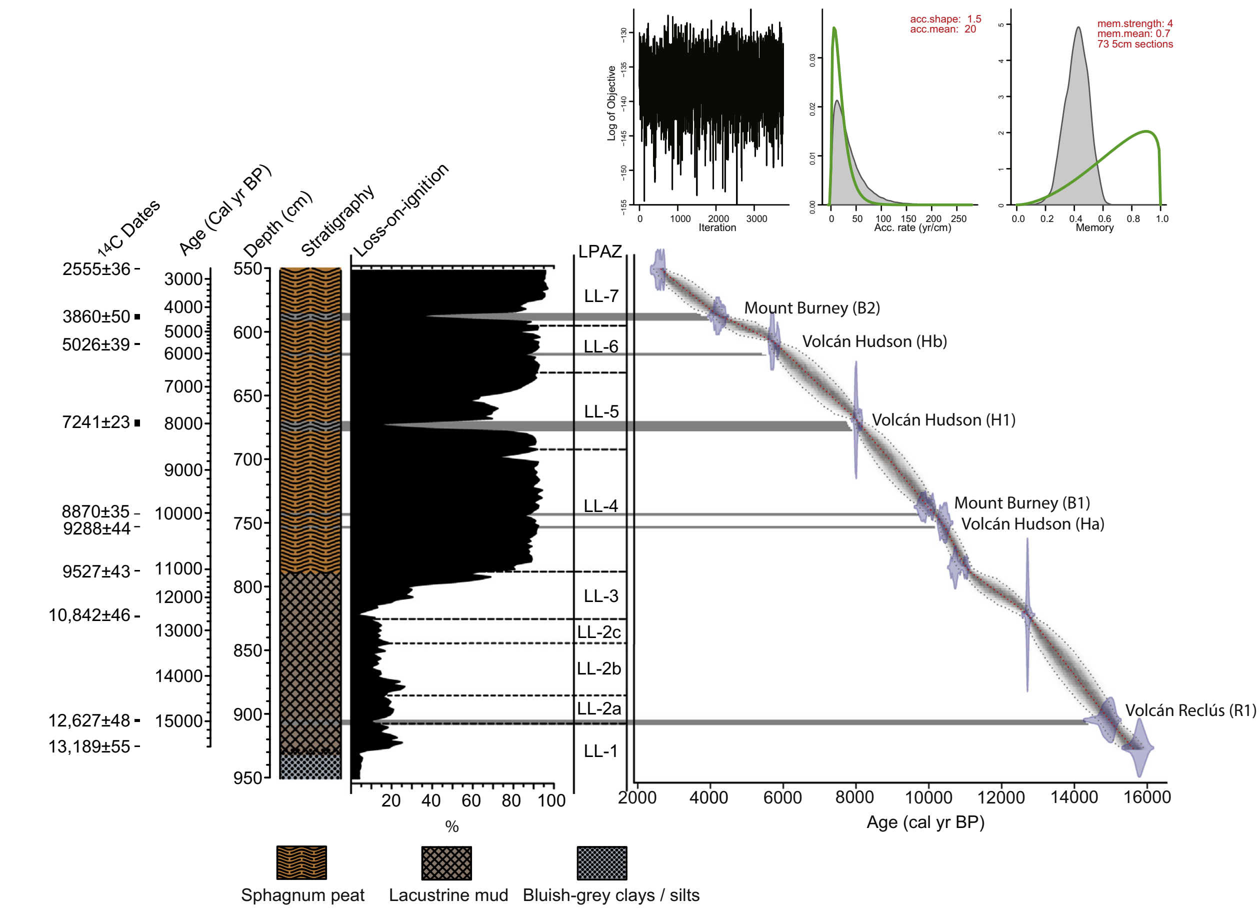

Fig. 3. The Lago Lynch record: sediment stratigraphy, organic content determined by LOI_{550}, the positions of the tephra layers are indicated across the figure and the LPAZs determined from the percentage pollen diagram (Fig. 5) by CONISS alongside the BACON age–depth model.

there is a change in dominant taxa as Poaceae increases to ~43% and Ericaceae decreases to ~35%. *Caltha* and Asteraceae (Subf. Asteroideae) also increase to ~3% and ~4%, respectively. *Myriophyllum* decreases to ~5% and, *Pediastrum* continues to fluctuate widely between ~60% and ~20%. *Nothofagus* increases to ~6% and charcoal particles appear but at low values of influx (~2 particles cm^{-2} yr^{-1}). The normal pollen preservation remains at ~53%.

3.4.3. LPAZ LL-3 (824–788 cm; c.12,760–11,050 Cal yr BP)

This LPAZ is distinctive due to the significant increase in the percentage of the herb *Galium* to ~11%, the pollen of which is not readily dispersed by wind. *Nothofagus* also increases to ~18% at 822 cm (*c.*12640 Cal yr BP) marking the establishment of *Nothofagus* forest-steppe ecotone. *Misodendrum* also appears at 818 cm (*c.*12,460 Cal yr BP) and is found continuously through this LPAZ. By 814 cm (*c.*12,270 Cal yr BP) *Nothofagus* increases to ~47% (open-canopy forest), corresponding with a decrease in dry-herbs, such as Poaceae, *Acaena* and Asteraceae (Subf. Asteroideae) to ~32%, ~3% and trace amounts respectively. *Myriophyllum* continues to be present at ~5% and *Pediastrum* fluctuates between 17% and ~62%. The total pollen influx increases dramatically to ~1350 grains cm^{-2} yr^{-1}, mainly due to increases in the contributions from *Nothofagus*, Poaceae and *Galium.* The proportions of normal pollen reach one of the highest values in the record at ~73% and the influx of charcoal continues to be low at ~9 particles cm^{-2} yr^{-1}.

3.4.4. LPAZ LL-4 (788–692 cm; c.11,050–8510 Cal yr BP)

This LPAZ is characterized by rapid and high magnitude fluctuations of Poaceae (from ~38% to ~80%) which reach the highest percentage in the record while the *Nothofagus* percentage fluctuates from ~20% to ~54%. *Misodendrum* is present in traces continuously through the LPAZ, while Asteraceae (Subf. Asteroideae) decreases to trace amounts. Cyperaceae increases in abundance to its maximum at ~17%. Also, concurrently *Lycopodium* increases to 4%. At 770 cm (*c.*10,690 Cal yr BP) and the aquatic flora finally disappear. The total pollen influx increases to ~1840 grains cm^{-2} yr^{-1} and the values remain relatively stable through the zone. The percentage of normal pollen decreases and fluctuates around ~42% and there is an increase in all of the categories of deteriorated pollen at ~35% until 595 cm (*c.*4640 Cal yr BP) and the lower boundary of LPAZ-7.

Charcoal influx also increases dramatically during LPAZ LL-4 to ~400 particles cm^{-2} yr^{-1} and remains high. Between 760 cm and 740 cm (*c.*10,500–9930 Cal yr BP), the total pollen influx decreases to ~1300 grains cm^{-2} yr^{-1}. Poaceae dominates this assemblage with the highest level in the record at ~74% while *Nothofagus* is sustained at ~22% and *Gunnera* and *Sphagnum* moss disappear during this interval. *Acaena* and Ericaceae appear at ~1% and trace amounts respectively. Asteraceae (Subf. Asteroideae) also remains in trace amounts and the degree of pollen preservation does not significantly change. Between 740 cm and 692 cm (*c.*9930–8510 Cal yr BP) Poaceae decreases to around 58% corresponding with an increase of *Nothofagus* to ~32%. Ericaceae and Asteraceae (Subf. Asteroideae) also increase in percentage to ~4% and ~2% respectively. *Sphagnum* increases dramatically and fluctuates from ~1% to ~44% corresponding with a decrease in *Lycopodium* (> 2%).

3.4.5. LPAZ LL-5 (692–632 cm; c.8510–6570 Cal yr BP)

This LPAZ is dominated by Poaceae, although the proportions of

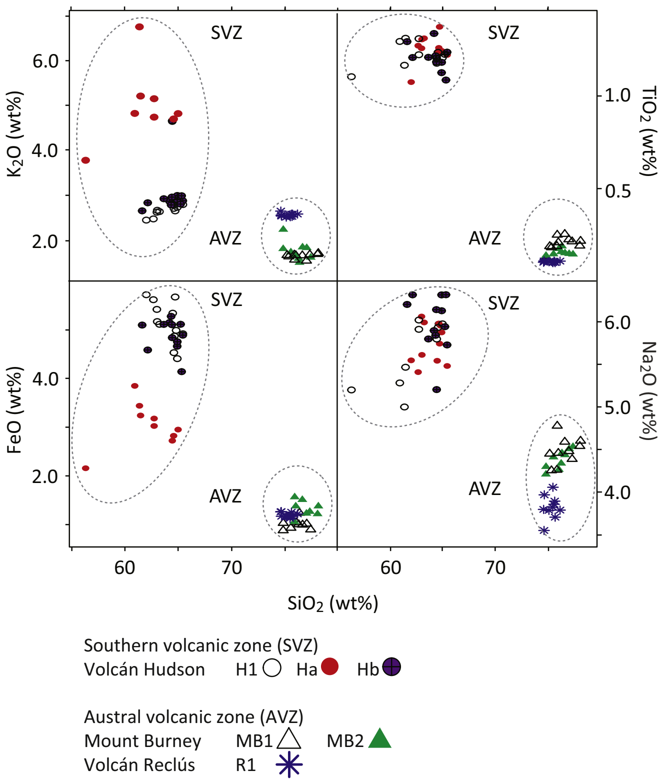

Fig. 4. Glass shards composition for selected major elements and its classification in two distinct volcanic groups, Southern Volcanic Zone andesitic and the Austral Volcanic Zone rhyolitic tephras. The data are expressed as percentage weight normalized to 100 wt%. See Supplementary information 2 for the complete data.

Poaceae decrease and fluctuate around ~40% while there is a small increase in *Nothofagus* to ~37%. *Misodendrum* is present in trace amounts continuously through the zone. In this LPAZ there is an increase in herbaceous and heath taxa such as Asteraceae (Subf. Asteroideae), Ericaceae and *Acaena* to around > 2%, ~5% and ~12%, respectively and Cyperaceae drops to ~8%. The pollen influx decreases to ~1600 grains $cm^{-2} yr^{-1}$ which is mainly contributed to by *Nothofagus*, Poaceae, Ericaceae, Asteraceae (Subf. Asteroideae) and Fabaceae. The charcoal influx also decreases dramatically and disappears from the record until it rises back at *c.*8100 Cal yr BP with ~1000 particles $cm^{-2} yr^{-1}$.

3.4.6. LPAZ LL-6 (632–595 cm; c.6570–4640 Cal yr BP)

This LPAZ is characterized by the increase and dominance of *Nothofagus* at ~58%. Herbaceous taxa, such as Poaceae and *Acaena* correspondingly decline to ~27% and ~2% respectively. Ericaceae increases to ~9% and Asteraceae (Subf. Asteroideae) remains at around ~3%. Cyperaceae and *Sphagnum* increase again to ~13% and ~42% respectively. Pollen influx decrease to ~1030 grains $cm^{-2} yr^{-1}$ and the influx of charcoal falls to ~90 particles $cm^{-2} yr^{-1}$ and continues decreasing to the top of the core.

3.4.7. LPAZ LL-7 (595–550 cm; c.4640–2640 Cal yr BP)

Nothofagus dominates the LPAZ at ~63%, the highest arboreal percentages in the record, while Ericaceae also increases to ~24%. Poaceae and Asteraceae (Subf. Asteroideae) correspondingly decline to ~7% and trace amounts. Cyperaceae and *Sphagnum* decrease dramatically to trace amount and ~5% respectively. The pollen influx increases dramatically to the highest value during the whole record (~28,000 grains $cm^{-2} yr^{-1}$) mainly contributed by Ericaceae. This LPAZ zone is also characterized by a dramatic increase in well preserved pollen to ~72% and a corresponding decrease in corroded and degraded pollen.

4. Discussion

4.1. Late glacial vegetation

The basal age taken from the contact between the organic lacustrine sediment and the underlying bluish-grey clay/silt glacial sediment from the Lago Lynch record provides a minimum age of *c.*15,610 Cal yr BP for ice retreat from the study site. However, it is likely that ice retreated from the area well before this time (Darvill et al., 2017). There is probably a substantial hiatus between deglaciation and sufficient growth, preservation and accumulation of organics to provide a measurable radiocarbon age estimate. The low pollen influx and organic

Table 1
Radiocarbon ages, calibrated age ranges and weighted mean age (WMA) from BACON Bayesian age model for the Lago Lynch record.

Laboratory code	Depth (cm)	Material	^{14}C yr (1σ)	δ^{13}C‰	Calibrated age range (95.4%) Cal. yr BP*	Calibrated age range (WMA) (95%) Cal. yr BP**
SUERC55284	551	Bulk	2555 ± 36	−26	2440–2746	2440–2790 (2640)
Tephra MB2	590	–	3860 ± 50	–	4013–4413	4070–4500 (4300)
SUERC55283	610	Bulk	5026 ± 39	−28.5	5604–5890	5580–5915 (5735)
Tephra H1	674	–	7241 ± 23	–	7949–8153	7870–8135 (7990)
Tephra MB1	743	–	8870 ± 35	–	9700–10,153	9790–10,200 (10,030)
Tephra Ha	750	–	9288 ± 44	–	10,266–10,556	10,050 - 10,430 (10,260)
SUERC55282	788	Bulk	9527 ± 43	−32.8	10,586–11,071	10,800–11,210 (11,045)
SUERC55281	824	Bulk	10,842 ± 46	−19.3	12,665–12,760	12,500–12,840 (12,720)
Tephra R1	905	–	12,627 ± 48	–	14,619–15,183	14,670–15,215 (14,980)
SUERC55280	926	Fine plant material	13,189 ± 55	−15.3	15,559–16,030	15,260–15,920 (15,610)

MB2 = Mount Burney tephra layer (McCulloch, 1994).
H1 = Volcán Hudson tephra layer (Stern et al., 2016).
MB1 = Mount Burney tephra layer (Mansilla et al., 2016).
Ha = Volcán Hudson tephra layer (Mansilla et al., 2016).
R1 = Volcán Reclús (Sagredo et al., 2011).
* Calibrated age ranges by OxCal 4.3 program (Bronk Ramsay, 2009) and SH13 curve (Hogg et al., 2013).
** Probability interval of calibrated ages and weighted mean age (WMA) from BACON (Blaauw and Christen, 2011).

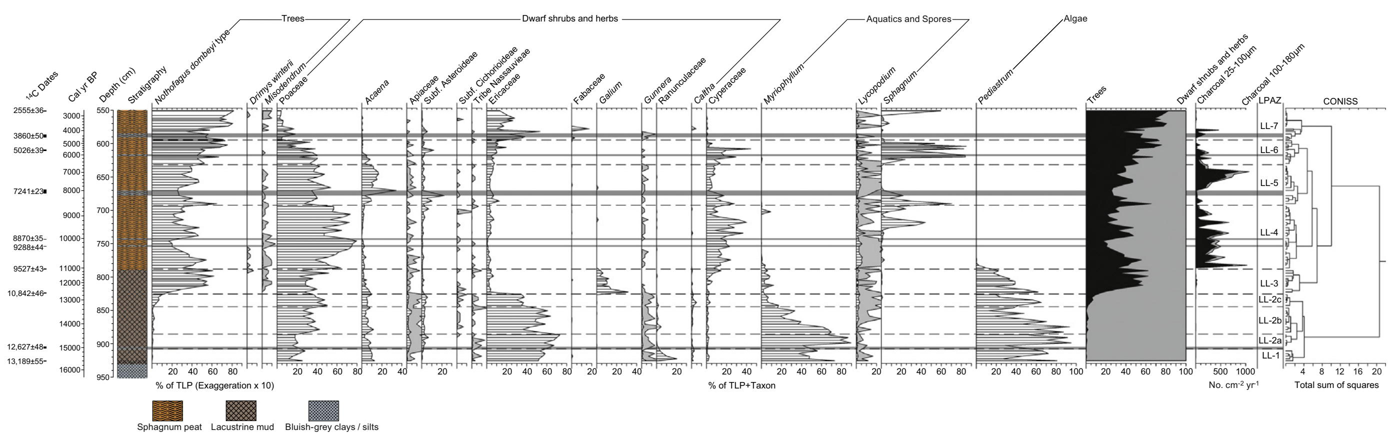

Fig. 5. Lago Lynch summary percentage pollen and spore diagram. *Misodendrum* is included in the trees group as it is a semi-parasite of *Nothofagus* trees.

content suggests limited terrestrial vegetation around the site but the water column in the basin was dominated by aquatic vegetation (*Myriophyllum*) and algae (*Pediastrum boryanum*). This suggests that the site was initially a relatively eutrophic lake with large inputs of minerogenic sediment from the surrounding recently deglaciated terrain (Komárek and Jankovská, 2001). The post-glacial landscape was characterized by a treeless Ericaceous heath-grassland, including Ranunculaceae, *Gunnera* and *Caltha* which was likely to have been marginal to the lake site. The high percentages of well-preserved pollen (~62%) also suggest that this was a period of gradual increase in effective moisture and a more favourable climate for the early development of vegetation.

Between *c.*14,980 Cal yr BP (R1 tephra layer) and *c.*14,410 Cal yr BP there was a gradual and rapid shift to drier conditions indicated by the reduction in wetland herbs and the increase in corroded and degraded pollen which suggests drier conditions on the land surfaces. These inferences are further supported by the increase in abundance of *Myriophyllum,* a shallow rooting aquatic plant, which may suggest lake level lowering and an expansion of suitable habitat. An increase in *Pediastrum* also probably suggests a shift to more eutrophic conditions.

Between *c.*14,410–13,300 Cal yr BP the Ericaceae heath was replaced by grassland vegetation (Asteraceae-Poaceae) and this was accompanied by a dramatic decrease in total pollen influx (TLP ~ 360 grains $cm^{-2}\,yr^{-1}$). The slight increase in the proportions of wetland taxa (Ranunculaceae and *Gunnera*) is probably due to the infilling of the lake and the formation of small ponds leading to the spread of the wetland taxa onto the site. During this interval *Myriophyllum* and *Pediastrum* also decreased and the organic content declined to ~10%. These changes suggest a shift to less eutrophic lake conditions and a reduction in bio-productivity probably driven by climatic cooling. This is consistent with the return of normally preserved pollen to ~60% probably due to an increase in relative humidity under cooler conditions. However, the temperature and humidity conditions continued to be below the critical limits for *Nothofagus* forest establishment. After *c.*13,300 Cal yr BP steppe vegetation persisted but with increasing patches of *Nothofagus* in the landscape from which an increase in effective moisture is inferred and a shift to more mesic-temperate conditions. Charcoal first appears in the record at *c.*12,930 Cal yr BP, which is probably related to the expansion of the forest concomitant with the ameliorating climatic conditions providing a larger amount of wood fuel (Huber et al., 2004).

4.2. Early Holocene period

From *c.*12,760 Cal yr BP to *c.*11,050 Cal yr BP *Nothofagus dombeyi* type continued to increase and reached ~18% at *c.*12,650 Cal yr BP which suggests the establishment of the *Nothofagus* forest-steppe ecotone. *Nothofagus* later reaches ~47% (by *c.*12,460 Cal yr BP) indicating the development of an open-canopy forest at Lago Lynch. *Misodendrum* also appears for the first time in the pollen record. This hemi-parasite requires *Nothofagus* as a host for germination and establishment and its pollen dispersion is closely related to the spread of its host (Tercero-Bucardo and Rovere, 2010). Therefore, *Misodendrum* is an indicator of the actual presence of *Nothofagus* at the site. The period between *c.*12,760 Cal yr BP and *c.*11,050 Cal yr BP marks the transition from the colder and fluctuating humidity of the Late glacial to the warmer and wetter climatic conditions of the early Holocene. A key component of the TLP at this time is *Galium* type*,* which would have expanded across the fen-margins of the site as the lake gradually infilled to form a mire through the process of hydroseral succession. This process of infilling and relative lake lowering may have been accelerated by the shift to warmer climate. The low proportions of *Pediastrum,* traces of *Myriophyllum* and the appearance of *Sphagnum* reflect the gradual disappearance of the lacustrine environment.

Between *c.*11,020 Cal yr BP and *c.*10,500 Cal yr BP, an increase in pollen influx (~1840 grains $cm^{-2}\,yr^{-1}$) occurs just after a transition from minerogenic-rich lacustrine sediment to organic-rich *Sphagnum* peat and so likely reflects the shift to more local pollen inputs. Contemporaneous with the transition from lake to mire was a further increase in fire activity at *c.*10,690 Cal yr BP. The proportion of normally preserved pollen decreases dramatically to ~42% suggesting the prevalence of aerobic conditions due to drying out of the mire surface. The drier climatic conditions would also have been conducive to the creation of drier fuel. Despite the apparent reduction in effective moisture, the vegetation continued to be mainly open-canopy mixed *Nothofagus* forest with scattered shrubs/trees of *Drimys* which favours small clearings in the forest.

Between *c.*10,500 Cal yr BP and *c.*9930 Cal yr BP the open-canopy mixed *Nothofagus* forest contracted dramatically accompanied by an increase in steppe vegetation dominated by Poaceae and an increase in fire activity. The combined evidence strongly suggests a significant reduction in effective moisture and a corresponding westward establishment of the forest-steppe ecotone. Between *c.*9930 and *c.*8510 Cal yr BP there were large fluctuations in the extent of the *Nothofagus* forest (~30%) and Poaceae-dominated steppe. These fluctuations probably reflect a continued interplay between periods of higher effective moisture driving eastwards and enabling forest expansion, followed by drier periods and westwards forest contraction. The large fluctuations in the proportions of Cyperaceae also highlight the extent to which the variations in effective moisture affected the mire surface wetness and fluctuating extent of shallow water levels at the site. The large amplitude of the forest-steppe changes recorded at Lago Lynch suggests the longitudinal margin of the forest is particularly vulnerable to changes in the SWWs and the east-west precipitation

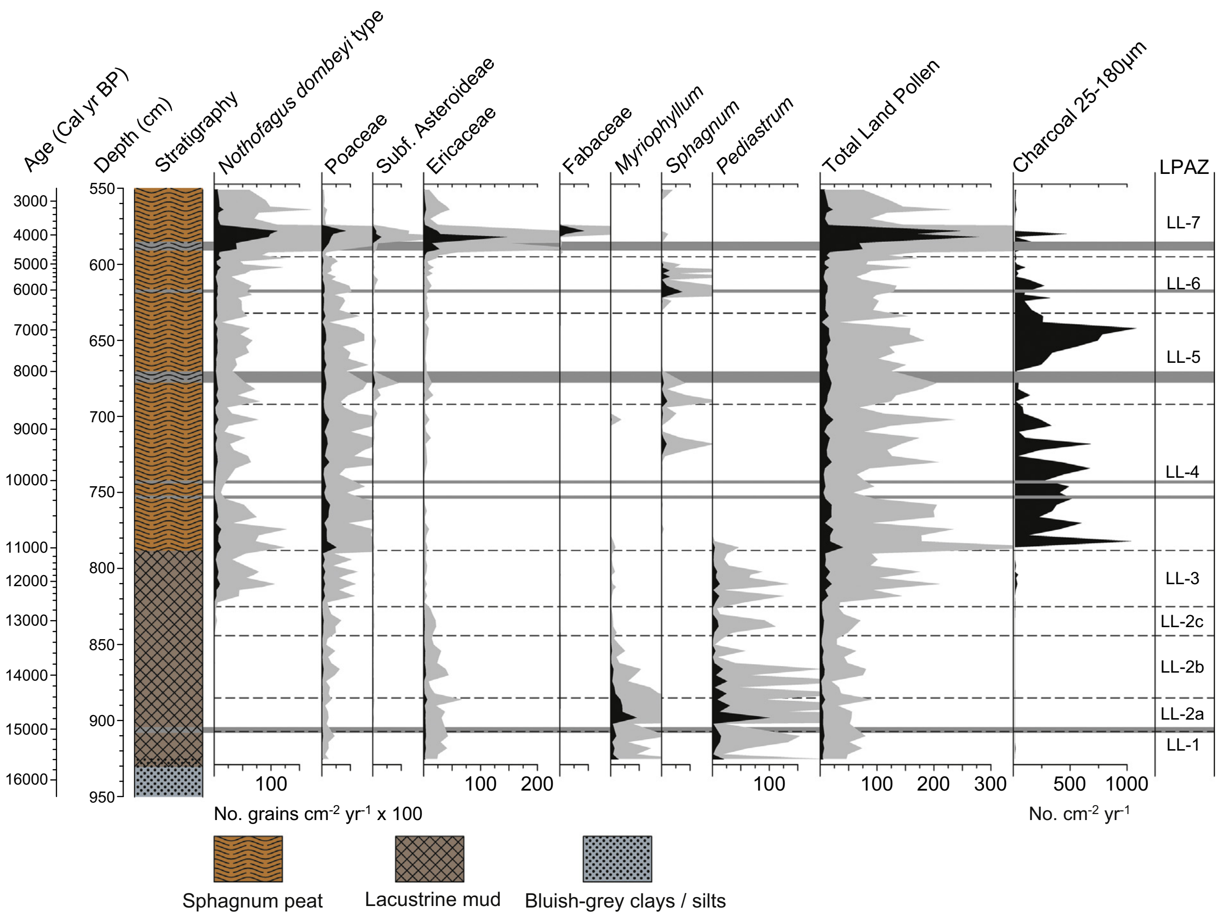

Fig. 6. Lago Lynch pollen and spore influx for selected taxa.

gradient.

4.3. Mid-Holocene period

Between *c.*8510 Cal yr BP and *c.*6570 Cal yr BP there was a sustained reduction in the extent of *Nothofagus* forest. In contrast to the previous period of lower effective moisture, the drier conditions led to an increase in dryland taxa such as Asteraceae (Subf. Asteroideae) and *Acaena*. This vegetation change indicates the expansion of grass-shrub steppe and suggests a persistent lowering of effective moisture levels. *Sphagnum* peat disappears at this time, there is a decrease in organic matter to ~70% (Fig.3) and in the pollen influx (~1600 grains cm^{-2} yr^{-1}) (Fig. 6). Together they probably reflect a drying of the mire surface and a slowing in the growth and preservation of peat (Fig. 6). This latter point is also indicated by high percentages of corroded and degraded pollen (Fig. 7) which suggest an expansion of the acrotelm and an increase in aerobic activity at the mire surface. This LPAZ is also characterized by the highest peak in fire activity (charcoal influx ~1800 particles cm^{-2} yr^{-1}) within the whole record. The drying of the mire surface and the increase in fire strongly suggests a prolonged period of intense aridity, which led to the contraction of the forest extent through both reduced moisture availability and fire. During this period, at *c.*8000 Cal yr BP, a large explosive eruption of Volcán Hudson deposited 5 cm thick tephra layer comprised of dark olive-green silt material. The CONISS cluster analysis (Fig. 5) shows a change in the vegetation assemblage before and after the tephra deposition. However, this change is not reflected in the ecological characteristics of the vegetation or the climatic inferences drawn from the period between *c.*8510 and *c.*6570 Cal yr BP.

Between *c.*6570 Cal yr BP and *c.*4640 Cal yr BP, there was an increase in *Nothofagus*, the replacement of the Ericaceae heath with Cyperaceae and *Sphagnum*, a dramatic improvement in the preservation of the pollen and a marked reduction in charcoal influx. Collectively, this evidence indicates a change to wetter climatic conditions and a concomitant sustained rise in the mire water-table. The increase in effective moisture facilitated a closed-canopy *Nothofagus* forest and the reduction in fire frequency is probably a reflection of the reduced availability of dry fuel.

4.4. Late Holocene period

The volcanic eruption of Mt. Burney (MB2 at *c.*4300 Cal yr BP) occurs at the start of the late Holocene period. Following this event, between *c.*4300 and *c.*3890 Cal yr BP there was a reduction in *Nothofagus* and a corresponding increase in Ericaceae pollen. This suggests a brief shift to drier conditions that would have allowed heath vegetation to colonize the drier areas of the mire surface and led to a contraction of the *Nothofagus* forest. It is not clear whether the MB2 volcanic eruption triggered these vegetation changes on the mire surface. However, the persistence of the heath vegetation for ~400 years suggests a climatic driver. Between *c.*3890 Cal yr BP and *c.*2640 Cal yr BP the proportions of *Nothofagus* pollen reached ~63%, and this is interpreted as the development of closed-canopy *Nothofagus* forest facilitated by higher levels of effective moisture. Also, a high level of well-preserved pollen ~72%, the maximal peak in pollen influx and low level of charcoal influx suggests that higher levels of effective moisture raised the mire water-table, permitted the maintenance of closed-canopy *Nothofagus* forest and led to the suppression of fire.

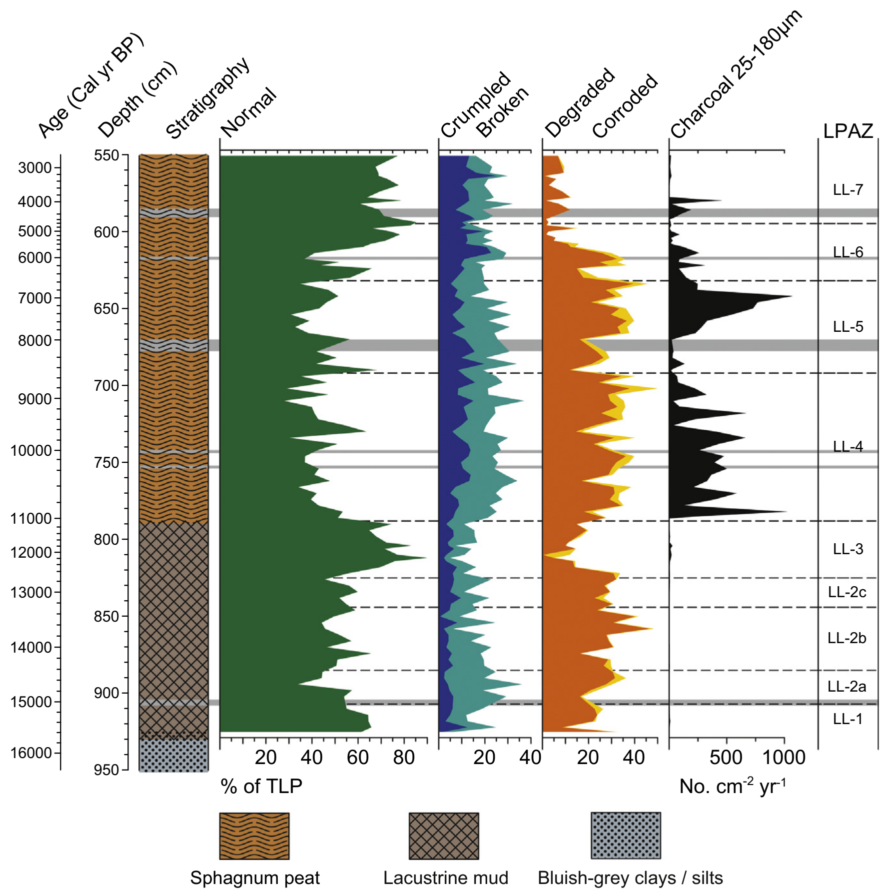

Fig. 7. Lago Lynch percentage pollen preservation diagram and charcoal influx. See Fig. 2 for examples of normal, broken, crumpled, corroded and degraded pollen.

5. Palaeoclimatic inferences for Tierra del Fuego

After *c.*18,800 Cal yr BP a strong warming of ~8 °C occurred in Fuego-Patagonia at ~53°S (Caniupán et al., 2011) which is consistent with the warming trend recorded in Antarctic ice cores (Lemieux-Dudon et al., 2010). The climatic warming led to the retreat of the Magellan glaciers after Glacial Stage D by *c.*17,700 yr BP (McCulloch et al., 2005; Kaplan et al., 2008). The initial vegetation at Lago Lynch after *c.*15,690 Cal yr BP appears to have been largely treeless and dominated by the cold resistant Ericaceae heath vegetation. This suggests the persistence of relatively cold climatic conditions across the region. However, the western-wetter sites, GCN, Isla Santa Ines and Isla Clarence (Fig. 1), were dominated by more moisture-demanding taxa, including Magellanic moorland, and indicates an already marked west-east precipitation gradient during the Late glacial.

The Lago Lynch palaeoenvironmental record indicates a significant shift to warmer interstadial conditions between *c.*14,980 Cal yr BP and *c.*14,410 Cal yr BP. This evidence is consistent with other records from along the Canal Beagle (Markgraf and Huber, 2010; Heusser, 1989) and central Fuego-Patagonia (McCulloch and Davies, 2001; Mansilla et al., 2016). This Late glacial warming trend recorded in Fuego-Patagonia has also been registered in Antarctic ice core records with the onset and end dated to *c.* 17,900 ± 300 Cal yr BP and *c.* 14,550 ± 130 Cal yr BP respectively (Lemieux-Dudon et al., 2010). The warming trend at Lago Lynch during the Late glacial was interrupted by a period of cooling indicated by the dominance of colder-drier tolerant vegetation between *c.*14,400 Cal yr BP and *c.*13,200 Cal yr BP. Similar climatic conditions have been identified from a limited number of sites in central Fuego-Patagonia (McCulloch and Davies, 2001; Mansilla et al., 2016). This period of colder and relatively humid conditions is contemporary with the beginning of the ACR (Lemieux-Dudon et al., 2010). Other pollen records located within different present ecosystems along the Canal Beagle and in western-wetter ecosystems in Fuego-Patagonia have not revealed an unambiguous cooling signal perhaps because the vegetation at these sites was more tolerant of colder-wetter climatic conditions.

After *c.*13,300 Cal yr BP, during the nadir of the ACR at Lago Lynch, the vegetation changed from the dominance of colder-drier tolerant species towards more mesic conditions leading gradually to the establishment of the forest by *c.*12,500 Cal yr BP. This increase in effective moisture levels continued during the early Holocene until before *c.*11,050 Cal yr BP. A similar pattern is seen in the palaeoenvironmental records located along Canal Beagle (Heusser, 1989, 1998; Markgraf and Huber, 2010), in south-eastern Tierra del Fuego (Musotto et al., 2016a, 2016b) and in the central part of Tierra del Fuego (Mansilla et al., 2016).

The Lago Lynch record is consistent with the idea of a *first pulse* of establishment of *Nothofagus* forest between *c.*13,500 and *c.*12,500 Cal yr BP in Tierra del Fuego, which was likely to have migrated from glacial refugia located in the south-eastern region of the Island. The spread of forest was facilitated by improving climatic conditions but limited to a longitudinal corridor along the east-west precipitation gradient and, therefore, the spread of *Nothofagus* forest was not a homogeneous event across Fuego-Patagonia.

Between *c.*11,050 Cal yr BP and *c.*6570 Cal yr BP there was a higher frequency of vegetation changes at Lago Lynch than those recorded during the Late glacial driven by trends to less effective moisture, with two arid phases: 1) early Holocene (*c.*10,500–9930 Cal yr BP) and 2) mid-Holocene (*c.*8510–6570 Cal yr BP). At the same time as the first arid phase at Lago Lynch, in the western-wetter areas of Fuego-Patagonia, such as Gran Campo Nevado (GCN) *c.*10,900 Cal yr BP, Isla Santa Inés *c.*10,500 Cal yr BP and Isla Clarence *c.*9800, cold-wet tolerant vegetation, including Magellanic moorland, was replaced by evergreen *Nothofagus* forest (Markgraf, 1983; Fesq-Martin et al., 2004; Fontana and Bennett, 2012). From these vegetation changes we infer a reduction in effective moisture due to a shift to warmer-drier climatic conditions in western Fuego-Patagonia. An arid phase coeval to this interval has previously been identified in central Fuego-Patagonia, at Puerto del Hambre I, Estancia Esmeralda II (McCulloch and Davies, 2001), Punta Yartou (Mansilla et al., 2016).

During the period between c.10,500 and 9930 Cal yr BP an expansion of *Nothofagus* forest is also recorded in sites located in south-eastern Tierra del Fuego at La Correntina (Musotto et al., 2016a, 2016b) and Isla de los Estados (Ponce et al., 2011) and along the Canal Beagle, southern Fuego-Patagonia (~54°S) (Heusser, 1989, 1998; Borromei, 1995; Markgraf and Huber, 2010; Borromei et al., 2016). The sites along the Canal Beagle also evidence an increase in fire activity at this time (Huber et al., 2004) although this may have been from the distal transport of charcoal particles from drier areas of the region. Overall, the palaeoenvironmental evidence from the Canal Beagle suggests that at *c.*10,500–10,000 Cal yr BP the humidity levels increased, probably consistent with the poleward migration of the SWWs through the Paso Drake (Bentley et al., 2009) and/or the westward penetration of moisture from south Atlantic air masses. This interplay between the south Atlantic and Pacific moisture sources has also been suggested for some parts of Central Patagonia when the SWWs had a very weak influence on the Pacific west coast (Whitlock et al., 2007).

At Lago Lynch between *c.*9930 and *c.*8510 Cal yr BP there was an increase in effective moisture coinciding with a re-expansion of the *Nothofagus* forest. A similar expansion in forest cover has also been registered at central and southern-east Tierra del Fuego *c.*9500 at Estancia Esmeralda II (McCulloch and Davies, 2001), Punta Yartou (Mansilla et al., 2016) and La Correntina (Musotto et al., 2016a, 2016b). This increase in effective moisture also coincides with the first establishment of *Nothofagus* forest in the eastern-drier areas of Fuego-Patagonia (~53°S) such as at Lago Yehuin and La Misión (Markgraf, 1983). In western-wetter areas of Fuego-Patagonia such as at Isla Santa Inés and GCN, a change from *Nothofagus* forest to wetter vegetation occurred at *c.*9000–8000 Cal yr BP and by *c.*9200 Cal yr BP respectively (Fesq-Martin et al., 2004; Fontana and Bennett, 2012). This increase in effective moisture is identified at Lago Lynch (*c.*9930–8510 Cal yr BP) but is not apparent in records from along the Canal Beagle, south of the Cordillera Darwin which suggests persistent wetter conditions. However, the fire activity decreased dramatically at these sites suggesting a reduction in the availability of drier combustible material (Huber et al., 2004). In contrast, the record from Isla de los Estados suggests warmer-drier conditions at this time (Ponce et al., 2011), which may be due to its geographical lee position in relation to the SWWs and the Patagonian landmass, and/or reduction in moisture sources from the South Atlantic.

During the second millennial intense mid-Holocene arid phase (*c.*8510–6570 Cal yr BP) at Lago Lynch, a similar drier phase is registered at central and south-eastern Fuego-Patagonia: La Correntina (*c.*8000–5000 Cal yr BP) (Musotto et al., 2016a) and Terra Australis (*c.*8500 Cal yr BP) (Musotto et al., 2016b), Punta Yartou (*c.*8080–5060 Cal yr BP) (Mansilla et al., 2016), Puerto del Hambre I and Estancia Esmeralda II (*c.*7500 Cal yr BP) (McCulloch and Davies, 2001) (south-east and central Tierra del Fuego). These sites are located within the present mixed evergreen and deciduous *Nothofagus* forest. Palaeoenvironmental records located in western-wetter areas, the more extreme eastern areas and areas next to Canal Beagle do not register such clear vegetation changes. However, all records show increased fire activity between *c.*8000 and *c.*5500 Cal yr BP. It has been suggested that the presence of higher fire activity is linked to drier summers with more fuel available during the season and the source of the charcoal particles could be either local wetland fires or adjacent vegetation without significantly affecting the characteristics of the forest cover (Huber et al., 2004). Regardless, the palaeoenvironmental evidence supports the inference of region-wide drier climatic conditions and higher fire activity during the mid-Holocene.

After *c.*6500 Cal yr BP closed-canopy forest became established and fire activity declined along the Canal Beagle and south-eastern Fuego-Patagonia due to an increase in effective moisture (Heusser, 1989, 1998; Markgraf and Huber, 2010; Borromei et al., 2016; Musotto et al., 2016a, 2016b). This period is relatively coeval with the increase of *Nothofagus* forest after *c.*6570 Cal yr BP at Lago Lynch, which gradually achieved a closed-canopy (~70%) by *c.*5400 Cal yr BP, suggesting higher levels of effective moisture. Also, by *c.*5800 Cal yr BP the forest had expanded eastwards to drier areas such as Onamonte (Heusser, 1993). The palaeoenvironmental records located at central (Estancia Esmeralda II and Punta Yartou) (McCulloch and Davies, 2001; Mansilla et al., 2016) and western-wetter areas (GCN and Isla Santa Inés) (Fesq-Martin et al., 2004; Fontana and Bennett, 2012) do not support the inference of wetter climatic conditions at this time. However, the decline in fire activity at all sites supports the idea of a gradual change to wetter climatic conditions in the region between *c.*6500 and *c.*4500 Cal yr BP.

After the volcanic eruption of Mt. Burney (MB2) at *c.*4300 Cal yr BP there was a brief period of *Nothofagus* forest contraction at Lago Lynch between *c.*4300 Cal yr BP and *c.*3890 Cal yr BP (~400 yr) probably driven by a shift to less effective moisture. There are a few studies that have mentioned the effect of volcanic eruptions on the vegetation of Fuego-Patagonia (Fesq-Martin et al., 2004; Kilian et al., 2006; Fontana and Bennett, 2012). These studies mention the potential impact on vegetation causing sustained damage to wetter ecosystems that may be sustained for up to 1400 years after a volcanic eruption. Therefore, the effects of this volcanic eruption on the vegetation cannot be excluded. However, many different strands of palaeoenvironmental evidence from Fuego-Patagonia: bulk organic geochemistry analysis from ~55°S (Moy et al., 2011), marine molluscs from ~54°S (Candel et al., 2009) and proxy-derived sea surface temperatures from ~53°S (Harada et al., 2013; Caniupán et al., 2011) all point towards a gradual decline in temperature between *c.* 4500 Cal yr BP and *c.* 3800 Cal yr BP thus it is likely that the decline in forest cover was a response to a climatic change to colder and/or drier conditions.

We argue that the periods of increased moisture and aridity inferred from Lago Lynch closely reflect the extent to which the southern westerly winds (SWWs) penetrated eastwards to the drier regions of Fuego-Patagonia during the Late glacial-Holocene. A synthesis of the palaeoecological records in the region suggests that the longitudinal variations in moisture recorded at Lago Lynch were driven by latitudinal shifts in the proximity and/or intensity of the SWWs. More significantly, the rapid and high-magnitude changes in the Lago Lynch pollen record indicates the forest-steppe ecotone is very sensitive to small-scale latitudinal shifts in the SWWs. This suggests that Nothofagus forest in the drier regions of Fuego-Patagonia may be highly vulnerable to future climate change.

6. Conclusions

The palaeoenvironmental evidence presented in this study provides a rare insight into the local site-specific environmental changes at Lago Lynch and a more regional perspective of movements in the forest-steppe ecotone driven by longitudinal shifts in the west-east precipitation gradient across Fuego-Patagonia. After deglaciation sometime before *c.*15.6 ka there was a significant shift to warmer interstadial conditions in the eastern region of Tierra del Fuego. This was followed by a significant reversal to colder conditions between *c.*14.4 and 13.3 ka coeval with the ACR. The first pulse of the establishment of *Nothofagus* forest occurred between *c.*13.5–12.8 ka, probably from refugia located in the south-eastern region of the Island. The dispersal of *Nothofagus* during the ACR suggests the spread of forest was more limited by moisture availability rather than by colder temperatures.

A shift to warmer-drier conditions leading to an arid phase is inferred from a contraction of the *Nothofagus* forest and an increase in fire activity at Lago Lynch between *c*.10.5–10.0 ka. The reduction in humidity in the east was also reflected in a shift to drier conditions in the wetter west which in contrast facilitated an expansion of *Nothofagus* forest in areas previously dominated by Magellanic moorland. These regional changes are consistent with a poleward migration of the SWWs through Paso Drake. Between *c*. 10.0 and 8.5 ka the establishment of *Nothofagus* forest in the eastern-drier areas of Fuego-Patagonia and the reversion of the western-wetter areas to Magellanic moorland suggest an increase in precipitation probably driven by a northward latitudinal shift in the SWWs. Between *c*.8.5–6.5 ka there was a second arid phase indicated by reduced *Nothofagus* forest and increased fire activity. These large amplitude changes in the extent of *Nothofagus* forest recorded at Lago Lynch suggests that even relatively small-scale changes in the east-west precipitation gradient resulted in large-scale geographical shifts in the eastern margin of the forest-steppe ecotone, which demonstrates the high vulnerability of the ecotone to shifts in the focus and intensity of the SWWs.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.07.014.

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