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Late Quaternary palaeoenvironmental reconstruction of central Tierra del Fuego (Argentina) based on pollen and fungi

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ABSTRACT

This paper presents the main palaeoenvironmental results obtained from two sites located in the eastern (La Correntina peat bog) and southern (Terra Australis peat bog) sectors of the Lake Fagnano area, situated at 54° S on the Tierra del Fuego island, at the southernmost extreme of Patagonia. Here, we provide an overview of the postglacial ecosystem and vegetation dynamics on both slopes of the Fuegian Andes by combining palynological records of pollen and fungal remains analyses, supported by radiocarbon datings and multivariate statistics. The pollen data from the two sites indicate initial shrubby and herbaceous vegetation with scattered trees, under drier and colder climate conditions than today. Expansion of *Nothofagus* forest began about 11,200 cal BP in the Terra Australis area, while an open vegetation of grasslands and shrubs developed around La Correntina site by 11,500 cal BP followed by the establishment of the forest-steppe ecotone after 9400 cal BP. These vegetation changes implied a modification of the climate toward warmer and drier climate conditions than present. At both sites, the predominance of the mycorrhizal *Glomus* was related to the presence of open ground grassland, indicating relatively dry local conditions. Closed-canopy forests dominated the landscape after 6500 cal BP at Terra Australis, and after 5000 cal BP at La Correntina, suggesting relatively cold and wet environmental conditions. However, the fungal assemblage in Terra Australis shows high abundances of epiphyllous Microthyriaceae, pointing that the *Nothofagus* trees grew closer than at La Correntina. These findings allow us to conclude that both mires have experienced dissimilar trends in the environmental evolution since Late-glacial times, probably due to their locations in two distinct flanks of the Andean range.

1. Introduction

Isla Grande de Tierra del Fuego (53–55° S; 66–74° W) is of particular interest for examining past environmental changes, since it constitutes the southernmost continental landmass in South America, offering the potential to assess the causes and effects of palaeoclimate fluctuations on terrestrial biota. It is a key region in which the Southern Westerly winds (SWW) are the main source of precipitation, and thus is ideal for reconstruction of wind variability patterns. Several palaeoenvironmental investigations have been carried out along the Beagle Channellowlands (Heusser and Rabassa, 1987; Heusser, 1989, 1995, 1998, 2003; Pendall et al., 2001; Borromei and Quattrocchio, 2008; Candel et al., 2009; Markgraf and Huber, 2010; Candel and Borromei, 2013; Borromei et al., 2014), on the inner valleys of the Fuegian Andes (Borromei, 1995; Borromei et al., 2007) and within some hanging valleys (Markgraf, 1993; Borromei et al., 2010; Markgraf and Huber, 2010). However, studies completed on northern and central areas of the archipelago are scarce (Markgraf, 1980; Heusser, 1993, 2003; Heusser and Rabassa, 1995; Burry et al., 2007; Musotto, 2013; Waldmann et al., 2014; Musotto et al., 2015, 2016). Taken together, these works show the development of an impoverished vegetation (steppe-tundra like) with scarce trees after last deglaciation, followed by *Nothofagus* woodland with high fire occurrences until about 6000 cal BP and

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closed-canopy forest since then, in response to an increase in moisture (Heusser, 2003; Markgraf and Huber, 2010; Kilian and Lamy, 2012). These past changes in vegetation have been interpreted to reflect fluctuations in temperature and precipitation regimes. These climate variations are in turn linked to shifts in the latitudinal location and/or intensity of the SWW, Antarctic sea-ice extension, position of the Antarctic Polar Front, solar irradiation, or a combination of these factors (Heusser, 2003; Markgraf and Huber, 2010; Waldmann et al., 2010).

Fungal microfossils, most often their spores and reproductive bodies, are an important part of the non-pollen information in peat deposits (van Geel and Aptroot, 2006; Cugny et al., 2010). They include types likely to represent the presence of decaying plant tissues, dung, fire or specific host plants, providing complementary information for a more accurate interpretation of depositional environments (Blackford et al., 2006). Because of the sporopollenin-like composition of their outer layer walls, fungal remains are often well preserved in fossil deposits and are not destroyed during chemical treatment of samples (Limaye et al., 2007). Despite the widespread use of fungal microfossils as a useful tool in palaeoecological reconstructions, studies on fungal remains in late Quaternary deposits of Tierra del Fuego are still scarce (Mauquoy et al., 2004; Borromei et al., 2010; Musotto, 2013; Musotto et al., 2013, 2015).

In order to gain a better understanding of the timing and structure of the vegetation and climatic changes since deglaciation in central Tierra del Fuego, two peat bog records retrieved at different locations from the Lake Fagnano area (Fig. 1) are considered. La Correntina mire is situated in the deciduous *Nothofagus* forest environment on the Atlantic side of the Fuegian Andes axis, while Terra Australis mire is located in the mixed evergreen—deciduous forest on the Pacific slope. In this paper, we use

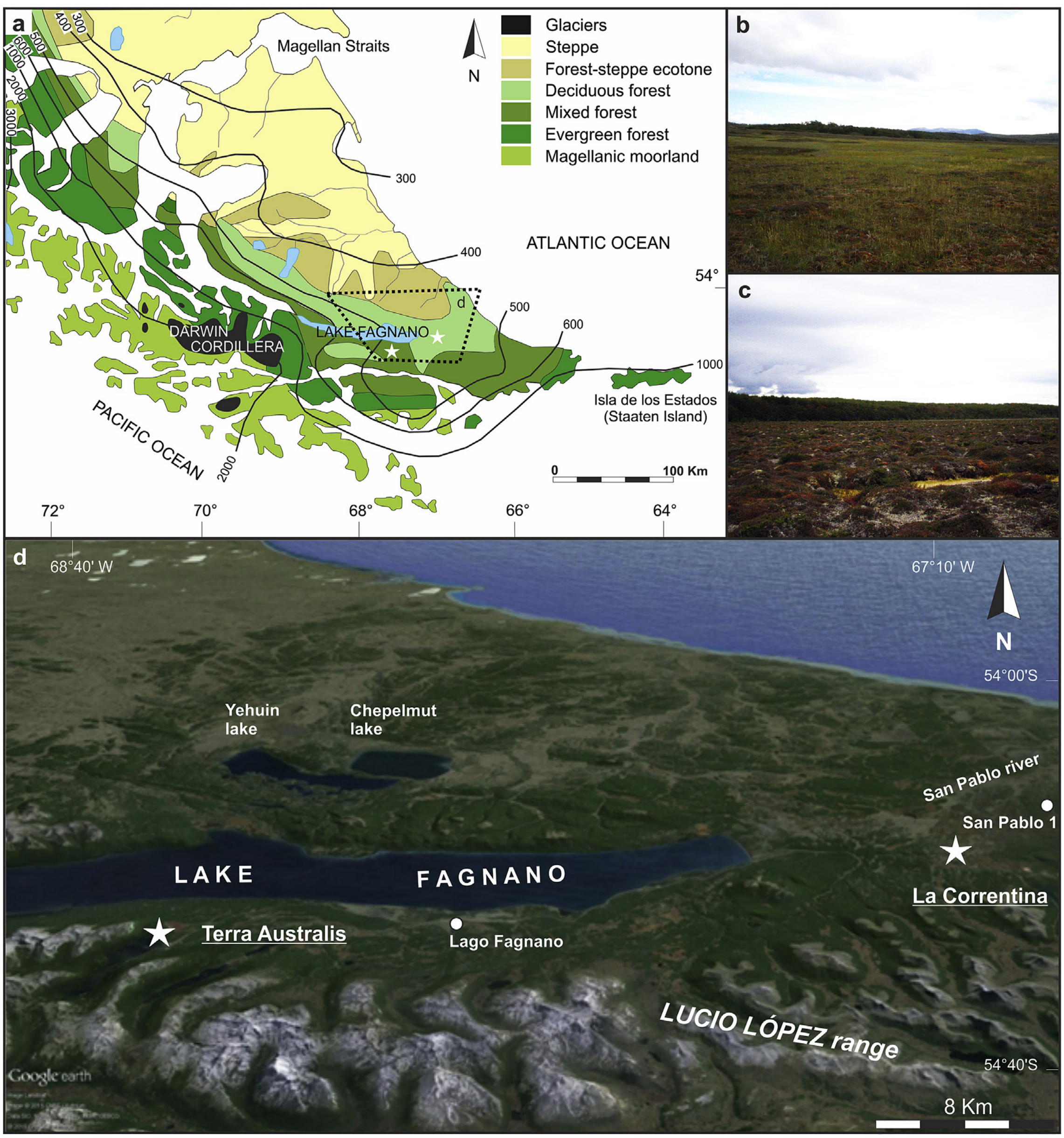

Fig. 1. (a) Modern-day vegetation map of the Isla Grande de Tierra del Fuego with the mean annual precipitation isohyets and the peat cores location (white stars). The highlighted area in the rectangle is shown enlarged in d (modified from Tuhkanen, 1992). (b) Ground photograph of La Correntina mire. (c) Ground photograph of Terra Australis mire. (d) Image showing the location of the study sites as well as of the other sites referred to in the text (taken from Google Earth Pro, free version).

particular fungal microfossils as proxies to complement the pollen/spores analysis with the aim of providing information on the past ecological conditions in the studied sites. Thus, the combined dataset allows assessment of the mechanisms controlling late Pleistocene–Holocene environmental changes on both flanks of the Fuegian cordillera.

2. Present climate and vegetation

The cold-temperate climate of Tierra del Fuego is mainly determined by Antarctic and Subantarctic air masses moving out from the Southern Pacific Anticyclone, and by the seasonal movements of the Antarctic Polar Front (Tuhkanen, 1992). The Fuegian Andes is a formidable topographic barrier to atmospheric circulation in the SWW, causing a progressive rain shadow to the north and east of the Andes. The Lake Fagnano has a semi-arid cold climate with mean annual precipitation and temperature of 550 mm and 6 °C, respectively. Lakeshore wind velocities are lowest during the winter months and highest during the summers, when the SWW belt migrates southwards. Precipitation reflects the annual cycle in wind speed, with maximum amounts registered during summer seasons (Moy et al., 2011). In winter, the climate is generally controlled by the Antarctic Oscillation (AAO), promoting drier and colder conditions (Waldmann et al., 2014).

Modern vegetation in Tierra del Fuego is characterized by the Fuegian–Patagonian steppe in the north, where mean annual precipitation is less than 400 mm, followed southward successively, by the deciduous beech forest and evergreen beech forest, which characterize areas with increased precipitation. Southern beech, *Nothofagus pumilio* and *N. antarctica*, predominates where precipitation exceeds 450 mm yr^{-1}; the former species under the most favourable conditions for growth (Pisano, 1977; Moore, 1983). Sheltered inland areas on the western and southwestern slopes of the Andes are mainly covered by enclaves of evergreen forest dominated by *N. betuloides* where the annual precipitation is >700 mm (Moore, 1983). Magellanic moorland occurs beyond the forest boundaries along the exposed outermost coast under conditions of increased precipitation of >1500 mm yr^{-1}, high winds and poor drainage. It consists of a mosaic of barren rock, marginal grassland, cushion bogs, scrub, and fragments of evergreen forest (Moore, 1983). Above the treeline in the Fuegian cordillera, Andean tundra is characterized by cushion plants, dwarf shrub heaths, and meadow communities (Pisano, 1977; Heusser, 2003).

3. Studied sites

In this paper, we compare two peat sequences from La Correntina and Terra Australis mires (Tierra del Fuego, Argentina) (Fig. 1). The reader is referred to some previously published reports (Musotto, 2013; Musotto et al., 2015, 2016) for details on the sites and peat cores descriptions and the methodology employed. Here, we just present a short description of the two core sites.

3.1. La Correntina site

La Correntina mire (54°33′ S, 66°59′ W; 206 m a.s.l.) is situated 14 km east of the southeastern tip of Lake Fagnano, at the bottom of a tributary valley of the Río San Pablo, on the northern slope of the Sierra Lucio López eastern Fuegian Andes. The local vegetation cover is mainly composed of hummocks of *Sphagnum magellanicum*, much overgrown by *Empetrum rubrum*, peaty grassland and scattered *Nothofagus antarctica* thickets. Deciduous forest communities surround the bog in the hills. The mire was formed at the bottom of the valley which follows the fault trace of continental boundary plates.

3.2. Terra Australis site

Terra Australis mire (54°36′ S; 67°46′ W; 120 m a.s.l.) lies 50 km west of La Correntina site and 3 km to the south of Lake Fagnano coast. The ombrogenous bog surface is formed primarily by hummocks of *Sphagnum magellanicum* accompanied by *S. fimbriatum*, Cyperaceae, Juncaginaceae, Juncaceae, and lichens, and covered by *Empetrum rubrum* and *Nothofagus antarctica*. Surrounding the bog is a mixed evergreen-deciduous *Nothofagus* forest. This mire has formed over late Quaternary drift composed of till, glaciolacustrine and glaciofluvial sediments emplaced during deglaciation.

4. Methods

4.1. Chronologies

Sediment cores were recovered from each site using a Russian corer with a chamber length 0.5 m and 5 cm diameter. Identification and correlation of tephras with known eruptions from specific source volcanoes (Stern, 2008) were based on geochemical and petrologic analyses carried out at the University of Calgary Laboratory for Electron Microbeam Analysis (UCLEMA), Canada. The chronology of the cores was constrained by AMS radiocarbon dates on bulk organic matter, obtained at the AMS Facility of the University of Arizona, U.S.A. (Table 1). The radiocarbon ages were converted to calendar years before present (cal BP) using the online version of the CALIB 7.1 program (Stuiver et al., 2015) and the Southern Hemisphere curve SHCal13 (Hogg et al., 2013). Based on these data, age–depth models were generated using Bacon (Blaauw and Christen, 2011).

Table 1
Radiocarbon and calibrated ages from the La Correntina and Terra Australis sites (data from Musotto et al., 2015, 2016).

Laboratory code	Depth (cm)	^{14}C yr BP	$\delta^{13}C$ (‰)	Median probability (cal BP)	1σ range	2σ range
La Correntina						
AA83315	29–30	217 ± 33	−25.8	193	148–220	138–231
AA86257	98–99	2241 ± 37	−25.4	2226	2154–2207	2145–2330
AA83316	159–160	4030 ± 37	−26.5	4469	4464–4518	4379–4570
AA83318	247–248	6410 ± 210	−27.2	7251	7145–7471	6775–7623
AA86263	255–256	7218 ± 48	−27.3	7992	7945–8025	7928–8069
AA83319	300–301	7686 ± 51	−25.7	8443	8388–8462	8365–8548
AA83317	465–466	12,775 ± 64	−29.7	15,168	15,076–15,277	14,872–15,400
Terra Australis						
AA86262	29–30	602 ± 35	−24.3	555	532–560	514–569
AA86256	90–91	1154 ± 36	−24.3	1012	1014–1056	934–1068
AA86261	501–502	5362 ± 43	−26.5	6099	6007–6083	5988–6214
AA86260	553–554	6881 ± 48	−26.5	7671	7612–7710	7586–7786
AA86259	558–559	7018 ± 46	−26.9	7808	7740–7858	7691–7879
AA83314	735–737	12,397 ± 62	−26.1	14,387	14,163–14,541	14,092–14,771

4.2. Palynological analysis

Samples were prepared according to standard Faegri and Iversen (1989) techniques. The material was systematically examined at 400× to 1000× magnification and the pollen sum was mostly ≥300 terrestrial pollen grains. The frequencies of terrestrial plant taxa were based on a total sum of pollen from trees, shrubs and herbs. Wetland herbs, aquatics and cryptogams were calculated as percentages of the total sum of pollen and spores. Fungal microfossils were calculated as the percentage of the total pollen/spores sum plus fungal remains sum. In this study only the curves of the main pollen and fungal taxa are presented. For the La Correntina record, other shrubs and herbs included Asteraceae (subfs. Mutisieae and Cichorioideae), *Berberis*, Brassicaceae, Chenopodiaceae, *Drapetes muscosus*, *Ephedra*, *Gentiana*, *Gunnera*, Plantaginaceae, Plumbaginaceae, Primulaceae, Rubiaceae, *Rumex acetosella*, Solanaceae and Urticaceae. Other aquatics and cryptogams included Iridaceae, Juncaceae, Juncaginaceae, *Lycopodium magellanicum*, *Myriophyllum*, Polypodiaceae, *Sphagnum*, and *Tetroncium*. For the Terra Australis record, other shrubs and herbs included *Astelia pumila*, Asteraceae (subfs. Mutisieae and Cichorioideae), Brassicaceae, Chenopodiaceae, *Ephedra*, Fabaceae, *Gentiana*, Plantaginaceae, Rubiaceae, Santalaceae, *Valeriana* and Verbenaceae. Also, *Caltha*, Iridaceae, Juncaceae, Liliaceae, *Lycopodium magellanicum*, *Myriophyllum*, Polypodiaceae, *Sphagnum*, *Tetroncium* and *Triglochin* were grouped and named as other aquatics and cryptogams. The diagrams were constructed using the TILIA and TGView 2.0.2 software package (Grimm, 2004) and zoned, using a stratigraphically constrained cluster analysis (CONISS; Grimm, 1987) and visual inspection. Reconstruction of the postglacial vegetation history was based on comparison of fossil pollen records with modern pollen assemblages (Heusser, 1989; Trivi de Mandri et al., 2006; Musotto et al., 2012) and present-day plant formations (Pisano, 1977; Moore, 1983).

Palynological richness, as determined by rarefaction analysis, has been interpreted to reflect primarily changes in plant biodiversity through time (Birks and Line, 1992). It provides the estimated number of pollen types that would be expected if all pollen counts had been of the same size. The analysis was performed using Psimpoll 4.27 software (Bennett, 2009).

In addition to pollen analysis, fossil fungal remains were assigned to modern taxa based on information provided in the specialised bibliography. For the Terra Australis record, Microthyriaceae included all the ascomata identified (mainly cf. *Microthyrium fagi*), as well as those fragments that could not be assigned to any genus. In the La Correntina sequence, Microthyriaceae included the ascoma indet. 2 and other unidentified reproductive bodies. The reader is referred to earlier reports (Musotto et al., 2012, 2013) for descriptions and illustrations of the fungal spores and ascomata. In this study, we used the surface fungi datasets for analysing the ecological requirements of living organisms, and for inferring environmental conditions in the studied area (Musotto et al., 2012).

4.3. Statistical analysis

Principal Component Analysis (PCA) was applied to explore the relationships between variables, describe the changes with depth/time, and relate them to the vegetation development in the Lake Fagnano area. The analysis was carried out on the covariance matrix of the percentage data of the major pollen and fungal taxa. Other steppe taxa plotted were *Acaena*, Apiaceae, Asteraceae subf. Asteroideae, *Azorella*, and Caryophyllaceae. Dryland/fire fungi indicators included *Gelasinospora* (HdV-1) and *Glomus* (HdV-1103). For the La Correntina record, wetland fungi indicators included *Anthostomella* cf. *fuegiana* (HdV-4) and Microthyriaceae s.l., while in Terra Australis they comprised *Byssothecium circinans* (HdV-16) and Microthyriaceae s.l. Prior to method application, all abundance data were square root transformed in order to stabilize their variances. The sample scores of the first two PCA-axes of the scatter plot allow the estimation of the rate of change within the palynological dataset. These scores were plotted for both sequences against a time scale expressed in calibrated years BP. PCA analysis was done using the free-access PAST 3.07 program (Hammer et al., 2001).

5. Results

5.1. Palynological data of the La Correntina and Terra Australis sequences

The palynological diagrams (Figs. 2 and 3) show selected taxa reflecting the vegetation, the landscape and environment dynamics in both La Correntina and Terra Australis records from the Lake Fagnano area. Main results of pollen and fungal remains are presented in Tables 2 and 3, respectively. The main fungal microfossils are shown in Fig. 4.

Table 2
Pollen/fungal assemblage zones and palaeoenvironmental interpretation from La Correntina mire (modified from Musotto et al., 2016).

Zones	Age (cal BP)	Pollen and fungal zone characteristics	Palaeoenvironmental interpretation
LC 3	Present–5000	Dominance of *Nothofagus* pollen (32–91%), with maximum abundance between 5000 and 3000 cal BP. Start of the continuous curve of *Misodendrum*. Decline of Poaceae (<32%). Increase of *Empetrum rubrum* and *Azorella* at around 400 cal BP. Cyperaceae decreases notably (<4%) and *Caltha* (<43%) occurs with fluctuating values. Microthyriaceae increases (<1%). *Anthostomella* cf. *fuegiana* (HdV-4) (<7) and *Glomus* (HdV-1103) (up to 18%) are also present.	Establishment of a closed-canopy *Nothofagus* forest; increase humidity and development of *Sphagnum* bog. Frequent occurrence of Microthyriaceae fungal remains. After 3000 cal BP, retraction of *Nothofagus* forest, expansion of mesic grasslands together with increase in mycorrhizal *Glomus*.
LC 2b	5000–8600	Dominance of Poaceae (that decline toward the top of the zone, ~40%). *Nothofagus* fluctuates between 10 and 63%. *Acaena* and *E. rubrum* are present. Rise of Cyperaceae (~64%) at around 7100 cal BP. Frequent occurrence of *Glomus* (<13%). Microthyriaceae (<0.5%) also occurs.	*Nothofagus* forest retraction; expansion of herb-like grasslands and cushion heaths interspersed with shrubs accompanied by spores of *Glomus*; abrupt shift in bog communities with increase of sedges.
LC 2a	8600–10,600	Dominance of Poaceae (28–79%), accompanied by Asteraceae subf. Asteroideae (up to 57%) and *Acaena* (<8%). Abrupt decline of *E. rubrum* (<12%). *Nothofagus* shows an increasing trend (up to 40%). Cyperaceae decreases (<45%). *Gelasinospora* (HdV-1) (<7%) and *Glomus* (<1.5%) spores are registered. Microthyriaceae (<0.5%) is present in some samples.	Development of grassland communities; decline of *E. rubrum* heaths; expansion of *Nothofagus* forest and establishment of forest-steppe ecotone; maximum prevalence of the carbonicolous fungus *Gelasinospora*; presence of Microthyriaceae remains; ombrogenous mire.

Table 2 (*continued*)

Zones	Age (cal BP)	Pollen and fungal zone characteristics	Palaeoenvironmental interpretation
LC 1b	10,600–14,400	Dominance of *E. rubrum* (21–70%) and Poaceae (13–48%), accompanied by *Acaena* (<31%) and Apiaceae (<8%). Caryophyllaceae and Asteraceae subf. Asteroideae are present. *Nothofagus* increases (<32%) and then declines (~5%) towards the end of the subzone. Cyperaceae increases notably (~85%). Onset of the mycorrhizal *Glomus* record at 12,900 cal BP. Microthyriaceae (<1%) also occurs.	Predominance of *E. rubrum* heath, grassland, and sedge plant communities accompanied by the occurrence of spores of *Glomus*; expansion and retraction of small populations of *Nothofagus* trees.
LC 1a	14,400–15,400	Dominance of *E. rubrum* (26–60%), accompanied by *Acaena* (12–44%) and Poaceae (<25%). *Nothofagus* pollen show low values (<12%). Among the aquatic taxa, Cyperaceae (14–42%) dominates. Microthyriaceous reproductive bodies (<1%) also occur.	Development of *E. rubrum* heaths accompanied by grasses and herbs growing on the deglaciated terrain; *Nothofagus* trees sparsely distributed; expansion of sedges under minerotrophic conditions.

Table 3
Pollen/fungal assemblage zones and palaeoenvironmental interpretation from Terra Australis mire.

Zones	Age (cal BP)	Pollen and fungal zone characteristics	Palaeoenvironmental interpretation
TA 3	Present–6600	Dominance of *Nothofagus* pollen (53–99%). *Misodendrum* (<5%) persists in low abundances. Sharp decline of Poaceae (<7%). *Empetrum rubrum* is variable, reaching frequencies up to 46%. Cyperaceae decreases notably (<9%). Microthyriaceae reproductive bodies increase (up to 17%). *Byssothecium circinans* (HdV-16) (<1%) and *Gaeumannomyces* (HdV-126) (<1%) also occur.	Establishment of a closed-canopy *Nothofagus* forest; increase humidity and development of *Sphagnum* ombrogenous bog; microthyriaceous remains associated to the expansion of woody elements.
TA 2	6600–11,300	Abrupt increase in *Nothofagus* pollen from 45 to 78%. Onset of the continuous and high frequencies of *Misodendrum*. Poaceae declines and fluctuates between 9 and 44%. *E. rubrum* (<24%), Asteraceae subf. Asteroideae (<11%) and *Acaena* (<5%) are also present. Frequent occurrence of *Arthrinium puccinioides* (<32%) and *Gaeumannomyces* (<20%). Mycorrhizal *Glomus* (HdV-1103) increases (<3%). *Gelasinospora* (HdV-1) decreases (<0.5%). Microthyriaceae (<1.5%) is recorded in some samples.	Expansion of *Nothofagus* forest and development of forest-steppe ecotone together with open ground vegetation of grasses, herbs, dwarf shrub heaths, scrubs, and ferns; the presence of *A. puccinioides*, *Gaeumannomyces*, *Glomus* and Microthyriaceae microfungi are related to the forest-steppe ecotone communities.
TA 1b	11,300–12,400	Dominance of Poaceae (88%) and *E. rubrum* (35%), accompanied by Asteraceae subf. Asteroideae (up to 45%). *Nothofagus* decreases (<22%). Cyperaceae diminishes (<37%). *Gelasinospora* (<1%) and *Glomus* (<1%) fungal spores are present.	Expansion of grasses, shrubs, cushion plants, and herbs accompanied by the record of spores of *Gelasinospora* and *Glomus*; retraction of small populations of *Nothofagus* trees; decline of sedges; low-humidity environments.
TA 1a	12,400–14,300	Dominance of Asteraceae subf. Asteroideae (up to 48%), *E. rubrum* (<27%) and Poaceae (16–25%). *Acaena* (19%), Caryophyllaceae (10%), and Apiaceae (7%) are also present. *Nothofagus* reaches 54% at the beginning of the subzone, declines and then increases to 60%. Cyperaceae values fluctuates between 12 and 74%. *Glomus* (<0.5%) and Microthyriaceae (<1.5%) are registered.	Pioneer vegetation composed by shrubs, grasses, herbs, and cushion plants; fungal remains of cf. *Microthyrium fagi* point to the local presence of small groups (low concentration values) of *Nothofagus* trees in the vicinity of the peat bog; expansion of sedges under minerotrophic conditions.

The La Correntina peat core contains two tephra layers derived from Volcán Hudson: the deeper has an interpolated age of 12,845 cal BP according to the age–depth model for the core, the upper corresponds to the mid Holocene tephra (H_1). Also, in the peat core of Terra Australis a tephra layer was recognized and attributed to the H_1 tephra erupted from Volcán Hudson. For a more detailed description on the tephra analyses and defined pollen and fungal assemblages, the reader is again referred to Musotto (2013) and Musotto et al. (2015, 2016).

5.2. Statistical analyses

The PCA scatter plots are shown in Fig. 5a and b. The analyses split the samples into clusters that are well in agreement with the zonation of the fossil pollen data.

In the La Correntina sequence, the Axis 1 (61.3%) contrasts Cyperaceae, *Empetrum rubrum*, Poaceae and other steppe taxa with *Nothofagus dombeyi*-type, *Misodendrum* and wetland fungi indicators. Axis 2 (16.8%) contrasts *N. dombeyi*-type, Cyperaceae and *Misodendrum* with *E. rubrum* and other steppe taxa. The record starts with samples dominated by *E. rubrum* (subzone LC-1a) and continues with samples containing higher abundances of Cyperaceae (subzone LC-1b). Samples from subzones LC-2a and LC-2b form a distinct group which corresponds to the decline of Cyperaceae and an increase in Poaceae. Samples from zone LC-3 are at the negative side of the axis 1 and are characterized by high proportions of *N. dombeyi*-type.

In the Terra Australis sequence, the Axis 1 (64.6%) contrasts Cyperaceae, Poaceae, other steppe taxa and *Arthrinium puccinioides* with *N. dombeyi*-type and wetland fungi indicators. Axis 2 (15.9%) contrasts *N. dombeyi*-type, Cyperaceae, *Misodendrum* and *A. puccinioides* with other steppe taxa, *E. rubrum* and Poaceae. The record starts with samples composed by Cyperaceae, Poaceae, other steppe taxa and *E. rubrum* (subzones TA-1a, TA-1b). Samples from zone TA-2 contain higher frequencies of Cyperaceae and *N. dombeyi*-type. Samples including mainly *Nothofagus* pollen (zone TA-3) are arranged in a tight circle at the negative side of the axis 1.

The Axis 1 and 2 scores for the La Correntina and Terra Australis records are represented in Fig. 6. The first principal component in both sequences, explaining most of the variance of the palynological composition of samples, seems to be related to forest cover: closed-canopy forest with negative values versus open grown vegetation with positive values. Thus, the axis 1 can be regarded as indicative of the moisture availability. At Terra Australis, the second principal component also appears to be associated with humidity level: *Nothofagus* woodland-more humid with positive values versus Fuegian steppe-less humid with negative values. In the case of the La Correntina record, the second component seems to reflect the closed-canopy forest and sedges with positive values versus heath, scrub and herb communities with negative values. Although these scores vary considerably throughout the sequence, some of the changes in the vegetation composition at local scale are most likely related to hydrological conditions within the bog. *Empetrum rubrum* is a dwarf shrub that generally grows on dry hummocks, while sedges grow in those wet areas of *Sphagnum* bogs (Moore, 1983).

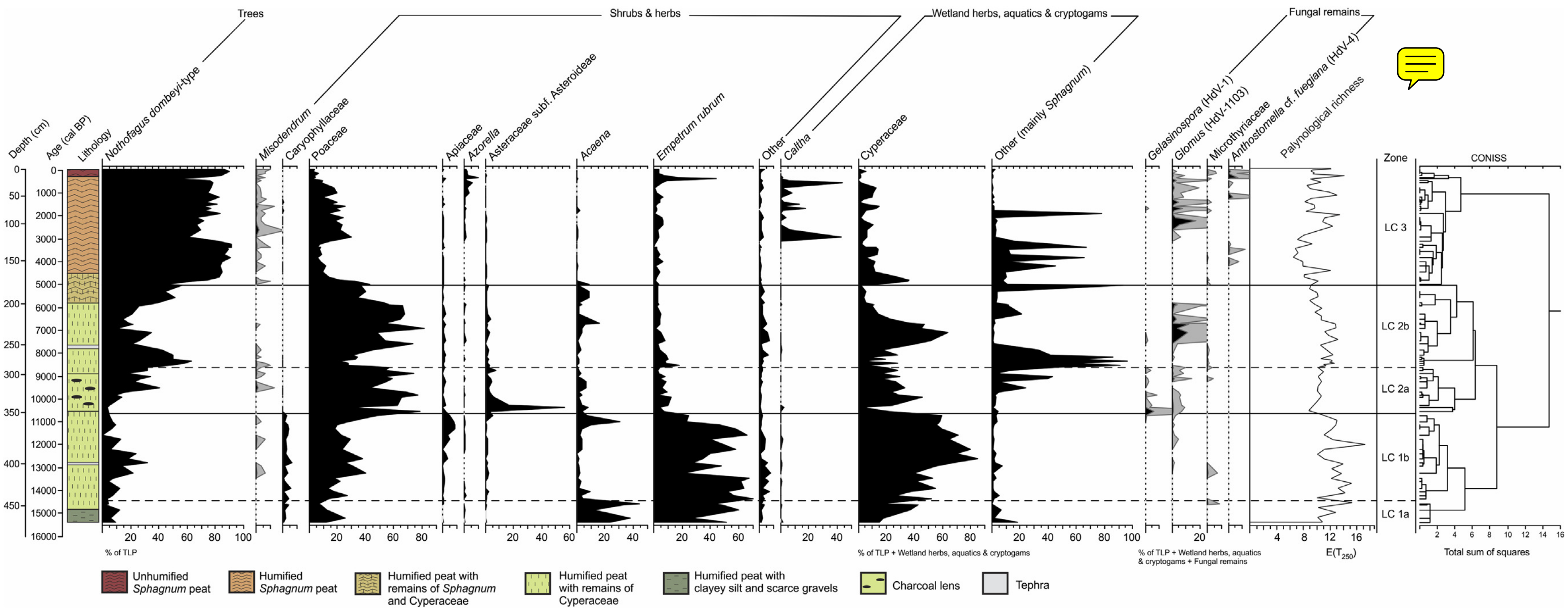

Fig. 2. Fossil pollen/spore frequency diagram (%) from La Correntina, including stratigraphy and palynological richness (base sum of 250). Exaggeration percentage curves (10×) are shown in grey for *Misodendrum* pollen and fungal microfossils. TLP: total land pollen. HdV: Hugo de Vries Laboratory.

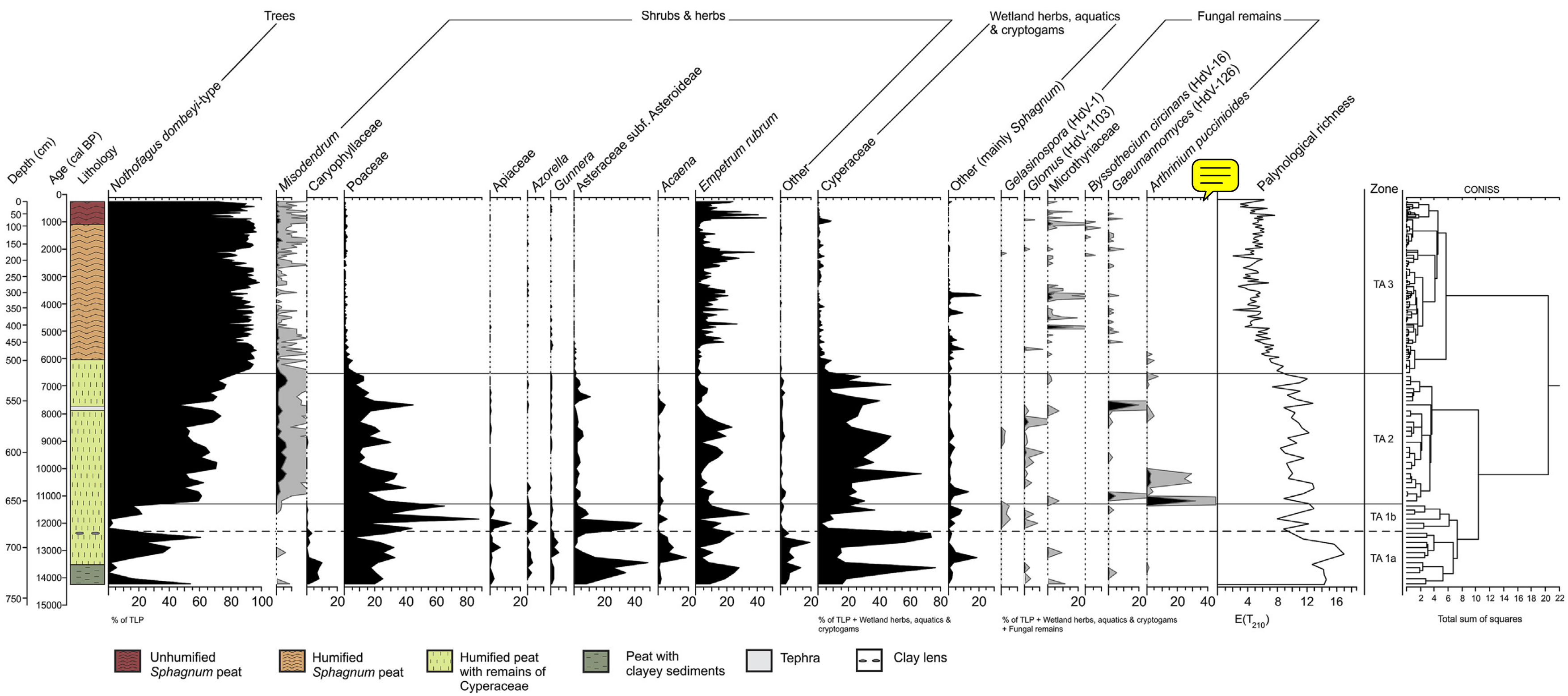

Fig. 3. Fossil pollen/spore frequency diagram (%) from Terra Australis, including stratigraphy and palynological richness (base sum of 210). Exaggeration percentage curves (10×) are shown in grey for *Misodendrum* pollen and fungal microfossils. TLP: total land pollen. HdV: Hugo de Vries Laboratory.

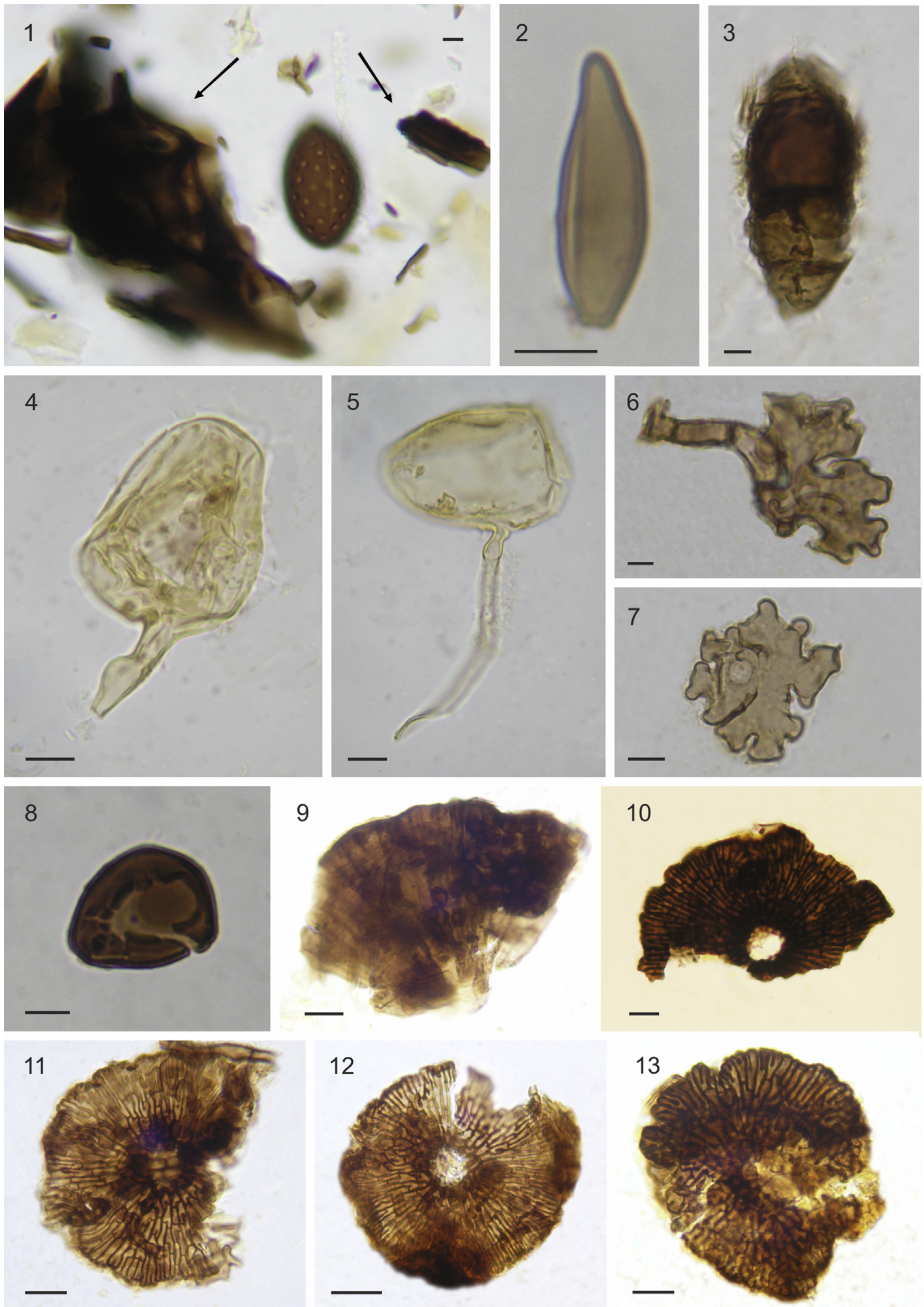

Fig. 4. Fungal remains found at La Correntina and Terra Australis mires. Each photograph indicates the sample number, and England Finder coordinates. 1. *Gelasinospora* (HdV-1), UNSP TLC 3301: Q29/4, arrows show oxidized phytoclasts; 2. *Anthostomella* cf. *fuegiana* (HdV-4), UNSP TLC 3524: Y27/1; 3. *Byssothecium circinans* (HdV-16), UNSP TTA 4074: N36/4; 4–5. *Glomus* (HdV-1103) (4: UNSP TLC 3521: Z33, 5: UNSP TLC 3522: L27/3); 6–7. *Gaeumannomyces* hyphopodia (HdV-206) (6: UNSP TTA 3737: O3, 7: UNSP TTA 3738: Z37); 8. *Arthrinium puccinioides*, UNSP TTA 3677: Z48/2; 9. Fragment of an unidentified reproductive body with ascospores, UNSP TTA 3975: P44/1; 10–13. cf. *Microthyrium fagi* (10: UNSP TTA 3819: W30, 11: UNSP TTA 3804: R49, 12: UNSP TTA 3804: O35/1, 13: UNSP TTA 3804: W25). Scale bar is 10 μm except in photos 1–3 and 6–8 where the scale bar is 5 μm.

6. Discussion

6.1. Palaeoenvironmental evolution in the eastern sector of Lake Fagnano

The Pleistocene glaciations of Tierra del Fuego have been very extensive. Large glaciers of the Darwin Cordillera (54–55° S, 69–70° W, Fig. 1) ice cap flowed north and eastwards following large, deep valleys known today as the Magellan Straits, Bahía Inútil-Bahía San Sebastián depression, Lake Fagnano, and the Beagle Channel (Rabassa and Coronato, 2009). During the Last Glacial Maximum (LGM; ca. 25,000 cal BP; Rabassa, 2008), the Fagnano glacier was confined to a relatively narrow zone, within an alpine-type landscape with almost 50 alpine-type glaciers flowing from the northern and southern mountain ranges. At its maximum extent, ice covered an area of ~4000 km^2 and its front extended

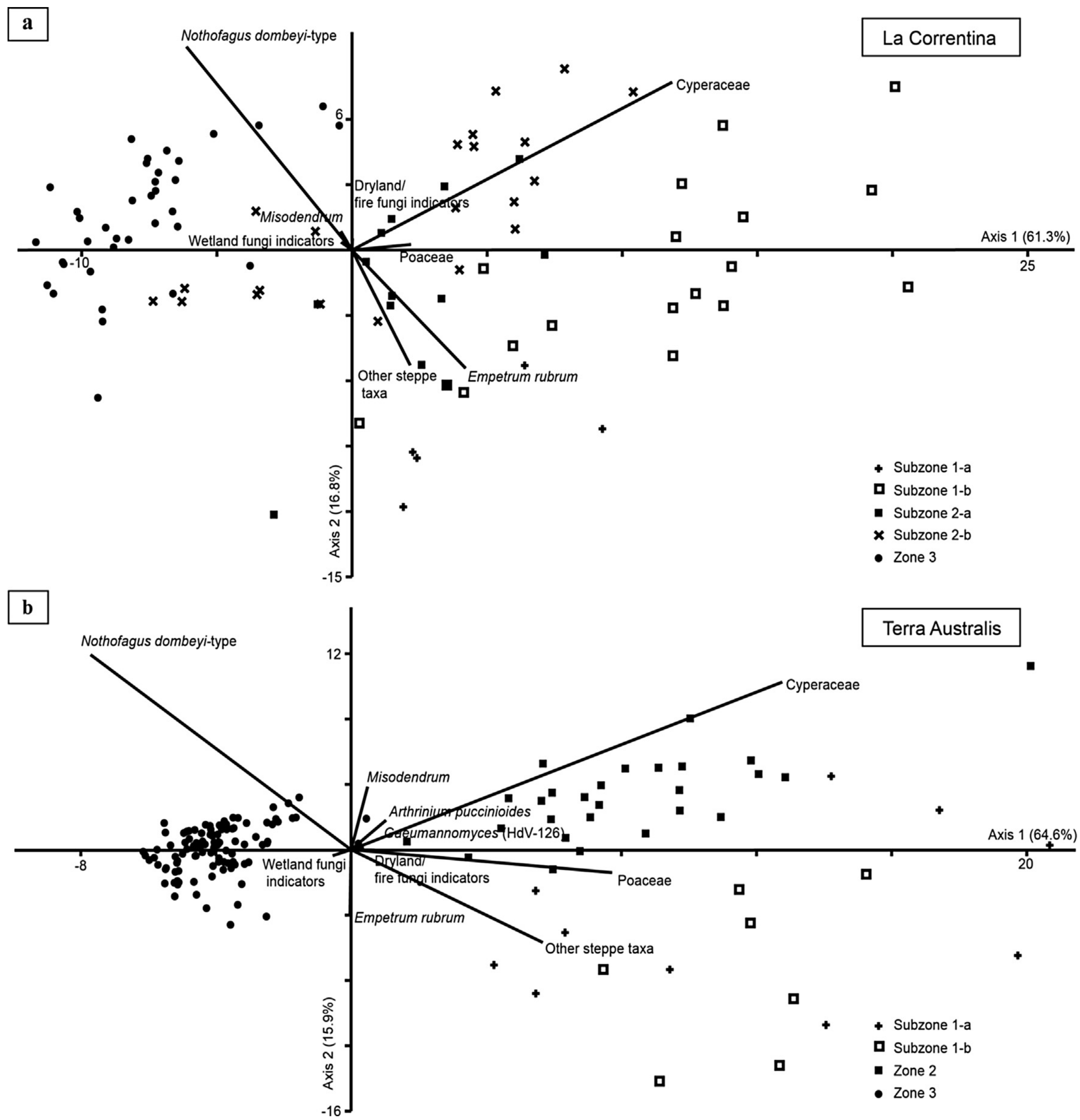

Fig. 5. (a) PCA distance biplot showing ordination of samples from La Correntina sequence. (b) PCA biplot showing ordination of samples from Terra Australis sequence. Zones and subzones are represented with different symbols in the PCA.

35 km eastward of the present lake coast. During the Late-glacial, this glacier retreated towards the west (Coronato et al., 2009). The basal ages of the La Correntina and San Pablo 1 peat bogs, located into the terminal position of the glacier during the LGM, show that the area was free of ice between 15,400 and 14,400 cal BP, respectively (Coronato et al., 2009; Musotto et al., 2016) (Fig. 1). The ice front had retreated from the southern-central coast of Lake Fagnano by 14,770 cal BP, as indicated by a basal radiocarbon date at the Terra Australis peat bog (Musotto et al., 2015).

Schematic palaeoenvironmental reconstructions from La Correntina and Terra Australis sites are illustrated in Fig. 7. The Late-glacial environment at La Correntina between 15,400 and 11,500 cal BP was dominated by heaths of *Empetrum rubrum*, grasses and pioneer herbs with scarce *Nothofagus* trees, suggesting conditions probably comparable to those on southeastern Patagonian steppe, where mean annual precipitation is <200 mm (Markgraf and Huber, 2010). At Terra Australis, the more mesic site, after 14,300 cal BP, the initial vegetation was composed by communities of scrubs (Asteraceae subf. Asteroideae), dwarf shrubs, grasses, herbs, cushion plants, and scattered trees. This plant assemblage resembles the present Fuegian steppe of the northern part of Tierra del Fuego, where precipitation values are less than 400 mm annually (Pisano, 1977; Moore, 1983). The low total pollen concentration recorded at both sites reflects a sparse vegetation cover possibly related to drier and colder than present climate. The pollen associations are characterized by the highest values in the palynological richness associated to the development of herbs and shrubs at that time. While both assemblages represent steppe communities, the Terra Australis sequence shows a low proportion of *E. rubrum* heaths and a significant occurrence of Asteraceae subf. Asteroideae scrubs, indicating that conditions were wetter than in La Correntina site. The low abundance of *Nothofagus dombeyi*-type pollen registered throughout the Late-glacial implies that pollen was transported from regional glacial refugia (Premoli et al., 2010) and/or small populations of trees close to these sites. Possibly, *N. antarctica* colonized the deglaciated

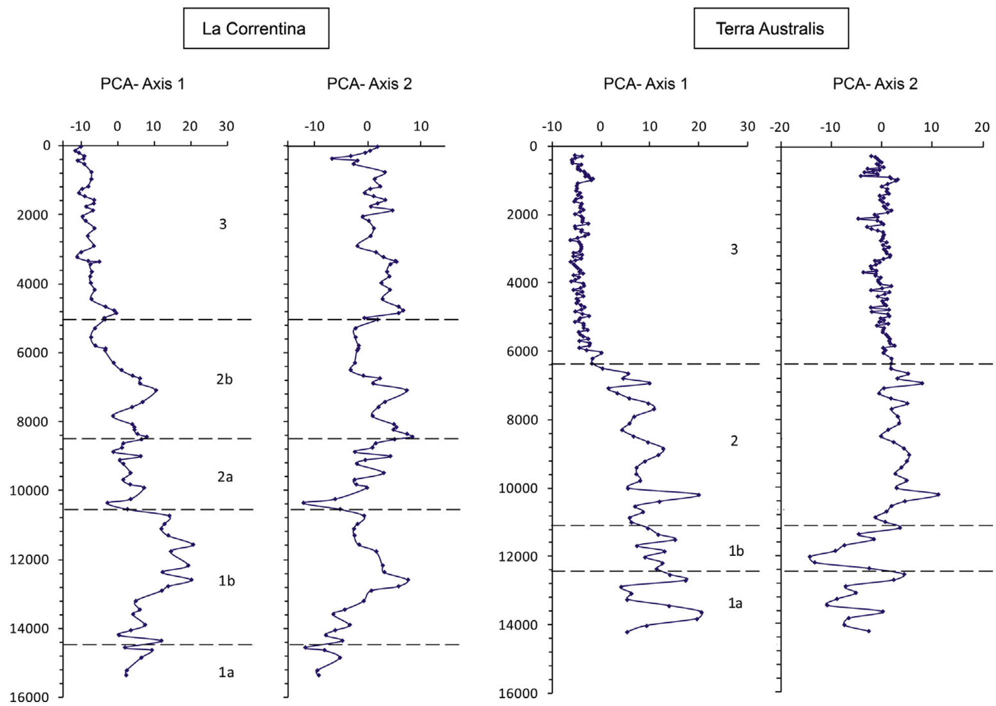

Fig. 6. Scores of the PCA axes of the palynological data from La Correntina and Terra Australis sequences presented on a time scale expressed in calibrated years BP. The boundaries of the identified pollen assemblage zones and subzones are marked in dashed lines.

terrain first, occupying less favourable habitats (Markgraf and Huber, 2010; Fontana and Bennet, 2012). Nowadays, *N. antarctica* is a pioneer species that colonizes the recently deglaciated areas (Donoso, 1993, in Fesq-Martin et al., 2004). It has wider ecological amplitude than *N. pumilio* and some adaptability to the open ground conditions, occurring on rocky, xeric and exposed sites (Veblen et al., 1996). At Terra Australis, the joint record of *Misodendrum* pollen and fungal remains of cf. *Microthyrium fagi* indicates that the *Nothofagus* trees were locally present from the onset. *Misodendrum* is the most abundant hemiparasitic plant in the subantarctic forests that specifically infects *Nothofagus* species (Tercero-Bucardo and Kitzberger, 2004). *Microthyrium fagi* is found on dead autumn leaves of *N. pumilio* (Arambarri and Gamundi, 1984); while other microthyriaceous fungi, including cf. *M. fagi*, have been recorded in surface soil samples from deciduous beech forest (Musotto et al., 2012). By this time, both mires were colonized by sedges and grasses under minerotrophic conditions related to the development of a fen. At present, herbaceous fens are located in parts of the arid steppe ecoregion where mean annual precipitations are less than 400 mm (Loisel and Yu, 2013).

Expansion of *Nothofagus* forest began about 11,200 cal BP in the Terra Australis area, the landscape was probably a forest-steppe ecotone with open ground vegetation of grasses, herbs, and shrubs. The increase in frequency and concentration values of *Misodendrum* argues for the local development of *Nothofagus*-dominated woodland. A decline in pollen richness is associated to the diminution of the open tracts in the landscape. In contrast, *Empetrum* heath, grassland and sedge communities developed around La Correntina site by 11,500 cal BP, where the spread of a forest-steppe ecotone occurred later, at 9400 cal BP. Modern manifestation of these communities is found in the northern Lake Fagnano area, where mean annual precipitation is 350–500 mm and summer temperatures average 11 °C (Pisano, 1977; Tuhkanen, 1992). These early Holocene vegetation changes implied a shift to warmer and drier climate conditions than today, which were probably due to the weakening and/or poleward displacement of the SWW (Whitlock et al., 2007; Moreno et al., 2012). The record of *Glomus* (HdV-1103) in both sequences during the late Pleistocene–early Holocene would indicate relatively dry local conditions and the presence of open ground grassland. This broadly concurs with the results of the modern study of fungal remains in Tierra del Fuego (Musotto et al., 2012), where *Glomus* was found to be restricted to the steppe environment. *Glomus* has been observed in rhizospheric soils around the most frequent grasses from degraded grasslands by sheep grazing in Tierra del Fuego (Mendoza et al., 2002). Furthermore, the record of *Gelasinospora* (HdV-1) may indicate less humid conditions related to the steppe communities. *Gelasinospora* species are terricolous, carbonicolous and lignicolous, with only a few coprophilous species (Cai et al., 2006; van Geel and Aptroot, 2006). It remains unclear whether these fungal spores indicate locally dry conditions, fire or an interaction of both factors (Yeloff et al., 2007). Although no charcoal analysis was performed, grass communities dominated the pollen spectra with simultaneous occurrence of *Gelasinospora* (HdV-1) towards the onset of the Holocene, probably in relation with regional fire events. High density of charcoal particles was documented at the Lago Fagnano site, 16 km east from Terra Australis, between about 11,000 and 8000 cal BP (Heusser, 2003; Huber et al., 2004). Fire occurrences in Tierra del Fuego have been attributed not only to a greater climate variability and overall decrease in precipitation of westerly origin (Whitlock et al., 2007), but also to deliberate burning by Paleoindian hunters (Heusser, 1994). In the Terra Australis record, high percentages of *Arthrinium puccinioides* and *Gaeumannomyces* (HdV-126) are registered during this interval. *Arthrinium puccinioides* is a dematiaceous fungus hosted on dead leaves of various species of Cyperaceae (Saccardo, 1886; Ellis, 1971). This may explain the higher abundance of this fungus in the samples where pollen of Cyperaceae is found. *Gaeumannomyces* species are parasitic on roots, crowns and lower stems and leaf sheaths of Poaceae and Cyperaceae (Walker, 1980). Presence of their lobed

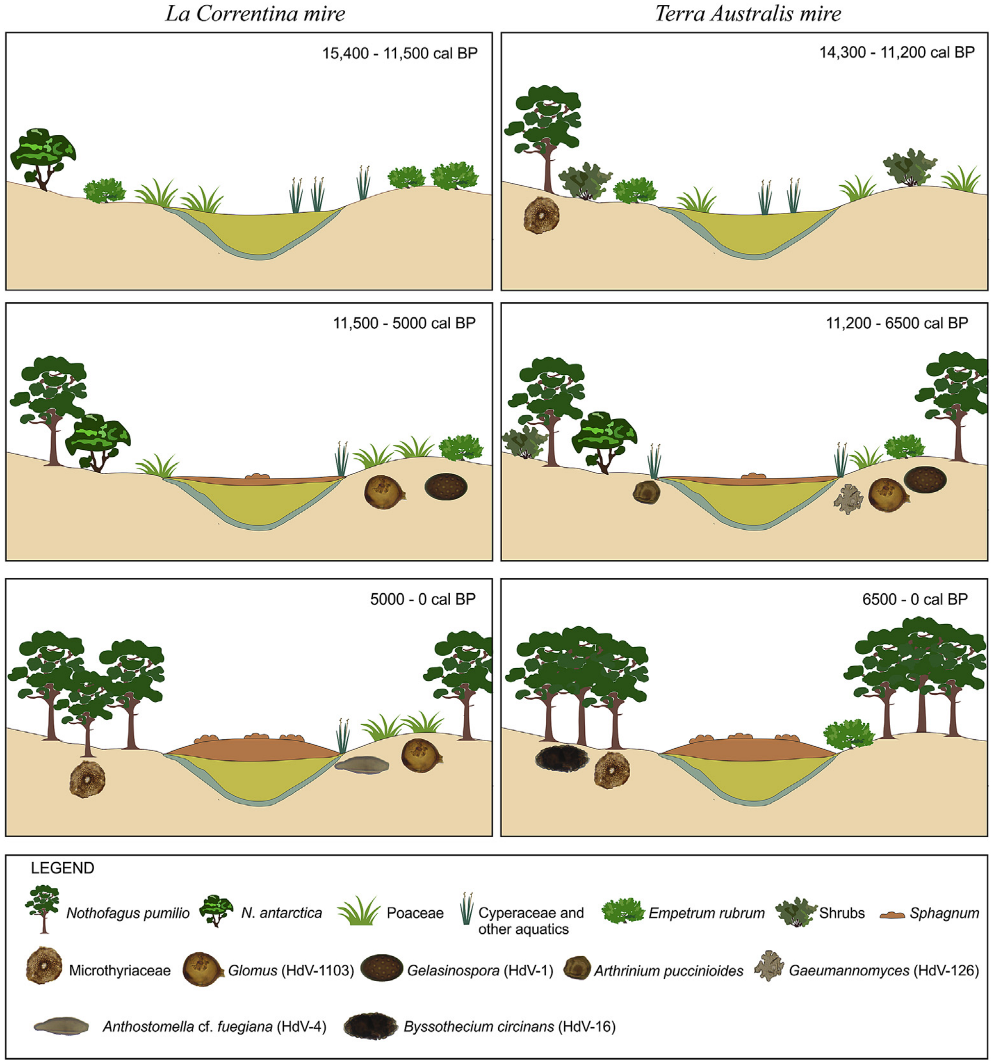

Fig. 7. Schematic palaeoenvironmental reconstructions during late Pleistocene and Holocene from La Correntina and Terra Australis mires.

hyphopodia appears to suggest the predominance of grasses and sedges in the mire.

The sequence from La Correntina documents the forest retraction and development of herb-like grasslands and cushion heaths interspersed with shrubs accompanied by increases in values of *Glomus* (HdV-1103) between 8600 and 5000 cal BP pointing to a low-humidity environment. In addition, the palaeoecological conditions in the bog changed and the sedges spread after the tephra deposition from the Hudson H_1 eruption, probably associated with nutrient enrichment in the mire. Menounos et al. (2013) reported geological evidences for one or more advances of glaciers sometime between 7960–7340 cal BP and 5290–5050 cal BP in hanging valleys of the Fuegian Andes. In central Patagonia (46° S), substantial glacial advances have been recognized at ca. 8500 and 6200 cal BP (Douglass et al., 2005).

The closed-canopy forest established after 6500 cal BP at Terra Australis, and after 5000 cal BP at La Correntina. A change in moisture availability is also evidenced by the development of ombrotrophic *Sphagnum* bog at both sites. Today, *Sphagnum*-dominated peat bogs are found on the lee side of the Andes as well as throughout the deciduous and evergreen cool-temperate ecoregions of Tierra del Fuego between 400 and 1000 mm of rain per year (Loisel and Yu, 2013). The floristic richness shows a decreasing trend, coincident with the spread of forest communities. Evidently, during this interval with dominant forest, pollen types derived from open vegetation are considerably underestimated (Berglund et al., 2008). Analogous communities exist today in the south of Tierra del Fuego, with annual precipitation estimated at 450–650 mm and summer temperatures averaging 10 °C (Tuhkanen, 1992). In agreement with these interpretations, the PCA Axis 1 scores show a clear shift at such times (Fig. 5), thus suggesting wetter conditions in the Lake Fagnano area. Similar climate conditions have been recorded in the lowlands of the Beagle Channel (Heusser, 1998) and in the Isla de los Estados (Ponce et al., 2011; Björck et al., 2012). Prominent increases in precipitation values were also documented in southern Patagonia (Tonello et al., 2009; Moreno et al., 2010). All these palaeoclimate evidences point to strengthening of the SWW at these latitudes during the late Holocene. At Terra Australis, high quantities of the reproductive bodies of Microthyriaceae (mainly cf. *Microthyrium fagi*) indicate that a closer forest developed likely reflecting more humid conditions than at La Correntina mire. Limaye et al. (2007) relate microthyriaceous fungi with heavy rainfall. Presumably, the accumulation of plant and wood remains provided a good substrate for the growth of saprotrophic fungi (particularly *Byssothecium circinans* (HdV-16)) in the vicinity of the Terra Australis mire.

At La Correntina, after 3000 cal BP, *Nothofagus* forest became more open, accompanied by the expansion of mesic grasslands, together with the reappearance of mycorrhizal *Glomus* (HdV-1103), apparently reflecting a somewhat drier local environment. In line with the opening of the canopy, the values of pollen richness increase. However, the development of ponds on the mire surface may have favoured the presence of moisture demanding taxa such as *Caltha* and *Anthostomella* cf. *fuegiana* (HdV-4). According to Ledru et al. (2006), *A. fuegiana* is an indicator of moist edaphic conditions along with the development of hygrophilous vegetation. In Terra Australis sequence, the closed-canopy forest remained until ca. 1000 cal BP, followed by an open landscape with less dense tree cover as is shown by the decline in the total pollen values (Musotto et al., 2015). Microthyriaceae drop along with occurrences of *Glomus* (HdV-1103) suggesting less humid local conditions during that time. At La Correntina, the forest cover decreased by 400 cal BP implying unsuitable conditions for forest growth, which appears to be in coincidence (within accuracy of the age model) with the Little Ice Age (LIA) in the Southern Hemisphere. However, in Terra Australis, the evidence for this cold event is less clear. Probably, the high levels of effective moisture recorded during this interval masked any evidence for climatic change towards colder conditions. After ca. 400 cal BP, *Nothofagus* forest expanded again around the La Correntina site, and the landscape displayed a physiognomy of a closed-canopy forest.

7. Final remarks

La Correntina and Terra Australis mires have experienced dissimilar environmental trends during the past ~15,000 years. As the mires are located in two different slopes of the Fuegian Andes axis, regional driving mechanisms should be considered as possible causes of the past environmental and climatic changes in the records. Today, La Correntina and Terra Australis are affected differently by the prevailing westerly circulation. The Terra Australis mire is situated between hills at the foot of the Fuegian Andes valleys, on the Pacific (windward side) slope, that impose the climatic conditions of mountain areas, particularly a relatively low number of daylight hours, rainfall originated by topographic relief and effect of the katabatic winds. Its position close to the Lake Fagnano coast would explain more favourable conditions for the arrival of the SWW into the site as the lake acts as a corridor for the passage of humid air-masses from Pacific Ocean. In contrast, La Correntina mire lies at the bottom of a valley oriented in the direction of the SWW, which may promote diurnal to seasonal temperature changes. Hence, its location on the Atlantic (leeward side) slope of the Andes makes this area specially sensitive to environmental changes. Within the uncertainty of the age–depth models, the timing for the climate shifts is different for both mires. The postglacial vegetation pattern observed at Terra Australis seems to be in agreement with palaeoenvironmental data available from the Beagle Channel area, at the southern Tierra del Fuego, whereas La Correntina mire seems to follow the vegetation pattern recorded in the centre of the island, particularly in the Lake Fagnano area.

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