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Palaeoenvironmental changes since Pleistocene–Holocene transition: Pollen analysis from a wetland in southwestern Patagonia (Argentina)

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ABSTRACT

Changes in pollen spectra of a sediment core from a wetland in the southern side of Lake San Martin, which is located at 49° 11′ S; 72° 22′ W (near the eastern limit of the Subantarctic Forest–Patagonian Steppe ecotone) reflect variations in the composition of vegetation since the Pleistocene–Holocene transition. Comparison of fossil to modern pollen assemblages allowed us to interpret these palaeoenvironmental changes in terms of moisture availability. Between 11 300 and 9500 cal yr BP, conditions with low moisture availability from Poaceae–*Ephedra*–Chenopodiaceae pollen assemblage were inferred. From 9500 to 8000 cal yr BP, the grass steppe dominance was interpreted as an increase in moisture availability. The steppe assemblage was replaced by shrub taxa suggesting drier conditions in the mid-Holocene (8000–3000 cal yr BP). Between 3000 and 100 cal yr BP, wetter conditions were inferred from an increase in herb taxa and a decrease in shrubs, while for the last century a grass steppe with higher amounts of shrubs suggests a decrease in moisture availability. Changes in these vegetation assemblages suggest changes in the precipitation patterns related to the position and strength of the westerlies.

1. Introduction

Southern Patagonia is an important area for the investigation of past variations in the Southern Hemisphere westerlies due to it is the only significant continental landmass that intersects the region of maximum zonal flow. Furthermore, the atmospheric circulation in the southern mid-latitudes is maintained by strong thermal gradients in the troposphere and sea-surface temperatures over the Pacific Ocean (Moy et al., 2009). Moreover, the Andean Cordillera is an important topographic barrier for the Pacific humid air masses therefore the mean annual precipitation decreases exponentially from west to east (Paruelo et al., 1998; Garreaud et al., 2009). The vegetation distribution in this region reflects the rain shadow effect generated by the Andes. Along the western Andean slopes, there are high rainfall environments, whereas in the eastern Andean precipitations decrease to around 800 mm annually and in semi-arid areas of the extra-Andean zone the precipitation is less than 200 mm annually. The climate of Patagonia can be defined as temperate or cool temperate; the mean annual temperature is 0–10 °C (Paruelo et al., 1998; Garreaud et al., 2009).

The landscape characteristics of southwestern Patagonia reflect events that occurred since the Miocene and which are related to past glacier movements and their deposits in different periods. Lateral moraines lining the pre-Andean lakes contain small basins that have accumulated sediments since the last glacial retreat (Auer and Cappannini, 1957; Rabassa et al., 2005). The relationship between these landscapes characteristics and the strong precipitation gradient determine the different vegetation units.

The ecotones of southwestern Patagonia are interesting because they are highly sensitive to climatic changes. Pollen studies have been carried out in southwestern Patagonia west and east of the Andes from different types of deposits such as mires, fens, lakes, peat bogs and archeological sequences (Auer and Cappannini, 1957; Ashworth et al., 1991; Schäbitz, 1991; Heusser, 1995; Mc Culloch and Davies, 2001; Mancini, 2002, 2009; Mancini et al., 2002; Huber and Markgraf, 2003; Markgraf et al., 2003; Huber et al., 2004; Villa-Martínez and Moreno, 2007; Wille et al., 2007; Moreno et al., 2009; Wille and Schäbitz, 2009). These records show changes in vegetation communities, mainly due to changes in precipitation, which are related to shifts in the position and strength of the westerlies. Thus, the history of vegetation is dissimilar for different latitudinal bands in Patagonia in terms of times and character of change (Markgraf et al., 1996).

With the aim to reconstruct the palaeoenvironmental changes at the eastern limit forest-steppe ecotone of Argentine Patagonia since the Pleistocene–Holocene transition, the pollen content of a core was analyzed. The place of sampling is located near Estancia La Tercera at

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the southern coast of the Lake San Martin basin (Santa Cruz Province, 49° 11′ S; 72° 22′ W) (Fig. 1). This record provides a contribution to the understanding of the vegetation and climate history in the Patagonian steppe adding valuable information to the knowledge of palaeoenvironmental conditions during the Holocene.

The analysis of modern pollen-vegetation relationship along climatic gradients (Mancini, 1993, 1998, 2002; Bamonte and Mancini, 2009) allowed inferring vegetation changes and palaeoclimatic conditions in southwestern Patagonia during the Holocene.

2. Study area

The study area is located in the southern shore of Lake San Martin (southwestern Santa Cruz Province), at the grass steppe near to the Subantarctic Forest–Patagonian Steppe ecotone (Fig. 1). The vegetation is related to a strong precipitation gradient that decreases from west to east. Wetlands, such as we studied for this research, are common in depressions within glacial deposits (Mazzoni and Vázquez, 2004).

The climate in the Lake San Martin basin is temperate-cold with an annual mean temperature below 5 °C; summers are fresh and winters are from cold to very cold with substantial snow accumulation. The western reach of Lake San Martin is characterized by moist conditions, while the eastern zone presents semiarid characteristics (Borrelli and Oliva, 2001).

The deciduous forest of the Subantarctic Province (Cabrera, 1976) or the Andean–Patagonian Forest (Dimitri, 1972), is represented by *Nothofagus antarctica* and *N. pumilio*, expanding along the wetter eastern slopes of the Andes between 800 and 400 mm mean annual precipitation. In more open forest, shrubs and herbs as *Berberis ilicifolia, Gaultheria mucronata, Osmorhiza chilensis, Acaena pinnatifida, Lathyrus magellanicus, Bromus catharticus, Poa patagonica* and *Festuca pallescens* are present. To the east of the 400 mm isohyet, *Nothofagus* forest appears only in edaphic and higher elevation sites where the water balance is favorable for this occurrence (Movia et al., 1987).

In the extra-Andean zone, with glacial deposits of terminal and lateral moraines, grass, shrub and dwarf-shrub steppes grow (Movia et al., 1987; Borrelli and Oliva, 2001) associated to the different precipitation ranks.

The grass steppe grows between 500 mm and 300 mm mean annual precipitations and at higher altitude areas where climatic conditions are colder and wetter. Around Lake San Martin, the grasslands are dominated by *Festuca pallescens* accompanied by *Festuca argentina* and the shrub *Nardophyllum obtusifolium.* Other grasses found in the area are *Poa ligularis, Stipa chrysophylla* and *Festuca pyrogea.* Also, *Carex andina, Polygala darwiniana* and *Nassauvia darwinii* are present. In some cases, *Junellia tridens, Senecio filaginoides* and *Berberis heterophylla* are found. The shrub steppe is characterized by a dense cover of shrubs growing between 400 and 200 mm mean annual precipitation. Along the eastern shore of Lake San Martin, high proportions of *Berberis heterophylla, Senecio filaginoides* and *Mulinum spinosum* are found. *Lycium chilense, Junellia tridens, Schinus polygamus* and *Senecio filaginoides* appear at the lowermost elevations. Where the moisture conditions are more favorable *Nardophyllum obtusifolium* dominates associated with *Festuca pallescens*. The dwarf-shrub steppe grows in areas where the precipitation is lower than 200 mm mean annual precipitation and is characterized by woody elements of low height and cover. The main species belong to the genera *Nassauvia, Chuquiraga, Acantholippia* and *Brachyclados. Nassauvia glomerulosa* associated with *Festuca pallescens* can be observed between the lakes San Martin and Tar. *Stipa* and *Poa* are also present (Movia et al., 1987). *Plantago patagonica* and *P.correae* are native species of this vegetation unit (Correa, 1999).

3. Methods

A core of 2.19 m was obtained by Vera Markgraf (University of Colorado, USA) using a Livingstone corer in 1985. Samples (N = 48) for pollen analysis were processed in the Laboratory of Palaeoecology and Palynology (Universidad Nacional de Mar del Plata) using standard procedures (Faegri and Iversen, 1989). Prior to pollen preparation samples were dried at 60 °C weighting between 0.7 and 10.2 g. *Lycopodium clavatum* spores were added to each sample in order to calculate pollen concentration per gram of sample. The samples were sieved through 120 μm mesh screens and were treated with KOH 10% and HCl 10%. The mineral fraction was separated by flotation in $ZnCl_2$ ($\delta = 2$ g/ml) and the silicates were removed using HF. Finally, acetolysis was performed. The pollen residues were mounted in glycerine. The pollen sums varied between 305 and 567 grains per sample. The pollen data of 39 modern surface sediment samples (Bamonte and Mancini, 2009) and 10 new samples, from different vegetation units, were used for the interpretation of fossil

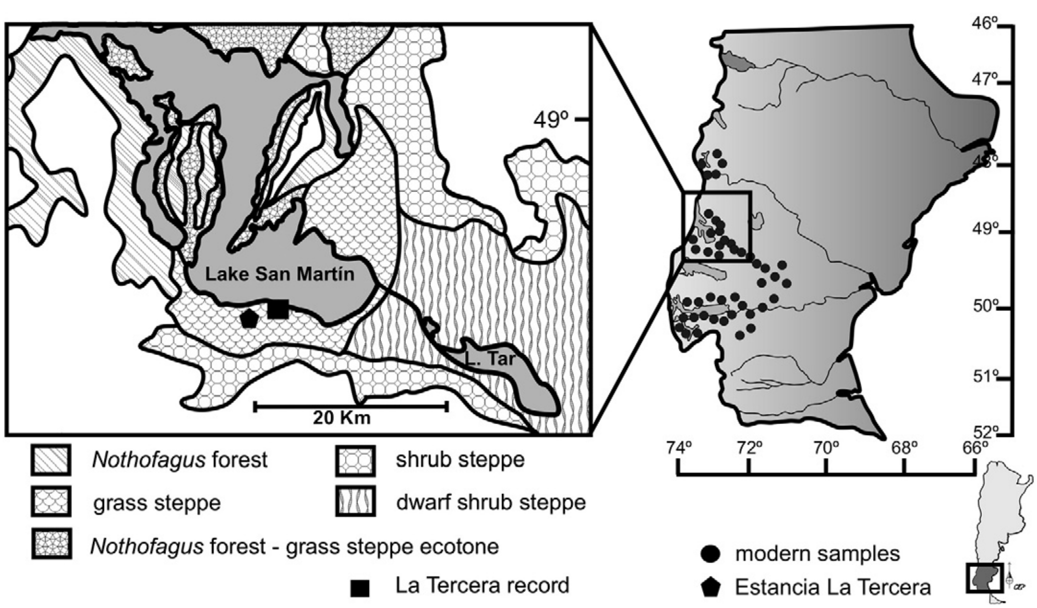

Fig. 1. Map of Santa Cruz showing vegetation units of Lake San Martín area (modified from Movia et al., 1987), the spatial distribution of modern pollen samples and the location of the studied core.

vegetational changes (Fig. 1). Modern sediment samples weighted around 20 g prior to pollen extraction. Each taxon is expressed as a percentage of the total pollen sum. Pteridophyta and Bryophyta spores, algae (Zygnemataceae and *Botryococcus*), *Myriophyllum* and Cyperaceae grains were not included in the pollen sum because they are the local wetland vegetation. Addittionally, *Rumex* was excluded because it is related to disturbed areas. Convolvulaceae, Euphorbiaceae and Campanulaceae were grouped and called as "other herbs". Plotting of pollen diagrams and statistical analysis were carried out using TILIA and TILIAGRAPH program (TGView 2.0.2, Grimm, 2004). Modern and fossil samples were grouped by Cluster Analysis, applying square root transformation with Edwards and Cavalli–Sforza' chord distance (TGView 2.0.2, Grimm, 2004).

The stratigraphy of the core was based on lithological description and analysis of organic matter and carbonate content using loss-on-ignition (LOI). The analyses were done on the same levels of the pollen samples. The samples were burnt overnight at 105 °C and followed by sequential combustion at 550 °C during 4 h and at 950 °C during 2 h in a muffle oven (Bengtsson and Enell, 1986; Heiri et al., 2001).

Age model developed based on four radiocarbon dates (Table 1). Radiocarbon dates were calibrated using CALIB 5.0.2 (Stuiver and Reimer, 1993; Stuiver et al., 2005) with the Southern Hemisphere calibration curve (SHCal04) (McCormac et al., 2004; Reimer et al., 2004). The post-bomb date at 10 cm depth was not included in the age model owing to its probably contamination and the 8900 ± 350 ^{14}C yr BP date has a high error. The age-depth model was constructed by MCAge software using a cubic smoothing spline and a bootstrap approach (Monte Carlo sampling) (Higuera et al., 2009) that allowed each date to influence the age model through the probability density function of the calibrated ages (Higuera et al., 2008). The final chronology represents the mean age of each depth from all the runs. By the method of extrapolation, the basal age of the core is 11 300 cal yr BP.

4. Results

4.1. Modern pollen data (Fig. 2)

Using cluster analysis the modern pollen assemblages reflect the different vegetation units along the precipitation gradient from west to east. The *forest* is characterized by high percentages of *Nothofagus* (40–95%) together with the mistletoe *Misodendrum* (<5%). The herbaceous layer is represented by Poaceae (35%). Among shrubs Asteraceae subf. Asteroideae (5%) are present. The transition between the forest and steppe is mainly characterized by *Mulinum* (15–45%), Ericaceae (<5%) and Asteraceae subf. Asteroideae (10–20%). *Nothofagus* percentages (<20%) are considerably lower than forest assemblage and Poaceae increase (15–40%). The *grass steppe* is dominated by 75% of Poaceae, accompanied by lower values of other herbs (<15%); while the shrubs show values near 15%. The *shrub steppe* is represented by high values of Asteraceae subf. Asteroideae (25–70%) together with other shrubs such as *Adesmia* (5–30%) and *Mulinum* (5–10%). Among the herbs, Caryophyllaceae and *Acaena* (5–10% and 5–25%, respectively) are the most representative. The *dwarf-shrub steppe* is characterized by Asteraceae subf. Asteroideae (until 30%), *Nassauvia* (30%), *Ephedra* (up to 25%) and Chenopodiaceae (up to 45%), while Poaceae present values between 5 and 50%.

4.2. Fossil records

4.2.1. Stratigraphy

From the base of the core (219 cm depth) to 185 cm depth, the sediment is primarily composed by clay associated to plant fibers; organic matter has low values (<5%), carbonates reach 15% and total pollen concentration values are low ($<7\times10^3$ g/gr) . The second sedimentary unit (185–137 cm) is mainly composed of a fine-grained carbonate mud (marl) and clay; carbonates and organic matter increase (10–30 and 5–50%, respectively) as well as total pollen concentration ($10–40\times10^3$ g/gr). The highest values of organic matter (50%) coincide with peat layers at the top of this unit. From 137 to 70 cm marl predominates interspersed by several organic-rich (gyttja) levels and clay. Organic matter presents percentages between 4 and 25% and carbonates between 2 and 27%. Total pollen concentration reaches 45×10^3 g/gr. In gyttja level, the sequence presents the lowest values of carbonates (2%), while in marl levels the carbonates reach 27%. Between 70 and 18 cm the sediment is mainly represented by gyttja; in this unit gyttja-peat levels show the highest values of organic matter (45%) and total pollen concentration (80×10^3 g/gr), besides marl and clay are also present. Carbonate values fluctuate between 2 and 25%. The uppermost unit from 18 cm to the top, is composed by clay and marl. Organic matter (<10%) and total pollen concentration values decrease (7×10^3 g/gr) with respect to the previous unit and carbonates reach 15% (Fig. 3). The mean deposition of sedimentation rate is around 0.02 cm/yr; at 9500 and at 100 cal yr BP the rate increases. The time resolution average shows an inverse effect (Fig. 4).

4.2.2. Fossil pollen record (Fig. 5)

The pollen sequence was divided into six zones according to cluster analysis.

4.2.2.1. Zone 1. (219–185 cm depth, 11 300–10 000 cal yr BP). This zone is characterized by Poaceae with values from 35 to 65%, accompanied by *Ephedra* (10 to 30%) and Chenopodiaceae (10%) which decrease towards the top. Among the herbs *Plantago* (5 to 20%) dominates. Asteraceae subf. Asteroideae increase from 5 to 15% towards the top of the zone. *Nassauvia* and Fabaceae show values around 5%. *Nothofagus* shows very low values (<5%). Within the excluded taxa, Cyperaceae increase from the base (10%) to the top (70%).

4.2.2.2. Zone 2. (185–175 cm, 10 000–9500 cal yr BP). This zone is characterized by a decrease of Poaceae (35%) and an increment of Asteraceae subf. Asteroideae (>35%). Asteraceae subf. Cichorioideae, Rubiaceae and Malvaceae increase (<10%) accompanied by *Plantago* (5%) and *Ephedra* (>5%). *Nothofagus* values are low. Cyperaceae (>70%) values are higher than those of the previous zone.

Table 1
Radiocarbon and calibrated ages from La Tercera core.

Depth (cm)	Laboratory No	^{14}C yr BP	Calibrated age yrs BP (median probability)	1 σ range	2 σ range	Material
10	AA 81418	Post-bomb	–	–	–	Marl-clay
53–54	AA 87093	1570 ± 37[a]	1399	1344–1418	1320	Gyttja-peat
111–113	AA 76035	5717 ± 45[a]	6444	6353–6365	6310–6564	Marl
142–144	A 4335	7540 ± 160[a]	8285	8056–8090	7978–8588	Marl-peat
171–172	A 4336	8900 ± 350	9931	9497–10297	9032–9054	Marl
173–174	AA 87094	8439 ± 52[a]	9408	9310–9359	9270–9523	Marl

[a] Included in the age model.

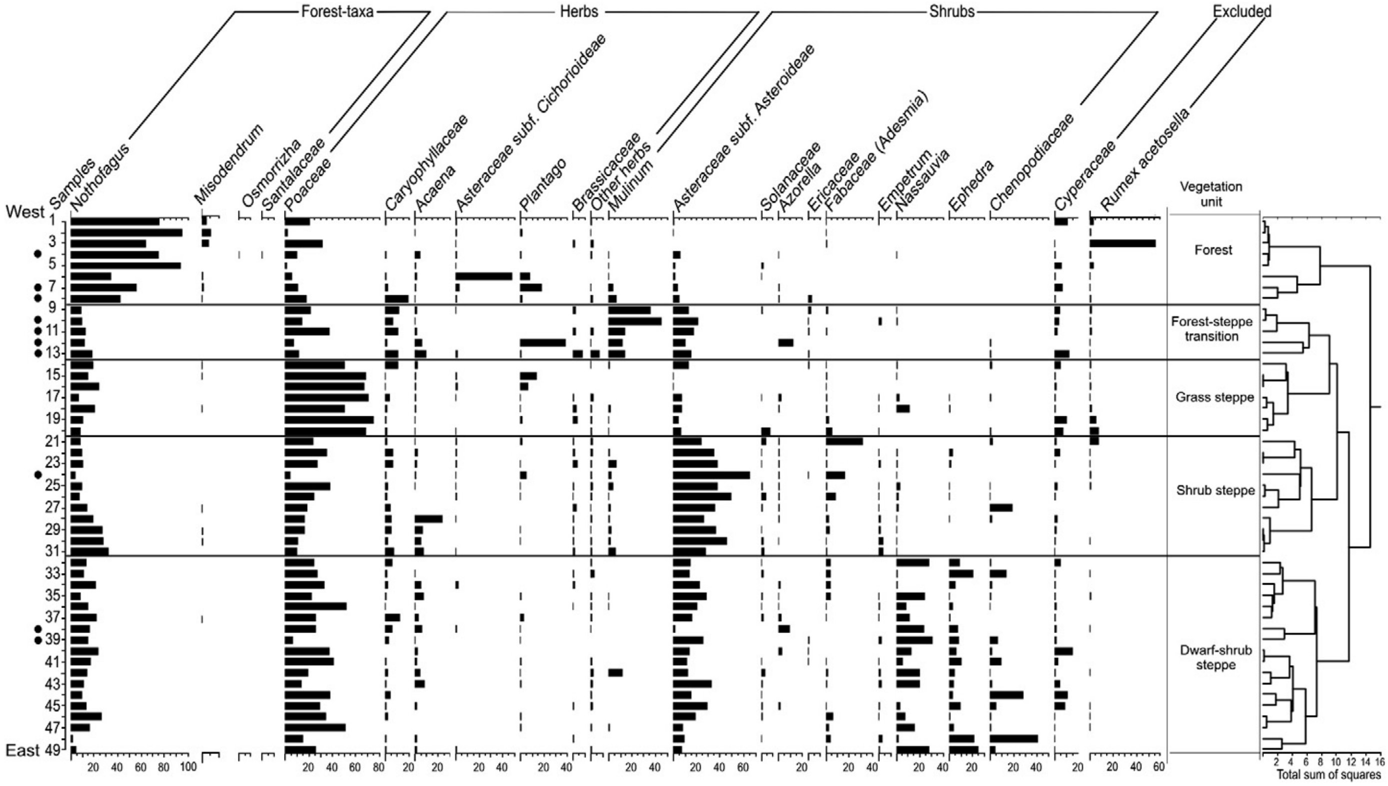

Fig. 2. Surface pollen diagram (in percentages) showing vegetation units. New samples respect to Bamonte and Mancini (2009) are showing with circles.

4.2.2.3. Zone 3. (175–140 cm, 9500–8000 cal yr BP). In this zone the pollen spectra is dominated by Poaceae (>80%) together with low values of herbs (<10%) such as Caryophyllaceae, Rubiaceae, Monocotyledoneae (mainly Amaryllidaceae), *Acaena* and Asteraceae subf. Cichorioideae. Asteraceae subf. Asteroideae (>20%) decrease considerably in relation to the previous zone. *Nothofagus* increases to 20%. Among the excluded taxa, Cyperaceae exceed 75% and both Pteridophyta and algae (Zygnemataceae and *Botryococcus*) increase to 15 and 10%, respectively.

4.2.2.4. Zone 4. (140–72 cm, 8000–3000 cal yr BP). This zone is characterized by an increase of Asteraceae subf. Asteroideae (40%), accompanied by Solanaceae and *Nassauvia* (>5%), and a decrease of Poaceae with values between 30 and 70%, and values lower than 20% regarding herbs. *Nothofagus* increases (30%) at the base of the zone. Cyperaceae decrease (15%) in the middle of the zone while Pteridophyta increase (55%); the reverse is seen towards the top where Cyperaceae increase (80%) while Pteridophyta and algae decrease (<5%).

4.2.2.5. Zone 5. (72–15 cm, 3000–100 cal yr BP). This zone is dominated by Poaceae (<80%) along with the other herbs (<10%) such as Caryophyllaceae, Rubiaceae and Monocotyledoneae. Asteraceae subf. Asteroideae decrease to values lower than 25%. *Nothofagus* shows values up to 25% throughout the zone. *Empetrum* is present with low percentages (<5%). Fabaceae present values lower than 10%. Cyperaceae reach up to 90%, Pteridophyta and algae decrease in relation to Zone 4. Bryophyta are present with low but constant values, as well as *Rumex*.

4.2.2.6. Zone 6. (15–0 cm, 100–0 cal yr BP). This zone is characterized by Poaceae (35–60%) together with Caryophyllaceae, Polemoniaceae and Asteraceae subf. Cichorioideae (<10%).

Asteraceae subf. Asteroideae (20%) dominate along with Solanaceae (10%) and Chenopodiaceae (30%) into the shrubs. *Nothofagus* decreases (15%). Cyperaceae show constant values (60%). *Myriophyllum* (15%) and *Rumex* (5%) are important in this zone and Pteridophyta and algae (10%) decrease.

5. Palaeoenvironmental interpretation

From the basal age of 11 300 cal yr BP until 9500 cal yr BP the pollen record reflects assemblages that are similar to those that are dominant in the dwarf-shrub steppe nowadays, represented by Poaceae, Plantago, *Ephedra* and Chenopodiaceae. Precipitation must have been less than 200 mm annually. The progressive increase of Cyperaceae could be related to the establishment of a wetland area. According to the lithology this interval may represent a low-energy environment. The clayed sediment with low organic matter and carbonate values would be associated with to the end of the glacier retreat period and with a low cover vegetation landscape.

The most important vegetation change occurred at the beginning of the Holocene. Between 9500 and 8000 cal yr BP, Poaceae dominance accompanied by other herbs and the low proportion of shrubs suggest the development of a grass steppe associated to an increase of precipitation to ca 300 mm annually whereas *Nothofagus* forest began to expand in the Andean zone. This vegetation type and the increment in organic matter and carbonates together with a decrease in clay and the presence of peat layers to the top of the zone could be related to temperature increase during the beginning of the Holocene.

Between 8000 and 3000 cal yr BP a steppe with shrubs developed indicating lower moisture. The predominant lower moisture conditions are reflected in the sediment by several marl layers. However, gyttja levels between 8000 and 6500 cal yr BP coincide with high *Nothofagus* values. The fluctuating algal values reflect the moisture variability during this period. Higher concentrations of *Botryococcus* may be attributed to dry periods (Limaye et al., 2007). However, it has been difficult to establish the criteria that lead to its proliferation because of the very variable conditions with which it has been associated. These include both deep and shallow water bodies and

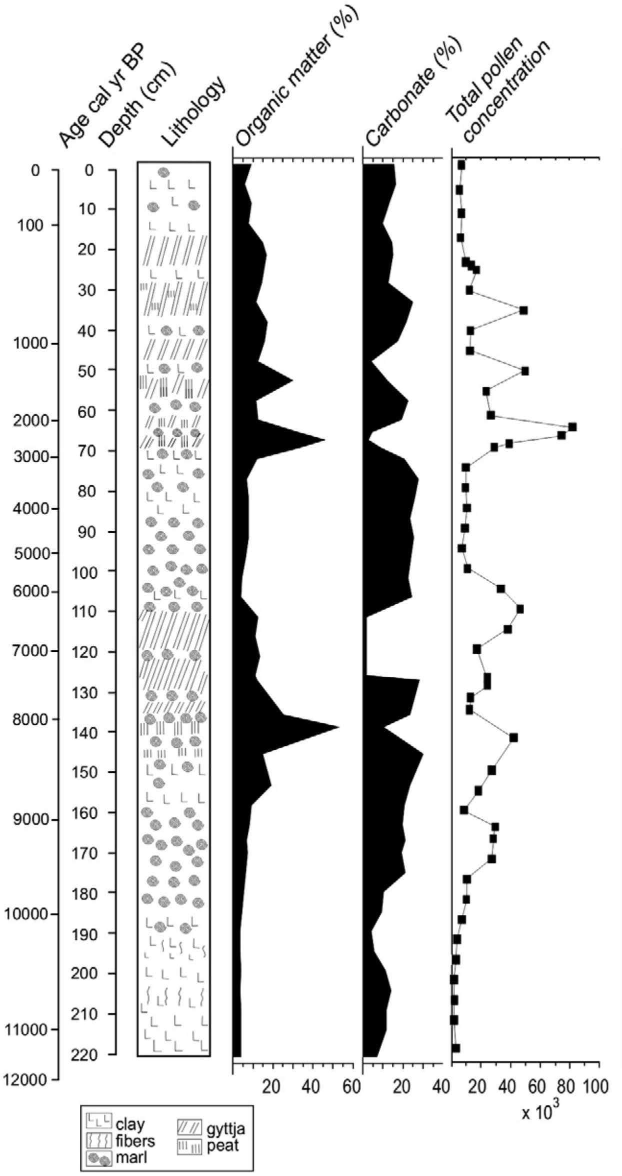

Fig. 3. Stratigraphic column, along the calibrated ages and results of the loss-on-ignition analysis and total pollen concentration.

high and low rainfall. It appears to compete with other particularly successful algae in areas where the water is shallow and the rainfall relatively low (Batten and Grenfel, 1996).

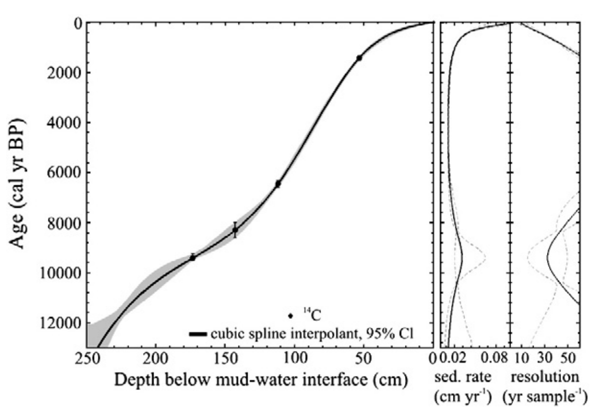

Fig. 4. Age-depth curve. The gray zones represent the 95% confidence intervals.

Between 3000 and 100 cal yr BP the increase in herbaceous taxa suggests the development of the grass steppe associated with higher moisture conditions. The organic matter increment and the presence of several gyttja-peat layers could be reflecting these wetter conditions that coincide with an increase in pollen concentration.

After 100 cal yr BP, a grass steppe with shrubs (mainly Asteraceae subf. Asteroideae and Solanaceae) is inferred, which indicates a trend towards a precipitation decrease. The sediment is mainly composed by clays. The wetland dynamics could be affected by seasonally fluctuating water levels reflected by variable values of Chenopodiaceae. In wet seasons *Myriophyllum* could develop. Signals related to the human (European) impact are represented by *Rumex acetosella.*

Reconstruction of past fire regime from La Tercera core enhances the paleoclimatic interpretation. CHAR (charcoal particles/cm^2 per yr) values in this sequence have significantly varied during the Holocene (Fig. 6; Sottile et al., in press).

Nowadays, La Tercera site is surrounded by grass communities. In a steppe environment, high CHAR values are associated to high Poaceae percentages; grass abundance favors horizontal fuel continuity allowing surface fires to take place in this environment. Steppe fires in La Tercera record show a clear relationship with grass spatial continuity during early and late Holocene when Poaceae values were the highest (Fig. 6). The high values of shrubs recorded in La Tercera, would have favor tussock grass biomass patchiness (such as *Festuca pallescens* grass) avoiding fire to spread to neighbor stands. Huber et al. (2004) suggested that the low accumulation together with the discontinuous fuel structure would have produced limiting factors for the occurrence of fires. These conditions were recorded in La Tercera during the Pleistocene–Holocene transition and mid-Holocene by low CHAR values (Fig. 6).

Gastropods were found at different levels (in zones 3 to 5). The species found were mainly *Succinea meridionales* and *Lymnaea viator*. These species are semi-aquatic, which suggest the development of a shallow water body, probably a damp habitat occasionally submerged. Specifically, *Limnaea viator* suggests a very shallow vegetated lacustrine habitat, with dominance of macrophytes, because this species perfectly lives in this type of environment (De Francesco et al., 2007). This is consistent both with the type of sediment and with pollen data suggesting that the site remained a wetland even in the period of low moisture during the mid-Holocene (Bamonte and Mancini, 2009). The gastropods absence in zones 1, 2 and 6 could be related with to the driest periods.

6. Regional analysis

Aridity conditions from 11 300 to 9500 cal yr BP are inferred from the pollen analysis carried out in the present study. Pollen sequences from the extra-Andean central plateau region in the Santa Cruz Province also show a dwarf-shrub steppe but the higher values of *Ephedra* suggest arid conditions with precipitations lower than 200 mm, different from the modern ones (Paez et al., 1999; de Porras, 2010). Toward the southwest, until 11 000 cal yr BP a grass steppe under relatively wet and cold conditions is recorded in areas closer to the forest, in the Cerro Frías (Mancini, 2009) and Vega Ñandú records (Villa-Martínez and Moreno, 2007). The precipitation in these areas was lower than at present-day (Tonello et al., 2009a). High charcoal depositional rates in the Cerro Frías record during Pleistocene–Holocene transition, could imply dry conditions or the occurrence of successive shifting from humid to dry periods dealing fuels to support fires (Sottile et al., in press).

High fire frequency for continuity in the fuel between 10 000 and 9000 cal yr BP (Sottile et al., in press) and the development of a grass steppe in the Lake San Martin area between 9500 and 8000 cal yr BP suggest relatively wetter conditions indicating an increment in the precipitation (Tonello et al., 2009b). The precipitation reached the area displacing the grass steppe/dwarf-shrub steppe ecotone eastward.

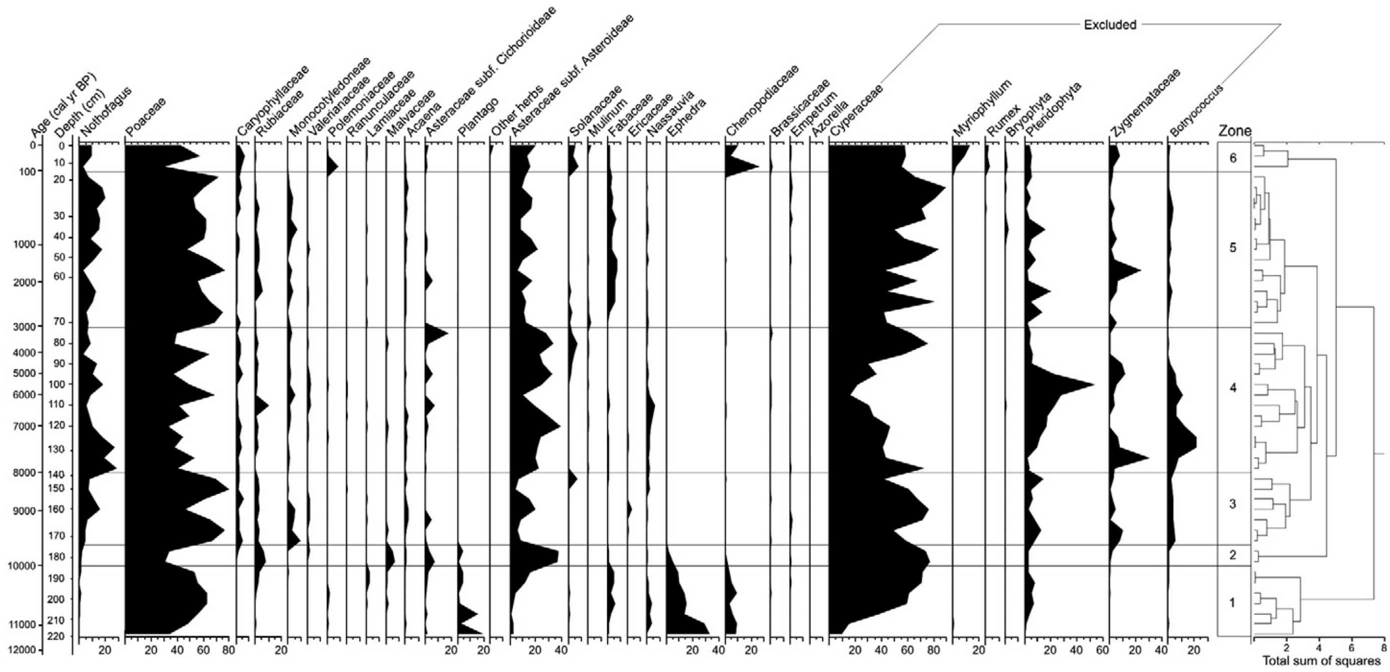

Fig. 5. Sequence fossil (in percentages) diagram and pollen zones.

In Laguna Potrok Aike a different signal between pollen/diatoms and sediments were recorded between 12 830 and 8700 cal yr BP. This might be due to responses to different environmental factors such as changes in winter precipitations that could have affected the water level but not the pollen/diatoms signal. Diatoms and pollen indicate a decrease both the lake level and moisture availability but the sediments suggest an increase in the lake level (Wille et al., 2007). This period with weakened Southern Hemisphere westerlies, air masses from easterly directions reached Laguna Potrok Aike more frequently giving rise to enhanced precipitation (Mayr et al., 2007). The Lago Cardiel levels were the highest during the interval between ca 9500 and 7500 cal yr BP, indicating precipitations substantially above present-day levels. According with Bradbury et al. (2001) and Markgraf et al. (2003) the precipitations came from the Atlantic Ocean. *Nothofagus* forest expansion suggests warmer and wetter conditions for the early Holocene at higher latitudes sites as Cerro Frías (Mancini, 2009), Torres del Paine (Heusser, 1995), Meseta Latorre (Schäbitz, 1991), Vega Ñandú (Villa-Martínez and Moreno, 2007) and Río Rubens (Huber et al., 2004). These vegetation communities inferred from records located in the forest-steppe ecotone and in drier extra-Andean areas suggest weaker westerlies periods with west-east precipitation gradient gentler than during higher intensities of westerlies (Whitlock et al., 2007; Moy et al., 2009).

Between 8000 and 3000 cal yr BP, a steppe with dominance of shrubs developed in Lake San Martin area suggesting a decrease in moisture availability, as well as, low fire activity by fuel discontinuity (Sottile et al., in press). In Laguna Potrok Aike, driest conditions started around 8700 cal yr BP until around 7300 cal yr BP (Wille et al., 2007),

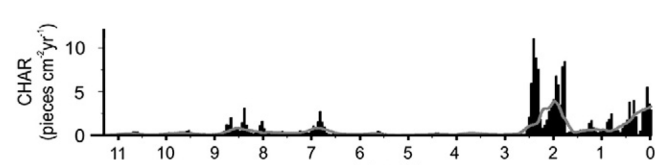

Fig. 6. CHAR values from La Tercera record. The interpolated charcoal accumulation rates (CHAR) are represented in black; the gray line represents the background CHAR (modified from Sottile et al., in press).

whereas fluctuations in geochemical parameters were interpreted in terms of lake levels fluctuations under overall drier conditions since 6300 cal yr BP (Haberzettl et al., 2005). These conditions are also observed in Chorrillo Malo 2 archeologic site, located in the south of Lago Argentino in the modern steppe, by an increment in shrub taxa from 8500 until 4000 cal yr BP (Mancini, 2002). This evidence as well as an increase in *Nothofagus* between 8000 and 8700 and 7500 cal yr BP in La Tercera and Laguna Potrok Aike records suggests that in these periods of time the westerly winds and the precipitation gradient were the strongest of the Holocene (Mayr et al., 2007; Wille et al 2007; Moy et al., 2009). The westerlies would bring more Andean-pollen to the steppe by a maximum in wind speed. Strong westerlies, which means higher wind speed and more precipitations in the west side, are also recorded by the dominance of *Nothofagus* forest in Río Rubens, Vega Ñandú and Brazo Sur, starting about 7700 cal yr BP (Huber and Markgraf, 2003; Villa-Martínez and Moreno, 2007; Wille and Schäbitz, 2009). Moreover, in the Cerro Frías record, an open *Nothofagus* forest between 8000 and 7000 cal yr BP and a dense *Nothofagus* forest between 5800 and 3200 cal yr BP similar to the modern one, developed (Mancini, 2009). The low fire activity in Cerro Frías during the mid-Holocene and the highest *Nothofagus* values, illustrate the highest Holocene precipitation values in this area which is close to the modern forest (Tonello et al., 2009a; Sottile et al., in press). Geochemistry and diatoms record from Isla de los Estados (eastern Tierra del Fuego island, and directly situated in the Southern westerlies belt during the austral summer) also indicate strong westerlies between 8500 and 4500 cal yr BP (Unkel et al., 2010).

In Lake San Martin area, between 3000 and 100 cal yr BP the pollen spectra shows conditions wetter than today that are interpreted from an increase in herb taxa and a pronounced decrease in shrubs. The signal of high levels of CHAR in La Tercera may be linked to an increment of fuel accumulation produced by high precipitation values (Sottile et al., in press). The fluctuations of the Lago Cardiel levels during the late Holocene are a good example for the illustration of the environmental variability during this time (Markgraf et al., 2003). Moisture levels in the Patagonian steppe became higher and grassy vegetation could expand (Wille et al., 2007). In Chorrillo Malo 2, the increment in grasses is observed after 4000 cal yr BP suggesting an increase in moisture (Mancini, 2002). At higher latitudes Huber et al.

(2004), Villa-Martínez and Moreno (2007), Wille and Schäbitz (2009) suggest an increase in moisture after 2500 cal yr BP. However, in the Cerro Frías record, *Nothofagus* values decreased suggesting an open forest and a grass steppe developed after 800 cal yr BP (Mancini, 2009). The evidence of four Neoglacial glacier advances of South Patagonian Icefield (Aniya, 1995; Glasser et al., 2004) suggests higher precipitation during the late Holocene (Villalba et al., 2005; Moreno et al., 2009) coincident with a strong cooling at this time (Glasser et al., 2004). Sedimentological analysis from Lago del Desierto (49°02′ S; 72°51′ W, close to the Southern Patagonia Icefield), allow inferences on past temperature during the late Holocene. This analysis allowed us to establish the start of the Medieval Climate Anomaly (MCA) after AD 850 (1100 cal yr BP). Moreover, the Little Ice Age (LIA) cooling and the subsequent 20th century warming can be traced in sediment records observed for southern South America (Kastner et al., 2010). As indicated by the chronology of human occupations, the impact of climatic oscillations on hunter-gatherer societies was strong. Very shrap fluctuations are recorded in the evidence of human presence during the last 1000 yr (Morales et al., 2009).

During the last century a change in the environmental conditions was observed from La Tercera core. The moisture availability decreased in comparison with the previous interval, and this is reflected by an increase in shrub taxa and Chenopodiaceae that would indicate fluctuating water levels. Sediment and pollen proxies from Laguna Potrok Aike (Wille et al., 2007) and grass steppe expansion with *Nothofagus* forest reduction in the Cerro Frías record (Mancini, 2009) also suggest a moisture decrease during the last century. Changes in response to the European settlement are also observed in Estancia La Tercera area by *Rumex acetosella* presence.

7. Conclusion

During the Pleistocene–Holocene transition, a dwarf-shrub steppe under arid conditions similar to the ones in the present day extra-Andean area was inferred. These arid conditions could have been the result of a southward shift of the westerlies. Since the beginning of the Holocene, the reconstructed steppe communities in Lake San Martin area resemble the present day ones. *Nothofagus* forest expansion started in the Andean zone, while in the extra-Andean zone a grass steppe dominated up to 8000 cal yr BP suggesting higher moisture availability than before. The westerlies appear to have exerted greater influence at 50° S by comparison with higher latitudes, producing strongly variable moisture conditions for *Nothofagus* forest expansion during the early Holocene (Heusser, 1995; Villa-Martínez and Moreno, 2007). A warming pulse of about 2.5 °C occurred between 8000 and 7500 cal yr BP, in the Southeast Pacific, might be related to palaeoclimatic changes during the early to mid-Holocene climatic transition (Kim et al., 2002). During the mid-Holocene, the record shows an increment in shrub taxa indicating low moisture availability, whereas *Nothofagus* forest expanded in the Andean zone. These vegetation patterns during the mid-Holocene imply an intensification of westerlies and a steepening in the west-east precipitation gradient. In the late Holocene until 100 cal yr BP the grasses began to increase again in the Lake San Martin basin suggesting the return of wetter conditions and a change from dense to open *Nothofagus* forest occurred in the Andean zone. In the last century important changes related to seasonal fluctuation and human impact are inferred from the record.

These vegetation and fire frequency changes from sites located in the modern forest-steppe ecotone and in the extra-Andean zone allowed us to evaluate changes in the precipitation gradient and intensity of westerlies since Pleistocene–Holocene transition when the limit between the grass steppe and the semi-arid region was shifted to the west. Thus, during the early Holocene the dominance of a grass steppe in the studied area suggests that this limit was shifted to the east. During the mid-Holocene, changes in the steppe are related to variations in conditions of moisture and temperature and a marked rainfall gradient from west to east, while the development of grass steppe suggests the return of more humid conditions in La Tercera area during the late Holocene. In the last centuries, the limits between different types of steppes were established as result of climate and human forcing. According to Tonello et al. (2009a), *Nothofagus* pollen-type is a good indicator of precipitation; the Andean forest extension and density would support the interpretations of changes in plant community ecotones and in the precipitation gradient; however changes in temperature and evaporation can force changes in the vegetation units.

The understanding of the palaeoenvironmental history during the Holocene is a contribution to the study of the human occupations that occurred in the southwest of Patagonia during the Holocene. The palaeoenvironmental interpretation suggests that past climatic conditions were different during the moments of human occupation of hunter-gatherer groups who lived in this area since the early Holocene continued intermittently until historical moments (Belardi et al., 2007; Belardi et al., 2010). The occupation history of Lake San Martin basin began during the Pleistocene–Holocene transition. During this time, the hunter-gatherers started to explore the area. The archeologic evidence shows that the occupation continued until historic times. Radiocarbon dates from *Lama guanicoe* with cut marks from archeologic sites near estancia La Tercera indicate that the highest levels of human occupation were during the late Holocene (Belardi et al., 2010) when the moisture availability increased as our interpretation reflects.

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