Veget Hist Archaeobot (2015) 24:267–277
DOI 10.1007/s00334-014-0473-z

ORIGINAL ARTICLE

Vegetation dynamics from Lago San Martín area (Southwest Patagonia, Argentina) during the last 6,500 years

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Received: 9 October 2013 / Accepted: 16 June 2014 / Published online: 29 June 2014

Abstract We report a palaeoenvironmental reconstruction since 6,650 cal. BP from the Lago San Martín area, from a peat-bog sequence, Mallín Paisano Desconocido, located at 48°58′S, 72°14′W. Between 6,650 and 4,500 cal. BP we can infer a shrub steppe dominated by Asteraceae subf. Asteroideae associated with other shrubs under relatively dry conditions, through an intensification of the westerly wind belt and a steepening in the west–east precipitation gradient. From 4,500 to 3,000 cal. BP a shrub-grass steppe development suggests a slight increase in moisture conditions although the environmental conditions remain dry. From 3,000 cal. BP a grass steppe represented by Poaceae and subordinate herbs developed, suggesting an increase in moisture availability and weaker westerly flow precipitation. The last 400 cal. BP were characterized by a change from grass to shrubby communities which could be related to the beginning of the Little Ice Age, whereas the last century shows signals of anthropic impact. The palaeoenvironmental interpretation from the Lago San Martín basin is based on moisture availability variations in relation to precipitation pattern changes of westerly origin. These trends are consistent with interpretations of records from the Andean and extra-Andean areas. The comparison with other sequences allows us to interpret the palaeoenvironmental changes in the Lago San Martín area and to integrate these variations within a regional framework, interpreting them in relation to southern past climatic changes. At a regional scale, the records show an increase in westerly intensity during the mid-Holocene, whereas weaker westerly flows are postulated for the late Holocene.

Keywords Southern Patagonia · Lago San Martín basin · Mid and late Holocene · Palaeoenvironmental reconstruction · West–east environmental gradient

Introduction

Geomorphological and climatic characteristics of southern Patagonia (46°–54°S; 73°–65°W) allow us to study the possible mechanisms and interactions between the responsible agents for environmental variability during the Holocene. Glaciological studies and palaeoenvironmental reconstruction based on multiproxy studies provide information for understanding palaeoenvironmental variability since the late Pleistocene (Mercer and Ager 1983; Mercer 1984; Rabassa and Clapperton 1990; Wenzens 1999; Glasser et al. 2004, 2011; Rabassa 2008; Hein et al. 2010; Strelin et al. 2011) until neoglacial events of the late Holocene (Aniya 1995; Porter 2000; Glasser et al. 2004; Masiokas et al. 2009). Several investigations in the area show changes in the glacial expansion, temperature and precipitation associated with variations of the westerly wind intensity and changes in fire regimes (e.g. Tonello

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Communicated by P. I. Moreno.

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et al. 2009; Glasser et al. 2011; Fletcher and Moreno 2012; Kilian and Lamy 2012; Sottile et al. 2012; Schäbitz et al. 2013). These environmental variations have been pointed out as the main driving forces for variability of the plant communities, inferred from the analysis of different proxies (e.g. pollen, sedimentary charcoal, tree rings, plant macrofossils). The Southern Patagonia Ice Field constitutes the largest continental ice-sheet which is highly sensitive to temperature as well as precipitation changes (Warren and Sudgen 1993). Westerly winds from the South Pacific Ocean are the major source of moisture, whereas temperature and precipitation are the main driving factors of vegetation distribution on both flanks of the Andean range. The strong west–east precipitation gradient produces highly sensitive ecosystems, from the forest on the hyper-humid western side to the dwarf steppe on the arid eastern side of the Andes. The correlation between precipitation and the zonal winds is generally strong in Southern Patagonia and offers an important tool for reconstruction of wind variability patterns using palaeoenvironmental records. The rain-shadow east of the Andes range (with the exception of areas near the Andes range) close to the present-day zone of maximum wind speeds (50°S), displays a negative correlation between zonal wind strength and local precipitation, which results from significant evaporative moisture loss as dry foehn winds strip moisture from the region under the strong westerly flow (Garreaud 2007; Garreaud et al. 2009, 2013). The topography of the Andes and potential advection of eastern moisture produce heterogeneities in the precipitation–atmospheric circulation relationship (Moy et al. 2009). The climatically induced regional vegetation zonation along the west to east environmental gradients can be used to infer past changes in precipitation regimes based on palaeoenvironmental reconstruction. Several authors have made palaeoenvironmental data revisions and syntheses considering diverse proxies. These studies allow us to obtain a picture of past ecosystem changes regarding past changes of the southern westerly wind belt ranging between 49° and 53°S (e.g. Markgraf and Huber 2010; Fletcher and Moreno 2012; Kilian and Lamy 2012; Moreno et al. 2012). However, Holocene palaeovegetation changes on eastern extra-Andean communities have been reconstructed from only few continuous records between 45° and 52°S (Lago Cardiel—Markgraf et al. 2003; Laguna Potrok Aike—Wille et al. 2007; La Tercera—Bamonte and Mancini 2011). La Tercera peat-bog and Laguna Potrok Aike records indicate a development of shrub communities during the mid-Holocene (until ca. 3,000 cal. BP) and an important forest signal suggesting an intensification of the southern westerly wind belt. Then, after ca. 3,000 cal. BP, the records indicate an increase in grass communities associated with more moisture availability, and a decrease in *Nothofagus* pollen type signalling a weakening westerly flow resulting in precipitation decreases in western areas and a lower evaporative potential to the east (Bamonte and Mancini 2011; Wille et al. 2007).

One of the first palaeoenvironmental reconstructions was developed by Aüer and Cappannini (1957) from pollen analysis of a peat-bog and geomorphological descriptions in the Lago San Martín area. Unfortunately, this sequence lacks an accurate chronology for interpreting the changes in the pollen spectrum integrated into a temporal framework. The analysis of a new peat-bog sequence (Mallín Paisano Desconocido), located on the northern shore of Lago San Martín 1 km to the east of the forest in the grass-shrub steppe ecotone, allows us to interpret vegetation dynamics and its possible causes since mid-Holocene, and to understand the establishment of vegetation communities on the west–east environmental gradient in relation to variations of the southern westerly winds. Comparison between Mallín Paisano Desconocido and other pollen sequences located in the Lago San Martín basin and southern Patagonia allows us to interpret the vegetation changes at different scales (meso and regional, Fig. 1) and assess if they respond to the main climatic changes occurred since mid-Holocene.

Environmental setting

The Lago San Martín basin (49°S, 72°W, 210 m a.s.l., Fig. 1) is the most northerly of the valleys reaching eastward from the Southern Patagonian Ice Field. Between the Southern Ice Field and the western side of the lake, a mountainous landscape covers the area with altitudes from 1,500 to 2,500 m a.s.l. On the southern and eastern shore of the lake, the landscape shows an undulating relief shaped by glacial action, surrounded by steep and rocky hillsides (Movia et al. 1987; Pereyra et al. 2002). The basin follows a northwest-southeast direction and is enclosed by a moraine system (Bonarrelli and Nágera 1921; Aüer and Cappannini 1957; Glasser et al. 2011). From cosmogenic nuclide exposure age estimates for glacial landforms, the set of moraines that encloses Lago San Martín is 22.4 ± 2.3 ka in age, representing the Last Glacial Maximum in the valley (Glasser et al. 2011). The present climate is mainly influenced by Southern Hemisphere westerly winds and the topography of the landmass (Mayr et al. 2007). The climate in the Lago San Martín basin is temperate-cold with an annual mean temperature below 5 °C (Borrelli and Oliva 2001). The Andean range slows the moist air passage from west to east generating an extensive rain-shadow effect that controls the climatic patterns in the Patagonian steppes to the east (Paruelo et al. 1998). The strong precipitation gradient decreases from 800 mm in the western shore of the basin to lower than

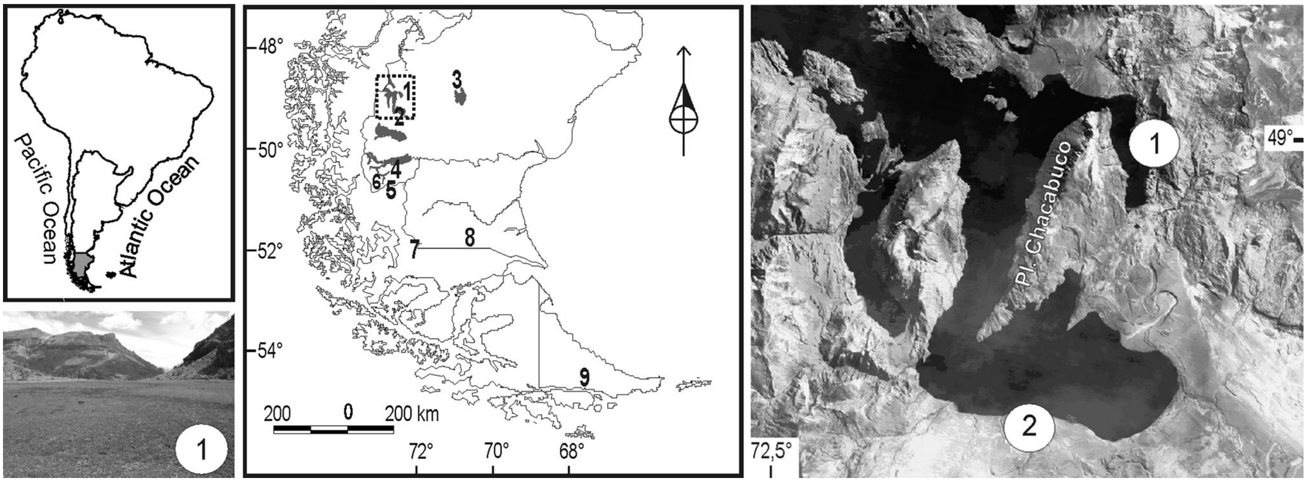

Fig. 1 Map of Southern South America showing the Lago San Martín area. The numbers correspond to sites mentioned in the text: *1* Mallín Paisano Desconocido; *2* La Tercera; *3* Lago Cardiel; *4* Cerro Frías; *5* Lago Guanaco and Vega Ñandú; *6* Brazo Sur; *7* Río Rubens; *8* Laguna Potrok Aike; *9* Haberton

Table 1 Radiocarbon and calibrated ages from the Mallín Paisano Desconocido sequence

Depth (cm)	Lab. code	^{14}C age (years BP)	Calibr. age (years cal. BP)	1 σ range (years cal. BP)	2 σ range (years cal. BP)	Material
30–31	AA93727	564 ± 34	535	518–548	502–560	Gyttja
53–54	AA92538	1,385 ± 43	1,259	1,185–1,203	1,172–1,329	Gyttja-clay
81–82	AA93728	4,317 ± 72	4,819	4,645–4,675	4,569–4,981	Clay
110–111	AA89406	4,491 ± 39	5,041	4,889–4,901	4,871–5,084	Gyttja-clay
187–188	AA89407	5,674 ± 41	6,394	6,319–6,373	6,305–6,488	Gyttja-clay

200 mm in the eastern zones. The vegetation units are not only related to this precipitation gradient (Borrelli and Oliva 2001) but also to topography and edaphic conditions. In the Andean region, where precipitation is the highest, *Nothofagus* forest grows. *Nothofagus pumilio* forest develops on the southwest of the basin, whereas *N. antarctica* patches and grass steppe mosaic covers the eastern península Chacabuco (1 km to the east of Mallín Paisano Desconocido, Fig. 1). The extra-Andean area surrounding the basin is covered by semiarid grass steppe dominated by *Festuca pallescens*, *F. argentina* and the shrub *Nardophyllum obtusifolium.* Other grasses present in the area are *Poa ligularis*, *Stipa chrysophylla* and *F. pyrogea.* Also, *Carex andina*, *Polygala darwiniana* and *Nassauvia darwinii* are present and in some cases, *Junellia tridens*, *Senecio filaginoides* and *Berberis heterophylla* (Movia et al. 1987). The shrub steppe is characterized by *Berberis buxifolia*, *Adesmia boronioides*, *Acaena pinnatifida*, *Taraxacum* sp., *Geranium molle*, *Calceolaria crenatifolia*, Poaceae (such as *Hordeum comosum*, *Stipa ibari*, *S. neaei*, *S. speciosa*, *Poa ligularis*, *Bromus setifolius*; Movia et al. 1987), *Senecio* sp., *Plantago lanceolata*, *Mulinum spinosum*, *Baccharis patagonica*, *Viola* sp., *Bolax* sp., *Cerastium arvense*, *Anemone multifide* and *Osmorhiza chilensis.* The shrub steppe associated with rocky slopes that surround the basin is dominated by *Nardophyllum obtusifolium* associated with *F. pallescens* and a high proportion of *Berberis heterophylla*, *Senecio filaginoides*, *Baccharis patagonica* and *Mulinum spinosum*. The dwarf-shrub steppe covers the easternmost part of the study area and it is composed of *Nassauvia glomerulosa* associated with *F. pallescens*, *Stipa* spp. and *Poa* spp. (Movia et al. 1987). Others important species are *N. ulicina* and *Ephedra frustillata*, cushion plants such as *Azorella caespitosa* and *Acantholippia seriphioides*, with isolated patches of the shrubs *Junellia tridens*, *Berberis heterophylla* and *Nardophyllum obtusifolium. Plantago patagonica* and *P. correae* are native species of this vegetation unit (Correa 1999).

Methods

Core sampling

The core Mallín Paisano Desconocido (1.98 m; 48°58′S; 72°14′W; Fig. 1) was obtained from the northeastern shore of Lago San Martín from a peat-bog located in a small canyon. The core was collected using a Livingstone piston corer. The core was then split along its length and sampled at 1 cm intervals.

Chronology

The chronology was based on five radiocarbon dates that were calibrated using CALIB 5.0.2 (Table 1; Stuiver and Reimer 1993; Stuiver et al. 2005) with the Southern Hemisphere calibration curve (SHCal04; McCormac et al. 2004; Reimer et al. 2004). The age-depth model was constructed with 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. 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 6,650 cal. BP.

Stratigraphy (LOI, lithostratigraphic characterization and magnetic susceptibility)

The stratigraphy of the core was based on analysis of organic matter and carbonate content using loss-on-ignition (*LOI*), lithological description and magnetic susceptibility (k). *LOI* analysis was carried out on samples taken at the same levels as the pollen samples. Samples were dried at 105 °C for 24 h, then ignited at 550 °C for 4 h and at 950 °C for 2 h in a muffle furnace (Bengtsson and Enell 1986; Heiri et al. 2001). The weight loss between each step measures the water, organic matter and carbonate content of the sediment, respectively. The entire core was analysed for magnetic susceptibility to assess changes in the sedimentology. Magnetic susceptibility measurements at low frequency (470 Hz) were performed on the split core with a Bartington MS3E point sensor at 1 cm intervals at the Instituto de Física Arroyo Seco (IFAS, UNCPBA). The calibration was checked every 10 measurements. If the value was within 10 % of the initial calibration value, the calibration was considered still valid.

Pollen analysis

Prior to pollen preparation, samples between 0.8 and 6 g were extracted each 4 cm and dried at 60 °C. Three tablets of *Lycopodium clavatum* spores were added as markers. The samples were sieved through 120 μm mesh screens and treated by the standard procedures of Fægri and Iversen (1989) for pollen extraction: KOH 10 % to remove clays and humic acids, HCl 10 % to remove carbonates, $ZnCl_2$ ($\rho = 2$ g/ml) to separate the mineral fraction by flotation, HF to remove silicates and finally acetolysis was performed. The treatment with $ZnCl_2$ ($\rho = 2$ g/ml) was omitted in some samples in which the sedimentology showed a high content of organic matter. To remove the coarse organic fraction, samples were sieved through 70 μm mesh screens and were treated by a short centrifugation technique to remove the fine organic fraction (Brown 1960). Each taxon is expressed as a percentage of the total pollen sum. *Podocarpus* was excluded because it represents an extra-regional taxon, and *Rumex* because it is related to anthropic impact. Also Cyperaceae and *Myriophyllun* grains, Pteridophyta spores and Zygnemataceae and *Botryococcus* algae were not included in the pollen sum as they represent wetland vegetation and were included in the "wetland taxa" category. Plotting of pollen diagrams and statistical analyses were carried out using the TILIA and TILIAGRAPH programs (TGView 2.0.2, Grimm 2004). Data were transformed to percentages and were grouped by cluster analysis, applying a square root transformation with Edwards dissimilarity coefficient and Cavalli-Sforza's chord distance (TGView 2.0.2, Grimm 2004).

Results

Stratigraphy

From the base of the sequence up to 110 cm, the sediment is composed mainly of gyttja and clays (Fig. 2). However, clays dominate between 160 and 135 cm. Organic matter fluctuates between 16 and 40 % and for this sedimentary unit carbonates average 1.29 %. Total pollen concentration increases up to 110 cm from 7×10^3 to 50×10^3 grain/sediment gram (gr/g). The k values are very low and vary between -0.3×10^{-5} and 3×10^{-5} SI. Between 110 and 70 cm the sediment is composed of clays and the organic matter decreases from 30 % at 110 cm to values lower than 10 % at 70 cm and the carbonate average is 1.16 %. Total pollen concentration fluctuates between 7.5×10^3 and 45×10^3 gr/g and k values increase in this section showing values between 1×10^{-5} SI and 12×10^{-5} SI. Between 70 and 50 cm depth, the clays are still present although gyttja sediments predominate. In this part, organic matter continues with low percentages around 8 % and the carbonate average is decreased to 0.98 %. Total pollen concentration reaches peak values of 350×10^3 gr/g at 60 cm depth. The k values oscillate around 6×10^{-5} SI, reaching the peak value of 30×10^{-5} SI at 51 cm. From 50 cm to the top of the sequence plant fibres appear and clays disappear. Organic matter increases up to 90 % at the top of the sequence; however, total pollen concentration fluctuates between 4×10^3 and 25×10^3 gr/g. The k values fluctuate between 24×10^{-5} SI at 49 cm and

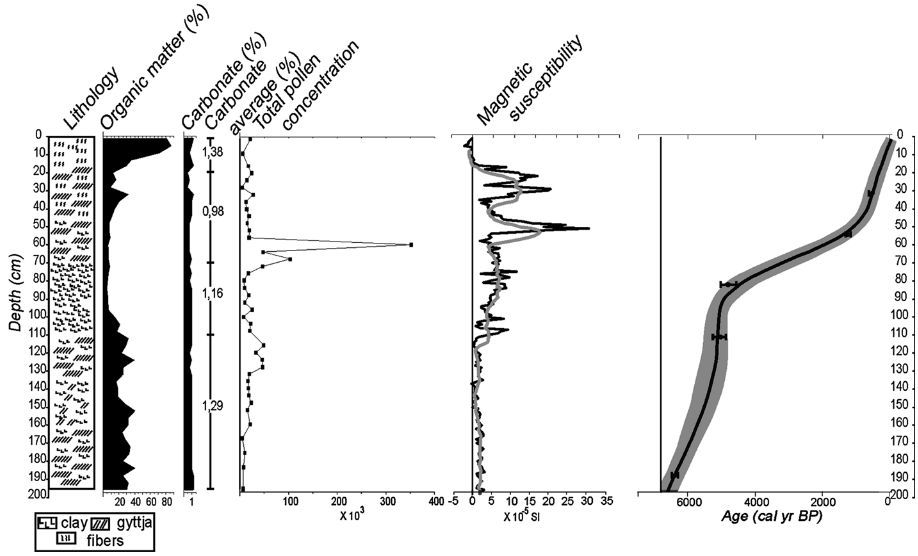

Fig. 2 Lithology, *loss on ignition*, total pollen concentration and magnetic susceptibility (*k*) from Mallín Paisano Desconocido core. A *grey line* represents the moving average values of *k*. Age-depth curve based on five radiocarbon dates, the *grey zones* represent the 95 % confidence intervals

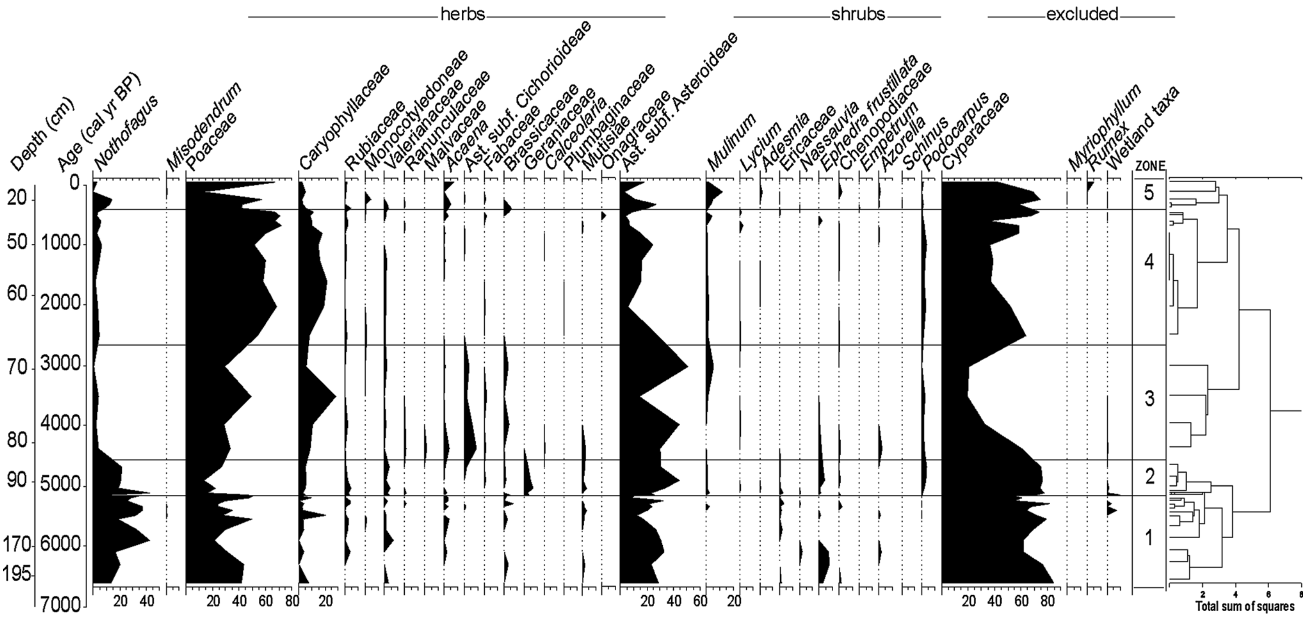

Fig. 3 Percentage pollen diagram and pollen zones

-2.3×10^{-5} SI at 5 cm. The top 20 cm present negative *k* values coinciding with the highest organic matter reached (85 %) and the highest carbonate average (1.38 %).

Pollen sequence

The pollen sequence was divided into five pollen zones by a cluster analysis (Fig. 3):

Zone 1 (196–108 cm; 6,650–5,150 cal. BP): This zone is characterized by high *Nothofagus* values (from 15 to 45 %), accompanied by Asteraceae subf. Asteroideae (between 10 and 35 %) and Poaceae (between 20 and 50 %). *Misodendrum* shows values below 5 %. Among herbs, Caryophyllaceae reaches 20 %, whereas Rubiaceae, Valerianaceae, *Acaena*, Brassicaceae and Mutisiae display values around 5 %. Among shrubs, *Ephedra* reaches 10 % and Ericaceae, *Nassauvia* and *Azorella* present low values (<5 %). Among the taxa excluded from the pollen sum, Cyperaceae fluctuates between 45 and 75 % and wetland taxa reach 5 %.

Zone 2 (108–85 cm depth; 5,150–4,500 cal. BP): *Nothofagus* fluctuates between 10 and 45 %, Poaceae between 15 and 50 % and Asteraceae subf. Asteroideae increases with respect to the previous zone and presents values between 10 and 45 %. Among herbs, Geraniaceae (<10 %), Rubiaceae, Valerianaceae, Mutisiae and Brassicaceae (<5 %)

are present. Among shrubs, Ericaceae (<5 %) decreases until it disappears, whereas *Ephedra*, Chenopodiaceae and *Mulinum* present 5 %. Among the taxa excluded from the sum, Cyperaceae shows 80 % and *Podocarpus* 5 %.

Zone 3 (85–68 cm depth; 4,500–2,800 cal. BP): In this zone a decrease of *Nothofagus* (5 %) is observed. Poaceae fluctuates between 30 and 50 % and Asteraceae subf. Asteroideae between 10 and 50 %. Among herbs, Caryophyllaceae (5–30 %), Asteraceae subf. Cichorioideae (<5–10 %), Brassicaceae, Fabaceae and *Acaena* (<5 %) are the most important taxa. Rubiaceae, Valerianaceae and Mutisiae decrease (<5 %). *Mulinum* shows values lower than 5 % at the top of the zone, whereas *Ephedra*, Chenopodiaceae and *Azorella* decrease until they disappear. Cyperaceae decreases to 20 % and *Podocarpus* continues with low values (<5 %).

Zone 4 (68–28 cm depth; 2,800–400 cal. BP): In this zone Poaceae (45–75 %) dominates along with Caryophyllaceae (5–25 %) and low values (5 %) of other herbs such as Rubiaceae, Monocotyledoneae, Valerianaceae, *Acaena* and Onagraceae. *Nothofagus* presents values between 5 and 15 %. Asteraceae subf. Asteroideae fluctuates between 5 and 30 %. *Mulinum*, *Lycium*, *Ephedra*, Chenopodiaceae and *Azorella* present values lower than 5 % in some samples. Cyperaceae increases (40–75 %) compared to the previous zone and *Podocarpus* continues with 5 %.

Zone 5 (28–0 cm depth; 400–0 cal. BP): The last zone displays a decrease of *Nothofagus* from the bottom (15 %) to the top (<5 %). Poaceae shows values between 20 and 70 %. Caryophyllaceae, Rubiaceae, Monocotyledoneae, Valerianaceae, *Acaena* and Brassicaceae shows values around 5 %. Among shrubs, Asteraceae subf. Asteroideae and *Mulinum* dominate, both with values between 5 and 15 %, whereas *Adesmia*, Chenopodiaceae and *Azorella* present low values (<5 %). Cyperaceae presents values between 40 and 65 % and *Rumex* reaches 5 %.

Discussion

Mallín Paisano Desconocido peat-bog dynamics since the mid-Holocene

From the base of the sequence up to ca. 5,000 cal. BP (110 cm) the record shows high proportion of Cyperaceae (60–85 %). These values suggest the presence of an active, productive peat-bog that could have been associated with the input of organic matter (Figs. 2, 3). Low *k* values suggest a possible reduction of water table levels resulting in low moisture availability. Between ca. 5,000 and 3,000 cal. BP (110–70 cm) the record shows intermediate *k* values, clay sediments and wetland taxa are frequent suggesting an increase in water table levels. From ca. 3,000 cal. BP to the present (70–0 cm), *k* values increase and fluctuate indicating more moisture availability. Higher values of organic matter in the sequence are registered between 100 cal. BP and the present. The Cyperaceae rise would be related to peat-bog recovery during this period and the *k* decline suggests drier conditions (Figs. 2, 3). The carbonate values were not considered in the interpretations of past environmental condition variations because they are minor at 5 % (Heiri et al. 2001).

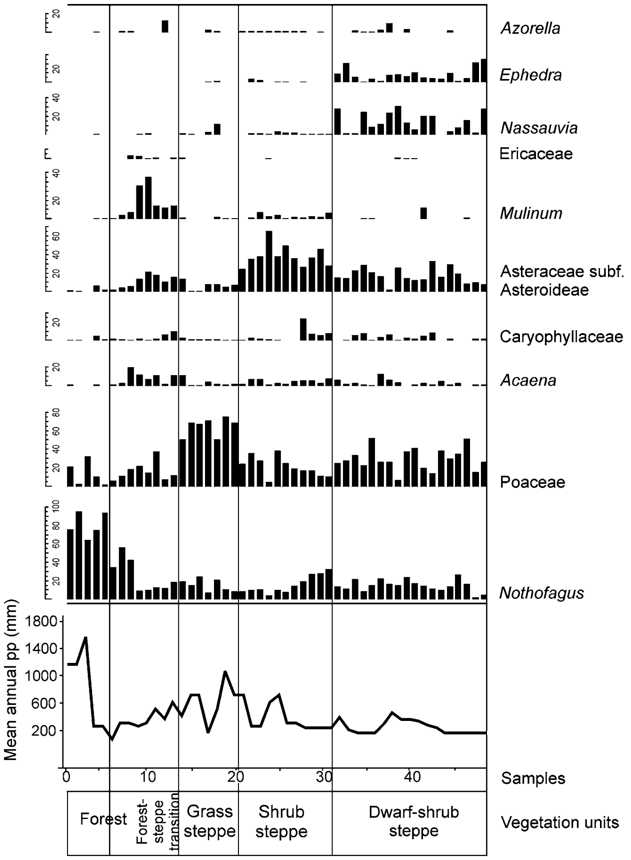

Fig. 4 Main pollen variables (in percentages) from surface samples across the west to east environmental gradient (modified from Bamonte and Mancini 2011). The precipitation values were obtained from Hoffman (1975)

Vegetation dynamics from Mallín Paisano Desconocido

Several investigations of pollen-vegetation relationships have been carried out in Patagonia at different scales throughout the west–east precipitation gradients (e.g. Bamonte and Mancini 2009, 2011; De Porras 2010; Mancini et al. 2012; Bamonte 2012; Marcos and Mancini 2012). In the modern analogous model published by Bamonte and Mancini (2011), 49 samples were included, representatives of different vegetation units between 73°–71.5°W and

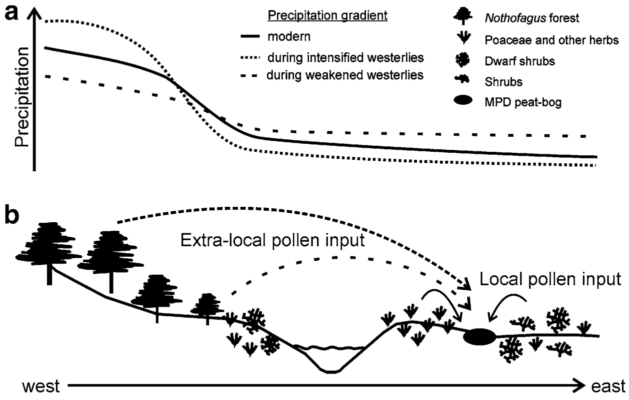

Fig. 5 **a** Schematic model of the modern and past west-east precipitation gradient on the northeastern shore of Lago San Martín. **b** Schematic model of the main local and extra-local pollen input tracks based on the assumptions of Jacobson and Bradshaw (1981) and Bianchi and Olabuenaga (2006). *Continuous arrows* indicates the main pollen input tracks, *dashed arrows* indicate lower pollen input tracks

47.5°–50.6°S, along an west–east precipitation gradient (Fig. 4) and the model was applied in the interpretation of the fossil samples. This model suggests close relationships between pollen–vegetation representation and precipitation at a regional scale. Combining this pollen–vegetation relationship with a pollen dispersion model (Jacobson and Bradshaw 1981), the Mallín Paisano Desconocido pollen record is probably influenced by local and extra-local pollen input. Thus variations of *Nothofagus* pollen percentages may be related both to variations in forest development westward (e.g. Península Chacabuco) or linked to intensification/weakening of the westerlies (extra-local pollen input). On the other hand, pollen types related to herbs and shrubs (usually less dispersed) make up most of the local pollen input (Fægri and Iversen 1989; Bianchi and Olabuenaga 2006) and allowed us to hypothezise about local extra-Andean past vegetation variations (Fig. 5). Linking both, Andean (extra-local) and extra-Andean (local) vegetation dynamics allowed us to compare the synchronicity and phase or antiphase variability of the moisture regimes.

From the base of the sequence at 6,650 up to 5,150 cal. BP, the pollen record shows a shrub steppe development over extra-Andean areas, suggesting drier conditions than present (Figs. 3, 4). This steppe was characterized by Asteraceae subf. Asteroideae (probably *Baccharis patagonica*) associated with *Ephedra*, *Nassauvia* and *Azorella* until 6,000 cal. BP. On the other hand, high values of *Nothofagus* suggest forest development in Andean zones near the studied site (península Chacabuco) together with Ericaceae at ca. 6,000–5,000 cal. BP suggesting a slight increase in moisture availability westward (Figs. 3, 4). The Ericaceae family is represented by *Gaultheria mucronata* that grows associated with forest zones (Guerrido and Fernandez 2007). The Brassicaceae family includes impact genera (e.g. *Chorispora tenella*), but also includes species that grow in humid areas in close relationship with the forest (e.g. *Draba andina*, *Noccaea magellanica* and *Cardamine* sp.) (Correa 1984; Guerrido and Fernandez 2007). This *Nothofagus*-Ericaceae (and Brassicaceae) association suggests the presence of forest cover in the Andean zone and the Chacabuco peninsula.

Between 5,150 and 4,500 cal. BP, the record shows a high proportion of shrubs and a notable decrease of Poaceae (Fig. 3). We infer that herbs such as Rubiaceae, Valerianaceae (e.g. *Valeriana carnosa*) and Geraniaceae might grow dispersed within the shrub matrix (Guerrido and Fernandez 2007). *Nothofagus* and Ericaceae decrease sharply towards 4,500 cal. BP indicating that steppe replaced forest communities over the Andean zone.

Between 4,500 and 2,800 cal. BP, the most significant changes in the sequence are observed. For this time we infer the beginning of a shrub-grass steppe development dominated by Asteraceae subf. Asteroideae and Poaceae, with subordinate Caryophyllaceae and Asteraceae subf. Cichorioideae (e.g. *Hypochaeris incana*) (Fig. 3). These changes in steppe composition suggest a gradual increase in moisture availability for the extra-Andean area; however, *Ephedra*, *Azorella* and Asteraceae subf. Asteroideae values suggest that environmental conditions remain dry. In the Andean zone, the forest shows an abrupt decrease inferred from *Nothofagus* values (Fig. 3).

Between 2,800 and 400 cal. BP, a grass steppe, represented mainly by Poaceae and Caryophyllaceae, dominates over extra-Andean areas suggesting an increase in moisture availability, while shrubs decrease markedly. *Nothofagus* values suggest that, in the Andean area, the forest remains as in the previous zone period.

The pollen record shows changes between 400 and 100 cal. BP. The *Mulinum*, *Adesmia*, *Acaena*, Caryophyllaceae, Brassicaceae and Asteraceae subf. Asteroideae association indicates a vegetation similar to the modern forest-steppe transition (Figs. 3, 4). The *Nothofagus* increase may be related to a slight forest re-establishment in the Andean zone. The last 100 cal. year BP are characterized by dry conditions over Andean zones as *Nothofagus* decreases showing an open forest, which may be related to a decreasing humidity trend or anthropogenic activities, such as forest clearance by fire and grazing pressure. On the other hand, the increase of shrubs also gives evidence of lower moisture availability. Chenopodiaceae could be reflecting seasonal variations in water table levels across the peat-bog where, during more humid seasons, *Myriophyllum* grows. The presence of *Rumex* indicates anthropic impact after European settlement (Fig. 3). The

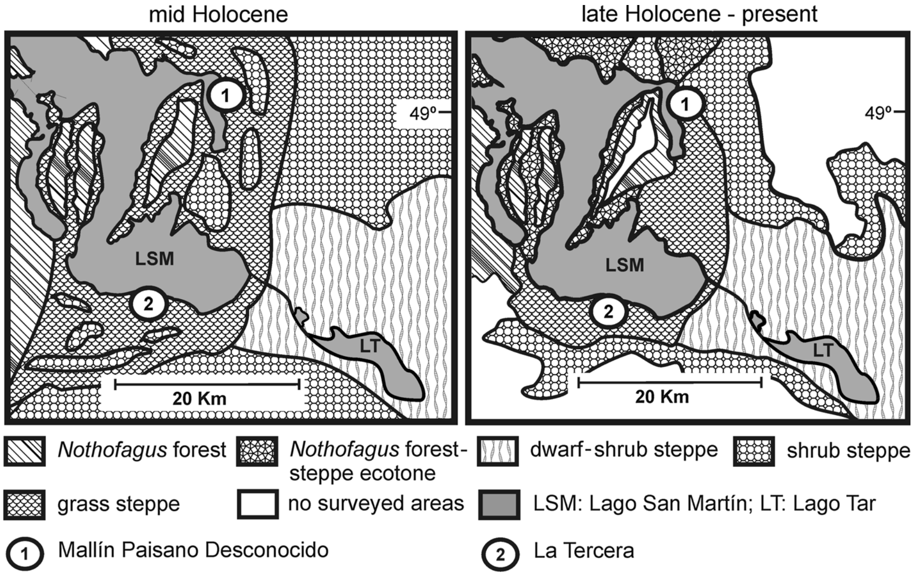

Fig. 6 Vegetation communities reconstruction from Lago San Martín area since the mid-Holocene. The late Holocene—present map was based on Movia et al. (1987)

development of the plant communities is consistent with the moisture availability conditions inferred from interpretation of the peat-bog dynamics from the mid-Holocene to the present.

Regional integration

On the southern shore of Lago San Martín, Bamonte and Mancini (2011) analysed the sequence from Mallín La Tercera. The integration of the La Tercera and Mallín Paisano Desconocido sequences allows us to establish the dynamics of the plant communities of Lago San Martín since the mid-Holocene (Fig. 6) and to contextualize these changes in a regional framework.

During the mid-Holocene (ca. 6,000–3,000 cal. BP) the La Tercera (Bamonte and Mancini 2011) and Mallín Paisano Desconocido palaeoenvironment reconstructions show a steppe dominated by shrubs suggesting low moisture availability in the extra-Andean Lago San Martín basin. In agreement with this scenario, Sottile et al. (2012) inferred low fire activity from the La Tercera peat-bog charcoal record, probably linked to fuel discontinuity in extra-Andean communities. On the northeast shore, Bamonte et al. (2013) studied a pollen sequence from an archaeological site Cueva del Paisano Desconocido; the top of this sequence includes the mid-Holocene represented by high shrub proportions. This sequence is composed mainly of local pollen communities, thus the pollen signal suggests low moisture availability over extra-Andean areas in agreement with inference from the continuous peat-bog sequence (Bamonte et al. 2013). At Mallín Paisano Desconocido *Nothofagus* values remain high up to the end of the mid-Holocene (ca. 4,500 cal. BP), probably related to high moisture availability in Andean communities. These palaeoenvironmental conditions for the Lago San Martín area are also observed in other lake and peat-bog sequences located further south. In Laguna Potrok Aike, shrub steppe increases since ca. 8,700. cal. BP and during the mid-Holocene suggest dry conditions in extra-Andean communities (Wille et al. 2007), whereas an increase in *Nothofagus* pollen type at 7,500 cal. BP suggests that the westerlies and precipitation gradient were the strongest of the Holocene (Mayr et al. 2007; Wille et al. 2007; Moy et al. 2009). At 50°S the Cerro Frías and Península Avellaneda Bajo (PAB) peat-bog records suggest the presence of a denser *Nothofagus* forest between 5,800–3,200 cal. BP and 5,500–3,500 cal. BP respectively (Mancini 2009; Echeverria et al. 2014), and the low fire activity suggests the occurrence of high amounts of precipitation over Andean communities (Tonello et al. 2009; Sottile et al. 2012; Echeverria et al. 2014). The high precipitation values in the Andean zone have also been evidenced by the dominance of *Nothofagu*s forest in Río Rubens, Vega Ñandú, Lago Guanaco, Brazo Sur and Harberton since 7,700–7,500 cal. BP (Huber and Markgraf 2003; Villa-Martínez and Moreno 2007; Moreno et al. 2009; Wille and Schäbitz 2009; Markgraf and Huber 2010). A synchronous and zonally symmetric anti-phased moisture regime change across the current zone of maximum westerly wind speeds reflects an increase in westerly intensity during the mid-Holocene (Fletcher and Moreno 2011, 2012). Stronger westerly flow inhibits the easterly-sourced precipitation, resulting in drier conditions over extra-Andean zone leading to higher evaporation (Garreaud 2007; Garreaud et al. 2009, 2013), whereas high moisture patterns were inferred for Andean communities (Fig. 5 a), between 7,000 and 3,000 cal. BP. The intensification of the southern westerly wind belt during the mid-Holocene has also been proposed by Fletcher and Moreno (2012) in a review of several pollen sequences from New Zealand, Australia, Africa and Patagonia.

Between ca. 3,000 and ca. 400 cal. BP, Mallín Paisano Desconocido and Mallín La Tecera (Bamonte and Mancini 2011) show an increase in moisture availability by development of a grass steppe while the forest signal decreases markedly. The fuel continuity in extra-Andean communities inferred from the La Tercera sequence between ca. 2,500–1,500 cal. BP probably favoured a higher fire frequency with respect to the previous period. This vegetation pattern may be linked to higher moisture availability by high precipitation values for extra-Andean areas (Sottile et al. 2012). The grass steppe development and a decrease in forest signal in the Andean zone are also observed in the Laguna Potrok Aike record (Wille et al. 2007). In south-western Andean communities (Vega Ñandú, Cerro Frías, Lago Guanaco, Brazo Sur and PAB), pollen records suggest the presence of open forest which may be related to lower moisture availability than during the mid-Holocene, probably linked to a weakening of the westerly winds (Fig. 5a) between 3,500 and 2,500 cal. BP (Villa-Martínez and Moreno 2007; Mancini 2009; Moreno et al. 2009; Wille and Schäbitz 2009; Echeverria et al. 2014). During weaker westerly flow, precipitation decreases in Andean areas. In eastern extra-Andean areas, weaker westerly flow enables the incursion of easterly precipitation sources (Garreaud 2007; Garreaud et al. 2009, 2013). The high palaeoenvironmental variability during the last millennium is related to events such as the Medieval Climate Anomaly (MCA, 950–750 cal. BP) and the Little Ice Age (LIA, 380–50 cal. BP). However, the magnitude, timing and nature of these events have not been clearly delineated in southern South America (Moy et al. 2009). The pollen records from Mallín Paisano Desconocido show a dominance of grass steppe in extra-Andean communities in the Lago San Martín basin during the MCA suggesting higher moisture availability than during the LIA. There is a significant change at the beginning of the LIA (ca. 400 cal. BP) from grass to shrubby communities. Palaeoclimatic models and glacier records suggest temperatures lower than present during the LIA (Masiokas et al. 2009; Neukom et al. 2010). Changes in temperature and moisture availability may have driven important vegetation changes, favouring dominance of cushion plants such as *Mulinum* and *Azorella* instead of grass species. During the last 100 cal. year BP, the increase in shrubs may be related to drier conditions, or have been driven by high grazing pressures. This lower moisture availability has also been pointed out at other sites (e.g. Cerro Frías and Vega Ñandú) by a signal of forest reduction. Human impact signals were recorded on a regional scale and were mainly indicated by the presence of *Rumex* in relation to European settlement.

There are two quantitative precipitation reconstructions for Southern Patagonia, the Cerro Frías record located in the modern forest-steppe ecotone (Tonello et al. 2009) and Laguna Potrok Aike in the grass steppe (Schäbitz et al. 2013), giving information on palaeoprecipitation from south-west and south-east Patagonia respectively. The palaeoenvironmental reconstruction from the Lago San Martín area shows a decrease in moisture availability during the mid-Holocene across extra-Andean communities, whereas after ca. 3,000 cal. BP the conditions became wetter up to the last 400 years cal. BP when humidity may have slightly decreased. This scenario is consistent with the inferences of Schäbitz et al. (2013) from the Laguna Potrok Aike pollen record. This showed lower precipitation between 8,000 and 2,500 cal. BP with pronounced dry phases between 4,600 and 3,800 cal. BP and the last century, whereas precipitation reconstruction from Cerro Frías suggests the highest values between 8,000 and 3,000 cal. BP (Tonello et al. 2009). These precipitation patterns suggest an intensification of the westerly wind belt and a steepening in the precipitation gradient from west to east. Since ca. 3,000 cal. BP, moisture availability became higher over steppe environments and decreased in western areas, as inferred from reconstructions of vegetation and precipitation patterns (Mancini 2009; Tonello et al. 2009; Sottile et al. 2012; Echeverria et al. 2014).

Conclusions

The southern Patagonia plant communities were sensitive to climatic changes that occurred during the Holocene. In the Lago San Martín area, since the mid-Holocene, pollen records and sedimentological inferences have recorded differences in plant communities and peat-bog dynamics associated with variations in moisture availability. During the mid-Holocene up to ca. 3,000 cal. BP, the records analysed for the area indicate a steppe with a high representation of shrubs, suggesting lower moisture availability through an intensification of the westerly wind belt and a steepening in the west–east precipitation gradient. However since ca. 3,000 cal. BP, grasses began to dominate due to an increase in moisture availability until 400 cal. BP when scrubland vegetation developed under drier conditions across extra-Andean areas through a weakening of the westerly wind belt. Changes of steppe communities in extra-Andean areas from 6,500 to ca. 1,000 cal. BP may have been opposite to those of Andean forest communities. The Mallín Paisano Desconocido record shows wet conditions during the MCA and a decrease in moisture availability and lower temperatures during the LIA period. According to this, from ca. 1,000 cal. BP to the present the records show the same trend as that for Andean forest communities. Nevertheless more continuous terrestrial records of pollen and other plant and geochemical proxies from the eastern extra-Andean areas are needed to disentangle past environmental changes in southern Patagonia.

Acknowledgments This research was financially supported by CONICET (PIP 1265) and UNMdP (EXA 510/10; EXA 602/12). We thank the National Science Foundation (NSF) Arizona and T. Jull for financial support for AMS radiocarbon dating. We are grateful to the Díaz (Ea. La Federica) and Muruzábal (Ea. Sierra Nevada) families for allowing access to the workplace and to Marcos Emanuel Echeverría for logistic support in the field and critical discussions.

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