

# New insights into postglacial vegetation dynamics and environmental conditions of Península Avellaneda, southwest Patagonia, revealed by plant macrofossils and pollen analysis

M.E. Echeverría<sup>1\*</sup>, G.D. Sottile<sup>1</sup>, M.V. Mancini<sup>1</sup> and S.L. Fontana<sup>2</sup>

<sup>1</sup> Universidad Nacional de Mar del Plata-IIMYC-CONICET, Argentina

<sup>2</sup> University of Göttingen, Germany

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## SUMMARY

Reconstruction of the history of past events becomes more objective when considering an increased number of possible indicators. Combining plant macrofossil analysis with pollen analysis has the potential to give a more detailed picture of the composition of the local vegetation. Patagonia has been the focus of several palaeoclimatic studies, in particular of latitudinal variations in southern westerly winds, which have global implications. However, palaeoecological reconstructions using plant macrofossils in conjunction with pollen analysis are still scarce. We analysed the plant macrofossils contained in two peat sequences from Península Avellaneda (located in the Lago Argentino basin, southwest Patagonia) and integrate these results with pollen information. Plant macrofossils and pollen records provide a well-resolved history of vegetation and catchment conditions starting from *ca.* 13,000 cal yrs BP. We also investigated the development of plant communities following the retreat of glaciers, with emphasis on the expansion of *Nothofagus* species (which were restricted under glacial climates) and particular reference to *Nothofagus pumilio*. These results provide an example of how plant macrofossil analysis (taxonomic, taphonomic and statistical) in combination with pollen analysis results in a better understanding of postglacial environmental history.

**KEY WORDS:** *Nothofagus* forest, palaeoecology, plant macrofossil analysis

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## INTRODUCTION

Palaeoecological reconstructions based on assemblages of fossils from South Patagonia have provided valuable information on changes in climate (Huber & Markgraf 2003, Villa-Martínez & Moreno 2007, Mancini 2007, Mancini 2009, Moreno *et al.* 2012), species provenance (Tonello *et al.* 2009, Sottile *et al.* 2015) and human impact on the vegetation (Huber & Markgraf 2003). Palaeoecological studies in Patagonia have provided information about changes in vegetation and climate during the late Quaternary at various spatial and temporal resolutions, focusing mainly on forest, forest-steppe ecotone or grass steppe areas (Schäbitz 1991, Huber & Markgraf 2003, Villa-Martínez & Moreno 2007, Mancini 2009, Moreno *et al.* 2009, Wille & Schäbitz 2009, Bamonte & Mancini 2011, Fontana & Bennett 2012, Echeverría *et al.* 2014). Pollen analysis has been the technique commonly used to reconstruct the history of vegetation in Patagonia and to infer the palaeobotanical, palaeoecological and palaeoclimatic history of Quaternary sedimentary sequences. In recent decades, the increased application of multi-proxy research has illustrated the importance of plant

macrofossils in answering questions relating to the environmental evolution of South America during the late Quaternary (Huber & Markgraf 2003, Mauquoy *et al.* 2004, Chambers *et al.* 2007, Recasens *et al.* 2012, Chambers *et al.* 2014). The integration of plant macrofossil analysis with pollen analysis gives a more detailed picture of the composition of the local vegetation and, therefore, a more accurate environmental and climatic reconstruction. Studies combining plant macrofossils and pollen have been productive, particularly in determining tree limits during the Holocene in the Northern Hemisphere (Watts & Winter 1966, Birks 1980, Birks & Birks 2003).

The different vegetation units that occur along the mountain ranges of Patagonia generally reflect gradients in climate variables. Thus, vegetation-scale reconstructions using pollen analysis are well suited for detecting patterns of climate change. However, there are a number of limitations. The lack of taxonomic precision in pollen identification is an important constraint, particularly in Patagonia where some of the most important trees share the same pollen type. Therefore, plant macrofossils, which can often be identified with greater taxonomic precision than pollen, can enhance the interpretation of pollen

records (Birks & Birks 1980) and allow a better reconstruction of vegetation history.

The term ‘macrofossils’ is used to identify parts of plants that are large enough to be seen without high magnification and have the potential to be incorporated into a lake or bog (Birks & Birks 1980). Plant macrofossils are not just seeds or fruits but also vegetative parts like leaves, cuticles, scales, buds, anthers, flower parts, stems, rhizomes and wood. In comparison with pollen, plant macrofossils are much larger and generally produced in smaller numbers. Plant macrofossils are not usually dispersed far from their point of origin, so a macrofossil assemblage reflects the local vegetation around the deposition site. This means that if fossils of upland taxa are found, they provide almost certain evidence that the taxa were growing locally. This information is valuable in reconstructing local upland vegetation and in tracing tree-limit changes, which are often under climatic control (Birks & Birks 2003). Macrofossil analysis complements pollen analysis by emphasising and defining the local vegetation and correcting false conclusions that may be drawn from pollen spectra containing large fractions of pollen which has been transported over long distances. Plant macrofossil assemblages have features that complement the results of pollen analysis, adding new dimensions when the two are studied in conjunction (Birks & Birks 2003). Therefore, plant macrofossils are increasingly being used in multiproxy studies, usually in conjunction with pollen analysis.

Amongst palaeoecological reconstructions in Patagonia using plant macrofossils in conjunction with pollen analysis, the pioneering work by Moore (1978) is notable. He used plant macrofossils from Cueva Mylodon (Última Esperanza, Chile) to provide valuable information on the postglacial vegetation composition of the region. Studies involving the analysis of plant remains from sedimentary sequences are rare. Van der Putten *et al.* (2004) studied macrofossil remains, bryophytes and seeds from a sequence in the sub-Antarctic island of South Georgia, aiming to reconstruct the ecological phases of bog development in the context of climatic changes during the Holocene. Mauquoy *et al.* (2004) and Chambers *et al.* (2007) carried out multiproxy studies on peat deposits in Tierra del Fuego (Argentina) aimed at the reconstruction of climatic changes during the Holocene, with emphasis on the Mediaeval Warm Period and the Little Ice Age and potential links to climatic changes in the Northern Hemisphere. The macrofossil analyses in these studies included the identification of vascular plants, bryophytes, fungi and testate amoebae. Markgraf &

Huber (2010) analysed the peat content, including mosses and roots of vascular plants, of the Rio Rubens sequence (Chile), giving insights into the vegetation history of southern Patagonia.

Reconstructions of the history of past events become more objective when they consider an increased number of possible indicators (Birks & Birks 2003). Watts & Winter (1966), Birks (1980) and Birks & Birks (2003) have shown the importance of combining macrofossil data with pollen analysis in building an understanding of vegetation and palaeoenvironmental changes. The aim of the work reported here was to reconstruct the postglacial vegetation changes and environmental conditions of Península Avellaneda, southwest Patagonia (Argentina). This area is located in the Lago Argentino basin at the eastern side of the Andes, within temperate forests of *Nothofagus* (Figure 1). Two peat sequences were analysed for plant macrofossil remains and pollen in order to characterise the development of local and regional plant communities following the retreat of glaciers. In addition, the hydrological conditions of the mires were evaluated in relation to changes in precipitation and humidity. The incorporation of plant macrofossil analysis into our pollen research allowed us to obtain a more detailed picture of the local vegetation composition and hence a more precise environmental reconstruction than either record alone. Indeed, the comparison between plant macrofossils and the pollen record enable us to hypothesise about past species distribution during the Holocene.

## GEOGRAPHICAL, GEOMORPHOLOGICAL AND CLIMATIC CONTEXT

Patagonia is the southern section of South America, extending from 37 °S to 56 °S (Figure 1a). It is the only landmass situated in the mid latitudes of the Southern Hemisphere (Coronato *et al.* 2008). In Patagonia, the north-to-south oriented Andes have a width of 150 to 200 kilometres and play a fundamental role in the distribution of precipitation across the region. The humid air masses from the Pacific are blocked by the mountain range, causing a rain shadow effect that results in contrasting conditions on the two sides of the Andes, with dry conditions in the east and wet conditions in the west. The general atmospheric circulation patterns, with westerly winds and the barrier of the Andes, determine the strong west–east gradient in precipitation (Garreaud *et al.* 2009, Berman *et al.* 2012). The highest annual precipitation in Argentinian Patagonia is registered at the border

between Argentina and Chile where it reaches 1800 mm, decreasing to 300 mm towards the eastern side of the mountains (Paruelo *et al.* 1998). Patagonia is strongly influenced by southern westerly winds (SWW), which control the amount and latitudinal distribution of precipitation (Bertrand *et al.* 2014). Temperature is also largely determined by the Andes. The distribution of isotherms indicates a southwest–northeast pattern, and mean annual temperature ranges from 3 °C in the southwestern part of Patagonia to 12 °C towards the northeast (Paruelo *et al.* 1998).

The high SWW precipitation in western Patagonia supports extensive rainforests and sustains the temperate glaciers that compose the Patagonian Icefields (Garreaud *et al.* 2009, Masiokas *et al.* 2009). Precipitation variability is one of the most important factors controlling the Patagonian glacier mass balance at millennial scales (Bertrand *et al.* 2014). The Andes are characterised by large valleys and deep basins, evidencing the action of Pleistocene glaciers. Several authors have reconstructed the glacial history of southwest Patagonia for the Last Glacial Maximum and the Holocene. According to Strelin *et al.* (2014), after the Late Glacial Maximum at 13000 cal yrs BP, Lago Argentino glaciers

retreated deep into the cordillera. This pronounced recession continued well into the early Holocene, interrupted only by a minor readvance at 12220 cal yrs BP. During the Holocene, several glacier readvances are documented for the region. A minor advance is recorded for the Lago Argentino basin at 7730–7210 cal yrs BP (Strelin *et al.* 2014), but a much more extensive advance occurred later, between *ca.* 6000 and 5000 cal yrs BP. This important glacier expansion is also well documented at several sites in the Southern Andes (Mercer 1982, Glasser *et al.* 2004, Aniya 2013). Subsequently, a minor advance occurred at *ca.* 3800 cal yrs BP (Moreno *et al.* 2009, Kilian & Lamy 2012, Aniya 2013). Younger glacier expansions are dated to *ca.* 2500–2000 cal yrs BP and *ca.* 1300 cal yrs BP (Glasser *et al.* 2004, Masiokas *et al.* 2009, Aniya 2013, Strelin *et al.* 2014). Readvances occurred during the Little Ice Age, between 600 and 50 cal yr BP. During this period, many glaciers reached their maximum extension at *ca.* 550 cal yrs BP then progressively retreated up to the present (Masiokas *et al.* 2009, Kilian & Lamy 2012).

In the study area, peatlands are formations of postglacial origin and of great importance (Auer & Cappannini 1957). These peatlands contain

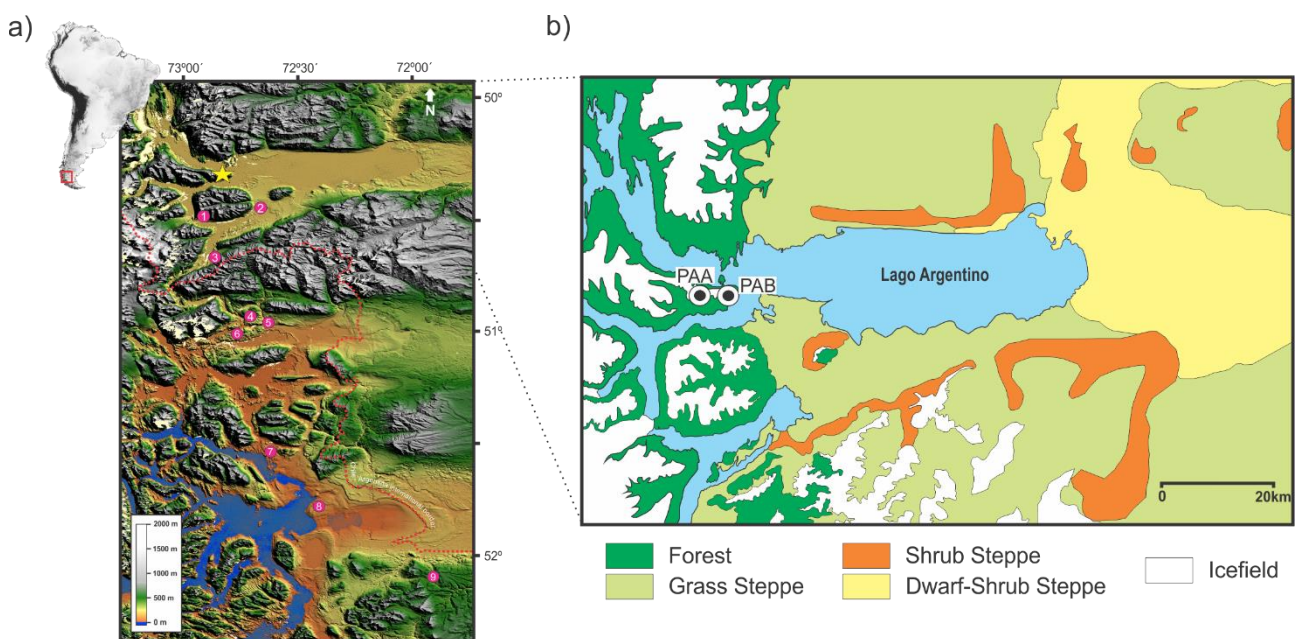


Figure 1. The study area. (a) Location of southwest Patagonia and digital elevation model showing Península Avellaneda (yellow star) and sites mentioned in the text: (1) Perito Moreno (Mercer & Ager 1983); (2) Cerro Frías (Mancini 2009, Tonello *et al.* 2009); (3) Brazo Sur (Wille & Schäbitz 2009); (4) Vega Ñandú (Villa-Martínez & Moreno 2007); (5) Torres del Paine (Heusser 1995); (6) Lago Guanaco (Moreno *et al.* 2009); (7) Lago Eberhard and (8) Pantano Dumestre (Moreno *et al.* 2012); and (9) Rio Rubens (Huber & Markgraf 2003). (b) Lago Argentino basin, showing vegetation units and the locations of the Península Avellaneda Alto (PAA) and Península Avellaneda Bajo (PAB) peat records.

sufficiently well-preserved micro- and macrofossils to represent valuable archives of environmental change during the Holocene. Peatlands of diverse types occur throughout the region. Fundamentally, two edaphic situations can be identified in Santa Cruz, Argentina: (1) mire with high organic matter accumulation, water level close to surface; and (2) mire on hill areas, constantly saturated humic soils (Martínez Carretero 2004). The latter are frequently found in valley bottoms and on gentle slopes and have often developed over lacustrine sediment after glacial retreat (Strelin & Malagnino 2000).

## METHODS

### Site description

The study area, Península Avellaneda, is located in the Patagonian Andes of Argentina, in the western part of the Lago Argentino basin (Figure 1b). It lies within a mixed deciduous forest of *Nothofagus antarctica* and *Nothofagus pumilio*, although in the eastern part of Península Avellaneda a shrub steppe of *Mulinum*, *Berberis*, *Escallonia*, *Gaultheria* and *Embothrium coccineum* has recently developed. This shrub steppe is the product of successional processes following fires that affected the Península during the 1950s (Pérez Moreau 1959). However, remnant patches of *Nothofagus pumilio*, *Nothofagus antarctica* and *Nothofagus betuloides* forest still survive today in the southeastern part of the Península.

The two peat sequences studied were located at different altitudes on the eastern slope of the Península, and in the following are referred to as the Península Avellaneda Alto (PAA) and Península Avellaneda Bajo (PAB) peat records (Figure 1b). The PAA core was collected from a flood mire adjacent to a small lake (Figure 2a) located at 50.26 °S, 72.85 °W, 460 m a.s.l. The bog is dominated by *Sphagnum magellanicum* and surrounded by a dense deciduous forest of *Nothofagus pumilio*. The PAB sequence was recovered from a mire (Figure 2b) located at 50.26 °S, 72.84 °W, 215 m a.s.l. This site is mainly dominated by Cyperaceae and grass species and surrounded by a mixed deciduous forest of *Nothofagus pumilio* and *Nothofagus antarctica*. Large cushions of *Mulinum spinosum* and other shrubs such as *Berberis*, *Escallonia*, *Gaultheria* and *Embothrium coccineum* are also common.

Human activities in Península Avellaneda are recorded in historical accounts beginning in 1873 (Echeverría *et al.* 2014). Farming was largely limited to livestock, while the cultivation of crops was restricted to a few hectares. In 1956, the Península was abandoned and became part of Los Glaciares National Park (Echeverría 2012). These activities have significantly shaped the present vegetation patterns.

### Chronology

The chronologies of the peat sequences (Península Avellaneda Alto and Península Avellaneda Bajo) are based on seven AMS radiocarbon samples and five bulk radiocarbon samples (Table 1). CALIB 7.1 (Stuiver *et al.* 2017) was used to convert the <sup>14</sup>C ages



Figure 2. Photographs of the cored peat bogs: (a) Península Avellaneda Alto; (b) Península Avellaneda Bajo.

to calibrated years before AD 1950 (cal yrs BP). Ages were calibrated with the Southern Hemisphere (SHCal13) calibration curve (Hogg *et al.* 2013).

The best fit to the dates of the PAA sequence was obtained by a Bayesian age-depth model, with the aid of the package "Bacon" using R software (Blaauw & Christen 2011). This method allowed calculation of a weighted mean and a 95 % confidence interval for the calendar age distribution of every level in the sedimentary sequence. In addition, the volcanic ash layers that presented between 102 and 164 cm in PAB and between 228 and 290 cm in PAA were extracted from the models. The age-depth model of the PAB sequence was obtained by MCAge software using a cubic smoothing spline and a bootstrap approach (Monte Carlo sampling, Higuera *et al.* 2009). The confidence intervals for the age-depth model, reflecting the combined uncertainty of all age estimates, were derived from 1000 bootstrapped chronologies. For each bootstrapped chronology, each age used to develop the chronology was selected randomly on the basis of the probable distribution of calibrated  $^{14}\text{C}$  dates. The final chronology represents the median age at each depth from all the runs.

#### Plant macrofossil analysis

Plant macrofossil analysis was performed in the Palaeoecology and Palynology Laboratory of Mar del Plata University (UNMdP) following standard methods (Mauquoy *et al.* 2010). Sub-samples of

known volume (2–15 cm<sup>3</sup>, measured by water displacement) were taken at different levels of the sequences. Clay-rich sub-samples were disaggregated with sodium pyrophosphate ( $\text{Na}_4\text{P}_2\text{O}_7 \cdot 10\text{H}_2\text{O}$ ) and each sub-sample was washed through a series of sieves (125 and 250  $\mu\text{m}$ ) with a gentle spray of water. Then, a small quantity of the residue was suspended in 2–3 mm of water in a shallow dish (e.g., Petri dish) and examined systematically under a stereomicroscope at about 12 $\times$  magnification. Remains that were of interest were picked out and sorted, identified, counted and tabulated. Results were presented as concentrations (number in a standard volume of sediment) calculated from the numbers counted in known sediment volumes. In order to compare macrofossil and pollen data, the macrofossil diagram was plotted using the pollen zonation obtained by CONISS analysis. The results were plotted using the TILIA.GRAPH program (TGView 2.0.4, Grimm 2004). The identification of fossil remains was based on collections of photographic references and herbarium material held by the Palaeoecology and Palynology Laboratory at UNMdP. During the analysis, animal remains (mostly aquatic invertebrates) were also found, identified and tabulated for interpretation. Remains of aquatic animals are common in sediments of lakes and bogs, and can contribute to the reconstruction of past ecosystems (Birks 2001). Fragments of Poaceae and Bryophyta dominated the macrofossil

Table 1. Radiocarbon ages for the PAA and PAB peat sequences. The material analysed was bulk organic matter.

| Core | Sample depth (cm) | Age $^{14}\text{C}$ yr BP | Age cal yrs BP (2 $\sigma$ ) | Lab. Code    |
|------|-------------------|---------------------------|------------------------------|--------------|
| PAA  | 26–27             | 835 $\pm$ 44              | 711 (661–774)                | AA99350      |
|      | 78–79             | 948 $\pm$ 35              | 819 (740–910)                | AA96517      |
|      | 155–156           | 2013 $\pm$ 37             | 1928 (1862–2004)             | AA96516      |
|      | 218–219           | 3782 $\pm$ 40             | 4094 (3972–4238)             | AA89352      |
|      | 318–318.4         | 6233 $\pm$ 28             | 7085 (6978–7179)             | D-AMS 017147 |
|      | 333–334           | 9634 $\pm$ 40             | 10936 (10747–11138)          | D-AMS 14677  |
|      | 352–353           | 10112 $\pm$ 69            | 11613 (11312–11844)          | UBA23299     |
| PAB  | 25–26             | 9 $\pm$ 38                | -2 (-4–0)                    | AA99349      |
|      | 53–54             | 365 $\pm$ 34              | 393 (310–473)                | AA93729      |
|      | 77–78             | 1550 $\pm$ 20             | 1385 (1340–1425)             | UGAMS10587   |
|      | 99–100            | 4555 $\pm$ 55             | 5159 (4968–5320)             | AA89351      |
|      | 181–182           | 7445 $\pm$ 46             | 8245 (8155–8360)             | AA89410      |

assemblages, and their data are expressed on a relative abundance scale: (1) rare, (2) uncommon, (3) frequent, (4) common, (5) abundant (Mauquoy *et al.* 2010).

**Pollen analysis**

Pollen sampling, processing and results from both records have been previously discussed in Echeverría *et al.* (2014) and Sottile (2014). Pollen samples were processed in the UNMdP Palaeoecology and Palynology Laboratory following standard methods. A known weight of sample was analysed after drying in an oven at 60 °C for 6 h. Sample weight ranged from ≤1 g to 8 g. *Lycopodium clavatum* was added to each sample prior to chemical treatment to enable estimation of the pollen concentration (Stockmarr 1971). Samples were sieved through 120 µm mesh and treated with KOH, HCl, ZnCl<sub>2</sub>, HF and acetolysis (Faegri & Iversen 1989). Pollen diagrams were presented as relative diagrams (percentage) of pollen grains and spores. Herbs include Rubiaceae, Scrophulariaceae, Monocotyledoneae, Caryophyllaceae, Lamiaceae, Apiaceae, Ranunculaceae, Polemonium, Plumbago, Malvaceae, Asteraceae subf. Mutisieae, Valeriana, Rosaceae, Chenopodiaceae, Brassicaceae, Convolvulaceae and Euphorbiaceae.

Shrubs comprise *Berberis*, *Empetrum*, *Mulinum*, Verbenaceae, *Gaultheria*, Solanaceae, Fabaceae and *Nassauvia*. Pollen zones were established using CONISS analysis of pollen percentage values, with TILIA.GRAPH 2.0.4 software (TGView 2.0.4, Grimm 2004). In order to compare selected pollen variables individually, pollen concentration data were recorded throughout the sequence so that the pollen accumulation rate (PAR) (grains g<sup>-1</sup> yr<sup>-1</sup>) could be calculated.

**RESULTS**

**Chronology**

Age-depth models and changes in composition of the sediments of the PAA and PAB sequences are detailed in Figure 3. Sedimentary changes are described in Table 2.

**Plant macrofossil and pollen analysis**

*Península Avellaneda Alto (PAA) sequence*

The chronology of the PAA sequence (Figure 3) suggested a basal age of *ca.* 11600 cal yrs BP. The pollen record (Figure 4) was divided into the following five assemblage zones by cluster analysis:

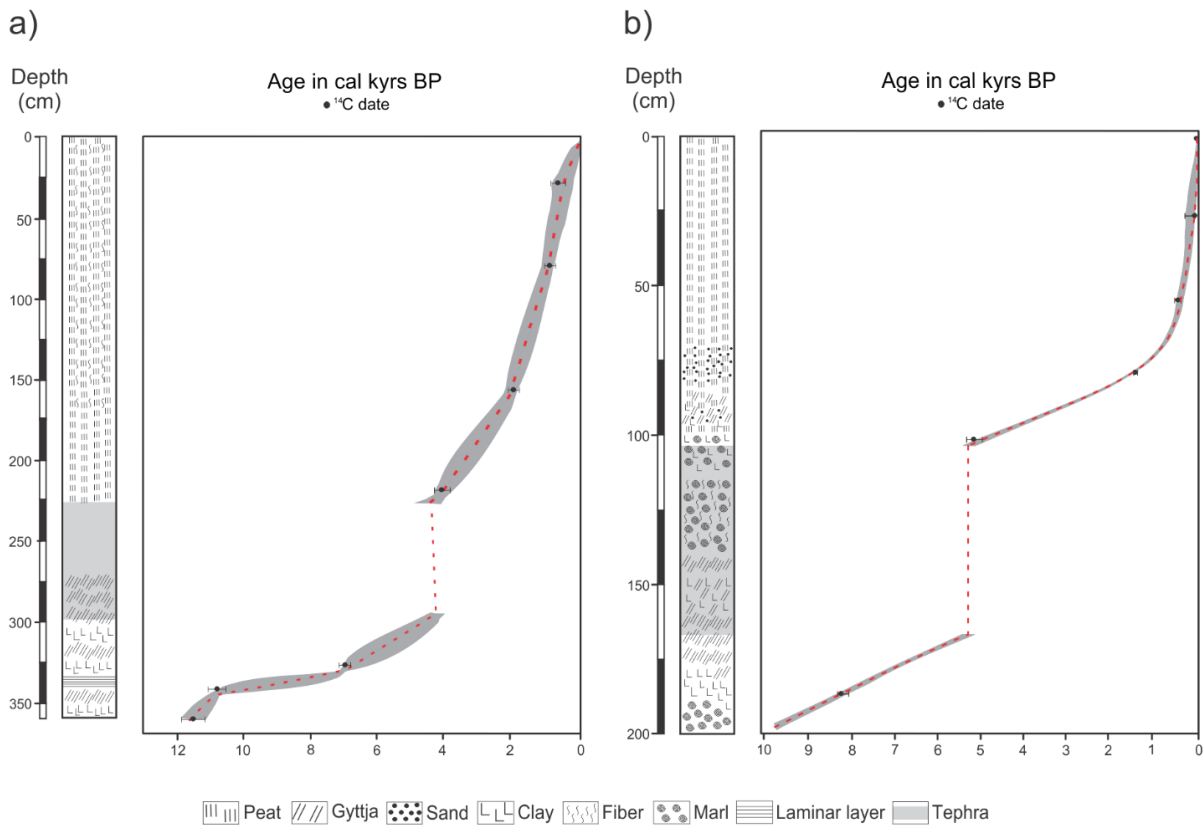


Figure 3. Sediment descriptions (modified from Sottile 2014 and Echeverría *et al.* 2014) and age-depth curves of the peat cores (a) Península Avellaneda Alto (PAA), and (b) Península Avellaneda Bajo (PAB).

Table 2. Sediment descriptions for the PAA and PAB peat cores.

| Core | Depth (cm) | Age (cal yrs BP)     | Character of the sediment   |
|------|------------|----------------------|---|
| PAA  | 0–170      | Present–2400         | peat with high concentration of plant fibres  |
|      | 170–228    | 2400–4500            | mainly peat   |
|      | 228–290    | <i>ca.</i> 4500–4600 | tephra layer with peat  |
|      | 290–333    | 4600–10000           | clay alternating with gyttja  |
|      | 333–342    | 10000–11200          | laminar layers  |
|      | 342–354    | 11200–11600          | primarily gyttja with clay  |
| PAB  | 0–68       | Present–800          | peat with high concentration of plant fibres  |
|      | 68–77      | 800–1500             | peat with presence of sand  |
|      | 77–94      | 1500–4000            | peat with low concentration of plant fibres and dark gyttja                             |
|      | 94–99      | 4000–5000            | primarily peat associated with high levels of clay and small amounts of sand and gyttja |
|      | 99–102     | 5000–5800            | clay and sand   |
|      | 102–165    | <i>ca.</i> 5800–6000 | tephra layer with marl and presence of fibres and clay                                  |
|      | 165–180    | 6000–8200            | peat layer  |
|      | 180–190    | 8200–9600            | mainly clay   |
|      | 190–196    | 9600–10500           | marl  |

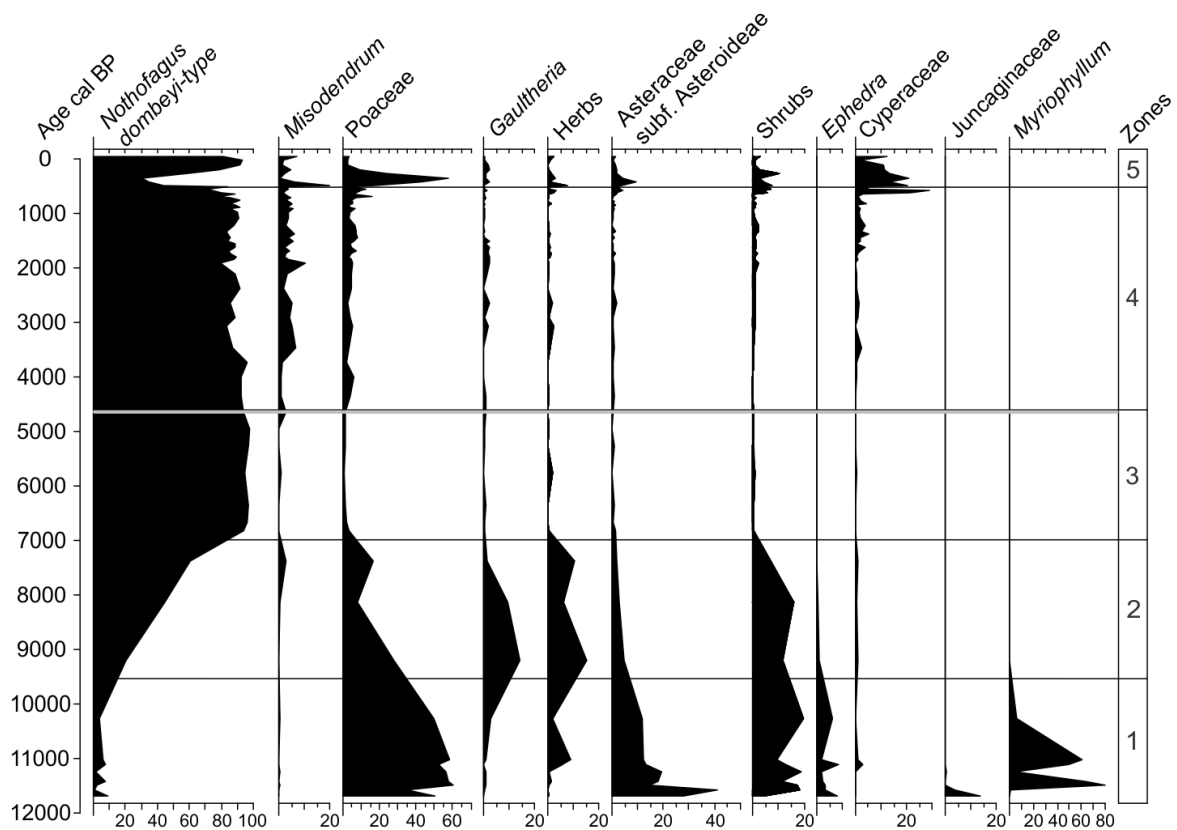


Figure 4. Península Avellaneda Alto (PAA) pollen diagram expressed in percentages (%). Pollen zones obtained by cluster analysis. The superposed grey line indicates the position of the tephra layer.

Zone PAA-1 (11600–9600 cal yrs BP). The pollen record was characterised by Poaceae (40–60 %), herbs, and shrubby taxa such as Asteraceae subf. Asteroideae (<40 %) and *Gaultheria* (<10 %) (Figure 4). *Ephedra* was also present (<10 %). High fractions of *Myriophyllum* (<80 %) accompanied by Juncaginaceae (<15 %) were recorded. Plant macrofossil analysis revealed high concentrations of Charophyta (100–400 oospores per 10 cm<sup>3</sup>), Juncaceae (10–20 seeds per 10 cm<sup>3</sup>), Chironomidae (200–800 head capsules per 10 cm<sup>3</sup>), claddisfly larval cases, oribatid mites (<40 per 10 cm<sup>3</sup>) and resting eggs of Turbellaria (Figure 5). In addition, abundant remains of Poaceae and *Sphagnum* were identified.

Zone PAA-2 (9600–7000 cal yrs BP). The pollen record was characterised by a pronounced decrease in Poaceae values. *Nothofagus* pollen percentages increased towards the top of the zone. *Gaultheria* (<20 %), other shrubs (<20 %) and herbs (<15 %) were also evident. The plant macrofossil record showed a decrease in concentrations of Poaceae, Juncaceae, *Sphagnum* and Charophyta, all of which were represented in only one sample. There was also a decrease in the diversity of aquatic microinvertebrates, in favour of Chironomidae (<800 remains per 10 cm<sup>3</sup>) and Turbellaria.

Zone PAA-3 (7000–4500 cal yrs BP). *Nothofagus* pollen had the highest percentages (90–100 %). *Misodendrum*, *Gaultheria* and other shrubs were also present but with low values. The plant macrofossil record showed high concentrations of *Nothofagus pumilio* leaves and *Nothofagus* spp. seeds, fruits and buds. Remains of *Sphagnum* and aquatic

microinvertebrates (head capsules of Chironomidae, oribatid mites, statoblasts of *Plumatella*, ephippia of *Daphnia*, caddisfly larval cases) were present.

Zone PAA-4 (4500–500 cal yrs BP). *Nothofagus* pollen values declined very slightly (75–90 %). *Misodendrum*, Poaceae, herbs, Asteraceae subf. Asteroideae, *Gaultheria*, other shrubs and Cyperaceae increased in this zone (<10 %). In the plant macrofossil record there was a large decrease in *Nothofagus* remains and an increase in Poaceae remains. *Sphagnum* values did not fluctuate appreciably within this zone. The diversity of aquatic microinvertebrates declined steeply.

Zone PAA-5 (500 cal yrs BP to present). *Nothofagus* pollen and macrofossil remains decreased, and Poaceae increased to close to 60 %. This condition persisted until 250 cal yr BP, when *Nothofagus* pollen increased to 90 % and the concentration of *Nothofagus* macrofossil leaves reached 100 per 10 cm<sup>3</sup>. The highest Cyperaceae pollen values (<30 %) were recorded in this zone. *Misodendrum*, *Gaultheria* and other shrubs were also present. The macrofossil concentrations of *Sphagnum* and Cyperaceae (50 seeds per 10 cm<sup>3</sup>) were high. The macrofossils of aquatic microinvertebrates showed low diversity, highlighting the presence of Oribatida mites (40 per 10 cm<sup>3</sup>).

#### Península Avellaneda Bajo (PAB) sequence

According to the age-depth model (Figure 3), the PAB sequence had a basal age of 10500 cal yrs BP. The pollen record (Figure 6) was divided into five assemblage zones:

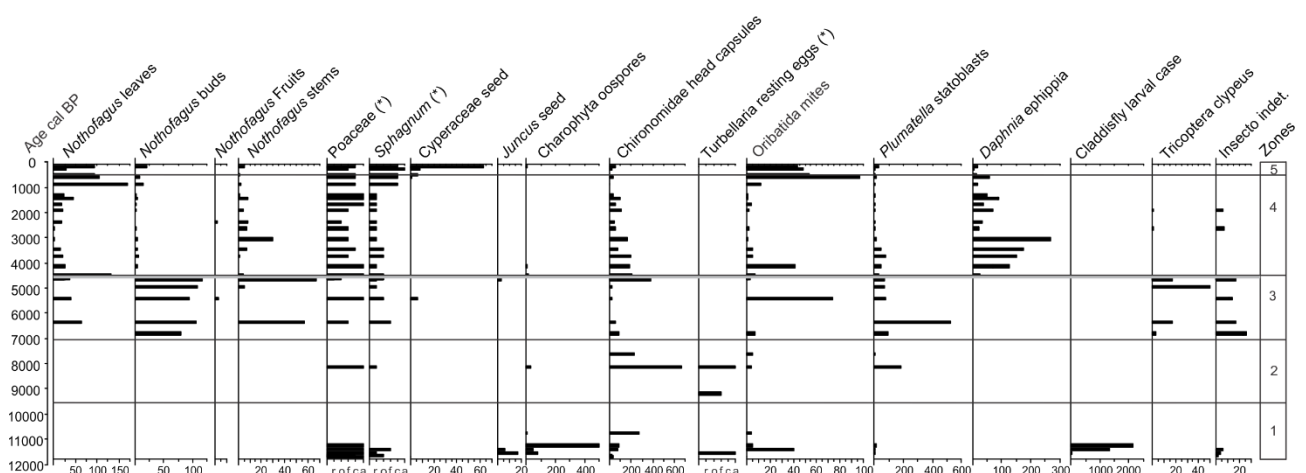


Figure 5. Península Avellaneda Alto (PAA) macrofossil diagram, expressed in terms of concentration (remains per 10 cm<sup>3</sup>), or (\*) relative abundance (r=rare, o=occasional, f=frequent, c=common, a=abundant). The grey line at 4500–4600 cal yr BP represents the tephra layer.



Zone PAB-1 (10500–6000 cal yrs BP). From 10500 to 8000 cal yrs BP the sequence was barren of pollen. After 8000 cal yrs BP the pollen analysis recorded *Nothofagus dombeyi*-type (<20 %), *Misodendrum* (<5 %), Poaceae (<55 %), herbs (<10 %) and Asteraceae subf. Asteroideae (<40 %). The plant macrofossil record (Figure 7) was characterised by an increase in the concentration of grass leaf fragments throughout the period. Stems of *Embothrium coccineum* (20 per 10 cm<sup>3</sup>) and *Gaultheria* (10 per 10 cm<sup>3</sup>) were also present. Seeds of *Juncus* and *Cyperus*, oospores of Charophyta, and annelid eggs were present towards the top of the zone.

Zone PAB-2 (6000–4000 cal yrs BP). *Nothofagus* pollen values increased during this period (<90 %), and Asteraceae subf. Asteroideae increased towards the top of the zone. The plant macrofossil analysis recorded a low concentration of remains. Leaf fragments of Poaceae (frequent and occasional) and *Gaultheria* stems (25 per 10 cm<sup>3</sup>) were present in all samples. Seeds of *Juncus* and *Eleocharis* and remains of Bryophyta were present in only one sample at the beginning of the period.

Zone PAB-3 (4000–2000 cal yrs BP). The pollen record was characterised by the presence of Asteraceae subf. Asteroideae (<55 %). Poaceae, herbs and shrubs were also present (<20 %). The plant macrofossil analysis showed the presence of *Nothofagus* leaves and *Gaultheria* stems (5–50 remains per 10 cm<sup>3</sup>), together with seeds of *Vicia* and *Silene*. The abundance of Poaceae remains did not fluctuate substantially within this zone. Macrofossils of Bryophyta, *Juncus*, *Scirpus* and *Potamogeton*, plus annelid eggs, were also recorded (Figure 7).

Zone PAB-4 (2000–350 cal yrs BP). *Nothofagus* pollen values had increased to 70 % by the end of this period, and *Misodendrum* reached the maximum values of the sequence (30 %). Poaceae, herbs and Asteraceae subf. Asteroideae were present (<20 %), and the Cyperaceae pollen percentage increased (<10 %). The plant macrofossil analysis indicated high concentrations of Poaceae and *Gaultheria* stems (50–120 per 10 cm<sup>3</sup>) together with an increase in the concentration of *Scirpus* seeds (20–100 per 10 cm<sup>3</sup>). Oribatid mites and annelid eggs were present at the top of the zone.

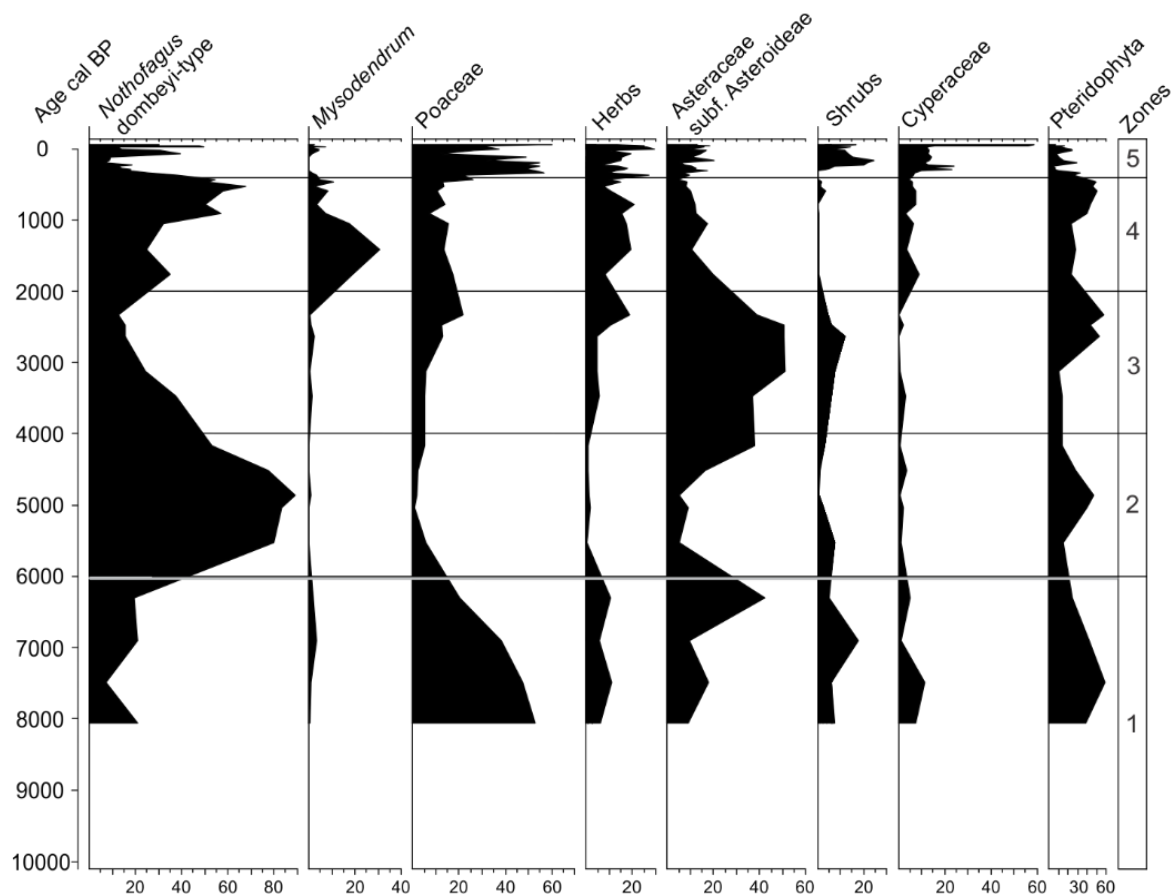


Figure 6. Península Avellaneda Bajo (PAB) pollen diagram expressed in percentages (%). Pollen zones obtained by cluster analysis. The superposed grey line indicates the position of the tephra layer.

Zone PAB-5 (350 cal yrs BP to the present). Poaceae pollen values first increased to 60 %, then declined slightly to the present. In contrast, *Nothofagus* pollen values had increased to about 40 % by the end of the period. The percentages of herb and shrub pollen increased substantially. The plant macrofossils indicated abundant Poaceae remains, *Gaultheria* stems and seeds of *Vicia* and *Silene*. *Nothofagus* leaf remains were present at the top of the zone (5 fragments per 10 cm<sup>3</sup>). In addition, macrofossils of Bryophyta, *Juncus*, Cyperaceae (*Scirpus*, *Eleocharis*, *Cyperus* and *Carex*) and *Potamogeton* were present. High concentrations of Chironomidae, oribatid mites and annelid eggs were also recorded in this zone.

## DISCUSSION

Mires contain detailed records of past biodiversity and environmental change. The value of analyses of plant macrofossils preserved in peat sediments, especially for reconstructing variability in local surface wetness conditions driven by changes in precipitation and evapotranspiration, has been demonstrated by Charman *et al.* (2009) and Chambers *et al.* (2010).

Plant macrofossil data have some features that must be taken into account during numerical analysis and interpretation. These data often contain many zero values, so palaeoecological interpretation is not straightforward. In plant macrofossil assemblages,

non-zero values always indicate presence in the local vegetation (true inference). In contrast, non-zero values in pollen data may reflect local or regional taxa (true presence and, therefore, true inference) or extra-regional taxa (false presence and, therefore, false inference) (Davis 2000).

On this basis it can be inferred that the pollen spectra for Península Avellaneda provide information about local, regional and extra-regional taxa whereas the plant macrofossil data indicate the arrival and local presence of taxa over time. In order to additionally infer the abundance of communities, the PAR values for the main taxa are compared in Figure 8. Thus, the combined results from pollen and plant macrofossil analysis document how the composition of the mire and surrounding vegetation has changed during the Holocene.

### Península Avellaneda Alto sequence

From 11600 to 9600 cal yrs BP the pollen record shows high values for Poaceae accompanied by herb and shrub taxa such as Asteraceae subf. Asteroideae and *Ephedra* (Figure 4). The PAR values for Poaceae and Asteraceae subf. Asteroideae are also high (Figure 8). Plant macrofossil analysis also indicates high concentrations of Poaceae. These data suggest local dominance of grass steppe in a dry environment, with high diversity of shrubs and herbs, on high-altitude areas in Península Avellaneda. Furthermore, the high pollen values for *Myriophyllum* accompanied by Juncaginaceae and

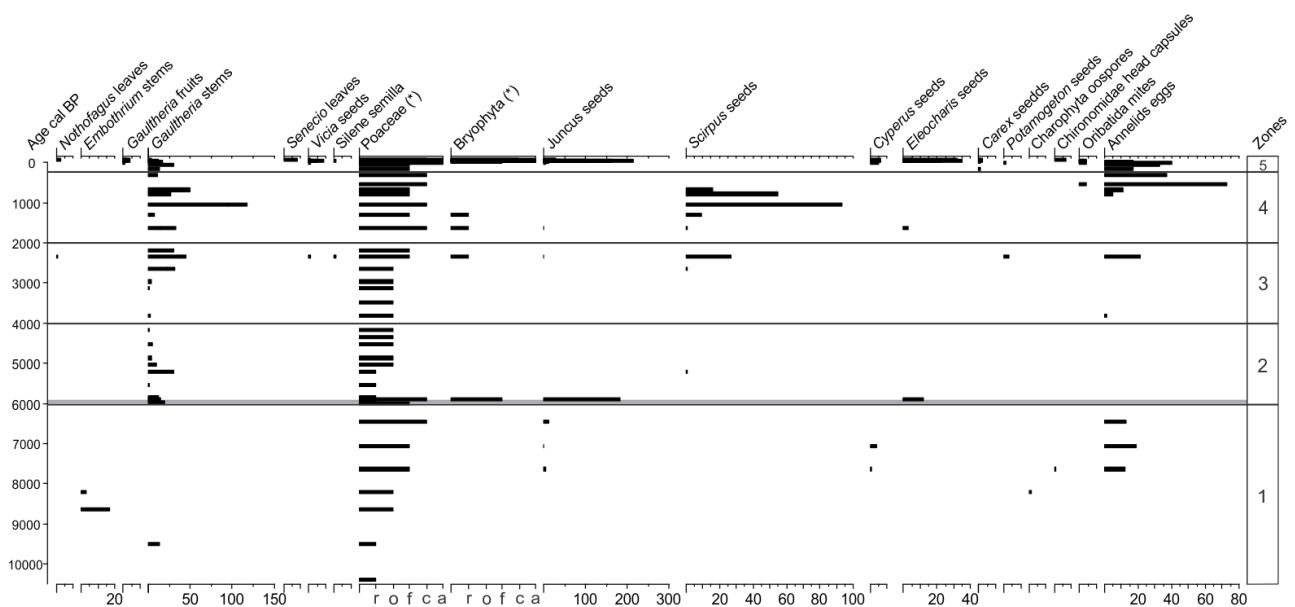


Figure 7. Península Avellaneda Bajo (PAB) macrofossil diagram, expressed in terms of concentration (remains per 10 cm<sup>3</sup>), or (\*) relative abundance (r=rare, o=occasional, f=frequent, c=common, a=abundant). The grey line at 5800–6000 cal yr BP represents the tephra layer.

the high concentrations of *Sphagnum* remains, Charophyta, Juncaceae, Chironomidae, Turbellaria, caddisfly larval cases and oribatid mites suggest the presence of a deeper and larger lake than today (Figure 2a), possibly reflecting the onset of glacial melting.

The period between *ca.* 9600 and 7000 cal yrs BP is characterised by low sedimentation rate (Figure 3). Pollen percentages show an ecotonal situation, with predominance of Poaceae and shrub taxa. Furthermore, the absence of *Myriophyllum* and Juncaginaceae in the pollen record, and the decline in Charophyta, Juncaceae and aquatic micro-invertebrate diversity in the macrofossil data (Figures 4 and 5), suggest lowering of the water level of the lake. The scarcity of pollen from herbs, *Gaultheria* and other shrubs in this section suggests an open landscape.

The pollen and plant macrofossil analyses indicate the development of a closed forest in Península Avellaneda between *ca.* 7000 and 3600/4000 cal yrs BP (Figures 4 and 5). There is further evidence in Figure 8, where the *Nothofagus* PAR shows an increase over the period. The high values of *Nothofagus* pollen and the abundance of *Nothofagus* remains such as leaves, seeds, fruits and buds indicate

the local presence and expansion of forest in the study area at around 6700 cal yrs BP. Identification of leaf fragments indicates the dominance of *Nothofagus pumilio* in the forest. Macrofossils of *Sphagnum* and Poaceae suggest that establishment of the bog was coincident with the expansion of *Nothofagus* (Figure 5).

Between *ca.* 3600/4000 and 2000 cal yrs BP, concentrations of *Nothofagus* macrofossils reduced substantially. This change is concomitant with deposition of a tephra layer between 4600 and 4500 cal yrs BP. After that, *Nothofagus* PAR estimates increase between 2500 and 500 cal yrs BP, reaching the highest values of the sequence (Figure 8). Furthermore, the pollen concentrations of *Misodendrum*, *Gaultheria*, Asteraceae subf. Asteroideae and other shrub taxa increase between 2500 and 500 cal yrs BP, suggesting an open mature forest for this interval. The abundance of aquatic microinvertebrates (*Chironomidae*, *Daphnia* and *Plumatella*) recorded during this period suggests a slight rise of the water level in the basin.

A marked decrease in *Nothofagus* pollen and macrofossil concentrations occurs between *ca.* 500 and 250 cal yrs BP. A pronounced PAR increase for Poaceae and high pollen levels for herbs, Asteraceae

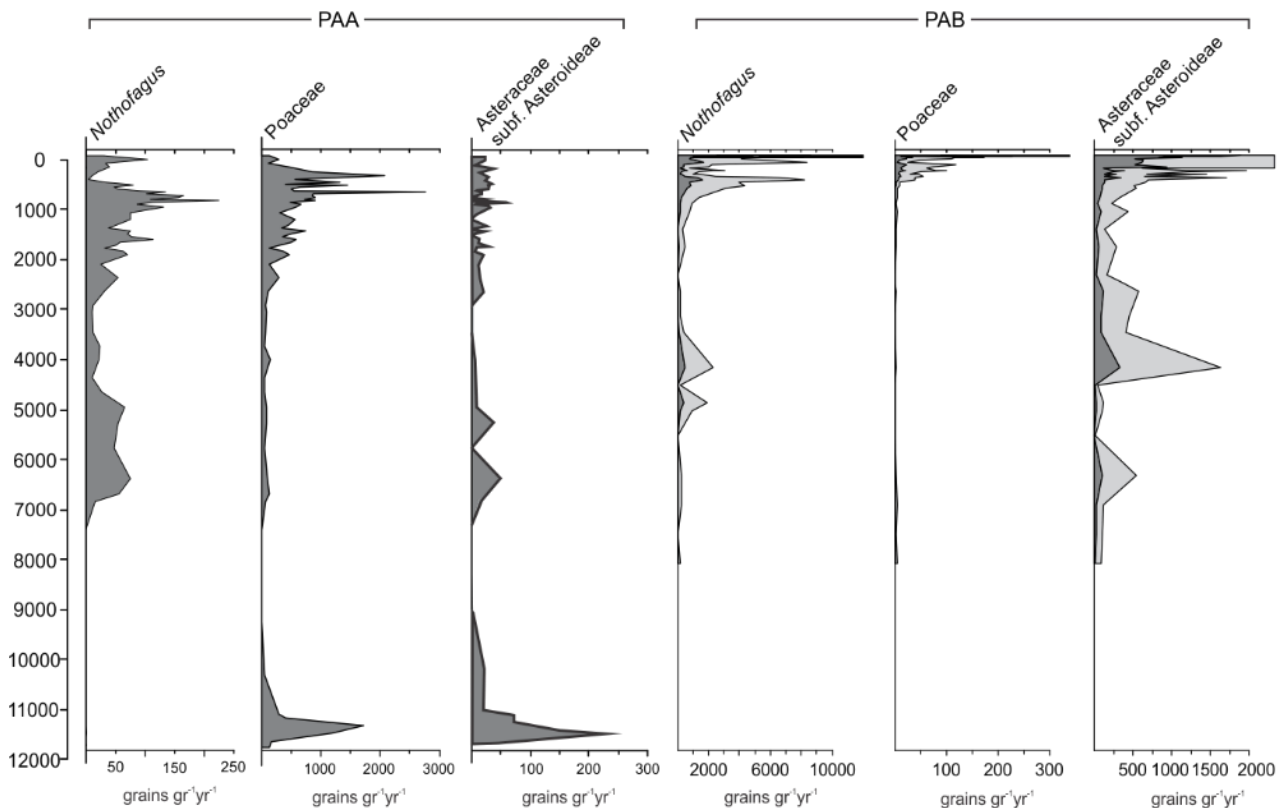


Figure 8. Pollen Accumulation Rate (PAR; dark grey shading) diagram for selected pollen types from Península Avellaneda Alto and Bajo. Light grey shading shows 5× exaggerations of the same data.

subf. Asteroideae and *Gaultheria* suggest an open landscape dominated by herbaceous and shrub elements during this interval. This condition continues until 250 cal yrs BP when the *Nothofagus* forest recovers (Figure 8). The pollen and macrofossil records evidence a bog dominated by *Sphagnum* and Cyperaceae for the last 500 years. Moreover, the decline in diversity of aquatic microinvertebrates indicates further lowering of the water level in the basin relative to the previous period.

### Península Avellaneda Bajo sequence

The vegetation for the period 10500–8000 cal yrs BP must be inferred from plant macrofossils only, as pollen has not been preserved. The record is characterised by the presence of Poaceae macrofossils in low concentration. *Gaultheria* and *Embothrium coccineum* stems were identified and dated at 9500 cal yrs BP and 8500 cal yrs BP, respectively (Figure 7). Towards 6000 cal yrs BP, the concentration of macrofossils of Poaceae increases, reaching maximum values. Furthermore, pollen of *Nothofagus*, *Misodendrum*, Poaceae and herbs characterise the assemblage between 8000 and 6000 cal yrs BP (Figure 7), suggesting local dominance of grass steppe rich in shrubs and herbs at low altitudes in Península Avellaneda. *Nothofagus* was present in secluded patches, and began to expand from high-altitude areas of the Península. This is supported by the presence of *Nothofagus* remains in the PAA sequence (Figure 5) and the low PAR values for *Nothofagus* pollen in the PAB record (Figure 8), interpreted as long distance transport (Figure 6). The macrofossil assemblages for this period suggest the presence of a mire dominated by *Juncus*, *Cyperus* and Poaceae.

From 6000 to 4000 cal yrs BP, pollen analysis shows an increase in *Nothofagus* values but no *Nothofagus* macrofossils are recorded. The *Nothofagus* PAR estimates show increasing values over the period (Figure 8). Macrofossils of *Gaultheria*, which is a typical understory species that colonises during the first stages of succession, are present. Therefore, it is likely that a high proportion of the *Nothofagus* pollen recorded here was wind-transported from higher altitudes and western areas of Península Avellaneda. Consequently, an ecotonal situation characterised the surroundings of the PAB mire. Also, light grey tephra layer is present at ca. 5500 cal yrs BP. This was probably produced by eruption of the Aguilera volcano (Stern 2008, Echeverría *et al.* 2014). This tephra deposition may have enhanced the change in vegetation. Remains of *Juncus*, Bryophyta and *Eleocharis* are present in only one sample for this period. Therefore, it is likely that

a mire dominated by Poaceae, Juncaceae and Bryophyta was present during this time.

The period 4000–2000 cal yrs BP is characterised by high PAR for Asteraceae subf. Asteroideae (Figure 8). Also, Poaceae and other herbs are registered (Figure 6). The plant macrofossil record shows a high concentration of Poaceae and *Gaultheria* stems. These data suggest a local dominance of shrub steppe with a high diversity of shrubs and herbs in the PAB area. Macrofossils of Bryophyta, *Juncus* and *Scirpus* are present at low concentrations and in few samples. These findings are consistent with a mire dominated by Poaceae, *Juncus*, *Scirpus* and Bryophyta, similar to the mire that was present during the previous period.

During the next period, 2000–500 cal yrs BP, the pollen data indicate a gradual increase in *Nothofagus* PAR up to 1000 cal yrs BP, suggesting development of forest patches, probably related to an increase in precipitation. *Misodendrum*, Poaceae, herbs and Asteraceae subf. Asteroideae are also present (Figures 6 and 8). The plant macrofossil record shows high concentrations of Poaceae and *Gaultheria* stems. These data support the interpretation that a grass steppe with forest patches and shrub elements was present in the area surrounding the PAB mire during that time. The macrofossil record suggests a mire dominated by *Scirpus*, Poaceae and Bryophyta.

During the last 350 cal yrs BP the pollen and plant macrofossil records suggest a grass steppe with a high diversity of herbs and forest patches, which has persisted to the present day. Furthermore, the macrofossil record indicates a mire co-dominated by Bryophyta, Juncaceae, *Scirpus*, *Eleocharis*, *Cyperus*, *Carex* and *Potamogeton* (Figure 7). In addition, the large numbers of Chironomidae, oribatid mites and Turbellaria suggest a flooded mire. Thus, the plant macrofossil and pollen analyses suggest a rapid downslope and eastward expansion of the forest patches during the last few centuries.

### Vegetation and climatic reconstruction for southwest Patagonia, inferred from pollen and plant macrofossil analyses

#### *Early Holocene: 11700–8200 cal yrs BP*

During the Last Glacial Maximum, the establishment of *Nothofagus* varied between different parts of South Patagonia. Several authors have postulated the expansion of *Nothofagus* forest from refugia populations between ca. 11000 and 9000 cal yrs BP, depending on the soil type, altitude and microclimatic conditions of each site (Mercer & Ager 1983, Heusser 1995, Villa-Martínez & Moreno 2007, Wille

& Schäbitz 2009, Mancini 2009, Moreno *et al.* 2010). This event could be related to a gradual rise in precipitation and temperature. A comparison of the different moments of *Nothofagus* forest expansion among southwest Patagonian sites shows that records from sites located to the north of 51°S, namely PAA, Cerro Frías, Perito Moreno and Brazo Sur (Figure 1a), date the *Nothofagus* expansion at *ca.* 9000, 10000, 9000 and 8000 cal yrs BP, respectively. On the other hand, records from Vega Ñandú, Torres del Paine, Lago Guanaco, Lago Eberhard, Pantano Dumestre and Río Rubens, which lie between 51°S and 52°S (Figure 1a), indicate *Nothofagus* expansion at *ca.* 11000, 10000, 12000, 11000, 13000 and 13000 cal yrs BP, respectively. This pattern in forest expansion could be related to a late deglaciation in the Lago Argentino basin, also recorded by the studies of Strelin *et al.* (2014) on glacier fluctuation on this area.

The Cerro Frías sequence recorded a grass steppe up to 9500 cal yrs BP, when the forest signal increased suggesting a change from dry to wet conditions (Mancini 2009). The quantitative precipitation reconstruction of Tonello *et al.* (2009) shows a continuous increase in precipitation for the Lago Argentino area during this period. The PAA sequence indicates grass steppe before 9000 cal yrs BP and an increase in *Nothofagus* pollen values after that, reaching 50 % at 8000 cal yrs BP (Figure 4). A similar trend was recorded in the Brazo Sur sequence, which showed shrub taxa (suggesting dry conditions) up to *ca.* 9000 cal yrs BP and an increase of Poaceae and *Nothofagus* inferring positive moisture availability between 9000 and 8000 cal yrs BP (Wille & Schäbitz 2009). The Lago Guanaco record showed Poaceae dominance during this period, associated with Asteraceae subf. Asteroideae, which increases up to 8500 cal yrs BP. Also, *Nothofagus* pollen values were less than 30 % (Moreno *et al.* 2010). Another site on the east Andes, Vega Ñandú, recorded variation in the abundance of *Nothofagus* and Poaceae, suggesting fluctuating precipitation conditions for this period (Villa-Martínez & Moreno 2007). Huber & Markgraf (2003) recorded grass steppe dominated by Poaceae on the Río Rubens bog until 8000 cal yrs BP. Also, *Nothofagus* pollen values were less than 50 %. On the basis of this synthesis, we can conclude that sites in southwest Patagonia were characterised by grass/shrub steppe until *ca.* 9000/8500 cal yrs BP, after which conditions became wetter, probably due to a strengthening of SWW.

#### *Mid Holocene: 8200–4200 cal yrs BP*

This work allows us to infer the presence of *Nothofagus* forest on the slopes of Península

Avellaneda at *ca.* 7000 cal yrs BP, as well as between *ca.* 5800 and 3200 cal yrs BP, probably due to an increase in SWW precipitation. Also, high abundance of *Nothofagus* remains such as leaves, seeds, fruits and buds indicates the local presence and expansion of forest in the Península Avellaneda at *ca.* 6700 cal yrs BP (Figure 5). PAB shows high *Nothofagus* pollen values between 6000 and 4000 cal yrs BP (Figure 6); however, no *Nothofagus* macrofossils are recorded for this period (Figure 7). Therefore, it is likely that the tree line never reached 180 m a.s.l. (PAB mire location) and the high fraction of *Nothofagus* pollen registered here was wind-transported from higher altitudes and the western parts of Península Avellaneda where *Nothofagus* macrofossils were recorded (Figure 5). Other Andean sites also infer high humidity for this period. The Cerro Frías pollen record suggests the development of *Nothofagus* forest between 8000 and 7000 cal yrs BP and between 6000 and 4000 cal yrs BP (Mancini 2009). Moreno *et al.* (2009) recorded high values of a *Nothofagus*/Poaceae index at *ca.* 4400 cal yrs BP, suggesting forest dominance on the Lago Guanaco area. Furthermore, a progressive increase in precipitation was registered by Tonello *et al.* (2009) for this period. The Brazo Sur, Vega Ñandú and Río Rubens sequences recorded high *Nothofagus* pollen values since 7500/7000 cal yrs BP (Huber & Markgraf 2003, Villa-Martínez & Moreno 2007, Wille & Schäbitz 2009). Also, positive Palaeohydric Balance Index values registered up to *ca.* 6000 cal yrs BP in southwest Patagonia have been related to an increase in precipitation through an intensification of the flow of storm tracks (Echeverría *et al.* 2017). The glaciological studies of Kaplan *et al.* (2016) suggest several glacier advances in the Lago Argentino area between 7000 and 4500 cal yrs BP, due to moisture accumulation and a decrease in temperature. In summary, a clear increasing trend of water availability allowed forest expansion in southwest Patagonia during this period, especially at *ca.* 7000 cal yrs BP, probably due to strengthened SWW.

#### *Late Holocene: 4200 cal yrs BP to the present*

The development of grass-shrub steppe from 4500/4000 to 2000 cal yrs BP indicated by the Cerro Frías and PAB pollen records suggests a decrease in water availability (Mancini 2009, Figure 6). Villa-Martínez & Moreno (2007) did not record significant changes during this period; nevertheless, Poaceae (*Nothofagus*) pollen values showed a slight decrease (increase) at *ca.* 2000 cal yrs BP. Wille & Schäbitz (2009) inferred the presence of a forest community on the southern part of Lago Argentino during this period, with an increase in grass and herbs elements

between 3500 and 2500 cal yrs BP. Similar conditions were registered by Moreno *et al.* (2009) in the Lago Guanaco sequence, with grass steppe dominance between 4000 and 1000 cal yr BP. Also, they interpreted an increase in *Pediastrum* values as evidence of warm conditions at *ca.* 3200–2900 cal yr BP (Moreno *et al.* 2009). Tonello *et al.* (2009) recorded a decrease in precipitation up to 2000 cal yrs BP. A positive to negative trend in Palaeohydric Balance Index, related to lower moisture availability, was registered in southwestern Patagonia from *ca.* 4000 to 1000 cal yrs BP (Echeverría *et al.* 2017). In addition, glaciological data indicate a decline in temperature towards 2500 cal yrs BP (Mercer 1982, Aniya 2013, Strelin *et al.* 2014). Based on this comparison, we can suggest that the presence of steppe communities with patches of forest in southwest Patagonia was due to a decrease in precipitation associated with a weakening of SWW up to 2000 cal yrs BP. Several sequences, such as Cerro Frías, PAA, PAB, Vega Ñandú and Brazo Sur, have suggested an increase in moisture availability after *ca.* 2500/2000 cal yrs BP due to an increase in dense forest development which continued until 700/600 cal yrs BP. This is possibly related to the increase in global temperature during the Mediaeval Climate Anomaly (MCA, *ca.* 950–750 cal yrs BP) and the increase in precipitation due to SWW strengthening. Also, Tonello *et al.* (2009) proposed an increase of precipitation up to *ca.* 1000 cal yrs BP. Towards the end of this period (*ca.* 400 cal yrs BP) a trend from wet to dry conditions was registered in the Lago Argentino area (Echeverría *et al.* 2014). Lower moisture availability in Cerro Frías and Vega Ñandú at this time has also been suggested (Mancini 2009, Villa-Martínez & Moreno 2007) on the basis of a reduction in forest pollen signal. These conditions could be related to the low temperature and drier bog surface conditions postulated for the Little Ice Age (LIA, 380–50 cal yrs BP) (Wenzens 1999, Villalba *et al.* 2003, Masiokas *et al.* 2009, Neukom *et al.* 2010, Aniya 2013, Chambers *et al.* 2014), which might have enabled glacier advances and restricted water availability, triggering a decrease in *Nothofagus* cover in southwestern Patagonia. The establishment of an open landscape suggests a reduction of precipitation in Andean areas by SWW weakening during the last few centuries.

## CONCLUSION

The integration of pollen and plant macrofossil analysis from two sediment sequences allowed us to reconstruct local and regional changes in the

vegetation of Península Avellaneda for the last *ca.* 11600 cal yrs BP (Figure 9). Early stages following the maximum extent of glaciers were characterised by herbaceous and shrubby elements throughout the area. *Nothofagus* colonised Península Avellaneda between 8000 and 7300 cal yrs BP. Furthermore, the concentration of *Nothofagus* pollen increased at 6700 cal yrs BP, suggesting that *Nothofagus* expanded on the Península at this time. The identification of leaf fragments indicated that those populations were composed by *Nothofagus pumilio*. The slopes of Península Avellaneda were covered by a dense forest from *ca.* 6700 to 4000 cal yr BP (Figure 9). After that, pollen and plant macrofossil records suggest a decrease in moisture availability and the development of open forest and grass-shrub steppe from *ca.* 4000 to 750 cal yrs BP. The last millennium was characterised by grass steppe until *ca.* 250 cal yrs BP, when woodlands started to recover (Figure 9).

In particular, the plant macrofossil study enabled a more accurate vegetation and environmental reconstruction. In addition, the plant macrofossil data served to confirm the pollen information and infer vegetation changes at different spatial scales. The timings of *Nothofagus* colonisation and expansion after glacial retreat in the Lago Argentino area were adjusted, allowing us to compare these results with those obtained by pollen analysis. Also, the analysis of plant macrofossils has proved to be very useful for reconstruction of changes in the composition of mires, and especially the fluctuations in hydrological conditions on the mire surface.

These results indicate the importance of using plant macrofossil analyses in conjunction with fossil pollen assemblages to enable more robust palaeoecological interpretations of the vegetation changes in Patagonia.

## ACKNOWLEDGEMENTS

We appreciate the assistance of and critical discussions with Dra Georgina del Fueyo from the Argentinian Museum of Natural Science (Buenos Aires, Argentina) on the identification of plant macrofossils. We thank Dmitri Mauquoy and an anonymous reviewer for their valuable comments on the manuscript. This work was financially supported by UNMdP EXA836/17; ANPCYT-PICT-2015-0763; CONICET-PIP 414; and DFG, German Research Foundation, FO 801/3-1. The authors thank “Administración de Parques Nacionales, Argentina (APN)” for allowing access to the workplace. We thank the (NSF)-Arizona AMS Facility and T. Jull for financial support for dating.

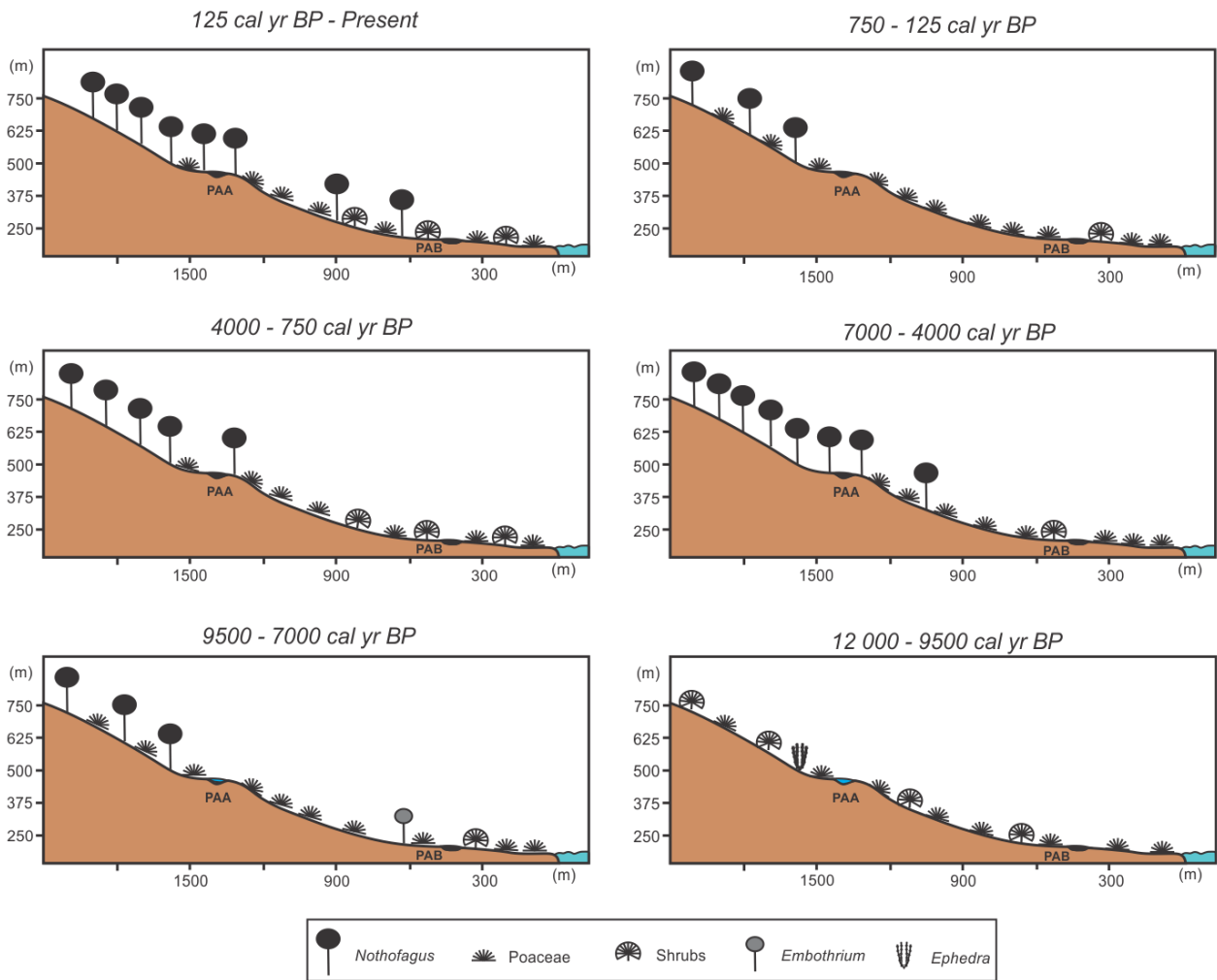


Figure 9. Reconstruction of postglacial vegetation communities at Península Avellaneda.

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- Submitted 26 Aug 2017, final revision 21 Sep 2018*  
*Editor: Frank Chambers*
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Author for correspondence:

Dr Marcos E. Echeverría, Paleocology and Palynology Laboratory, Universidad Nacional de Mar del Plata-IIMYC-CONICET, Funes 3250 (7600) Mar del Plata-ARGENTINA.  
Tel: +54 0223 4753554; E-mail: [echeverriamarcos@hotmail.com](mailto:echeverriamarcos@hotmail.com)