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Paleoenvironmental Changes for the Last 3000 Cal Years BP in the Pueyrredón Lake Basin, Southern Patagonia, Argentina

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Abstract: Patagonian shrub and ecotonal communities were sensitive to past environmental changes and thus may also be affected by future ones. Therefore, their paleoecological study constitutes a valuable tool to understand the way in which these plant communities respond to the forcings responsible for environmental variability. The aim of this paper is to reconstruct the vegetation dynamics of the Pueyrredón Lake area (47°25′55′′ S; 72°0.7′7′′ W) for the last 3000 cal yr BP and to contextualize these changes in a regional paleoclimatic framework. The results indicate that at the beginning of the 2900 cal yr BP, the vegetation in the northwest of Santa Cruz, Argentinian Patagonia, was represented by a grass-shrub steppe associated with forest–shrub steppe ecotonal elements. This information correlates with the larger-scale environmental inferences described for the period, which indicate an increase in moisture availability due to the weakening of the westerly winds. A marked change to arid conditions is indicated in the last 1050 cal yr BP, with the establishment and development of different shrub steppe communities and the lack of ecotonal elements. Although vegetation was sensitive to changes in moisture conditions related to the variability of the westerly winds, there is evidence of differences in the composition of shrub vegetation regarding the sequences analyzed. Variations in pollen proportions of the shrub steppes in the Pueyrredón Lake area suggest that changes in vegetation are not only due to climate variability but also local factors in the areas where shrub communities grow. The integration of the information with other Patagonian sequences allowed to frame these changes in a regional context. The results obtained provide useful information to understand the way vegetation changed in the past and the manner in which it may respond to future changes.

Keywords: Patagonia; late Holocene; pollen; paleoenvironmental changes

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1. Introduction

The physical and climatic characteristics of South America favor the study of past environmental variability. The combined effect of the westerly winds and the topographic barrier of the Andean mountain range represents the main force behind changes in precipitation [1–3]. The composition and distribution of plant communities are determined by these forcings and by topographical characteristics, thus inducing a marked west–east vegetation gradient. Different records have detected that this region is sensitive to climate changes [4–8] and vegetation [9–14], among others, during the Holocene. Paleoecological reconstructions based on fossil pollen sets have provided valuable information on the dynamics of plant communities in Andean areas [15–17] and extra-Andean Patagonia [12,18–20]. Particularly at 47° S, the wide Patagonian physiographic and climatic diversity has enhanced paleoenvironmental [21–24], paleogeographic [25–27] and archaeological studies [28–31], among others.

The late Holocene was characterized by a highly variable climate, which records periods of moisture and drought that had a different impact on the Andean and extra-Andean plant communities. Paleoenvironmental variability during the last millennium was particularly related to the Medieval Climate Anomaly (MCA, 950–750 cal yr BP) and the Little Ice Age (LIA, 380–50 cal yr BP), though the nature and timing of these events in South America have not been accurately established [2]. Paleoenvironmental studies indicate that the extra-Andean plant communities were similar to those currently present in physiognomy and distribution, with minimal modifications in internal composition [20,32]. On the contrary, Andean communities seem to have been more strongly affected by the changes recorded during the late Holocene [15,17]. Due to their uniqueness and global importance, the Patagonian steppe and its ecotones have been identified as one of the most vulnerable terrestrial ecoregions with a high conservation priority in Latin America [33]. Therefore, obtaining information about the past environmental dynamics of Patagonia, its main forcings and the way they affected vegetation in the past is imperative. This paper focuses on changes in vegetation during the late Holocene through the analysis of a pollen record located at 47° S, 72° W, near the Subantarctic forest–Patagonian steppe ecotone. The geographical location of this sedimentary sequence offers a high potential to detect the environmental changes that have occurred in the last 3000 cal yr BP.

The comparison with other paleoenvironmental studies will help to understand the way vegetation responded in the past, assess similarities and differences in the patterns of environmental changes, and indicate the probable consequences of current environmental changes.

1.1. Environmental Characteristics and Vegetation of the Pueyrredón Lake Area

The Pueyrredón–Posadas–Salitroso basin is the relict of a paleolake product of the melting of extensive ice masses during the late Pleistocene and early Holocene [25]. The configuration of the lake systems in northwestern Santa Cruz, Argentinian Patagonia, is characterized by a retracted glacial and periglacial landscape [34–36]. The average annual rainfall in the area is 500 mm/year on the eastern flank of the Andes Mountains, Argentine side. Towards the east, it decreases steeply, reaching 200 mm/year a few kilometers away from the Andes (Figure 1). The average annual temperature is 7–8 °C, reaching 0–1 °C in winter and increasing to up to 11 °C in summer.

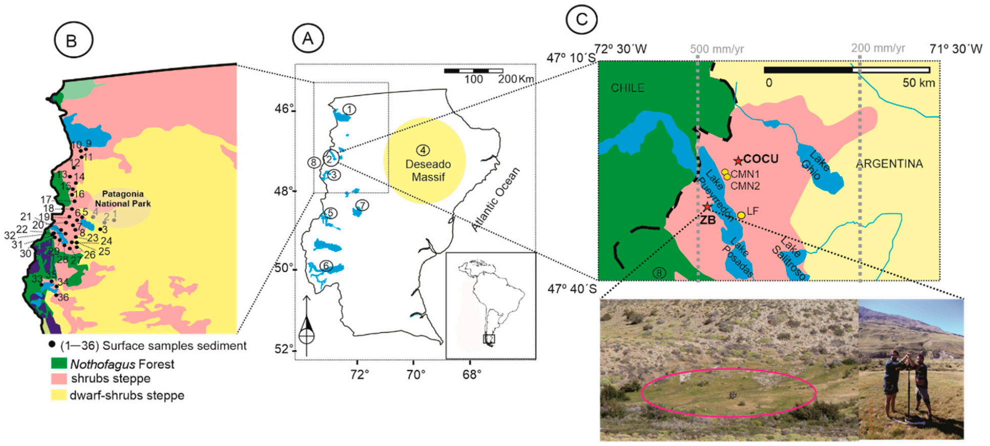

Figure 1. (**A**) Map of South America and Santa Cruz, Argentinian Patagonia, that shows the geographical location of the study site and other paleoenvironmental records used in regional paleoenvironmental reconstruction. 1—Buenos Aires Lake [21]; 2—Pueyrredón Lake [22–24,26,27]; 3—Belgrano Lake (PNPM) [37]; 4—The Deseado Massif [20,32]; 5—San Martín Lake [18,19]; 6—Argentino Lake [15,16]; 7—Cardiel Lake [38,39]; 8—Mallín Casanova [40]. (**B**) Geolocation of sediment samples (1–36) and vegetation units. (**C**) Location of the study area, Zorro Bayo wet meadow (ZB), CMN1, CMN2, COCU archaeological sites and Los Flamencos (LF) used for the paleoenvironmental reconstruction of Pueyrredón Lake.

According to [41,42], vegetation in Patagonia is very heterogeneous due to the restrictions imposed by the environment at regional scale and mesoscale. Thus, the distribution of vegetation is determined by the strong precipitation gradient that results in a dense forest to the west and an open forest and steppes to the east [43–45]. The subantarctic forests of *Nothofagus* grow in the Andean regions, where rainfall varies between 1200 and 400 mm annually. To the east, the precipitations in the area of the open *Nothofagus* forest reach 400 mm/year where soil conditions and water balance are appropriate [44]. Further east, with precipitations ranging between 400–200 mm/year, the shrub steppes are conformed by different communities with representatives such as *Mulguraea*, *Nardophyllum*, *Senecio*, *Mulinum* and *Berberis* [46]. Along the distribution gradient of *Mulguraea* it occurs as a shrub and as a dwarf-shrub. The dwarf-shrub steppe grows where precipitation levels are lower than 200 mm/year, and its dominant representatives are *Nassauvia glomerulosa*, *N. ulicina* and *Ephedra frustillata* [44,45]. The vegetation in the area of Pueyrredón Lake is particularly represented by a shrub steppe of *Mulinum spinosum*, *Berberis heterophylla* and *Nardophyllum* sp., accompanied by *Senecio filaginoides*, *Schinus polygamus* and grasses such as *Festuca pallescens* and *Stipa* sp., among others.

1.2. Previous Paleo-Environmental Investigations

The first palynological studies of archaeological sequences in the northwest of Santa Cruz were carried out by [47–50], which provided valuable information for the first reconstructions of vegetation history. Paleoenvironmental and archaeological studies of the Pueyrredón Lake area [22–24,28–30,51,52], among others, allowed to relate the archaeological and palynological information of different archaeological sites as Cueva Milodón Norte 1 (CMN1), Cueva Milodón Norte 2 (CMN2) and Cerro Cuadrado (COCU) [22,23] and the information of the Los Flamencos sedimentary sequence [24] with variations in the lake level, and helped to understand the way these environmental changes were relevant in the use of space and resources and in the dynamics of hunter–gatherer groups during the Holocene [26,27].

During the early Holocene (around 8500 cal yr BP) the vegetation was represented by a grass steppe associated with dwarf-shrubs. A change in vegetation was evidenced in the middle Holocene, with the development of a shrub steppe associated with forest elements. Around 5000 cal yr BP, the separation of the Posadas and Salitroso Lakes generated a new landscape and new ecological niches in which the shrub steppe developed [26,27]. The floristic diversity of this period allowed greater availability of resources for the hunter–gatherer groups that inhabited the area. Los Flamencos sequence allowed to reconstruct the paleoenvironmental history up to 3500 cal yr BP, so the information available about the late Holocene originates from the archaeological sites (CMN1, CMN2 and COCU) that indicate the development of a shrub steppe with characteristics similar to the current one [22,23,26,27]. Although these sites have provided important data that contribute to the paleoenvironmental reconstruction of the area, they only represent temporary windows of information; therefore, the paleoenvironmental history is incomplete. In addition, in order to adjust the paleoenvironmental information derived from archaeological records as well as the chronological discontinuity between archaeological layers, [23] also considered the effect of pollen preservation problems in paleoenvironmental reconstructions. For this reason, pollen deterioration rates related to biochemical (degraded grains) and mechanical damage (broken and crumpled grains) were calculated. Based on this background, the Zorro Bayo sequence constitutes a continuous sequence of the last 2800 cal yr BP that will enable us to learn more precisely about the vegetation dynamics associated with the environmental changes that occurred during the Late Holocene, and to contextualize it on a regional scale.

2. Materials and Methods

2.1. Study Site

Zorro Bayo (ZB) is located on the western shore of Pueyrredón Lake (47°25′55′′ S; 72°0.7′7′′ W) (Figure 1a,c). It is located in a depressed area of wet meadows, which consist of wetlands of great ecological value for the current ecosystem [53] and which have been widely used for paleoenvironmental reconstruction and post-glacial chronology in Patagonia [11,13,17,18,20,54–58], among others, obtaining valuable paleoenvironmental information with good chronological resolution. They are associated with a wide variety of communities, from *Nothofagus* forests to steppes in arid and semi-arid environments [59]. The classification of meadows based on the degree of moisture is directly related to the vegetation [53]; in agreement with this, ZB corresponds to a semi-humid wet meadow whose water level is below the surface and whose vegetation cover is grasses (*Festuca* sp.). In this way, some pollen types from the fossil record can be classified as indicators of wet–arid periods. In the surroundings, there are slopes covered by shrubs such as *Mulinum spinosum*, *Berberis heterophylla* and Asteraceae subf. Asteroideae. The annual rainfall of the area is 350 mm/year. According to [22], three shrub communities are distinguished at local scale: 1. Shrub community of *Mulinum,* Asteraceae subf. Asteroideae and *Colliguaja,* 2. Shrub community of *Mulinum,* Asteraceae subf. Asteroideae and *Berberis*, and 3. Shrub community of *Mulinum* with shrubs. Some *Nothofagus pumilio* forest patches cover mountain slopes 7 km westward from the wet meadow, near the border with Chile. On the eastern margin of Pueyrredón Lake, 12 km from the ZB wet meadow, the sequence LF [24] and the archaeological sites CMN1, CMN2, and COCU [26,27] (Figure 1c) are located. COCU archaeological site is located on the southern bank of the lake at 300 m.a.s.l., the archaeological layers are made up of laminated silty clayey sediments indicating lacustrine deposits. Lithic technology and guanaco remains were discovered on the archaeological site COCU. Dating done on layer 2 (493 cal yr BP) and layer 3 (2040 cal yr BP) indicate human occupation during the late Holocene. Previous studies in COCU show a good preservation of pollen grains, inferring a local signal in the reconstructed vegetation [23]. More details of the geomorphological and archaeological characteristics of those archaeological sites are described in [22,23,26–30].

For this study, a sedimentary sequence (ZB) of 120 cm long was extracted using a Russian core sampler. Pollen, organic matter and carbonate content analyses were conducted, as well as a stratigraphic description. The sedimentary sequence was interpreted in conjunction with the modern pollen model and compared with the archaeological sequence COCU [22,27], since it presents the same chronological resolution. The LF sequence and the CMN1 and CMN2 sites were used to contextualize the paleoenvironmental dynamics of the Pueyrredón Lake area.

2.2. Sedimentological Analysis

The ZB sequence was sedimentologically described in the Laboratory of Paleoecology and Palynology (IIMyC-CONICET, UNMDP). Subsequently, organic matter and carbonate content analyses were performed using the loss on ignition method (LOI) at the same levels as those used for pollen analysis. Each sample was placed in crucibles previously weighed on a precision scale. In order to eliminate the water content, they were dried in an oven overnight at 105 °C, and then the weight of each was recorded. For the calculation of organic matter and carbonate content, the samples were burned in a muffle at 500 °C (4 h) and 950 °C (2 h), respectively. At the end of each of these procedures, the samples were weighed on a precision scale [60,61]. The results are expressed as percentages of weight loss of the sediments at each step in relation to the dry weight of the samples prior to combustion [60].

2.3. Chronological Data

Table 1 shows the 5 radiocarbon datings made from the ZB fossil sequence and 2 radiocarbon ages from COCU. Radiocarbon dating was calibrated using the CALIB 8.2 program [62] and the Southern Hemisphere curve (SHCal 20) [63]. Subsequently, a Bayesian-type age–depth model was built using the "Bacon" package of the R program [64] with 13 sections for its run. The method allowed calculation of a weighted mean and a 95% confidence interval for the cal age distribution of every level in the sedimentary sequence. This analysis contributed to a reliable chronological control of the sequence and its subsequent comparison on a regional scale with other fossil records.

Table 1. Radiocarbon ages of ZB, COCU and calibrations in accordance with [63].

ZB				
Code Lab	**Depth (cm)**	**Age ^{14}C**	**Median Probability (CAL BP)**	**2 Range**
DAMS-028827	35	264 ± 25	277	274–315
DAMS-028031	51	843 ± 23	706	673–740
DAMS-028032	72	1722 ± 24	1578	1532–1614
DAMS-028826	100	2188 ± 24	2123	2051–2146
DAMS-014678	120	2845 ± 29	2912	2840–3004
COCU				
Code Lab	**Depth (cm)**	**Age ^{14}C**	**Median Probability (CAL BP)**	**2 Range**
UGAMS-5883	Layer 2	460 ± 20	493	451–510
UGAMS-5884	Layer 3	2080 ± 20	2040	1986–2055

2.4. Pollen Analysis

Between 0.90 and 1.25 g of sediment in ZB and 5–9 g of modern sediment and the COCU, archaeological sequence was used for pollen extraction. The extraction of modern and fossil pollen grains was conducted using standard physicochemical techniques [65–67]. The procedures include: hot KOH 10% to remove clays and humid acids, HCl 10% to remove carbonates, heavy liquid with $ZnCl_2$ (δ = 2) to separate the mineral fraction by flotation, HF to remove silicates and acetolysis to eliminate organic matter. The residues were mounted in glycerine and analyzed under microscope (1000×). The samples were analyzed under light microscope by counting at least 300 grains. For the recognition of the grains, the palynological reference collection of the Laboratory of Paleoecology and Palynology (UNMdP) and the pollen atlases [68,69] were used. Three *Lycopodium clavatum* spore tablets (BATCH No. 177.445, x = 18.584) were added to the sample processing in order to obtain a pollen marker and to subsequently estimate the sums and concentration of pollen.

This paper presents an expanded modern pollen model from that published in [23] and in [9]. With that aim, 16 surface pollen samples from the north and northeast of Pueyrredón Lake and 4 samples from the pollen database of the Laboratory of Paleoecology and Palynology (UNMDP-IIMyC, CONICET) were added (Figure 1b). All samples were taken following the multiple sub-sampling technique, and each sample consisted of 5 randomly collected sub-samples [70]. There is also a current pollen model on a local scale published in [23]. Modern palynological information at regional and local scale will be used as an analog model in order to compare with fossil records and to facilitate paleoenvironmental inferences.

Modern and fossil pollen diagrams were plotted with the TILIAGRAPH program (TGView 2.0.2.) [71]. Fossil sequence zoning was performed using a stratified cluster analysis (CONNIS) [71] applying a square root transformation using the Edwards and Cavalli-Sforza distance. Each taxon was expressed as a percentage of the total pollen sum.

In the modern pollen diagram, the pollen types *Eupatorium*, *Gilia*, *Phacelia*, *Calceolaria*, Rubiaceae, *Ranunculus*, *Oenothera*, *Adesmia*, Euphorbiaceae, Poligonaceae, *Fuchsia*, Iridaceae, Malvaceae, *Vicia patagonica, Oxalis*, Apiaceae, *Gentianella*, Saxifragaceae, *Oreopolus*, *Epilobium*, Calyceraceae, *Polemonium*, *Sisyrinchium*, Lamiaceae, *Plantago*, *Hypochaeris* and *Valeriana* were grouped as "other herbs". *Rumex,* Brassicaceae and Myrtaceae were grouped as anthropogenic impact pollen types. In the pollen diagram of the archaeological site COCU, Euphorbiaceae, Apiaceae, Malvaceae, Iridaceae, *Gilia*, *Phacelia*, *Adesmia* and Ranunculaceae were grouped as "other herbs".

3. Results

3.1. Modern Pollen Data

Group 1 samples are geolocated from the northeast of the study area to the Patagonia National Park (Figures 1b and 2). The pollen group is characterized by dwarf-shrubs such as *Mulguraea* (2–25%), *Nassauvia* (7–22%), Amaranthaceae subf. Chenopodioideae (5–25%), *Chuquiraga*, *Ephedra*, *Arjona* with 2–5% and *Empetrum* (2%). There are accompanying shrubs such as *Mulinum* (2–10%), *Berberis* (2–5%), Asteraceae subf. Asteroideae (5–25%), *Schinus* (2–5%) and *Colliguaja* (2–15%). Poaceae (5–30%) and low percentages of herbs constitute the herbaceous layer. *Nothofagus* (5–25%) and *Podocarpus* (2–10%) are also present. Pollen types of impact with low values of (2–5%) are present.

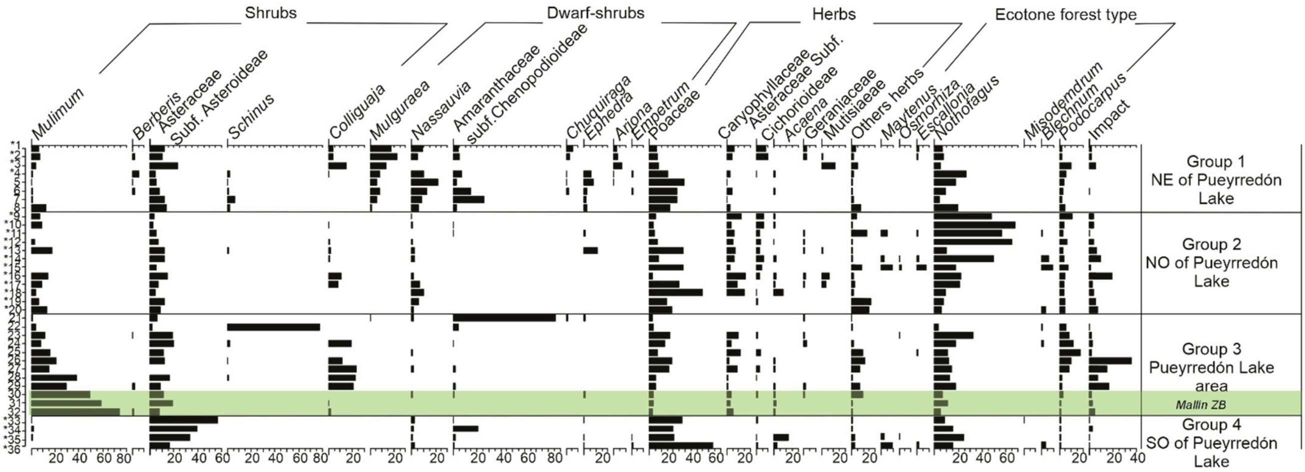

Figure 2. Pollen diagram in percentages (%) of surface samples at regional scale. New samples in respect to [9,22] are shown with asterisk.

Group 2 consists of the surface samples located in a northern direction between the Buenos Aires and Pueyrredón Lakes (Figures 1b and 2). The pollen assemblage is mainly characterized by *Mulinum* shrubs (5–20%), Asteraceae subf. Asteroideae (2–15%), and *Colliguaja* (2–12%). Compared to the previous group, there is a decrease in the dwarf-shrubs *Nassauvia* (2–10%) and *Ephedra* (only in two samples, 2–10%), while the representation of herbs such as Poaceae (5–45%) and Caryophyllaceae (5–15%), among others, increases. *Nothofagus* has high percentages ranging from 5 to 67% together with *Podocarpus* with the range of 5–10%, pollen types associated with ecotone such as *Maytenus*, *Osmorhiza* and *Escallonia* with low percentages, and *Blechnum* (2–10%). Impact pollen types are present at 2–20%.

Group 3 consists of the samples from the area of Pueyrredón Lake in which ZB wet meadow and the archaeological site COCU are located (Figures 1b and 2). This group is characterized by high percentages of *Mulinum* (2–75%) along with other shrubs such as Asteraceae subf. Asteroideae (2–20%) and *Colliguaja* (10–25%). *Schinus* is present in some samples of the group, with percentages of 80% in Sample 22. The dwarf-shrubs (*Nassauvia*, Amaranthaceae subf. Chenopodioideae, *Chuquiraga* and *Ephedra*) present low percentages (2%), except for Sample 21, which exhibits 85% of Amaranthaceae subf. Chenopodioideae. Poaceae has moderate percentages (2–20%), accompanied by other herbs ranging from 2 to 12%. *Nothofagus* (5–30%), *Podocarpus* (2–15%) and *Blechnum* (1–2%) are present as well. Pollen types of impact (2–35%) are present.

Group 4 consists of sediment samples located to the southwest and close to Belgrano Lake (Figures 1b and 2). The predominant shrub is Asteraceae subf. Asteroideae (60-15%), and dwarf-shrubs such as *Nassauvia* and *Ephedra* (1%), and Amaranthaceae subf. Chenopodioideae (2–20%) constitute low percentages. Grasses are represented by Poaceae (20–55%) and other herbs with low percentages (2–10%). There is a moderate representation of *Nothofagus* (10–25%), *Podocarpus* (2%) and pollen types associated with the ecotone

(2–7%). *Misodendrum* (1%) is present in Sample 33. Impact pollen types (2–5%) have low values.

3.2. Stratigraphy of Fossil Record

The sedimentary characteristics of ZB sequence allowed to determine four sections: 120–100 cm depth, 100–50 cm depth, 50–20 cm depth and 20–0 cm depth. The section of the base up to 100 cm is mainly characterized by silt associated with small quartz rocks, values of organic matter ranging between 10 and 30% and pollen concentration ranging between 220 and 300 gr/g. Between 100 and 50 cm of depth, the sediment is characterized by peat, plant fibers and gyttja; the percentages of organic matter for this section are the highest of the sequence, and the pollen concentration ranges between 100 and 300 gr/g. From 100 cm, the percentages of organic matter increase notoriously from 25 to 75% at 69 cm, and then decrease to 25% at 50 cm. The section between 50 and 20 cm is characterized by peat associated with plant remains. The percentages of organic matter range from 25 to 45% and the pollen concentration increases up to 1250 gr/g. The last section (20–0 cm) is mainly characterized by plant fibers, and the percentages of organic matter reach values of 60% at 10 cm and decrease to 35% at centimeter zero. The pollen concentration of the latter section fluctuates between 100 and 1250 gr/g. Carbonate percentages vary between 0 and 5% (0–10 cm) and then remain low (1%) throughout the sequence. According to [61], carbonates were not considered in paleoenvironmental interpretations because they had values lower than 5%. The average accumulation rate is 20 yr/cm, with records of a low accumulation rate between 120 and 50 cm (2800–650 cal yr BP), which suggests a quiet environment and later a higher sedimentation rate between 650 cal yr BP and present (Figure 3).

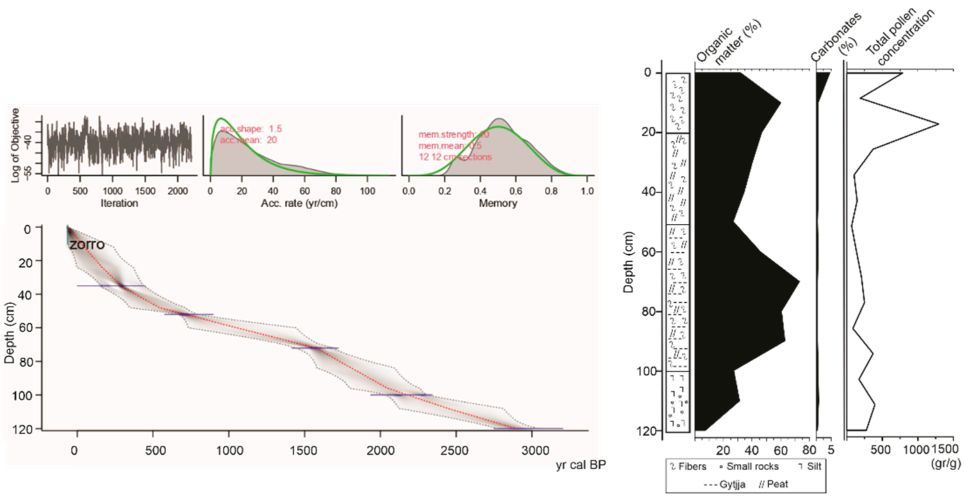

Figure 3. Stratigraphy, loss on ignition, pollen concentration and age model of Zorro Bayo wet meadow.

3.3. Fossil Pollen Record

3.3.1. Zorro Bayo Sequence

In the pollen sequence of the Zorro Bayo wet meadow, two pollen zones were differentiated according to the cluster analysis (Figure 4).

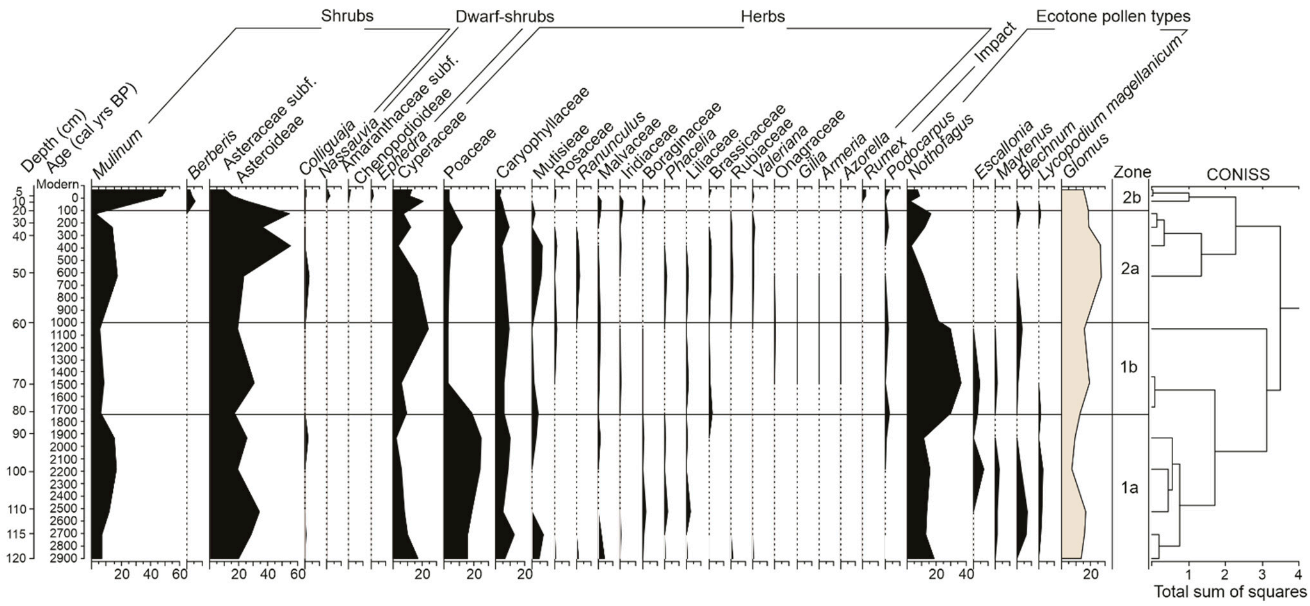

Figure 4. Pollen diagram in percentages and pollen zones of the Zorro Bayo wet meadow.

Zone 1. It has two subzones.

Subzone 1a (2900-1750 cal yr BP; 120-80 cm depth). It is characterized by shrubs such as Asteraceae subf. Asteroideae (20–37%) and Mulinum (10–15%), grasses such as Poaceae (15–25%), Cyperaceae (5–15%), Caryophyllaceae (7–12%) and other herbs (2%). Nothofagus (10–25%), Escallonia (7%), Blechnum (7%) and Lycopodium magellanicum (2%) are also present. Glomus presents values between 7 and 15% in this subzone.

Subzone 1b (1750-1050 cal yr BP; 80-60 cm depth). There is a slight decrease of shrubs such as Asteraceae subf. Asteroideae (15–30%) and Mulinum (5–9%) compared to the previous subzone. Poaceae decreases from 25% to 5% towards the end of the subzone, while Cyperaceae varies from 5% to 22%, and the percentages of Caryophyllaceae decrease slightly (5–9%). Nothofagus increases significantly (35%) with respect to the previous subzone together with Escallonia (5%), Maytenus (2%), Blechnum (2–5%) and Lycopodium magellanicum (1%). Glomus percentages vary between 10 and 19%.

Zone 2. It consists of two subzones characterized by a significant increase in shrubs.

Subzone 2a (1050-120 cal yr BP; 60-20 cm depth). It presents a marked increase in Asteraceae subf. Asteroideae (20–55%) and Mulinum (5–15%), and a decrease in Poaceae (5–13%), Caryophyllaceae and Mutisieae (5–7%). Cyperaceae fluctuates between 5 and 20%. In regards to the ecotonal pollen types, Nothofagus (5–20%) and Blechnum (1%) decrease their values. Glomus presents the highest values of the sequence (20–25%).

Subzone 2b (last 120 cal yr BP; 20-0 cm depth). It is characterized by high values of Mulinum (25–50%), a decrease in Asteraceae subf. Asteroideae with respect to the previous subzone (40-10%), and the presence of Berberis in percentages of 2–5%. Dwarf-shrubs (Nassauvia, Amaranthaceae subf. Chenopodioideae and Ephedra) values range between 1 and 2%. Cyperaceae (10–20%), Poaceae (5–7%) and Caryophyllaceae (5%), among other herbs, are present. Nothofagus is present in low percentages (5–12%), so is Podocarpus (2%). Rumex (2–4%) represents an anthropogenic impact pollen type. Glomus (15–20%) are present.

3.3.2. Archaeological Site COCU

The pollen sequence of the COCU archaeological site was divided into two zones (Figure 5).

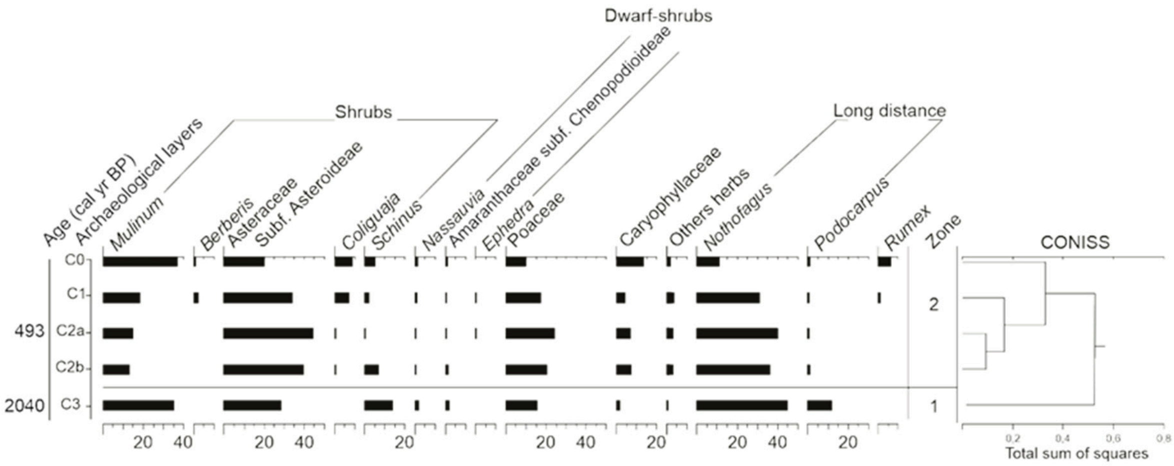

Figure 5. Pollen diagram in percentages (%) of the COCU archaeological sequence.

Zone 1 (2040 cal yr BP) is represented by shrubs such as Mulinum (35%), Asteraceae subf. Asteroideae (27%) and Schinus (15%), and dwarf-shrubs such as Nassauvia and Amaranthaceae subf. Chenopodioideae (2%). Grasses are represented by Poaceae (15%) together with other herbs (1–2%). Nothofagus and Podocarpus are present in 45% and 12%, respectively.

Zone 2 (the last 493 cal yr BP) is characterized by the development of shrubs such as Mulinum (15–37%), Berberis (3%), Asteraceae subf. Asteroideaea (20–45%), Colliguaja (1–10%) and Schinus (1–7%). Among the subshrubs, Nassauvia, Amaranthaceae subf. Chenopodioideae and Ephedra are found in low percentages (1–2%). Poaceae (10–25%), Caryophyllaceae (7–14%) and other herbs (2%) represent herbaceous vegetation. Nothofagus values fluctuate between 10 and 40%, while Podocarpus percentages are low (2%). Rumex (2–7%) represents an anthropogenic impact pollen type.

4. Discussion

4.1. Modern Pollen Representation

The modern pollen assemblages represent the distribution of vegetation that grows along the west–east precipitation gradient on a regional scale (Figures 1b and 2).

The samples located northeast of Pueyrredón Lake, Group 1, represent the shrubs and dwarf-shrub steppe associated with a lower availability of moisture and high temperatures. *Mulguraea*, *Nassauvia*, Amaranthaceae subf. Chenopodioideae, *Ephedra*, *Chuquiraga*, *Arjona* are the main representatives of the regional vegetation that grows on high slopes and the Patagonian plateau [46] (Figure 2).

Samples from Groups 2 (NW from Pueyrredón Lake) and 4 (SW from Pueyrredón Lake) show two ecotonal areas between the shrub steppe and the patches of forest of *Nothofagus pumilio*. Both groups exhibit a notorious contribution of elements of the forest-steppe ecotone such as *Nothofagus pumilio* along with *Maytenus*, *Osmorhiza*, *Escallonia*, *Blechnum* and *Misodendrum*. The shrub steppes of each group differ in their composition. In Group 2, the shrub steppe is mainly characterized by *Mulinum* and Asteraceae subf. Asteroideae, while Asteraceae subf. Asteroideae predominates in Group 4. Both groups indicate areas of greater availability of moisture due to their proximity to the Andes, which favors the development of ecotonal vegetation (Figure 2).

Samples from Group 3 represent the shrub steppe of *Mulinum spinosum*, *Berberis heterophylla* and Asteraceae subf. Asteroideae that grows in the surroundings of Pueyrredón Lake. According to [45], although on a regional scale the shrub steppe is considered a homogeneous unit, it is considerably heterogeneous on a local scale and presents important differences in its composition as a result of the geomorphological features of Patagonia. Furthermore, it is important to consider dispersion syndromes in the interpretation of pollen sets. For example, the percentages of *Berberis* pollen are low in all the samples, but its representation in the modern vegetation is high, especially in the surroundings of the ZB wet meadow. However, this situation is not reflected by the pollen samples (Samples 30, 31, 32), since this taxon presents an entomophilous dispersion that explains these differences between pollen and vegetation. Based on [72], it is important to note that pollen analyses in temperate and semi-arid regions are based almost exclusively on anemophilous taxa, which dominate the fossil pollen record. However, entomophilous taxa must be highly considered since they are representatives of many types of vegetation. The percentages of *Colliguaja* must be analyzed considering that they correspond to samples taken near the edges of the roads; therefore, although it is part of the native vegetation, places of disturbance favor their presence. The Samples 21 and 22 are particular cases with high percentages of Amaranthaceae subf. Chenopodioideae and *Schinus*, respectively; these values are possibly associated with the presence of anthers where the samples were collected and their corresponding overrepresentation in the pollen set. The high percentages of *Rumex* reflect the expansion of species introduced since the European settlement (Figure 2).

4.2. Vegetation Dynamics of the Last 3000 Cal Years BP

The reconstruction vegetation changes of the last 3000 cal yr BP has been possible due to the pollen assemblage analysis (modern and fossil). The paleoenvironmental information from ZB sequence between 2900 and 1750 cal yr BP indicates that the vegetation was characterized by a grass–shrub steppe codominated by Asteraceae subf. Asteroideae and *Mulinum* with some forest elements analogous to Group 2 of the modern pollen model (Figures 2 and 4). The presence of *Nothofagus* together with *Escallonia*, *Maytenus*, *Blechnum* and *Lycopodium magellanicum* provides information on the presence of patches of a forest of open characteristics within a predominant shrub–grass steppe, thus suggesting a contribution of moisture in this period. In addition, the herbs of this time signal a greater diversity in vegetation. A landscape heterogeneous in its floristic composition, with greater development of forest patches and shrub community of Asteraceae subf. Asteroideae and *Mulinum* continues up to 1050 cal yr BP. *Nothofagus* increases notoriously accompanied by elements of the forest–steppe ecotone such as *Escallonia*, *Maytenus, Blechnum* and *Lycopodium magellanicum*. This increase in *Nothofagus* is also recorded in the COCU sequence at 2040 cal yr BP, although without the presence of ecotonal pollen types. It should be considered that the COCU archaeological site provides information for the reconstruction of the vegetation at a local scale. However, the detection of local and regional pollen signals in the different sequences analyzed strengthen the reconstruction of the study area. The shrubs and Poaceae pollen types decrease slightly while Cyperaceae increases, which signals a pulse of local moisture (Figures 4–6). The palynological information from the archaeological sites CMN1 and CMN2 [26,27] provides clues at 2600 cal yr BP that the vegetation was characterized by a forest–steppe ecotonal community that later evolved to the modern shrub steppe.

From 1050 cal yr BP until 120 cal yr BP, a change in vegetation is evidenced with a greater development of the shrub steppe of *Mulinum* and Asteraceae subf. Asteroideae. There is a drastic decrease in grasses such as Poaceae and Cyperaceae and elements of the forest-steppe ecotone, thus suggesting more arid conditions for the period (Figures 4 and 6). In addition, the increase in *Glomus* (an arbuscular mycorrhizal fungus) is evident, which has been considered a good indicator of aridity conditions in other paleoenvironmental reconstructions of Patagonia [20]. According to [73], *Glomus* allows plants to resist these adverse conditions by increasing to drought and nutrient absorption. These dry conditions are also recorded in the COCU sequence at 493 cal yr BP the development of a shrub steppe of *Mulinum*, *Berberis* and Asteraceae subf. Asteroideae, together with other shrubs and dwarf-shrubs. For this moment (around 500-450 cal yr BP), there is also evidence of a slight decrease in *Nothofagus* and a lack of elements associated with the forest in ZB. This arid signal in sequences ZB could be related to the low temperatures proposed for the Little Ice Age (LIA) [74–79], and would be characterized by advances in glaciers and decrease in rainfall in the Andean zone due to the weakening of the westerly winds. In other paleoenvironmental records, at 49° S, arid conditions have also been inferred at 400 cal yr BP, probably associated with the LIA [18,19].

Moisture availability	Age (yr cal BP)	Pollen zones	Palaeoenvironmental plant communities	Sequence
(-)	Last 120	2b	Shrub community dominated by *Mulinum* with *Berberis*, Asteraceae subf. Asteroideae and dwarf-shrubs	ZB
	493	2	Shrub community of *Mulinum*, *Berberis* and Asteraceae subf. Asteroideae and *Colliguaja*	COCU
	1050-120	2a	Shrub community dominated by Asteraceae subf. Asteroideae with *Mulinum*	ZB
	1750-1050	1b	Shrubs steppe codominated by Asteraceae subf. Asteroideae and *Mulinum* with forest patches	ZB
(+)	2900-1750	1a	Shrubs-grass steppe codominated by Asteraceae subf. Asteroideae, *Mulinum* and Poaceae with forest patches	ZB

Figure 6. Reconstruction of the dynamics of the plant communities of the Pueyrredón Lake area (47° S) using the pollen information of the ZB wet meadow sequence and the COCU archaeological sequence for the last 2900 cal yr BP.

The last 120 cal yrs BP indicate the establishment of the current shrub steppe that grows in the study area and is analogous to Group 3 of the modern pollen model (Figures 2 and 4). These shrub and dwarf-shrub steppes are physiognomically and floristically heterogeneous. This heterogeneity has been related to the spatial variation of rainfall, the redistribution of runoff and the diversity of soil [46]. In our records, the increase in shrubs such as *Mulinum*, the presence of *Berberis*, Asteraceae subf. Asteroids and dwarf-shrubs (Amaranthaceae subf. Chenopodioideae, *Nassauvia*, *Ephedra*), and the decrease in Poaceae could be indicators of evaporation processes associated with aridity conditions similar to the current one (Figures 4 and 6).

While the development of the shrub steppe coincides chronologically in both sequences (ZB and COCU), there are signals in the ZB sequence located further west of the Andes that indicate greater sensitivity to variations in moisture availability during the late Holocene, which is documented by the pollen types associated with the forest. In this area, the signal of the forest is recorded as patches within a dominant shrub steppe, which is accounted by the association between the pollen types that accompany *Nothofagus*. The COCU archaeological sequence has provided greater details of the changes in the pollen proportions of plant communities recorded at the local scale [22]. These local changes are important since, although they did not change the physiognomy of the vegetation, they allowed modifications in the internal composition of the arid steppes (Figure 6). Thus, small changes in temperature, precipitation and topography can result in changes of different magnitude in the composition and biodiversity of steppe communities [42,80,81]. In this sense, [82] indicated that low availability of water, low temperature and high speed and frequency of winds are the physical factors that determine the structure and functioning of the Patagonian communities and morpho-physiological characteristics of the species.

On the other hand, on a local scale, wet meadows are subject to high grazing pressure [59]. In ZB, the presence of the pollen type associated with impact such as *Rumex* has been observed in the last 50 years (Figure 4). *Rumex acetosella* has become one of the most frequently introduced taxa for expeditions in Patagonia [83]. *Rumex* and other impact pollen types are present in the fossil record and modern pollen model, associated with the intense grazing pressure caused by the introduction of sheep from the Pampa Húmeda, Patagonia and Malvinas Islands in the last 100 years [84].

4.3. Regional Integration

In the Pueyrredón Lake area, [22–24] reconstructed vegetation dynamics during the Holocene using the sequences of LF, CMN1, CMN2 and COCU. The integration of paleoenvironmental information to the ZB sequence makes it possible to complement changes in vegetation, particularly in the late Holocene, and to contextualize them regionally.

During the late Holocene, there is a change in environmental conditions that indicates greater water availability associated with the weakening of the westerly winds and the influence of Atlantic humid air masses that penetrated the continent [85] in Patagonia in the last 3000 cal yr BP. In [86], it was reported that the weakest west–east hydric gradient (48–52° S) occurred between 2500 and 1200 cal yr BP. On a global scale, a change associated with variations in solar UV irradiation was evidenced around 2700 cal yr BP, which decreased the production of ozone in the atmosphere. The reduction of insolation would have caused consequences such as the relocation of the atmospheric circulation cells to the Equator [87] and a drift of the westerly winds [88].

In the NW of Santa Cruz, the vegetation in the area of Pueyrredón Lake (47° S) was represented by a shrub steppe with patches of forest indicating humid conditions. At 46° S, [21] indicate after 2100 cal yr BP the temperate humid conditions with a shift to the east of the forest–steppe ecotone limit. To the southwest, the inferences about the Perito Moreno National Park (48° S) indicate the development of a discontinuous forest associated with sporadic rainfall and the decrease in temperature [37]. From the 2700 cal yr BP, possible forest fluctuations associated with conditions of greater moisture than the current ones and environmental heterogeneity are inferred [37]. All these results suggest a fluctuation in the moisture availability. In addition, the formation of a transgressive pulse of the paleolake after the retreat of the glacier is also postulated, which would have reached 100 m above the current level of Lake Belgrano [89]. This greater water availability in the different paleoenvironmental records mentioned seems to coincide with the paleoenvironmental reconstruction carried out in ZB, which indicates the development of patches of forests from 2900 cal yr BP. Other studies have also recorded the increase in lake levels and the expansion of forest south of 44° S, both west and east of the Andes, associated with an increase in moisture [16,40,90,91]. In addition, the fluctuations recorded in Cardiel Lake [38,39] also exemplify the climate variability during the late Holocene. The comparison with sequences located east of the 47° S in the Deseado Massif (Los Toldos, La Martita, La Primavera) indicate semi-arid conditions similar to the current ones [20,47,49]; these conditions correlate with the moisture pattern recorded in the west–east gradient of Patagonia. In line with the previously mentioned data, the sites located between 49° and 50° S indicate the establishment of an open forest [17] and the development of a grass steppe associated with high moisture values and the decrease in shrubs in the La Tercera wet meadow, Paisano Desconocido wet meadow and Chorrillo Malo 2 [18,19,92]. In addition, a period of greater incidence of fires is noted between 3000 and 2000 cal yr BP in the communities of Argentino Lake and the extra-Andean steppe of San Martín Lake, which suggests conditions that favored the drying of logs in the forest and the continuous supply of fuel in extra-Andean communities [93]. This regional scenario between 46 and 50° S seems to be compatible with the weakening of the west–east precipitation gradient associated with westerly winds [15].

From the last 1050 cal yr BP to the present, ZB wet meadow indicates a change to arid conditions with the development of the current shrub steppe. This is coincident with other paleoenvironmental records that indicate a decrease in effective moisture at 47° S in the west of the Andes [40], and the loss of forest cover in the last 500 cal yr BP. To the east of the Andes and at the same latitude, the paleoenvironmental sequences in the Deseado Massif record for the last millennium a shrub and dwarf-shrub steppe under dry conditions [20,49,94]. Between 500 and 100 cal yr BP, the sequences located at 49°

S (San Martín Lake) suggest a grass steppe with shrubs associated with lower moisture availability in the area [18,19]. In the southern Patagonia, inferences made by calculating palaeohydric index indicate lower values in eastern environments between 700 and 500 cal yr BP [86]. The paleoenvironmental records of Argentino Lake at 50° S [15–17] indicate a change from wet to dry conditions at 400 cal yr BP with reduction of forest pollen. In addition, pollen data from archaeological sequences at the same latitudes [49] also indicate the development of a shrub steppe associated with dry conditions. On a larger scale, geochemical evidence [95] and speleothems [96] indicate for this period a decrease in water availability due to the weakening of westerly winds.

5. Conclusions

The pollen records studied allowed to reconstruct the paleoenvironmental history of the NW of Santa Cruz, Patagonia, for the late Holocene. The plant communities of the Pueyrredón Lake area were sensitive to the climate changes registered. These changes signal variations in water availability, indicating wet and dry periods in the last 3000 cal yr BP. The ZB sequence indicates for the last 2900 cal yr BP the development of a shrub–grass steppe with Asteraceae subf. Asteroideae and *Mulinum* and the increase in pollen types associated with the forest, which signals wetter conditions. Then, from 1000 cal yr BP, dry conditions were accentuated, which was recorded in our sequence by the expansion of the shrub and dwarf-shrub steppe. Moreover, changes in the composition and dominance of steppes over time were evidenced.

Small-scale changes in the composition of the shrub steppes of the Pueyrredón Lake area were also detected when comparing with archaeological sequences, which account for the heterogeneity of steppe vegetation. In addition, although the paleoenvironmental information agrees with data previously obtained of the archaeological sequences (COCU, CMN1, CMN2), it must be considered that they represent temporary windows of information and that said information may contain some anthropic bias. Therefore, the comparison with continuous sequences (ZB) strengthens the paleoenvironmental reconstruction at local and regional scale. In this sense, the information provided from the COCU archaeological site has made it possible to reconstruct the landscape locally.

The integration of the information with other Patagonian sequences allowed to frame in a regional context the changes that occurred. Although the synchronicity of the environmental changes recorded for this period varies according to the geographical location of the different Patagonian paleoecological records studied, the regional context indicates an increase in wet conditions around 3000 cal yr BP and a change to drier conditions in the last millennium. Thus, the changes detected in vegetation agree with the west–east gradient variations in moisture availability, in which Andean and extra-Andean communities behave antagonistically.

Although the plant communities in the study area were sensitive to changes in moisture conditions related to variations of the westerly winds, they responded differently according to local conditions resulting from the geomorphology of the site. In this sense, modern pollen models have shown variations among the pollen proportions of each shrub community that develops in the area. These variations can be associated not only with changes in moisture availability but also soil factors on a local scale. Thus, the small variations detected within the shrub communities indicate that the vegetation changed not only its physiognomy, but also in the internal composition of the steppes in the last 3000 years.

In addition, the analysis of the modern pollen model provided relevant information on the types of dispersion present in the pollen spectrum and their consideration in the interpretation of the fossil record. The taxa related to the current anthropogenic impact and that found in the last century indicate mainly landscape modifications caused by the European settlement and the introduction of sheep in Patagonia.

The results obtained provide useful information to understand changes in vegetation in the past and the way it can respond to changes in the future.

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