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Late-Holocene vegetation dynamics and disturbance regimes in north Patagonia Argentina (40°S)

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Abstract
Natural disturbance processes such as volcanic eruptions, fire and human activities are important vegetation drivers in north Patagonia. Here, we tested the impact of volcanic ash fall and fire on vegetation composition analysing two sediment records, Lake Avutarda and Lake Bruja, located in the forest-steppe transition at 40°S. In addition, our analysis provides the first account on the history of *Nothofagus alpina* at its eastern distribution limits. Our results comprise the last 3000 years, indicating the persistence of the vegetation despite evident volcanic activity documented by numerous tephra layers in both records. Eleven fire episodes were identified, while redundancy analysis indicates a non-significant influence of fire activity on the vegetation. The population increase of *Nothofagus alpina* represents the most important change in vegetation composition in the last three millennia. We speculate that the presumed change in climate, which led to the expansion of *Austrocedrus chilensis* south of the study area, also caused the increase of *Nothofagus alpina* populations in the region.

Keywords
ash, fire, human activities, late-Holocene, *Nothofagus alpina*

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Introduction

The eastern side of the Patagonian Andes is characterized by a remarkable vegetation gradient, with a sharp transition from the forest to the steppe. The modern geographic position of the ecotone is largely determined by effective moisture and follows the decrease in precipitation from west-to-east (Garreaud, 2009), which in turn is determined by the orographic effect of the Andes Cordillera and the prevailing westerly winds. The exact position of the ecotone may depend on the latitudinal position and strength of the Southern Westerlies (Villalba et al., 2003). Nevertheless, natural disturbances such as fires and volcanic eruptions are frequent in this region and may play an important role in controlling the vegetation composition as well (Kitzberger, 2012; Veblen et al., 1992).

Many characteristics of the vegetation, including richness, dominance and structure are under the influence of disturbance events (Pickett and White, 1985; Theurillat and Guisan, 2001). The strength or frequency of some disturbance processes depends on the mean state of other abiotic components (Baker, 1995; Turner et al., 1998). For example, the severity and frequency of fire varies with changes in precipitation and temperature (Dale et al., 2001; Jolly et al., 2015; Veblen et al., 2000). In addition, human activities represent additional disturbance factors, such as logging, animal pasture and through the introduction of new species.

In addition to climate and disturbance regimes controlling vegetation history, the initial distribution of plants at the end of the last glaciation play an important role in explaining postglacial vegetation change. The survival of plants on both sides of the Andes Cordillera has been proposed by palynological and genetics studies, for some important tree taxa in the region (Heusser, 1983; Marchelli and Gallo, 2006; Markgraf et al., 2009; Paredes, 2003; Pastorino and Gallo, 2002; Premoli et al., 2000; Villagrán, 1991). *Nothofagus alpina* has been largely investigated in genetic studies (Donoso et al., 1990; Marchelli and Gallo, 2004), while palaeoecological studies have hitherto not addressed its history along its eastern distribution limit, especially at 40°S, where *Nothofagus alpina* as well as *Nothofagus obliqua* (same pollen type) have their largest abundance (Sabatier et al., 2011).

These deciduous southern beech species occur at both sides of the Andes Cordillera. The latitudinal range of *Nothofagus alpina* in Chile extends from 35°13′S until 40°22′S and its Argentinean distribution comprises a latitudinal range from 39°25′S to 40°35′S. The geographical distribution of *Nothofagus obliqua* is wider extending in Chile from 30°30′S to 41°S and, on the eastern side of the Andes, its distribution ranges from 36°50′S to 40°15′S. In general, both species grow under a humid-temperate climate,

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where winter precipitation plays an important role in the development and persistence of these species during the following summer (Donoso, 2013).

Based on these settings and previous research in the region we address the following questions: (1) What changes did the vegetation experience at 40°S during the last 3000 years? (2) Did natural and anthropogenic disturbances processes strongly influence vegetation composition through time? (3) What is the history of *Nothofagus alpina* in Northern Patagonia? To answer these questions, we investigated the sediments of two small lakes positioned in the transition of the forest-steppe ecotone, south of Lake Lácar in the Neuquén Province, Argentina. The area is currently largely affected by the deposition of volcanic ash, lightning and resulting fires, and human activities. Our study sites are located within the Lanín National Park, home to the main populations of *Nothofagus alpina* and *Nothofagus obliqua* on the eastern side of the Andes.

Modern environmental setting

The study sites are located in north Patagonia Argentina at 40°S, on the eastern flank of the Andes Cordillera, in the southwestern part of the Neuquén Province. The western flanks of the Andes receive precipitation in excess of 3000 mm a year, which drops within 100 km to below 200 mm per year. The air masses discharge most of the humidity on the way up the mountains on the western slopes of the Andes. Dry air descends on the eastern slopes undergoing adiabatic heating: because of the difference between wet and dry lapse rates the descending air is warmer. In the valleys, precipitation is generally less than 800 mm (Garreaud et al., 2013). Maximum precipitation occurs in the winter season (June–August). To the east, the climate is drier and with regular frost periods and warmer summer temperatures (Fernández-Long and Müller, 2006). In the study area, the average precipitation varies between 2100 and 1700 mm per year. The average temperatures are 4.1°C in winter and 20.1°C in summer (Administración de Parques Nacionales, 2012).

The vegetation in the region responds to the sharp precipitation gradient and topography. A vegetation transition from rain forest to open woodland and to steppe on the eastern flanks characterize this gradient. The rainforest elements *Podocarpus nubigenus, Saxegothaea conspicua, Drimys winteri* are present in the westernmost areas (Donoso, 2013). The transition zone between rain forest and the steppe is dominated by an open woodland of *Nothofagus antarctica* with *Austrocedrus chilensis* and *Maytenus boaria* together with shrub species of *Berberis, Discaria* and *Escallonia*. The steppe is mainly characterized by shrubs belonging to the family Asteraceae, Chenopodiaceae, and to the genus *Mulinum* and herbs of Poaceae, *Senecio, Acaena* and *Phacelia*.

The forest is dominated by several southern beech species of the genus *Nothofagus*. Their distribution in the landscape is determined by effective moisture, elevation and soil. Five species of *Nothofagus* are present in the region, of which *Nothofagus alpina* and *Nothofagus obliqua* are restricted to some lake basins in their Argentinean distribution. Large and dense mixed forests of these two species develop around Lake Lácar (Sabatier et al., 2011), while in other overlapping areas of their distribution the two species occur as monospecific forests. Within those mixed forests, however, the species abundance differs with altitude. *Nothofagus obliqua* dominates the forests between 650 and 800 m a.s.l., while *Nothofagus alpina* becomes dominant at 950 m a.s.l., occurring up to 1350 m a.s.l. *Nothofagus alpina* grows under an annual precipitation average between 1800 and 2800 mm year^{-1} and *Nothofagus obliqua* occurs with a precipitation average between 950 and 2300 mm year^{-1} (Sabatier et al., 2011). *Nothofagus alpina* extends its south range of distribution in Argentina to 40°35′S, while *Nothofagus obliqua* reaches its southern limit of distribution at 40°14′S, south of the Lake Lácar basin. In Argentina, *Nothofagus alpina* is more than twice as abundant as *Nothofagus obliqua*.

The other three *Nothofagus* species have a wider distribution in Argentina as well in Chile. *Nothofagus pumilio* is a deciduous tree widely distributed along the Andes in Argentina and Chile (Donoso, 2013), defining the upper tree limit at high altitudes (Cuevas, 2000). Different morphological forms occur according to the altitude and environmental conditions, with some individuals growing as shrubby krummholz form at the highest elevations and others growing as trees up to 20 m tall (Young and León, 2007). *Nothofagus dombeyi* dominates slopes in the western parts in an elevation belt below *Nothofagus pumilio*, where the mean annual precipitation fluctuates between 1000 and 2800 mm. *Nothofagus antarctica* possesses the greatest ecological amplitude among the South American *Nothofagus* species (Donoso, 2013) and adopts different morphotypes according to the environment in which it develops (Premoli, 1991; Ramírez and Figueroa, 1987). In our study site, this species is forming monospecific woodland and mixed patches of open vegetation towards the dry end of the precipitation gradient.

The study sites are located within the Lanín National Park in Neuquén Province, Argentina (Figure 1c). Lake Bruja (40°14′S; 71°30′W; 1060 m a.s.l.; Figure 1b) is situated on the north-east slope of Cerro Escondido. It has a basin of about 1.6 ha. It is located in a wide valley, which is used for summer pasture of cows and horses that roam in the forest around the lake. The immediate surroundings of the lake consist of a closed mixed forest of *Nothofagus dombeyi* and *Nothofagus alpina* with few individuals of *Nothofagus antarctica* growing at the lake shore, while a mosaic of *Nothofagus antarctica* and patches of open grassland characterize the lower slopes and valley bottom. A dense population of bamboo *Chusquea culeou* characterizes the understory. *Austrocedrus chilensis* is present within the valley on slopes with northerly aspects. At Lake Bruja, precipitation is about 2100 mm year^{-1}.

Lake Avutarda (40°23′S; 71°25′W; 1610 m a.s.l.; Figure 1a) is located 30 km south of San Martin de Los Andes, east of Cerro Ezpeleta. It is situated at the treeline of *Nothofagus pumilio. Nothofagus alpina* occurs on the western slopes up to about 1350 m a.s.l. It is a shallow lake of 0.75 ha, with a depth of 1.5 m at the time of sampling. Shrubs and herbs such as Asteraceae, Caryophyllaceae, Iridaceae, Poaceae, Ranunculaceae, *Valeriana, Geranium, Acaena*, Brassicaceae, *Gaultheria, Senecio* and *Quinchamalium* occur around the lake. Krummholz forms of *Nothofagus pumilio* grow at the eastern side of the lake, while a forest of erect *Nothofagus pumilio* trees is found to the west. At Lake Avutarda precipitation is about 1700 mm year^{-1}.

Materials and methods

The sediment–water interface at both lakes was collected using a gravity sampler, recovering 17 and 11 cm for Lake Bruja and Lake Avutarda, respectively. Further 1-m long core sections were obtained using a square rod Livingstone sampler (Wright, 1967). A 140 cm long core was obtained from Lake Bruja and a sediment sequence of 116 cm length was recovered from Lake Avutarda. Cores were described visually using the Munsell Soil Colour Chart. Loss on ignition was carried out at 550°C (Heiri et al., 2001) from the same sample depth used for pollen analysis.

Samples of 0.5 cm^3 were taken for pollen analysis at 2-cm intervals, along both cores avoiding tephra layers. In addition, contiguous pollen sampling was conducted before and after major tephra layers in order to analyse the effect of ash deposition on the vegetation. Pollen processing followed the methodology outlined by Bennett and Willis (2001), excluding sieving. Identification was carried out using the reference collection from the Department of Palynology and Climate Dynamics of the University of Göttingen together with reference literature by Heusser (1971)

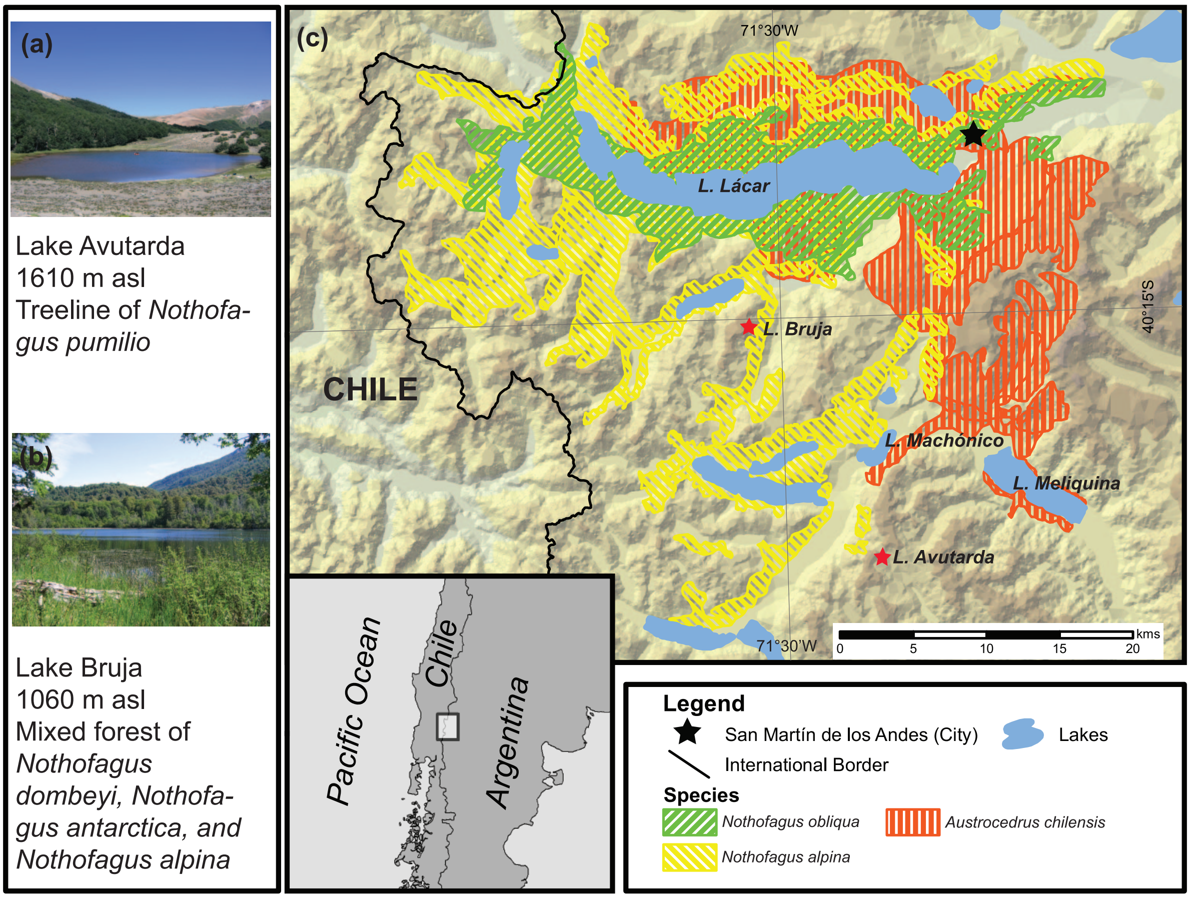

Figure 1. Location of the study sites: (a) Lake Avutarda and (b) Lake Bruja photographs; (c) position of the study sites (red stars), and the modern distribution of *Nothofagus alpina, Nothofagus obliqua* and *Austrocedrus chilensis* on the Argentinean side around Lake Lácar basin based on Sabatier et al. (2011), Administración de Parques Nacionales (2012) and Dezzotti and Sancholuz (1991). Notice that the studied lakes are small (Avutarda 0.75 and Bruja 1.6 ha) and therefore not distinguishable on the map.

and Markgraf and D'Antoni (1978). A tracer of *Lycopodium* was added to each sample to calculate pollen concentration. A minimum of 500 pollen grains was counted at 40× magnification. Terrestrial pollen percentages were based on the sum of trees, shrubs and herbs. Cyperaceae pollen grains were not included in the sum of aquatic taxa as these plants grow at the margin of the lakes.

In the absence of macrofossils, four bulk sediment samples per lake were radiocarbon dated. The age-depth models were constructed based on these dates (Table 1) and pollen stratigraphical control points using Clam 2.2 (Blaauw, 2010) with SHCal13.14C calibration curve (Reimer et al., 2013). Linear interpolation was applied, without considering the width of tephra layers with a thickness >1 cm.

Pollen diagrams were constructed using C2 (Juggins, 2003). Constrained cluster analysis was performed with Tilia 2.0 (Grimm, 1993) using incremental sum of squares on the chord distance matrix. Principal component analysis (PCA) was conducted to explore directional changes and compare the two sites. The analysis was carried out on the covariance matrix of the taxon-combined percentage data. We conducted a redundancy analysis (RDA) examining possible relationships between changes in the vegetation composition and tephra deposition as well as fire episodes. The distance of each sample to the prior tephra layer and tephra thickness are the variables considered to evaluate whether tephra deposition had an effect on the vegetation. Fire frequency and fire magnitude are the variables used to investigate if the fire regime had influenced the vegetation. All ordinations were performed using CANOCO 5.0 (Ter Braak and Šmilauer, 2012) with square root transformed percentage data. For visual comparison, samples from both lakes were assigned to the clusters corresponding to the numerical zonation of each record. Palynological richness (E (Tn)) (Birks and Line, 1992) was estimated using 'vegan' package version 2.4.4 (Oksanen et al., 2017) with R (R Development Core Team, 2017).

Macro charcoal analysis was carried out based on 1 cm^3 sediment contiguously sampled at a 1-cm interval following the methodology outlined by Stevenson and Haberle (2005), avoiding tephra layers. The material was sieved at 125 µm, and counted under a stereomicroscope. The results were analysed using CharAnalysis (Higuera et al., 2009). This analysis was carried out for Lake Bruja, because of its position within a major forest of *Nothofagus* species.

Results

Chronology, lithology and loss on ignition

The age-depth models for the cores from Avutarda and Bruja indicate basal ages of 2800 and 3600 cal. yr BP, respectively (Figure 2a and b). To constrain the age model for the youngest samples, we added two control points. A date of 1880 ± 20 was added for the arrival of the first European settlers to the area (Kitzberger, 2012; Veblen and Lorenz, 1988), indicated by the onset of the *Rumex acetosella* curve in the diagram. A second date was used to mark the onset of *Pinus* plantations in the region (1970 ± 10) (Rehfeldt and Gallo, 2001; Schlichter and Laclau, 1998).

The sedimentation rate of both cores fluctuates between 0.1 and 0.8 mm yr^{-1}. In the last 100 years, Avutarda shows the fastest sedimentation rates (2 mm yr^{-1}), while the fastest sedimentation rates at Bruja (2 mm yr^{-1}) occurred around 3500 cal. yr BP. The sediments from both lakes show alternations between gyttja and basaltic-ash layers throughout the record (Table 2 and Figure 2). In addition, the core from Avutarda contains a thick pumiceous-ash

Table 1. Radiocarbon ages for the cores Avutarda and Bruja based on bulk sediment. Control points based on first pollen appearance: CPa marks the establishment of *Pinus* plantations. CPb arrival of first European settlers indicated by *Rumex acetosella*.

Depth (cm)	Uncalibrated age	Calibrated age (cal. yr BP)	Calibrated age ranges at 95% confidence intervals (yr min/yr max [probability (%)])	Control point	Laboratory code
Lake Avutarda					
150.5–151		−30	−49/−11 [95]	1970 ± 20	CPa
153.5–154		71	21/118 [95]	1880 ± 10	CPb
167.5–168	1229 ± 25	1103	993/1017 [7] 1054/1179 [87.9]		UBA-19650
200.5–201	1944 ± 26	1846	1747/1772 [9.8] 1789/1791 [0.4] 1801/2086 [84.7]		UBA-19652
219.5–220	2088 ± 28	2007	1930/1979 [27.3] 1981/2086 [67.6]		UBA-19654
263–263.5	2708 ± 50	2792	2720/2879 [94.8] 2914/2915 [0.2]		UBA-19656
Lake Bruja					
685.5–686		−30	−49/−11 [95]	1970 ± 20	CPa
687.5–688		70	31/108 [95]	1880 ± 10	CPb
715–715.5	837 ± 41	709	670/752 [94.2] 758/760 [0.8]		UBA-21609
747–747.5	1761 ± 45	1721	1537/1722 [95]		UBA-21610
792.5–793	1963 ± 35	1867	1748/1772 [5.7] 1788/1791 [0.4] 1800/1933 [84] 1963/1992 [4.8]		UBA-21611
836–836.5	3359 ± 33	3543	3455/3636 [95]		UBA-21612

segment between 253 and 236 cm depth. Tephra layers recorded in both cores >1 cm thick consist entirely of volcanic material. Not organic or minerogenic material mixed with the volcanic glass is observed. It can therefore be assumed that inwash of allochthonous material into the lake during or following the volcanic eruptions must have been low. Consequently, tephra layers represent a particular volcanic event and their thickness gives an idea of the magnitude of the eruption. Although both sites are situated 15 km apart, the tephra layers in both cores could not be matched visually (Figure 2).

Avutarda and Bruja pollen record and fire history of Lake Bruja

Changes in pollen composition were summarized for both Avutarda and Bruja in Table 3 and scarce pollen types (up to three grains per sample) are presented in Table 4. The constraint cluster analysis indicated three distinct groups for both sites and the diagrams were subdivided into three zones accordingly (Figure 3). The different *Nothofagus* species occurring in the region can only be separated into two distinct pollen types: *Nothofagus dombeyi*-type corresponding to *Nothofagus antarctica, Nothofagus pumilio* and *Nothofagus dombeyi* and *Nothofagus obliqua*-type produced by *Nothofagus alpina* and *Nothofagus obliqua*. At both sites, pollen of *Nothofagus obliqua*-type is mostly attributed to *Nothofagus alpina*. This pollen type is large and heavy, with short distance pollen dispersal (< 35 m, Marchelli et al., 2012), and therefore has a restricted pollen source area. *Nothofagus alpina* occurs today around Lake Bruja and ca. 250 m downslope on the western side of Lake Avutarda (1610 m a.s.l.), between ca. 800 and 1350 m a.s.l. These tree populations of *Nothofagus alpina* may have largely contributed to the total pollen of *Nothofagus obliqua*-type recorded at Avutarda, because of upslope pollen transport by the prevailing westerly winds. Pollen input of *Nothofagus obliqua* into the lake basins is of regional origin (sensu Prentice, 1985), and therefore contributing in a small proportion to the pollen records. The southern distribution limit of *Nothofagus obliqua* occurs ca. 5 km north/north-east of Lake Bruja and 20 km north of Lake Avutarda. In addition, both sites are above the modern altitudinal optimum of *Nothofagus obliqua* in the region, making it unlikely the tree occurred in the proximity of the lakes during the last 3000 years. Cupressaceae pollen is attributed largely to *Austrocedrus chilensis*, although individual grains may come from the rainforest taxa *Fitzroya cupressoides* or *Pilgerodendron uviferum* via long-distance transport.

The location of the lakes determines the type of pollen signal captured. Bruja, situated on the mountain slope at 1060 m a.s.l. within a dense forest, is documenting mainly changes in the local vegetation, reflected by the high percentage of *Nothofagus dombeyi*-type corresponding to the dominance of *Nothofagus dombeyi* occurring around the lake, *Nothofagus pumilio* above 1150 m a.s.l. and few individuals of *Nothofagus antarctica* growing at the lake shore as well as downslope in the valley. Lake Avutarda is located at the tree line (1610 m a.s.l.), where the persistent westerlies bring extra local components. Therefore, pollen from extra local origin is stronger represented including *Podocarpus nubigenus, Saxegothaea conspicua, Weinmannia trichosperma* and *Eucryphia/Caldcluvia*.

The accumulation of macroscopic charcoal in the sediments of Bruja is low with an average of 0.65 particles cm^{-2} yr^{-1}. Most of the charcoal counted correspond to grass (>80% in all the samples counted). Nevertheless, distinct peaks are visible and the signal-to-noise index (SNI) of 4.6, which indicates a consistently good separation of the signal from background noise (Kelly et al., 2011). Eleven fire episodes were detected during the last 3600 years. Fire frequency was high between 2000 and 1600 cal. yr BP and 1000 and 500 cal. yr BP with a maximum of four episodes/500 years during the former period.

High fire magnitude indicates large or intensive fires (Whitlock et al., 2006). In Bruja, these episodes took place between 2000 and 500 cal. yr BP. The highest peak magnitudes were registered between 1700 and 600 cal. yr BP. Fire-free intervals, with at least 400 years between fire events were observed along the record. Time between fire events was shorter between 2000 and 800 cal. yr BP, with an interval of 100–200 years.

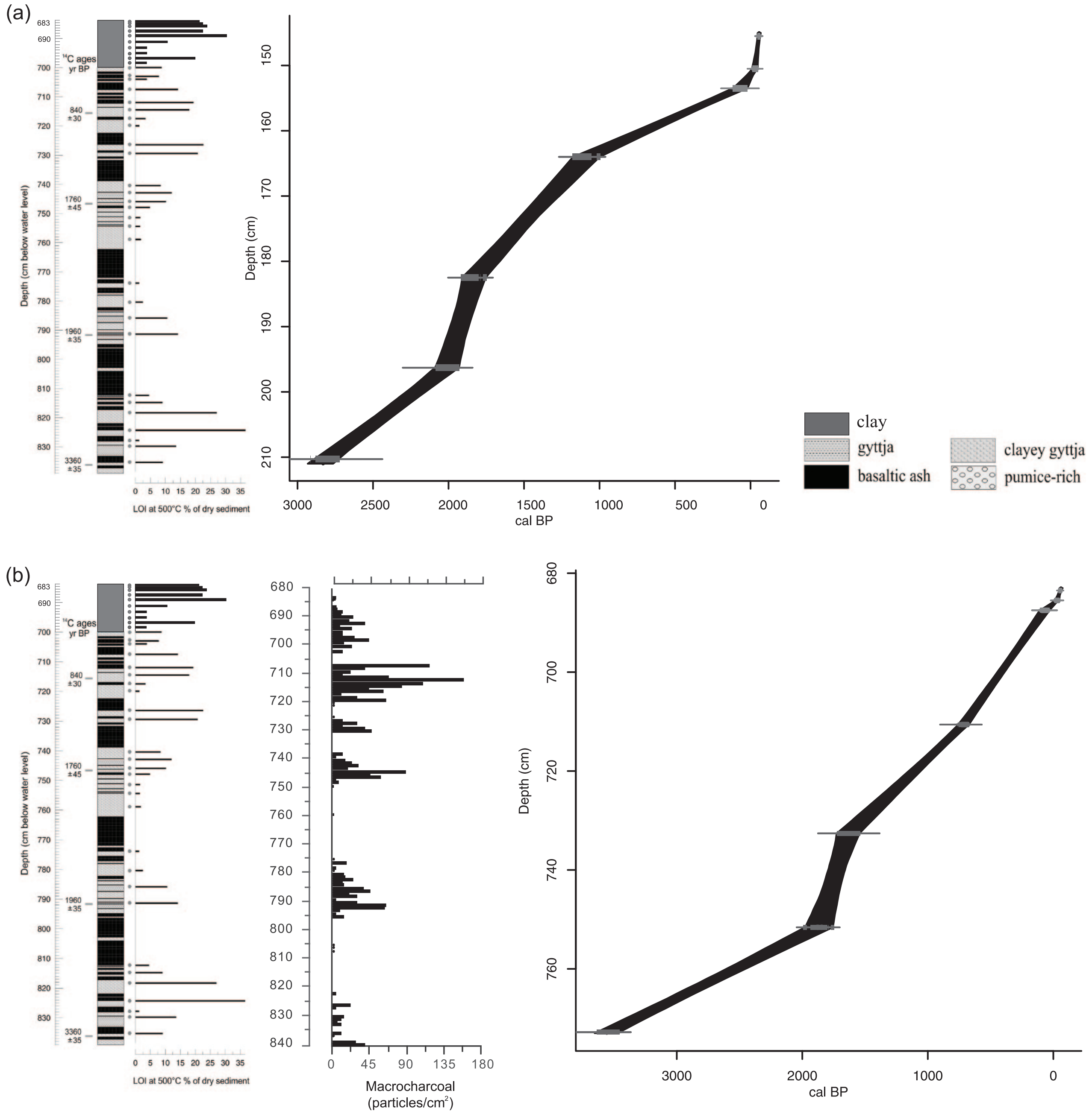

Figure 2. Lithology and age-depth model of (a) Avutarda and (b) lithology, macrocharcoal (particles/cm^2), and age-depth model of Bruja. Notice adjusted depth in *Y* axis in age-depth model.

Table 2. Sediment description of cores Avutarda and Bruja.

Depth (cm)	Age cal. yr BP	Sediment characteristics
Lake Avutarda		
150–145.5	Present	Clay. LOI between 5% and 22%
181–150	Present–1550	Alternate gyttja/black-basaltic ash layers. LOI between 2% and 12%
191–181	~1550	Grey-pumice-rich segment
236–191	1550–2300	Alternate clayey-gyttja/black-basaltic ash layers. LOI between 1% and 20%. Minimum LOI % between 213 and 203 cm
253–236	~2300	Thick grey-pumiceous segment
265–253	2300-2800	Reddish gyttja with three fine bands of basaltic ash. LOI between 4% and 14%
Lake Bruja		
700–683.5	Present	Clay. LOI between 2% and 32%
772–700	Present–1800	Series of thick clayey-gyttja and basaltic ash layers with varied thickness. LOI between 1% and 22%
795–772	1800–2200	Various layers of clayey-gyttja and narrow layers of basaltic ash. LOI between 1% and 14%
812–795	~2200	Two thick bands of basaltic ash with an incursion of a clayey-gyttja layer
835–812	2200–3300	Alternate laminations of clayey-gyttja, basaltic ash, and gyttja. LOI between 1% and 36%
840–835	3300–3600	Light clayey-gyttja and basaltic ash segment

Table 3. Vegetation history of Avutarda and Bruja records.

Zone	Age cal. yr BP	Pollen zone characteristics	Interpretations
Avutarda			
Avu-3	Present–100	Presence of human land-use indicator taxa: *Rumex acetosella, Plantago lanceolata* and *Pinus* (in that order of appearance); reduction in the percentage of Poaceae, *Ranunculus*, Asteraceae subf. Asteroideae and *Nothofagus dombeyi*-type. Palynological richness = 20–28 taxa	Forest clearing and animal husbandry close to the lake
Avu-2	100–1200	Gradual increase in the percentage of *Nothofagus obliqua*-type (2.7%, peak around 500 cal. yr BP), as well as an increase in the percentage of rainforest taxa, and a decrease in *Hydrangea* and *Misodendrum*. Asteraceae subf. Asteroideae remains high as the prior zone. Palynological richness = 14–26 taxa	Increase of downslope population abundance of *Nothofagus alpina*
Avu-1	1200–2800	Decline of *Nothofagus dombeyi*-type and increase of Poaceae between 2500 and 2000 cal. yr BP. First encounter of *Nothofagus obliqua*-type pollen at 2300 cal. yr BP. Asteraceae subf. Asteroideae shows its highest percentage (3.7%). Epiphytic taxa show a continuous presence (~1%). *Ranunculus* shows the maximum percentage (4.8%), followed by *Gunnera* (2.6%). The end of this zone is characterized by an increase of *Nothofagus dombeyi*-type and a decrease of Poaceae percentage. Palynological richness = 16–27 taxa	Local and regional decrease of *Nothofagus pumilio*. Expansion of herbs and grasses
Bruja			
Bru-3	Present–88	Appearance of *Rumex acetosella, Plantago lanceolata* and *Pinus*. Reduction in the percentage of *Nothofagus dombeyi*-type with a slight increase of Poaceae percentage. Palynological richness = 18–25 taxa.	Use of natural open areas for grazing. Short-scale timber activities
Bru-2	88–1200	Slight reduction in the percentage of *Nothofagus dombeyi*-type and Cupressaceae, and increase in the percentage of *Nothofagus obliqua*-type. Slight decrease in the percentage of *Misodendrum*, Asteraceae subf. Asteroideae and Poaceae. The end of this zone is marked by the appearance of the human introduced taxa *Rumex acetosella*. Palynological richness = 10–17 taxa	Closest forest. Reduction of the diversity of herbaceous taxa. Local increase of *Nothofagus alpina* populations occurring around the lake
Bru-1	1200–3600	Frequent occurrence of Cupressaceae and *Misodendrum*. Rise of *Nothofagus obliqua*-type at 2200 cal. yr BP (10.9%). Presence of rain forest element decreasing at 2700 cal. yr BP. Continuous presence of *Isoëtes* (0.7%) and its later disappearance from the record at 1600 cal. yr BP. Abundance of Poaceae, Asteraceae subf. Asteroideae and Chenopodiaceae. Presence of steppe elements (e.g. *Azara, Maytenus, Discaria*) lower than 7%. Palynological richness = 12–23 taxa	Open forest. Codominance of *Nothofagus* and grass. High diversity in the herbaceous stratum

PCA and RDA

For both records the PCA analyses show that the composition of samples was relatively stable through time with the first PCA-axis explaining only 23% and 17% of the variance for Avutarda and Bruja, respectively. The grouping obtained in the constrained cluster analysis was not reproduced by the PCA. In Avutarda the PCA only separates the samples from the youngest pollen zone, while no clear grouping of samples was obtained for Bruja. The first axis in the PCA for Avutarda separates the samples according to their proportion of *Ranunculus*, Caryophyllaceae and Poaceae versus *Pinus* and *Rumex acetosella* and *Plantago lanceolata* (Figure 4a). Therefore, it may be considered that the first component represents a land-use gradient that increases from left to right. It is interesting to note that Poaceae are not associated with the human impact indicator taxa, suggesting that the area around Lake Avutarda was not intensively used for agrarian and pastoral activities. The second axis explaining 12% of the variance separated the samples according to the proportion of *Nothofagus dombeyi*-type versus *Nothofagus obliqua*-type.

The first PCA axis in Bruja separated the samples according to their percentage of Poaceae and *Misodendrum* versus *Nothofagus dombeyi*-type. The second axis explained 16% of the variance and split the samples according to their proportion of Cupressaceae and Asteraceae subf. Asteroideae versus human indicator taxa (Figure 4b). The sample arrangement on the PCA shows two main vegetation phases through time. The first phase (lower two quadrants corresponding to 3600 and 1100 cal. yr BP), with samples characterized by steppe taxa; and a second phase (upper two quadrants corresponding to the last 1100 years) characterized by *Nothofagus obliqua*-type.

Submitting both records to the same PCA analysis revealed a clear separation between both sites (Figure 4c) with the first axis explaining 68% of the variance. The first axis is representing the environmental gradient between the two sites, which is a combination of the altitudinal difference and the precipitation gradient. On the right-hand side, the samples from Lake Avutarda were characterized by Asteraceae subf. Asteroideae, Poaceae and *Ranunculus*, which is in accord with the high elevation position of this lake, at the treeline of *Nothofagus pumilio*. By contrast, samples from Lake Bruja (left side, squares) were characterized mainly by *Nothofagus obliqua*-type and some rain forest elements such as *Weinmannia trichosperma* and *Drimys winteri* (not shown here). The second axis explained 5% of the variance, and separates the samples according to the presence of human indicator taxa such as *Rumex acetosella, Plantago lanceolata* and *Pinus*. These species are present in the youngest samples (on top) and they have a negative correlation with Poaceae and a positive correlation with *Nothofagus dombeyi*-type. The taxa arrows belonging to Avutarda quadrant indicate the extra local input represented in this site, which also includes *Nothofagus dombeyi*-type.

We applied RDA analysis to the pollen data from both sites to investigate whether the deposition of tephra layers had any effect on the pollen composition of the next younger samples (Table 5, Figure 5), but found no significant effect (Lake Bruja: explained variation of the distance to the tephra 2.0%; and tephra thickness 2.1%). However, in individual cases we visually observed changes in pollen percentages and/or a reduction in taxonomic richness in both records. The samples following the two thickest tephra layers in Bruja contain higher proportions of Poaceae pollen (11%) with a decrease in *Nothofagus dombeyi* pollen, while the sample with an even higher Poaceae proportion (14%) is not following a tephra layer. For Bruja, we also tested whether changes in fire frequency and magnitude explain changes in pollen composition, but also here found no significant influence of the fire regime on the vegetation (explained variation 4.4% and 3.4% respectively).

Table 4. Rare pollen types (up to three pollen grains per sample) at Lakes Avutarda and Bruja (not shown in the pollen diagrams).

	Avutarda			Bruja		
Age (cal. yr BP)	0–100	100–200	1200–800	0–88	88–1200	1200–3600
Taxa/pollen zones	Avu-3	Avu-2	Avu-1	Bru-3	Bru-2	Bru-1
Araucaria araucana					*	
Alnus acuminata		* * *	* *			
Lomatia hirsuta	* *	*		*	*	
Drimys winteri			* * *		*	
Maytenus	*	* *	* * *			
Embothrium coccineum		*				
Ribes	*		*			
Aster. subf. Cichorioideae	* * *			*		
Nassauvia						* *
Quinchamalium					*	
Valeriana				*	*	
Viviania					*	*
Ranunculus					*	
Berberis			*			
Azorella						*
Armeria			*			
Verbenaceae						*
Iridaceae	* *					
Adesmia			*			
Rubiaceae		* *	*			
Mulinum	*					
Polygonaceae	*		* *			
Escallonia	* *	* *	*	*	*	*
Unknown	* *	* *	*	*	*	*
Isoëtes		* *				
Hymenophyllum			*			
Polypodium feuillei					* *	
Anthoceros/Phaoceros						*
Litorella/Plantago			*			

*represents the number of pollen grains found per zone.

Discussion

Vegetation history and population increase of Nothofagus alpina

The most pronounced result of this investigation is that the vegetation was stable around Avutarda and Bruja over the last 3600 years, regardless of tephra depositions of up to 20 cm, fire activity, and presumed increase in ENSO variability (Flantua et al., 2016; Moy et al., 2002). The increase in the percentage of *Nothofagus obliqua*-type, attributed here mostly to *Nothofagus alpina*, appear as one of the most noticeable changes in our records; however, this change is gradual and most likely not triggered by a single disturbance event, such as a large-scale fire. Documentation of the vegetation history of *Nothofagus alpina* in palynological records is limited, especially on the Argentinean side of the Andes, where its distribution is restricted to valleys between 39° and 40°S (see Sabatier et al., 2011), and most of the investigations have so far focused on sites further south or north, capturing scarcely its presence. Thus, our records provide a first account of the late-Holocene history of *Nothofagua alpina* as the lakes are located close to the main population of this species in the Lake Lácar basin in the Lanín National Park.

Lake Bruja is surrounded by a dense forest of *Nothofagus alpina* and located 6 km south of Lake Lácar, where the largest populations of *Nothofagus alpina* as well as *Nothofagus obliqua* occur today (Figure 1c). The uppermost surface sample from Lake Bruja comprises 9.1% of *Nothofagus obliqua*-type pollen that increased from 3.3% at the beginning of the record around 3600 years ago (Figure 3b). Lake Avutarda collects 1% of *Nothofagus obliqua*-type pollen in the modern samples, with the continues pollen curve starting around 1500 cal. yr BP (Figure 3a). At Avutarda, the closest *Nothofagus alpina* population occur 250 m downslope (Figure 1c), while the closest *Nothofagus obliqua* population is found at 20 km north-west, around Lake Lácar.

This late-Holocene increase of *Nothofagus obliqua*-type finds a parallel in the late-Holocene expansion of *Austrocedrus chilensis* to the south of the study region. Several pollen diagrams from the forest-steppe ecotone between 41° and 43°S document the expansion of *Austrocedrus chilensis* between 5000 and 2000 years ago (Iglesias et al., 2014). *Austrocedrus chilensis* is also abundant on the eastern end of Lake Lácar, while its pollen type is scarcely represented at Avutarda and declines at Bruja. In this case, Cupressaceae pollen decline from an initial 3–1% coinciding with the increase of the *Nothofagus obliqua*-type pollen. This may suggest either a decrease of *Austrocedrus chilensis* individuals or an override-effect of the Cupressaceae pollen signal, because of the large amount of pollen production of the *Nothofagus* species (Fontana and Bennett, 2012) in comparison with *Austrocedrus chilensis*, which has a locally restricted pollen dispersal (Markgraf et al., 1981).

Austrocedrus chilensis is a drought-resistant taxon. However, its growth and distribution are mainly depending on moisture availability and precipitation, especially during the growing season (Kitzberger et al., 2000; Villalba and Veblen, 1997). Where the expansion of *Austrocedrus chilensis* occurs at sites towards the steppe (e.g. Lago Mosquito, Iglesias et al., 2011), it is interpreted

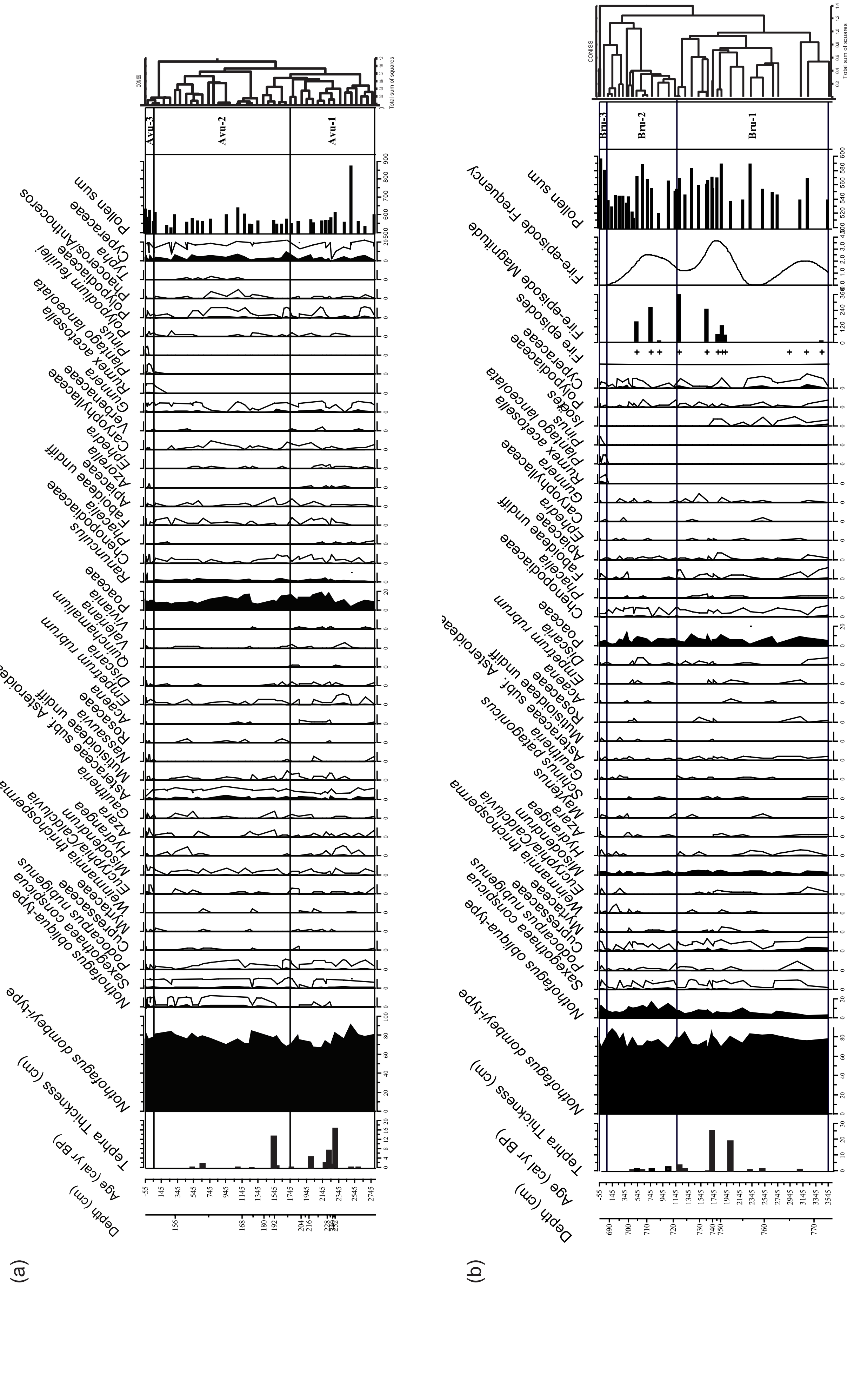

Figure 3. Percentage pollen diagram from (a) Avutarda record and percentage pollen diagram and macrocharcoal results from (b) Bruja, including pollen sums. Outline curve represent 10× exaggeration for minor taxa.

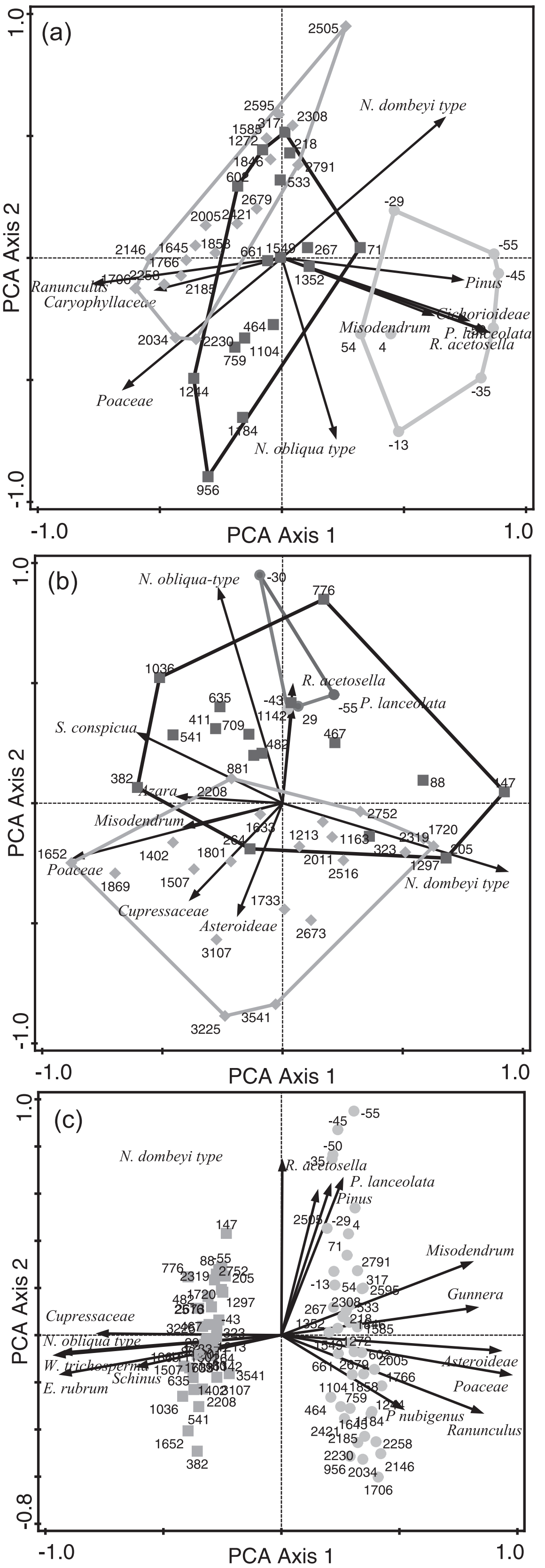

Figure 4. Species/sample scores of the PCA of pollen percentage data of (a) Lake Avutarda and (b) Lake Bruja. Grouping by CONISS shown by different symbols in the PCA: rhombus = zone 1; squares = zone 2; and circles = zone 3. (c) Combined ordination of Lake Bruja (squares) and Lake Avutarda (circles).

as a reaction to a more humid climate while other climatic shifts or changes in the fire regime may have triggered the expansion elsewhere (Iglesias et al., 2014). However, the general trend in late-Holocene climate change in Northern Patagonia is towards more humid conditions (Lamy et al., 2001; Mancini et al., 2008). Causes for increased humidity during the late-Holocene may be the northward shift and or enhanced strength of the Southern Westerlies (Fletcher and Moreno, 2011; Moreno et al., 2010). At the same time the climate may also have become more variable with enhanced ENSO activity (Flantua et al., 2016; Montecinos and Aceituno, 2003), possibly leading to alternations of drought and wet years perhaps providing an opportunity for a gradual replacement of tree taxa though gap dynamics. *Nothofagus alpina* and *Nothofagus obliqua* occur in areas with winter precipitation and dry summers (Alberdi, 1987; Conticello et al., 1996; Donoso, 2013; Ramírez et al., 1997), while it is most likely their requirement for growing season warmth that limits their distribution in the east and south. Both trees would have benefitted from increased late-Holocene moisture availability.

Although our records do not provide a strong evidence related to changes in precipitation seasonality and ENSO variability, the population increase of *Nothofagus alpina* during the late-Holocene is consisted with interpretations of late-Holocene climate change for southern South America (Lamy et al., 2001; Stine and Stine, 1990).

Table 5. RDA results performed on pollen percentages of lakes Avutarda and Bruja.

Explanatory variables	Explained variation (%)	Pseudo-*F*	*p*	*p* (adj)
Lake Avutarda				
Distance to the tephra	3.4	1.4	0.096	0.192
Tephra thickness	2.0	0.8	0.704	1
Lake Bruja				
Fire frequency	4.4	1.7	0.474	1
Fire magnitude	3.4	1.3	0.322	1
Tephra thickness	2.1	0.8	0.658	1
Distance to the tephra	2.0	0.8	0.832	1

Disturbance history

The lithologies of the cores from Avutarda and Bruja document a constant and significant volcanic activity in the region (Table 2 and Figure 2a and b) and one would expect that the vegetation should respond to this disturbance agent. High volcanic activity is reported for the entire Holocene in southern South America (Fontijn et al., 2014; Naranjo et al., 1993; Naranjo and Moreno, 1991). Due to the westerlies, most of the ash falls on the eastern flank of the Andes Cordillera (Gaitán et al., 2011), affecting flora and fauna (Berenstecher et al., 2017).

For the last 3600 cal. yr BP captured in our records, frequent volcanic activity occurred between 2300 and 900 cal. yr BP, which coincides with minor changes in the percentage and concentration of *Nothofagus dombeyi*-type. Simi et al. (2017) report volcanic activity in two records in the Aysén region in southwest Chile, showing a minimal variation in arboreal pollen, similar to our records. In both cases, these slight changes in pollen percentage are reflecting the persistence of the forest despite the constant disturbance processes related to volcanic activity. Montiel et al. (2016) analysed the impact of tephra layers on populations of *Nothofagus* species after the eruption of the Puyehue-Cordón Caulle Volcanic complex in June 2011. According to their results, based on tree-stands and tree-ring analysis, they concluded that some trees died because of the mechanic damage caused by the massive ash fall (>50 cm), and surviving trees showed no ring development after the event. Nevertheless, they observed a considerable regeneration of *Nothofagus* seedlings but they could not show that this effect is directly related to the ash deposition. Since

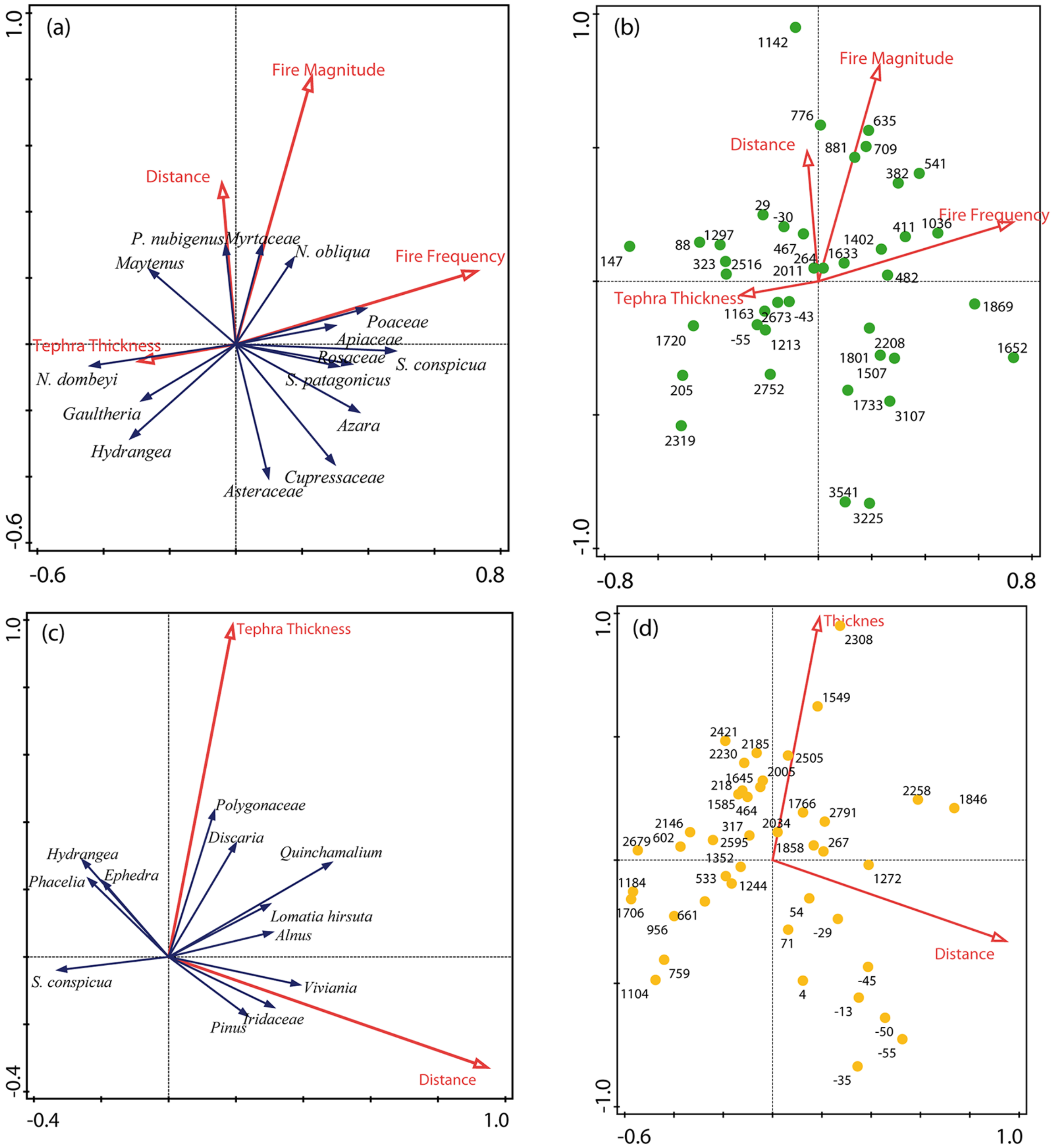

Figure 5. Redundancy analysis (RDA) biplot of selected species and samples, and explanatory variables for (a, b) Lake Bruja and (c, d) Lake Avutarda.

the thickest tephra layer in our records is 30 cm, mechanic damage on the branches of *Nothofagus* because of the ash fall may not have occurred here. Nevertheless, we cannot reject the possibility that ash deposition could have caused some impact on the foliage, as is demonstrated in some post-volcanic event studies (Chaneton et al., 2014) and therefore, it could affect pollen productivity. The finding that thick tephra deposits did not show significant effects on the vegetation may account for specific strategies of some plant species to reduce a negative effect. For example, the development of adventitious roots in *Nothofagus antarctica* (Veblen et al., 1977). González et al. (2014) reported the establishment of *Nothofagus pumilio* sprouts 1 year after the Hudson volcano eruption, as well as the surviving of understory species. Likely, these strategies are the consequence of an adaptative response to the systematic occurrence of this disturbance process (Veblen et al., 1977).

Another example of the effect on the vegetation composition after a volcanic eruption indicates that the chemical composition of the ash plays an important role for the establishment or the decline of some taxa. An increase in soil acidification because of ash deposition may facilitate the establishment of new species or hindering the recovery of pre-existing species (Fontana and Bennett, 2012). In our case, the short-term effect of ash deposition likely is not noticeable because of the constant influx of *Nothofagus* pollen into the lake.

The RDA results show that the effect of tephra deposition on the vegetation in both records is detectable, but not statistically significant as to have caused repeatedly a noticeable change in vegetation composition (p value >0.05 and explained variation $<4.5\%$ in all the variables tested; Table 5 and Figure 5). The slight decline in *Nothofagus* and the increase in shrubs and herbs after one of the tephra layers may have been caused by volcanic ash deposition. In addition, during periods of large ash deposition, fire events started to be frequent and possibly, these two local disturbance agents may have caused together the observed changes on the vegetation after single events. Moreover, when disturbance processes (fire and ash fall) and climate act simultaneously it is quite difficult to identify which factor caused the observed changes on the vegetation (De Porras et al., 2014). In the analysed records, the response in terms of increase or decrease in percentage and concentration (not shown) of individual taxa seems random. For example, at Avutarda percentage values of *Nothofagus dombeyi*-type pollen decrease from 83% to 70% after 18 cm of tephra. However, in the same record, the same taxon increase from 78% to 83% after 17 cm of tephra. In the case of Poaceae percentage, this random effect of ash is also observed. From 8% to 15% after 18 cm of tephra deposition and later, after 17 cm of tephra the percentage of Poaceae decrease from 10% to 7%. Nevertheless, studies in Argentina as well as in Chile report the importance of major disturbance processes in the development and dynamics of *Nothofagus* forests and in some cases, the forest as well as the understory seem to be resistant to the disturbance events (González et al., 2014).

Several studies have assessed the impact of tephra deposition from different perspectives: tree-growth (Magnin et al., 2017), soil properties (Cremona et al., 2011; González et al., 2015), fauna changes (Berenstecher et al., 2017; Lallement et al., 2014) and leaf-litter decomposition (Chaneton et al., 2014; Piazza et al., 2018), among others. However, all these investigations have evaluated the impact of ash deposition at a short time scale, and potential long-term effects or the lack therefore are not clear. Based on our data, it is difficult to disentangle the several factors that are acting at the same time, like fire, ash deposition and climate. Moreover, one or more of these factors could strengthen or weaken the individual effect they have on the vegetation structure. Even in this situation, the vegetation reflected in both pollen diagrams seems to be stable.

Fire plays an important role in North Patagonia, and its effect on the vegetation composition has been extensively studied (Dudinszky and Ghermandi, 2013; Kitzberger et al., 1997; Kitzberger and Veblen, 1999; Mermoz et al., 2005; Veblen et al., 1999; Whitlock et al., 2006, among others). Palynological and macrocharcoal analysis in North Patagonia show that fire activity during the late-Holocene is associated with the strengthening of ENSO frequency/intensity, especially after 3000 cal. yr BP (Iglesias and Whitlock, 2014). Assessing the influence of fire events on the vegetation around Bruja, it was possible to identify eight fire episodes between 3500 and 1100 cal. yr BP, among which just five represent large or intensive fires and fire frequency increased between 2100 and 1100 cal. yr BP. Three fire episodes, with a frequency of 1–2 fires every 200 years were identified for the second zone (Bru-2; 1100–100 cal. yr BP). We expected a correlation between fire and Poaceae since most of the charcoal counted comes from grass. However, the influence of fire frequency on Poaceae percentages is only strong in one sample (Figure 5). The RDA results indicate a non-significant influence of fire frequency and fire magnitude on the vegetation composition. Overall, the explanatory variables tested in this work (fire frequency, fire magnitude, tephra thickness and distance to the preceding tephra) account for 13.7% of the variation. However, since pollen sampling was carried out contiguously only before and after major tephra layers, it is possible that variation on the percentage of some taxa because of fire were not detected in other sections of the core. Despite this, it is possible to suggest that the local fire signal captured by Lake Bruja corresponds to surface-fires, at low magnitude and possibly promoted by lightning. The source of the charcoal found in Bruja could come either from the *Chusquea* bamboo understory around Lake Bruja or the open grassland patches in the valley north-east of the lake. Nowadays, farmers use this place for cattle and low-scale timber extraction.

Human impact

Northern Patagonia has been under the influence of human activities since before the arrival of European settlers (Veblen and Lorenz, 1988), changing the vegetation and adding to the natural disturbance regimes. However, it is difficult to find evidence of these early land-use activities in pollen diagrams. The pollen diagram from Lake Bruja and Avutarda show the presence of pollen from the introduced plants *Rumex acetosella, Plantago lanceolata* and *Pinus* in their topmost samples. Based on the abundance of these pollen types, the area close to Lake Avutarda was more intensively used by European settlers than the area surrounding Lake Bruja. Today, *Pinus* plantations and a few farms are located 3 km north-west of Lake Avutarda.

The presence of *Rumex acetosella* and *Plantago lanceolata* in pollen records from southern South America has been used as an indicator for livestock grazing (Iglesias et al., 2017). A common pattern related to the arrival of European settlers is a decline in tree pollen with an increase in grass, because of forest clearance for pastureland (Fletcher and Moreno, 2012; Mancini et al., 2005; Szeicz et al., 1998). Our results do not show an increase in Poaceae pollen at the time of the rise in *Rumex acetosella* and *Plantago lanceolata*. The PCA for Avutarda and Bruja (Figure 4a and b) shows a negative correlation between the Poaceae vector and human indicators taxa. At the time of grazing activities, Poaceae percentages are stable or decreased, indicating that the area likely was not suitable for pasture.

The pollen diagram from Bruja shows a decline in the percentage of *Nothofagus obliqua*-type, immediately before the appearance of the human indicator pollen type. The age model in this section is not well constrained; however, it may be that the first European settlers around Lake Lácar area conducted selective-timber activities for house-building with a preference for *Nothofagus alpina*, because of its high wood-quality (Azpilicueta and Marchelli, 2016). Lanín National Park was created in 1937 (Administración de Parques Nacionales, 2012) and protective measures were established and timber extraction was controlled, but initially continued at low rate. The result of this measure may be observed in the pollen diagram from Bruja where percentages of *Nothofagus obliqua*-type increase in the last 50 years, potentially indicating the effectiveness of those measures.

Human-set fires in north Patagonia have been widely documented, based on reports written by eyewitnesses that indigenous people used fire for hunting (Veblen et al., 1999, 2003). Thus, anthropogenic fires are not only related to European settlers. Fire frequency in the Bruja record declined in the last 500 cal. yr BP and fire activity is practically null towards current times, probably because of the measures adopted by the authorities in charge of the National Park. In the light of these results, it is possible to speculate that neither indigenous people nor European settlers have promoted significant changes on the vegetation composition close to Lake Bruja, as it is evidenced by our results. Moreover, our fire record during the last decades suggests effective fire suppression activities in the region.

Conclusion

During the late-Holocene, the local vegetation around both Avutarda and Bruja lakes shows minimal changes, indicating the stability of the vegetation during the last 3600 years at 40°S. Although we documented fire and volcanic activity in the region, we do not find evidence of large-scale vegetation reactions to these disturbances. The population increase of *Nothofagus alpina* was the most important change in vegetation composition during the last three millennia. Here, our records offer a first account of the vegetation history of this southern beech species. We speculate that the increase in effective moisture suggested in other investigations for the expansion of *Austrocedrus chilensis* in the region also determined the development of *Nothofagus alpina*. Human impact in the last century was detected by the presence of introduced taxa. However, the detected land-use change has not caused a significant impact on the vegetation composition in the region, accounting for the effectiveness of the measures carried out by the authorities of the National Park.

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