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Nanavati, W., Whitlock, C., Outes, V., & Villarosa, G. (2020). A Holocene history of monkey puzzle tree (pehuén) in northernmost Patagonia. Journal of Biogeography. 10.1111/jbi.14041

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Journal of Biogeography

TITLE

A Holocene history of monkey puzzle tree (pehuén) in northernmost Patagonia

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Holocene history of monkey puzzle tree

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ACKNOWLEDGEMENTS

This research was supported by grants from the National Science Foundation (OISE0966472, GSS1461590, SPRF-FR2004941), Fondo para la Investigación Científica y Tecnológica (PICT 2011 2046), and the Neuquén Volcanic Hazards Assessment, CONICET-Legislatura Provincial de Neuquén. We would like to acknowledge collaboration from Copahue Provincial Park, Neuquén Province, Argentina. Devin Quick assisted with field and lab work. Dr. Virginia Iglesias and Dr. David Roberts provided help with the statistical analyses. Dr. Mark Bush and Dr. Jean Larmon provided useful comments on the manuscript.

ABSTRACT

Aim: Although it is established that climate and fire have greatly influenced the long-term ecosystem dynamics of Patagonia south of 40°S, the environmental history from northernmost Patagonia (37-40°S), where endemic and endangered monkey puzzle tree (*Araucaria araucana*) occurs, is poorly known. Here, we ask: (1) What is the Holocene vegetation and fire history at the northeastern extent of *A. araucana* forest? (2) How have climate and humans influenced the past distribution of *A. araucana*?

Location: Northernmost Patagonia, Argentina and Chile (37-40°S)

Taxa: *Araucaria araucana*, *Nothofagus*, Poaceae

Methods: Sedimentary pollen and charcoal from Laguna Portezuelo (37.9°S, 71.0°W; 1730 m; 11,100 BP) were evaluated using statistical methods and compared with other paleoecological, independent paleoclimate, and historical records to assess how changes in climate and land use influenced local-to-regional environmental history.

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Results: An open forest-steppe landscape persisted at L. Portezuelo throughout the Holocene with generally low-to-moderate fire activity. Increased *Nothofagus* pollen after ~6590 BP suggests increases in shrubland and moisture in association with cooler conditions and greater seasonality and ENSO activity. *Araucaria* pollen appeared at L. Portezuelo at ~6380 BP, but was low in abundance until ~370 BP, when it rose with charcoal levels. This increase in *Araucaria* and fire coincided with a regional influx of Mapuche American Indians. *Nothofagus* deforestation and *Pinus* silviculture marked Euro-American settlement beginning in the 19-20th century.

Main conclusions: (1) Rapid postglacial warming and drying limited the distribution of *Araucaria* in the central valley of Chile. In the middle and late Holocene, decreased temperatures and greater seasonality and ENSO activity increased precipitation variability allowing *Araucaria* expansion at its northeastern limit. (2) Greater abundance of *Araucaria* and heightened fire activity at L. Portezuelo after 370 BP coincided with increased Mapuche-Pehuenche American Indian land use, suggesting that *Araucaria* may have been managed in a human-altered landscape.

KEYWORDS: American Indians, fire history, Holocene, land use, paleoecology, vegetation history

INTRODUCTION

Although it is well established that climate and fire have greatly influenced the long-term dynamics of the Patagonian forest-steppe ecotone south of 41°S (Iglesias, Whitlock, Markgraf, & Bianchi, 2014; Nanavati, Whitlock, Iglesias, & de Porras, 2019; Whitlock et al., 2006), the vegetation and fire history of Patagonia north of this latitude is poorly understood, given the paucity of well-dated records (i.e., Abarzúa et al., 2014; Fletcher & Moreno, 2012b) (Table 1; Fig. 1). Northernmost Patagonia (here defined as Argentina and Chile, 37-40°S) is notable for the presence of monkey puzzle tree (*Araucaria araucana*), an endemic, endangered, and culturally significant conifer that presently grows on both sides of the Andes and in disjunct populations in the Cordillera de Nahuelbuta, Chile (Fig. 1) (Aagesen, 2004; dos Reis, Ladio, & Peroni, 2014; Premoli, Quiroga, & Gardner, 2013). Within the last few hundred years, the clearance of native forest for Euro-American settlement, agriculture, livestock grazing, and timber has reduced the distribution of *A. araucana* by nearly 60%, and currently, it is confined to an area of less than 400 km^2 (Mundo, Kitzberger, Juñent, Villalba, & Barrera, 2013; Premoli et al., 2013). The recent decline of *A. araucana* warranted its listing as an endangered species by the International Union for Conservation of Nature in 2013 (Premoli et al., 2013).

Araucaria araucana is a shade-intolerant, dioecious species that survives surface fire when mature and has a limited capacity for pollen and seed dispersal (González, Muñoz, González-Reyes, Christie, & Sibold, 2020; Sanguinetti & Kitzberger, 2009; Shepherd & Ditgen, 2013; Veblen, 1982). *A. araucana* occurs in pure stands on north-facing slopes in the Andes or within mixed stands alongside *Nothofagus pumilio* near timberline, *N. dombeyi* and/or *Austrocedrus chilensis* near the southern extent of *A. araucana* distribution, *N. alpina* and/or *N. obliqua* at low elevations west of the Andes, and *N. antarctica* at low elevations along the forest-steppe border east of the Andes (Veblen, 1982). According to historical and ethnographical accounts (Aagesen, 2004; dos Reis et al., 2014), *A. araucana* is sacred to Mapuche-Pehuenche American Indians, who actively managed the species through seed sowing, transplantation, and

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possibly the use of fire to facilitate the collection of piñons and maintain the fire-tolerant species. Despite the wealth of research documenting the modern ecology of *A. araucana*, little is known about its Holocene paleoecological history and the role that American Indian management may have had on the distribution of this species through time.

Araucaria angustifolia occurs in subtropical southern Brazil and northeastern Argentina, between 18 and 30°S, and is the only other member of Araucariaceae native to the Americas (dos Reis et al., 2014). Similar to the Patagonian *A. araucana*, these trees assume a sacred importance to the local American Indian populations and provide vital food and material resources (dos Reis et al., 2014). In *A. angustifolia* forest, it is hypothesized that American Indian management facilitated the regional expansion of the species during the last 1500 years (Bitencourt & Krauspenhar, 2006; Iriarte & Behling, 2007; Robinson et al., 2018). A similar hypothesis about American Indian management of Patagonian *A. araucana* forest has been made based on ethnographic and genetic records (e.g., Aagesen, 2004; Ruiz et al., 2007), but this hypothesis has not been examined with paleoecological records, which can provide a nuanced understanding of vegetation and fire history. Here, we present an 11,100-year-long record of climate, vegetation, fire, and land use from Laguna Portezuelo in northernmost Patagonia (37.91°S, 71.04°W; 1733 m elev.; 1.66 ha; 5.6 m maximum water depth) at the northeastern limit of *Araucaria araucana* distribution. In this region, the conifer grows on moist, south- and east-facing slopes and in rocky settings at the lower forest-steppe ecotone. The L. Portezuelo reconstruction is compared with independent paleoclimatological, paleoecological, archaeological, and ethnohistorical information from northernmost Patagonia to address the questions: (1) What is the Holocene vegetation and fire history of L. Portezuelo? (2) How have climate and humans influenced the distribution of *A. araucana*?

Study Area

L. Portezuelo lies in an ice-block depression on a lateral moraine of late-Pleistocene age. It is fed by a spring from the southwest and has a small outflowing stream that drains into Lago Caviahue. The site is 13 km southeast of the active Copahue stratovolcano (Fig. 1). Along the Patagonian Andes (37-55°S), annual precipitation ranges from >3000 mm yr^{-1} at the crest of the Andes to <100 mm yr^{-1} in the steppe to the east (Garreaud, Lopez, Minvielle, & Rojas, 2013). The resulting precipitation gradient produces a transition in the vegetation from wet forest in the western Andean foothills, to alpine heathland at high elevations, dry forest in the eastern foothills, and steppe at low elevations. Near L. Portezuelo, average annual temperature is 8.8°C, with an average summer temperature of 2.8°C (DJF) and 15.1°C in winter (JJA) (University of East Anglia Climatic Research Unit; Harris, 2017). The area receives most of its annual precipitation between May and August (average of 93.5 mm $month^{-1}$) (University of East Anglia Climatic Research Unit; Harris, 2017). The climate is influenced by El Niño-Southern Oscillation (ENSO), where El Niño events result in increased winter precipitation and warmer-than-average annual temperature, and La Niña is associated with decreased winter precipitation and cooler-than-average annual temperature (Garreaud, Vuille, Compagnucci, & Marengo, 2009).

L. Portezuelo lies within heavily grazed steppe composed of native *Acaena*, *Azorella trifulata*, *Berberis empetrifolia*, *Colliguaja integerrima*, *Fabiana* spp., *Stipa* spp., and members of Rhamnaceae (including *Ochetophila trinervis*). Stands of *Araucaria araucana* grow less than a kilometer from the site and extensive *A. araucana* forests are present ~4 km to the southwest and northwest (Fig. 1). *Nothofagus antarctica* shrubland grows nearby in moist and protected

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habitats. *Scirpus* is present along the lake margin, and *Myriophyllum* and *Potamogeton* grow as aquatics.

American Indians were present along the Chilean coast of Patagonia by ~14,500 BP (Dillehay et al., 2015) and east of the Andes by ~11,200 BP (Barberena, Prates, & Eugenia de Porras, 2015). Here and below, all dates are provided in calibrated radiocarbon years before 1950 Common Era (henceforth, BP) and/or years Common Era (CE). The archaeological record suggests that groups were small in number, dispersed, and reliant on nomadic hunter-gather subsistence strategies until the late Holocene (Barberena et al., 2015; Dillehay et al., 2007; Pérez, Postillone, & Rindel, 2017). According to 19th-century travelers, American Indians in Patagonia used fire to signal distant parties, facilitate hunting, and improve grazing for European-introduced livestock and horses (Cox, 1863; Moreno, 1897; Musters, 1871). The isotopic analysis of human remains indicates that *Araucaria* has been an important food source in northernmost Patagonia for the last ~11,000 years (Gordón, Perez, Hajduk, Lezcano, & Bernal, 2016).

METHODS

Three cores were collected in February 2013 from the center of L. Portezuelo (LP13A-LP13C) with a 5-cm-diameter modified Livingstone piston corer. Cores were extruded in the field and wrapped in cellophane and aluminum foil for transport to the laboratory. A fourth core, LP13D, was retrieved with a polycarbonate tube using a UWITEC gravity corer. In the laboratory, cores were split lengthwise, and lithology and tephra layers were described (Villarosa et al. in prep). Organic, carbonate, and non-carbonate inorganic content was measured from 1 cm^3 samples by loss-on-ignition analysis (LOI; Heiri, Lotter, & Lemcke, 2001). Cores LP13D and LP13A were correlated based on lithostratigraphy, chronology, and LOI results to create a composite core that was 719 cm long.

A Bayesian age-depth model was developed based on 11 AMS radiocarbon dates calibrated in Bacon using the SHCal13 calibration curve (Blaauw & Christen, 2011; Hogg et al., 2013), the initial rise in *Pinus* (marking arrival of *Pinus* plantations, ~1960 CE), tephra from the 2012 CE Copahue eruption, and 2013 CE collection date. Tephra layers ≥0.5 cm in thickness were treated as instantaneous deposition events in 'rbacon' (i.e., "slump"; Blaauw and Christen, 2011). Mean deposition time was set to 20 yr cm^{-1} and section thickness was set to 10 cm.

Pollen was analyzed at 1-cm intervals for the top 39 cm to provide a high-resolution record of the last ~1000 years and between 2- and 16-cm intervals for the remainder of the composite core. Samples were prepared with standard procedures (Faegri, Kaland, & Krzywinski, 1989), and a tracer of *Lycopodium* spores was added to each sample to calculate pollen accumulation rates (PAR; grains cm^{-2} yr^{-1}). At least 1000 terrestrial pollen grains were counted for the first 10 cm of the composite core to increase the probability of recording rare taxa. Below 10 cm depth, at least 300 terrestrial pollen grains were tallied. Terrestrial pollen percentages were calculated based on a sum of all terrestrial pollen and spores. Percentages of aquatic and wetland taxa were based on a denominator of all pollen and spores. Local pollen and charcoal zones were identified by visual inspection and CONISS (Grimm, 1987).

Nothofagus dombeyi-type pollen in this region likely comes from *N. antarctica*, which grows locally forming shrubland, and possibly from extralocal *N. dombeyi* and *N. pumilio*, which occur in forests to the south and west. *N. obliqua*-type pollen is attributed to *N. alpina*, *N. glauca*, and/or *N. obliqua* from extralocal forests to the west. Established modern pollen-vegetation relationships from east of the Andes (40 and 45°S) were used to discriminate major

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vegetation formations: steppe (<41% *N. dombeyi*-type pollen), shrubland or open forest (41-67% *N. dombeyi*-type pollen), and closed forest (>67% *N. dombeyi*-type pollen) (Iglesias, Quintana, Nanavati, & Whitlock, 2017). Poaceae pollen includes species from steppe, forest, and tundra, including bamboo (*Chusquea* spp.). Cupressaceae pollen, which was present in low percentages, is attributed to long-distance transport from *Fitzroya cupressoides* to the west or *Austrocedrus chilensis* to the south (Pastorino, Fariña, Bran, & Gallo, 2006). *Araucaria* is neither an abundant pollen producer nor disperser, and generally is underrepresented in pollen records (Heusser, Rabassa, Brandani, & Stuckenrath, 1988; Paez, Schäbitz, & Stutz, 2001). Modern surface samples within the present distribution of *A. araucana* commonly show <5% pollen in *Araucaria*-steppe ecotonal regions east of the Andes (Moreno-Gonzalez, Giesecke, & Fontana, 2020; Paez et al., 2001). Because of its underrepresentation, *Araucaria* pollen, even in low percentages, is a conservative indicator of the conifer's presence in the watershed. Human-indicator pollen types include native and exotic taxa. Although Asteroideae subfamily Cichorioideae (henceforth, Cichorioideae) and *Rumex* pollen types include native and exotic (nonnative) species, their marked increase at the time of European arrival to the region suggests exotic *Taraxacum* species and *R. acetosella* as the pollen source. Although anomalously early arrival of exotic taxa may be attributed to wind-transportation from other settlements in the region, early botanical surveys of Patagonia suggest that exotic weeds were prolific decades prior to Euro-American settlement (Berg, 1877).

Samples for charcoal analysis (1 cm^3) were taken from contiguous 1-cm intervals from the composite core, soaked in 10% tetrasodium diphosphate ($Na_4P_2O_7$), and then washed through a 125-µm mesh sieve to reconstruct the local fire history (Whitlock & Larsen, 2001). CharAnalysis version 1.1 (Higuera, Brubaker, Anderson, Hu, & Brown, 2009) was used to identify statistically significant increases in charcoal accumulation rate (CHAR, particles cm^{-2} yr^{-1}) that denote fire episodes. Prior to the analysis, the sedimentation rate was interpolated to a constant temporal resolution based on a cubic spline fitted to Bacon mean ages. In CharAnalysis, charcoal concentration values (particles cm^{-3}) were divided by 16 years cm^{-1}, the median sampling resolution, to interpolate CHAR data. A moving median with an 800-year window was used to describe background charcoal (BCHAR) and maximize signal to noise. Fire episodes were identified as charcoal peaks (i.e., the positive residuals of CHAR above BCHAR) that surpassed the 95th percentile of a locally defined Gaussian distribution model by a probability of at least 0.3 (minCountP). The frequency of fire episodes greatly underestimated the frequency of fires denoted in dendroecological records from <10 km away (6 yr $fire^{-1}$; Mundo et al., 2013), which suggests that CHAR peaks in our data are local, large, and/or severe fire episodes that occurred less often than the surface fires recorded by fire scarred tree-rings. Because we do not think charcoal peaks in the L. Portezuelo record adequately capture the frequent, low-to-mixed severity fires suggested in the regional dendroecological literature (González et al., 2020; Mundo et al., 2013; Whitlock & Larsen, 2001), our interpretation of fire history is based on the trends in CHAR and BCHAR results, as defined in Table 2.

A canonical correspondence analysis (CCA) was used to determine the relationships between the L. Portezuelo terrestrial pollen assemblages and explanatory variables: sea-surface temperature (SST; Kaiser, Lamy, & Hebbeln, 2005), insolation seasonality (DJF-JJA; Berger & Loutre, 1991), ENSO activity (i.e., L. Pallcacocha red-band intensity; Moy, Seltzer, Rodbell, & Anderson, 2002) and CHAR from L. Portezuelo. Insolation seasonality is considered here because periods of low seasonality (low summer and high winter insolation) may allow warm conditions in winter to "carry-over" into spring, increasing fuel accumulation and the fire season

length (Whitlock, Moreno, & Bartlein, 2007). Changes in CHAR, in-part representing fuel loads, were expected to coincide with changes in pollen, and unidirectional causality was not interpreted. Time-since-tephra-deposition was also considered as an explanatory variable, but the results were insignificant and are not discussed further. CCA was completed using the 'vegan' package and plotted using 'ggplot2' (Oksanen et al., 2019; Wickham et al., 2016). Percent abundance of *Araucaria* was plotted, connecting samples chronologically to show how *Araucaria* abundance changed through time.

RESULTS

Lithology and chronology

Sediment from L. Portezuelo consisted of brown clayey silt, intercalated by 54 tephra layers of ≥0.5 cm in thickness (maximum tephra thickness was 4 cm; Fig. 2). Based on LOI, organic content varied from 1 to 25% of dry mass, carbonate content from 0 to 6%, and non-carbonate inorganic content from 42 to 99%. One date (OS-144515) was rejected as too old based on exceeding the 95% highest posterior density (HPD) intervals, essentially Bayesian confidence limits (Fig. 2). Deposition time was generally between ~8 and 25 yr cm^{-1}, except for a period of slow deposition, between 40 and 29.5 cm depth (~1120-430 BP), where deposition time increased to ~100 yr cm^{-1}. The age-depth model indicates an extrapolated mean basal age of ~11,100 BP (Table 3, Fig. 2).

Pollen and charcoal record

The L. Portezuelo record (Fig. 3) is plotted by age BP and depth, and divided into four local pollen zones based on visual inspection and CONISS (Grimm, 1987):

Zone LP-1 (710-448 cm depth; ~10,960-7360 BP) featured an increase in *Nothofagus dombeyi*-type pollen (from 12 to 33%) and a decline in Cupressaceae (<4%), Poaceae (from 61 to 50%), Fabaceae (<4%), and Rhamnaceae (<6 %). Cyperaceae was present (1-10%), and *Myriophyllum* was scarcely present (<2%). Trends in PAR at L. Portezuelo were strongly governed by variations in deposition time (Fig. 2) and are not discussed further. CHAR values were between 0 and 4 particles cm^{-2} yr^{-1}.

Zone LP-2 (448-82 cm depth; ~7360-2260 BP) displayed a punctuated increase in *Nothofagus dombeyi*-type pollen (to 48%) at the expense of Cupressaceae and steppe pollen taxa (i.e., Poaceae, Fabaceae, and Rhamnaceae). *Araucaria* pollen first appeared at 354 cm depth (~6380 BP), but had low, discontinuous representation (<1%). Cyperaceae increased from 2 to 13%. *Myriophyllum* was elevated (2.0-38.3%) between 378 and 264 cm depth (~6600-4520 BP). CHAR values were between 0 and 2 particles cm^{-2} yr^{-1}.

Zone LP-3 (82-30 cm depth; ~2260-460 BP) displayed increased Poaceae percentages from 34 to 55% and decreased *Nothofagus dombeyi*-type (from 44 to 29%) and Ranunculaceae (<2%) (Fig. 3). Although low in abundance (<1%), *Araucaria* pollen was consistently present above 57 cm depth (~1870 BP). At 33 cm depth (~500 BP), *N. dombeyi*-type abundance increased from 29 to 48% at the expense of Poaceae (from 55 to 36%). Cyperaceae was elevated throughout Zone LP-3 with a brief increase to 17% at 49 cm depth (~1670 BP). *Myriophyllum* pollen was abundant (7-14%) between 39 and 36 cm depth (~1000-840 BP). CHAR values were generally between 0 and 2 particles cm^{-2} yr^{-1}, but were 0 particles cm^{-2} yr^{-1} between 58 and 50 cm depth (~1900-1740 BP).

Zone LP-4 (30-0 cm depth; ~460 to -13 BP) featured an increase in *Araucaria* pollen abundance until 10 cm depth (~30 BP; 0-3%) that was followed by a decrease to 2% by the top

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of the core (~-63 BP), as well as increased native disturbance taxa (i.e., Apiaceae, Asteraceae subfamily Asteroideae (henceforth, Asteroideae), and Fabaceae) and exotic taxa (e.g., Cichorioideae, *Echium vulgare*, *Plantago*, *Pinus*, and *Rumex*) at the expense of *Nothofagus dombeyi*-type (from 47.8 to 24.7%) (Fig. 3). Poaceae abundance decreased between 29 and 17 cm depth (~430-100 BP) from 42 to 19%, increased to 27% at 16 cm depth (~80 BP), largely at the expense of *N. dombeyi*-type, and remained high (26-39%). *Pinus* appeared in the record at 12 cm depth (~-9 BP) and was rare (≤1%) until 7 cm depth (~-40 BP), when values increased to 5% by present. Between 30 and 26 cm depth (~460-340 BP), CHAR values were between 0.7 and 2 particles cm^{-2} yr^{-1}. CHAR values decreased to 0.5 particles cm^{-2} yr^{-1} at 20 cm depth (~170 BP), suggesting a decrease to low fire activity (Fig. 3). CHAR values increased to 6 particles cm^{-2} yr^{-1} at 8 cm depth (~-30 BP), and then decreased to present CHAR values (to 2 particle cm^{-2} yr^{-1}).

Multivariate analysis

The CCA constrained 32% of the total inertia (Fig. 4; results summarized in Table 4). A "horseshoe" effect in the CCA results exaggerates differences along the CCA2 axis and makes the earliest and latest pollen samples from L. Portezuelo appear more similar than is correct. Focusing largely on the CCA1 axis, two clusters are evident: one containing samples from ~10,964 to 455 BP and another from ~426 to 13 BP. This difference in ordination space is supported by the clear separation of Zones LP-3 and LP-4 by CONISS. Given the present importance of ENSO activity on effective moisture and ecosystem dynamics in Patagonia (Holz, Kitzberger, Paritsis, & Veblen, 2012; Veblen & Kitzberger, 2002), we attribute the weak explanatory value of ENSO activity to a combination of the temporal uncertainties inherent in the age-depth models for the L. Portezuelo and L. Pallcacocha records, the sub-decadal frequency of ENSO (where multiple El Niño/La Niña events may occur in the time span of a pollen sample), and the rate at which vegetation would have responded to interannual climate variability. Pollen taxa important to the clustering of samples from the last 400 years include native *Araucaria* and exotics such as *Rumex*, *Plantago*, and Cichorioideae.

DISCUSSION

The Holocene vegetation and fire history of L. Portezuelo was interpreted based on pollen, charcoal, and CCA results, and compared with ethnohistorical and dendroecological fire-scar records near the site (e.g., Moreno, 1897; Mundo et al., 2013; Villalobos, 1989). The influence of past changes in climate and land use on the distribution of *Araucaria araucana* forest in northernmost Patagonia was assessed by comparing the environmental history of L. Portezuelo with other well-dated sites in the region (37-40°S) (Table 1; Fig. 1 and 5; i.e., Abarzúa et al., 2014; Fletcher & Moreno, 2012b; Moreno-Gonzalez et al., 2020). The regional trends were examined in light of changes in seasonal insolation (Berger & Loutre, 1991), SST (Chilean coast, 41°S; Kaiser et al., 2005), ENSO history (Moy et al., 2002) and dendroecological fire records from *A. araucana* forest (González et al., 2020; Mundo et al., 2013) (Fig. 5). The local and regional reconstructions were also compared with archaeological and ethnohistorical records (e.g., Aagesen, 2004; Barberena et al., 2015; Dillehay et al., 2007) (Fig. 5).

Holocene vegetation and fire history at L. Portezuelo

Steppe vegetation grew near L. Portezuelo throughout the Holocene; however, increasing *N. dombeyi*-type pollen suggests an expansion of woody cover through time, which we attribute

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to increased *N. antarctica* shrubland. CHAR levels suggest generally low-to-moderate fire activity prior to 6590 BP, with a period of high fire activity between ~9480 and 7970 BP, implying fire activity varied during the early Holocene (Fig. 3 and 5; fire activity defined in Table 2). After ~6590 BP, increased abundance of Cyperaceae and *Myriophyllum* pollen indicates an expanded riparian area, which given the gradual slope of the lake basin, we attribute to higher water levels.

Between ~6590 and 2330 BP, levels of CHAR indicate a decline in fire activity to low-to-moderate levels. Increased *Nothofagus dombeyi*-type pollen suggests expanded shrubland. *Araucaria* first appeared in the pollen record at ~6380 BP, and even in low amounts, its pollen suggests local tree presence. CCA results suggest that middle- and late-Holocene changes in vegetation history were driven by decreasing temperatures (Kaiser et al., 2005), increasing insolation seasonality (Berger & Loutre, 1991), and, to a lesser degree, increased interannual climate variability after 6130 BP (Moy et al., 2002) (Table 4; Fig. 4 and 5).

Between ~2330 and 1900 BP, the pollen data indicate a transition from shrubland to steppe. Higher CHAR levels imply moderate-to-high fire activity at this time (Fig. 3 and 5). The last two millennia were characterized by fluctuating levels of Poaceae, *Nothofagus,* and *Araucaria* pollen at L. Portezuelo, which based on CCA, were likely driven by strengthened ENSO activity, increased insolation seasonality and decreased temperatures (Table 4, Fig. 4 and 5). For example, between ~1900 and 1640, high Poaceae and low CHAR suggest the dominance of steppe and low fire activity. Between ~480 and 370 BP (1470-1580 CE), increased *Nothofagus* and *Araucaria* and moderate-to-high CHAR suggest more woody cover associated with moderate-to-high fire activity.

Evidence of land use near L. Portezuelo is noted after ~370 BP (1580 CE; 95% Bacon HPD = 470-240 BP), with the rise in native and exotic pollen types indicative of disturbance (e.g., Asteroideae, *Plantago*, and *Rumex*) and an increase in fire (Fig. 3, 4, and 5). *Araucaria* pollen abundance also increased during this time of cooler and wetter conditions and more, possibly humans-set fires. The presence of disturbance taxa and high fire activity at L. Portezuelo predated local Euro-American settlement (1870s CE; Moreno, 1897). Instead, these changes coincided with the translocation of the Mapuche peoples from the Chilean coast and foothills to east of the Andes, and the introduction of cattle to the region in the mid-16th century (Crespo, Dubois, Russo, Lanata, & Dejean, 2017; Ortelli, 1996; Torrejón, 2001; Villalobos, 1989). Between ~70 and 14 BP (1880-1936 CE), dendroecological records from *Araucaria* stands <10 km north of L. Portezuelo indicate a fire return interval of 6 yr fire^{-1} (Mundo et al., 2013). During this period, increased fire activity is evidenced by high CHAR and BCHAR values.

Subsequent increases in exotic taxa and a decline of *Nothofagus* pollen occurred at ~60 BP (1890 CE), coincident with Euro-American settlement on the Caviahue-Copahue region. Decreased *Araucaria* pollen after ~30 BP (1920 CE) marks a decline in trees due to increased grazing and logging prior to provincial, federal, and international efforts to protect the species in 1948 CE (CITES, 2007; Premoli et al., 2013). Exotic *Pinus* pollen appeared at ~-10 BP (1960 CE), is related to establishment of *Pinus* plantations in the region.

Climatic and human influence on *Araucaria araucana* distribution (37-40°S)

In addition to L. Portezuelo, two well-dated paleoecological records lie within the modern range of *Araucaria araucana*: El Valle Bog, spanning the last ~26,500 years (38.05°S, 72.97°W; 70 m elev.; Abarzúa et al., 2014) and Laguna San Pedro, beginning at ~1500 BP

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(38.43°S, 71.32°W; 913 m elev.; Fletcher & Moreno, 2012b) (see Table 1; Fig. 1 and Fig. 5). Moreno-Gonzalez et al. (2020) also describe a set of lake cores that span the last few centuries of environmental history in northernmost Patagonia. We focus our discussion on records with well-constrained Holocene chronologies but refer to other sites more generally.

The fire history from El Valle and the sites presented by Moreno-Gonzalez et al. (2020) were based on microscopic charcoal concentrations (particles cm^{-3}) instead of macroscopic charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) as at L. Portezuelo and L. San Pedro. Microscopic charcoal concentration data are sensitive to variations in sediment deposition time and the smaller particles come from a larger fire source area (Carcaillet, Bouvier, Fréchette, Larouche, & Richard, 2001; Whitlock & Larsen, 2001); these differences limit precise comparisons between sites, so we rely on the fire-history interpretations of the original authors.

Late Pleistocene and early Holocene (~20,000-7000 BP)

Winter insolation increased and summer insolation decreased from 20,000 to 10,000 BP (Berger & Loutre, 1991) (Fig. 5), resulting in low seasonality throughout Patagonia (Whitlock et al., 2007). ODP-1233 SST data off the Chilean coast (41°S) suggest rapid warming from ~20,000 to 10,000 BP, with highest temperatures at ~11,500 BP (Kaiser et al., 2005). During the early Holocene, increased fire activity and dry conditions throughout southern South America are attributed to a southward shift and/or weakening of the Southern Westerly Winds (SWW) (Moreno, Villa-Martínez, Cárdenas, & Sagredo, 2012; Nanavati et al., 2019; Whitlock et al., 2007).

Pollen data from El Valle suggest that the central valley of Chile was a glacial refugia for *Araucaria* (~20% abundance at 26,500 BP), when conditions were generally cool and wet (Fig. 5) (Abarzúa et al., 2014; Heusser, 1984; Ruiz et al., 2007; Villagrán, 1991). As the climate warmed between ~20,000 and 8,000 BP, vegetation near El Valle shifted first to an open warm-temperate forest with *Prumnopitys* and Myrtaceae and moderate fire activity and then to a closed forest and high fire activity after 7000 BP. The near-absence of *Araucaria* pollen at El Valle after ~12,000 BP points to a shift in the conifer's distribution, but the rarity of late-glacial records from northernmost Patagonia leaves much in question regarding the path and timing of this range shift. Villagrán (1991, 2001) suggests that the species may have migrated to higher, previously glaciated areas, such as the Cordillera de Nahuelbuta <50 km to the west. East of the Andes, the L. Portezuelo region supported steppe with moderate-to-high fire activity, with no *Araucaria* at this time.

Middle Holocene (~7000-4000 BP)

Winter insolation decreased and summer insolation increased, resulting in a gradual increase in seasonality and a decrease in temperature from previous conditions (Fig. 5) (Berger & Loutre, 1991; Kaiser et al., 2005). Precipitation increased across Patagonia, as storm tracks associated with the SWW reached their modern position and intensity between 40-60°S, (Fletcher & Moreno, 2012a; Garreaud et al., 2013; Nanavati et al., 2019). Strengthened ENSO activity after ~6800 BP (Moy et al., 2002) likely led to greater interannual moisture variability at this time (Garreaud et al., 2013; Garreaud et al., 2009; Veblen & Kitzberger, 2002).

During the middle Holocene, El Valle and L. Portezuelo show evidence of expanded woody cover, consistent with increased moisture (Fig. 5). Decreased charcoal levels between ~7000 and 4000 BP at both sites suggest a shift from high to low-to-moderate fire activity. Increased moisture likely favored *Nothofagus* near L. Portezuelo. At El Valle, increased

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Eucryphia/*Caldcluvia* suggests an expansion of temperate humid forest associated with moderate fire activity from 7000 to 4000 BP (Abarzúa et al., 2014), and *Araucaria* became slightly more abundant. *Araucaria* first appeared in the L. Portezuelo record at ~6380 BP in association with low fire activity. Pollen from Laguna Las Totoras (37.80°S, 71.13°W; ~6180 BP basal date; Table 1) indicates the presence of *Araucaria* in the coastal Cordillera de Nahuelbuta (Villagrán, 2001) by about this time. The contrasting fire histories between El Valle and L. Portezuelo may reflect differences in fuel biomass along the west-to-east moisture gradient and/or land-use differences, as American Indians were present at sites throughout northernmost Patagonia by ~7000 BP (Barberena et al., 2015; Pérez et al., 2017).

Late Holocene (since ~4000 BP)

Higher summer and lower winter insolation compared with the previous periods and similar-to-present temperatures mark the establishment of present-day climate conditions after ~4000 BP (Berger & Loutre, 1991; Garreaud et al., 2013; Kaiser et al., 2005). Changes in the position and intensity of SWW-related storm tracks in recent millennia are attributed to strengthened ENSO variability across Patagonia (Fletcher & Moreno, 2012a; Holz et al., 2012; Iglesias et al., 2014; Nanavati et al., 2019).

Between ~4000 and 1500 BP, pollen and charcoal data from El Valle suggest increasingly open conditions in the central valley of Chile and decreased fire activity until ~1500 BP (Fig. 5) (Abarzúa et al., 2014). At L. Portezuelo, shrubland expanded from ~4000 to 2500 BP, and conditions were likely wetter than before, followed by a dry period from ~2500 and 1500 BP, when high amounts of Poaceae mark a replacement of shrubland by steppe. Between ~1500 and 800 BP, shrubland returned at L. Portezuelo and forest increased at El Valle and L. San Pedro (Abarzúa et al., 2014; Fletcher & Moreno, 2012b). This regional expansion of woody cover coincided with three major El Niño wet phases (16-31 events 100 yr^{-1}) at ~1600-1500, 1300-1200, and 900-600 BP (Moy et al., 2002).

From ~4000 to 800 BP, *Araucaria* was absent at El Valle (Abarzúa et al., 2014), and in low abundance at L. Portezuelo (Fig. 5). The L. San Pedro watershed in the center of present-day *Araucaria*-*Nothofagus* forest distribution had highest levels of *Araucaria* pollen (1-6%) between ~1500 and 800 BP (Fletcher & Moreno, 2012b). After ~800 BP, sclerophyllous forest (e.g., *Maytenus* and *Schinus*) replaced *Nothofagus dombeyi* forest at El Valle in association with dry conditions (Abarzúa et al., 2014). Between ~800 and 100 BP at L. San Pedro, increase of *N. dombeyi*-type pollen, decrease in *Araucaria* and low CHAR values suggest that *Nothofagus* forest was favored by wetter, less fire-prone conditions (Fletcher & Moreno, 2012b). At L. Portezuelo, *Nothofagus* pollen declined while *Araucaria* pollen and CHAR values increased after ~370 BP, implying that increased fire activity facilitated *Araucaria* expansion.

Abarzúa et al. (2014) suggest that American Indian agriculture was common at El Valle and possibly the central valley of Chile after ~5000 BP, and archaeological evidence shows widespread and intensive Mapuche agriculture during the last 1000 years in that region (Fig. 5) (Dillehay et al., 2007). The earliest evidence of land use at L. Portezuelo comes at ~1580 CE (370 BP), with increased disturbance taxa (i.e., *Plantago lanceolata* and *Rumex acetosella*) and high CHAR values that suggest local livestock grazing and anthropogenic fire, prior to local Euro-American settlement. Pollen and charcoal records throughout northernmost Patagonia demonstrate similar increases in disturbance taxa in the last 200 years, including *Pinus* after ~1950 CE (0 BP) (Abarzúa et al., 2014; Fletcher & Moreno, 2012b; Moreno-Gonzalez et al., 2020). Interestingly, fire activity in the 20th century varied greatly among sites, demonstrating

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local differences in fuel, catchment area, and land use along the west-to-east moisture gradient (Abarzúa et al., 2014; Fletcher & Moreno, 2012b; Moreno-Gonzalez et al., 2020). Similar variability in fire activity across northernmost Patagonia is noted by Mundo et al. (2013), who show that fire-return intervals in *Araucaria* stands initially decreased with Euro-American settlement, but lengthened in some areas as increased ranching and logging fragmented and limited burnable biomass.

These results raise the question: To what extent did American Indians alter the northern Patagonian landscape and influence *Araucaria araucana* distribution? Discussions regarding "anthropogenic", "altered", or "manufactured" landscapes depend on the spatial and temporal scales being considered (Bush & Silman, 2007; Iglesias & Whitlock, 2014; Munoz, Mladenoff, Schroeder, Williams, & Bush, 2014; Roos, 2020). Although climate has been the major driver of ecosystem dynamics at a regional scale in Patagonia (Iglesias & Whitlock, 2014; Moreno, 2020; Nanavati et al., 2019; Whitlock et al., 2007), the results presented here suggest that past American Indian land use likely significantly altered natural ecosystem dynamics at a local-to-landscape spatial scales in northernmost Patagonia. Variations in human population size and land-use intensity in the late Holocene likely created a mosaic of landscapes that ranged from the nearly-pristine to highly altered prior to European arrival (Whitlock, Colombaroli, Conedera, & Tinner, 2018). At El Valle, the pollen data indicate that the adoption and expansion of agriculture at 5000 BP, may have resulted in the loss of temperate forest, creating a highly-altered landscape (Abarzúa et al., 2014; Dillehay et al., 2007). In contrast, at L. San Pedro, there is no clear paleoecological evidence for pre-European land use, suggesting a near-pristine landscape at the time of Euro-American settlement (Fletcher & Moreno, 2012b). Near L. Portezuelo, the landscape was likely near-pristine until ~370 BP, when Mapuche-Pehuenche altered the landscape through livestock grazing and the management of forests for the procurement of *Araucaria* seeds (Aagesen, 2004; dos Reis et al., 2014; Torrejón, 2001; Villalobos, 1989). Unintentionally- or deliberately-set fires by Mapuche-Pehuenche peoples likely facilitated *A. araucana* at its northeasternmost extent, in a manner that was similar to stewardship of *A. angustifolia* forests of southern Brazil and northeastern Argentina (Bitencourt & Krauspenhar, 2006; Iriarte & Behling, 2007; Robinson et al., 2018).

CONCLUSIONS

1. At L. Portezuelo, steppe with moderate-to-high fire activity was slowly replaced by *Nothofagus* shrubland with low-to-moderate fire activity between ~11,100 and 2260 BP. Increased shrubland is attributed to more moisture as a result of grater seasonality, decreased temperatures, and strengthened ENSO activity. Between ~2260 and 1900 BP, shrubland was replaced by steppe and fire activity decreased, consistent with dry conditions and reduced fuels. Fluctuations between shrubland and steppe in last 2000 years likely responded to ENSO activity and increased land use after 370 BP.

2. *Araucaria araucana* was likely present in the central valley of Chile during the last glaciation until rapid postglacial warming and drying limited its distribution in the valley. It first appeared at its northeasternmost extent, near L. Portezuelo, at ~6380 BP in sporadic abundance, suggesting few trees in the area until ~370 BP. *Araucaria* was abundant in the L. San Pedro area until 800 BP, when its decline is associated with lower fire activity and *Nothofagus* dominance.

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3. Increased abundance of *Araucaria* and exotic *Plantago* and *Rumex*, and moderate-to-high fire activity at L. Portezuelo after ~370 BP (1580 CE) is attributed to American Indian land use prior to local Euro-American settlement, coinciding with a major migration of Mapuche peoples from the Chilean coast and foothills to east of the Andes. The early appearance of exotic taxa indicate that the spread of exotic weeds outpaced local Euro-American settlement. These results suggest that the L. Portezuelo was a human-altered landscape for the last 400 years, but this hypothesis warrants further testing through archaeological survey and excavation.

4. Throughout northernmost Patagonia, Euro-American settlement and American Indian displacement were marked by subsequent increases in exotic and steppe taxa at the expense of native arboreal taxa (i.e., *Nothofagus* and *Araucaria*). The timing and scale of changes in fire activity recorded throughout northernmost Patagonia varied, but generally increased with initial Euro-American settlement and decreased to present as agriculture, ranching, and logging limited burnable biomass.

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Tables

Table 1. Pollen and charcoal records discussed in text.

Site name	Lat. (°S)	Long. (°W)	Elev. (m)	Temporal range (~BP)	Pre-European vegetation**	Citation
Lagunas Las Totoras	37.8	73.1	1225	6200 to 0	Valdivian forest with Araucaria	Villagrán (2001)
El Valle Bog*	38.1	73.0	70	26,500 to 0	*Nothofagus* forest with very few, scattered *Araucaria*	Abarzúa et al. (2014)
Lomocura	38.8	71.8	1015	75 to -66	*Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Laguna San Pedro*	38.4	71.3	913	1500 to -59	*Araucaria-Nothofagus* forest	Fletcher and Moreno (2012b)
Quinquen	38.6	71.3	1690	220 to -66	*Araucaria-Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Los Piñones	38.8	71.3	1280	70 to -66	*Araucaria-Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Koywija	38.9	71.2	1189	-5 to -60	*Araucaria-Nothofagus* forest	Moreno-Gonzalez et al. (2020)
Paso del Arco	38.9	71.1	1200	2500 to 0	*Araucaria-Nothofagus* forest	Heusser et al. (1988)
Relem*	39.0	71.1	1265	360 to -66	Steppe with patches of *Araucaria*	Moreno-Gonzalez et al. (2020)
Laguna Portezuelo*	37.9	71.0	1730	11,100 to -62	Steppe with patches of *Araucaria*	This manuscript
Lonco Luan	38.6	71.0	1230	-30 to -64	Steppe with patches of *Araucaria*	Moreno-Gonzalez et al. (2020)

Sites with well-constrained chronologies. The age-depth models of sites without an "" are limited by unconstrained reversals, hiatuses, and/or basal dates, making comparison difficult.
**Interpretations are based on cited publication.

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Table 2. Fire activity definitions with evidence specific to the L. Portezuelo CHAR record.

Fire activity category	Fire regime characteristics	Evidence (CHAR, particles cm^{-2} yr^{-1})
Negligible	If fires present: Very low severity, small, and/or distant	Extended periods with 0
Low	Low severity, small, and/or distant	<1
Moderate	Intermediate severity, size, and/or proximity	1-2
High	High severity, large, and/or nearby	>2

Table 3. Calendar and AMS radiocarbon ages from L. Portezuelo.

Lab ID	Depth (cm)	Radiocarbon Age (^{14}C yr BP)	Calibrated Age (BP; 1-σ range)[a]
Core top	0.0	-63 ± 0.1[b]	
Copahue tephra	0.1-0.5	-62 ± 0.5[b]	
Pinus rise[c]	10.0-11.0	-23 ± 5[b]	
OS-144514	29.0-30.0	430 ± 15	495-465
D2	46.5-47.5	1770 ± 30	1700-1648, 1626-1593
Da3	78.0-79.0	2230 ± 30	2304-2235, 2203-2194, 2187-2151
D3	110.0-111.0	2630 ± 30	2757-2716
OS-144384	161.0-162.0	3400 ± 20	3635-3569
D4	251.0-252.0	3930 ± 30	4408-4287, 4264-4259
OS-144385	341.0-342.0	5490 ± 30	6292-6266, 6246-6212
D5	446.0-447.0	6450 ± 30	7415-7353, 7335-7302, 7296-7295
OS-144515[d]	552.0-553.0	9070 ± 40	10,233-10,188
D6	609.0-610.0	8340 ± 40	9415-9258
D7	717.0-718.0	9980 ± 40	11,394-11,255

[a] Calibrated with CALIB 7.10 using the ShCal13 calibration curve (Hogg et al., 2013; Stuiver, Reimer, & Reimer, 2017).
[b] Dates for the core top, Copahue tephra, and *Pinus* rise are in calendar years before present.
[c] *Pinus* rise marks establishment of *Pinus* plantations in the 1970s CE.
[d] Date rejected by the 95% highest posterior density of the Bacon age-depth model.

Table 4. Biplot scores from the constraining variables in the CCA.

Constraining variables[1]	CCA1 (77%[2])	CCA2 (17%)	CCA3 (4%)	CCA4 (2%)
CHAR[3]	-0.85	-0.53	-0.05	0.06
SST	0.85	-0.48	0.05	0.21
Insolation Seasonality	0.74	0.64	0.06	0.18

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El Niño activity	0.29	0.08	-0.91	0.29

[1]The constraining variables constrained 32% of the total inertia.
[2]The provided precents are of the total inertia constrained.
[3]In agreement with the strong interaction between vegetation and fire, not unidirectional causality.

Figure Legends

Fig 1. Map of southern South America, showing a conservative distribution of *Araucaria araucana* (orange; CONAF-CONAMA, 1999; Lara et al., 1999). The inset map shows the location of Laguna Portezuelo and other sites discussed in-depth in the text (i.e., Abarzúa et al., 2014; Fletcher & Moreno, 2012b; Moreno-Gonzalez et al., 2020). The triangle northwest of L. Portezuelo marks the Copahue stratovolcano. Satellite map data: Google, Maxar Technologies. Photo taken from L. Portezuelo (2013) facing a stand of *A. araucana* about 0.5 km south of the site.

Fig 2. Age-depth model for Laguna Portezuelo using Bacon 2.2 (Blaauw and Christen, 2011). Green areas represent calendar ages provided for different layers (see Table 3), blue areas represent probability distributions of the calibrated dates, red area represents the Bacon-rejected date (OS-144515), dotted red line shows weighted mean age, and dotted gray lines depict the 95% highest posterior density (HPD) intervals. Vertical gray bars show location and thickness of tephra layers (≥0.5 cm thickness). Deposition time (black), percent composition of non-carbonate inorganic (blue), and organic (orange) are discussed in text.

Fig 3. Pollen percentage diagram from Laguna Portezuelo showing pollen taxa and zones discussed in text, with resulting CONISS dendrogram (Grimm, 1987). Charcoal accumulation rates (CHAR; black) and background CHAR (BCHAR; red) describe variations in fire activity.

Fig 4. CCA plot of the terrestrial pollen data from Laguna Portezuelo with explanatory variables: sea-surface temperature (SST; Kaiser et al., 2005), insolation-driven seasonality (DJF-JJA; Berger & Loutre, 1991), and ENSO activity (i.e., L. Pallcacocha red-band intensity; Moy et al., 2002) and CHAR from L. Portezuelo. Changes in CHAR were expected to coincide with changes in vegetation, so unidirectional causality was not interpreted. Pertinent pollen taxa (blue dots) are labeled: RU = *Rumex*, PN = *Plantago*, LG = Cichorioideae, AR = *Araucaria*, V = Asteroideae, LU = Fabaceae, ND = *Nothofagus dombeyi*-type, RZ = Rhamnaceae, UM = Apiaceae, G = Poaceae, J = Cupressaceae. Samples (black dots) are labeled chronologically and connected by a line colored based on the abundance of *Araucaria* pollen in a given sample. Biplot scores of the constraining variables are provided in Table 4.

Fig 5. Vegetation, fire, climate, and human history based on published interpretations. Darker shades denote greater inferred abundance of *Araucaria araucana*. Summer (DJF; red) and winter (JJA; blue) insolation values (Berger & Loutre, 1991), temperature anomalies from present (green) (Kaiser et al., 2005), and El Niño event frequency (black) (Moy et al., 2002). Interpretations from the independent paleoclimate data are also provided. Abbreviations in text: BP = calibrated years BP (cal yr BP); ka = thousands of years; CE = Common Era.

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Figures

Fig 1.

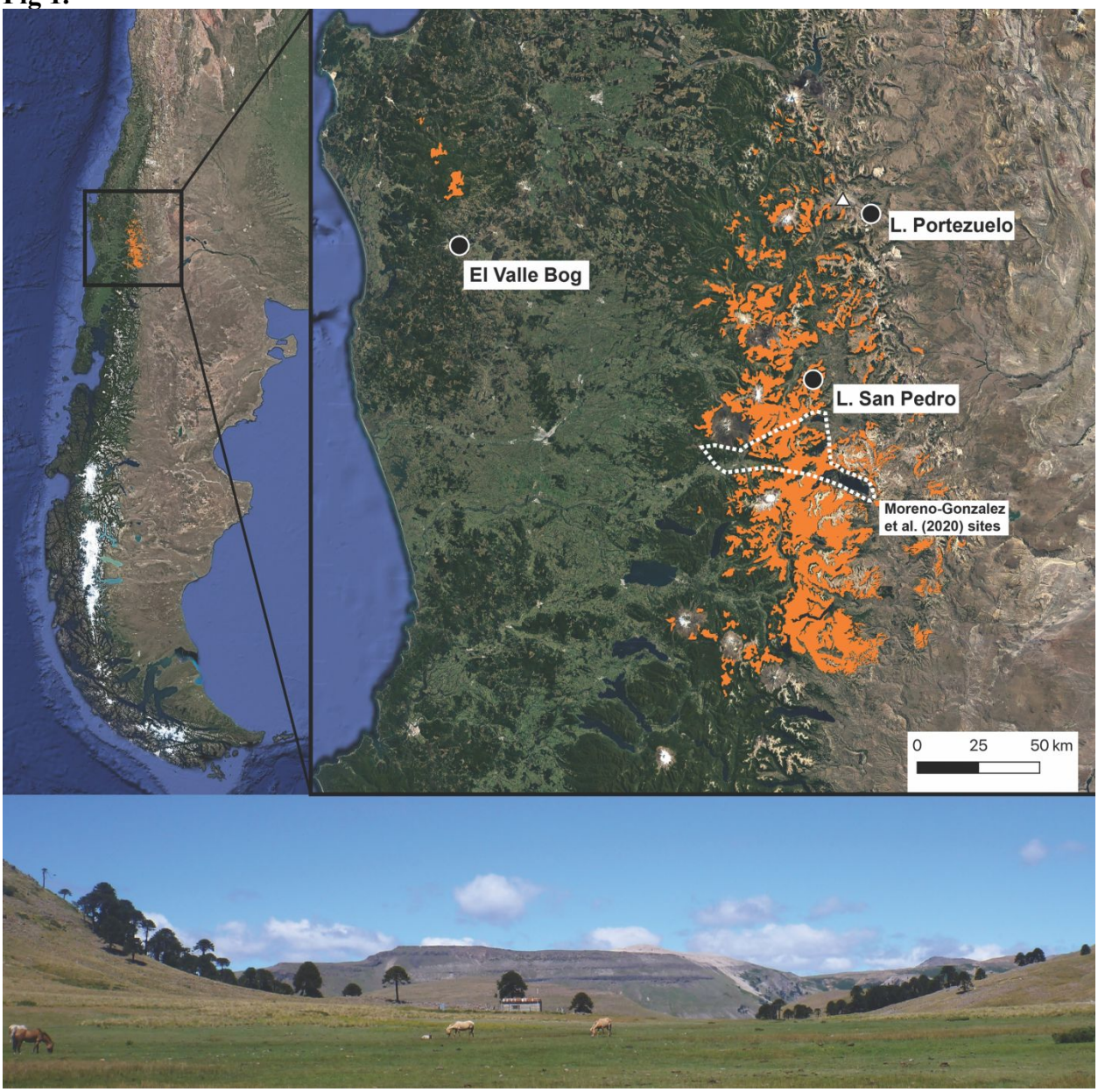
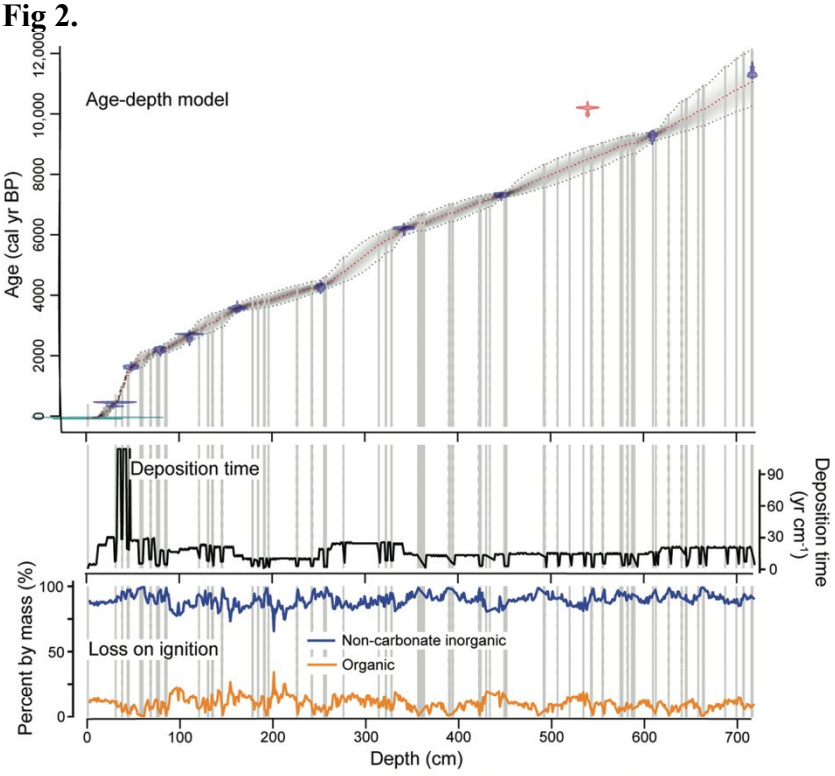
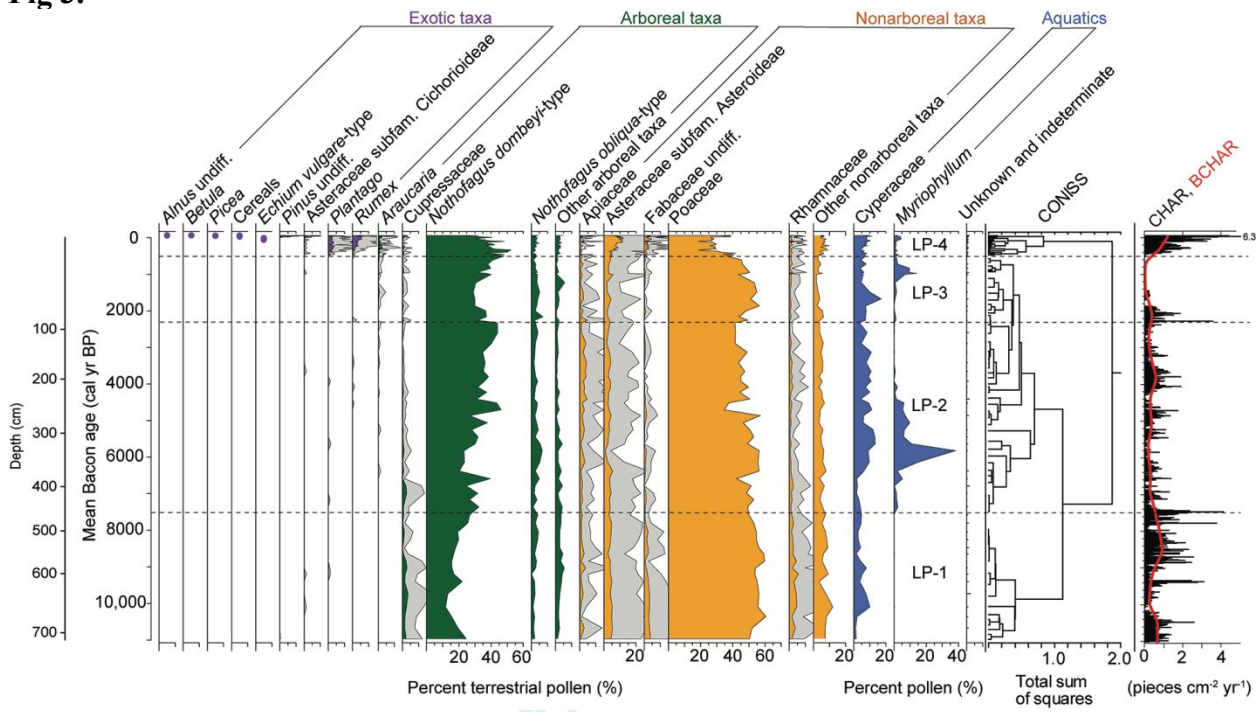


Fig 2.



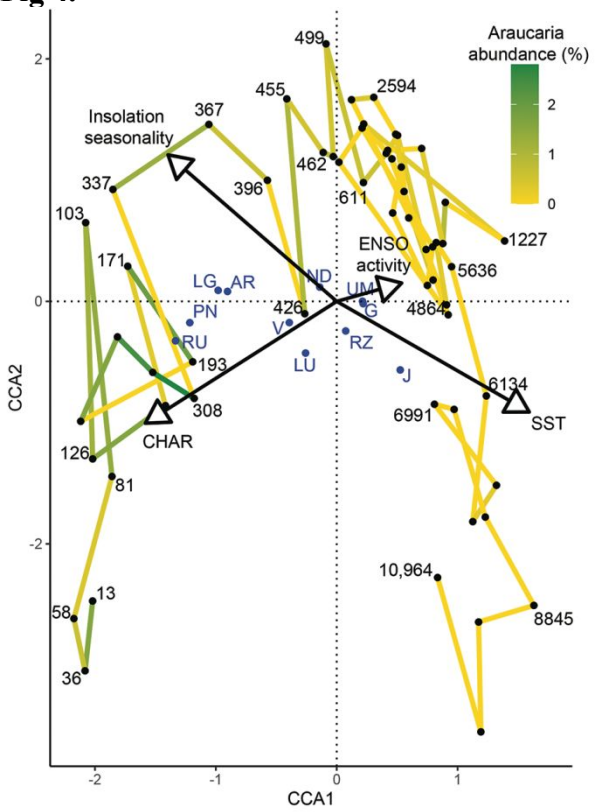
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Fig 3.



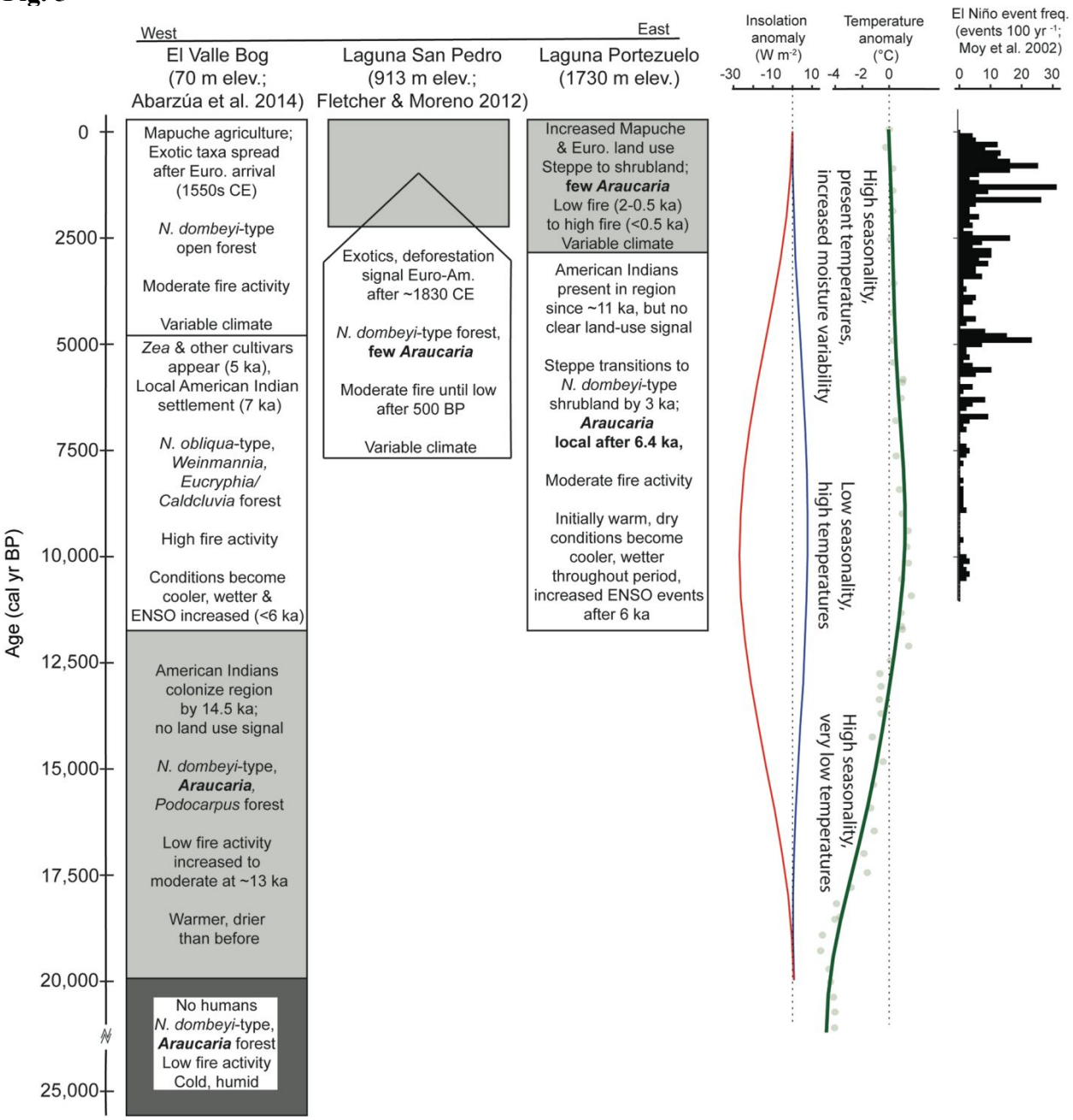
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Fig 4.



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Fig. 5



DATA AVAILABILITY STATEMENT

The pollen and charcoal data as well as information to reconstruct the age-depth model from Laguna Portezuelo are deposited in the Neotoma Paleoecology Database (www.neotomadb.org; Dataset IDs: 48751-48753) and the Global Charcoal Database.

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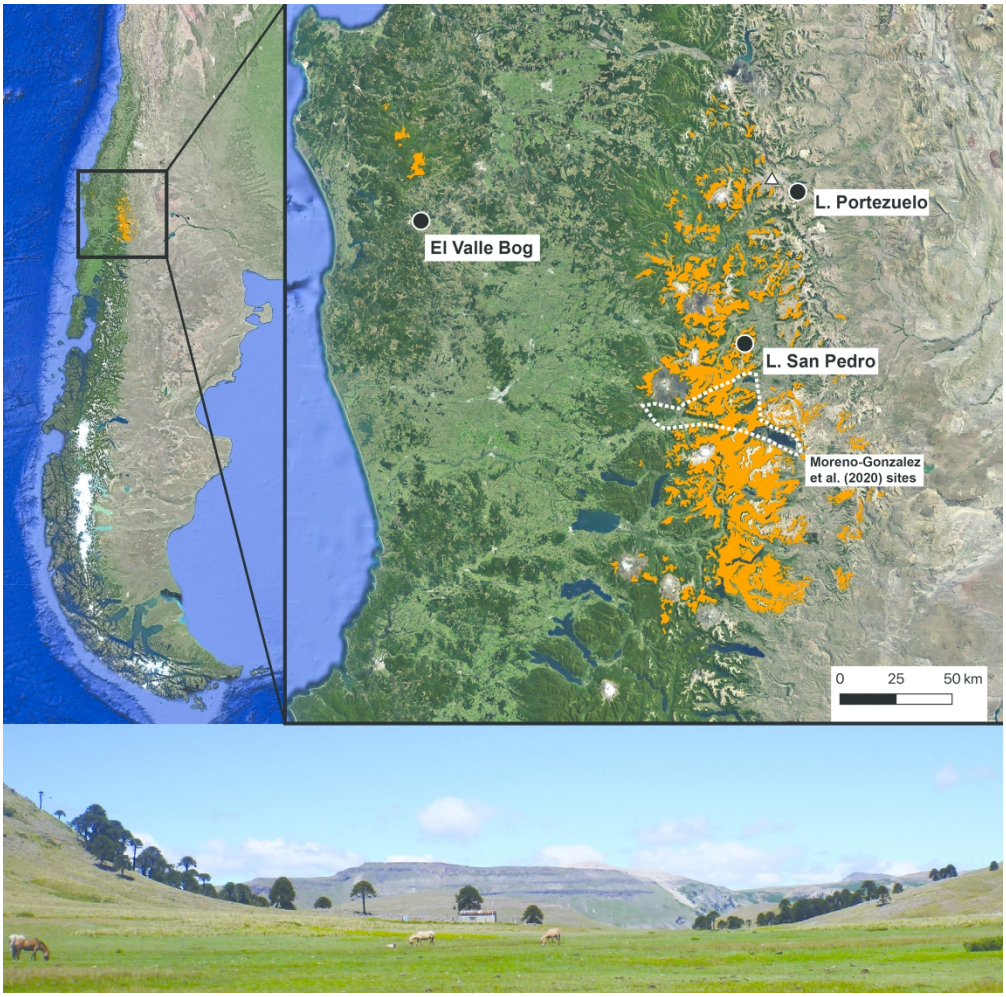
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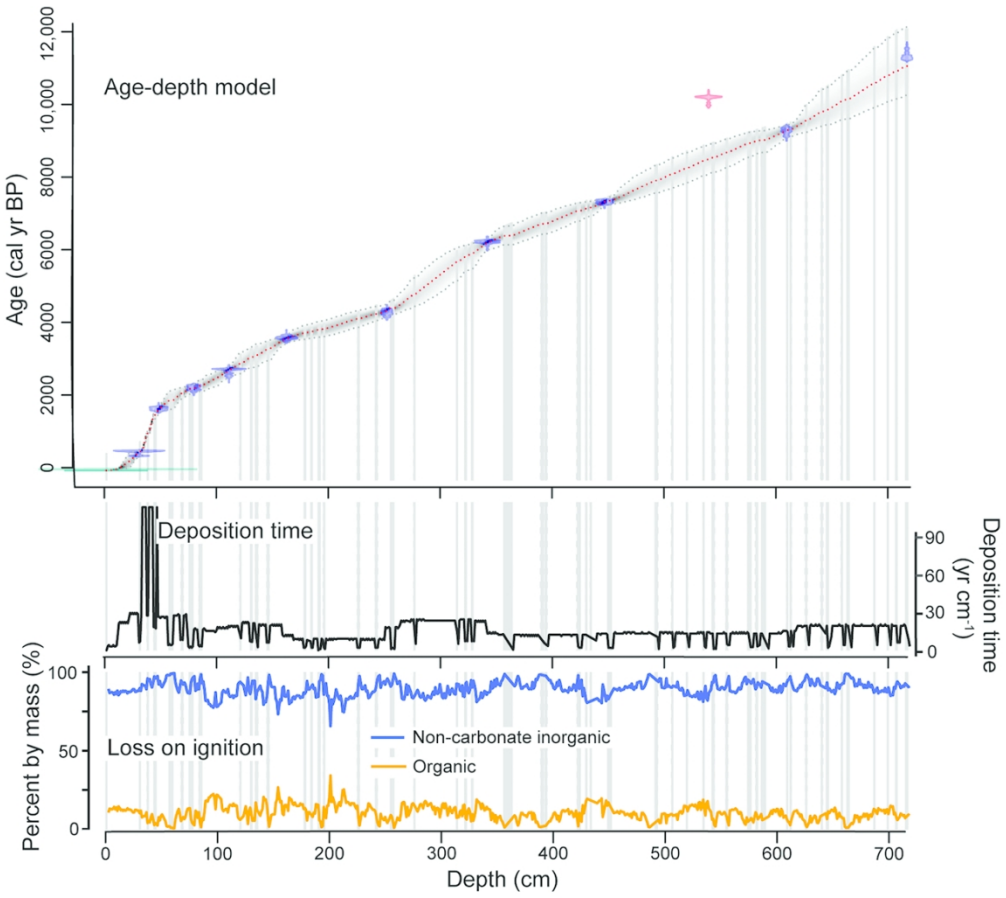
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Author contributions: All authors conceived the research questions, conducted the fieldwork analyzed the data, and participated in writing the manuscript.

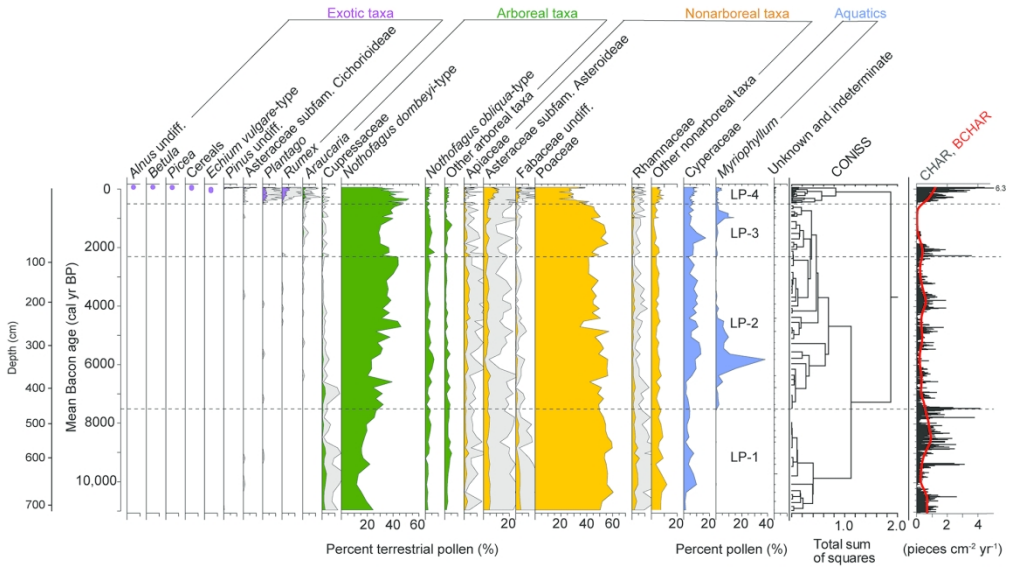
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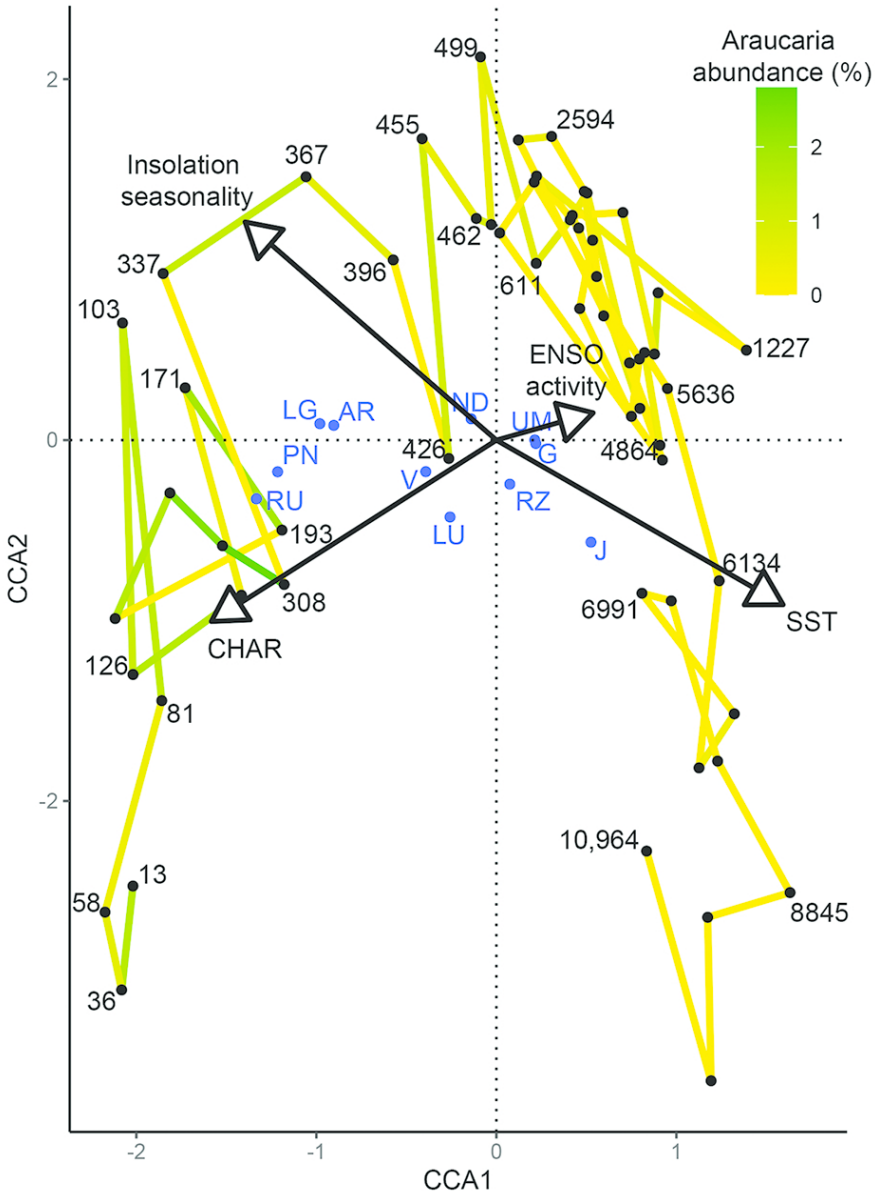
Map of southern South America, showing a conservative distribution of *Araucaria araucana* (orange; CONAF-CONAMA, 1999; Lara et al., 1999). The inset map shows the location of Laguna Portezuelo and other sites discussed in-depth in the text (i.e., Abarzúa et al., 2014; Fletcher & Moreno, 2012b; Moreno-Gonzalez et al., 2020). The triangle northwest of L. Portezuelo marks the Copahue stratovolcano. Satellite map data: Google, Maxar Technologies. Photo taken from L. Portezuelo (2013) facing a stand of *A. araucana* about 0.5 km south of the site.



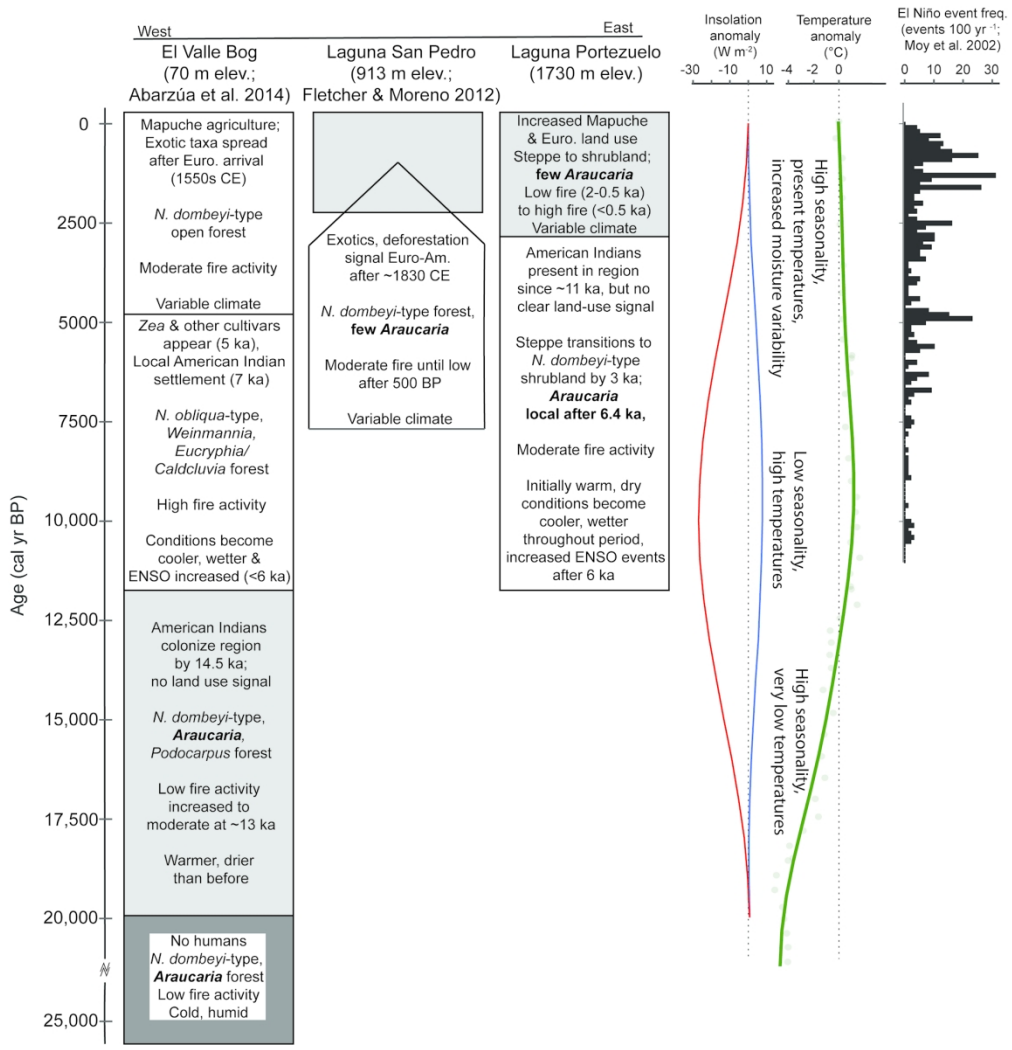
Age-depth model for Laguna Portezuelo using Bacon 2.2 (Blaauw and Christen, 2011). Green areas represent calendar ages provided for different layers (see Table 3), blue areas represent probability distributions of the calibrated dates, red area represents the Bacon-rejected date (OS-144515), dotted red line shows weighted mean age, and dotted gray lines depict the 95% highest posterior density (HPD) intervals. Vertical gray bars show location and thickness of tephra layers (≥0.5 cm thickness). Deposition time (black), percent composition of non-carbonate inorganic (blue), and organic (orange) are discussed in text.



Pollen percentage diagram from Laguna Portezuelo showing pollen taxa and zones discussed in text, with resulting CONISS dendrogram (Grimm, 1987). Charcoal accumulation rates (CHAR; black) and background CHAR (BCHAR; red) describe variations in fire activity.



CCA plot of the terrestrial pollen data from Laguna Portezuelo with explanatory variables: sea-surface temperature (SST; Kaiser et al., 2005), insolation-driven seasonality (DJF-JJA; Berger & Loutre, 1991), and ENSO activity (i.e., L. Pallcacocha red-band intensity; Moy et al., 2002) and CHAR from L. Portezuelo. Changes in CHAR were expected to coincide with changes in vegetation, so unidirectional causality was not interpreted. Pertinent pollen taxa (blue dots) are labeled: RU = *Rumex*, PN = *Plantago*, LG = Cichorioideae, AR = *Araucaria*, V = Asteroideae, LU = Fabaceae, ND = *Nothofagus dombeyi*-type, RZ = Rhamnaceae, UM = Apiaceae, G = Poaceae, J = Cupressaceae. Samples (black dots) are labeled chronologically and connected by a line colored based on the abundance of *Araucaria* pollen in a given sample. Biplot scores of the constraining variables are provided in Table 4.



Vegetation, fire, climate, and human history based on published interpretations. Darker shades denote greater inferred abundance of *Araucaria araucana*. Summer (DJF; red) and winter (JJA; blue) insolation values (Berger & Loutre, 1991), temperature anomalies from present (green) (Kaiser et al., 2005), and El Niño event frequency (black) (Moy et al., 2002). Interpretations from the independent paleoclimate data are also provided. Abbreviations in text: BP = calibrated years BP (cal yr BP); ka = thousands of years; CE = Common Era.



Photo taken in 2018 of the *Araucaria araucana* forest-steppe ecotone at its northeastern limit near L. Portezuelo, with *Nothofagus antarctica* growing in the foreground and the Copahue stratovolcano in the background.

1422x1066mm (72 x 72 DPI)