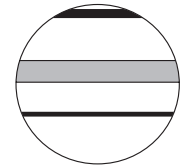


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The impact of recent land-use change in the *Araucaria araucana* forest in northern Patagonia

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Abstract

Land-use change in the form of extensive *Pinus* plantations is currently altering the natural vegetation cover at the forest–steppe ecotone in northern Patagonia. Providing recommendations for conservation efforts, with respect to this recent and earlier land-use changes, requires a longer time perspective. Using pollen analysis, we investigated to what degree the colonization of the area by Euro-American settlers changed the forest composition and the vegetation cover, and to explore the spread of the European weed *Rumex acetosella*. This study is based on short sediment cores from six lakes in the *Araucaria araucana* forest region, across the vegetation gradient from the forest to the steppe. Results document that although *Araucaria araucana* has been extensively logged elsewhere, near the investigated sites, populations were rather stable and other elements of the vegetation changed little with the initiation of Euro-American settlements. A reduction of *Nothofagus dombeyi*-type pollen occurred at some sites presumably due to logging *Nothofagus dombeyi* trees, while toward the steppe, *Nothofagus antarctica* shrubs may have been removed for pasture. The appearance of *Rumex acetosella* pollen is consistent with the initiation of land use by Euro-American settlers in all cores, probably indicating the onset of animal farming. The rise of the *Rumex acetosella* pollen curve during the 1950s marks more recent land-use change. These observations indicate that the spread and local expansion of the weed requires disturbance. Overall, the study shows that the initial colonization of the area by Euro-American settlers had little effect on the natural vegetation structure, while developments since the 1950s are strongly altering the natural vegetation cover.

Keywords

Araucaria araucana, biological invasion, forest–steppe ecotone, human impact, land-use change, North Patagonia, *Rumex acetosella*, vegetation disturbance

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Introduction

Over the past centuries, human activities have become the main driver for vegetation change globally (Foley et al., 2005). In some cases, this has led to species-diverse cultural landscapes worth conserving (Birks et al., 1988), while modern land use often leads to homogeneous areas with a loss in diversity (Foster et al., 1998). Recent land transformations to intensive forestry, agriculture, and urbanized areas threaten many ecosystems (McKinney, 2002). Restoration or sustainable management projects are often being initiated to counteract the loss of ecosystem services. These projects require knowledge of the vegetation and natural disturbance regimes prior to the recent land use. Paleoecological investigations provide this baseline information and a long perspective of land use (Whitlock et al., 2018; Willis et al., 2010). This has been successfully demonstrated by many studies such as determining the natural variability of the fire regime, for example, in the north-west United States (Whitlock et al., 2003) or information on whether plants were native or introduced on the Galapagos Islands (Coffey et al., 2011). Likewise, paleoecological investigations would be useful in the confirmation of conservation status of a species or to assess the rate and patterns of spread of invasive species (Froyd and Willis, 2008).

In Europe, land-use change occurred gradually with pulses due to technological progress, starting perhaps with the onset of farming in the Neolithic (Kaplan et al., 2009). The development in the

Americas was interrupted by the arrival of Europeans in AD 1492 (hereafter all dates are given as AD), initially leading to a decline in the indigenous population due to the introduction of diseases. The extent to which pre-European land use altered vegetation in the Americas is still debated. Many indigenous communities had developed agriculture in the Americas prior to the arrival of Europeans (e.g. McKey et al., 2010); however, the extent of their impact was likely small and/or locally restricted. Few of the 182 pollen diagrams reviewed by Flantua et al. (2016) from Latin America indicate clear human land-use prior 1500. The study also indicates that post-Columbian land use occurred earlier in the north spreading to the south, consistent with European settlement history of the continent. Similar patterns are more clearly documented for North America, where initial deforestation started

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around 300 years ago on the east coast, but only 150 years later on the western side of the continent (McAndrews, 1988). Events in North and Central America resulted in land-use pulses in southern South America. For example, the gold rush in California leads to large-scale deforestation for wheat farming about the mid-1800s in south-central Chile. This connection lasted until the construction of Panama Canal, reducing the cost for sea transport between east and west North America (Armesto et al., 2010). Around 1800, the spread of colonies and nations in the Americas accelerated the conversion of the natural vegetation into cropland, pastures, and urbanized areas (Kaplan et al., 2011). Later, during the 19th century, new technologies, such as the introduction of stream-powered and mobile sawmills, enhanced the pace of deforestation in western Patagonia (Armesto et al., 2010).

Detecting the initial arrival of Euro-American settlers in a region based on pollen analysis is not always trivial. The best indicators are native taxa reacting to disturbance such as *Ambrosia* in eastern North America (McAndrews, 1988) or *Cecropia* in the humid neotropics (Flantua et al., 2016). While these taxa may also indicate natural disturbance or the Native American land use, the concomitant appearance of introduced taxa with a high pollen production, such as *Plantago lanceolata* and *Rumex acetosella*, may add confidence. While the genera *Plantago* and *Rumex* have native species in the Americas with somewhat similar pollen morphology, pollen from the introduced *Plantago lanceolata* and *Rumex acetosella* can be identified in most cases. Both taxa are native to Europe and document the changing strength of human pressure over the past millennia in European pollen diagrams (Behre, 1981). Of the species belonging to the genus *Rumex*, in Europe, particularly, *Rumex acetosella* has spread around the world with European farmers, and potentially with whalers. It may have been introduced deliberately in some places as it was regarded as a medicinal plant (Stopps et al., 2011). It was naturalized in eastern North America by 1634 (Mack, 2003), and pollen diagrams show the pollen type to increase with the rising curve of *Ambrosia*, for example, at Linsley Pond around 1700 (Brugam, 1978).

For South America, the early establishment and spread of this weed is not as well documented. The earliest appearance of *Rumex acetosella* in pollen records from South America varies between 500 and 580 years ago including sites from the tropical Atlantic and Pacific coasts to Patagonia (Flantua et al., 2016; Markgraf et al., 2009). *Rumex acetosella* has become one of the most frequent introduced taxa in several disturbed environments (Stopps et al., 2011). Particularly in Patagonia, abundant regeneration occurs after fire or in overgrazed pastureland (Speziale and Ezcurra, 2011). It is not well known when and where *Rumex acetosella* was first introduced to Patagonia. The pollen diagram from Mallín Vaca Lauquen, a site located c. 200 km north of the study area, documents the presence of *Rumex acetosella* during the 16th century together with the arrival of Spanish colonist (Markgraf et al., 2009). The presence of European weeds there is attributed to grazing and logging. Furthermore, *Rumex acetosella* is also recorded at the beginning of the 16th century at Lake Torta, a site located 30 km south of the study area (Fontana, unpublished data). These are the earliest occurrence of the pollen type in Patagonia until now. At Rio Rubens, in southern Patagonia, *Rumex acetosella* is recorded as early as 1620 (Huber and Markgraf, 2003). The continuous encounter of the pollen type predates the establishment of a settlement, suggesting that *Rumex acetosella* had spread through the intentional release of livestock by sealers and whalers or from the unsuccessful establishment of two Spanish colonies on the Straits of Magellan during the 1580s.

Another consequence of the arrival of European settlers is the extraction of timber, initially to clear the area for agriculture and the construction of houses (Rothkugel, 1916). Timber extraction was particularly intense on the western side of the Andes between

the mid-19th and the first half of the 20th centuries. Two characteristic trees of Patagonia, *Fitzroya cupressoides* and *Araucaria araucana*, suffered from this exploitation. In the Chilean Lake District, *Fitzroya cupressoides* was a particular target and nearly all stands at low elevations were extensively logged by the 1950s (Fraver et al., 1999). *Araucaria araucana* was targeted since the early 20th century and approximately 30,000 ha were exploited by the wood industry and for exportation (Otero, 2006). *Araucaria araucana* is a tree considered a cultural symbol by indigenous people, which also provides food (Herrmann, 2006). Past selective logging has severely reduced and fragmented *Araucaria araucana* populations (Hechenleitner et al., 2005; Premoli et al., 2013). Despite the successes of early protected areas, such as Lanín National Park founded in 1937, and the logging ban since the 1970s, the overall population of the tree seems to be in continuous decline due to a lack of regeneration (Roig et al., 2014). Recent threats affecting natural regeneration include the reduction of habitat through substitution of native vegetation with *Pinus* plantations, frequent human-induced fires, and livestock grazing (Gonzalez et al., 2006).

The Patagonian Andes, including the larger part of the *Araucaria araucana* forest region, were one of the last areas to be colonized by Euro-American settlers at the end of the 19th century (Bandieri and Blanco, 1996; Camus Gayán, 2006). During the 16th century, indigenous people had adopted horses and cattle after the establishment of Spanish colonies in what is now North and Central Chile and Argentina (Aagesen, 1998; Michell, 2017). Within the study region, the towns of Lonquimay, Chile and Aluminé, Argentina were founded in 1897 and 1915, respectively. In this region of the forest–steppe ecotone, fire was an effective means to clear land for pasture and the ownership of the land was divided during this time (Rothkugel, 1916). Initially, livestock farming and tree logging were the major activities in the area. Plantations of introduced trees, mainly *Pinus*, started in the 1970s and since then have increased particularly by converting previously open vegetation types at the forest–steppe boundary into *Pinus* plantations. Over the past decades, tourism is becoming the main economy, leading to a spread of summer lodges and holiday houses along the lake shores. Villa Pehuenia as an important destiny, founded in 1989 with an initial population of 155 inhabitants. The permanent population has increased to more than 2000 inhabitants, and tourism is starting to exert pressure on the environment. Thus, the change of land use and its impact on the natural vegetation are rather recent in this area, where nature conservation, tourism, and forestry have conflicting aims.

We are using this setting for a palynological case study, investigating the impact of recent land-use change on the *Araucaria araucana* forest. In particular, we aim to determine (1) how the vegetation has changed with the recent land use, (2) which indicator taxa are related to the recent history of land-use changes in *Araucaria araucana* forest, and (3) the impact of this land use on the *Araucaria araucana* forest.

Study area

Araucaria araucana occurs in the Andes between 37°30' and 39°40' S on the western flank and between 37°45' and 39°50' S on the eastern flank (Gonzalez et al., 2006). The study area is located almost in the center of the latitudinal distribution of *Araucaria araucana*, but was also selected due to the relatively well-documented human history (Table 1). The study area encompasses both slopes of the Andes Cordillera in a west-east transect around 39° S (Figure 1a and b). The climate is temperate with average monthly temperatures above freezing and a precipitation minimum during the austral summer, giving it a Mediterranean character, while under oceanic influence (Luebert and Plissock, 2006). Precipitation in the Andes arrives with westerly winds from the

Table 1. Brief description of human history with environmental significance.

Period	Date range, AD	
Exploitation	1950 to present	Overgrazing in the steppe; forestry with exotic species, mainly <i>Pinus</i> ; spread of <i>Pinus</i> into open areas and native forests; decreased logging of the native forest; increase in tourism, creation of touristic infrastructure but unregulated access to natural vegetated areas; many areas remain unprotected, while <i>Araucaria araucana</i> is protected
Colonization	1850–1930/1950	Use of fire to ‘open’ the forest; foundation of the town Aluminé, Argentina, in 1915, and Lonquimay, Chile, in 1897; population expansion, livestock intensification, and intense logging; the ownership of the land was divided.
Exploration	1530–1850	First contacts between indigenous communities and European explorers; indigenous communities adopted horses and cattle; hunting activity decreased.
Pre-European	<1530	Indigenous people were present in the area, gatherer and hunters, but probably seasonally; possible use of fire to hunt native games, for example, Guanaco (<i>Lama guanicoe</i>).

After Armesto et al. (2010), Camus Gayán (2006), and Otero (2006).

Pacific Ocean (Garreaud, 2009; Garreaud et al., 2013). The Andes Cordillera reaches elevations exceeding 2000 m a.s.l. creating a sharp rain-shadow effect with the Pacific air masses discharging most of the precipitation on the western slopes (Mundo et al., 2013). Here, total annual precipitation ranges between 1200 mm at 800 m a.s.l. and 2500 mm or more at 1600 m a.s.l., while on the eastern slopes rainfall decreases exponentially to 200 mm toward the steppe (Bianchi et al., 2016; Paruelo et al., 1998). Annual mean temperature on the western slopes ranges between 12°C and 8°C at high elevations, and increases up to 16°C on the eastern side (Bianchi et al., 2016). The interannual variability of precipitation and temperature are higher east of the mountains (Paez et al., 1997; Paruelo et al., 1998), which has consequences for the distribution and abundance of plants (Paruelo et al., 1998).

Araucaria araucana forest at 39° S occurs mainly above 1000 m a.s.l. up to the tree line at c. 1700 m a.s.l., in fragmented populations (Gonzalez et al., 2006) (Figure 1b). Because of the complex interaction between climate, topography, and the disturbance regime, *Araucaria araucana* shows a variety of plant associations that create a complex landscape (Kitzberger, 2013; Roig et al., 2014). The plant associations in *Araucaria* forest have not always clear limits; however, zones of major abundance and the absence of species can be recognized along the gradient (e.g. Gonzalez et al., 2006; Roig et al., 2014). For instance, under the humid climate condition on the western slopes of the Andes, *Araucaria araucana* forms dense multi-layered forests with dominance of *Nothofagus dombeyi* and *Nothofagus pumilio*, as well as understory species typical for the rainforest. Under mesic climate conditions, *Araucaria araucana* forms open forests with *Nothofagus antarctica* dominating in the understory. Under xeric climate conditions, scattered individuals of *Araucaria araucana* occur without or with scarce presence of *Nothofagus antarctica* or *Austrocedrus chilensis*. Bunch grasses and shrubs, such as *Berberis microphylla*, *Discaria chacaye*, and *Colletia hystrix*, often dominate these dry sites. Estimates of *Araucaria araucana* forest cover loss since the 1970s to the present are difficult (Miranda et al., 2018). The general trend in the lowland westward from the *Araucaria araucana* forest shows that the forest coverage decreased about 19% (Miranda et al., 2017). However, due to the existence of the tree on steep isolated mountains and the existence of many protected areas created since the 1930s, the loss of *Araucaria araucana* may be less toward the west of its distribution.

In the following, we describe the vegetation around the lakes from west to east (Table 2; Figure 1b):

1. Lake Lomocura has no *Araucaria araucana* in the immediate surroundings and is dominated by *Nothofagus dombeyi* and *Nothofagus pumilio*, with a dense understory of *Drimys andina*, *Myrceugenia chrysocarpa*, *Berberis microphylla*, *Gaultheria phillyreifolia*, *Escallonia rosea*, and *Escallonia rubra*. After logging, common weeds, such as *Rumex acetosella* and *Taraxacum officinale*, are frequent.

In other places, *Nothofagus pumilio* dominates together with the perennial evergreen bamboo *Chusquea culeou* in the understory. After the 1970s, native forest was replaced by unsuccessful *Pinus* and *Eucalyptus* plantations (landowner, personal communication). Species of the genera *Poa*, *Carex*, *Uncinea*, and *Acaena* are also present.

2. Lake Quinquen is located close to the altitudinal tree line, where *Araucaria araucana* forms small groups or scattered individuals mixed with *Nothofagus pumilio*, *Nothofagus dombeyi*, and *Nothofagus antarctica*. The forest understory is densely covered by *Chusquea* sp., *Myrceugenia chrysocarpa*, *Drimys andina*, *Berberis microphylla*, *Berberis serrato-dentata*, and other herbs such as *Perezia pedicularidifolia*, *Valeriana lapathifolia*, and *Alstroemeria aurea*. Above the tree line, alpine herbs, such as *Senecio* spp., *Viola reichei*, *Quinchamalium chilensis*, and *Acaena ovalifolia*, occur together with Poaceae and Cyperaceae. The area was logged during the 1970s and is now protected allowing indigenous people to collect *Araucaria araucana* seeds and dead-wood.
3. Lake Los Piñones is located in the mesic zone. *Araucaria araucana* is mixed with *Nothofagus dombeyi*, and some elevated areas are mixed with *Nothofagus pumilio*. In surrounding areas, *Nothofagus antarctica* occurs as a shrub below *Araucaria araucana* in flat areas near the lake. Isolated populations of *Nothofagus obliqua* occur in the wider area. The open forest is used for livestock grazing, wood collection, and tourism. Herb species, such as *Rumex acetosella*, *Plantago lanceolata*, *Cerastium arvense*, *Acaena ovalifolia*, *Viola reichei*, *Fragaria chilensis*, *Galium hypocarpium*, and *Alstroemeria aurea*, grow near the lake.
4. Lake Koywija is located on the eastern side of the hydrological divide on a peninsula between the lakes Aluminé and Moquehue. Individuals of *Araucaria araucana* are growing close to the lake. *Austrocedrus chilensis*, *Nothofagus antarctica*, and the small trees *Lomatia hirsuta* and *Aristotelia chilensis* are components of the open canopy. Other associated species are *Chusquea culeou*, *Ranunculus peduncularis*, *Rumex acetosella*, and *Acaena antarctica*. While livestock grazing was important in the past, the area is increasingly developed for tourism.
5. Lake Relem is situated in a *Pinus* plantation established in 1985. The native vegetation close to the lake is characterized by *Nothofagus antarctica*, *Ephedra*, Poaceae, *Ranunculus peduncularis*, *Discaria chacaye*, *Mulinum spinosum*, *Berberis microphylla*, *Escallonia rosea*, *Baccharis* sp., *Gamochaeta spicata*, *Acaena ovalifolia*, and *Acaena magellanica*. Outside the plantation, vegetation cover is sparse, with the presence of dispersed individuals of *Araucaria araucana* associated with *Discaria chacaye*, *Eryngium paniculatum*, and *Azorella trifurcata*. Open areas within the *Pinus* plantation are used for cattle grazing.

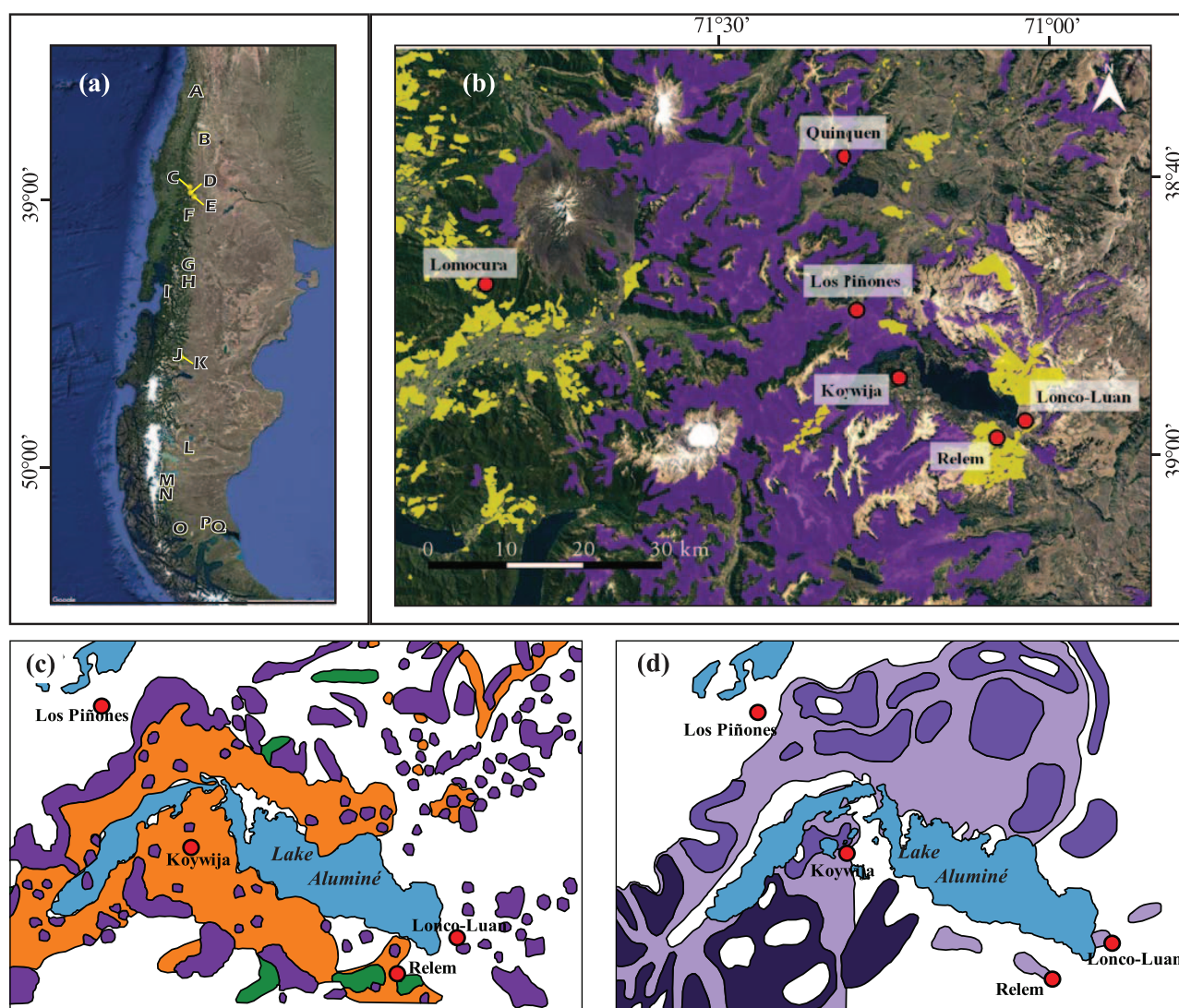


Figure 1. Study area. (a) Location of the study area within Patagonia and location of cited studies (Table 4) with the presence of pollen from introduced taxa. Letters follow the order in the table. (b) Location of study sites (red circles), modern distribution of dense *Araucaria araucana* (purple) and *Pinus* plantations (yellow). (c) Early 20th century estimate (Rothkugel, 1916) of the burned area (orange), the area covered by *Araucaria araucana* (purple), and *Nothofagus pumilio* (light green) in the Argentine study area. (d) Structure of *Araucaria araucana* forest in the Argentine study area (Tortorelli, 1942): dense (dark purple), open (purple), and parkland forest (light purple). Note that in Rothkugel and Tortorelli's map, the units are generalized and therefore scale is not provided.

6. The vegetation around Lake Lonco Luan is sparse, mainly composed of bunch grasses, *Azorella*, *Mulinum spinosum*, *Ephedra chilensis*, *Acaena ovalifolia*, and *Acaena magellanica*. The closest *Pinus* plantation was established in 1985. Dispersed individuals of *Araucaria araucana* occur in the surrounding area on rocks. To the south, individuals of *Araucaria araucana* grow together with *Austrocedrus chilensis*. The area around the lake is used as pasture for goats.

Methods

Sampling and pollen analysis

Six lakes of similar size were chosen along the west–east precipitation and vegetation gradient within the distribution of *Araucaria araucana* (Figure 1b). Using a gravity sampler launched from an inflatable boat, short cores were collected from selected lakes. The cores range between 16 and 31 cm in length (Table 2). Koywija and Lonco Luan were sampled in 2010 and 2015, respectively, and all other samples were collected in February 2016. In the field, the cores were cut into 1-cm-thick slices and stored in sealed plastic bags. At Relem, a longer sediment sequence was

collected by means of a modified Livingstone sampler (Wright, 1967). All sediments were stored at 5°C until processing.

Samples of 0.5 cm³ were taken at 2 cm intervals for pollen analysis and prepared following standard techniques (Bennett and Willis, 2001), excluding sieving. *Lycopodium clavatum* tablets were added to estimate pollen and micro-charcoal concentration. Pollen were counted using light microscope at $\times 400$ and $\times 1000$ times magnifications. A minimum of 400 terrestrial pollen grains were counted for Quinquen, Relem, and Lonco Luan due to a low pollen concentration and at least 500 grains were identified at all other sites. These higher pollen counts compared with the commonly used 300 grains allow for a better detection of rare pollen types and for a lower uncertainty in assessing abundance changes of less abundant pollen types (Birks and Line, 1992; Maher, 1972).

The identification of pollen grains and spores was carried out with atlases of Heusser (1971), Markgraf and D'Antoni (1978), Beug (2004), and pollen reference stored in Department of Palynology and Climate Dynamics, University of Göttingen. Pollen grains of the introduced weed *Rumex acetosella* were easily differentiated from native *Rumex* species according to their morphological features, for example, shape and size. *Rumex acetosella* produce small and spherical pollen grains of 22.5–27.5 μm

Table 2. General characterization of the studied lakes and cores.

Lake name	Lake location		Lake feature		Core		Pinus plantation		Modern vegetation
	Coordinate	Elevation (m a.s.l.)	Size (ha)	Water depth (m)	Length (cm)	Collection year	Plantation year	Distance (km)	
Lomocura	38° 47' S 71° 50' W	1015	3.59	8	29	2016	1980	5	Degraded <i>Nothofagus dombeyi</i> forest, with <i>Pinus</i> and <i>Eucalyptus</i> plantation
Quinquen	38° 38' S 71° 18' W	1690	0.44	0.5	31	2016	1985	24	<i>Araucaria araucana</i> with <i>N. antarctica</i> , <i>N. pumilio</i> , and <i>N. dombeyi</i>
Los Piñones	38° 49' S 71° 17' W	1280	1.36	3.5	31	2016	1985	3.4	<i>A. araucana</i> with <i>N. antarctica</i> , <i>N. obliqua</i> , and <i>N. dombeyi</i>
Koywija	38° 54' S 71° 13' W	1189	5.12	4	24	2010	1985	6.5	<i>A. araucana</i> , <i>N. antarctica</i> mixed forest; Scatter individual of <i>Austrocedrus chilensis</i>
Relem	38° 58' S 71° 04' W	1265	0.84	2.5	65	2016	1985	0.2	<i>Pinus</i> plantation; small patches of <i>A. araucana</i> and <i>N. antarctica</i> ; in open areas, steppe grasses and shrubs.
Lonco Luan	38° 57' S 71° 02' W	1230	7.33	4.3	25	2014	1985	1	Steppe grasses and shrubs. <i>Pinus</i> plantations and isolated individuals of <i>A. araucana</i>

The ages are presented as AD.

(average 25.2 μm) (Beug, 2004), while pollen grains of the native *Rumex magellanicus* are of medium size and spheroidal to subspheroidal, 42–46 $\times$ 38–40 μm (Heusser, 1971). These measurements are based on material mounted in glycerine gel. The pollen taxonomy follows the information on present plant distribution (Rodríguez et al., 2018; Zuloaga et al., 2008; and the database of the herbarium of Concepción, Chile, CONC), linking morphological pollen types to species and genera present in the study area (Fontana and Bennett, 2012). In this region, *Nothofagus dombeyi*-type pollen includes *Nothofagus dombeyi*, *Nothofagus pumilio*, and *Nothofagus antarctica*. The *Nothofagus obliqua*-type pollen is produced by *Nothofagus obliqua*, *Nothofagus glauca*, and *Nothofagus alpina*. While *Nothofagus obliqua* occurs in this region, *Nothofagus alpina* is found scarcely only westward of the study area, therefore can be assumed to be represented by this pollen type. Micro-charcoal particles were counted in the pollen slides to assess regional and temporal trends in the fire activity. Charcoal particles were recognized as black, opaque, and angular particles larger than 10 μm (Clark, 1988).

Chronology

The sediment of Lake Relem was radiocarbon dated. Three samples of bulk sediment were submitted for radiocarbon dating, attempting to capture the bomb peak with two samples and constraining the base with a sample dating prior the plateau for the last 300 years in the calibration curve (Hua, 2009). Radiocarbon dates were calibrated using the southern Hemisphere calibration curves (SHCal13, Hogg et al., 2013; postbomb_SH1-2, Hua et al., 2013). The age–depth model was constructed using Clam 2.2 (Blaauw, 2010) with a smooth spline (0.1 smooth).

The initiation of *Pinus* plantations is well documented in the region; this information was used to match it to the appearance of *Pinus* pollen in the sediments to obtain a time marker. *Pinus* plantations in Chile are mainly *Pinus radiata*, while *Pinus ponderosa* and *Pinus contorta* are planted in Argentina. These species start flowering at the age of 10 years (Bocos and Laclau, 2017, personal communication). The age of the closest plantation (Table 2) plus 10 years was assigned to the depth where the percentage of *Pinus* pollen rise. Using this date and the year of sampling for the sediment surface, a linear sedimentation was assumed to estimate the respective age–depth relationship for each lake. *Pinus* pollen is recorded with values of up to 15%. Maximum values are encountered when large plantations occur in the surroundings of the sites such as lakes Lonco Luan and Relem. Even though *Pinus* is a high pollen producer, *Nothofagus dombeyi*-type also produces abundant pollen, making up to 80% of the pollen sum. Both are

wind-dispersed pollen taxa that can be transported over long-distance. The percentage cover of forest of *Nothofagus dombeyi*-type is far much larger than *Pinus* plantation. The beginning of the continuous curve of *Pinus* pollen is interpreted as an indication of extra-local presence of *Pinus*, and the initial increase as local presence around the site.

Data analysis

The sum of terrestrial taxa was used to calculate percentages of taxa pertaining to that sum. The sum of all terrestrial and aquatic pollen types was used for the percentage calculation of aquatic taxa. The sediment accumulation rate changes in the upper unconsolidated sediments and the charcoal concentration would reflect that, rather than changes in fire activity. Therefore, counts of charcoal particles were expressed as percentages of the terrestrial pollen sum (e.g. Clark, 1988; Whitlock and Larsen, 2001). Pollen diagrams were constructed with TILIA v.2.0.41. Palynological richness was estimated using rarefaction analysis (Birks and Line, 1992) to the minimum common sum of 400 pollen grains. Trends in the compositional changes of the terrestrial taxa were explored using ordination analysis. Multivariate analysis in ecology relies basically on the assumption of linear or unimodal response of taxa to environmental explanatory variables (Legendre and Legendre, 2012; Ter Braak and Smilauer, 2012). Though non-linear and multi-modal responses can be found in ecological gradients, the multivariate ordination methods allow interpretations of vegetation patterns of any transitional type (Ter Braak and Smilauer, 2012). Correspondence analysis (CA) was chosen assuming unimodal response of the species on the environmental gradient from west to east. The CA for all lakes together was carried out excluding aquatic taxa, using square-root transformation and without down-weighting rare taxa. The lengths of the first axis from a Detrended CA, a special form of CA (Ter Braak and Smilauer, 2012), were used to describe compositional changes. In further CA, introduced taxa and *Nothofagus dombeyi*-type were excluded to explore potential changes in the composition of native taxa and remove the dominance and abundance shifts of *Nothofagus dombeyi*-type, respectively. Rarefaction and ordination analysis were conducted using the vegan-package 2.4-2 (Oksanen et al., 2017) and Canoco 5 (Ter Braak and Smilauer, 2012).

Results and interpretation

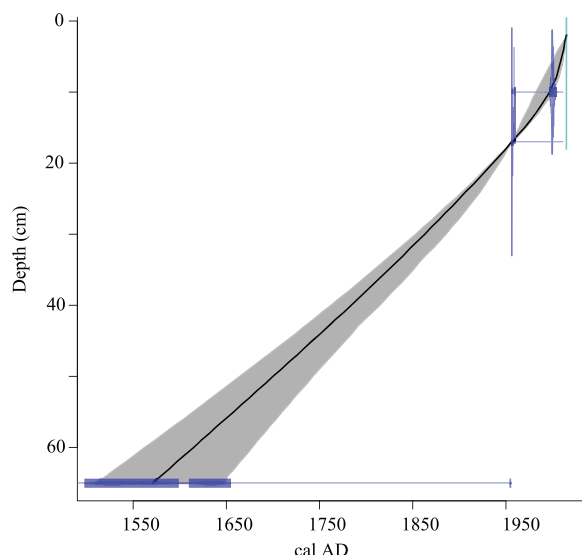
Chronology and age estimation

The two radiocarbon dates from the most recent sediments of Lake Relem provide high precision ages (Table 3). One of the dates

Table 3. Radiocarbon dates only for Lake Relem.

Lab. No.	Depth (cm)	Age (^{14}C yr BP)	%pMC	Age, cal. yr AD	Probability (%)
UBA-29237	270–271		109.88 ± 0.34	2003.4–1997.0 1958.8–1958.7	93 2
UBA-29238	277–278		100.37 ± 0.32	1957.4–1955.1	95
UBA-29239	325–325.5	330 ± 24		1503–1592 1615–1651	70 30

Material analyzed: bulk sediment at the CHRONO Centre, Queen's University of Belfast, UK (UBA). Calibrated dates presented as 2σ .

**Figure 2.** Age–depth model for Lake Relem.

corresponds unambiguously to the rise of the bomb peak in the year 1956 ± 1 . This makes the period 1997–2003 the most likely age for the topmost radiocarbon date. Together with the basal date and the age of the top sample, a simple age model was produced (Figure 2).

The time of the establishment of *Pinus* plantations in the study area is well documented, and the radiocarbon dates allow dating the rise of the *Pinus* pollen curve in Relem. Around Relem, *Pinus* plantation started in 1985. Adding 10 years for the onset of flowering results in an expected rise of the *Pinus* pollen curve around 1995. The independent age model for Relem (Figure 2) yielded an age of 1992 for the first sample with increased *Pinus* pollen percentage at 11 cm depth. This comparison shows that the rise of the *Pinus* pollen curve is indeed occurring approximately 10 years after plantation and provides a good chronological marker for the other short cores. For all lakes, the closest *Pinus* plantations were established after the 1980s (Table 2), consequently ages in the 1990s were assigned to the rise of the *Pinus* curves. The length of the gravity cores varied between 25 cm (Lonco Luan and Koywija) and 31 cm (Quinquen and Los Piñones) (Table 2). The rise of *Pinus* occurred at 15 cm in Lonco Luan, 9 cm in Koywija, 6 cm in Lomocura, 3 cm in Quinquen, and 5 cm in Los Piñones (Figure 4). Applying a linear extrapolation based on the year of sampling and the age for the rise of the *Pinus* curve yields age estimates for the gravity cores between 30 years (Lonco Luan) and 300 years (Quinquen). These age estimates correspond to sedimentation rates of around 0.6 cm yr^{-1} at Lonco Luan, 0.5 cm yr^{-1} at Koywija, 0.2 cm yr^{-1} at Quinquen and Lomocura, and 0.3 cm yr^{-1} at Los Piñones. For Relem, we obtained a sedimentation rate of 0.6 cm yr^{-1} in the uppermost 5 cm and an average of 0.13 cm yr^{-1} for the older sediments (Figure 2).

Patterns of vegetation land-cover and land-use change

Nothofagus dombeyi-type is the dominating pollen taxon at the six sites (Figure 3). In the study area, this pollen type comprises

Nothofagus dombeyi, *Nothofagus antarctica*, and *Nothofagus pumilio*, which represent the dominant trees in the study area. The pollen production of other forest trees like *Araucaria araucana* is much lower and thus the proportion of *Nothofagus dombeyi*-type pollen is a good indicator of overall forest cover. The highest percentages of *Nothofagus dombeyi*-type occur at the westernmost sites Lomocura and Quinquen with an average of 82% and 86%, respectively (Figure 4b). The lowest abundance of around 40% was found in the top samples of Lonco Luan, where tall *Nothofagus* species are absent and patches of shrubby *Nothofagus antarctica* occur within c. 5 km of the site. Thus, the proportion of *Nothofagus dombeyi*-type pollen below 40% may indicate patches of open forest and steppe vegetation types as suggested by Iglesias et al. (2017) as a threshold differentiating the forest from the steppe in an area 200 km to the south with somewhat different vegetation composition.

Araucaria araucana occurs throughout the study region, and its pollen was present in all six sites with values around 4%. The highest percentages occurred in Koywija (6.5%) and the lowest in Lonco Luan (3.2%) (Figure 3). There is no common temporal trend in changing *Araucaria araucana* pollen among the lakes. Percentages decreased in Lomocura and Quinquen, while they increased in Koywija and Lonco Luan. At the mesic site Los Piñones and the more xeric site Relem, *Araucaria araucana* pollen proportions did not change. *Nothofagus obliqua*-type pollen is present in all lakes (Figure 3) with low abundance. In lakes Lomocura, Quinquen, Koywija, and Lonco Luan, the abundance is lower than 3%, but stable. In Los Piñones, the pollen type increased from 4% before 1970 to c. 10% in recent samples.

At the westernmost site, Lomocura, rainforest-tree pollen taxa (e.g. *Weinmannia trichosperma*, *Eucryphia/Caldcluvia*, and *Saxegothea conspicua*) together represented 2.1% in samples between 10 and 30 cm depth and decreased to 1.3%, while herbaceous taxa increased in the top samples, suggesting a dense forest prior to the appearance of *Pinus* pollen (Figure 3a, Supplemental Material, available online). The most relevant change in Quinquen was the increase in *Nothofagus dombeyi*-type, which may influence the relative abundance of other taxa. The pollen of *Araucaria araucana* and the pollen of the understory shrub *Escallonia* were more abundant in the past (Figure 3b, Supplemental Material, available online). In Los Piñones, the rainforest taxon *Saxegothea conspicua* was more abundant in samples from 20 to 30 cm depth, approximately before 1900 (Figure 3c). The xeric shrub *Discaria*, as well as other herbaceous taxa Asteraceae subf. Cichorioidae, Apiaceae undiff., and Verbenaceae, increased after approximately 1970 (Figure 3c, Supplemental Material, available online). In Koywija, the pollen from the shrubs taxa *Discaria*, *Escallonia*, and *Ephedra* were more abundant than in bottom samples and *Austrocedrus chilensis* increased toward the top (Figure 3d, Supplemental Material, available online). The most notable change in Koywija was the rise of *Lomatia hirsuta* pollen about 1970 reaching more than 2% in top samples. The pollen type corresponds to the small tree *Lomatia hirsuta*, nowadays widespread in the surroundings of the lake. In Lonco Luan, few changes in vegetation composition occurred during the short time captured by the core. The oldest sample corresponding perhaps to

around 1960 contained 68% *Nothofagus dombeyi*-type pollen, which declined in the following sample with the increase in Poaceae (Figure 3e, Supplemental Material, available online). *Rumex acetosella* proportions only increased in the next younger sample. In Lake Relem, *Discaria* and *Ephedra* were relatively stable for the whole period, varying between 1% and 3%, with a peak of 4.3% before the plantation of *Pinus*. The relative abundance of *Azorella* and *Littorella* declined gradually since around 1900 (Figure 3f, Supplemental Material, available online).

Presence of introduced taxa

In all lakes with close proximity to a *Pinus* plantation, *Pinus* pollen (Figure 4a) is the most abundant introduced pollen taxon. The highest pollen abundance of *Pinus* in the top samples was found in Relem (15%), which at the time of sampling was surrounded by a 19-year-old *Pinus* plantation, and Lonco Luan (14%), with a plantation within less than 1 km from the site. Lomocura is also close to a *Pinus* plantation, but also surrounded by remnants of tall *Nothofagus dombeyi* forest. Here, *Pinus* pollen reached only 7% in top samples. The lowest amounts were found in Koywija (4.8%) and Los Piñones (3.5%) with a c. 5 km distant plantation and Quinquen (1.6%) without a close plantation and situated in a dense forest (Table 2).

The *Rumex acetosella* pollen curves show long continuous presence at low abundance, starting approximately in 1900 (Relem and Los Piñones) and a later increase in abundance after 1950 (Figure 4a). The timing of the onset of the curve seems delayed at Lomocura (15 cm; c. 1950) and Quinquen (7 cm; c. 1950). In none of the sites, *Rumex acetosella* or other introduced taxa were registered in single samples prior to about 1900, assuming a linear sedimentation rate before *Pinus* plantation. In Relem, the relative abundance of *Rumex acetosella* increased after the 1970s (15 cm) associated with the increase in *Pinus* pollen, probably indicating intensification of the land use at that time. Also at the other lakes, the rise of *Rumex acetosella* was relatively recent, reaching maximum values between 5% and 15%. *Rumex acetosella* is slightly more abundant in the lakes from xeric environments and open forests compared with more humid and closed canopy sites (Lomocura and Quinquen). The pollen of *Plantago lanceolata* also increased after the 1970s, but its abundance never exceeded 5% and decreased in top samples.

In Quinquen and Relem, the abundance of *Nothofagus dombeyi*-type increased from bottom to c. 1950s, while it was stable before 1950 at lakes Lomocura, Los Piñones, and Koywija. This indicates that forest cover was not reduced during the time of the initial Euro-American colonization in the late 19th to early 20th centuries. At all sites, the abundance of *Nothofagus dombeyi*-type declined with the increase in introduced taxa dating to around 1950 at Relem and Lonco Luan and somewhat later at Lomocura, Los Piñones, and Koywija. Changes in Poaceae percentages show mirror images of the trends in *Nothofagus dombeyi*-type proportions for most sites (Figure 4b). The increase in Poaceae since c. 1950 was related to the *Nothofagus dombeyi*-type reduction indicating a recent decline in forest cover. Due to the rise of introduced taxa in the topmost samples at all sites, the abundance of Poaceae decreased together with *Nothofagus dombeyi*-type. In Koywija, Poaceae remained stable in low percentage despite the fall in *Nothofagus dombeyi*-type, perhaps due to the major presence of *Lomatia hirsuta* (Figure 3d) which covers the surrounding area of the lake currently.

Compositional changes

Despite the differences in vegetation cover around the sites, ranging from closed forest to open steppe, the overall compositional

gradient estimated by the first DCA-axis is short (1.3 SD). In order to focus on compositional changes of indicator taxa, a CA was carried out on a dataset combining all individual sites by taxon (Figure 5). When introduced taxa are included in the analysis, their increasing abundances determine the temporal trend in the first ordination axis. They also cause the distance between top and bottom samples of individual cores to be larger than the distance between the top samples of the different sites (Figure 5a). Here, the second axis captures the position of the sites regarding their position on the gradient from the forest to the steppe. The exclusion of introduced taxa results in relatively tight clusters for individual sites, arranged along the environmental gradient on the first axis, with little compositional change through time (Figure 5b). In both ordination plots, the environmental gradient is characterized by the occurrence of spores from the epiphytic fern *Synammia feuiliei* at Lomocura to *Azorella* and *Mulinum*, characteristic components of the steppe at Relem. Samples from Lonco Luan were separated from Relem by their presence of Apiaceae and Asteraceae subf. Cichorioidae.

Discussion

Changes in woodland composition

Two vegetation maps with generalized mapping units are available for the eastern study region including the sites of the Lake Aluminé basin (Figure 1c and d), providing snapshots of the vegetation around the years 1915 (Rothkugel, 1916) and 1940 (Tortorelli, 1942). A large mapping unit in the Rothkugel map (Figure 1c) indicates burned areas reaching all around Lake Aluminé from the area that is today dominated by open vegetation types in the east to tall *Nothofagus* forests including stands of *Nothofagus obliqua* (Sabatier et al., 2011) around Lake Moquehue to the west. Although Relem is situated at the edge of the mapped burned area, no pronounced micro-charcoal peak or an obvious response in pollen composition was found in the samples corresponding to the early 20th century. Also at Los Piñones few kilometers to the north-west, we could not find evidence of a large extensive fire corresponding to that time. Therefore, the mapped burned area either corresponds to an earlier fire or was created by several small and low severity fires (sensu Keeley, 2009). The subsequent map (Figure 1d) indicates that much of the woodland had recovered and was dominated by *Nothofagus antarctica* (Tortorelli, 1942). Nevertheless, Rothkugel (1916) estimated that Euro-American settlers had burned about 40% of the forest on the eastern side of the Andes at the beginning of the 20th century. However, at all sites capturing the time of this early phase of land-use change there is hardly any change in the pollen record that would identify it, save the beginning of the continuous curve of *Rumex acetosella* at Relem and Los Piñones.

Before 1900, forest exploitation focused on the Pacific coast, and lowlands of Chile and Andean forest were only targeted after the 1930s when technologies improved (Armesto et al., 2010). The town of Lonquimay (40 km north of Los Piñones) was connected to the Chilean railroad network in the 1930s, where a single sawmill working with *Araucaria araucana* consumed approximately 30,000 ha of *Araucaria araucana* forest between 1915 and 1970 (Otero, 2006). A planned train connection across the mountains to Zapala was motivated by the potential extraction of *Araucaria araucana* wood from the study region; however, this train was never realized. The survey by Tortorelli (1942) was an inventory of the available *Araucaria araucana* standing volume that may be logged on the Argentinean side of the mountains. Tortorelli (1942) observed *Araucaria araucana* trees being diseased in some open stands at the dry end of the distribution and recommended logging the mature trees in the dense forest. While his recommendations on establishing a large sawmill at the south-eastern end of Lake Aluminé were not realized, small sawmills

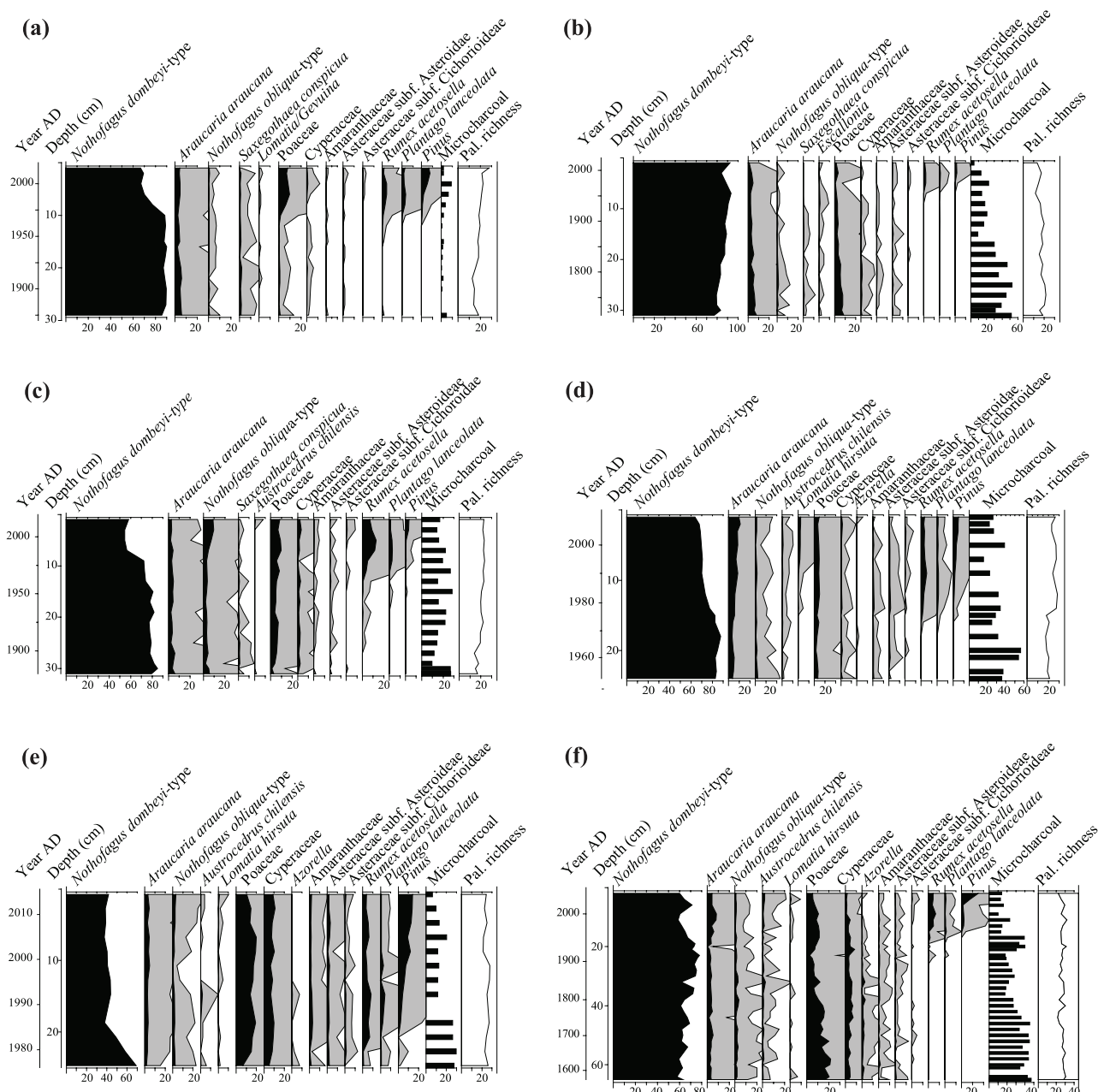


Figure 3. Pollen diagrams, ordered along the precipitation gradient from west to east: (a) Lomocura, (b) Quinquen, (c) Los Piñones, (d) Koywija, (e) Lonco Luan, and (f) Relem.

Pollen percentages in black, $\times 10$ exaggeration light-gray silhouettes. Microscopic charcoal particles expressed as percentage of the terrestrial pollen sum. Palynological richness estimated in base, a minimum sum of 400 terrestrial pollen grains.

existed in the area, but their activities were not documented. The *Araucaria araucana* pollen curve at none of the sites shows a strong decline that could be attributed to logging. This lack of *Araucaria araucana* utilization may be due to the initial inaccessibility of the sites in Chile and the long distance of the Argentinian region to larger commercial centers that hampered exploitation until the tree was protected. A pollen diagram 3 km from Lonquimay (Laguna San Pedro, Fletcher and Moreno, 2012) depicts a gradual decline of *Araucaria araucana* pollen from 3% to 1% prior the establishment of the town in 1890, while it documents an abrupt decline in *Nothofagus dombeyi*-type pollen at around 1900. However, the diagram indicates no change in the proportion of *Nothofagus obliqua*-type pollen during this time.

A strong decline in *Nothofagus dombeyi*-type pollen is also documented for several of the here investigated sites, however, after 1950. In the valley near the westernmost site Lomocura, logging started to be the major economy in the 1930s (Neira et al., 2011). Nevertheless, the forest around the site remained

unchanged until the 1970s, when after logging an initial *Eucalyptus* and *Pinus* plantation failed and a secondary *Pinus* plantation is currently growing (landowner, personal communication). The logging event is clearly visible in the abrupt reduction of *Nothofagus dombeyi*-type with the rise in Poaceae pollen. Based on the current distribution of *Nothofagus* species and historical documents (Otero, 2006), the sharp decline in *Nothofagus dombeyi*-type at Los Piñones is most likely also related to logging nearby *Nothofagus dombeyi* stands for timber. The decline in the pollen type in the lowermost two samples at Lonco Luan may be related to cutting of *Nothofagus antarctica* for firewood or the clearance of land for animal pasture. At Koywija, the decline in *Nothofagus dombeyi*-type pollen does not coincide with an increase in Poaceae, but with the appearance and increase in pollen from *Lomatia hirsuta*. Indeed, *Lomatia hirsuta*, a low-growing tree, is physiologically adapted to nutrient-poor soils and hydraulic stress (Alberdi, 1995; Delgado et al., 2018) and it has been reported to grow rapidly after fire and grazing or in abandoned farmlands

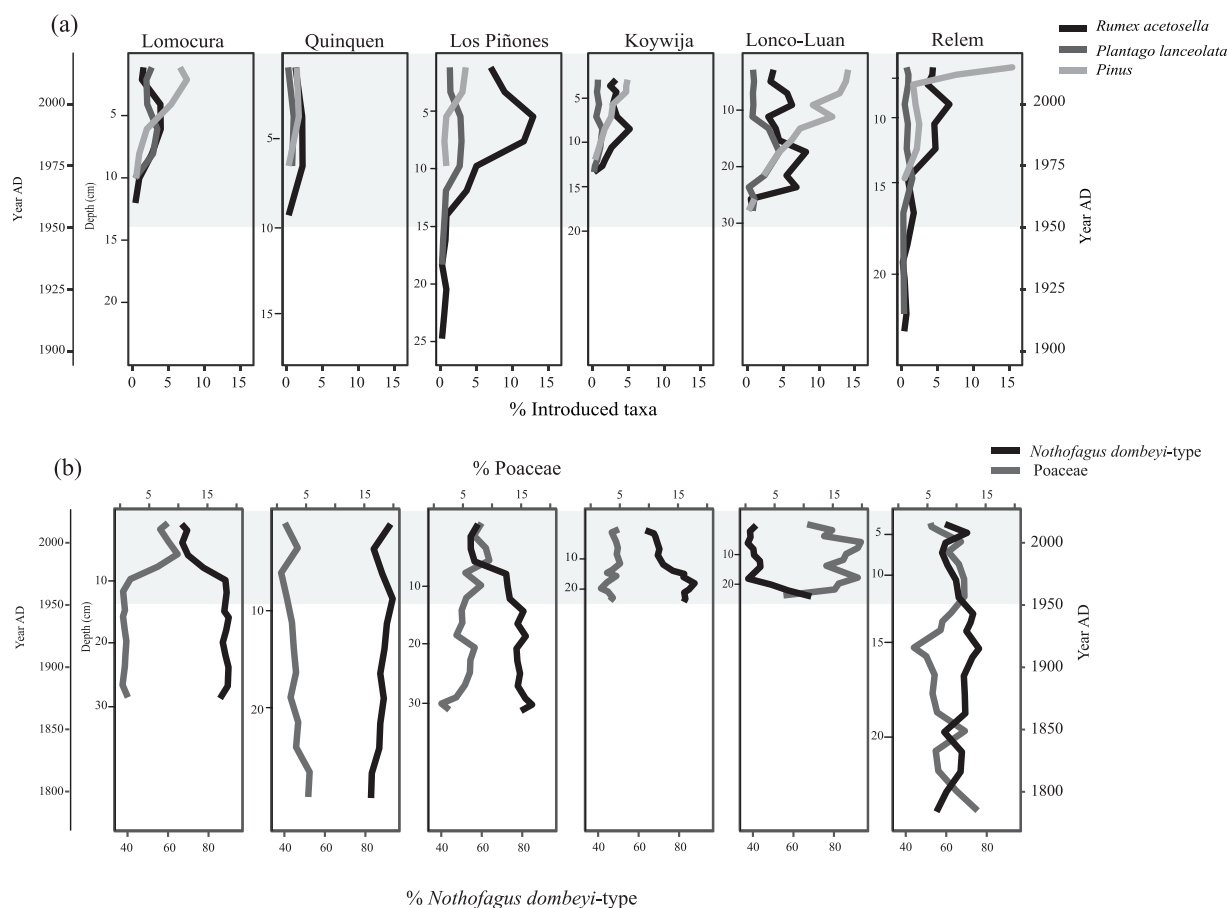


Figure 4. Relative abundance of (a) introduced taxa and (b) *Nothofagus dombeyi*-type and Poaceae.

Lakes are ordered in a west–east gradient from left to right. Ages are shown for Relem and the depth scale at all other sites was adjusted to this time scale, assuming a linear sedimentation rate and using the time of the expansion of *Pinus*.

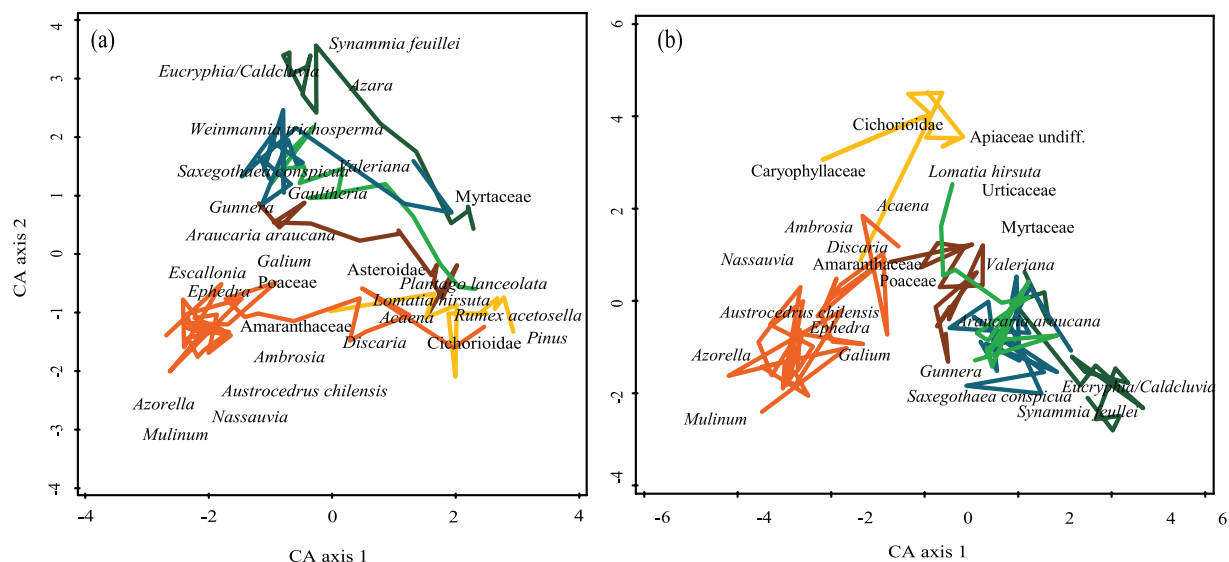


Figure 5. Correspondence analysis of the taxa combined datasets (a), and without human indicators taxa (b).

Lomocura (dark green), Quinquen (blue), Los Piñones (light green), Koywija (brown), Lonco Luan (yellow), and Relem (orange). Note different axis scales.

(Donoso and Escobar, 2006; Raffaele and Veblen, 1998). These characteristics make it a potential disturbance indicator; however, the low pollen production requires *Lomatia hirsuta* to be abundant before the pollen type is registered. The mean and maximum abundance of *Lomatia* pollen in modern surface samples from Patagonia varies between 0.08% and 3.7% (Paez et al., 2001). The current abundance of *Lomatia* around Lake Alumín coincides with the burned areas registered by Rothkugel (1916).

In north-western Patagonia, *Nothofagus obliqua* was extensively used for the construction of houses and railways (Otero, 2006). However, the here investigated sites do not show a decline in the abundance of *Nothofagus obliqua*-type pollen. In contrast, during the period of most intense logging, its pollen abundance remained stable and even increased in the top samples of Los Piñones since approximately 1970. The presence of young stands close to Los Piñones by 1970 was documented by Naveas et al.

Table 4. Selection of paleoecological studies mentioning the occurrence of introduced taxa in Patagonia.

Sites		Site location		Age ^a of appearance and rise of pollen types of introduced taxa	Authors
ID ^b	Name	Lat. S	Long. W		
A	Laguna Aculeo	33°50'	70°54'	No mention of <i>Rumex</i> . <i>Plantago</i> started 1900* (age interpolated), together with <i>Pinus</i> increase after 1960***	Villa et al. (2004)
B	Lago Maule	36°04'	70°29'	Appearance of <i>Rumex</i> 12 cm depth (c. 1900*), increase at 10 cm (c. 1960**). Dating with reservoir effect and age reversal.	Carrevedo et al. (2015)
C	Laguna Sn. Pedro	38°26'	71°19'	Presence of <i>Rumex</i> in top 20 cm (c. 1880s**), decrease toward top. Presence of <i>Pinus</i> 10 cm depth (c. 1970***) increase monotonically.	Fletcher and Moreno (2012)
D	Lago Galletue	38°41'	71°17'	No mention of <i>Rumex</i> . Presence of <i>Pinus</i> and <i>Plantago</i> from 13 cm (c. 1960 ***), <i>Pinus</i> increase to c. 10% abundance at 5 cm.	Urrutia et al. (2007)
E	Mallín Paso del Arco	38°52'	71°04'	Presence of <i>Rumex</i> in top 15 cm. (c. 1800*) always below 5%. <i>Pinus</i> is not documented.	Heusser et al. (1988)
F	Mallín Rio Malleo	39°36'	71°24'	Presence of <i>Rumex</i> in top two samples, 10 cm (c. 1900***). Presence of <i>Pinus</i> only in top sample (c. 1980***), below 1%.	Heusser et al. (1988)
G	Mallín Ser-rucho	41°46'	71°25'	Traces of <i>Rumex</i> and <i>Plantago</i> in the top 10 cm (c. 1800*). Youngest date 110.	Markgraf et al. (2013)
H	Lago Mosquito	42°29'	71°23'	Presence of <i>Rumex</i> and <i>Pinus</i> (not shown) found in small amounts above top 40 cm, since 1740**. First two ages are reversals.	Whitlock et al. (2006)
I	Lago Teo	42°54'	72°42'	Presence of <i>Rumex</i> and <i>Plantago</i> in the first 10 cm, <1% abundance (1600**).	Henríquez et al. (2015)
J	Lago Venus	45°41'	72°01'	Presence of <i>Rumex</i> since 1920**. Abundance rises up to 5% by 1940***. <i>Pinus</i> in first 3 cm, reaching 5% in the top.	Szeicz et al. (1998)
K	Mallín Pollux	45°41'	71°50'	Presence of <i>Pinus</i> and <i>Plantago</i> in two samples on top 20 cm (c. 1940**)	Markgraf et al. (2007)
L	La Tercera	49°11'	72°22'	<i>Rumex</i> in first 10 cm (approx. 1850–1900**). Around 1% abundance.	Sottile et al. (2011)
M	Mallín Cerro Frías	50°24'	72°42'	Presence of <i>Rumex</i> in first 3 samples (approx. 1850–1900**). Around 1% abundance.	Sottile et al. (2011)
N	Mallín Vega Nandu	50°55'	72°45'	Presence of <i>Rumex</i> in top 2 cm, abundance >1% (1800*). Youngest radiocarbon date c. 50 at 31 cm depth.	Villa-Martínez and Moreno (2007)
O	Laguna Azul	52°05'	69°35'	Presence of <i>Rumex</i> in top 25 cm (c. 1900 **), increasing in last 10 cm (c. 1980**). Chronology considered youngest dates from two different cores.	Mayr et al. (2005)
P	Mallín Rio Rubens	52°08'	71°52'	Presence of <i>Rumex</i> in top 25 cm (c. 1600**), increase (~5%) after c. 1950***. Presence of <i>Plantago</i> (<0.5%) in uppermost samples (c. 1980)	Huber and Markgraf (2003)
Q	Lago Potrok Aike	51°58'	70°23'	Presence of <i>Rumex</i> in c. 1850**, growth in c. 1950**. No data for <i>Pinus</i> and <i>Plantago</i> .	Haberzettl et al. (2006)

^aAll ages are expressed as AD: uncertainty of age determination: *>60 years; **<60 years; ***<20 years.

^bLetters correspond to Figure 1a.

(1979), and also the pollen diagram from San Pedro (Fletcher and Moreno, 2012) documents an increase in the pollen type over the past 60 years. Perhaps, in the study area, *Nothofagus obliqua* benefited from the opening of the forest and reduced competition with other trees. *Nothofagus obliqua* has been found growing after disturbance in lowlands in Chile or in the valleys around 40°–41° S, in Argentina, in secondary forest (e.g. Donoso et al., 2006; Kitzberger and Veblen, 1999).

Introduced taxa as human impact indicators in Patagonia

In all here investigated sites, the native taxa showed little reaction to land-use change, except for *Lomatia hirsuta* at Koywija and the abundance of grass pollen indicating forest clearance. *Rumex acetosella* was the earliest introduced pollen taxon appearing at the sites, however never before the time land-use change had commenced in the wider area. Today *Rumex acetosella* is widespread in Patagonia, particularly in non-forested and degraded areas (Pauchard and Alaback, 2004). It has been documented to spread rapidly after fire disturbance (Ghermandi et al., 2004). The pollen of *Rumex acetosella* is present in many modern pollen samples throughout Patagonia, generally with higher abundances in the steppe and grassland (10–20%) compared with forested areas (Iglesias et al., 2017; Paez et al., 1997).

The occurrence of the plants *Rumex acetosella* and *Plantago lanceolata* was documented in 1851 and 1860, respectively, for an

area close to the Pacific coast around 40° S (Fuentes et al., 2014). Closer to the study area, collections of the two species were made by Gunkel in 1942 (38°42' S; 71°44' W; 950 m a.s.l.) (Herbarium CONC, personal communication). While herbarium lists have limitation, they document an early expansion phase of all introduced taxa in Chile after 1910 (Fuentes et al., 2008).

We reviewed published pollen diagrams from southern South America documenting the appearance of introduced taxa and assessed, where possible, the primary data in the Latin American Pollen Database (Table 4). Like in the here presented diagrams, most sites show a continuous or discontinuous tail with the presence of *Rumex acetosella* below 1% and a later rise of the curve. As mentioned in the introduction, the oldest account of *Rumex acetosella* pollen comes from the north Patagonian steppe at 36°45' S (Markgraf et al., 2009) as well as from within the region, 30 km of the study sites (Fontana, unpublished data). Both records date the presence of the weed to the 16th century. In the latter record, Lake Torta, the history of introduced taxa for the last 500 years, is supported by five radiocarbon dates. The only other pollen diagram depicting the early presence of *Rumex acetosella* with dating certainty is Lago Teo (Table 4) located about 1 km north of the town of Chaiten at the Gulf of Corcovado. Here, the first appearance at 10 cm below the core top was dated to about 1600 or earlier; however, the authors consider that the age estimate may be biased due to the slow sedimentation rate. The published date of 1740 for Lake Mosquito (Whitlock et al., 2006) is somewhat uncertain as the two uppermost radiocarbon dates in

the sequence are reversed. Other diagrams depicting *Rumex acetosella* before about 1900 base the chronologies on interpolation where the youngest radiocarbon date is 1000 years or older (Markgraf et al., 2013; Villa-Martínez and Moreno, 2007). This results in larger uncertainties in the order of more than 100 years.

The diagram from Laguna San Pedro (Fletcher and Moreno, 2012) is the best-dated diagram near the study region and has a high sample resolution depicting changes in the past centuries. The diagram depicts a sudden rise to about 4% *Rumex acetosella* pollen coinciding with a deforestation event. This event dates to around 1900 according to the published age model constrained by ^{210}Pb ages with an uncertainty of about 30 years for this event. This sudden rise in *Rumex acetosella* pollen is present in many diagrams from Patagonia associated to major land-use change with inferred ages around the 1950s (e.g. Huber and Markgraf, 2003; Mayr et al., 2005). In the here presented diagrams, this change dates to the 1980s which is rather late and may be connected to the establishment of *Pinus* plantations in the region. Enhanced building activity creating touristic infrastructure add to the increased disturbance regime and also the tourist may have contributed to the dispersal of *Rumex acetosella*. These changes had a stronger impact on the vegetation cover compared with the initial land-use change with the establishment of ranches and pastures. *Pinus* plantations within the forest-steppe ecotone are monocultures without any understory vegetation and replace a diverse vegetation of low-growing shrubs and herbs. In addition to the direct effect of *Pinus* plantations in the landscape, *Pinus* has become an invasive species in the region spreading into *Araucaria araucana* forest as well as in open vegetation types toward the steppe.

Conclusion

The period of initial land-use change with the establishment of small-scale sawmills, ranches, and pastures had apparently little impact on the forest structure and the position of the forest–steppe ecotone. However, recent *Pinus* plantations in the study area are large alterations of an until recently near natural vegetation, which make a marked impression in the pollen diagrams.

Among the native taxa, only Poaceae and *Lomatia hirsuta* may indicate land-use change. The introduced *Rumex acetosella* seems to be a good indicator of human activity after the arrival of Euro-American settlers. Due to the lack of pollen diagrams with adequate chronology, it is difficult to assess whether the long and often discontinuous tail in the pollen type marks the spread of the plant after initial introduction without human assistance or an early phase of land use as in the here presented diagrams. However, the pollen type seems to mark the time when land-use change was initiated without a discernible delay due to prior absence of the plant.

Although there were plans in place to exploit the *Araucaria araucana* forest in the study region, we do not find evidence for a significant reduction in the abundance of the tree over the last 100 years along the climatic gradient. Combining historical documentation with our data suggests that logging reduced mainly *Nothofagus dombeyi* in more humid areas, while *Nothofagus antarctica* was likely removed for firewood and pastures at the dry end of the gradient. Less abundant trees like *Nothofagus obliqua* and *Austrocedrus chilensis* did not change in abundance or perhaps even increased. This study shows that general patterns of deforestation did not occur throughout Patagonia and that the vegetation cover in inaccessible mountain regions in Chile and Argentina remained close to its natural state until recently.

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Supplemental material

Supplemental material for this article is available online.

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