Zentrum
für Biodiversität und Nachhaltige Landnutzung
Sektion
Biodiversität, Ökologie und Naturschutz

-Centre of Biodiversity and Sustainable Land Use-
Section: Biodiversity, Ecology and Nature Conservation

Holocene Vegetation and Disturbance Dynamics in the *Araucaria araucana* Forest

a paleoecological contribution for conservation

Dissertation
For the award of the degree
"Doctor of Philosophy" (Ph.D. Division of Mathematics and Natural Sciences)
of the Georg-August-University of Göttingen

Within the doctoral program Biodiversity and Ecology

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I dedicate this effort to all what I love… those present and those gone; to my emotions intensifiers, Jana, Ema and Paulo; to my ethereal mother and to my father; to the nature I belong…

Mi historia se acerca a la tuya
Yo soy tu, movido por el viento y respirando a veces el aire sulfurado de los volcanes
Yo soy tu, solitario o acompañado por la diversidad
Yo soy tu, resistente, con tu corteza gruesa y con hojas punzantes
Yo soy tu, dando mis semillas, cauteloso y observando
Quiero que permanezcas y que te expandas, tú me darás la libertad de las montañas
Tu se la darás a mis hijos cuando te vean... y te ayudaremos

Ya voy… ya voy a tu lado, y te contare mi historia en silencio

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PREFACE

Araucaria araucana is an endangered species with a high socio-ecological value. Populations decline and fragmentation are among the main problem to the persistence of the species. The situation has inspired many people from science, art and political sphere, as well as the indigenous and other social organizations to protect the species. Several initiatives have started to conserve and restore the degraded populations, while the concern is still increasing in the face of the current global and regional change. There are many possible causes, however it is not clear if its current conservation status corresponds to the human impacts in the last centuries, or due to natural variability in the climate, or it is a result of past disturbances. Little is known about the history of *A. araucana* over millennia where we could distinguish those patterns, process and causes, which utterly could help to the conservation. Paleoecological multi-proxy studies can help to elucidate the problem, however few studies have been conducted in this regard or are of relatively short time frame.

Aims and outline of the thesis

This thesis aims to reconstruct the Holocene vegetation and disturbance history of the *A. araucana* at the forest-steppe ecotone in northern Patagonia in order to contribute to the understanding of the long-term dynamics of *A. araucana* forests. I especially investigate the vegetation responses to the disturbances such as land-use, fire and volcanic eruptions in order to evaluate the role of disturbance regime for *A. araucana* populations in the past and to make it applicable for the conservation of *A. araucana*.

The results of this thesis are structured in three chapters to assess long-term vegetation patterns and its response to disturbances:

- *Chapter 3 – The impact of recent land-use change in the Araucaria araucana forest in northern Patagonia.*

  The human activities since the European arrival have transformed the land-use threatening the persistence of several species, especially of *A. araucana* at the forest-steppe ecotone.

To evaluate the anthropogenic impact on the vegetation, I carried out a palynological study where I reconstructed the recent vegetation history with six lakes across an environmental gradient dominated by *A. araucana.* The main goal is to analyze compositional changes and the expansion of introduced invasive plant species as indicator of human disturbances.

- *Chapter 4 – Fire and vegetation dynamics of the endangered Araucaria araucana at the forest-steppe ecotone in northern Patagonia.*
  In the last centuries fire regime change in the *Araucaria* forest may have threated its conservation status. To understand recent and long-term vegetation patterns regards fire regime, I investigated the vegetation and fire history based on the 9000-year-old sediment from the Lake Relem. The reconstructions help to evaluate the role of fire on the vegetation dynamic and the long-term trend of the population of *Araucaria*.

- *Chapter 5 – Vegetation responses to volcanic disturbances at the Araucaria forest-steppe ecotone in southern South-America.*
  Volcanic eruptions play a principal role in vegetation dynamics and the natural history of the *A. araucana,* although the impacts on the vegetation have been seldom assessed. In the region, volcanoes are very active and may affect the *Araucaria* population and distribution. To provide insights into the vegetation responses to past volcanic disturbances, we conducted a palynological study in Lake Relem to reconstruct the vegetation history and compared it to the volcanic regime, which was reconstructed based on the tephra layers.

In the last Chapter 6, I synthetize these three main disturbances and discuss differences and similarities of vegetation response and diversity changes in the study area. To get insights into the historical range of variability of *A. araucana,* past distribution and its current conservation status, I compare the results from my study with other records.

Summary

Climatic changes have changed the vegetation distribution in northern Patagonia over millennial time-scale; while, fire and volcanoes disturbance might play an important role in the vegetation dynamics, especially in the *Araucaria araucana* forest. The Holocene history of the *Araucaria araucana* is poorly studied despite of its evolutionary, ecological, and social importance. *Araucaria araucana* is well adapted to resist moderate disturbances, and it is though that human activity has threatened the persistence of the *Araucaria araucana*. Little is known about the history of *Araucaria araucana* forest, its natural variability and past disturbances regime. An insight into the long-term patterns and process could provide information for conservation management. Therefore, this thesis aims to reconstruct the Holocene vegetation and disturbance history throughout the analysis of pollen, charcoal, and tephra deposited in lake sediments. In addition, I assessed the impacts of recent land-use change, fire and volcanic events in the *Araucaria araucana* forest in three separated chapters.

The results show that land-use change since early colonization of the northern Patagonia have had a strong impact on the vegetation only for the last 50 years, in the form of *Pinus* plantation. In the long term, interpreted from a 9000-years-old sediment record from Lake Relem, an overall change in pollen dominance from Poaceae toward *Nothofagus dombey*i-type about 4.5 ka was observed, suggesting that the landscape shift from a grassland to a forest and scrubland. The forest-steppe ecotone was probably fragmented, but the degree was likely less than today. This general trend has been disrupted by 20 fire and 39 volcanic events. Volcanic eruptions buried the vegetation around the studied lake by tephrafall. Tephrafall were relatively frequent, but with low impacts on the vegetation. Only one large eruption, the Sollipulli-Alpehue, triggered a dramatic change about 3 ka. Vegetation recovered short after with dominant *Ephedra*, yet return to pre-eruption condition after c.500 years. Fire regime, was variable between 6-3 ka BP when fire frequency and magnitude increased. Pollen abundance related to macro-charcoal denotes small severity of disturbances though. Fire during Euro-American colonization was comparatively small, and with the data I cannot confirm the change in fire regime. Although the early colonization does not change vegetation until more recent time, the magnitude and rate of changes produced by humans can be compared with the largest eruption in the region. The vegetation shows some sensitivity to past fire and volcanic disturbances; however, could recover fast to small-scale disturbances.

In synthesizing records from the area, the comparison suggests that *Araucaria araucana* might reach the Andes before 10 ka, and that during the Holocene history until present there is no unique trend of decreasing populations or distribution changes of *Araucaria araucana*. During the Holocene, *Araucaria araucana* pollen abundance in Lake Relem suggests a low variability, disregard of disturbance. Future trend are unpredictable and more studies are required, but surely the spread of invasive *Pinus* toward natural areas is already affecting regeneration process and increasing the fuel biomass. Despite of some limitations, paleoecological studies are powerful tools to understand present vegetation patterns, thus could contribute to develop conservation strategies to *Araucaria araucana* forest.

CHAPTER 1-

1. Introduction

1.1 Distribution, ecology and conservation status of *Araucaria araucana*

The natural history and ecology of *Araucaria araucana* have attracted researchers from diverse areas for a long time. This conifer is a single monotypic species of *Araucaria* in southern South America (Veblen et al., 1995). Due to low species diversity and disjunct distribution in the southern hemisphere, *Araucaria* species are considered as a relict from the Cenozoic and, therefore, as a key taxa to biogeography because of its ancient origin and its dominant role in some forests (Kershaw & Wagstaff, 2001). This relictual status leads to the hypothesis that the *Araucaria* species could evolve from tropical rainforest probably because of a special adaptation to frequent, destructive volcanic disturbances which are quite common in the Andes (Kershaw & Wagstaff, 2001). The authors added that shade-tolerance and longevity maybe helpful under this disturbance to persist. After continental drift divided Gondwana, the members of the Araucariaceae family in South America were isolated by the formation of the Arid Diagonal and the uprising of the Andes (Villagrán & Hinojosa, 2005). During the last glacial and interglacial periods, as the ice-sheet expanded on high Andean mountains, *A. araucana* should have migrated to low-lands west and east of the Andes below 600 m elevation (Villagrán, 2001). Deglaciation within the current *A. araucana* distribution occurred around 17 ka BP (Hulton et al., 2002). Pollen evidence indicated that *A. araucana* was present in low-land (<200 m a.s.l.) in Chile during the last-glacial-maximum until about 16 ka BP (Abarzúa, 2009), but due to the lack of studied sites covering this time frame, no pollen records indicates its presence in mountains refugia or eastward of the Andes, as phylogenetic analysis suggested (Bekessy et al., 2002). Therefore, it remains unknown since when, how fast, and from where *A. araucana* reached its current distribution at high elevation.

The current range of *A. araucana* distribution along the Andes is relatively reduced (37°30’S-39°50’S), covering ~390 km^2, mainly over 1000 m a.s.l. (Gonzalez et al., 2006) giving a strong fragmented and isolated character (Figure 1.1.b). Fragmentation is even more notorious in driest section to the north and east of its distribution, where the easternmost populations at ecotonal areas are severely influenced by grazing, *Pinus* plantation and more recently by touristic pressure (Veblen et al., 2008). However, the reasons of the fragmentation are not well defined and could be due to long-term climatic trends, natural disturbance such as volcanism or fire, or the land-use change since European colonization

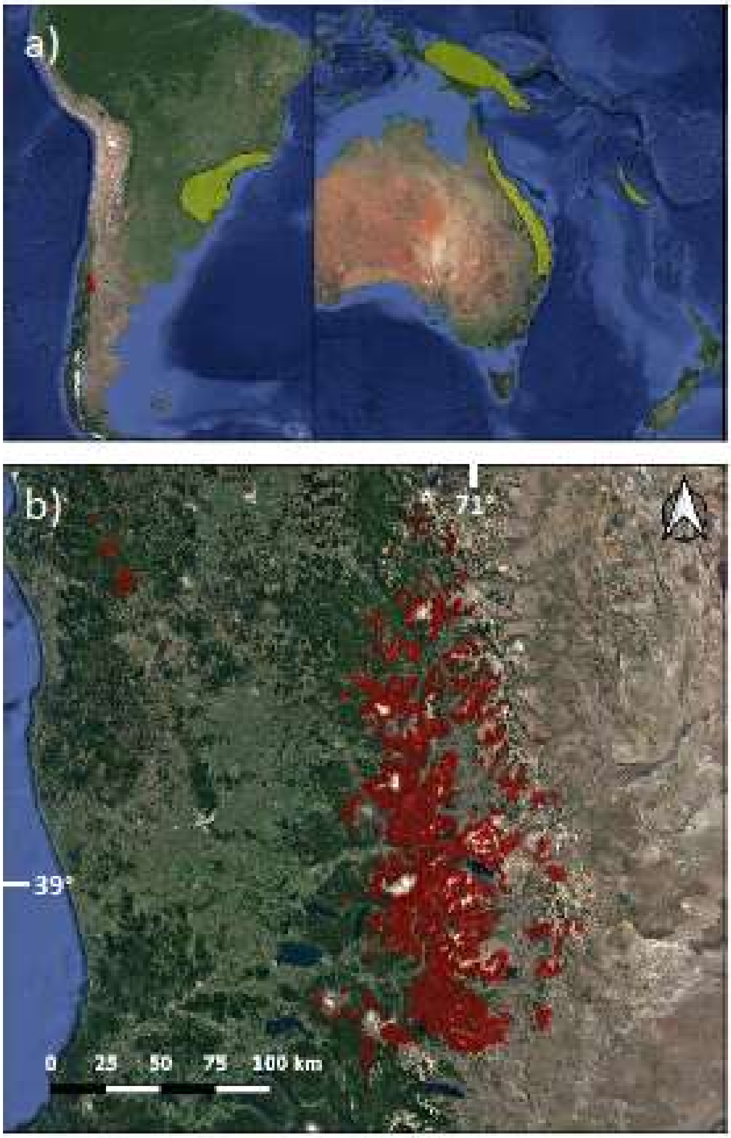

Figure 1.1 (a) Distribution of *Araucaria* in southern hemisphere (green-yellowish polygons). Note that areas indicating the *Araucaria* distribution is not exact and only used as references and no coordinates are provided. (b) Current distribution of *Araucaria araucana* in southern South America (red polygons, also in panel a).

A. araucana is classified as an endangered species principally because of a strong reduction in almost 50 percent of its area of occupancy caused by intense selective logging and land-use change (Gonzalez et al., 2006; Premoli et al., 2013). At least 30,000 ha were logged between 1900-1950 (Otero, 2006) and more than ¼ of the *A. araucana* cover was burned during the Euro-American colonization (Rothkugel, 1916). Throughout the analysis of fire-scar in tree-ring records, it was established that the land-use change might shift the fire-disturbance regime during the last hundred years (e.g., Mundo et al., 2014). There is also a large concern about low rates of regeneration and its replacement by angiosperm species (e.g., Schmithüsen, 1964), principally by Patagonian steppe vegetation due to aridification in the last 2 ka (e.g., Kalela, 1941; Tortorelli, 1942). In some moist areas *A. araucana* forest present abundant regeneration protected by dense understory (Gonzalez et al., 2002), while under xeric conditions gaps of regeneration for the last ~100 years has been observed (Roig et al., 2014). However, the regeneration mode of *A. araucana* is broadly considered disturbance-driven (e.g., Burns, 1991) and several studies demonstrated that discontinuities in age structure are normal and can be explained by disturbances event (Veblen et al., 1995).

Despite most of the *A. araucana* coverage is under protection in Chile and Argentina, and different conservation actions have been carried out, stage of *A. araucana* populations causes increased concerns in the last decades due to severe fire burned ~20,000 ha of *A. araucana* forest during the austral summer of 2001-2002 (González & Veblen, 2007) and ~600,000 ha between 2010-2015 related to a strong drought (Gonzalez et al., 2018). Furthermore, although still not confirmed and investigation are being conducted, the same mega-drought might cause widespread disease in *A. araucana* populations.

The ecological knowledge for *A. araucana* still presents several gaps, and new research is required with a special priority given to the analysis and long-term monitoring of *A. araucana* population size, distribution, and trends (Premoli et al., 2013). For this, paleoecological records provides powerful insights to understand long-term population and vegetation changes through the use of subfossil pollen, and simultaneously possible causes of the variability such as disturbance (e.g., land-use change, fire, volcanism) through the use of macro-charcoal particles and tephra layer content in sediment soils in lakes.

1.2 Vegetation dynamics and disturbance paleoecology: implications for the nature management.

The management of nature, such as conservation, restoration, silviculture, relies fundamentally on ecological knowledge of patterns and process, which required the study of disturbances mechanism to understand vegetation dynamic. It is known that climatic changes and disturbance agents drive the vegetation dynamic in a millennia scale. But, while climate might exert a long and gradual pressing disturbance, episodic disturbance event act as pulses that might trigger vegetation change (Davies et al., 2018). Among others, the major ecological disturbances affecting vegetation in temperate climatic zones are glacial activity, human land-use change, fire, and volcanism (Veblen et al., 2005). In my work, I will refer to disturbances as follows: Disturbance is a relatively discrete event in time disrupting the ecosystem, community or population, while the disturbance regime can be characterized by its frequency, return interval, and magnitude (White & Pickett, 1985).

The disturbance agents can interact in different ways in a given climatic context, triggering unpredicted patterns and pathways in the successional process as the climatic conditions shift from one state to another. Disturbance magnitude varies in intensity and severity and can be heterogeneously distributed in the landscape (Turner et al., 1998), as a consequence of the interaction between topographic, vegetation and meteorological factors (White et al., 1996). The disturbances will leave different types and amount of biological and non-biological legacies in the impacted area (Franklin et al., 1990), creating complex mosaics of vegetation (Veblen, 1992), and possibly increasing the diversity in the landscape at intermediate disturbance level (Connell, 1978). Indeed, some ecosystems require disturbances to keep diversity and other ecological functions or to keep continuous regeneration as the case of *A. araucana* (Armesto et al., 2009). Likewise, the type, amount, and arrangement of biological legacies after buried by tephra might result in the rate of recovery (e.g., Zobel & Antos, 2018). Therefore, identifying the biological legacies are a keystone to nature management activities after a disturbance (Franklin, 1990). To understand disturbance regime is of especial interest in silviculture management, where the basic harvesting techniques in a close-to-nature silviculture attempt to emulate natural disturbances in terms of size, frequency and biological legacies (e.g., Franklin et al., 2002; O’Hara, 2016).

The stability of the vegetation is of particular interest for conservation and restoration activities, since vegetation responses after a disturbance may not recover original composition and structure while shifting to a different stable state (Holling, 1973). For example, based on the last 300 years of fire regime history in northern Patagonia it has been suggested an increase in the fire frequency could facilitate the persistence of fire-prone vegetation, leading to an alternative-stable-state of the original forest (Kitzberger et al., 2016; Paritsis et al., 2015). This hypothesis should consider a longer time perspective to avoid misinterpretation (e.g., Petraitis & Latham, 1999) by means of paleoecological tools such as pollen and macro-charcoal (e.g., Jackson & Hobbs, 2009; Willis, et al., 2010). If the vegetation is changing because of fire frequency change, then the same community, or some indicator taxa in paleoecological records, should be seen increasing in the past after a period of frequent fire. For example, Gil-Romera et al. (2019) designed a paleoecological study case in Ericaceous belt in tropical African mountains to assess the resilience and positive feed-back between Ericaceous re-sprouting and burning regime. Their results show a positive interaction between *Erica* pollen abundance with fire occurrence throughout the Late-glacial and Holocene and interpret the results as an example of long-term fire resilience.

Large-disturbance (area and intensity) are infrequent, and generally, vegetation responses show general common patterns of regeneration leads by heterogeneous patterns of surviving organism (Turner et al., 1998). However, each kind of disturbance presents its characteristic depending on the kind of impact and regime (Foster et al., 1998); therefore, each case should be analyzed independently. It is essential to know the frequency and size variation of the disturbance and recovery process to better design nature management (Pickett & Thompson, 1978). Thus, paleoecological records provide insights about the historical range of variability of disturbances as well as its ecological effects (Hayward et al., 2012). In Patagonia, for example, volcanic and fire disturbances are ubiquitous during the Holocene history (Armesto et al., 2009). During the last two decades in Patagonia, the use of sedimentary macro-charcoal and the development of statistical techniques allows the reconstruction of fire regime (Nanavati et al., 2019; Whitlock et al., 2007), while the Postglacial volcanic history is relatively known in this region (Fontijn et al., 2014). This information about the historical events would provide of rough reference in Patagonia for nature management but, as I will discuss later, further studies are required to be integrated into plans. Likewise, to know the historical range of variability of *A. araucana* at the forest-steppe ecotone in northern Patagonia would also be useful in determining the conservation status of the species and future trends.

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Chapter 2 -

2. Materials and Method

2. 1 Study area: climate and vegetation

A. araucana occurs in the Andes between 37°30’-39°40’ S on the western flank, and 37°45’-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 *A. araucana*, but was also selected due to the relatively well documented human history. Specifically, for the third chapter, to analyze the recent human impacts I selected 6 lakes in the study area crossing both slopes of the Andes Cordillera in a west-east transect around 39° S (Chapter 3). Later, to extend the chronology and to assess long-term vegetation and disturbance dynamics I used one of these lakes, Lake Relem, to analyze the pollen, macrocharcoal and tephrafall (Chapter 4 and 5).

The climate around 39° S is temperate with average of all months temperatures above freezing and a precipitation minimum during the austral summer, giving it a Mediterranean character, while under oceanic influence (Luebert and Pliscoff, 2006). Precipitation in the Andes arrive with westerly winds from the Pacific Ocean (Garreaud, 2009; Garreaud et al., 2013). The Pacific air masses discharge most of the precipitation on the western slopes of the Andes Cordillera which reaches elevations over 2000 m a.s.l., creating a sharp rain-shadow effect (Mundo et al., 2013). Here total annual precipitation ranges between 1200 mm at 800 m a.s.l. to 2500 mm or more at 1600 m a.s.l., while on the eastern slopes rainfall decreases exponentially to 200 mm towards the steppe (Bianchi et al., 2016; Paruelo et al., 1998). Annual mean temperature range on the western slopes between 12°C to 8°C at high elevations, and increase to about 16°C on the eastern side (Bianchi et al., 2016). Geographical patterns of precipitation and temperature are shown in Figure 2.1. 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).

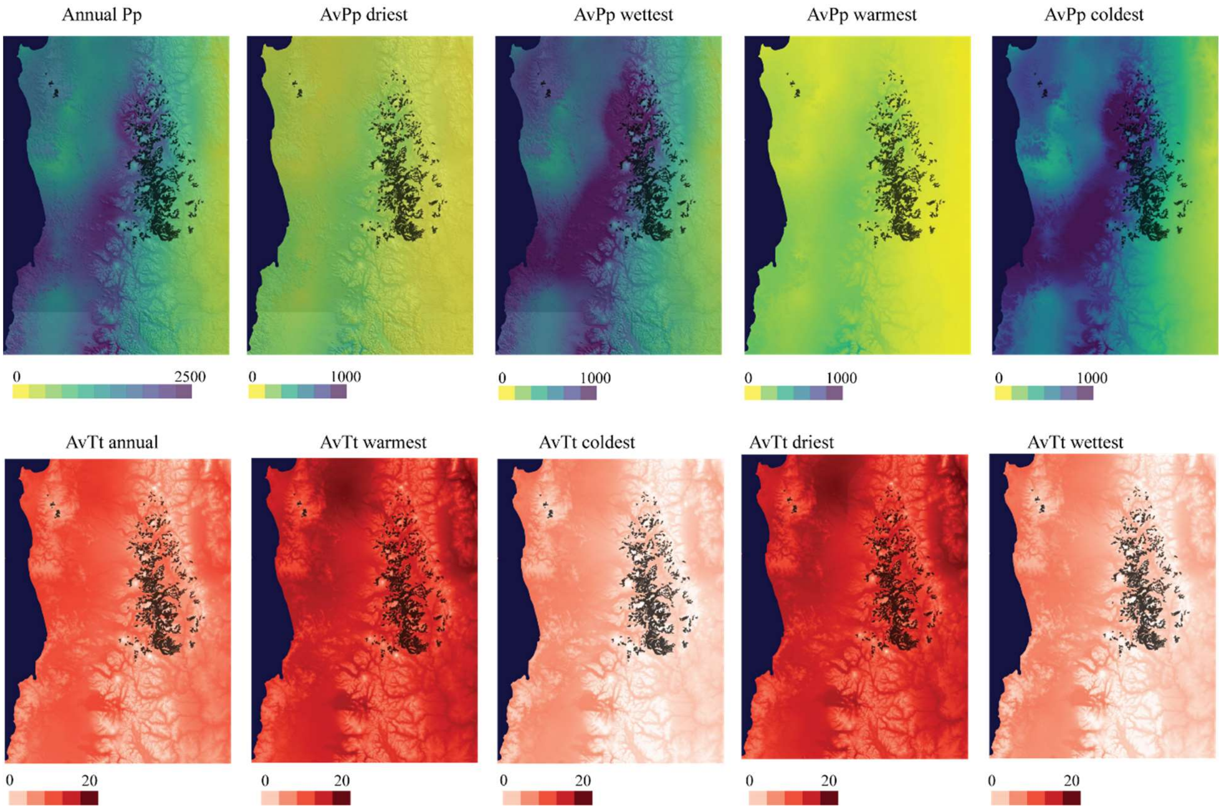

Figure 2.1 Climatic parameters describing precipitation (mm; upper row) and temperature (°C; bottom row) annual and extreme monthly variability in the study area (source WorldClimV1; Hijmans et al., 2005). Black polygons correspond to *Araucaria araucana* distribution. Av: average; Pp: precipitation; Tt: temperature.

The interaction between climate, topography and the disturbance regime, creates a complex landscape in the Patagonian Andes, therefore the vegetation in the *Araucaria* forest shows a variety of plant association (Kitzberger 2009). Under moist climate conditions *Araucaria* forms dense, multilayer forest with dominance of *Nothofagus dombeyi*, and *N. pumilio* associated with the species *Drimys andina, Berberis microphylla, B. montana, Maytenus magellanica, Gaultheria mucronata, Escallonia virgata, Desfontainia spinosa* in the understory. Herbs such as *Alstroemeria aurea, Adenocaulon chilense, Valeriana lapathifolia, Shoenus andinus, Senecio trifurcatus, Ozmorhiza chilensis* and *Viola reichei* are relatively common. Under disturbed condition *Chusquea culeou* can form dense understory. Under mesic-climate condition, *Araucaria* araucana forms mixed forest with *Austrocedrus chilensis* and/or *Nothofagus obliqua,* or open forest with dominance of deciduous *Nothofagus antarctica.* Common understory shrubs such as *Schinus patagonicus, Azara alpina, Empetrum rubrum, Escallonia virgate, Maytenus disticha, Gaultheria pumila* and *G. mucronata, Baccharis patagonica, Berberis darwinii* and *B. microphylla*; and herbs such as, *Ranunculus peduncularis, Poa pratensis, Azorella caespitose,* *Galium antarcticum, Anemone multifidi, Caltha appendiculata, Calceolaria tenella, Osmorhiza chilensis, Festuca pallescence, Fragaria chiloense, Acaena pinnatifida.* Under xeric condition, scatter individuals of Araucaria occur without or scarce *N. antarctica*, *Austrocedrus chilensis,* and it is broadly dominated by bunch grasses and shrubs as *Discaria and Colletia*. At the extreme of the gradient eastward of the lake Alumine *Araucaria araucana* is normally absent, steppe vegetation is characterized by herbs such as *Festuca pallescens, Cerastium arvense, Azorella caespitosa, Nassauvia abreviata, Poa spp., Elymus patagonicus, Bromus spp., Quinchamalium chilense, Sencecio patagonius, Sisyrinchium junceum, Acaena pinnatifida* and *A. macrocephalla, Adesmia longipes* and *A. retusa, Galium antarcticum* and *G. fuegianum*; and shrubs: *Discaria serratifolia D. chacaye, Gaultheria myrtilloides* and *G. pumila, Baccharis magellanica, Berberis empetrifolia* and *B. microphylla, Mulinum spinosum, Colliguaja integerrima, Ephedra chilensis.*

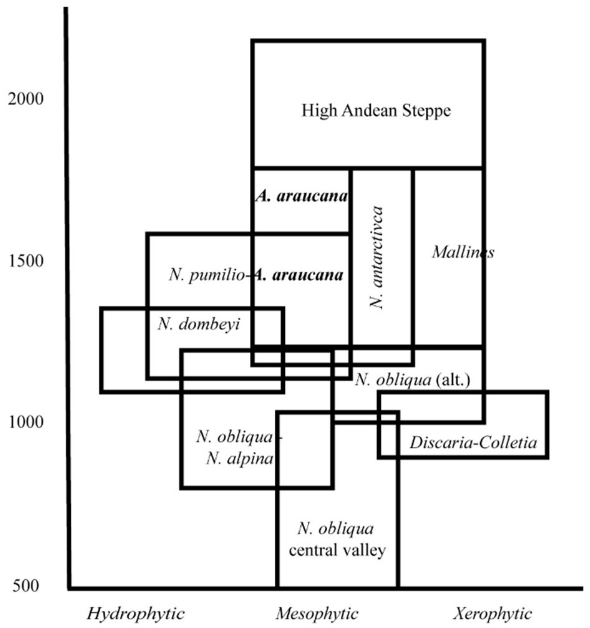

Figure 1.2 Schematic representation of vegetation along both altitudinal and moist gradient (West-East) (adapted from Michell 1980).

2.2 Environmental human history in northern Patagonia

At the arrival of the European, the indigenous in Patagonia were hunters-gatherers (Salemme and Miotti, 2008; Scheinsohn, 2003), based in a transhumance system and reaching the mountains only during summer (Bengoa, 1987, 1992). Indigenous used fire to hunt (Veblen and Lorenz, 1988; Veblen and Markgraf, 1988), and might manage forest regeneration (Aagesen, 2004). However, their activity until this time might have a poor environmental fingerprint traceable in sedimentary records. Since approximately 1520 CE the European started exploring Patagonia and placed cities close to Atlantic and Pacific Coast, but the Andes were not colonized until the end of 19th century (e.g., Bengoa 1992, Aagesen 2004). Nevertheless, it is supposed they adopted the European livestock since the first contact (Aagesen, 1998).

Cattle and sheep were introduced around 1550-1580 to northern Argentina and Chile from Peru, and distributed in northern Argentina (e.g. Carrazzoni 1997, Martinez et al. 2000). First sheep in Patagonia were introduced from Chile to Argentina in 1703 in the surrounding area of Lake Nahuel Huapi (~40°S, Argentina) (Carrazzonni, 1997). Many explorations between 1550-1880 failed in crossing the river Neuquen from the north, or reach the Andes from the Atlantic coast in Patagonia (Bandieri, 2005), hence most likely wild-cattle also could not. Albeit cattle in Patagonia were never widespread, the massive production of sheep started only after the second-half of the19th century from the Atlantic coast in province of Santa Cruz (south of ~ 50°S), (e.g., Frontoms, 2009).

Between 1850-1880 Chile and Argentina started the territorial expansion to north Patagonia displacing native people by Euro-American settlers (Bengoa 1992, Bandieri 1991). In both side of the Andes, close to the *Araucaria* forest, two towns were founded: Lonquimay in Chile (1897); and Aluminé in Argentina (1915). The *Araucaria* forest by this time was considered undisturbed (Matthei, 1939), but the land was burned and logged for colonizers (e.g., Rothkugel 1916). Bandieri and Blanco (1996) proposed that cattle were introduced massively in Patagonia as a cause and consequence of economic expansion, leading to speculate that impact before 1900 were not significant.

The first half of 20th century the land was reconfigured, population increased, and resource exploitated. In Chile there are three economical periods with environmental consequence: 1) Livestock farming (1881-1920), 2) mineral extraction (1920-1938) and 3) timber exploitation (1916-1976) mainly focused in *A. araucana* species (Paillacheo-Cancino, 2009). Around 1950 was the boom of the forestry industry, decaying in 1976 after *A. araucana* was protected by law. Immediately after, the industry logged other native species (Paillacheo-Cancino 2009). In the region protected areas were created in high, inaccessible mountains since 1907. Forest plantations with *Pinus radiata* started massively in 1970 but kept unimportant here due to unfavorable climatic conditions. *Pinus contorta* is colonizing Araucaria forest and non-vegetated areas during last decades (Franzese et al., 2017). Tourism and conservationism became important after 1990s, when the first Indigenous protected area was created (Molina and Paves, 2012).

In the Argentinean northwest Patagonia, the colonization and exploitation of the territory started during 1900-1950. Mining were developed north from the study area, while intense livestock farming and low-scale forestry were the main economic activities in the province (Bandieri, 1991; Bandieri and Blanco, 1996). Rothkugel (1916) estimate that approximately 40% of Patagonian forest were burned because the farming colonization between 1850-1900, while mountainous areas were not disturbed importantly by fire (Figure 3.1c). Early establishment of Lanín National Park in 1937 stopped felling the *Araucaria* forest and protecting most of the Argentinean populations, nevertheless in the north, several populations are still unprotected and grazing is an intense and non-regulated activity disturbing natural regeneration (Roig et al., 2014). Livestock farming was the principal resource during 1900-1950, which pastured freely in yet open forest and grassland. Since c.1960 the economical develop is based in tourism and *Pinus* plantations (Wallingre, 2011, Schlichter and Laclau 1998). *Pinus* plantations started in the area c.1980 (Schlichter and Laclau, 1998), covering today more than 100 k ha in Patagonia, (CIEFAP-UCAR, 2017). Nowadays *Pinus* are colonizing non-vegetated areas, increasing the risk of fire and preventing the potential regeneration of native species (Taylor et al., 2017).

2.3 Chronology

To build a chronology of the short cores, I matched the age of the closest plantation with the appearance of *Pinus* pollen in the sediments to obtain a time marker (Chapter 3.3.3). The initiation of *Pinus* plantations is well documented in the region and these species start flowering at the age of 10 years in Patagonia (Bocos and Laclau, 2017, personal communication). The age of the closest plantation (Chapter 3, Table 3.2,), plus 10 years because of the age of flowering 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. Further details are given in the third Chapter.

To obtain a chronology for the long core in Lake Relem used in Chapter 4 and 5, the age of 7 samples were obtained by accelerator mass spectrometry (AMS) on bulk sediment. The samples were submitted to the CHRONO Centre, Queen's University Belfast, UK (UBA) (Chapter 4, Table 4.1). Later, Radiocarbon dates were calibrated with SHCal13.14C (Hogg et al., 2013) and the postbomb_SH1-2.14C for post-bomb dates (Hua et al., 2013). I also used the volcanic eruption of the Sollipulli-Alpehue dated in 2990±0.09 BP (Naranjo et al., 1993). Tephra layers were excluded from the total original depth to build the age-depth model, as they deposited in a short time. The age-depth model was carried out with smooth spline (0.1 smooth), with a 95% of confidence interval (1000 iterations). Calendar age point for depths are based on weighted average of all-depth curves. Calibration and age-depth model were conducted with Clam 2.2 (Blaauw et al., 2010).

2.4 Sediment and Pollen analysis

The cores were subsamples to estimate the dry bulk density and organic content of the sediment. The 0.2 cm^3 subsamples were dried at 105° C for 24 hrs and then burned at 550° C for 4 hrs (Heiri et al., 2001). Pollen samples of 0.5 cm^3 were taken along the cores, particularly in the long-core the tephra layers were avoided. Pollen analysis were done following standard techniques, but without sieving (Bennett & Willis, 2001). The pollen concentration and the Pollen-Accumulation-Rate (PAR) were calculated for all cores. Pollen were tallied using light microscope at 400-1000x. I counted a minimum of 400 pollen grains, due to low pollen concentration. The identification of pollen and spores was carried out with atlases of Heusser (1971), Markgraf and D'Antoni (1978) and pollen reference stored in the Department of Palynology and Climate Dynamics, Göttingen University. Pollen taxonomy follows modern plant distribution within the study area then linking the pollen types to this species and genera (Fontana & Bennett, 2012).

2.5 Fire regime: Macro-charcoal analysis

To reconstruct the fire history in Chapter 3, I followed procedures proposed by Whitlock and Larsen (2001) to process macro-charcoal particles in sedimentary records. Subsamples of one cubic centimeter were extracted every centimeter and sieved in 125 µm mesh. Charcoal accumulation rate (CHAR) were interpolated to the median sampling interval of 20 years and smoothed with Robust Lowess method for a 500-yr time window. Row data were not transformed.

To estimate high-frequency CHAR I used the ratio between Charcoal interpolated and the charcoal background. Peaks events (cPeak) were detected with a local threshold, modelled with a mean Gaussian cut-off at 90% confidence. Pre-treatment and analysis of Charcoal data were conducted with CharAnalysis v.1.1 (P. Higuera, 2009).

2.6 Volcanic regime: Tephra analysis

In the Chapter 5, I aim to reconstruct the volcanic disturbance regime, where we considered each tephra layers >0.5cm as a single-independent event since tephrafall is limited to a short time. I used the tephra thickness as a measure of the magnitude of the impact. Furthermore, each tephra was coded as quantitative explanatory variable and modelled as a simple exponential decay process following the proposal by Lotter and Birks (1993) with a small modification described in Chapter 5.3.2. The frequency of volcanic events was calculated as the sum of events over 1000 years.

2.7 Data handling

Pollen of the terrestrial taxa was summed within respective levels to obtain the relative abundance. Aquatic plants were summed apart from the total of the terrestrial taxa and expressed. For the long record of Lake Relem, zonification was defined by means of depth-constrained cluster analysis with all terrestrial taxa. Statistical significant zones were defined by broken stick model (Bennett, 1996). Compositional trend of the terrestrial taxa was explored through multivariate analysis, in the second chapter a Correspondence Analysis (CA) and for the third and fourth chapters through principal component analysis (PCA). To assess the compositional turn-over in all the records, I used a Detrended Correspondence Analysis (DCA) (Ter Braak & Smilauer, 2012). For both PCA and CA the taxa abundance was square-root transformed. Furthermore, to assess the vegetation responses to fire regime and volcanic regime, the compositional data were constrained against fire and volcanic parameters (see respective chapters for further details). All analyses were conducted with RStudio v.3.3.1 (RStudio Team, 2016), vegan-package 2.4-2 (Oksanen et al., 2017), Rioja-package (Juggins, 2015).

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CHAPTER 3 -

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

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The Holocene (2020): on-line first published

https://doi.org/10.1177/0959683620913918

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 change, 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 towards 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

Human impact, Vegetation disturbance, *Rumex acetosella*, Biological invasion, Forest-steppe ecotone, *Araucaria araucana,* North Patagonia, Land-use change.

3.1 Introduction

Over the last 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 homogenous 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 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 northwest 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 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 500-80 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 century. 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 last decades, tourism is becoming the main economy, leading to a spread of summer lodges and holidays 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 is 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 i) how the vegetation has changed with the recent land use, ii) which indicator taxa are related to the recent history of land-use changes in *Araucaria araucana* forest, and iii) the impact of this land use on the *Araucaria araucana* forest.

3.2 Study area

Araucaria araucana occurs in the Andes between 37°30’-39°40’ S on the western flank and 37°45’-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 3.1). The study area encompasses both slopes of the Andes Cordillera in a west-east transect around 39° S (Figure 3.1a, 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 Pliscoff, 2006).

Table 3.1 Brief description of human history with environmental significance. After Armesto et al. (2010), Camus Gayán (2006), Otero (2006).

Period	Date range AD	
Exploitation	1950 to present	Over grazing in the steppe; forestry with exotic species, mainly *Pinus*; spread of *Pinus* into open areas and native forests; decrease logging of the native forest; increase of tourism, creation of touristic infrastructure but unregulated access to natural vegetated areas; many areas remain unprotected, while *Araucaria araucana* is protected
Colonization	1850-1930/50	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, e.g. Guanaco (*Lama guanicoe*).

Precipitation in the Andes arrives with westerly winds from the 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. to 2500 mm or more at 1600 m a.s.l., while on the eastern slopes rainfall decreases exponentially to 200 mm towards the steppe (Bianchi et al., 2016; Paruelo et al., 1998). Annual mean temperature ranges on the western slopes between 12°C to 8°C at high elevations, and increase 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).

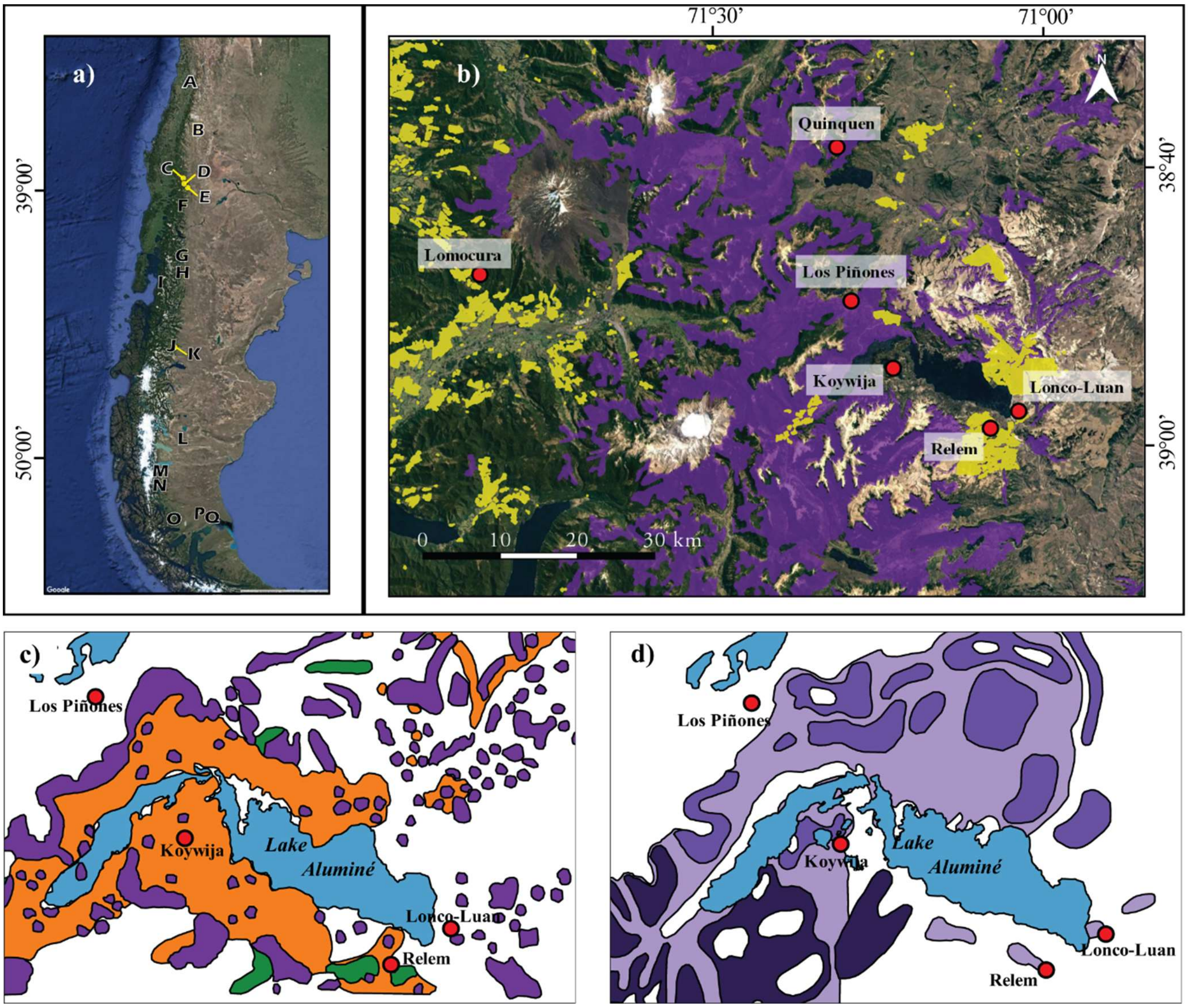

Figure 3.1 Study area. (a) Location of the study area within Patagonia and location of cited studies (Table 4) with the presence of pollen from introduced taxa. Letters follow the order in the table b) Location of study sites (red circles), modern distribution of dense Araucaria araucana (purple) and 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) The 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 Tortorellis’ map the units are generalized and therefore scale is not provided.

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 3.1b). 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 histrix* 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 low-land 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 towards the west of its distribution.

In the following we describe the vegetation around the lakes from west to east (Table 3.2; Figure 3.1b): i) 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.

Table 3.2 General characterization of the studied lakes and cores. The ages are presented as AD

Lakes names	Lakes location		Lakes 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 *Nothofagus dombeyi* forest, with *Pinus* and Eucalyptus plantation
Quinquen	38° 38' S 71° 18' W	1690	0.44	0.5	31	2016	1985	24	*Araucaria araucana* with *N. antarctica, N. pumilio and N. dombeyi*
Los Piñones	38° 49' S 71° 17' W	1280	1.36	3.5	31	2016	1985	3.4	*A. araucana* with *N. antarctica, N. obliqua and N. dombeyi*
Koywija	38° 54' S 71° 13' W	1189	5.12	4	24	2010	1985	6.5	*A. araucana, N. antarctica* mixed forest; Scatter individual of *Austrocedrus chilensis*
Relem	38° 58' S 71° 04' W	1265	0.84	2.5	65	2016	1985	0.2	*Pinus* plantation; small patches of *A. araucana* and *N. antarctica*; 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. *Pinus* plantations and isolated individuals of *A. araucana*.

ii) 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 laphathifolia, Alstroemeria aurea.* Above the tree-line alpine herbs such as *Senecio* spp., *Viola reichei*, *Quinchamalium chilensis*, *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.

iii) Lake Los Piñones is located in the mesic zone. *Araucaria araucana* is mixed with *Nothofagus dombeyi*, and some elevated areas 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 chiloensis, Galium hypocarpium, Alstroemeria aurea* grow near the lake.

iv) 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 antartica* 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, Acaena antartica*. While livestock grazing was important in the past, the area is increasingly developed for tourism.

v) Lake Relem is situated in a *Pinus* plantation established in 1985. The native vegetation close to the lake is characterised 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.

vi) The vegetation around Lake Lonco Luan is sparse, mainly composed of bunch grasses, *Azorella,* and *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.

3.3 Methods

3.3.1 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 3.1b). 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 3.2). 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 was counted using light microscope at ×400 and ×1000 time 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 to 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 (average 25.2 µm) (Beug, 2004); while pollen grains of the native *Rumex magellanicus* are of medium size and spheroidal to sub-spheroidal: 42-46 × 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*. Whilst *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).

3.2.2 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).

Table 3.3 Radiocarbon dates only for Lake Relem. Material analyzed: bulk sediment at the CHRONO Centre, Queen's University of Belfast, UK (UBA). Calibrated dates presented as 2σ.

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	[93]
				1958.8-1958.7	[2]
UBA-29238	277-278		100.37±0.32	1957.4-1955.1	[95]
UBA-29239	325-325.5	330±24		1503-1592	[70]
				1615-1651	[30]

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 *P. radiata*, while *P. ponderosa* and *P. 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 rises. 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.

3.2.3 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 (Ter Braak and Smilauer, 2012; Legendre and Legendre, 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 were 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 analysis 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).

3.3 Results and interpretation

3.3.1 Chronology and age estimation

The two radiocarbon dates from the most recent sediments of Lake Relem provide high precision ages (Table 3.3). One of the dates 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 3.2).

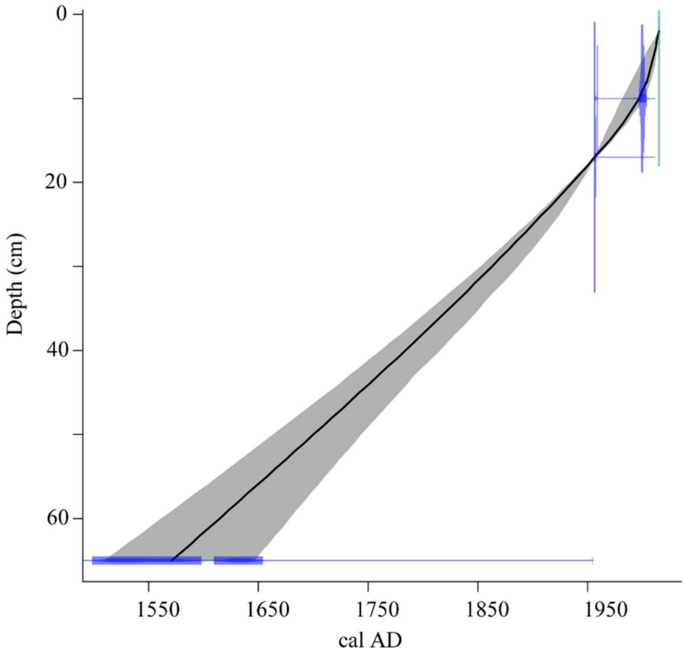

Figure 3.2 Age-depth model for Lake Relem.

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 3.2) 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 3.2), 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 3.2). 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 3.4). 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 at Lonco Luan, 0.5 cm/yr at Koywija, 0.2 cm/yr at Quinquen and Lomocura, and 0.3 cm/yr at Los Piñones. For Relem we obtained a sedimentation rate of 0.6 cm/yr in the uppermost 5 cm and an average of 0.13 cm/yr for the older sediments (Figure 3.2).

3.3.2 Patterns of vegetation land-cover and land-use change

Nothofagus dombeyi-type is the dominating pollen taxon at the six sites (Figure 3.3). 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 average 82% and 86% respectively (Figure 3.4b). 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.

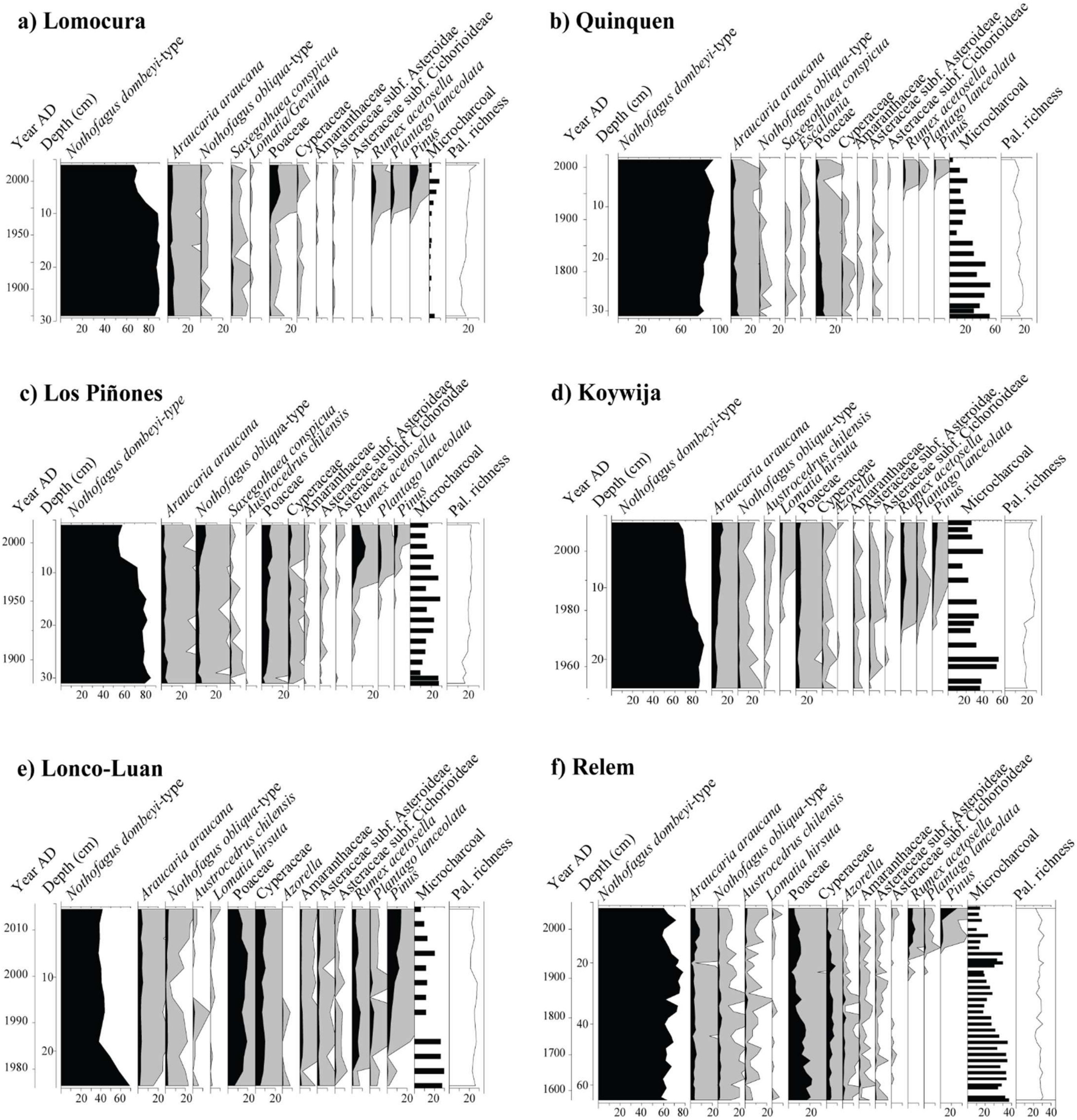

Figure 3.3 Pollen diagrams, ordered along the precipitation gradient from west to east: a) Lomocura, b) Quinquen, c) Los Piñones, d) Koywija, e) Lonco Luan, and f) Relem. Pollen percentage in black, ×10 exaggeration light-grey silhouettes. Microscopic charcoal particles expressed as percentage of the terrestrial pollen sum. Palynological richness estimated in base a minimum sum of 400 terrestrial pollen grains.

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 3.3). 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 3.3) 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 *Saxegothaea conspicua*) together represented 2.1% in samples between 10-30 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 3.3a, Supplement material). The most relevant change in Quinquen was the increase of *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 3.3b, Supplement material). In Los Piñones, the rainforest taxon *Saxegothaea* conspicua was more abundant in samples from 20-30 cm depth, approximately before 1900 (Figure 3.3c). The xeric shrub *Discaria*, as well as other herbaceous taxa such as Asteraceae subf. Cichorioidae, Apiaceae undiff. and Verbenaceae increased after approximately 1970 (Figure 3.3c, Supplement material). In Koywija, the pollen from the shrubs taxa *Discaria*, *Escallonia* and *Ephedra* were more abundant than in bottom samples and *Austrocedrus chilensis* increased towards the top (Figure 3.3d, Appendix b). 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 3.3e, Appendix b). *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 1-3%, with a peak of 4.3%

before the plantation of *Pinus*. The relative abundance of *Azorella* and *Littorella* declined gradually since around 1900 (Figure 3.3f, Appendix b).

3.3.3 Presence of introduced taxa

In all lakes with close proximity to a *Pinus* plantation, *Pinus* pollen (Figure 3.4a) 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 plantations and Quinquen (1.6%) without a close plantation and situated in a dense forest (Table 3.2).

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 3.4a). 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 of *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 5-15%. *Rumex acetosella* is slightly more abundant in the lakes from xeric environments and open forests compared to 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.

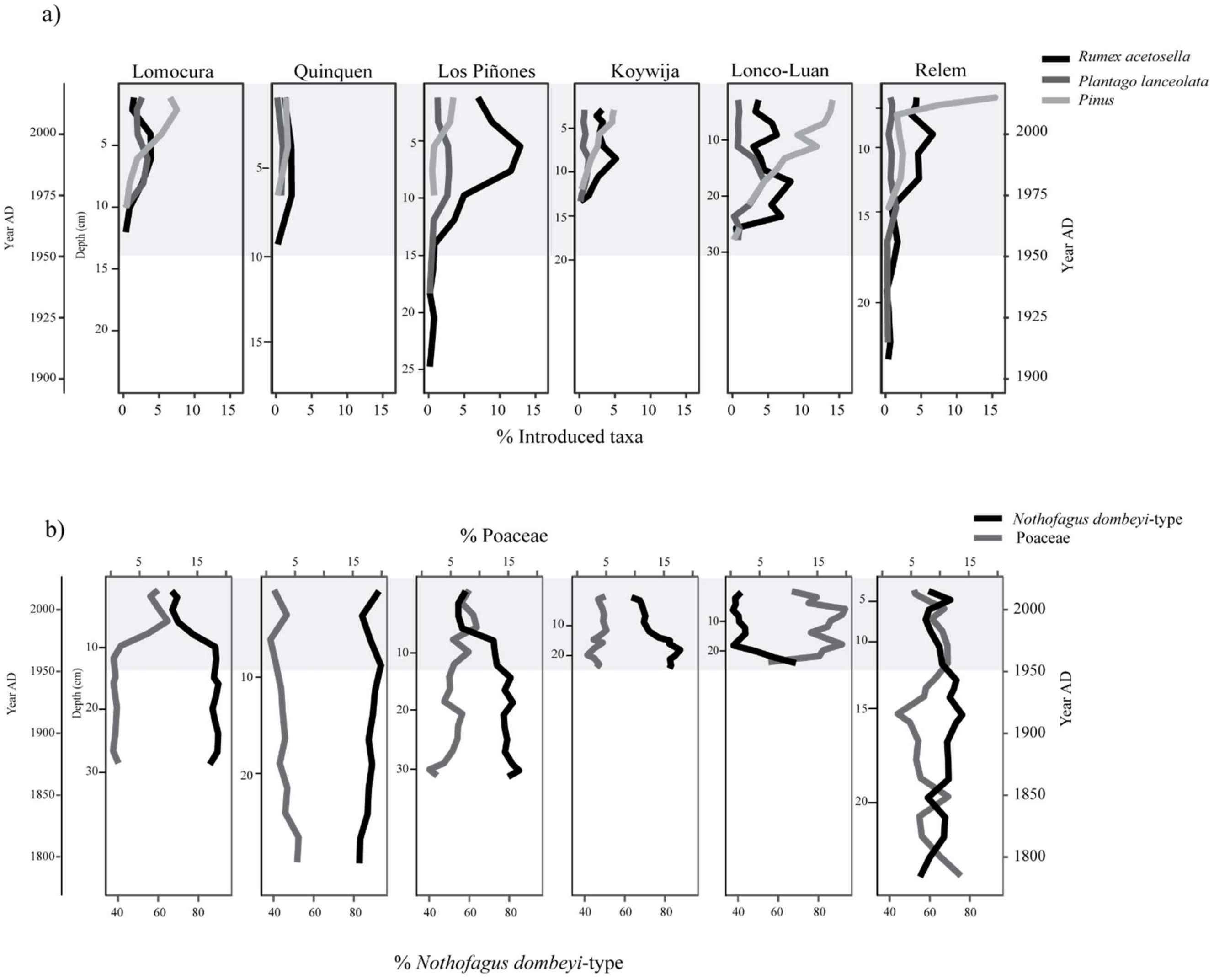

Figure 3.4 Relative abundance of (a) introduced taxa and (b) Nothofagus dombeyi-type and Poaceae. Lakes are ordered in a west-east gradient from left to right. Ages are shown for Relem and the depth scale at all other sites was adjusted to this time scale, assuming a linear sedimentation rate and using the time of the expansion of Pinus.

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 century. At all sites the abundance of *Nothofagus dombeyi*-type declined with the increase of 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 of 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 kept stable in low percentage despite the fall in *Nothofagus dombeyi*-type, perhaps due to the major presence of *Lomatia hirsuta* (Figure 3.3d) which covers the surrounding area of the lake currently.

3.3.4 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 Correspondence Analysis (CA) was carried out on a dataset combining all individual sites by taxon (Figure 3.5). 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 3.5a). 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 3.5b). In both ordination plots the environmental gradient is characterized by the occurrence of spores from the epiphytic fern *Synammia feuillei* at Lomocura to *Azorella* and *Mullinum*, characteristic components of the steppe at Relem. Samples from Lonco Luan were separated from Relem by their presence of Apiaceae and Asteraceae subf. Cichorioidae.

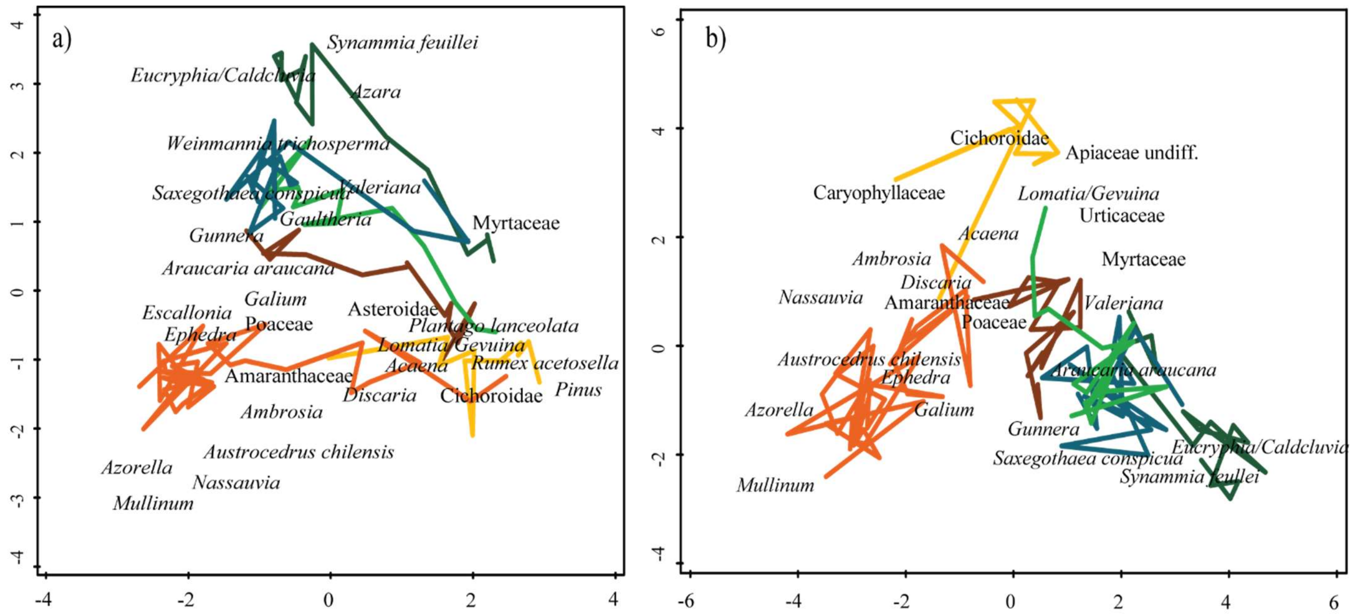

Figure 3.5 Correspondence analysis of the taxa combined datasets (a) and without human indicators taxa (b). Lomocura (dark green), Quinquen (blue), Los Piñones (light green), Koywija (brown), Lonco Luan (yellow), Relem (orange). Note different axis scales.

3.4 Discussion

3.4.1 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 3.1c, d) providing snapshots of the vegetation around the year 1915 (Rothkugel, 1916) and 1940 (Tortorelli, 1942). A large mapping unit in the Rothkugel-map (Figure 3.1c) 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 continues 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 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 in 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 of 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 of 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 (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 Aluminé 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 were documented by Naveas et al. (1979), and also the pollen diagram from San Pedro (Fletcher and Moreno, 2012) documents an increase of the pollen type over the last 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 low-lands 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).

3.4.2 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 to forested areas (Iglesias et al., 2017; Paez et al., 1997).

Table 3.4 Selection of paleoecological studies mentioning the occurrence of introduced taxa in Patagonia.

Sites		Site Location		Age[2] of appearance and rise of pollen types of introduced taxa	Authors
ID[1]	Name	Lat. S	Long. W		
A	Laguna Aculeo	33° 50’	70° 54’	No mention of *Rumex*. *Plantago* started 1900* (age interpolated), together with *Pinus* increase after 1960***	Villa-Martínez et al., 2004
B	Lago Maule	36° 04’	70° 29’	Appearance of *Rumex* 12cm 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 *Rumex* in top 20cm (c.1880s**), decrease toward top. Presence of *Pinus* 10cm depth (c.1970***) increase monotonically.	Fletcher and Moreno, 2012
D	Lago Galletue	38° 41’	71° 17’	No mention of *Rumex*. Presence of *Pinus* and *Plantago* from 13cm (c.1960 ***), *Pinus* increase to c.10% abundance at 5 cm.	Urrutia et al., 2007
E	Mallín Paso del Arco	38° 52’	71° 04’	Presence of *Rumex* in top 15cm. (c.1800*) always below 5%. *Pinus* is not documented.	Heusser et al., 1988
F	Mallín Rio Malleo	39° 36’	71° 24’	Presence of *Rumex* in top two samples, 10cm (c.1900***). Presence of *Pinus* only in top sample (c.1980***), below 1%.	Heusser et al., 1988
G	Mallín Serrucho	41° 46’	71° 25’	Traces of *Rumex* and *Plantago* in the top 10 cm (c.1800**). Youngest date 110.	Markgraf et al 2013
H	Lago Mosquito	42° 29’	71° 23’	Presence of *Rumex* and *Pinus* (not shown) found in small amounts above top 40cm, since 1740**. First two ages are reversals.	Whitlock et al 2006
I	Lago Teo	42° 54’	72° 42’	Presence of *Rumex* and *Plantago* in the first 10 cm, <1% abundance (1600**).	Henríquez et al., 2015

J	Lago Venus	45° 41’	72°01’	Presence of *Rumex* since 1920**. Abundance rises up to 5% by 1940***. *Pinus* in first 3cm, reaching 5% in the top.	Szeicz et al., 1998
K	Mallín Pollux	45° 41’	71° 50’	Presence of *Pinus* and *Plantago* in two samples on top 20 cm (c.1940**)	Markgraf et al., 2007
L	La Tercera	49° 11’	72° 22’	*Rumex* in first 10 cm (approx. 1850-1900**). Around 1% abundance.	Sottile et al., 2011
M	Mallín Cerro Frías	50° 24’	72°42’	Presence of *Rumex* in first 3 samples (approx. 1850-1900**). Around 1% abundance.	Sottile et al., 2011
N	Mallín Vega Ñandu	50° 55’	72° 45’	Presence of *Rumex* in top 2cm, 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 *Rumex* in top 25cm (c. 1900 **), increasing in last 10cm (c.1980**). Chronology considered youngest dates from two different cores.	Mayr et al., 2005
P	Mallín Rio Rubens	52° 08’	71° 52’	Presence of *Rumex* in top 25cm (c.1600**), increase (~5%) after c.1950***. Presence of *Plantago* (<0.5%) in uppermost samples (c.1980)	Huber and Markgraf, 2003
Q	Lago Potrok Aike	51° 58’	70° 23’	Presence of *Rumex* in c.1850**, growth in c.1950**. No data for *Pinus* and *Plantago*.	Haberzettl et al., 2006

Note: [1]Letters correspond to Figure 1a. [2]All ages are expressed as AD: Uncertainty of age determination: *** <20yr; ** <60; * >60

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, pers. 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 3.4). Like in the here presented diagrams, most sites show a continuous or discontinues 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 one 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 last 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, 2001; 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 to 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 towards the steppe.

3.5 Conclusions

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.

Acknowledgements
Our sincere thanks to Mr Bocos and Dr Laclau (INTA) for providing valuable information on Pinus plantation in Argentina, Dr Muñoz (UCV) who provided files with the distribution of Araucaria, and Mr Iglesias for geo-referencing the historical map of Rothkugel. We are grateful to MSc Marticorena (herbarium CONC) and Dr Fuentes (LIB) who enabled data about the introduced taxa. We are thankful to Prof. Dr Behling for supporting part of this research, and to the anonymous reviewers for helpful comments on the original version.

Funding

This work was supported by a scholarship to RM through program DAAD/BECAS Chile, 2014 (57144001), and by the DFG Grant FO 801/3-1. TG acknowledges funding from the DFG Grant GI 732/9-1. The authors declare that there is not conflict of interest.

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CHAPTER 4 -

4. Fire and vegetation dynamics of the endangered *Araucaria araucana* at the forest-steppe ecotone in northern Patagonia.

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Manuscript

Abstract

Questions

In the last centuries fire regime change in the *Araucaria* forest may have threated its conservation status. Although, *Araucaria* does not depend of fire to persist, natural-fires are part of the ecosystem and *Araucaria* may resist moderate fires. To understand recent and long-term vegetation patterns and process that help in conservation task, we reconstructed the vegetation and fire history to find out the role of fire on the vegetation dynamic and the long-term trend of the population of *Araucaria*.

Location

Lake Relem, northern Patagonia.

Methodology

Pollen and macro-charcoal analysis.

Results

Vegetation history and fire regime were reconstructed for the last c.9 ka. Before 4.5 ka steppe vegetation dominates the landscape. After 4.5 ka, steppe changed gradually to scrublands and woodland. Forest and woodland may cover the landscape from 2.5 ka until the establishment *Pinus* plantations. Local fire regime indicates 20 fire events of low magnitude, most frequently between 6-2.5 ka. Vegetation dynamics is not determined by fire event and its magnitude, but strongly related with fire-frequency. *Araucaria* spread around Relem between 8-6 ka and then decayed suddenly. There is no evidence that fire caused this drop. After that, the abundance is slightly increasing up to the present.

Conclusion

These results are the first longest reconstruction of fire regime and vegetation dynamics. For the last millennia forest and woodlands was abundant, likely a patchy landscape less fragmented than today. Holocene fire regime was less frequent and severe than in other areas of the ecotone. Individual events had no influence on vegetation, but fire frequency. Results do not evidence change in fire regime due to Euro-American colonization. The causes of drastic decline in *Araucaria* population are not clear, yet likely a disease. After that, population is slightly increasing until present.

Keywords: *Araucaria araucana*, forest-steppe ecotone, Patagonian Andes, Fire disturbance regime, Vegetation dynamics, lightning, endangered species

4.1 Introduction

Change in the fire regimes due to climate and land-use change might be altering vegetation structure and composition at forest-steppe ecotone in Patagonia (Mundo et al., 2014). Although fire is a natural component in the Patagonian Andes ecosystems (e.g., Whitlock et al., 2007), there is still a concern on the conservation status of the vegetation due to the shifts in the fire regimes. Increasing trends of fire frequency and severity during the last decades (González et al., 2018) keep up the discussion on the stability of the vegetation boundaries and the persistence on endangered species at the ecotone. During the Euro-American colonization in the late 19th century about 25% of the forested areas close to the steppe was burned (Rothkugel, 1916). The recolonization of grasses and shrubs short after leads to the early interpretation of progressive expansion of steppe vegetation toward the forest due to aridification (e.g., Kalela, 1941). But later, Veblen and Lorenz (1988) realized that some of those burned areas were subsequently colonized by trees. Moreover, the authors argued that by this time the precipitation trend was not clearly decreasing. Therefore, vegetation composition and structure were mainly associated to humans setting fires while tree species recolonized the area as result of decreased fire frequency (Veblen & Markgraf 1988). Recent advances and a long-term perspective suggest that precipitation is in fact decreasing through the last centuries (e.g., Villalba et al., 2012), while repeated fire may drive to a persistent vegetation dominated by pyrophytic shrubs species in alternative to tree species (Kitzberger et al., 2016). Thus current vegetation patterns at the forest-steppe ecotone are the results of the historical complex interaction between climate, human and fire disturbance (Kitzberger, 2012; Whitlock et al., 2007). To understand the role of fire disturbance on the vegetation dynamic at the ecotone, aiming to contribute in conservation tasks, it is required a longer time perspective into the historical range of variability.

In the past, the distribution of the forest-steppe ecotone boundaries in northern Patagonia have changed regard its modern setting (Iglesias et al., 2014). Today *Araucaria* forests are mostly distributed in mountains above 600 m elevation (Roig 1998), an area covered by ice before ~15 ka (Hulton et al., 2002). During the transition to the Holocene, pollen records suggest a progressive replacing of steppe vegetation by an open forest of *Nothofagus* (Iglesias et al., 2014). As the temperature increased during the early and mid-Holocene (Lamy et al., 2002), *Nothofagus dombeyi*-type pollen indicate an expansion of the forest (e.g., Iglesias et al., 2014; Whitlock et al., 2006). The pollen abundance of *Nothofagus dombeyi*-type apparently increased from north to south in Patagonia and keeps high until the Late-Holocene (Nanavati et al., 2019). Late-Holocene in northern Patagonia is also characterized by the spread of *Austrocedrus chilensis,* creating a mixed forest until today, likely due to an increase in fire frequency (Whitlock et al., 2006; Iglesias et al., 2012).

Fire disturbances that occurred throughout the Holocene might play an important role on the vegetation at the forest-steppe ecotone (e.g. Whitlock et al., 2007; Iglesias et al., 2018). During the Holocene, the pace of fire along the Patagonian forest-steppe ecotone is clearly variable (Nanavati et al., 2019). Factors responsible for this variation are not well resolved (Whitlock et al., 2015). The studies have focused on climatic drivers fire, such as the intensification of Southern Westerly Wind and the onset of El-Niño-Southern-Oscillation (ENSO) (e.g., Fletcher & Moreno, 2012a), lightning-strike (Holz et al., 2012; Whitlock et al., 2007) or by indigenous peoples (Veblen & Markgraf, 1988). While SWW and ENSO may account for dry periods allowing the expansion of fires, the most likely mechanism that sparks a fire are lightning and humans. However, little is known about mechanism behind lightning fires in Patagonia, and despite the humans perhaps used fire to hunt, the pace that indigenous populated Patagonia may not necessarily follow periods of fire. The spread of fire is spatial and temporal limited by fuel biomass available and climatic factors that can by modified by the human actions such as increasing fuel biomass or suppressing fire (Whitlock et al., 2015). Along the northern Patagonian forest-steppe ecotone, the fire starting in the grasslands and scrublands in the steppe is normally suppressed when reaching the forest due to more humid conditions into the forest (Mermoz et al., 2009). Fire dynamics in the past are result of complex interaction of many variables, sometimes unknown or unmeasurable. Notwithstanding, palaeoecological reconstruction of fire and vegetation dynamics may help in the conservation of endangered species in Patagonia.

Araucaria araucana have a limited distribution area in the Patagonian Andes (~390 km^2; Premoli et al., 2013), fragmented and with some isolation in the mountains above 1000 m a.s.l. (Gonzalez et al., 2006). *Araucaria* is an endangered species because of a strong reduction in almost 50 percent of its area of occupancy caused by intense selective logging and land-use change (Gonzalez et al., 2006; Premoli et al., 2013). Further concern pointed out for gaps of regeneration for about 100 years in northern and eastern areas of its distribution (Roig et al., 2014); humans, birds and mice consumed the seed, while coats graze the seedling (Gonzalez et al., 2006). However, understory plants can protect the seedlings (Gonzalez et al., 2006; Roig et al., 2014). In addition, decreasing tree-ring growth trends across *Araucaria* distribution is related to precipitation diminution at centennial scale (Muñoz et al., 2014). Recent humans settlement might change the fire regime from ubiquitous infrequent catastrophic events to more frequent (Armesto et al., 2009). To its favor, *Araucaria* shows adaptation to tolerate low and medium intensity fires disturbances such as a thick bark, protected terminal buds and shoot re-sprouting after fire (e.g. Veblen et al., 1982; Burn 1993; Gonzalez et al., 2006). Vegetation recovery after fire disturbance is complex, but mostly it is expected an abundant regeneration of *Nothofagus* species (Veblen et al., 1992). Severe and infrequent fires under humid condition should be follow by regeneration pulse of *Nothofagus* species; whilst under xeric-conditions with lower biomass vegetation fires are frequent but less severe (Gonzalez et al., 2005). However, records longer than 1000 years are scarce in the area which allows confirming the frequency of catastrophic fires, the responses of vegetation, and whereas *Araucaria* populations are decreasing.

During the Holocene the vegetation dynamics of the *Araucaria* forest at the steppe ecotone is poorly known. Pollen abundance of *Araucaria* in the longest high resolution study was found decreasing over the last 1.5 ka (Fletcher & Moreno, 2012b). On the contrary, Heusser et al. (1988) published two records, where the first shows a slight increase in *Araucaria* pollen, while the second southward of *Araucaria* distribution the pollen abundance did not change. Regards the recent history for the last 300 years approximately Moreno-Gonzalez et al. (2019; Chapter 3) suggested that in some areas of *Araucaria* forest the vegetation did not change significantly, but rather during the last decades due to extensive *Pinus* plantation. Here we aim to contribute a new record with a longer term perspective into the vegetation and fire disturbance regime that would add more confidence to recent vegetation changes and the trend of *Araucaria* populations. By asking what role played the fire, and whereas there is a common decreasing trend of *Araucaria,* the objective of this work is 1) to reconstruct the local vegetation and fire history, and 2) to assess the vegetation response to past fire disturbances. We emphasized in the long-term dynamic of the *Araucaria* and what role played the fire in its natural variability and current conservation status.

4.2 Study area

The study area is located in the current forest-steppe ecotone, in northern Patagonia. Lake Relem is shallow (~2.5 m depth), small (~1 ha), without river inflow, located in 38°58'39.64"S; 71° 4'51.13"W, at 1268 m a.s.l. (Figure 4.1). The Andes Cordillera reaches elevations exceeding 2000 m creating a sharp rain-shadow effect with the storm tracks and westerly winds arrive from the Pacific Ocean discharging most of the precipitation on the western slopes (Garreaud, 2009; Mundo et al., 2013). The climate is temperate with monthly average temperatures above freezing and a marked precipitation minimum during the austral summer (DJF), giving it a mediterranean character (Luebert and Pliscoff 2006). Precipitation nearby Lake Relem in average is 200 mm, decreasing from about 2500 mm at elevation over 1600 m a.s.l. westward in the Andes (Bianchi et al., 2016; Paruelo et al., 1998). Annual mean temperature ranges on the western slopes between 12 °C to 8 °C at high altitudes, and increases to about 16 °C on the eastern side (Bianchi et al., 2016). For the last 100-year rainfall decreased between 20-40% (Garreaud et al., 2017). Lightning strike are common in the Patagonian Andes with ~2 lightning km^2 year^{-1} (WWLLN 2017), although 10-fold lower than tropical and subtropical areas (Garreaud et al., 2014). Lightning strikes in the area are probably caused by the uprising of the moist air masses on the windward of the Andes, followed by rain discharge that alter the electric charge of the clouds mainly during dry summer (Garreaud et al., 2014).

Fires have burned ~600,000 ha in the last decade in Chile central-south, where the region around *Araucaria* forest was one of the most affected (Gonzalez et al., 2018). Abnormal mega-drought in 2010-2015 for the last 1000 years (Garreaud et al., 2017) may have helped to fire expansion and more lightning-strike (Gonzalez et al., 2018; Mariani et al 2019). In Argentina, close to 25% of the forest were burned in northern Patagonia during the Euro-American colonization (1880-1920 CE) (Rothkugel 1916). The study of fire scare in *Araucaria* trees evidenced an increase of fire-frequency during the Euro-American colonization compared with previous 300 years (Mundo et al., 2013; Gonzalez et al., 2005). Although, the periods of increasing frequency are clearly related to human, the climate conditions have played an important role. For example, periods of ENSO events are negatively correlated with fires events (e.g. Mundo et al., 2013) and low precipitation (Garreaud 2009). Apparently, lightning strike are more frequent during ENSO (Mariani et al., 2018). However, less than 5% of fires occurred in last decades were produced by natural causes (Gonzalez et al., 2018).

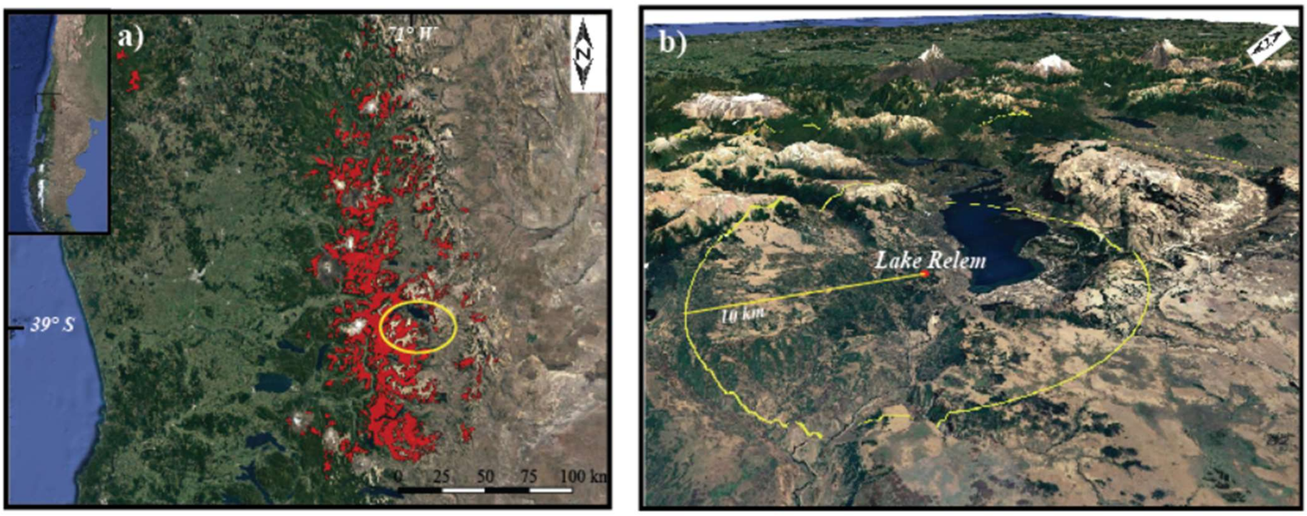

Figure 4.1 a) Map of the study area indicating the distribution of Araucaria (red polygones) and the approximate location of Lake Relem (yellow circle). B) Zoom in to Lake Relem and the theoric pollen source area of 10 km for small lakes (yellow circle)

The interaction between climate, topography and the disturbance regime, at the ecotone shows a variety of plant association, creating a complex landscape (Kitzberger, 2012). Within the theoretical pollen source area studied (Figure 4.1b), *Araucaria* present different association. 1) Dense, multilayer forest with dominance of *Nothofagus dombeyi*, and *N. pumilio,* associated with *Drimys andina, Berberis microphylla, Maytenus magellanica, Gaultheria mucronata, Escallonia virgata, Desfontainia spinosa* in the understory among others. Under disturbed condition *Chusquea culeou* can form dense understory. 2) Mixed forest with *Austrocedrus chilensis* and/or *Nothofagus obliqua,* or open forest with dominance of deciduous *Nothofagus antarctica*. Common understory shrubs such as *Schinus patagonicus, Empetrum rubrum, Escallonia virgate, Maytenus disticha, G. mucronata*; and the herbs *Poa pratensis, Azorella caespitose, Galium antarcticum, Caltha appendiculata, Festuca pallescence, Acaena pinnatifida.* 3) scatter individuals of *Araucaria* without or scarce *N. antarctica* and *A. chilensis,* and broadly dominated by bunch grasses and shrubs as *Discaria* and *Colletia*. At the steppe *Araucaria* is normally absent and the vegetation is characterized by herbs such as *Festuca pallescens, Cerastium arvense, Azorella caespitosa, Nassauvia abreviata, Poa spp., Elymus patagonicus, Quinchamalium chilense,* *Sencecio patagonius, Acaena pinnatifida, Adesmia longipes, Galium antarcticum*; and the shrubs: *Discaria serratifolia, G. pumila, Baccharis magellanica, Mulinum spinosum, Colliguaja integerrima, Ephedra chilensis.*

4.3 Methodology

4.3.1 Chronology

The age of 7 samples were obtained by accelerator mass spectrometry (AMS) on bulk sediment submitted to the CHRONO Centre, Queen's University Belfast, UK (UBA) (Table 4.1). Radiocarbon dates were calibrated with SHCal13.14C (Hogg et al., 2013) and the postbomb_SH1-2.14C for post-bomb dates (Hua et al., 2013). We also made use of a well-known volcanic eruption in the area, the Sollipulli-Alpehue dated in 2990±0.09 BP (Table 4.1; Naranjo et al., 1991). The age-depth model was carried out with smooth spline (0.1 smooth), with a 95% of confidence interval (1000 iterations). Calendar age point for depths are based on weighted average of all-depth curves. Calibration and age-depth model (Figure 4.2) were conducted with Clam 2.2 (Blaauw et al., 2010).

4.3.2 Sediment and Pollen analysis

Subsamples of 0.2 cm^3 were taken to obtain an estimation of the dry bulk density and organic content of the sediment; the samples were first dried at 105° C for 24 hrs and then burned at 550° C for 4 hrs (Heiri et al., 2001). A total of 176 pollen samples of 0.5 cm^3 were taken along the core avoiding tephra layers. Pollen analysis were done following standard techniques (Bennett & Willis, 2001). The samples were not sieved. By adding *Lycopodium clavatum* tablets we estimated pollen concentration, then the results were multiplied by sedimentation rate to estimate the Pollen-Accumulation-Rate (PAR). Pollen were counted using light microscope at 400-1000x. Pollen concentration was low, therefore a minimum of 400 terrestrial pollen grains were counted. The identification of pollen and spores identification was carried out with atlases of Heusser (1971), Markgraf and D'Antoni (1978) and pollen reference stored in the Department of Palynology and Climate Dynamics, Göttingen University. Pollen taxonomy follows modern plant distribution within the study area then linking the pollen types to this species and genera (Fontana & Bennett, 2012).

4.3.3 Macro-charcoal analysis

To reconstruct the fire history we followed procedures proposed by Whitlock and Larsen (2001) to process macro-charcoal particles in sedimentary records. Subsamples of one cubic centimeter were extracted contiguously every centimeter and sieved in 125 µm mesh. Charcoal particles were counted in a stereomicroscope. Charcoal morphotypes calculate the Grass-to-total charcoal index follows a simplified classification of Enache & Cumming (2006). Charcoal accumulation rate (CHAR) were interpolated to the median sampling interval ($C_{interpolated}$) and smoothed with Robust Lowess method for a 500-yr time window to estimate low-frequency CHAR ($C_{background}$). Row data were not transformed. To estimate high-frequency CHAR we used the ratio between $C_{interpolated}$ and $C_{background}$ as suggested by Higuera et al., (2010) to be unbiased method for unequal CHAR average and variance. Peaks events (cPeak) were detected with a local threshold, modelled with a mean Gaussian cut-off at 90% confidence. Fire Frequency (FF) and Fire-Return-Interval (FRI) were analyzed over 1500-yr time windows. Pre-treatment and analysis of Charcoal data were conducted with CharAnalysis v.1.1 (Higuera, 2009).

4.3.4 Data analysis

Pollen of the terrestrial taxa was summed within respective levels to obtain the relative abundance. Only taxa >1% abundance were plotted in the pollen-diagram for the manuscript. Aquatic plants were summed apart from the total of the terrestrial taxa and expressed. Zonification was defined by depth-constrained cluster analysis of the pollen samples based on the Euclidian distance of all terrestrial taxa. Statistical significant zones were defined by broken stick model (Bennett, 1996). Compositional trend of the terrestrial taxa was explored through principal component analysis (PCA), and to assess the compositional turn-over we used a Detrended Correspondence Analysis (DCA) (Ter Braak & Smilauer, 2012). For both PCA and DCA the taxa abundance was square-root transformed and centralized. Later, to assess the vegetation responses to fire regime we constrained the compositional data against CHAR, FF, FRI, cPeak, and Fire-Magnitude. All analyses were conducted with RStudio v.3.3.1 (Rstudio Team, 2016), vegan-package 2.4-2 (Oksanen et al., 2017), Rioja-package (Juggins, 2015).

4.4 Results

4.4.1 Chronology and sedimentary process

The core has a total length of 743 cm (442 cm without tephra layers). The base of the core was dated to ~9000 cal. BP (hereafter all dates correspond to cal. BP). Using 6 additional radiocarbon dates and the published radiocarbon age of one tephra (Table 4.1) we obtained an age-depth model (Figure 4.2a) indicating a relatively constant sedimentation rate between < 0.1 to 0.2 cm yr^{-1}. Near the top of the core the sedimentation rate increases up to 0.5 cm yr^{-1}. Organic content in the sediment, expressed as the percentage of organic material loss after ignition (LOI %), shows strong variation along the core, with an increasing trend from c. 500 cm depth to the top (Figure 4.2b). Dry bulk density (Figure 4.2c) mirrors LOI for most samples. Peaks in bulk density and drops in organic material are related to tephra layers (Figure 4.2d), in particular after the Sollipulli-Alpehue eruption. In the core, were detected 42 tephra layers with more than 0.5 cm thickness, most of them range in between 1 and 5 cm and one of ~200 cm thick (Figure 4.2d).

Table 4.1 AMS Radiocarbon dates from Lake Relem. Bulk sediment was analyzed in the CHRONO Centre, Queen's University Belfast, UK (UBA).

Lab. no.	Depth (cm)	Age (^{14}C yr BP)	%pMC	Age cal yr BP (2σ)	Probability (%)
UBA-29237	270-271		109.88±0.34	-53.4 - -47 -8.8 - -8.7	93 2
UBA-29238	277-278		100.37±0.32	-7.4 - -5.9	95
UBA-29239	325-325.5	330±24		295.9 - 340.5 351.8 - 451.3	28.8 66.2
UBA-29242	431.5-432	1949 ±22		1750.9 - 1768.3 1815.7 - 1916.8	5.1 89.9
So-A*	483	2990±0.09		2847.1 - 3054.8	95
UBA-29243	576-576.5	4576±26		5049.5 - 5193.5 5211.7 - 5312.5	61 34
UBA-29244	643.5-644	6359±30		7167.4 - 7313	95
UBA-23305	706.5-707	7994±47		8641.1 - 8989.5	95

*So-A date corresponds to Sollipulli-Alpehue eruption (Naranjo et el., 1991). The age was assigned to the adjusted depth, just below the tephra (original depth, 724cm).

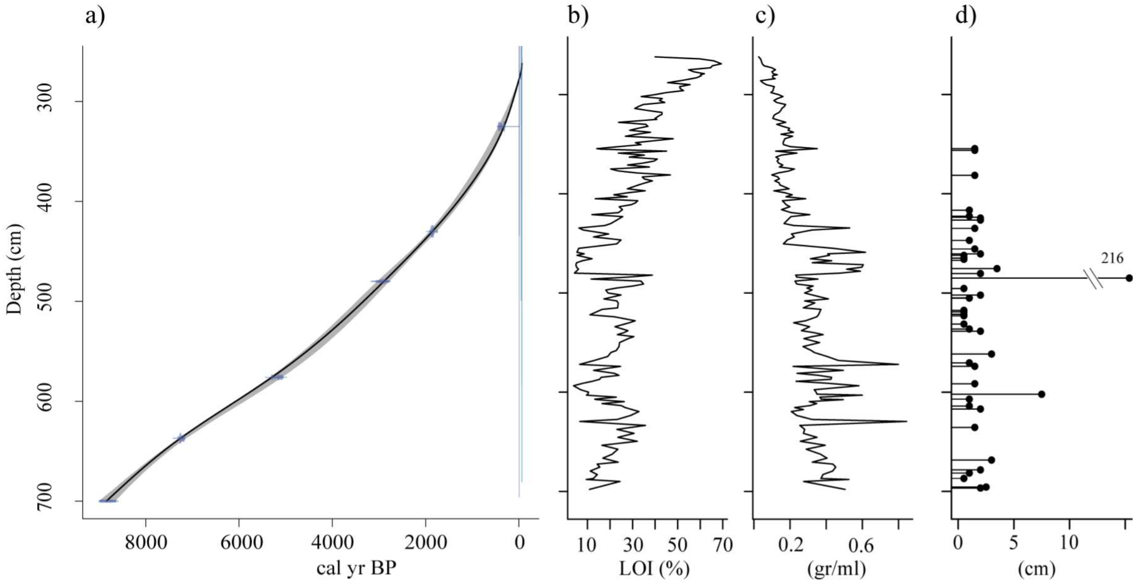

Figure 4.2 a) Age-depth model; b) Percentage of organic content loss after ignition (LOI); c) the dry bulk density; d) tephra thickness. All tephra layers >0.5 cm were excluded from the age-depth model.

4.4.2 Vegetation history

The general trend in vegetation composition over the last 9 ka shows an overall vegetation transition from steppe grassland (Poaceae) to forest (*Nothofagus dombeyi*-type) (Figure 4.3). The pollen type *N. dombeyi*-type in the study area is represented by three *Nothofagus* species*, N. dombeyi, N. pumilio* and *N. antarctica*, while Poaceae might represent over 100 species (CONC Herbarium pers. comm.). Results for DCA indicate a low compositional turnover for the whole period (1.25 SD), however the results of the cluster analysis differentiate five significant local pollen zones in the pollen diagram (Figure 4.3). The taxa in the pollen diagram are ordered according to their weighted average, from left-bottom to the right-up. Between 9-4.5 ka the pollen assemblage is characterized by higher abundances of *Mulinum*, Verbenaceae, Cyperaceae, Amaranthaceae and Poaceae (Figure 4.3, 4.4, 4.5a). These taxa are typical for the modern steppe vegetation. Although they are present along the record, the relative abundance decreases towards the present while PAR remains relatively stable. Pollen from *Prumnopitis andina* was found sporadically in low percentage, but is more abundant between 9-4.5 ka. Likely it corresponds to long dispersal pollen or represents scarce individuals nearby. *Araucaria* pollen shows maximum abundance between 8-6 ka (Figure 4.3 and 4.4). Starting from the bottom, a small drop in *Araucaria* pollen percentage occurred about 7.4 ka, but later the pollen increased up to 15% around 6.7 ka. Similar pollen percentages over consecutive samples suggest a relatively stable population near the lake for approximately 200 years before drastic population decay. This trend is also reflected in the *Araucaria* PAR reaching between 400-500 grains cm^2 $year^{-1}$ at around 6.7 ka (Figure 4.4). After the steep decline, the pollen abundance remains between 1-3%, with a steady increase from 2 ka to the present (Figure 4.3 and 4.4). Pollen from *Schinus patagonicus*, occur throught the record at low abundances, however, somewhat more frequently before 4.5 ka. *Nothofagus dombeyi*-type pollen shows a stepwise abundance increase around 4.5 ka with values around 45% before 4.5 ka, and 60% after the increase. Low values before 4.5 ka suggest the presence of dispersed patches from likely the shrubby *N. antarctica*. Likely small patches of tall *Nothofagus* forest remained somewhere in protected hills westward of Lake Relem (Figure 4.1b and Figure 4.1b), due to the still high amount of *Nothofagus dombeyi*-type, and the presence of vines pollen (e.g., *Muehlembeckia* and *Hydrangea*, Figure 4.3).

This increase in *Nothofagus dombeyi*-type around 4.5 ka is accompanied by a decline in Poaceae pollen indicating an expansion of the forest into the steppe. A steep decline in *Nothofagus dombeyi*-type and Poaceae pollen occurred around 3 ka as a consequence of the Sollipulli-Alpehue eruption. This eruption had a strong imprint on the vegetation (Figure 4.3, LR-3). The pollen percentage of *Nothofagus dombeyi*-type (Figure 4.3) reached high proportions for the last ~2.5 ka, ranging between 60-80%. The same trend is observed in the PAR (Figure 4.4). Poaceae pollen remained at low percentage after 2.5 ka, with almost constant PAR. The pollen abundance of Poaceae denotes the close proximity of the steppe and/or the presence of patches with open forest and shrubs. Pollen from *Araucaria*, *Nothofagus obliqua*-type, *Saxegothaea conspicua*, and *Austrocedrus chilensis* are slightly more abundant after 2.5 ka. Pollen from introduced taxa characterize the topmost samples with significant increase of *Rumex acetosella* and *Pinus* reaching both together up until 20% on top (Figure 4.3, LR-5).

More frequent aquatic taxa found were *Myriophyllum, Potamogeton, Sagittaria* (Figure 4.3). Between ~ 8-6 ka all taxa decreased the abundance with low and sporadic appearance. After 6 ka *Potamogeton* and *Sagittaria* increased again and remained relatively stable until present, but

Myriophyllum were dominant between 6-2 ka. The fall of *Myriophyllum* after 2 ka and the quasi-continuous presence of *Potamogeton* might indicate strong change within the lake until the present and perhaps some variation in lake level and water condition.

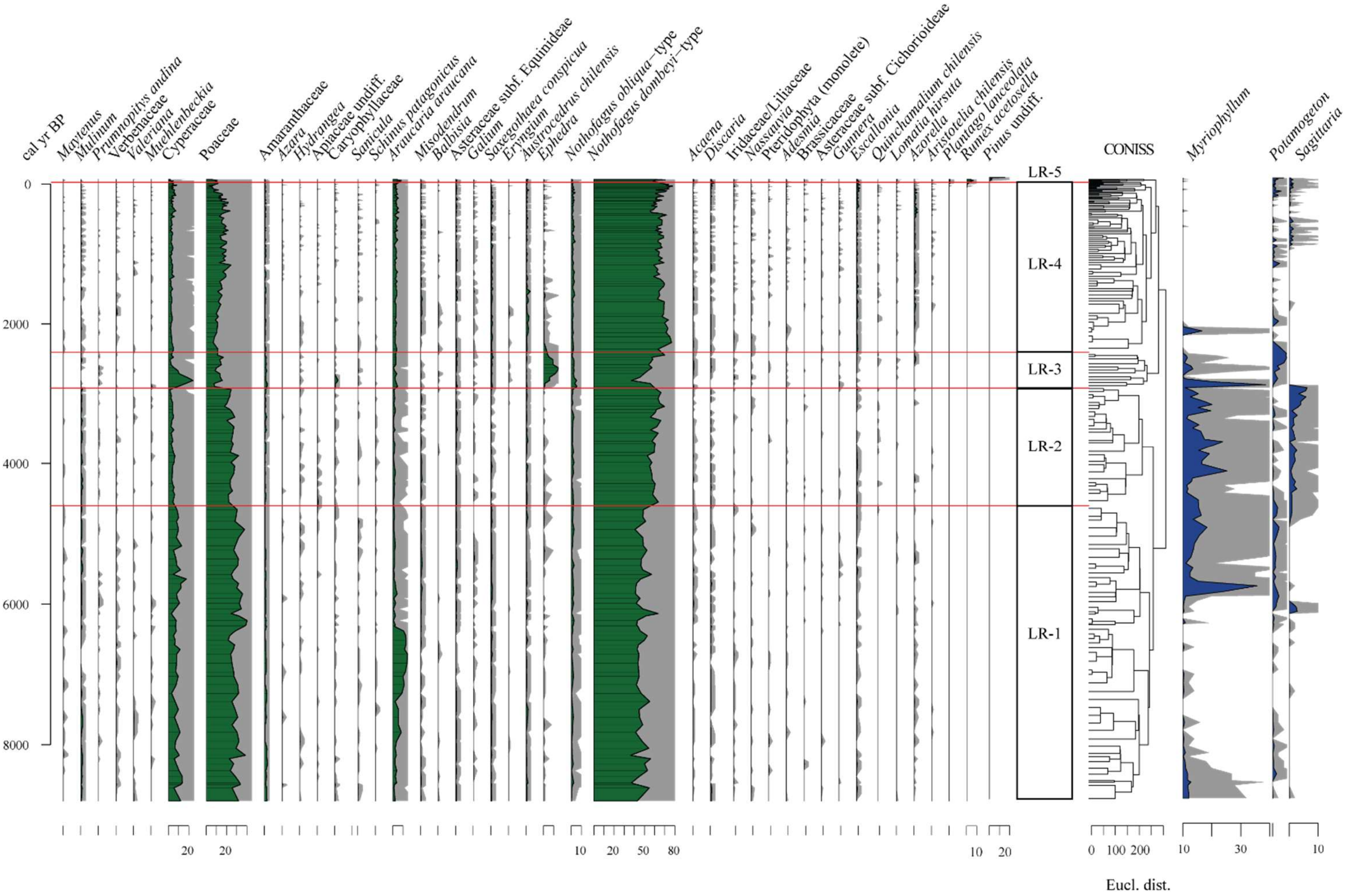

Figure 4.3 Shows the pollen diagram for the most abundant taxa (>1%). Taxa are order according their weighted average, with taxa showing highest abundances towards the bottom of the core being placed. Grey silhouette indicate magnification ×10. CONISS and Zonification were calculated only with terrestrial pollen taxa. The pollen percentage of aquatic taxa were calculated based on terrestrial pollen sum.

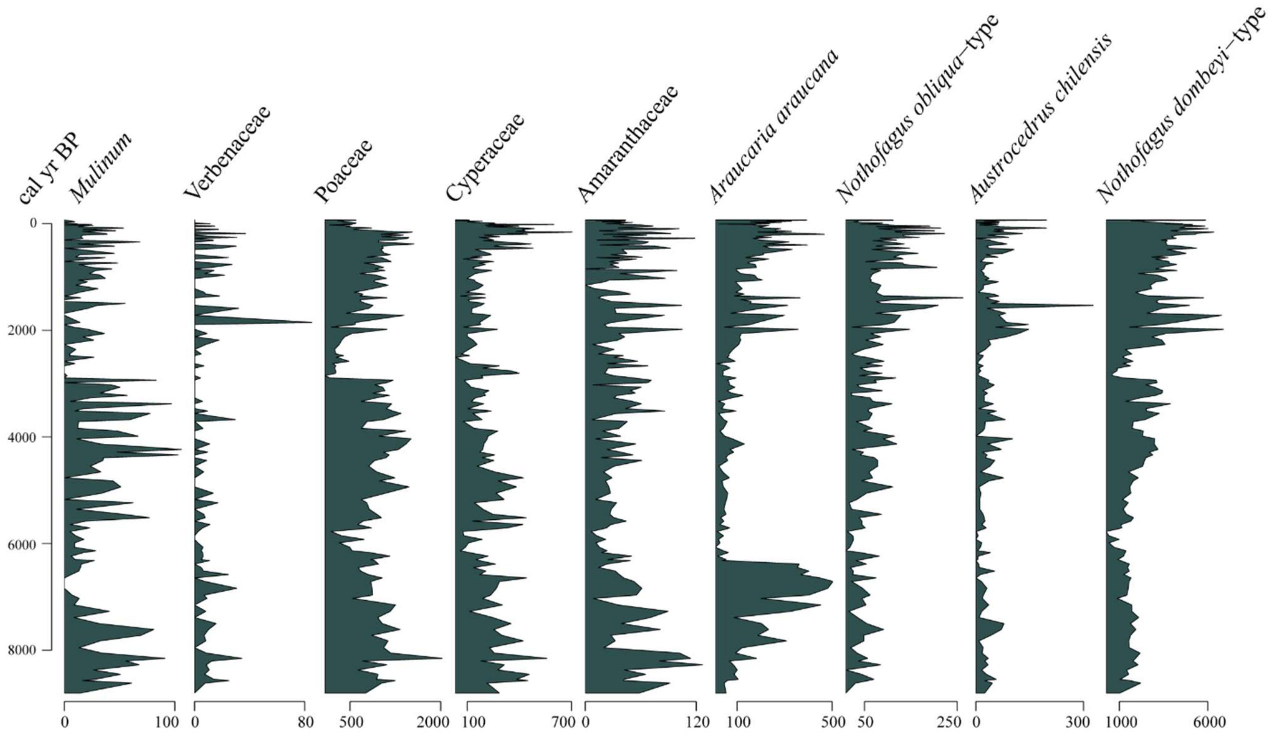

Figure 4.4 Pollen accumulation rate (grains cm^{-2} yr^{-1}) of selected taxa along the record. Taxa are order regard their weighted average of the PAR. Note different x-scale for readability of the diagram.

4.4.3 Fire history

Fire history is reconstructed following the pollen zones. CHAR (Figure 4.5a) shows variation along the records with periods of high accumulation (5-10 pieces cm^{-2} yr^{-1}) between 9-8 ka and 5.8-3 ka. The grass-to-total charcoal index (Figure 4.5b) indicates that grass was the main fuel combusted during the last 9 ka. The CHAR analysis detected 20 significant fires for the last 9 ka in the area close to Lake Relem (Figure 4.5c). Although, peaks in the interpolated charcoal were observed, some of them could not pass threshold remaining insignificant. Of those significant peaks, most of them have a SNI close or higher than 3 (Figure 4.5d) adding confidence to the results. Fire magnitude were normally <40 pieces cm^{-2} yr^{-1}, but only one peak registered 520 pieces cm^{-2} yr^{-1} approximately at 5.6 ka (Figure 4.5e). Between 9-6 ka fires were fairly infrequent; with almost a single fire every 1.5 ka (Figure 4.5f). Fires became more frequent between 6-2.5 ka, when a fire event would have occurred almost every 200 years.

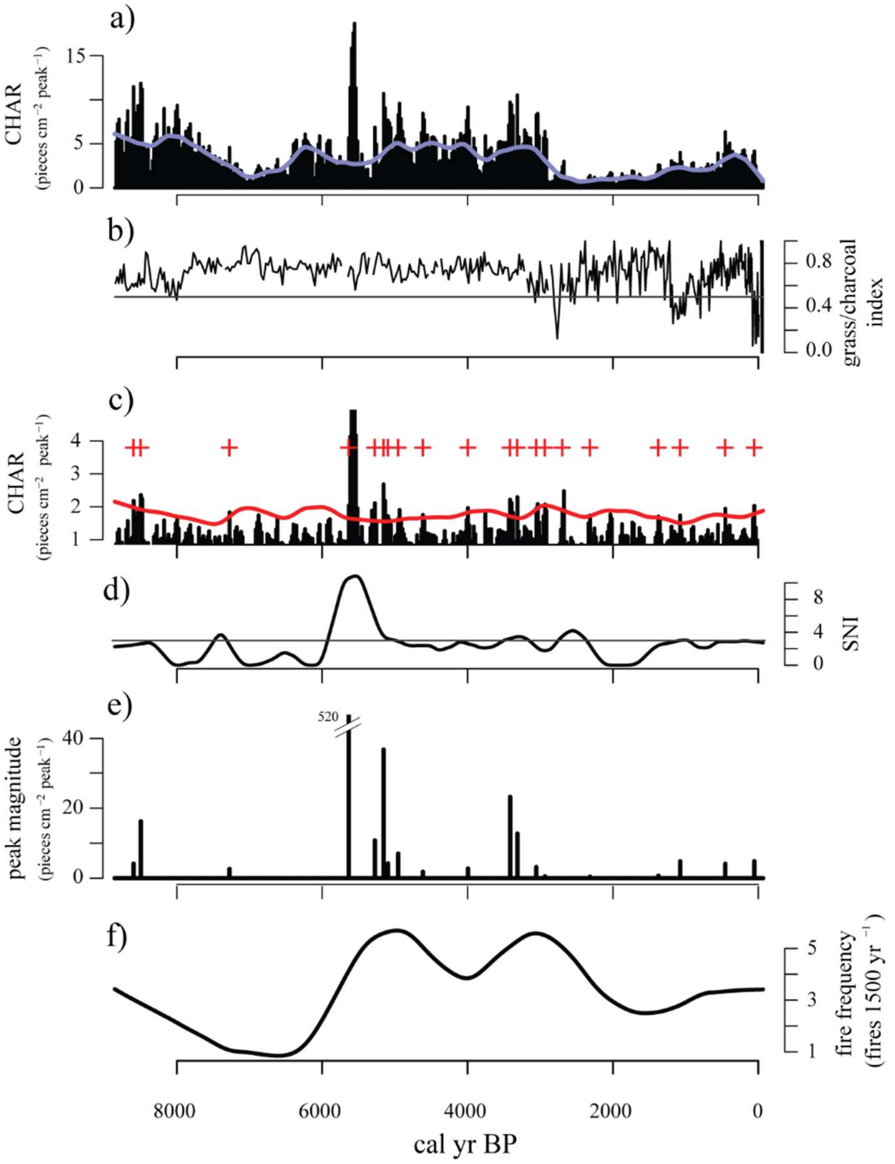

Figure 4.5 Local fire history for lake Relem. a) $C_{interpolated}$ to 20yr and $C_{background}$ defined by 500yr trend with robust Lowess method (blue line). b) Grass-to-total charcoal index, threshold indicate values >0.5 with dominance of grass charcoal and <0.5 dominance of wood charcoal particles. c) shows the peak magnitude, C_{peak}, obtained from the ratio between $C_{interpolated}/C_{background}$, threshold defining C_{noise} (90%) and identification of the significant events detected; d) Local Signal-to-Noise Index, values ≥3 indicate consistent peak detection. e) peak magnitude of significant fires. f) fire frequency for time span of 1500 years.

Charcoal parameters of fire regime explain a small part of pollen variation (Figure 4.6b). Fire frequency (smPeakFrequ) and fire return interval (smFRIs) are significantly related with the pollen composition, while the fire event (peaksFinal) and the magnitude of the event (peakMag) have no significant relation with pollen (Figure 4.6b). The highest abundance of *Araucaria araucana* pollen occurred during a time when fire frequency was lowest (Figure 4.5b, 4.6). On the contrary, *Ephedra, Nothofagus obliqua*-type and Caryophyllaceae are positively related to high fire frequency since the abundance of these taxa increase during period of major fire frequency.

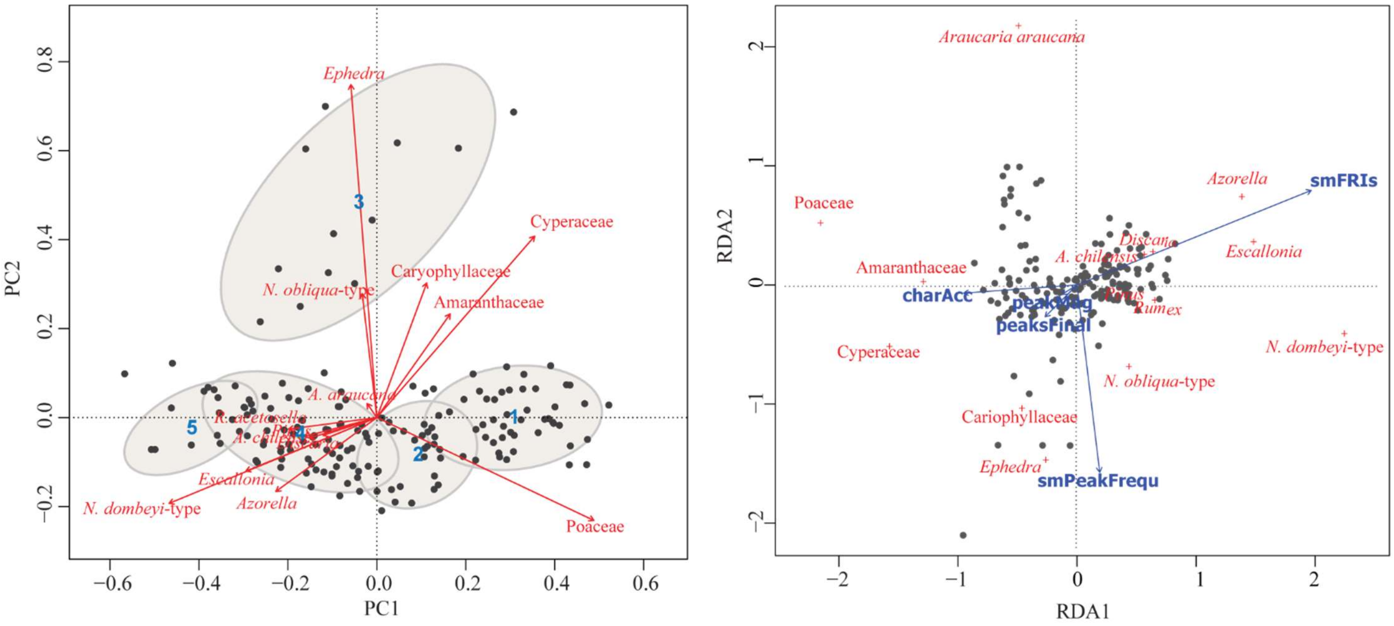

Figure 4.6 Ordination diagrams, only most abundant taxa are plotted. a) Results of Principal Component Analysis for unconstrained pollen data. Ellipses indicate groups of samples regards significant pollen zones as result of cluster analysis. b) Constrained pollen data by fire parameters: Charcoal accumulation rate (charAcc, P 0.001), fire event (peakFinal, P 0.331) and the magnitude of the peak (peakMag; P 0.27), fire frequency (smPeakFrequ, P 0.001) and Fire return interval (smFRIs, P 0.001).

4.5 Discussion

4.5.1 Vegetation and fire dynamics at the ecotone

Changes in pollen abundance of *Nothofagus dombeyi*-type and Poaceae in Patagonia, indicators of forest and grassland respectively, suggest that the position of the forest-steppe ecotone have changed through the Holocene (Iglesias et al., 2014; Whitlock et al., 2006). As the ecotone is determined by the steep precipitation gradient from west to east, the increasing (decreasing) pollen abundance of *N. dombeyi*-type (Poaceae) is related to the expansion (contraction) of the forest and to the increasing precipitation throughout the Holocene. Composite curve for relative abundance of *N. dombeyi*-type in northern Patagonia (41-44° S) decreased between 11-7.5 ka (Nanavati et al., 2019), however high variability during the lower maxima (~7.5 ka) suggest local changes rather than regional. The authors show that *N. dombeyi*-type increased again about 7 ka reaching a maximum around 5 ka. The increase of *N. dombeyi*-type at Lake Relem lags for about 1.5 ka regard sites between 41-44° S. The causes for the lag in *N. dombeyi*-type expansion are not clear. Perhaps the influence of persistent arid condition during early and mid-Holocene (Jenny et al., 2003) were likely sharper and enhanced north of 41° S. Current annual precipitation is lower at Lake Relem than in those sites studied south of 41° S, where around 39° S the summers are driest and the temperature range are more extreme (Bianchi et al., 2016). Lake Relem is also at a higher altitude and most to the east, what limit the distribution and abundance of tree taxa such as *Nothofagus dombeyi*, *Nothofagus pumilio,* and *Austrocedrus chilensis*. From 5 ka to the present, *N. dombeyi*-type at the ecotone, between 41-44° S, decreased as *Austrocedrus chilensis* expanded. *Austrocedrus chilensis* reached abundance between 10-30%, more notoriously around 41° (Iglesias et al., 2014). The expansion of *Austrocedrus chilensis* might form a mixed forest, but not a displacement of the position of the forest-steppe ecotone since Poaceae does not show significant long-term increase (Iglesias et al., 2014). In Lake Relem, the pollen of *Austrocedrus chilensis* account for sparse groups of individuals eastward of the lake and represented marginally through the record (Figure 4.3). Therefore, through the Holocene *Austrocedrus* may play a negligible role at the ecotone around 39° S. It seems that the shifts of the ecotone boundaries at the *Araucaria* section have followed a different pattern as showed by Nanavati et al. (2019) for northern (41°-44° S), central (44°-50° S) and southern (50°-55° S) Patagonia.

The fire history in Relem indicates that fire frequency (Figure 4.5e) increased when precipitation rose about 6 ka (Jenny et al., 2003; Lamy et al., 2001), while on the contrary fire frequency was lower during the driest period. Relatively low PAR before 6 ka suggests a low fuel biomass and from 6 ka to the present PAR augmented. Increasing precipitation and temperature may triggered increasing biomass, but increasing ENSO event frequency from 6 ka to the present which added more variability to the climate (Moy et al., 2002). Nowadays, ENSO at this latitude is related with a dry period (Garreaud, 2009). Furthermore, recently was found that lightning-strikes are coupled with ignited fire in years of high temperature during ENSO-events (Mariani et al., 2018). However, during the recent decade fires caused by lightning account by less than 5% (Gonzalez et al., 2018), which might explain the low fire frequency around Lake Relem. Perhaps, frequent fires between 6-4.5 ka ameliorate gradually the grassland in favor of *Nothofagus* species, and later the increasing moist condition allow the expansion of *N. antarctica* and the development of *N. dombeyi* and *N. pumilio* in protected hills nearby of Relem (Figure 4.1b). As *Nothofagus dombeyi*-type and precipitation remain relative constant for the last 2.5 ka (Jenny et al., 2003; Lamy et al., 2001), the fire frequency decrease. It is not clear if lightning could decouple of ENSO-events and explain absence of fire. But also the lack of fire-events coincides with the highest indigenous population before the arrival of Spaniard (Perez et al., 2016). Alternatively, lightning might keep occurring but could not burn the vegetation or consume the forest due to predominant moist condition; also because the forest at the ecotone tend to act as fire-breaker (Mermoz et al., 2009; Morales et al., 2015).

The Euro-American colonization between 1850-1900 CE burned approximately 25% of the forest in eastern flank of the Andes (Rothkugel 1916). For the same period dendrochronological evidences record an increase in fire occurrence more or less synchronic across the *Araucaria* region (González et al., 2005; Mundo et al., 2013). Our analysis recorded a single peak for this period (Figure 4.5c; ~1895 CE) suggesting that the surrounding of Lake Relem was in fact burned, but the record do not identify a change in the frequency. Perhaps, the increase in macrocharcoal accumulation (Figure 4.5a) for the last 200 years would correspond to this several small-areas burned. The analysis of macrocharcoal in Relem also indicates that fire caused during this time was as big as other in the local history (Figure 4.5e). But, this particular event burned mostly non-grass material (Figure 4.5b). Nevertheless, this event might have a small effect in dominant taxa, where *Nothofagus dombeyi*-type (Poaceae) shows a small decrease (increase) for a very short time before recover to previous abundance.

In Lake Relem vegetation responses to fire regime indicate that it is more sensitive to change in the frequency and FRI than to the fire event and its magnitude (Figure 4.6b). In sedimentary records, the responses of vegetation to individual event have not been asses at the ecotone so far (but e.g. Henriquez et al., 2015 in western lowlands of the Andes). Studies document that *Nothofagus* species can regenerate vigorously within a decade after severe fire disturbance (Gonzalez et al., 2005; Veblen et al., 1992). However, vegetation in the mixed *Nothofagus-Austrocedrus* forest (around 41°S), may present alternative-stable-state in response to repeated fire disturbances caused by humans (Kitzberger et al., 2016; Paritsis et al., 2015). The authors observed that vegetation after repeated fire during the 20th century were re-colonized by pyrophytic shrubs species (e.g., *Discaria, Berberis, Ephedra*). This vegetation response created a mosaic of vegetation at the landscape level in an otherwise forest dominant species. In our results *Ephedra* is well related with high fire frequency, while *Discaria* is rather associated with periods free of fires (Figure 4.6b). The results for the study area suggest that vegetation can resist light disturbances without changing the composition at the landscape level, and recover pre-disturbance values relatively fast. Other taxa do not show any trend and no indicator taxa could be defined since sporadic appearance in the record.

4.5.2 The role of fire in the natural variability of *Araucaria* dynamics

The development of *Araucaria* was independent of fire events and only small changes can be visually attributed to past fire events (Figure 4.6). Charcoal accumulation rate (CHAR) in Patagonia is commonly considered as an indicator of fire activity; however, we found no effect on the *Araucaria* (Figure 4.6b). On the other hand, we expected that intense fire should have strong negative effect on the abundance but the fire magnitude does not show any effect in *Araucaria* pollen too (Figure 4.6b). It seems the fuel biomass were rather low in the past, or even lower when Poaceae was dominant before 4.5 ka, thus fire was likely of low intensity. This could explain the lack of impacts on the pollen abundance after fire events. On the contrary, the abundance of *Araucaria* in Relem was strongly influenced by changes in fire frequency. The pollen abundance of *Araucaria* during the period of frequent fire is lower than the overall average, while long period free of fire coincide with abundance above the average (Figure 4.6).

Although the rise and fall of *Araucaria* between 8 and 6.2 ka (Figure 4.7a) was also found by the same time in Lake Torta ~20 km south of Relem (Fontana & Giesecke, 2017), two other sites in the same valley of Lake Torta do not show the same pattern (Fontana & Giesecke, 2017; Moreno et al., 2018). In modern pollen rain *Araucaria* can reach up to 23% nearby Relem around Paso Los Arcos (Paez et al., 2001). The vegetation in this area is not abundant, composed by few grasses in the underground, the shrubby *N. antarctica* is almost absent*,* while *Araucaria* is the unique tree forming groups of dense woodland. In Relem, the relative abundance of *Araucaria* is not only enhanced by the lack of pollen of *Nothofagus dombeyi*-type, since *Araucaria* PAR (Figure 4.4) is also high. The origin of the pollen rise and persistence is unknown, but it coincides with a long period of low precipitation (Lamy et al., 2001; Jenny et al., 2003), and with long period free of fires (Figure 4.7b). Maybe, the established population of *Araucaria* could take advantage of local fire about 8 ka (Figure 4.7b) to colonize and expand into the area. Likely the lack of shrubs competing and the absence of fire killing young individuals may allow the expansion. Seedlings of *Araucaria* tend to be abundant under canopy and can present continuous regeneration with multi-age stand (Gonzalez et al 2006; Roig et al., 2014). Later, after prolonged dry period (Lamy et al., 2001; Jenny et al., 2003) the population around Relem might weakened, many individuals died and the load of pollen decrease drastically. Since there is no significant fire peak around 6.2 ka, the fall in *Araucaria* pollen is not related to fire. A possible explanation would be a catastrophic disease.

To identify the population trends for *Araucaria* is one of the research priorities to assess its conservation status (Premoli et al., 2013). The relative abundance for the last 50 years is higher than the overall mean abundance, around 3% (Figure 4.7a, dotted line). Probably as result of logging ban and the creation of protected areas, but also due to localized logging and perhaps not a strong land-use change before 1950s (Moreno-Gonzalez et al., 2019; Chapter 3). High resolution of pollen and macrocharcoal depict a sudden drop in abundance related with a fire event dated to 1895 CE, during colonization (Figure 4.7a, b). However, the pollen drop was relative small and recovered short after. This event was of low-magnitude and burned principally grasses, suggesting that the event was not severe for *Araucaria*. However, the response of *Araucaria* pollen presented in this work account for its sensibility to fire disturbance, the resistance of mature individuals to moderate fire intensity (Burn 1993), and for a fast recovering. Perhaps the most relevant current risk to the stability of *Araucaria* are the *Pinus* plantation. Nearby of Lake Relem is cover by *Pinus* plantation with scarce *Araucaria* individual. On the four topmost samples (from 2000 until 2015 CE) the abundance of *Araucaria* falls from 8 to 4% as *Pinus* increase up to 15%. The impact of these plantation to the vegetation include the *Pinus* regeneration in non-vegetated areas, the homogenization of the landscape (Garcia et al., 2018; Moreno-Gonzalez et al., 2020; Chapter 3), as well as an increasing risk of severe fire (Taylor et al., 2017).

A comparison of short records for the last 200 years found none common significant decreasing of *Araucaria* (Moreno-Gonzalez et al., 2020; Chapter 3). Instead, these records indicate that in moist sites with *Araucaria* the pollen abundance decrease slightly, other shows small increasing under mesic to xeric condition, while others do not show any trend. Heusser et al (1988), showed in the Mallín Paso del Arco (c. 12 km north of Lake Relem) *Araucaria* tends to increase since the last 2 ka, while decreasing on the last 2 uppermost samples (Heusser et al., 1988). The same authors showed that in Mallín Río Malleo (~75 km south-west of Relem) there is no change for the same period. In Mallín Miraflores (~38 km north-west of Relem), although a low sample resolution, the pollen abundance of *Araucaria* tends to increase from 3 ka to the present (Reyes 2001). On the contrary, Fletcher and Moreno (2012), in Lake Sn Pedro (~64 km north-west from Relem) observed a continuous decrease from 1.5 ka to the present. This comparison indicates that there is not a general decreasing of *Araucaria* and the natural variability seems to present rather local patterns.

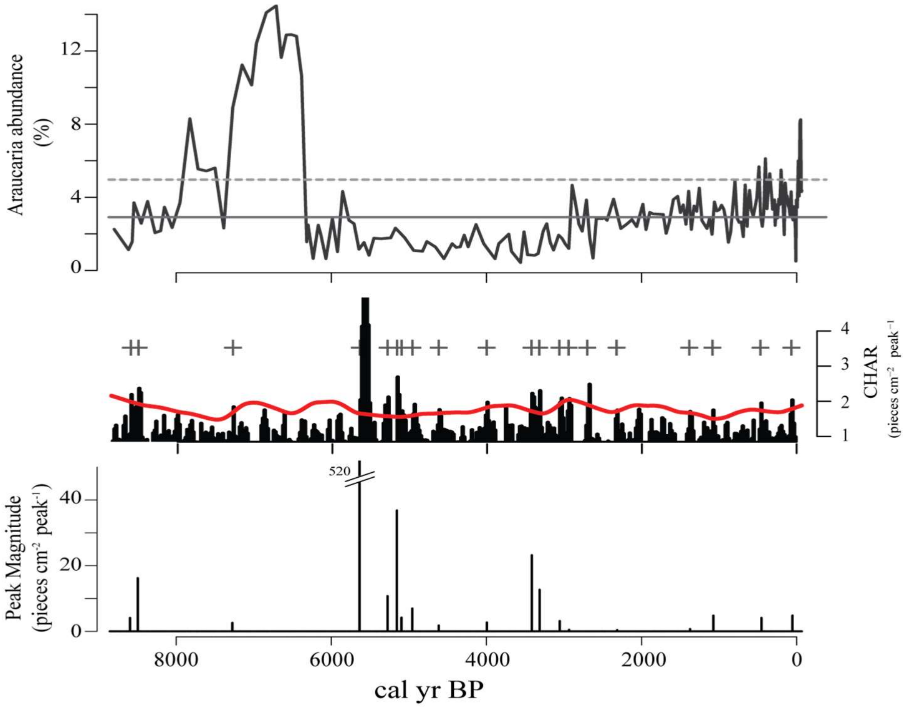

Figure 4.7 a) Long-term variation of *Araucaria araucana* pollen abundance (~8.5 ka), horizontal lines reference the mean abundance for the last 50-yr (5%, dotted line) and for the whole period (3%, continuous line). b) Fire events history (red line indicating threshold) and c) magnitude of the events.

4.6 Conclusions

The results suggest that major driver of vegetation changes along the last 9 ka in the *Araucaria* forest was apparently the change of climatic condition, while secondarily small fire disturbance altered the general patterns. The pollen analysis in study area indicate that steppe vegetation dominated between 9-4.5 ka while gradually change for about 1.5 ka towards forest condition. After 3 ka to the present *Nothofagus dombeyi*-type became more abundant, but the range of variability suggest that tall trees and forest never was fully developed here, and rather a patchy landscape less fragmented than today. For more specific relationship between fire and vegetation, we found that:

- In the study area fire events are ubiquitous for the last 9 ka, however are seemingly stochastic and normally non severe. Climatic reconstructions suggest some relation with our fire and vegetation reconstruction, but the underlying mechanism triggering fire in the past, such as drought, human, and lightning, are not conclusive.

- Clear signal of human disturbance occurs only with *Pinus* plantation. Fires during the colonization period were captured as a single event, therefore no evidences of change in fire regime. Also, the magnitude of this event was not higher than other past events.
- Fire in the study area is rather infrequent but variable with long periods free of ignition. The severity of fire was rather low, and vegetation could resist and/or recover short after events.
- The rise of pollen abundance of Araucaria may indicate an outstanding dense population. In absence of fire evidence, the decay of the population around Relem was likely by a disease. Although current information available is not conclusive, there is no a common large-scale population decreasing, but rather a more local variability. Current populations trend seems to be part of the historical range of variability, however the recent expansion *Pinus* plantation is a novel kind of disturbance in the region that could increase the risk of *Araucaria* persistence.

Acknowledgements

This work was supported by a scholarship to RM through program DAAD/BECAS Chile, 2014 (57144001), and by the DFG Grant FO 801/3-1. TG acknowledges funding from the DFG Grant GI 732/9-1. The authors declare that there is not conflict of interest. We are thankful to Prof. Dr Behling for supporting part of this research.

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Chapter 5-

5. Vegetation responses to volcanic disturbances at the *Araucaria* forest-steppe ecotone in southern South-America.

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Abstract

1. Volcanic eruptions play a principal role in vegetation dynamics and its natural history. However, large events are infrequent and eruptions with significant imprint in today vegetation patterns occurred in the past. Volcanoes in southern Andes are particularly active during the last 10 ka, and support unique ecosystems such as the Araucaria forest. Although volcanism might have impacted the genetic variability and distribution of Araucaria, it is considered that Araucaria have evolved to resist volcanic disturbances and depend of the disturbances to persist. However, some question remains unanswered. To provide insights into the vegetation responses to past volcanic disturbances, paleoecological studies allow the reconstruction of the vegetation and the disturbance regime.

2. We conducted a palynological study in a small lake located at the *Araucaria araucana* forest-steppe ecotone to reconstruct the vegetation history. To reconstruct the volcanic regime, we made use of the tephra layers. We investigated the successional patterns caused by volcanic eruptions during the Holocene, especially the Sollipulli-Alpehue eruption (So-A), one of the largest eruption in the zone.

3. During the last 9 ka, 39 tephrafall have buried the vegetation around Lake Relem. Tephra layers range between 1-7 cm thick, whilst So-A eruption deposited ~2 m. Between 4-2 ka tephrafall were more frequent, whereas none tephra layer was registered from 2 ka until present.

4. The vegetation was sensitive to the impact of small tephrafall but seldom caused significant change. After tephrafall, we also found variable patterns of palynological richness. So-A eruption left a strong imprint in the vegetation, where forest and grassland were severely affected. Early vegetation succesion was dominated by *Ephedra*, while original condition may recover after c.500 years. Slight increase of pollen percentage from *Araucaria* and *Nothofagus obliqua*-type could be indicative of undisturbed patches.

5. Vegetation was buried several time by tephrafall at irregular intervals with small impacts on the vegetation, nonetheless it had slightly more impacted grasses and shrubs. The vegetation resisted without permanent changes, recovering relatively fast after the large So-A eruption with unexpected *Ephedra* as keystone species. The relative stability of *Araucaria* pollen suggests no change in its geographical distribution at the steppe.

Keywords: *Araucaria araucana,* disturbance regime, vegetation response, long-term vegetation dynamics, volcanic ecology

5.1 Introduction

Volcanic eruptions are among the most important disturbance agents on Earth, and the impacts can trigger sudden and large environmental changes, particularly on the vegetation (Crisafulli & Dale, 2018). Large volcanic eruptions are infrequent, episodic and stochastic events in the history of an ecosystem (Turner et al., 1998). In general, volcanic disturbance can be characterized by the return interval, intensity and severity (White and Picket 1985). Volcanism creates dynamic processes depending on the disturbance mechanism and the magnitude, which in turn can create complex patterns on the vegetation at the landscape or regional scale (e.g., Crisafulli & Dale, 2018; Foster, Knight, & Franklin, 1998). In example, Zobel & Antos (2018) observed that the vegetation growth rapidly after being buried by tephrafall, while del Moral & Grishin (1999) observed that the type and arrange of biological legacies in disturbed areas drove regeneration patterns and the rate of vegetation development after disturbance. In addition, the interaction with other disturbances and random process made it difficult to understand the ecology of the volcanoes (Buma, 2015; Swanson & Crisafulli, 2018). Understanding the lasting effects of process and patterns of vegetation responses like the resistance and recovery may help in designing nature management (Dale, Swanson, & Crisafulli, 2005; Franklin et al., 2002). However, the study of the vegetation dynamic is challenging since active volcanoes are located in remote areas, the long-term monitoring requires many resources, the responses last too long to be monitored in human-life span, or had occurred far in the past (Swanson & Crisafulli, 2018). Well-designed paleoecological studies, through the study of tephra layers and pollen sub-fossil in sedimentary records, could help to understand past volcanic disturbances and vegetation responses.

Paleoecological studies have attempted to illustrate past impact of eruption and aimed to contribute to disturbance ecology. However, the reconstruction of volcanic disturbance regime and the vegetation responses from sedimentary records is not straightforward. For example, the potential effects of large-eruptions of Icelandic volcanoes on the Britain and Ireland vegetation have been largely studied for more than 20 years. Several published pollen records show contradictory and/or weak evidences, therefore it was concluded that there is a lack of evidence of volcanic disturbance in the European vegetation (Paine et al., 2013). In addition, in the Cascade Range, in the western North America, an experiment was conducted in a small lake located 500 km eastward of Mt. Mazana, to infer the impacts on local and regional vegetation after three different eruptions (Egan et al., 2016). The thickness of the tephra layers varied between 10-40 mm. In this study, the authors concluded that eruptions did not trigger significant changes in terrestrial pollen taxa, but the aquatic taxa changed due to enrichment of nutrients. Unlike those areas, after Taupo eruption (~1850 BP) in North-Island, New Zealand, pollen evidences indicate that this eruption destroyed the forest in the surrounding areas, and up to 170 km east of the vent the vegetation suffered a variable degree of disturbance (Wilmshurst and McGlone, 1996). In many areas the forest could not recover to its original conditions, and unexpectedly far sites from the crater covered by thin tephra layer were strongly impacted.

Active volcanoes during the Holocene are dispersed in the Earth, but one of the most active areas is located in the south-eastern part of the Pacific (Stern, 2004). The subduction of the Nazca-plate underneath the south American-plate has triggered several large-eruptions in the last 10 ka (Fontijn et al., 2014). The southernmost section of the Andes supports unique forest ecosystems which have been influenced by these volcanoes through the time. Volcanic disturbance is a major ecological disturbance affecting structure and functions in this Andean forest and surrounding vegetation (e.g., Veblen et al., 2016). As result of the eruptions the elevation of the tree-line can be depressed (Daniels & Veblen, 2004; Veblen et al., 1977), or sustain uneven age forest in the landscape (Kitzberger, 2012). Moreover, volcanism would be responsible to keep pioneer species such as *Nothofagus* species and *Araucaria araucana* as dominant (Veblen and Ashton 1978; Burns, 1991).

Despite the volcanic characteristics and the unique vegetation, few studies have been carried out to document the vegetation responses after eruptions. For instance, after the eruption of the Puyehue-Cordon del Caulle Volcanic Complex (PCC) in 2011, *Nothofagus pumilio* was the principal species resprouting in zones buried by ~50 cm tephra, and several cohorts would correspond to past eruptions (Montiel et al., 2016). Eastward from PCC, the steppe vegetation was buried by <5 cm tephra, and rhizomatous geophytes species such as *Poa* sp. and *Rumex acetosella* increased while therophytes disappear (Ghermandi et al., 2015). Another case is the 2008-eruption of Chaitén volcano. Swanson et al. (2013) described the early responses of the different types of disturbance as similar to those happened after Mount St. Helens, where each disturbance type impacted specific areas that created different patches of disturbance in the landscape, therefore the type of damage produced to the vegetation. Furthermore, Moreno-Gonzalez et al. (2019) pointed out that in the direct blast-zone of the disturbance gradient the early vegetation establishment is associated with elevation gradient, and that the regeneration depend on life-traits strategy and the types of biological legacies remaining in the area.

The vegetation history in the eastern Patagonian Andes has been also largely studied throughout pollen analysis (e.g., Iglesias et al., 2018; Whitlock et al., 2018; Nanavati et al., 2019). However, palynological evidences are not always clearly linked to the volcanic impacts, especially when *Nothofagus* forest is dominant and the magnitude of the eruptions are small (Álvarez-Barra et al., 2019). Other cases the volcanic impacts on the vegetation have not been weighed. For example, close to Chaitén and Michinmahuida volcanoes the vegetation history was reconstructed from two sites, Lake La Zeta and Lake Theobald, located ~80 km eastward of these volcanoes (Iglesias et al., 2014). The lakes are ~60 km distant from each other and present different amount of tephra layers. Even though the age-depth model are not exact, both records show one tephra layer that could correspond to one of the Michinmahuida eruption about 5.1-6.3 ka (Amigo et al., 2013). The pollen diagram from Lake Theobald indicates a small decrease of the total Pollen-Accumulation-Rate (PAR) and Poaceae percentage in samples dated after 6 ka, plus a slight increase of shrubs and steppe taxa. In the contrary, in the record of Lake La Zeta the pollen percentage and PAR did not change. This example gives an account of differential vegetation responses, or the lack of, for sites which are situated close to each other. Another example could be the PCC and Antillanca-group which register large-eruptions during the Holocene that can be observed in sedimentary records. Despite several pollen records, there is no evidence of significant change due to volcanic eruption. Instead, vegetation changes around Lake Nahuel-Huapi are mostly attributed to climatic and fire-regime change (e.g., Iglesias et al., 2014; Whitlock et al., 2006).

Several gaps of knowledge on the role of volcanic disturbance and how they have impacted the current forest-steppe ecotone in Patagonia are still remaining. In the northernmost section of the forest-steppe Patagonian vegetation, *Araucaria* is located on an active volcanic area too. Volcanic eruptions might influenced the genetic variability of *Araucaria*, but also the population distribution and regeneration dynamics (e.g., Bekessy et al., 2002; Veblen et al., 2016). Furthermore, *Araucaria* is an endangered species that normally constitutes a part of the tree-line on the volcanoes, or grows close to the steppe in the form of woodlands or isolated trees. Despite its social and ecological importance, few long-term vegetation reconstructions have been made so far in the *Araucaria* forest-steppe ecotone. To contribute to the knowledge of vegetation dynamics and the volcanic disturbance regime in the *Araucaria* forest-steppe ecotone we aim 1) to reconstruct the long-term vegetation and the volcanic disturbance history in the *Araucaria* forest-steppe ecotone, and 2) to assess the vegetation responses to past volcanic disturbance.

Due to the distance to the volcanic source, the forest-steppe ecotone eastward of the Andes is affected mostly by tephrafall that buries the vegetation. Tephrafall therefore is the main disturbance type around Lake Relem. We hypothesized that vegetation responses should be related with the tephra thickness, where vegetation would be more resistant and/or recover faster to thin tephrafall than to thick tephrafall.

5.2 Study area

5.2.1 Climate and Vegetation

The study area is located in the current forest-steppe ecotone around 39° S, in northern Patagonia (Figure 5.1). Lake Relem (38°58'39" S; 71°4'51" W; 1268 m a.s.l.) is a shallow and small lake (~2.5 m depth, ~1 ha, respectively), without river inflow or outflow. The macroclimate is temperate, due to oceanic influence on the average monthly temperature above freezing. The precipitation is minimum during the austral summer (DJF), giving it a mediterranean character (Luebert & Pliscoff, 2006). Year round precipitation arrives with dominant westerly winds (Garreaud, 2009). The Pacific air masses discharge most of the precipitation on the western section of the Andes, which reaches elevations above 2000 m, creating a sharp rain-shadow effect (Mundo et al., 2013). At high elevation the mean precipitation reaches 2500 mm or more and decreases abruptly to approximately 200 mm around Lake Relem (Bianchi et al., 2016; Paruelo et al., 1998). The annual mean temperature ranges between 8-12 °C on the western slopes, and about 10-16 °C at the eastern side (Bianchi et al., 2016).

Araucaria araucana forest at 39° S occurs mainly above 1000 m elevation up to the tree-line around 1700 m a.s.l., in fragmented populations (Gonzalez et al., 2006) (Figure 5.1). The interaction between disturbance regime, topography and climatic conditions create complex pattern and niches for different plants associated with *Araucaria araucana* (Kitzberger, 2012;

Roig, 1998). As a general pattern, *Araucaria araucana* can form: 1) dense, multilayer forest with dominance of *Nothofagus dombeyi*, and *N. pumilio* mixed with typical understory Rainforest species under humid conditions, 2) open forest or woodland with dominance of deciduous *N. antarctica* and other shrubs in the understory under more mesic-climatic conditions, 3) in xeric conditions, scattered individuals of *Araucaria* without or scarce *N. antarctica*, *Austrocedrus chilensis*, *N. obliqua* and broadly dominated by bunch grasses and shrubs as *Discaria* and *Colletia* (Luebert & Pliscoff, 2006). *Araucaria* and *Nothofagus* species are considered the tree pioneer species after volcanic disturbances (e.g., Veblen et al., 1982).

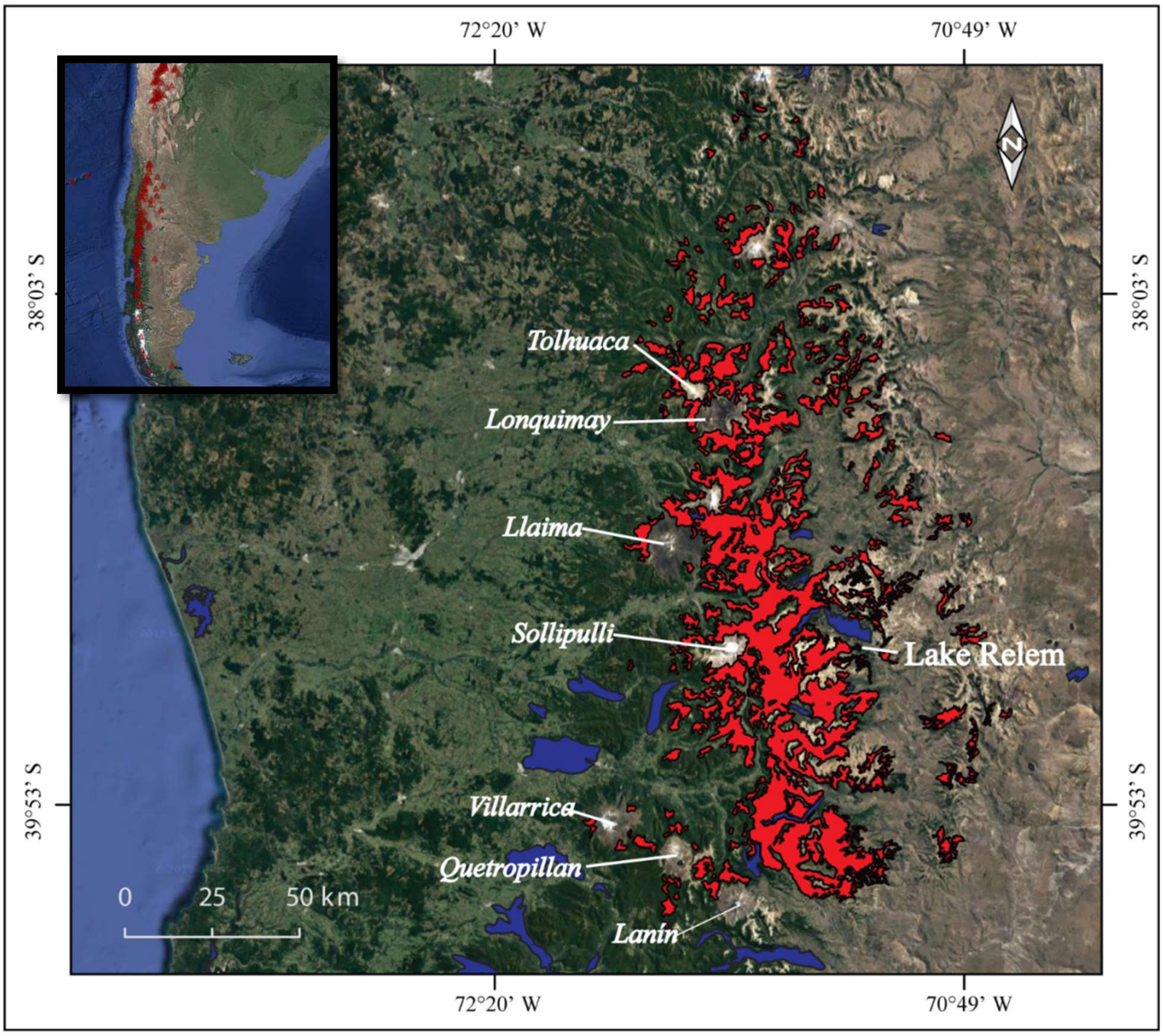

Figure 5.1 a) Figure showing active volcanoes (red triangles) during the Holocene in southern South America (Global Volcanism Program, 2013). b) Map of the study area representing the position of Lake Relem, the location of volcanoes closes to Lake Relem, and the distribution of *Araucaria araucana* (red polygons).

5.2.2 Volcanic setting and eruptive history

The study area lies in the Southern Volcanic Zone of the Andes (SVZ). The SVZ is a result of the subduction of the Nazca plate beneath the continental South American plate, and is extended between 33° S to 46° S (Gilbert et al., 2014). In a radius of 100 km around Lake Relem there are 7 volcanoes that have been active during the Holocene (Figure 5.1). Fontijn et al. (2014) list all the eruptions recorded so far to the SVZ, which are summarized in Table 5.1. The Lonquimay volcano has had more regular eruptions of considerable magnitude. In relation to the Sollipulli-Alpehue eruption, Lake Relem is located within the isopach of 2 m (Fontijn et al., 2016). Two large eruptions have occurred recently in the temperate forest of Patagonia: Chaitén (2008-2009) and PCC volcanic complex (2011). However, these kinds of eruptions are not unprecedented in the Holocene history of this forest. The Andes Cordillera where this forest lies are one of the most active areas in the SVZ with diverse volcanoes. Here some volcanoes have erupted every 10 years (e.g., Villarrica volcano) or have erupted at least once during the last 10 k years (Fontijn et al., 2014). The Sollipulli-Alpehue eruption (hereafter the So-A eruption) was one of the largest in the recent past in northern Patagonia, it is dated back to 2951 cal. yr. BP (Naranjo et al., 1993).

Table 5.1 Location of potential source volcanoes close to Lake Relem, its frequency (further details for each eruption are found in Fontijn et al., 2014)

Volcano name	Distance and direction from Lake Relem	Total eruptions last 10 ka	Eruptions VEI ≥3
Tolhuaca	88 km; 326° NNW	1	1
Lonquimay*	80 km; 326° NNW	26	25
Llaima	64 km; 299° WWN	55	3
Sollipulli	38 km; 270° W	2	2
Villarica	89 km; 236°WWS	150**	10
Quetropillan	80 km; 223° WS	3	1
Lanin	81 km; 205° WSS	5	4

*In Lonquimay VEI is not provided by Fontijn et al. (2014), but the composition of tephra fall (mainly dacite), probably ejected about 0.01 km3 of tephra, equivalent to VEI ≥3 (Gilbert et al., 2014)

** Some of the eruptions the dates are uncertain. Most of them occurred in the last 500 years

5.3 Methodology

To explore the vegetation and volcanic history of the *Araucaria araucana* forest-steppe ecotone we made use of the 9000-years-old long-core retrieved from Lake Relem. More detailed description about the chronology is given in Chapter 4, and here only a brief description of the pollen analysis and more compressive data analysis.

5.3.2 Pollen analysis

Along the core, a total of 176 samples of 0.5 cm^3 were taken from the cores. Pollen samples were processed following the techniques proposed by Bennett and Willis (2001), but not sieved. By adding *Lycopodium clavatum* tablets we estimated the pollen concentration, which was multiplied by the sedimentation rate to obtain the Pollen-Accumulation-Rate (PAR). A minimum of 400 terrestrial pollen grains were counted and identified using light microscope at 400-1000x. The identification of pollen grains and spores was carried out with atlases of Heusser (1971), and Markgraf and D'Antoni (1978), and pollen reference stored in the Department of Palynology and Climate Dynamics, University of Göttingen. Pollen taxonomy follows modern plant distribution within the study area, linking the pollen types to this species and genera (Fontana and Bennett, 2012). For instance, *Lomatia/Gevuina* pollen type is assumed to be produced mostly by *Lomatia hirsuta,* which is widely dispersed in the area. Other pollen taxa that cannot be differentiated (such as *N. dombeyi*-type) would correspond to the species *N. antarctica*, *N. dombeyi*, and *N. pumilio.* In some cases, we assumed the shrub *N. antarctica* since it is the most common and well adapted to growth close to steppe.

5.3.2 Data analysis

Pollen of the terrestrial taxa per sample were summed to obtain the relative abundance, expressed as pollen percentage. Later, we conducted a stratigraphically constrained cluster analysis (CONISS) for the pollen samples based in Euclidean distances (Bennett 1996). To assess pollen diversity changes, individual rarefaction analysis is a powerful tool (Birks & Line, 1992). Using rarefaction analysis, we estimated the palynological richness at the minimum terrestrial pollen count of 400 pollen grains ($E(T_{400})$), the pollen diversity estimated at $E(T_{10})$, and pollen evenness was calculated as the ratio $E(T_{10})/ E(T_{400})$ (Matthias et al., 2015). Compositional trend of the terrestrial taxa was explored through principal component analysis (PCA). The percentage was square root transformed and centralized, the samples were grouped regarding to significant zones defined previously by the cluster analysis. Furthermore, we fitted a Principal Curve (PC) to the compositional data. The starting point was based on the age of the samples, and the curve was fitted through a smooth-spline method with complexity of 5. To estimate the Rate-of-Change (RoC), we interpolated the pollen samples at a regular time interval of 50 years with smooth-spline, and then with the Euclidean distances as a dissimilarity coefficient (Bennett & Humphry, 1995).

Every tephra layer that was >0.5 cm and being evident in the core was used to reconstruct the volcanic disturbance regime. Here we considered each of these tephra layers as a single and independent disturbance event, since tephrafall is limited to a short time, and the tephra thickness is considered as a measure of the magnitude of the impact. Furthermore, each tephra was coded as a quantitative explanatory variable and modelled as a simple exponential decay process (Lotter and Birks 1993). This model is a simple but robust equation ($x^{-\alpha t}$), where x is the value for the ash (arbitrarily set to 100 by the authors), α is the decay coefficient equal to -0.5, and t is the sample depth (=time). Also, the authors arbitrarily assigned a value before tephra deposition of 0. In this manuscript, we preferred to describe the magnitude of the event of each tephra by giving the ash-value corresponding to the tephra thickness in centimeters. Unlike the record of Lotter and Birks (1993), in sedimentary records from Patagonian the occurrence of multiple tephra is quiet normal, therefore the value below a tephra layer corresponded to 0 only in some cases. In doing so, we aim to describe the magnitude of the eruptions. The frequency of volcanic events was calculated as the sum of events over 1000 years, and then was modelled with smooth-spline method (spar=0.7). Both variables, frequency and magnitude, were later used as an explanatory variable to constrain the pollen samples assessing vegetation responses to volcanic disturbance regime. All statistical analyses were conducted through RStudio 3.3.1 (RStudio Team, 2016), vegan-package 2.4-2 (Oksanen et al., 2017) and Rioja 0.9-15 (Juggins, 2015).

5.4 Results

5.4.1 Vegetation history and volcanic disturbance regime

The vegetation history from the pollen record encompasses the last 9000 cal. BP (hereafter all ages are given as calibrated years BP). (A thorough description of this pollen record was exposed in the previous chapter 4 of this thesis, here I only show some of the most relevant data related with the volcanic history of the study area). Along this period, the general trend of dominant taxa shows an overall vegetation change from steppe grassland (Poaceae) to forest (*N. dombeyi*-type) (Figure 5.2). The results of the cluster analysis indicate five significant pollen assemblage zones (Figure 5.2). The description and the interpretation of the principal results are given in Table 5.2. *N. dombeyi*-type is clearly the most abundant pollen taxa through the history, however its average was low between c. 9-4.5 ka but more variable than from 4.5 ka to the present (Table 5.2). At the time of So-A eruption, the pollen of *N. dombeyi*-type (Poaceae) was increasing (decreasing), however the abundance of both *N. dombeyi*-type and Poaceae taxa fall drastically after this eruption. *Araucaria* registered a noticeable period of high abundance, unique for the last 9000 years in the study area. A small increase in *Araucaria* pollen abundance after the So-A eruption suggests that it could resist the impact but did not expand. The same may have happened to *N. obliqua*-type.

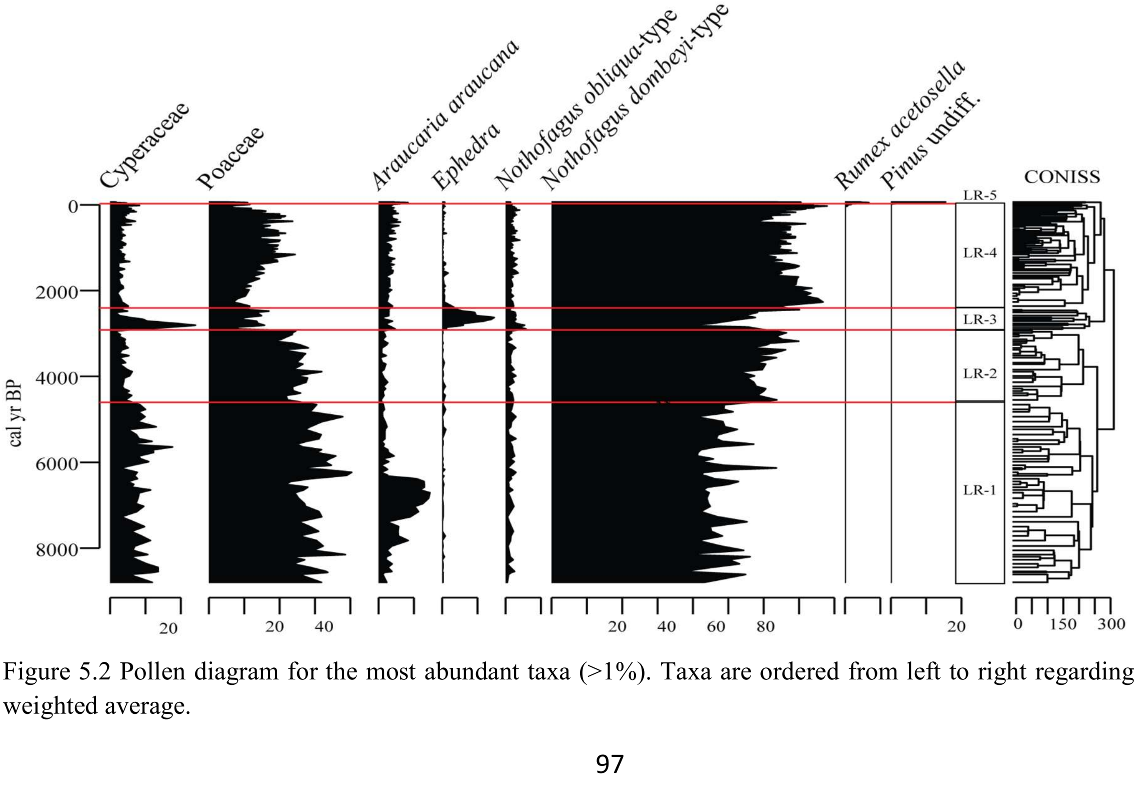

Figure 5.2 Pollen diagram for the most abundant taxa (>1%). Taxa are ordered from left to right regarding to their weighted average.

Table 5.2 Brief description of the vegetation history of Lake Relem.

Pollen zones [cal. yr. BP]	Pollen taxa	Pollen abundance		Interpretation
		Max.	mean ± sd	
LR-5 [-31: -65]	*Araucaria araucana*	8	5.6±2	Decline of *N. dombeyi*-type, and other native taxa to its present abundance. Sharp increase of *Pinus* and *Rumex*. Human disturbance through land-use change towards *Pinus* plantation. Non-analog pollen ensemble to past composition.
	N. dombeyi-type	70	62±4.4	
	Pinus	15	5.2±5.5	
	Poaceae	11	8.1±2.3	
	Rumex acetosella	7	4.7±1	
LR-4 [2414: -19]	*Araucaria araucana*	6	3.3±1	*N. dombeyi*-type recovery after So-A eruption reaching high abundance. Closed forest westward of the study area, while likely dense shrubby *N. antarctica* around the lake. *Ephedra* and Poaceae decay.
	Ephedra	3	0.3±0.4	
	N. dombeyi-type	78	66±4.9	
	N. obliqua-type	4	1.9±0.7	
	Poaceae	24	14±4.5	
LR-3 [2491: 2487]	*Araucaria araucana*	5	2.8±1.1	Post disturbance vegetation dynamics after So-A eruption. Early establishment dominated by *Ephedra*. Sharp drop in *N. dombeyi*-type compared to Poaceae. Slight increase of *N. obliqua*-type and *Araucaria*, as possible biological legacies in protected areas.
	Ephedra	15	7.6±4.6	
	N. dombeyi-type	70	54±8.4	
	N. obliqua-type	6	3.0±1.4	
	Poaceae	17	12±3.2	
LR-2 [4579: 2987]	*Araucaria araucana*	3	1.4±0.6	Vegetation change from steppe to shrub and woodland. Establishment and expansion of *N. dombeyi*-type species into open areas or grassland.
	Ephedra	1	0.2±0.3	
	N. dombeyi-type	70	60.7±4	
	N. obliqua-type	3	1.5±0.7	
	Poaceae	32	24±2.9	
LR-1 [8777: 4687]	*Araucaria araucana*	14	4.6±4.3	Steppe-like condition dominated by Poaceae Cyperaceae, Verbenaceae, *Mulinum*. Variable condition for Poaceae and N. *dombeyi*-type during short periods. *Araucaria* reached highest abundance in its history.
	Ephedra	1	0.2±0.2	
	N. dombeyi-type	64	46±5.3	
	N. obliqua-type	3	1.5±0.7	
	Poaceae	40	29±4.5	

The volcanic history and its disturbance regime were reconstructed from the tephra layer content in the sediment of Lake Relem (Figure 5.3). In total, the sediment core registers 39 tephra layers well-defined >0.5 cm thick. Most of them are between 0.5-7.5 cm thick (Figure 5.3a) but only 18 are >1.5 cm thick, what could be considered as significant peaks (red-cross, figure 5.3a). The tephra layer corresponding to the So-A eruption is the biggest one, which in the core records 216 cm. The tephra-value, modelled as an exponential decay, shows similar patterns regards the tephra thickness, but indicates a lowest effect respect the eruption magnitude and missing peak above the threshold (Figure 5.3b). Considering all the tephra layers, volcanic disturbance regime is relatively frequent (Figure 5.3c). The disturbance frequency indicates that around 7 eruptions had occurred every 1000 years between 4-1.8 ka. Before 4 ka volcanic frequency was lower than 6 events/1000 years, with periods without any disturbance around 7 and 5 ka. For the last 1.5 ka up to the present, few tephrafall are recorded, but none deposited more than 1.5 cm of tephra into the lake.

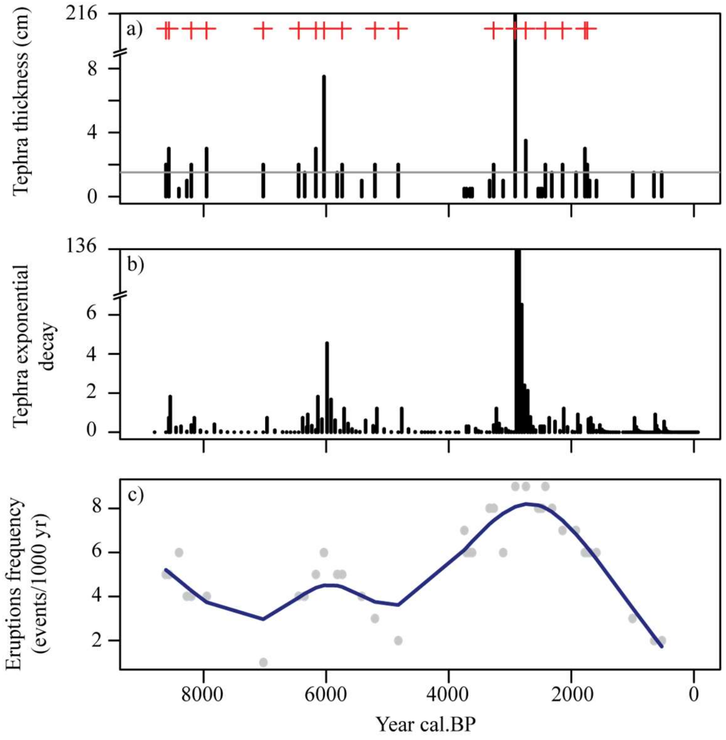

Figure 5.3 Volcanic eruption regime. a) Indicates the thick of tephra layers deposited into the Lake Relem. Grey horizontal line shows arbitrary threshold of >1.5 cm to determine relevant eruptions (red crosses). b) Tephra thickness modelled as the exponential decay after eruption. c) Eruption frequency every 1000 years. Grey points indicate the sum of frequency every 1000 years. Trend of frequency was obtained by smooth spline function (blue line) with spar =0.7.

In the unconstrained ordination diagram (Figure 5.4a) the compositional trends represent the gradual vegetation change from zone 1 to 5 showed in the pollen diagram (Figure 5.2). The first component explains 78% of the total variance, and would be interpreted as the long-term shift from steppe taxa dominance (e.g., Poaceae) to a forest with the dominance of *N. dombeyi*-type. Poaceae, *Mulinum* and Cyperaceae, among others, are more abundant in the zone 1, located on the left side of the ordination diagram. The second component explains 11% of the variance and split the overall trend where *Ephedra* is dominant. The abundance of *Ephedra* rose short after the So-A eruption (Figure 5.2), therefore the second axis is mostly related to the response of So-A (Figure

5.4a). The volcanic eruptions have a significant influence on vegetation composition (Figure 5.4b) explaining 20 % of the data. Both explanatory variables, the volcanic frequency and the magnitude (Exp.Dec), have a significant influence on the vegetation. Further analysis excluding samples after the So-A eruption indicate that the other small tephra-layers had no significant influence in the pollen composition.

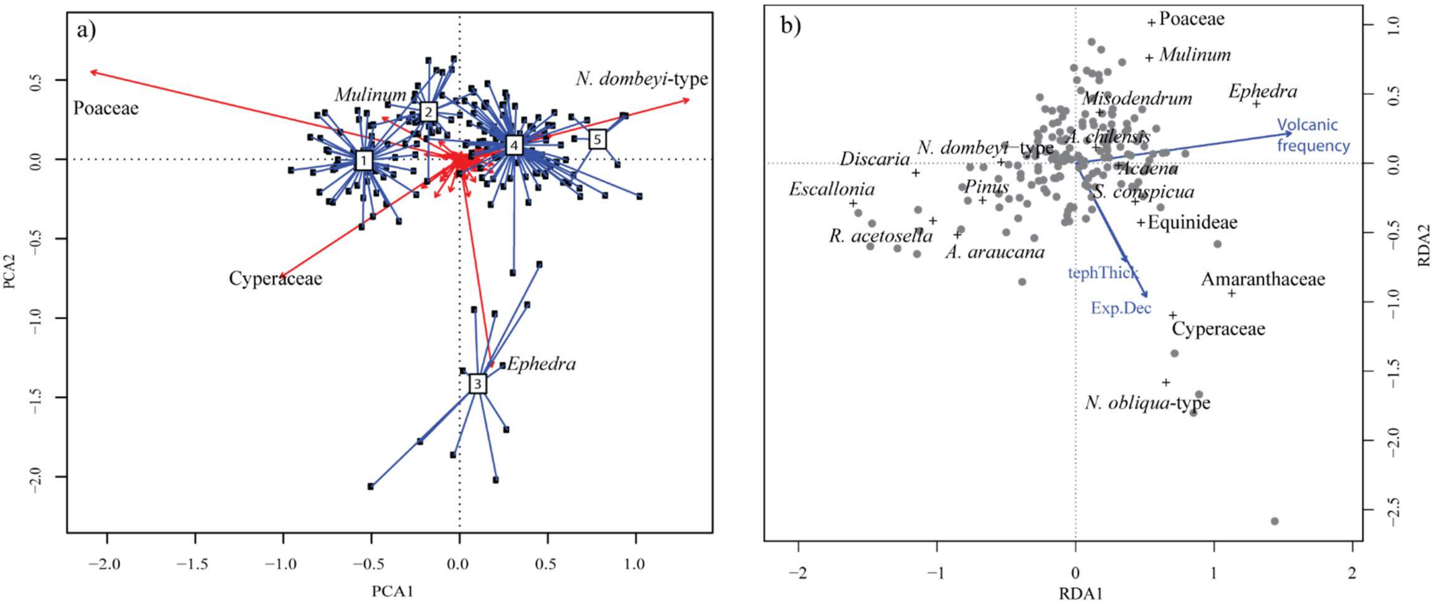

Figure 5.4 Ordination diagrams of pollen composition for Lake Relem, a) unconstrained and b) constrained.

5.4.2 Vegetation responses to volcanic events

Due to the distance of Lake Relem to the crater and direct blast zone of the volcanoes (Figure 5.1), the type of volcanic impact would correspond to the zone buried by tephra. In figure 5.5 we compare several indicators of the vegetation with the So-A eruption (vertical red line) and other unknown tephra <10 cm thick (vertical grey lines). Tephrafall that mark a disturbance event, normally caused a decrease (increase) in Poaceae (*N. dombeyi*-type) pollen percentage (Figure 5.5a). The decrease is not proportional to tephra thickness, but is always more notorious before 4.5 ka, when vegetation was likely dominated by Poaceae and other grasses. Only So-A eruption depressed the abundance of both dominant taxa, while the few events after So-A do not seem to have affected any of both pollen taxa. Along the record, PAR of all taxa together is variable (Figure

5.5b), where PAR could be interpreted as an indicator of vegetation biomass. Volcanic events normally caused small decrease in PAR between 100-500 grains cm^{-2} yr^{-1}, while after So-A eruption PAR decayed more than 2000 grains cm^{-2} yr^{-1}. Other drops in PAR can be related to sedimentary processes or other disturbances. The Principal Curve fitted after 21 iterations. The variation in distance gradient units indicates some sensitivity of the vegetation composition to volcanic disturbances, notwithstanding only few significant changes (Figure 5.5c). The most relevant changes occurred at the time of So-A, but the curve also suggests that pollen composition was relatively stable along the time. On the contrary, peaks depicted by the rate of change were not sensitive to volcanic events, except for So-A (Figure 5.5d). The result indicates that the small changes after small tephra deposition did not have long lasting effects on the vegetation and could recover rapidly after the events. Changes in palynological richness are variable and not always related to volcanic disturbance (Figure 5.5e). In responses to volcanic disturbance, palynological richness can increase or decrease. In particular, before the So-A eruption, palynological richness reached the smaller values coinciding with the expansion of *N. dombeyi*-type in the area; but interestingly after So-A eruption palynological richness increased. Perhaps vegetation was not completely destroyed, and some biological legacies and survival individual remained in sheltered areas. As the dominant taxa was depressed, palynological evenness increased (Figure 5.5f), a pattern that normally occurred after other small volcanic eruptions in this study.

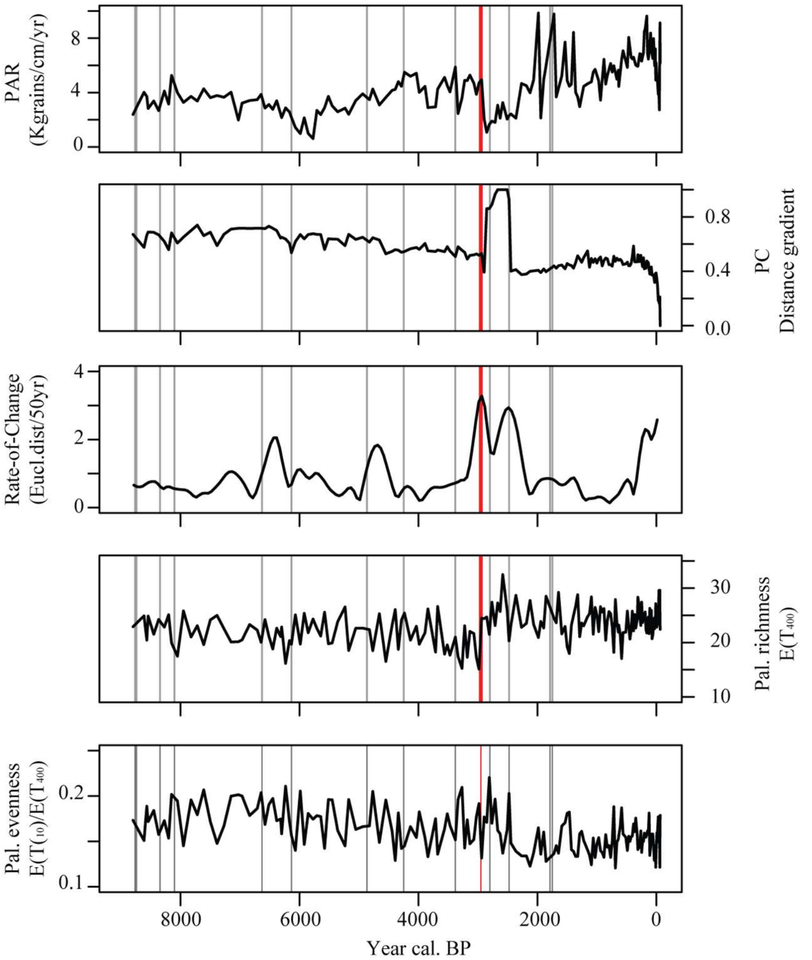

Figure 5.5 Vegetation responses to volcanic eruptions registered in the sediment record from Lake Relem. a) All pollen taxa Pollen-Accumulation-Rate used as a proxy for vegetation biomass changes. b) Principal Curve and c) the rate of change showing significant compositional changes along the time. d) Palynological richness $E(T_{400})$) and e) palynological evenness $E(T_{10})/E(T_{400})$ comparing diversity changes after volcanic disturbances. Red vertical line indicates the Sollipulli-Alpehue eruption; grey vertical lines indicate other tephra deposited >1.5cm thick into the lake.

5.5 Discussion

5.5.1 Reconstruction of disturbance regime: some methodological implications

The variety and frequency of eruptions of the Andean Southern Volcanoes Zone (SVZ), and the unique characteristics of the vegetation in southern South-America (Armesto et al., 1995), present excellent conditions to test ecological hypothesis on vegetation dynamics and volcanic disturbances. The Holocene eruptive history in SVZ is relatively well-known; the volcanic source of some tephra layers are well documented in time and magnitude, and have generally an adequate geochemical characterization (e.g., Fontijn et al., 2014, Fontijn et al., 2016). However, the reconstruction of the volcanic disturbance regime and of the vegetation responses from sedimentary records is not straightforward. For instance, during small-eruptions the tephra might be mixed within the sediment and/or the impacts on the environment are not traceable in pollen records. Also, when the vegetation is distant from the volcanic source, there might be a lack of palynological evidences even after large-eruptions (Paine et al., 2016). When large-eruption deposit tephra layer into the sediment, the thickness of the layer may be altered by some taphonomic process, therefore alter the signal to reconstruct the disturbance magnitude. This could happen in lakes with inflow and/or outflow rivers (Fontijn et al., 2014), as well as due to superficial runoff and erosion processes after the disturbance, particularly on steep slopes (Swanson et al., 2013; Wilmshurst and McGlone 1996). Those factors seem irrelevant in Lake Relem since the slope around the lake basin is very low and the catchment area does not have any rivers. Hence the thickness of the tephrafall deposited into the lake could be similar to the offshore affecting terrestrial vegetation. Of the volcanic history in the region (Table 5.1), not all the eruptions are registered in Lake Relem, likely due to the wind directions and the magnitude of the volcanic eruption, principally those from Llaima and Villarrica volcanoes in the last 500 years. Besides the So-A eruption, we avoided to designate a given tephra layer to a respective volcano since geochemical analysis was not conducted. Instead, to reconstruct the volcanic regime nearby Lake Relem, we stressed on the potential impacts of tephrafall as the main mechanism disturbing the vegetation, independently of the volcanic source and its chemical characteristics.

5.5.2 Reconstruction of disturbance regime: a regional comparison

Volcanic eruptions play a fundamental role in structuring the vegetation in the eastern Andes forest-steppe ecotone (e.g., Veblen, 2016), but there are still gaps in our understanding about how the vegetation responses to large-eruptions. The vegetation history in this region have also been studied largely (e.g., Iglesias et al., 2018; Whitlock et al., 2018; Nanavati et al., 2019), but the published results do not show significant changes due to volcanic disturbances. It is contrary to what we could expect considering the several large-eruptions during the Holocene. In order to analyze the impact of tephrafall on the vegetation, in the following we contrast the eruptive history of some volcanoes in the region with past vegetation reconstructions based on pollen analysis from sites located close to the addressed volcanoes. Fontijn et al. (2014) reconstructed the eruptive history of the Chaitén and Machinmahuida volcanoes, and the volcanoes belonging to the PCC and the Antillanca-group. These volcanoes are of particular interest due to recent large-eruptions and ongoing ecological monitoring.

Close to Chaitén and Michinmahuida volcanoes the vegetation history was reconstructed from two lakes, Lake La Zeta and Lake Theobald, located ~80 km eastward from these volcanoes (Iglesias et al., 2014). Both lakes are located ~60 km apart from each other. The lithology accounts for the presence of different amount of tephra layers (La Zeta 19 layers; Theobald 2 layers). Based on their published chronology, one tephra layer, identified about 6 ka in both records, might be related with a large eruption of the Michinmahuida volcano dated approximately between 5.1-6.3 ka (Amigo et al., 2013). The pollen diagram from Lake Theobald indicates small changes in samples dated after 6 ka: a small decrease in total PAR and Poaceae percentage; whilst a slight increase of shrubs and steppe taxa (*Ephedra* among them). Nevertheless, the Lake La Zeta record does not account for changes in pollen percentage and PAR after the deposition of ~20 cm.

In the last 10 ka the PCC volcanic complex and the Antillanca-group recorded 5 large-eruptions (Fontijn et al., 2014). Maybe one of these eruptions played a more important role than previously thought. Iglesias et al. (2014) show an expansion of *Austrocedrus* around 6 ka, somehow synchronously on all the records described around lake Nahuel-Huapi (~41°S). The expansion of *Austrocedrus* might have occurred due to the increase in effective moisture and climate variability what in turn triggered a change in the fire disturbance regime (Whitlock et al., 2006). However, one of the most prominent PCC eruptions occurred likely at 6.2 ka, ejecting c.1 km^3 of tephra and burying the surrounding of Lake Nahuel-Huapi by ~1 m tephra (PCC2 in Fontijn et al., 2016). Although age-depth models of those several records are poorly constrained by this time, it is possible to differentiate the regarding tephra layer on most of the records (Fontijn et al., 2014). The PCC2 eruption occurred after a prolonged dry period, as it is suggested by Lamy et al. (2001) and Whitlock et al. (2006). The vegetation was dominated by *Nothofagus* species, likely shrubs of *Nothofagus antarctica* were contributing the most to the *N. dombeyi* pollen type (Iglesias et al., 2014; Nanavati, et al., 2019), since this species is well adapted to dry conditions (Donoso, Steinke, & Premoli, 2006). It is possible that this eruption devastated the *Nothofagus* species and supported the expansion of *Austrocedrus* into the area, a hypothesis not considered so far. Although there are no reports of *Austrocedrus* sprouting after buried by tephra, it is able to resprout from the stump, and the seeds can spread long-distances and produce abundant regeneration (e.g., Donoso, Escobar, et al., 2006). Moreover, *Austrocedrus* along its distribution grows normally on volcanic soils. *Austrocedrus* is well adapted to dry and poor soil conditions, and small populations out of the distribution can be found on volcanic lava or tephra deposits as well (Donoso, Escobar, et al., 2006). Whitlock et al. (2006) also observed that the expansion of *Austrocedrus* occurred from wettest to drier zones. However, this gradient is also related to a disturbance gradient due to increasing distance from the volcano, where the closest areas to the volcano are more humid. Thus, in this humid area close to volcano, the tephrafall was likely thickest and with more severe impacts on the vegetation. Furthermore, at the same latitude on the other slope westward of the Andes, in Lake Pichilafquen, Jara & Moreno (2014) recorded a considerable decrease (increase) in *N. dombeyi*-type (*Eucryphia*) after an eruption dated between 6.1-6.7 ka accounting for a widespread impact.

If the hypothesis is true, then the PCC2 eruption changed the structure and composition of the vegetation for more than 2 ka. Perhaps, *N. dombeyi*-type could not recover as happened after So-A. Maybe, *Austrocedrus* was able to persist in the landscape due to high fire-frequency (e.g., Whitlock et al., 2006) and the increasing volcanic activity during the Late-Holocene (Fontijn et al., 2016). Both examples account for different vegetation responses, or the lack of, for close sites in the forest-steppe ecotone. This difference could be likely due to the influences of wind on the tephrafall dispersion and/or topography, but also due to vegetation characteristics and the type of volcanic disturbance. It is an alternative hypothesis that needs to be tested though.

5.5.3 Local patterns of vegetation responses to volcanism in the Araucaria forest-steppe ecotone

The vegetation resistance and the rate of recovery may be controlled by many interacting factors, such as climatic conditions, type of the impact and topographic factors (del Moral and Grishin, 1999), by plants traits (Antos & Zobel, 1986), and biological legacies (e.g., Dale et al., 2005). However, vegetation recovery may not return to its original condition. In the following paragraph we attempt to review those patterns occurring around Lake Relem.

Ephedra was the unexpected dominant taxa after the So-A eruption. Little is known about its ecology and its paleoecological significance in Patagonia. *Ephedra* might have a nursery effect on *Nothofagus* and *Austrocedrus* after fire disturbance (e.g., Raffaele & Veblen, 1998). In that study *Ephedra* is not the most abundant species after disturbances and it has been studied around ~200 km southward. In modern pollen-samples it averages 2.7%, with maxima of 32.4%, but close to Lake Relem is founded up to 20% (Paez et al., 2001). *Ephedra's* pollen grains could disperse several kilometers far from the source area (Maher, 1964). The pollen abundance of *Ephedra* before So-A eruption was always low, but such increase in pollen percentage and PAR should only be indicative of local presence and a result of the So-A eruption. For instance, Mallín Paso del Arco is a record within the 2 m isopach zone of the So-A (Heusser et al., 1988) which depict a slight increase on *Ephedra* around 3 ka, above a thick tephra layer. Unlike, other sites out of the 2 m isopach, but still close to Sollipulli volcano, do not show an increase in *Ephedra* (Fontana & Giesecke, 2017) and to our knowledge none of the palynological records in north-western Patagonia show significant increase of *Ephedra* after an eruption.

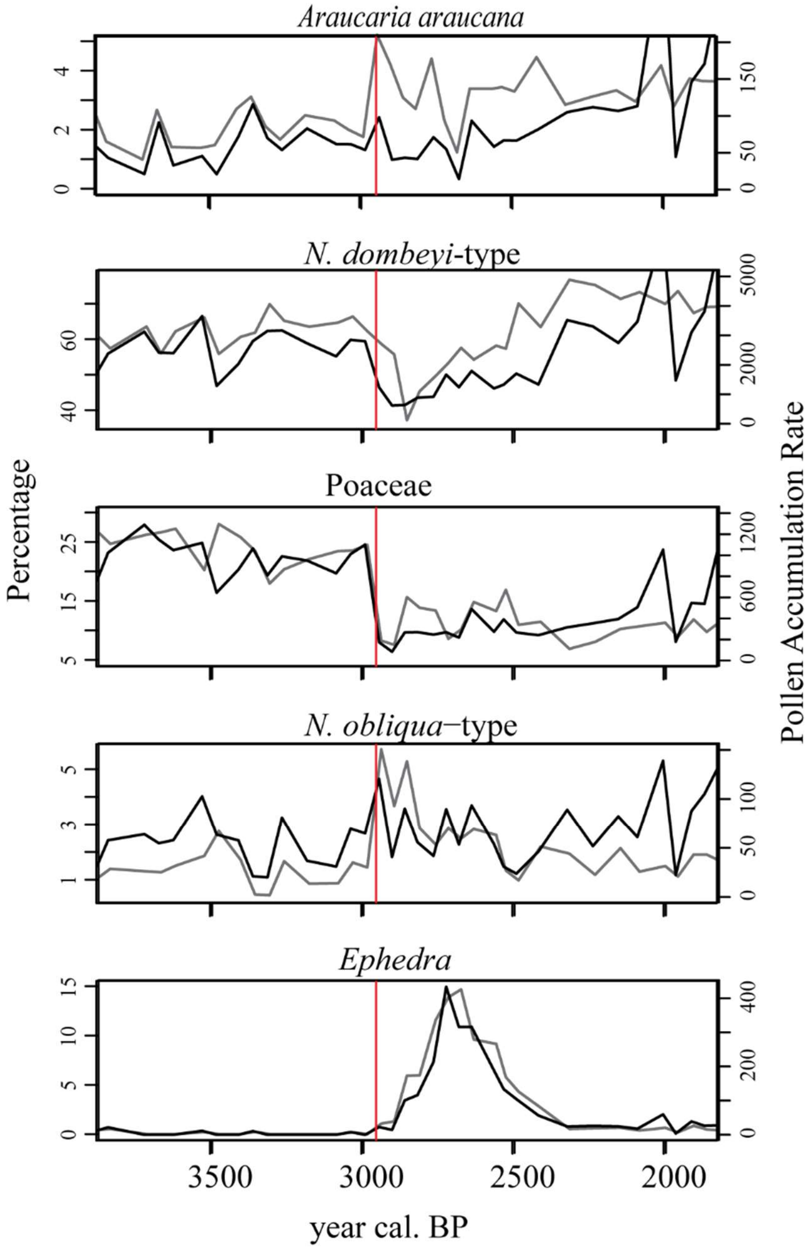

Figure 5.6 Change in pollen relative abundance (grey curve) and Pollen Accumulation Rate (black curve) of selected taxa to the Sollipulli-Alpehue eruption (Vertical line).

Climatic condition may play a role in the environmental responses, by determining the vegetation composition and structure, which in turn influence potential colonizer species and the rate of revegetation after disturbance. For example, before 4.5 ka when precipitation was low (Jenny et al., 2003; Lamy et al., 2001) the vegetation was dominated by grasses (Table 5.1). Small tephrafall left some impact to the vegetation dominated by grasses (Figure 5.5b), but recovering fast enough to not register a peak in the rate-of-change analysis (Figure 5.5c). After So-A, revegetation started short-after with *Ephedra* whilst forest developed later. This eruption evidenced strong imprint in vegetation composition, but due to relatively stable climatic conditions in a millennial-scale it returned close to its original state after approximately 500 years (Figures 5.5 and 5.6). In comparison, after Taupo eruption in New Zealand, the vegetation returned to its original condition after about 120-250 years (Wilmshurst & McGlone, 1996). Later, when precipitation augmented in Patagonia, it promoted the development of *Nothofagus* species in the area, the vegetation was less sensitive to small tephra deposition or did not disturb significantly.

Plant traits play an important role to resist tephra deposition and may determine the species performance in function of the tephra thickness. For example, Antos & Zobel (1986) found that herbs could not resist being buried by ~15 cm, while the early establishment was dominated by the shadow tolerant trees and shrubs under the undisturbed canopy. Regarding to the So-A eruption, the success during the early establishment of *Ephedra* was likely due to special adaptation to poor soil, resprouting shoots, and the capacity to resist arid and cold weather conditions (Luebert & Pliscoff, 2006). Roots regrowing seem to be a common mechanism of plants in response to buried disturbance by tephrafall. For example, after the Taupo eruption (1850 BP), the spore of *Pteridium,* a fern species with rhizome root system, were found increasing in several records in a wide area buried by tephrafall, thus suggesting that the species spread after resisting the impacts of the eruption (Wilmshurst & McGlone 1996). The same occurred with the fern *Lophosoria quadripinnata* after the 2008-eruption of Chaitén volcano. The species, also with rhizome root system, that normally grows under the forest canopy in the low elevation of the temperate forest. Close to the blast-zone *Lophosoria* was one of the first species regrowing one year after the eruption in low and mid-elevation zones (Moreno-Gonzalez et al., 2019). Remarkably, after repeated past eruptions in the areas close to Chaitén Volcano, *Lophosoria* responded positively short after the eruptions (Henríquez et al., 2015). Furthermore, the following expansion of *Ephedra* in the area can be related to its fleshy-fruit and dispersal mechanism, principally through birds and rodents (Loera et al., 2015). Probably *Ephedra* was the main food supply for birds and rodents in a wide area devastated after So-A eruption. A similar mechanism of plant dispersal was suggested after Taupo eruption, where the pollen of some fleshy-fruits taxa were found (Wilmshurst and

McGlone 1996); and in the last eruption of the Chaitén volcano, the species with fleshy-fruits were also found playing an important role in the early vegetation establishment (Moreno-Gonzalez et al., 2019).

Trees are expected to be less affected by small tephrafall, particularly *Araucaria* and *Nothofagus* species are considered pioneer species after volcanic disturbances (Veblen, 1982). After the recent eruption of Puyehue, *Nothofagus pumilio* species were found regrowing in areas buried by tephra (Montiel et al., 2017). However, in the blast-zone of the last eruption from Chaitén Volcano none *Nothofagus* seedling were found one year after the eruption (Moreno-Gonzalez et al., 2019). In palynological records the abundance of *N. dombeyi*-type is always variable, and few studies have been assessed directly the responses to volcanic events. Álvarez-Barra et al. (2020) demonstrated that well developed forest was not affected in the long-term by tephrafall smaller than 20 cm. However, after the large-eruption of So-A, the pollen abundance of *N. dombeyi*-type was strongly affected.

Multivariate analysis and simple comparison of the curves point to that *Araucaria* was not affected by any of the small-eruption. It is well documented the physiological characteristic to resist moderate disturbance (Burns, 1991; Veblen et al., 1995). For example, thick bark, flexible branches and smooth leafs. Hence, it is possible that small tephrafall during the Holocene did not cause physical damage. If chemical change to soil occurred after tephra deposition, possible physiological harms such as decreasing tree-ring growth (Tognetti et al., 2012) did not last for a long time, therefore unlikely to found significant change in pollen abundance from sedimentary records. Since *Araucaria* did not indicate significant change in pollen percentage and PAR after the So-A eruption, it is improbable that volcanism affected the distribution of the populations distant from volcanic source as it suggested by Bekessy et al. (2002).

5.6 Conclusions

This study is a contribution to understand the effects of volcanic eruptions on the *Araucaria* vegetation dynamics at the forest-steppe ecotone. Although further studies are required, some concluding remarks can be done from this first Holocene reconstruction of the volcanic disturbance regime and assessment of the impacts to the dynamics of *Araucaria* at the forest-steppe ecotone:

- The Holocene volcanic history at the *Araucaria* forest-steppe ecotone is solely represented by tephrafall impacts, with variable frequency and intensity. The severity of the impacts caused by the tephrafall is influenced by climatic and topographic factors that determine vegetation conditions at the time of the disturbance. After volcanic disturbance episodes, the pollen richness and evenness, as well as PAR, do not show a unique pattern of decreasing biodiversity and biomass.
- Due to the distance and normally thin tephrafall, shrubs and trees were not significantly affected, which in turn suggest that long-term successional patterns here are not strongly driven by volcanism. However, large-infrequent disturbance as the So-A eruption did. With our record we cannot model a full gradient of disturbance intensity to determine vegetation threshold of maximal resistant. Vegetation responses after the So-A eruption shows similar patterns of regeneration with other large-volcanic disturbance in Patagonia and New Zealand.
- *Nothofagus* species, principally *N. dombeyi*-type pollen taxa in the record, do not represent a pioneer status after volcanic disturbance. After So-A eruption, it colonized the impacted area around Lake Relem about 500 years later, and maybe helped by the nurse effect of *Ephedra,* (likely protection against herbivory, temperature extremes and evapo-transpiration, and organic matter input). *Ephedra* played a more important role than expected
- The Holocene history of *Araucaria* around Relem seems to be independent of volcanic disturbance, thus unlikely to modify dynamics and distribution of the population tens of kilometer far from the volcanic source

Acknowledgments

This work was supported by a scholarship to RM through program DAAD/BECAS Chile, 2014 (57144001), and by the DFG Grant FO 801/3-1. TG acknowledges funding from the DFG Grant GI 732/9-1. The authors declare that there is not conflict of interest. We are thankful to Prof. Dr Behling for supporting part of this research.

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Chapter 6- Synthesis

6. Synthesis of the main results

The changes in the Andean vegetation and in the fire regime in the last centuries might have driven some species to critical conservation status. To achieve restoration tasks in the Andean vegetation is not easy, and the lack of long-term perspectives of the vegetation is critical in determining the threshold of persistence for *Araucaria araucana*. In this respect, the use of palynological records in sediments provides a baseline for restoring degraded ecosystems. In the following, I synthesize the results of previous chapters that reconstruct the impacts of the human land-use, fire, and volcanic tephra deposition on the vegetation. To gain more information about the historical range of variability of the *Araucaria*, I compare the results published here with other studies conducted within the *Araucaria* region.

6.1 Disturbance history and the vegetation stability at the *Araucaria araucana* forest-steppe ecotone

The disturbance history reconstructed from the sediments of Lake Relem confirms that fire and volcanoes are important disturbance events at the *Araucaria* forest-steppe ecotone (Chapter 4 and 5). The 9000-years-old record from Lake Relem indicates a total of 39 volcanic eruptions and 20 fires episodes (Figure 6.1d, e). Interestingly, both, fire and tephra deposition frequency was lower between 8-6 ka and from 2 ka to the present, indicating long disturbances free periods (Figure 6.1). The period of high fire frequency between 6 and 2 ka in Relem is corresponding to a time of high fire activity in northern Patagonia (Nanavati et al., 2019), albeit fire events are less frequent at the Lake Relem area. The period with major frequency of tephra deposition is recognized as a time of increased volcanic activity in the area (Fontijn et al., 2014). The magnitude of impacts from these fire events around Lake Relem were lower in comparison with published results from northern Patagonia due to the low available fuel in the open vegetation at the forest steppe ecotone (Chapter 4). On the other hand, the impact of some volcanic eruptions in northern Patagonia may have been underestimated (Chapter 5). The multivariate analysis of the fire and tephra disturbance events indicates that there is no significant direct effect of small scale disturbance events on the vegetation. However, the frequency trends of both, fire and tephra significantly influence the pollen assemblages (Chapter 4 and 5).

The largest fire event registered in the Relem record did not yield a characteristic change in pollen composition; the largest eruption of the Sollipulli-Alpehue produced a strong change in pollen composition. This event is characterized by deposition of 2 m of tephra that produced a severe damage on the vegetation as indicated by the abrupt decline of dominant pollen taxa and strong changes in pollen composition (Figure 6.1). Perhaps some groups of *A. araucana* and *N. obliqua* trees, whose pollen abundance did not change, survived the impact in protected areas. In the long centennial time-scale, the early successional stage of vegetation was dominated by the *Ephedra*, contrary to the expected *Nothofagus* species or *A. araucana. Ephedra* may have a nurse effect in the recovery of the vegetation close to the original in a process that lasted more than 500 years, likely by creating protection conditions against herbivory, temperature extremes and evapo-transpiration. This eruption has been the most prominent natural disturbance in the history of *A. araucana* vegetation around Lake Relem.

There is no clear evidence in the pollen record that humans impacted on the vegetation before the arrival of the Europeans, and the macro-charcoal analysis did not show any evidences of increasing fire frequency during the period of highest indigenous population density (Chapter 4). Probably, extensive burning to hunt was seldom exercised because the indigenous population density was comparatively low before the Euro-American colonization and because some basic elements as the use of horses were still absent. The comparison of fire and volcanic events during the Holocene indicates that the impact of indigenous on vegetation played a minor role before the Euro-American colonization of northern Patagonia. On the contrary, the magnitude of the human impact on the vegetation is strong for the last 50 years due to *Pinus* plantations as indicated by its pollen imprint on the pollen records (Chapter 3). The magnitude of the vegetation change produced by

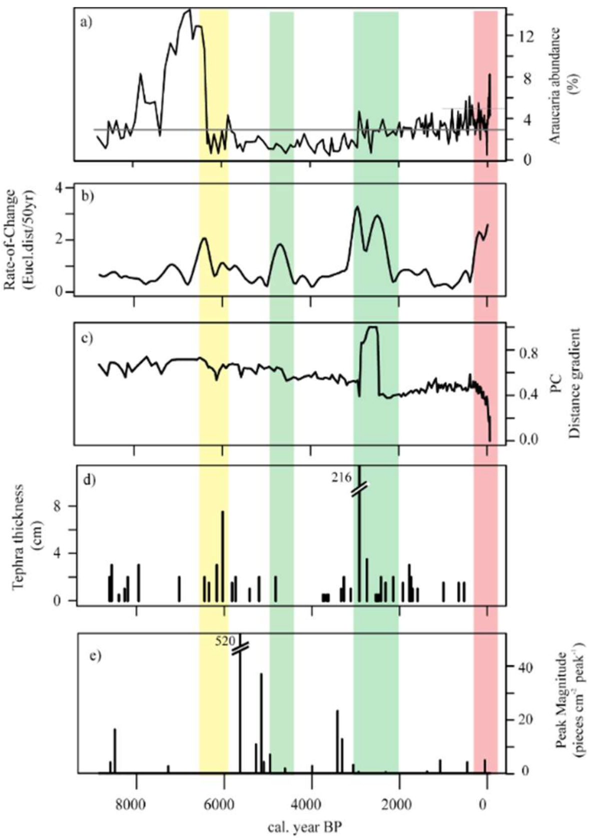

Figure 6.1 Long-term trends in Araucaria pollen (a), vegetation composition (b) and the rate of change (c) in contrast to the tephra deposition (d) and the fire regime (e). Gray horizontal line in panel (a) indicates the average abundance of Araucaria pollen. Colored vertical areas highlight the peaks in the Rate-of-Change, in relation with the fall of Araucaria pollen (yellow), the change from grassland to forest and the impact of the Sollipulli-Alpehue eruption (green), and the human impact caused by Pinus plantation (red)

humans in the last 400 years can be compared with the largest disturbance caused by the Sollipulli-Alpehue eruption in terms of the amount of change (Figure 6.1c), and the rate of the change (Figure 6.1b). These results indicate that the present pollen composition is quite different from the past, and that the change in vegetation occurred rapidly.

The understanding of the ecosystem stability is highly important for conservation. Therefore, it is necessary to examine the causes that alter the stability of the vegetation dynamics in northern Patagonia, in particular for the endangered *Araucaria* at the forest-steppe ecotone. Recently the idea of alternative-stable-state is being used to explain possible positive feed-back between fire-prone species and increasing fire-frequency due to current global warming and human activities. For instance, Kitzberger et al. (2016) and Paritsis et al. (2015) observed an alternative-stable-state of the vegetation in northern Patagonia resulting from the shift to more frequent fire disturbances during the last 150 years. Based on the 6 sites studied here (Chapter 3) it is difficult to confirm the hypothesis of alternative-stable-state in the f *A. araucana* forest-steppe ecotone since there is no significant changes in abundance. Also the fire reconstruction does not indicate a change in the frequency for this period (Chapter 4). In addition, the last 9 ka of vegetation and fire reconstruction around Lake Relem demonstrate that the vegetation was never stable, as revealed by the pollen of the dominant taxa and the disturbance return interval of about 200 years or less (Chapter 4 and 5). Hence, it seems that this hypothesis cannot be generally applied in entire northern Patagonia. The main problem in assessing the alternative-stable-state hypothesis is the short time scale to compare a reference ecosystem to (Petraitis & Latham, 1999). For example, the pollen record from Lake Relem indicates that *Ephedra* likely dominated the area for about 500 years after the So-A eruption, but later the composition of the vegetation changed again returning to the previous stage (Chapter 5).

The study of the ecosystem stability dominated by *Araucaria* is challenging from the palynological point of view, since small-scale vegetation patterns and processes may be hidden in pollen records. Since the surface of Lake Relem is small (~1 ha), the pollen record (Chapter 4 and 5) has a pollen source area of ~3000 ha, it is possible to reconstruct the vegetation at the landscape-scale but not at the stand-scale. Moreover, samples at the top-core have a time resolution of ~10 years; therefore, short-term successional patterns cannot easily be detected. As disturbances create a mosaic of vegetation in the landscape (Turner et al., 1998) and the complex topography creates different habitats, the record from Lake Relem suggests that likely the vegetation is a diverse and dynamic arrangement of patches in a landscape with changing structure and composition. As disturbance occurs in the long-term the patches interchange and/or persist in the landscape for variable time. Thus, the vegetation dynamics might be seen as multiple, in non-equilibrium states (*sensu* Sutherland, 1974).

The changes of vegetation at the *Araucaria* forest-steppe ecotone are part of the natural dynamics. As long as the species recolonizing disturbed areas are native, short-term alternative-states are of no concern, since vegetation and fire dynamics seem to be part of the historical range of variability. Furthermore, the results of the pollen records have demonstrated that vegetation can resist disturbance of moderate magnitude and can even recover rapidly after large-disturbance. However, human activities that change the composition and structure of vegetation lead to novel ecosystems and disturbance agents (Hobbs et al., 2006). At the *Araucaria* forest-steppe ecotone, introduced species, such as *Pinus*, are the main risk for the stability of the vegetation, due to their expansion into areas vegetated by native species (Chapter 3). While there is not a significant change in the composition during the European colonization and the palynological richness indicates that there is no decrease of plant richness, the *Pinus* plantations are homogenizing the vegetation of the *Araucaria* region. The spread of *Pinus* out of the plantations is leading to a novel competition and will exclude some slow growing and shadow intolerant native species. Moreover, *Pinus* plantations might cause severe wildfires due to the increase of biomass (Taylor et al., 2017) together with the current increasing trend in fire frequency (e.g., Gonzalez et al., 2018), the risk is higher. As most fire events involved principally grasses around Lake Relem (Chapter 4), suggest that increasing magnitude of fires would be out of the historical range of variability.

6.2 The historical range of variability of *Araucaria* populations

To understand the current conservation status of *A. araucana* it is necessary to look back into the long-term historical range of variability. Searching for keystone periods and events may help to comprehend whether *A. araucana* has an increasing fragmentation or a declination of the Andean populations. The results of this thesis provide insight into the historical range of variability in *A. araucana* abundance, which is useful for conservation. Here I compare with other records to gain information on population and range of changes in response to past climate change, disturbances events and diseases.

6.2.1 Glacial and Post-glacial history of *Araucaria*

The distribution of *Araucaria* prior to the Last-Glacial-Maximum (LGM) is unknown. It is generally assumed that populations may have migrated from the Andean high elevations to the east and to the west into the lowlands (e.g., Bekessy et al., 2002). In the current *Araucaria* region, glaciers likely melted by ~17 ka (Hulton et al., 2002). Only one record confirmed the presence of *A. araucana* in the western lowlands between 26-14 ka BP (Abarzúa, 2009; Figure 6.2a). In this record, the pollen abundance reached ~15%, suggesting a forest dominated by *A. araucana*. In addition, the pollen record from Lake Espejo, does not show *A. araucana* pollen during the last 10 ka (Abarzúa et al., 2012; Figure 6.2b). Villagrán (2001; Figure 6.2c) found that *Araucaria* may have reached elevations above 1000 m in the Coastal Range by about 6 ka. The author also suggested that the Andes might have been colonized later than the coast. On the other hand, there are no strong evidences confirming the presence of *A. araucana* sheltered in the eastern slope of the Andes during the LGM. Traces of *A. araucana* pollen were found between ~33-27 ka in a non-glaciated area (Markgraf et al., 1986; Figure 6.2d). The oldest records in the eastern *A. araucana* region present low pollen abundance (1-3%) from ~15 ka (Fontana & Giesecke, 2017; Figure 6.2e, f; Moreno et al., 2018; Figure 6.2g). These sites are located in valleys glaciated during the LGM. The records from the eastern Andes suggest that probably *A. araucana* was present close to glaciated areas and expanded from here to the north and to the west in the Andes as the glaciers melted. Although more data are required, it is possible that this area was one of the centers of dispersion and likely *A. araucana* colonized the Andes earlier than proposed by Villagran (2001).

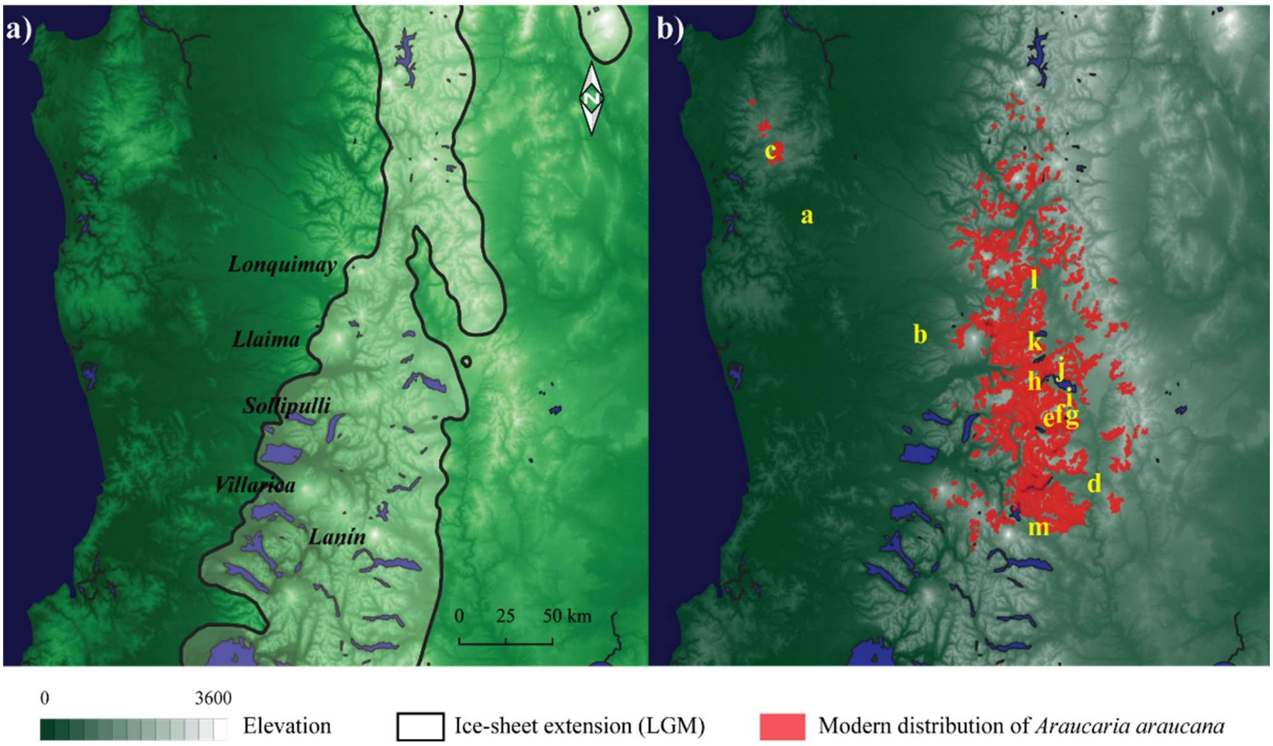

Figure 6.2 a) Representation of the maximal extension of the ice cap during the Last-Glacial-Maximum (LGM; after Ehlers et al., 2011) and the location of principal volcanoes. b) Current distribution of *Araucaria araucana* in the Andes. Letters indicate referenced sites used for the comparison in Chapter 6.2. a: Mallin el Valle, Abarzúa, 2009; b: Lake Espejo, Abarzua et al., 2012; c: Nahuelbuta, Villagran 2001; d: Bajada Rahue, Markgraf et al., 1986; e: Lake Torta, Fontana & Giesecke, 2017; f: Lake Tonkol Fontana & Giesecke, 2017; g: Lake Seco, Moreno et al., 2018; h: Lake Cilantro, Fletcher et al., 2019; i: Lake Relem, this thesis; j: Mallin Paso los Arcos, Heusser et al 1988; k: Mallin Miraflores, Rondanelli-Reyes 2001; m: Mallin Rio Malleo, Heusser et al., 1988; l: Lake San Pedro, Fletcher and Moreno, 2012). Note the positions of letters are not exact to the referred sites and used only for orientation.

6.2.2 Early and mid-Holocene history of *Araucaria*

The pollen records covering the early-Holocene in eastern Patagonian Andes are relatively close to each other, and all indicate a low abundance of *A. araucana* (around 1%): Lake Torta and Lake Tonkol (Fontana & Giesecke, 2017) and Lake Seco (Moreno et al., 2018). At the beginning of the mid-Holocene (8.2-6 ka), the pollen records from lakes Seco and Tonkol kept low and relatively stable abundance (<3%) of *A. araucana* pollen. But other sites show a high abundance (between 15-20%), for example, Lake Cilantro (Fletcher et al., 2019; Figure 6.2h), Lake Torta and Lake Relem (Figure 6.2i). The causes for the local expansion are not clear in all sites, but for Lake Relem there is no evidence that small-scale fire or tephra deposition events had some influence (Figure 6.1; see also Chapter 4 and 5). Modern pollen in surface samples indicate a maximum abundance (~20%) close to Paso Los Arcos (Paez et al., 1997). The vegetation around Paso Los Arcos represents dense, multi-age *A. araucana* woodland with few associated species. Since not all records show the same abundance, it is possible that *A. araucana* was dispersed in the landscape as a mosaic of uneven-age stands or groups of different densities, likely less fragmented than today.

The decline of *A. araucana* pollen abundance occurred suddenly in Lake Relem (Figure 6.1a) in comparison with the record from Lake Cilantro (Fletcher et al., 2019) and Lake Torta (Fontana & Giesecke, 2017). Figure 6.1 shows that the decrease of *A. araucana* around Lake Relem is not directly linked to a fire or a tephra event; nevertheless, the magnitude of the decrease in pollen abundance in a relatively short time produced a high rate of change. Thus, in the absence of fire and volcanic evidence at Lake Relem, it is possible that insects or a disease attacked several populations and caused this strong decline. Furthermore, if the high pollen abundance is related to population density, then those dense populations were more affected than the others, since these less-dense populations showed no change during the same time. This is indicating that there was not a general phenomenon affecting all the populations, despite that the precipitation reconstructed for the period between 8-6 ka was lower than at present along a broad region (Jenny et al., 2003; Lamy et al., 2001). To understand this event, it is highly relevant to examine the current, still unknown disease which is threatening the persistence of many populations of *A. araucana* (e.g., Parra et al., 2018) since the persistent and strong drought during 2010-2015 (Garreaud et al., 2017). Perhaps paleoecology can contribute to the understanding of these rare episodes of massive mortality affecting the persistence of the species today.

6.2.3 Late-Holocene variability of the *Araucaria* populations

Current major vegetation forms in the Andes may have established since the Late-Holocene. Since climate conditions have not changed strongly during this period, the last 4 ka could be considered as a baseline to assess the degree of fragmentation or tipping points in population trends. The history of *A. araucana*, for the last 300 years, interpreted from relative pollen abundance in 6 lakes (Chapter 3), suggests different trends across a precipitation gradient covering the distribution of *A. araucana*. Populations in sites under humid conditions showed a decrease, while under mesic or more xeric conditions populations did not change or even increased. To get longer perspectives, I compare the evidences exposed in this thesis with other records conducted in the *A. araucana* forest region, some of them already mentioned in the above paragraphs (for geographical reference see Figure 6.2). Again, the responses were variable. The pollen records show that in some sites the populations are increasing (Heusser et al., 1988; Figure 6.2j, also lakes Relem, Torta, Tonkol), in other areas the pollen abundance is decreasing (Fletcher & Moreno, 2012; Figure 6.2l; and Lake Cilantro, Fletcher et al., 2019), while other sites hardly show a trend (Heusser et al., 1988; Rondanelli-Reyes, 2000; Figure 6.2, points k, and m respectively). The records discussed before, cover a relatively small area of the *A. araucana* distribution (Figure 6.2), therefore, with the data available so far, it is not possible to depict a regional common pattern towards increasing fragmentation or population decreasing. In turn, this synthesis points to local patterns characterized by different pathways, likely determined by other factors than past human activity, fire or volcanic disturbance. However, fire and volcanic disturbance should not be ruled out in all sites due to still few evidences.

Bekessy et al., (2002) suggested that in particular volcanism played a role in the genetic variability, but also in the population distribution and dynamics of *A. araucana*. The frequency of tephra has a significant influence in the long-term vegetation dynamics. The results in Chapter 5 (Figure 5.4) show a strong negative effect of frequent tephra deposition and *A. araucana* pollen abundance, but it coincides with increasing fire-frequency and a long-term depression in the precipitation trend (Chapter 4). In addition, the multivariate analysis indicates no significant relationship with individual events, hence indicating some change in the dynamics. At the physiological level, it was demonstrated that after two recent moderate-eruptions the tree-ring growth of *A. araucana* trees close to Lonquimay volcano declined within the following 3 years (Tognetti et al., 2012).

Nonetheless, the growth recovered to normality after the third year, and no abnormal mortality has been reported after the events. Furthermore, along the Holocene, few large eruptions have occurred in the region (Chapter 5), and even after the huge So-A eruption the *A. araucana* population around Lake Relem was not significantly affected. Thus, it is unlikely that moderate to small volcanic events affected the distribution of populations within a distance of a few tens of kilometers towards the steppe. Finally, the pollen percentage of *A. araucana* after fire or volcanic disturbance did not increase significantly in continuous samples. At least from the palynological perspective, the results do not support the hypothesis of episodic pulses of regenerations and the later increase of *A. araucana* populations favored by competition exclusion. Therefore, these results suggest that volcanism and fire played a small role in *Araucaria* population dynamics and distribution from nearby Lake Relem at the current forest-steppe ecotone.

6.3 Concluding remarks and future prospections

A. araucana might have reached high-altitudes in the Andes earlier than 6 ka as previously thought. Current pollen evidences do not allow determining a precise date for the spread of the tree in the Andes after deglaciation, but it must have occurred before 10 ka. Likewise, it is not sure if populations moved from the low-lands westward and from the east more or less simultaneously, or if they expanded from glacial refugia in the Andes. Climatic changes throughout the Holocene influenced the *A. araucana* dynamics and determined composition and structure of the vegetation at the forest-steppe ecotone. Long-term dynamics have been variable with local contractions and expansions of *A. araucana* populations, suggesting a probably patchy landscape with uneven-age stand, as well as a variable degree of fragmentation over time. Topography plays an important role creating a complex array of niches for regeneration, habitat for the species, protection against natural disturbance, and microclimatic conditions.

Fire and volcanic disturbance events did not trigger any characteristic pulses in the pollen record, e.g., increase of diversity (interpreted by pollen richness) or decrease in biomass (interpreted by PAR). The magnitude of the fire and tephra was comparatively low, and eventually promoted small changes in vegetation, which apparently was more sensitive to small-scale disturbance before the expansion of *Nothofagus* species eastward (~4.5 ka to present). Even though, *A. araucana* populations may have not been affected severely by tephra far from the volcanic source or affected by fire in areas with low fuel biomass at the forest-steppe ecotone. No drastic and permanent vegetation change caused by persistent disturbance can be observed from the pollen record of Lake Relem. The huge So-A eruption caused severe negative impacts to the dominant vegetation and to grasses, but likely left several dispersed biological legacies that assisted the revegetation of the impacted area. Some species such as *A. araucana* and *Nothofagus obliqua* could survive the impact of the tephra deposition. *Ephedra* expanded after the So-A eruption and likely dominated the landscape due to its ecological traits. It might have facilitated the recolonization of other species later on.

Future vegetation changes at the *A. araucana* forest-steppe ecotone are unpredictable. The results of this thesis and other records cannot assure that all populations of *A. araucana* are decreasing or whether the current fragmentation is greater than in the past. Nevertheless, they enable to differentiate local patterns and pathways for *Araucaria* population dynamics for about the last 4 ka until present. To assert the conservation status and to determine population trends, further quantitative paleoecological studies are required. However, the current expansion of *Pinus* out of plantations is threatening the persistence of *Araucaria* and the natural process at the forest-steppe ecotone. Under this novel scenario caused by *Pinus* plantations, natural disturbance increases the risk of more severe impacts to the vegetation, apparently out of the historical range of variability.

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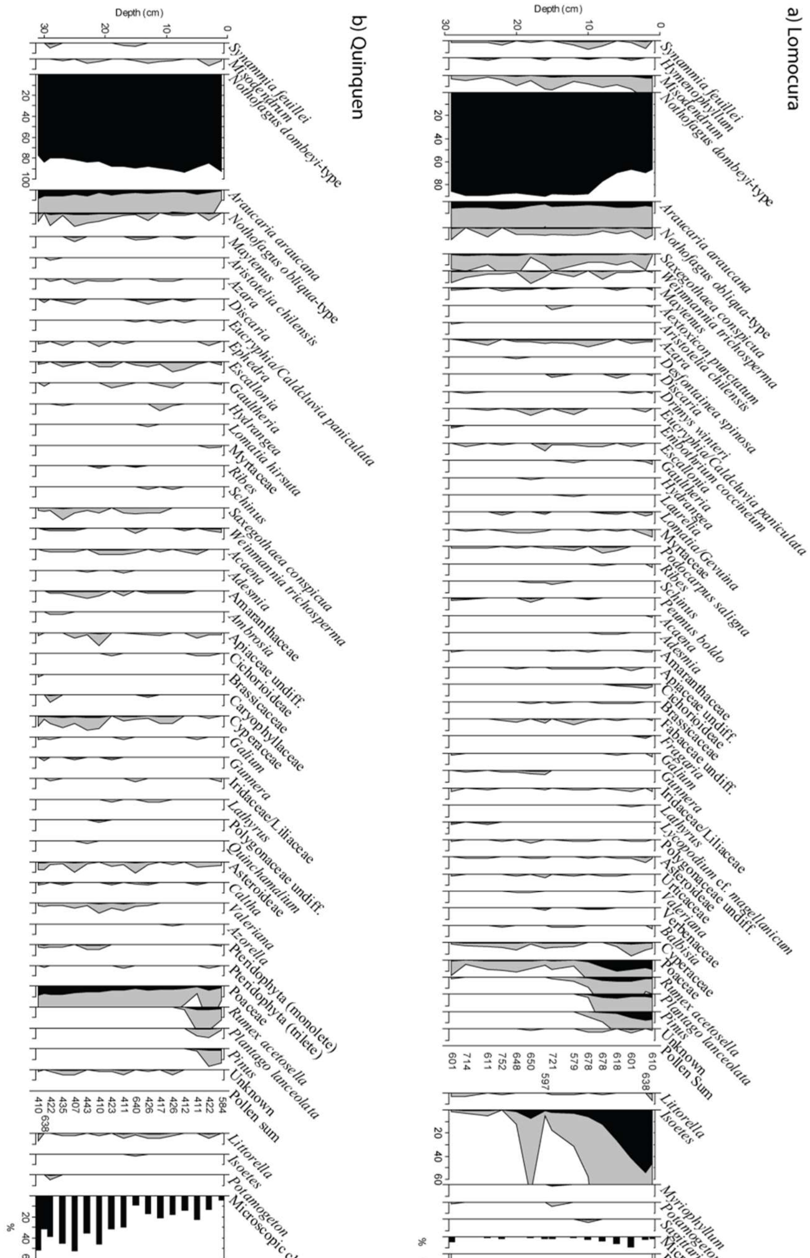
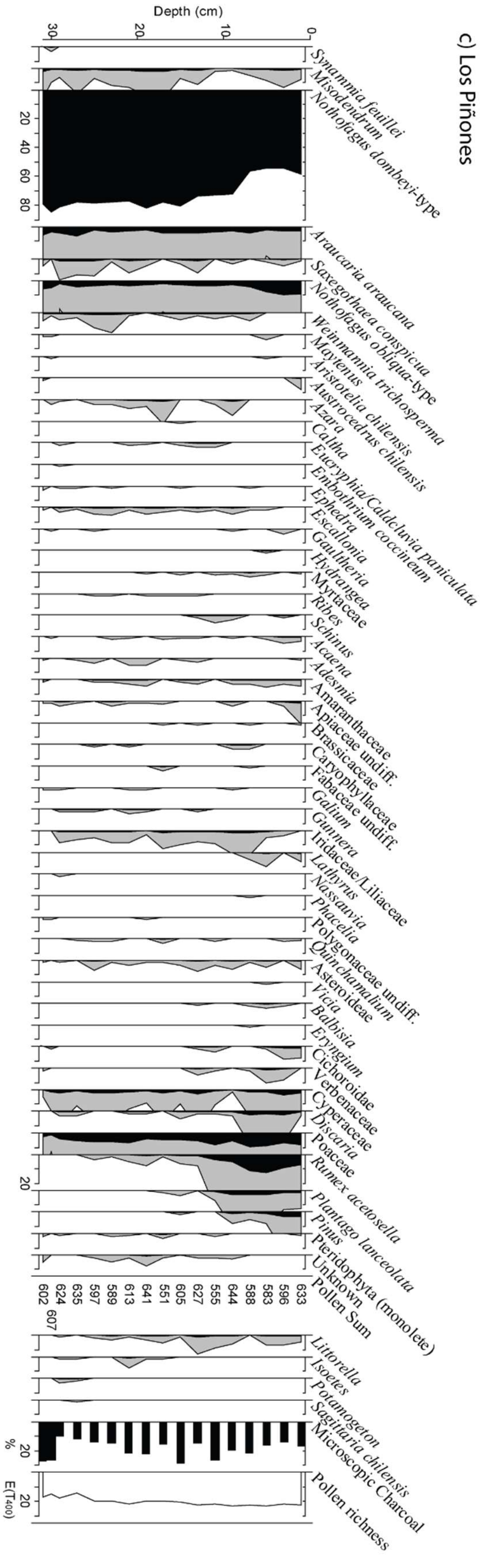
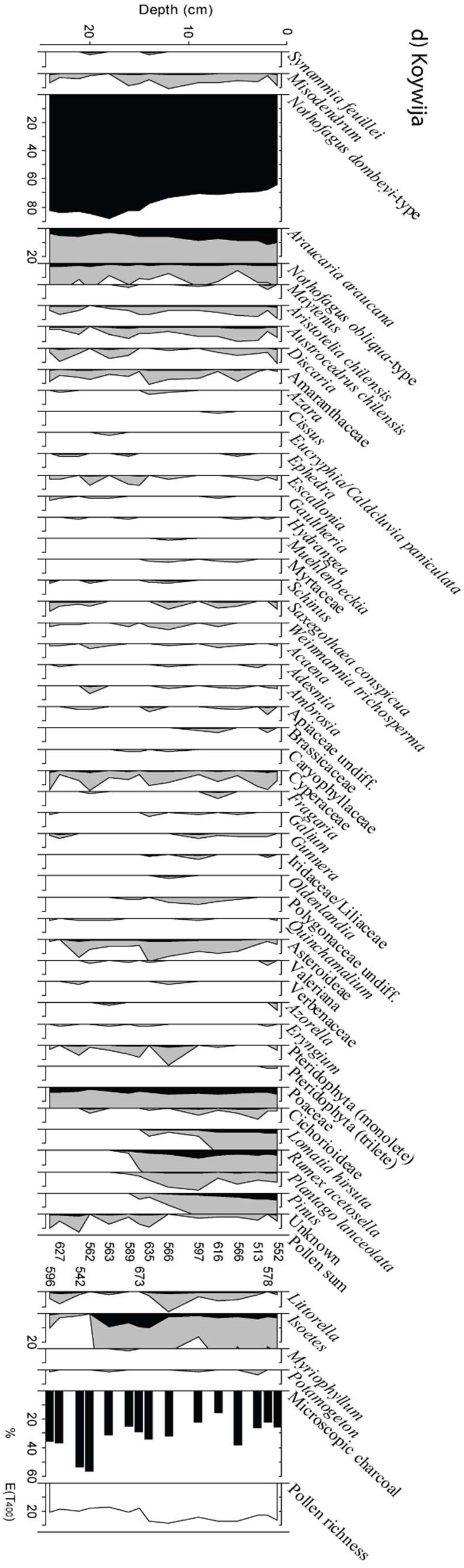
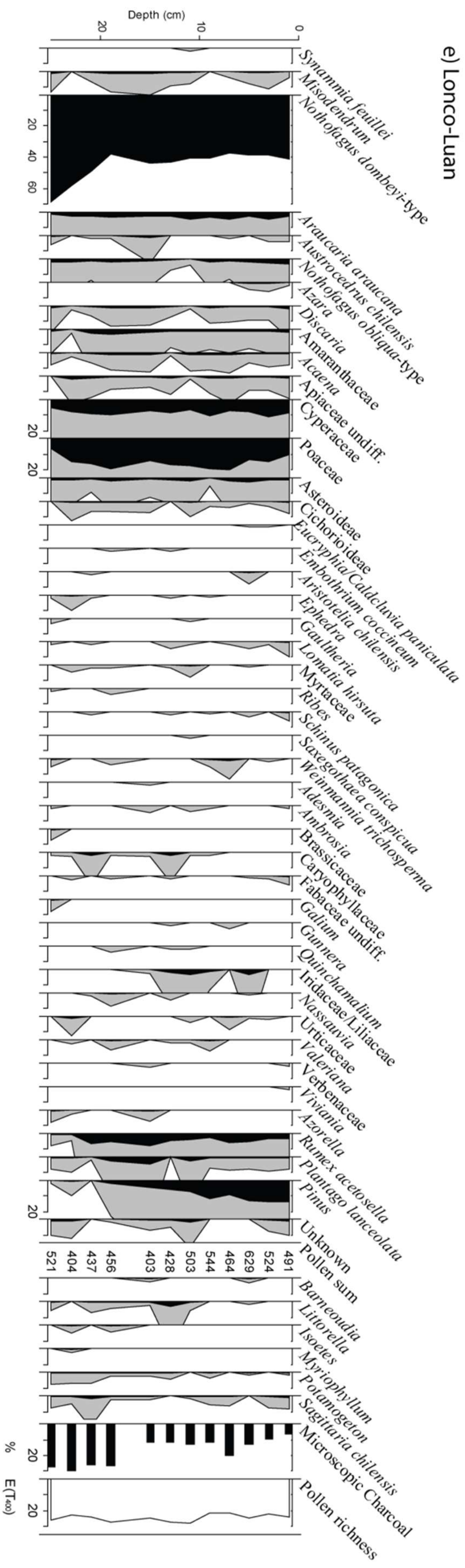
Appendix

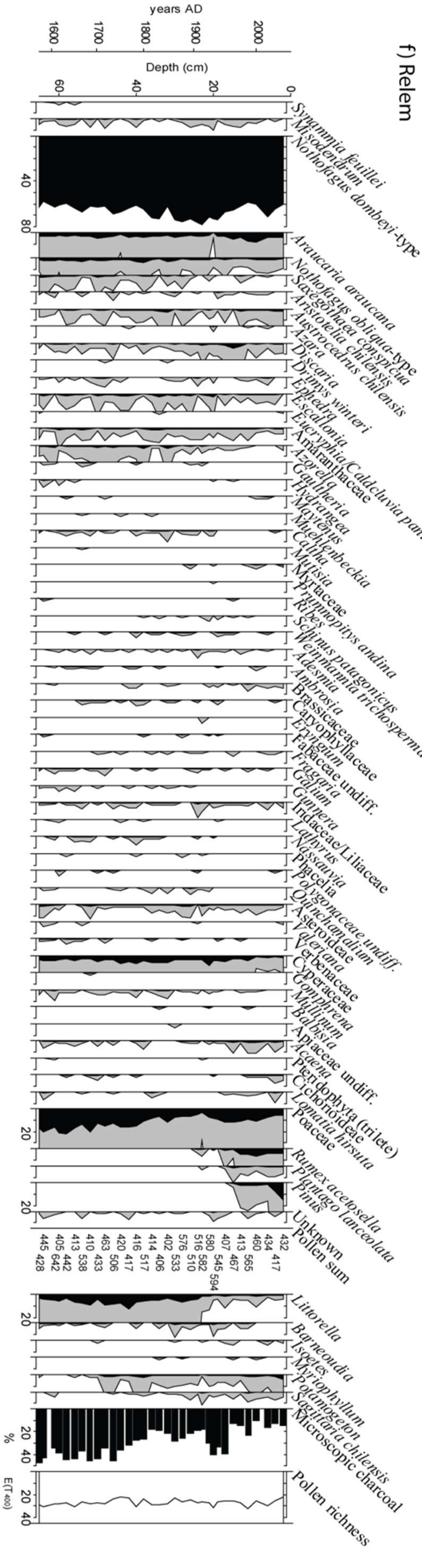
Appendix A: Full pollen diagrams




c) Los Piñones
Depth (cm)
0
10
20
30
Synammia feuillei
Misodendrum
Nothofagus dombeyi-type
20
40
60
80
Araucaria araucana
Saxegothaea conspicua
Nothofagus obliqua-type
Weinmannia trichosperma
Maytenus
Aristotelia chilensis
Austrocedrus chilensis
Azara
Caltha
Eucryphia/Caldcluvia paniculata
Embothrium coccineum
Ephedra
Escallonia
Gaultheria
Hydrangea
Myrtaceae
Ribes
Schinus
Acaena
Adesmia
Amaranthaceae
Apiaceae undiff.
Brassicaceae
Caryophyllaceae
Fabaceae undiff.
Galium
Gunnera
Iridaceae/Liliaceae
Lathyrus
Nassauvia
Phacelia
Polygonaceae undiff.
Quinchamalium
Asteroideae
Vicia
Balbisia
Eryngium
Cichoroidae
Verbenaceae
Cyperaceae
Discaria
Poaceae
20
Rumex acetosella
Plantago lanceolata
Pinus
Pteridophyta (monolete)
Unknown
Pollen Sum
633
596
583
588
644
555
627
605
551
641
613
589
597
635
624
607
602
Littorella
Isoetes
Potamogeton
Sagittaria chilensis
Microscopic Charcoal
%
20
Pollen richness
E(T400)
20


d) Koywija
Depth (cm)
0
10
20
Synammia feuillei
Misodendrum
Nothofagus dombeyi-type
20
40
60
80
Araucaria araucana
20
Nothofagus obliqua-type
Maytenus
Aristotelia chilensis
Austrocedrus chilensis
Discaria
Amaranthaceae
Azara
Cissus
Eucryphia/Caldcluvia paniculata
Ephedra
Escallonia
Gaultheria
Hydrangea
Muehlenbeckia
Myrtaceae
Schinus
Saxegothaea conspicua
Weinmannia trichosperma
Acaena
Adesmia
Ambrosia
Apiaceae undiff.
Brassicaceae
Caryophyllaceae
Cyperaceae
Fragaria
Galium
Gunnera
Iridaceae/Liliaceae
Oldenlandia
Polygonaceae undiff.
Quinchamalium
Asteroideae
Valeriana
Verbenaceae
Azorella
Eryngium
Pteridophyta (monolete)
Pteridophyta (trilete)
Poaceae
Cichorioideae
Lomatia hirsuta
Rumex acetosella
Plantago lanceolata
Pinus
Unknown
Pollen sum
552
578
513
566
616
597
566
635
673
589
563
562
542
627
596
Littorella
Isoetes
20
Myriophyllum
Potamogeton
Microscopic charcoal
%
20
40
60
Pollen richness
E(T400)
20

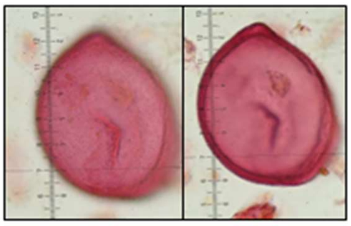

e) Lonco-Luan
Depth (cm)
0
10
20
Synammia feuillei
Misodendrum
Nothofagus dombeyi-type
20
40
60
Araucaria araucana
Austrocedrus chilensis
Nothofagus obliqua-type
Azara
Discaria
Amaranthaceae
Acaena
Apiaceae undiff.
Cyperaceae
Poaceae
20
20
Asteroideae
Cichorioideae
Eucryphia/Caldcluvia paniculata
Embothrium coccineum
Aristotelia chilensis
Ephedra
Gaultheria
Lomatia hirsuta
Myrtaceae
Ribes
Schinus patagonica
Saxegothaea conspicua
Weinmannia trichosperma
Adesmia
Ambrosia
Brassicaceae
Caryophyllaceae
Fabaceae undiff.
Galium
Gunnera
Quinchamalium
Iridaceae/Liliaceae
Nassauvia
Urticaceae
Valeriana
Verbenaceae
Viviania
Azorella
Rumex acetosella
Plantago lanceolata
Pinus
20
Unknown
Pollen sum
521
404
437
456
403
428
503
544
464
629
524
491
Barneoudia
Littorella
Isoetes
Myriophyllum
Potamogeton
Sagittaria chilensis
Microscopic Charcoal
%
20
E(T400)
20
Pollen richness


f) Relem
years AD
1600
1700
1800
1900
2000
Depth (cm)
0
20
40
60
Synammia feuillei
Misodendrum
Nothofagus dombeyi-type
40
80
Araucaria araucana
Nothofagus obliqua-type
Saxegothaea conspicua
Aristotelia chilensis
Austrocedrus chilensis
Azara
Discaria
Drimys winteri
Ephedra
Escallonia
Eucryphia/Caldcluvia paniculata
Amaranthaceae
Azorella
Gaultheria
Hydrangea
Maytenus
Muehlenbeckia
Caltha
Mutisia
Myrtaceae
Prumnopitys andina
Ribes
Schinus patagonicus
Weinmannia trichosperma
Adesmia
Ambrosia
Brassicaceae
Caryophyllaceae
Eryngium
Fabaceae undiff.
Fragaria
Galium
Gunnera
Iridaceae/Liliaceae
Lathyrus
Nassauvia
Phacelia
Polygonaceae undiff.
Quinchamalium
Asteroideae
Valeriana
Verbenaceae
Cyperaceae
Gomphrena
Mulinum
Balbisia
Apiaceae undiff.
Acaena
Pteridophyta (trilete)
Cichorioideae
Lomatia hirsuta
Poaceae
20
Rumex acetosella
Plantago lanceolata
Pinus
20
Unknown
Pollen sum
445
428
405
642
442
413
538
410
433
463
506
420
417
416
517
414
406
402
533
576
510
516
582
580
545
594
407
467
413
565
460
434
417
432
Littorella
20
Barneoudia
Isoetes
Myriophyllum
Potamogeton
Sagittaria chilensis
Microscopic charcoal
%
20
40
E(T400)
20
40
Pollen richness

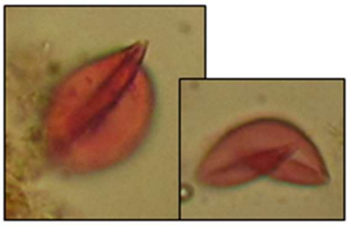
Appendix b: Pictures of the Pollen reference

Gymnospermae

1) *Araucaria araucana*



2) *Austrocedrus chilensis*

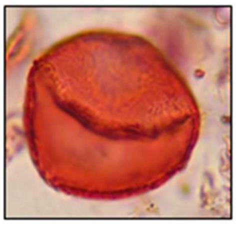


3) *Prumnopitis andina*

4) *Podocarpus salignus*

5) *P. nubigenus*

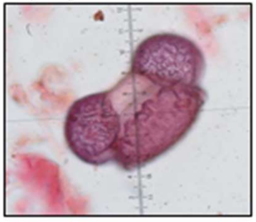
6) *Saxegothaea conspicua*



7) *Ephedra*

8) *Pinus contorta*

9) *P. ponderosa*

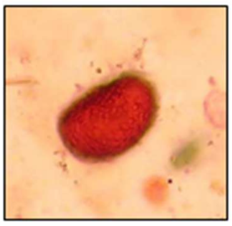


10) *P. radiata*

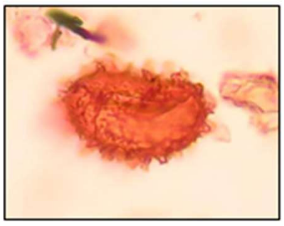
Pteridophyta-monolete

11) *cf. Cystopteris*

12) *cf. Blechnum*



13) *cf. Asplenium*

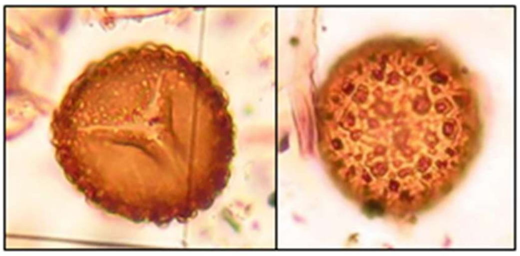


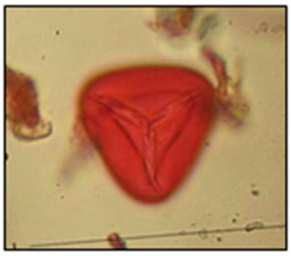
14) *cf. Thelipteris*

15) *Synamia feullei*

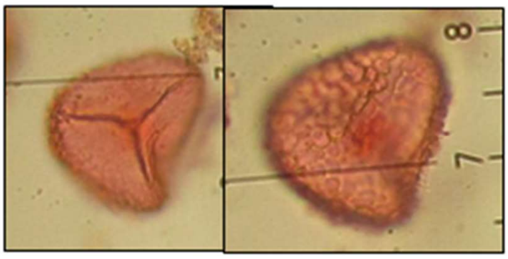
16) *Vittaria*

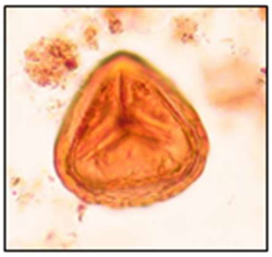
Pteridophyta - trilete

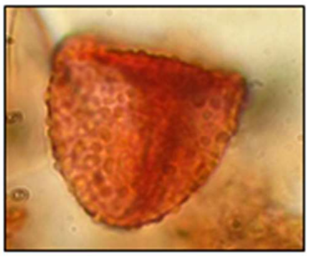

17) *cf. Marsilea*


18) *cf. Notholaena*


19) *cf. Pteris chilensis*

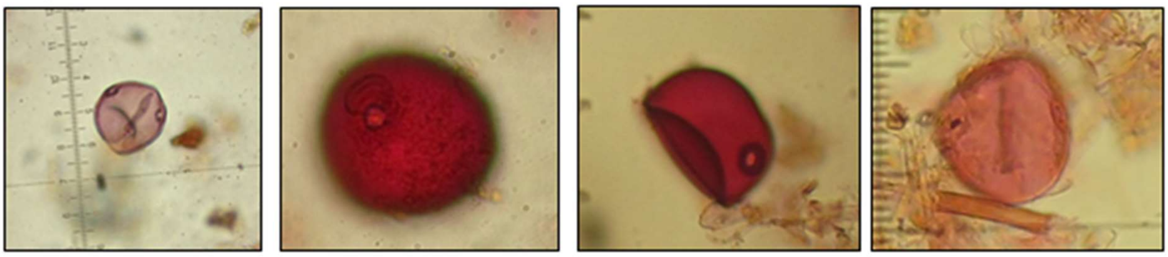

20) *Lycopodium cf. magellanicum*


21) *Lophosoria*


22) *cf. Cryptogramma*

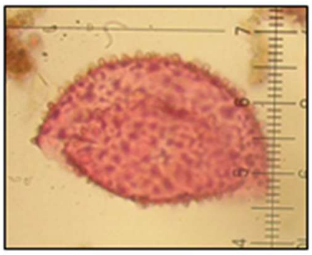
Angiospermae - Monocotyledoneae


23) Iridaceae/Liliaceae


24) Poaceae


25) Amarillidaceae

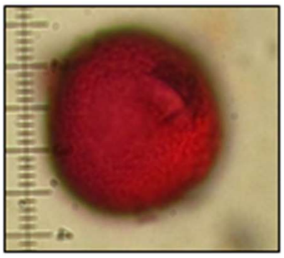

26) Cyperaceae


27) *Lapageria rosea*

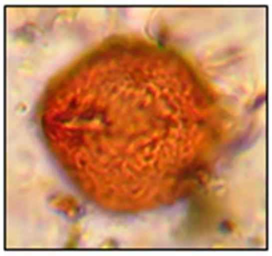

28) *cf. Gaimardia*

Angiospermae - dicotiledoneae

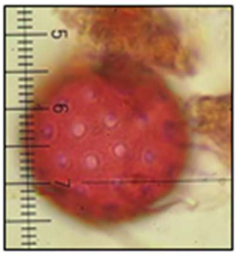
29) *Acaena*



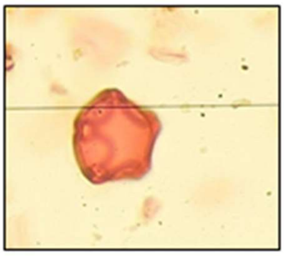
30) *Acaena cf. trifida*



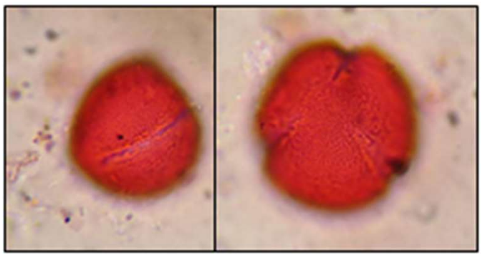
31) Amaranthaceae



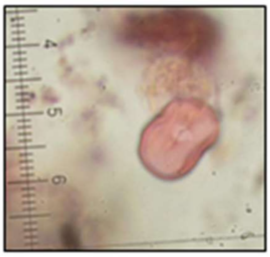
32) *Alnus*



33) *cf. Alonsoa*



34) *cf. Apium*



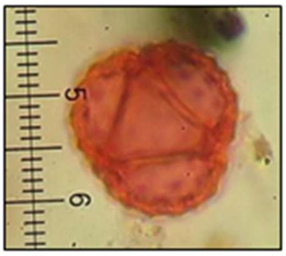
35) Apiaceae undiff.

36) *Mulinum*

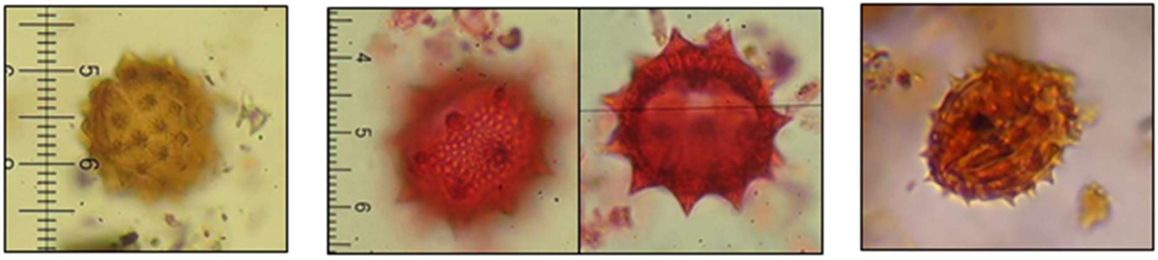
37) *Pozoa*

38) *Azorella*

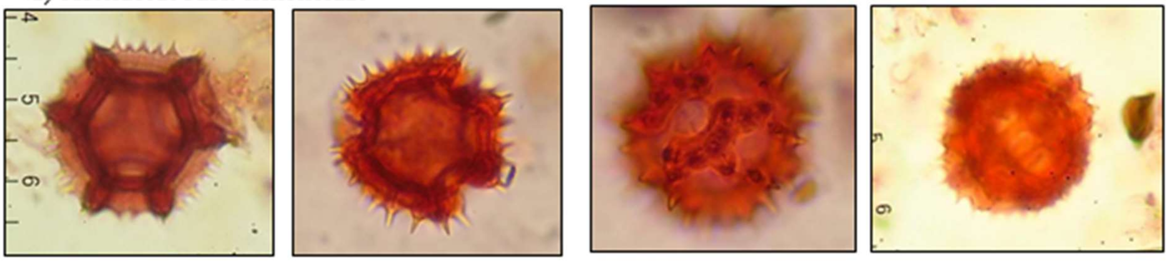
40) *Ambrosia*



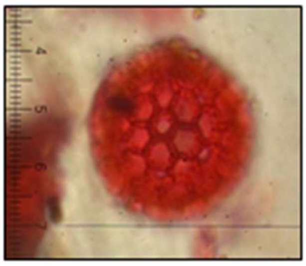
41) Asteraceae subf. asteroidae



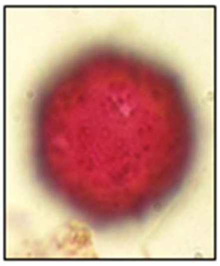
42) Asteraceae subf. cichorioidae



43) *Balbisia*

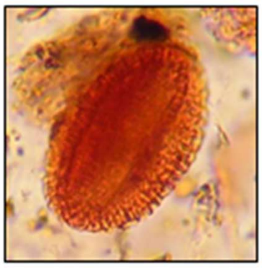


44) *Barneoudia*

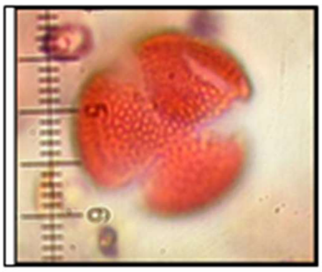


45) *Berberis*

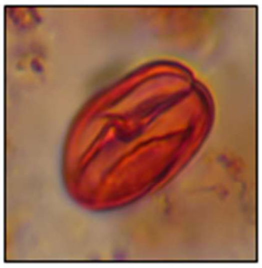
46) *Brassicaceae*



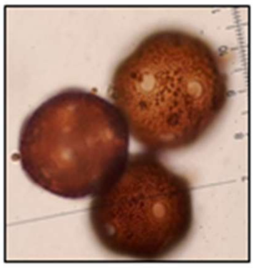
47) Brassicaceae



48) *cf. Budlejia*

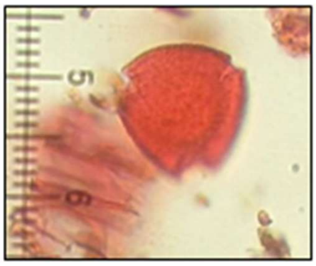


49) *Cerastium arvensis*



50) *cf. Cryptocaria*

51) *Desfontainea spinosa*



52) *Discaria*

53) *Drimys winteri*

54) *Eryngium*

55) *Embothrium coccineum*

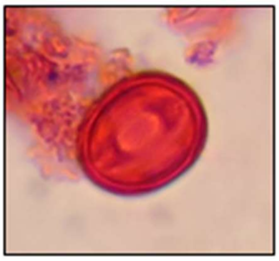
56) *Escallonia*

57) *Escallonia*

58) *Eucryphia/Caldcluvia*

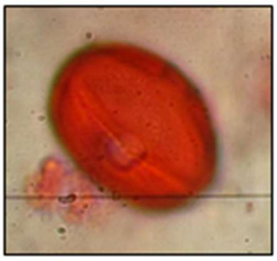
59) *Euphorbia*

60) Fabaceae - *Adesmia*



61) Fabaceae - *Lathyrus*

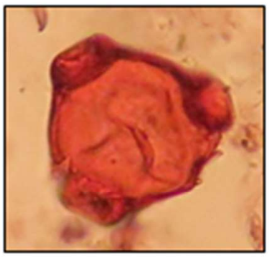
62) Fabaceae *undiff.*



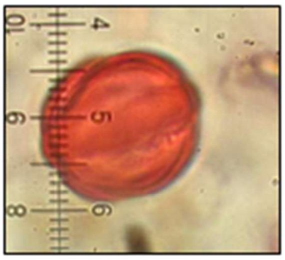
63) Fabaceae *undiff.*

64) Fragaria

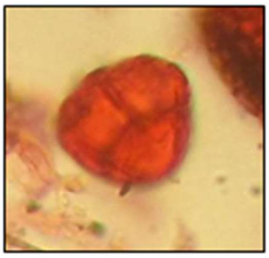
65) Fuchsia



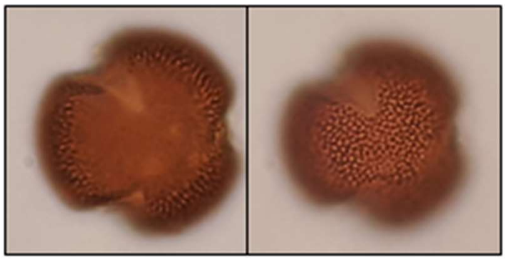
66) Galium



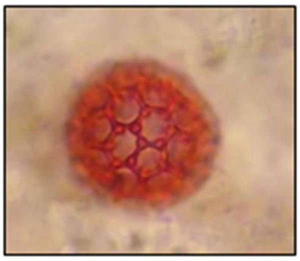
67) Gaultheria



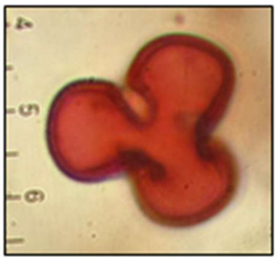
68) Gentianaceae



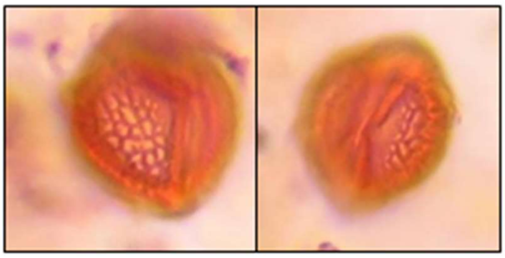
69) cf. Gomphrena



70) Gunnera

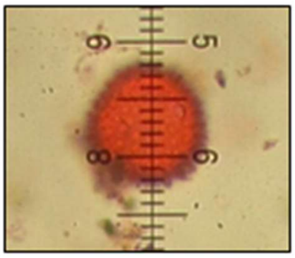


71) *Hydrangea*

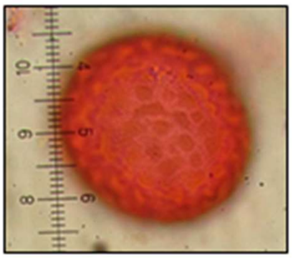


72) *Laurelia*

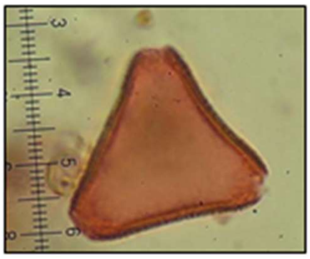
73) *Lepidoceras*



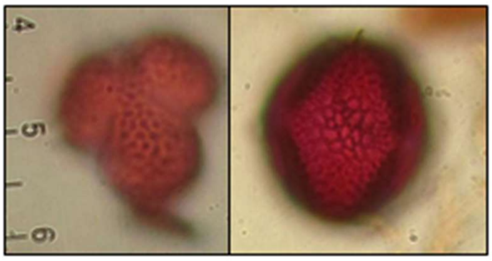
74) *Littorela*

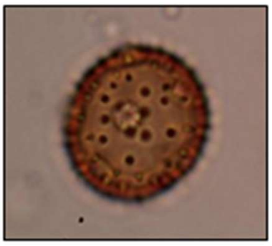


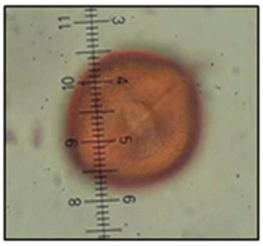
75) *Lomatia/Gevuina*

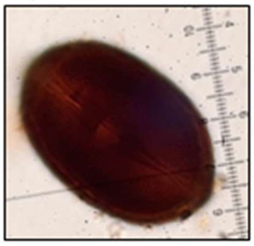


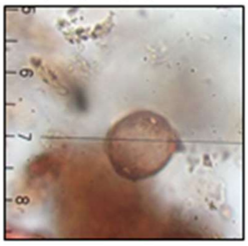
76) *Maytenus*



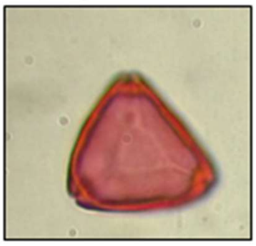

77) *Misodendrum*

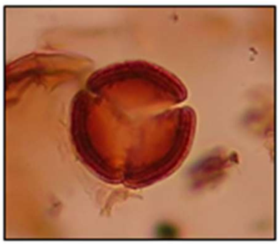

78) *Muehlenmbeckia*

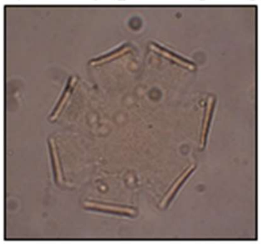

79) *Mutisia*


80) *Myriophyllum*


81) Myrtaceae

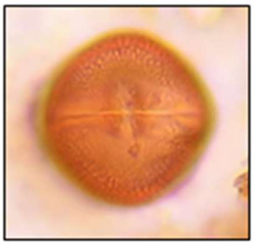

82) Myrtaceae

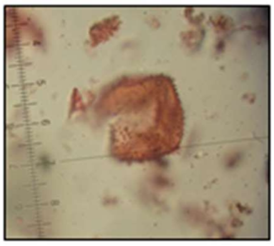

83) *Nassauvia*


84) *Nothofagus obliqua*-typ

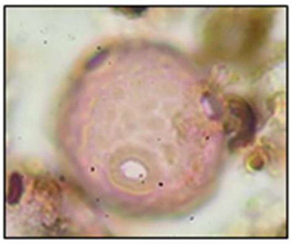

85) *N. dombeyi*-type

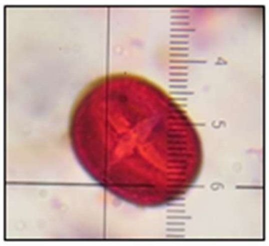

86) *Oldenlandia*

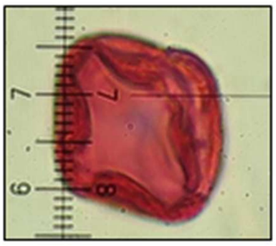

87) *cf. Oxytheca*


88) *Peumus boldo*


89) *Phytolacca*


90) *Plantago lanceolata*

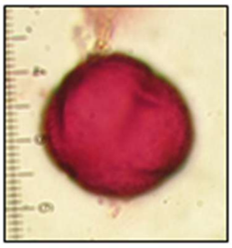

91) Polygonaceae undiff.


92) *Potentilla*


93) *Quinchamalium*


94) *Ribes*

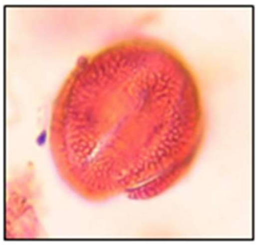
95) *Rumex acetosella*



96) *Rumex magellanica*

97) *Sanicula*

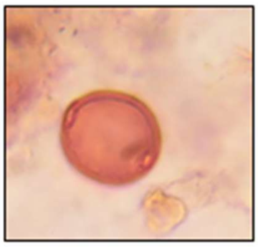
98) *cf. Satureja*



99) *Schinus*

100) *Solanum*

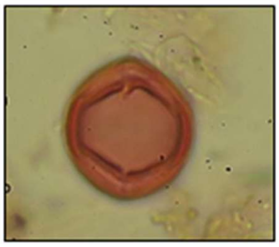
101) *Urtica*



102) *Valeriana*

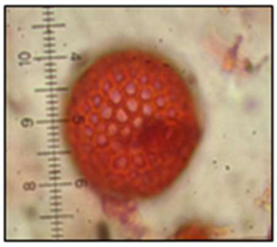
103) Verbenceae

104) Verbenceae



105) *Viola*

106) *Wendtia*



Appendix c: Age estimation of the tephra layers identified in the sediment from Lake Relem

tephra ID	Original depth (cm)	Modified depth (cm)	Radiocarbon age (yr BP)	min95%	max95%	Tephra thickness (cm)
1	347	354,5	747	729	839	1,5
2	359	356	769	751	860	1,5
3	386	381,5	1138	1113	1211	1,5
4	422	416,5	1645	1571	1703	1
5	429	422,5	1732	1648	1788	1
6	433	424,5	1761	1674	1817	2
7	437	426,5	1790	1701	1847	2
8	447	435	1939	1852	1992	1,5
9	460	447	2192	2128	2243	1
10	470	455,5	2371	2306	2427	1,5
11	477	460,5	2477	2405	2539	2
12	479	462	2508	2436	2572	0,5
13	482	464,5	2561	2486	2629	0,5
14	484	466	2593	2517	2664	0,5
15	497	475,5	2793	2701	2878	3,5
16	504	480,5	2898	2794	2994	2
17	724	484,5	2989	2879	3085	216
18	753	495,5	3266	3154	3341	0,5
19	762	502	3430	3313	3493	2
20	766	505	3505	3389	3564	1
21	779	517,5	3821	3693	3861	0,5
22	781	519	3858	3728	3895	0,5

23	784	521,5	3921	3789	3956	0,5
24	786	523	3959	3825	3993	0,5
25	831	561,5	4930	4725	4941	3
26	841	570,5	5156	4933	5166	1
27	846	574	5245	5012	5254	1,5
28	865	591,5	5748	5561	5758	1,5
29	883	602	6056	5894	6070	7,5
30	889	607	6202	6052	6221	1
31	897	614	6407	6273	6431	1
32	902	617	6494	6368	6523	2
33	922	635,5	7036	6946	7106	1,5
34	958	668,5	7899	7781	7972	3
35	970	678,5	8151	8011	8235	2
36	974	681,5	8227	8079	8315	1
37	980	687	8365	8206	8464	0,5
38	991	695,5	8580	8395	8695	2,5
39	994	696,5	8605	8418	8723	2

Declaration of Academic Integrity

I hereby confirm that the present dissertation is solely the work of myself. All scientific collaborators appear as co-authors of the manuscripts. If any passages or figures/diagrams from books, papers, the Web or other sources have been copied or in any other way used, all references, including those found in electronic media, have been acknowledged and fully cited.

Ricardo A. Moreno Gonzalez

Acknowledgements

I am thankful with many people during the time of this PhD research, but the story start much before this important keystone in my scientific life. I want to thank all those engaged in my early formation in science; here you go my first wave Iván, Carlos, Duncan, thanks for your motivation and support; to the entire “disturbance agents” at the Institute, KDP, Ariel, Waldo, Rafael and Jorge, and many other friends.

I want to acknowledge the labor of my advisors. First, I am grateful to Prof. H. Behling for the opportunity to conduct a PhD research at the department, and for his support in finishing this thesis. Thanks to my early advisors, Dr. Sonia L. Fontana and Dr. Thomas Giesecke, for the time they spend in helping me and improving my scientific skills. It was a pity what happened by the end. I wish you both all the best, I learned a lot from you. I want to thank to Prof. F. Shäbitz and Prof. H. Bergmeier who accepted to be on the board committee in the last stage of my PhD. I wish it would be another way to meet you in others working condition. Finally, I am also grateful to the scholarship granted by DAAD/CONICYT and the support they provide.

I want to express all my gratitude to my colleagues at the department. Thanks Paula for your honesty and friendship. Thanks Lyudmila, Vincent, Caro and Angi for your friendship, I had a lot of fun with you. Thanks Daniela and Christina, for your happiness and kindly chat. Of course, my especial thanks go to Valentina, my dear *coleguita*. My friends, I would like I could share more time with you all and know you much better. I feel in debt with you, but let hope we will meet again. To all of you, all my consideration, big hugs, my best wishes, and have good luck in science.

Thousands of words will not be sufficient to express all my affection, appreciation and thoughtfulness to my family. To my wife Jana, for all the support and encourage, all her sacrifice and patient, but permanent love. To my children, with their incomparable daily help in enjoying the moment and abilities to move myself. Special warms go to my father who slowly walk closing his cycles and filling the story. Thanks for parenting me, will apply your best. It is also for you my brothers and sister, many thanks for your affects. My unearthly thanks for my mother, untouchables words you can receive wherever you are now. Thanks for being part of all.