

# Vegetation responses to past volcanic disturbances at the *Araucaria araucana* forest-steppe ecotone in northern Patagonia

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## Abstract

**Aims** Volcanic eruptions play an important role in vegetation dynamics and its historical range of variability. However, large events are infrequent and eruptions with significant imprint in today vegetation occurred far in the past, limiting our understanding of ecological process. Volcanoes in southern Andes have been active during the last 10 ka, and support unique ecosystems such as the *Araucaria-Nothofagus* forest as part of the Valdivian Temperate Rainforest Hotspot. *Araucaria* is an endangered species, strongly fragmented and well adapted to disturbances. Yet it was suggested that volcanism might have increased the fragmentation of its populations. To provide an insight into the vegetation responses to past volcanic disturbances, a paleoecological study was conducted to assess the role of volcanic disturbance on the vegetation dynamics and if the current fragmentation has been caused by volcanism. Location *Araucaria* forest-steppe ecotone in northern Patagonia. Methods Pollen and tephra analysis from a sedimentary record. Results During the last 9 kyr, 39 tephrafall buried the vegetation around Lake Relem, more frequently between 4-2 ka. The vegetation was sensitive to small tephrafall but seldom caused significant changes. However, the large eruption of Sollipulli-Alpehue (~3 ka) might change the environmental conditions affecting severely the forest and grassland, as suggested by the pollen record. Ephedra dominated early successional stage, perhaps facilitating *Nothofagus* regeneration recovering original condition after ~500 years. Slight increase of pollen percentage from *Araucaria* and *Nothofagus obliqua*-type could be indicative of sparse biological legacies distributed in the landscape. The analysis showed that vegetation resisted without permanent changes, recovering relatively fast after the large eruption. Conclusion The relative stability of *Araucaria* pollen in the study area after several tephrafall suggests no change in its past geographical distribution at the current forest-steppe ecotone, thus I found no evidence that volcanic eruptions would have affected its current conservation status.

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Running title

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### Abstract

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paleoecological study was conducted to assess the role of volcanic disturbance on the vegetation dynamics and if the current fragmentation has been caused by volcanism.

#### Location

Araucaria forest-steppe ecotone in northern Patagonia.

#### Methods

Pollen and tephra analysis from a sedimentary record.

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During the last 9 kyr, 39 tephras buried the vegetation around Lake Relem, more frequently between 4-2 ka. The vegetation was sensitive to small tephras but seldom caused significant changes. However, the large eruption of Sollipulli-Alpehue (~3 ka) might change the environmental conditions affecting severely the forest and grassland, as suggested by the pollen record. *Ephedra* dominated early successional stage, perhaps facilitating *Nothofagus* regeneration recovering original condition after ~500 years. Slight increase of pollen percentage from *Araucaria* and *Nothofagus obliqua* -type could be indicative of sparse biological legacies distributed in the landscape. The analysis showed that vegetation resisted without permanent changes, recovering relatively fast after the large eruption.

#### Conclusion

The relative stability of *Araucaria* pollen in the study area after several tephras suggests no change in its past geographical distribution at the current forest-steppe ecotone, thus I found no evidence that volcanic eruptions would have affected its current conservation status.

**Keywords** : disturbance regime, vegetation resilience, long-term vegetation dynamics, volcanic ecology, Valdivian Temperate Rainforest hotspot

## Introduction

Volcanic eruptions are 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). Volcanism creates complex patterns and dynamic processes on the vegetation depending on the disturbance mechanism and the magnitude (e.g., Crisafulli & Dale, 2018; Foster, Knight, & Franklin, 1998). In example, the vegetation growth rapidly after being buried by tephras (Zobel & Antos, 2018), while the type and arrange of biological legacies in disturbed areas drove regeneration patterns and the rate of vegetation development after disturbance (del Moral & Grishin, 1999). Understanding the lasting effects of process and patterns of vegetation responses like the resistance, recovery or the develop of diversity patterns may help in designing nature management (Dale et al., 2005; Franklin et al., 2002) especially in highly diverse biogeographical areas influenced by volcanism. 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. For example, for large-eruptions of Icelandic volcanoes that could affect past climate conditions, palynological studies showed contradictory or weak evidences that volcanoes disturbed the vegetation in western Europe (Paine et al., 2013). Also in the Mt. Mazana, western North America, an experiment was conducted in a small lake to infer the impacts on local and regional vegetation (Egan et al., 2016). The authors concluded that eruptions did not trigger significant changes in terrestrial pollen taxa in a distant area, but the aquatic taxa changed due to enrichment of nutrients. Unlike those areas, after

Taupo eruption (~1850 yrs BP), New Zealand, pollen evidences indicate that this eruption destroyed the forest nearby, and up to 170 km east of the vent the vegetation suffered a variable degree of disturbance (Wilmshurst & McGlone, 1996). In many areas the forest could not recover to its original conditions, and sites far from the crater covered by thin tephra layer were strongly impacted. Despite the expected role of volcanoes in several global biodiversity hotspots little is known about the mechanism that volcanic eruption drove past vegetation dynamics and their influence in the diversity patterns needs to be further explored.

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 kyr in the Andes region (Fontijn et al., 2014). The southernmost section of the Andes supports unique forest ecosystems, featured by a high endemism, which also have been influenced by these volcanoes affecting structure and functions in this Andean forest and surrounding vegetation (e.g., Veblen et al., 2016). As result of the eruptions, the tree-line location 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). The evidences show 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 in 2011, the steppe vegetation was buried by <5 cm tephra and rhizomatous geophytes species such as *Poa* spp. 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 in the landscape. 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.

Despite the volcanic characteristics and the unique vegetation, little is known about the role of volcanic disturbance on the vegetation dynamics in northern Patagonia, the rate of recovery or the capability to resist disturbance, particularly in the *Araucaria araucana* forest. It was hypothesized that past volcanic eruptions might influenced the genetic variability of *Araucaria*, but also affected negatively the population distribution and regeneration dynamics (e.g., Bekessy et al., 2002; Veblen et al., 2016). Yet the hypothesis is contradictory with the recognized morphological adaptation to resist volcanic disturbance (Burns, 1991) that might helped to persist in an angiosperm dominated ecosystems (Kershaw & Wagstaff, 2001). Despite *Araucaria*'s socio-ecological importance and its current conservation status, few long-term vegetation reconstructions have been conducted so far in the *Araucaria* forest-steppe ecotone. To contribute to the knowledge of vegetation dynamics and the volcanic disturbance regime, this work aims 1) to reconstruct the volcanic disturbance history in the *Araucaria* forest-steppe ecotone, 2) to assess the vegetation responses to past volcanic disturbance and 3) to evaluate if *Araucaria* distribution was influenced by volcanism at the current forest-steppe ecotone affecting its conservation status. To this end, I made use of a published pollen record (Moreno-Gonzalez et al., 2021) and re-analysed to have a separate insight into the volcanic influence on the *Araucaria* forest dynamics. Due to the distance to the volcanic source of the forest-steppe ecotone eastward of the Andes, it is affected mostly by tephrafall that buried the vegetation. Tephrafall therefore is the main volcanic disturbance type around the study area. Following this assumption, I predict that the magnitude of 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. Then, forest fragmentation should increase after thick tephrafall.

## Methods

The study area is located in the current *Araucaria* forest-steppe ecotone around 39° S, in northern Patagonia (Figure 1). In particular, vegetation history was reconstructed from a sediment core obtained from Lake

Relem (38°58'39" S; 71°4'51" W; 1268 m a.s.l.), Lake Relem is a shallow and small lake (~2.5 m depth, ~1 ha, respectively), without river inflow or outflow. The climate in the region is temperate with oceanic influence. The Pacific air masses arriving with westerly winds create a sharp rain-shadow effect discharging most of the precipitation on the western section of the Andes (Mundo et al., 2013). Climatic conditions when interacting with local topography and natural disturbances generate complex vegetation patterns and plants associations (Kitzberger, 2012; Roig, 1998). *Araucaria* forest occurs mainly above 1000 m elevation, normally reaching the tree-line at 1700 m a.s.l. (Gonzalez et al., 2006) showing a strong fragmentation (Figure 1). Further details on climate and vegetation description, as well as a full description of the sediment analysis, pollen analysis and the chronology can be found in Moreno-Gonzalez (2020) and Moreno-Gonzalez, Giesecke, and Fontana (2021).

## 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 1). Fontijn et al. (2014) list all eruptions recorded so far to the SVZ, which are summarized in Table 1. The Lonquimay volcano has had more regular eruptions of considerable magnitude (VEI [?]3) while other 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). In relation to the So-A eruption, Lake Relem is located within the isopach of 2 m (Fontijn et al., 2016).

## Data analysis

Here we used only pollen data from terrestrial taxa per sample and expressed as 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. 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).

To reconstruct the volcanic disturbance regime, we made use of every tephra layer >0.5 cm thick. Here we considered each of these tephra layers as a single and independent disturbance event -since tephra fall 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 ( $\xi^{-\alpha t}$ ), where  $x$  is the value for the ash (arbitrarily set to 100 by the authors),  $\alpha$  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 centimetres. In doing so, we aim to describe the magnitude of the eruptions. 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. 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 in a multivariate analysis (Redundant Analysis) 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).

## Results

### Reconstruction of the volcanic regime

The volcanic history and its disturbance regime were reconstructed from the tephra layer content in the sediment of Lake Relem (Figure 2). 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 2a) but only 18 are >1.5 cm thick, what could be considered as significant peaks (crosses in Figure 2a). The tephra layer corresponding to the So-A eruption is the biggest one, which in the core recorded 216 cm. The tephra-value, modelled as an exponential decay, shows similar patterns regards the tephra thickness, but indicates a lowest effect regarding to the eruption magnitude while missing some peaks above the threshold (Figure 2b). Considering all the tephra layers, volcanic disturbance regime is relatively frequent (Figure 2c). 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 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.

### Vegetation responses to volcanic events

A full description of the vegetation history was published in Moreno-Gonzalez (2020). It encompasses the last 9 kyr and it is characterized by an overall vegetation transition from steppe grassland (Poaceae) to forest (*Nothofagus dombeyi* -type) that occurred ~4.5ka (Appendix 1), likely as result of a change in precipitation regime rather than fire (Moreno-Gonzalez et al., 2021). Likewise, in the unconstrained ordination diagram (Figure 3a) the compositional trends represent the gradual vegetation change. 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* in the pollen record rose after the So-A eruption (Figure 3, Appendix 1), therefore the second axis is mostly related to the response of So-A (Figure 3a). The volcanic eruptions had a significant influence on vegetation composition (Figure 3b) explaining 20% of the data. The explanatory variables, volcanic frequency and magnitude, had a significant influence on the vegetation too. However, further analysis excluding samples after the So-A eruption indicate that the other small tephra-layers had no significant influence in the pollen composition. In the multivariate analysis, *Araucaria* shows a weak negative relation with volcanic frequency, while somewhat related with volcanic magnitude suggesting that *Araucaria* increased its abundance following the eruptions.

The figure 4 shows 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 marked a disturbance event, normally caused a decrease (increase) in Poaceae (*N. dombeyi* -type) pollen percentage (Figure 4a). The decrease is not proportional to tephra thickness, but it is 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 4b), where PAR could be interpreted as an indicator of vegetation biomass. Volcanic events normally caused small decrease in PAR between 100-500 grains cm<sup>-2</sup>yr<sup>-1</sup>, while after So-A eruption PAR decayed more than 2000 grains cm<sup>-2</sup> yr<sup>-1</sup>. Other drops in PAR can be related to sedimentary processes or other disturbances. The Principal Curve fitted after 21 iterations. The variation in the distance gradient units indicates some sensitivity of the vegetation composition to volcanic disturbances, notwithstanding only few significant changes (Figure 4c). 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 4d). 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 4e). 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, with some biological legacies and survival individual remained in sheltered areas. As the dominant taxa was depressed, palynological evenness increased (Figure 4e), a pattern that normally occurred after other small volcanic eruptions in this study.

## Discussion

After volcanic disturbance episodes, the pollen richness and evenness, as well as PAR, do not indicate a unique pattern of decreasing biodiversity and biomass. The traditional successional model suggests an overall decrease in plant biomass and diversity caused by volcanism that initiate a new ecological succession, likely dominated by pioneer and shadow-intolerant species. Contrary to this expected model, the findings presented here showed a more complex dynamic in the *Araucaria* forest-steppe ecotone, what may be controlled by many interacting factors. Recent advances in volcanic ecology (Crisafulli et al., 2015) point that the vegetation resistance and the rate of recovery is a result of factors such as climatic conditions, type of the impact and topography (del Moral and Grishin, 1999), plants traits (Antos & Zobel, 1986), and biological legacies (e.g., Dale et al., 2005). Moreover, those operating factors can vary in time and spatial extension from one eruptive event to another. In the following paragraph, I attempt to contextualize those patterns occurring around Lake Relem.

*Ephedra* was the unexpected dominant taxa during the early successional stage after the So-A eruption since *Nothofagus* species and *Araucaria* are considered pioneer tree in the region (Figure 5). Little is known about its ecology and its palaeoecological 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 from Lake Relem. 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 kilometres 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 a very local presence –perhaps suppressed or co-existing with other species- and the following increase as result of the So-A eruption that facilitate its expansion under certain conditions. For instance, Mallín Paso del Arco (Heusser et al., 1988), a record within the 2 m isopach zone of the So-A, depict a slight increase on *Ephedra* around 3 ka, above a thick tephra layer at the core bottom. Unlike, other sites do not show an increase in *Ephedra* (Dickson et al., 2020; Fontana & Giesecke, 2017) and, to my knowledge, none of the palynological records in northern Patagonia show a significant increase of *Ephedra* after an eruption nor have been reported during recent eruptions.

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 (Figure 4). Small tephra fall left some impact to the vegetation dominated by grasses (Figure 4b), but recovering fast enough to not register a peak in the rate-of-change analysis (Figure 4c). 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 4 and 5).

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 also an important role to resist tephra deposition and may determine the species performance. 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 early establishment of *Ephedra* was likely due to special adaptation to poor soil, sprouting shoots, and the capacity to resist arid and cold weather conditions (Luebert & Plissock, 2006). Roots growing seem to be a common mechanism of plants in response to buried disturbance by tephrafall. 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 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 (Figure 5, Phase II) 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 that 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 (this study and Dickson et al. 2020). Indeed, the data presented here shows that *Nothofagus* species did not behave as pioneer and expanded into the area after 500 years in advanced successional stages following the decay of *Ephedra* (Figure 5, phase III).

Multivariate analyses indicated that *Araucaria* was not affected by any of the small tephrafall. It is largely documented that the thick bark, flexible branches and smooth leaves allow the species to resist moderate disturbance (Burns, 1991; Veblen et al., 1995). Hence, it is possible that small tephrafall deposited in the trees crown did not cause significant physical damage to the whole population. If chemical change to soil occurred after tephra deposition, physiological harms such as decreasing tree-ring growth might not last for a long time (Tognetti et al., 2012), 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 (the largest eruption in the area for the last 9 ka), it is unlikely that volcanism affected negatively the distribution of the populations increasing the fragmentation distant from volcanic source as it suggested by Bekessy et al. (2002). A recent pollen record from Lake Cilantro (Dickson et al., 2020) shows similar patterns as those observed in Lake Relem, neither changes in pollen relative abundance after small tephra layers nor changes in PAR after So-A eruption. Although not a generalised pattern, Dickson et al. (2020), Moreno-Gonzalez et al. (2021) and Nanavati et al., (2020) showed that pollen abundance in areas nearby the current ecotone have been slightly increasing for the last ~4 ka despite of the influence of

several volcanic eruptions. Further palaeoecological studies need to be done to understand the role of past volcanic eruptions in determining current diversity patterns in Araucaria forest and that can be used in the conservation of certain threatened species in the Valdivian Temperate Rainforest hotspot.

#### Data accessibility statement

Moreno-Gonzalez, Ricardo; Giesecke, Thomas; Fontana, Sonia L (2020): Pollen and macro-charcoal analysis of Lake Relem sediment core, northern Patagonia. PANGAEA, <https://doi.org/10.1594/PANGAEA.923741>

#### Reference

Álvarez-Barra, V., Giesecke, T., & Fontana, S. L. (2020). Late Holocene vegetation dynamics and disturbance regimes in north Patagonia Argentina (40°S). *The Holocene* 30(8):1115-1128. doi:10.1177/0959683620913920.

Antos, J. A., & Zobel, D. B. (1986). Recovery of Forest Understories Buried by Tephra from Mount St. Helens. *Vegetatio* ,64 (2/3), 103–111. <https://doi.org/10.2307/20037246>

Bekessy, S. A., Allnutt, T. R., Premoli, A. C., Lara, A., Ennos, R. A., Burgman, M. A., Cortes, M., & Newton, A. C. (2002). Genetic variation in the Monkey Puzzle tree, detected using RAPDs. *Heredity* ,88 , 243–249. <https://doi.org/10.1038/sj/hdy/6800033>

Bennett, K. D., & Humphry, R. W. (1995). Analysis of late-glacial and Holocene rates of vegetational change at two sites in the British Isles. *Review of Palaeobotany and Palynology* , 85 (3–4), 263–287. [https://doi.org/10.1016/0034-6667\(94\)00132-4](https://doi.org/10.1016/0034-6667(94)00132-4)

Birks, H. J. B., & Line, J. M. (1992). The use of Rarefaction Analysis for Estimating Palynological Richness from Quaternary Pollen-Analytical Data. *The Holocene* , 2 (1), 1–10. <https://doi.org/10.1177/095968369200200101>

Burns, B. R. (1991). *The regeneration dynamics of Araucaria araucana* . University of Colorado.

Crisafulli, C. M., & Dale, V. H. (2018). *Ecological responses at Mount St. Helens : revisited 35 years after the 1980 eruption* . Springer.

Crisafulli, C. M., Swanson, F. J., & Clarkson, B. D. (2015). Volcano Ecology : Disturbance Characteristics and Assembly of Biological Communities. *The Encyclopedia of Volcanoes , March 2018* , 1265–1284. <https://doi.org/10.1016/B978-0-12-385938-9.00073-0>

Dale, V. H., Swanson, F. J., & Crisafulli, C. M. (2005). Ecological perspectives on management of the mount St. Helens landscape. In V. H. Dale, F. J. Swanson, & C. M. Crisafulli (Eds.), *Ecological Responses to the 1980 Eruption of Mount St Helens* (pp. 277–286). Springer. [https://doi.org/https://doi.org/10.1007/0-387-28150-9\\_19](https://doi.org/https://doi.org/10.1007/0-387-28150-9_19)

Daniels, L. D., & Veblen, T. T. (2004). Spatiotemporal Influences of Climate on Altitudinal Treeline in Northern Patagonia. *Ecology* ,85 (5), 1284–1296. <https://doi.org/10.1890/03-0092>

del Moral, R., & Grishin, S. Y. (1999). Volcanic disturbances and ecosystem recovery. In L. R. Walker (Ed.), *Ecosystems of Disturbed Ground* (1st ed., p. 868). Elsevier.

Dickson, B., Fletcher, M., Hall, T. L., & Moreno, P. I. (2020). Centennial and millennial-scale dynamics in *Araucaria* –*Nothofagus* forests in the southern Andes. *Journal of Biogeography* , jbi.14017. <https://doi.org/10.1111/jbi.14017>

Fontana, S. L., & Giesecke, T. (2017). Processes and patterns of vegetation change during the Holocene at the forest-steppe ecotone in northern Patagonia, Argentina. *Pages-OSM* , 234.

Fontijn, K., Lachowycz, S. M., Rawson, H., Pyle, D. M., Mather, T. A., Naranjo, J. A., & Moreno-roa, H. (2014). Late Quaternary tephrostratigraphy of southern Chile and Argentina. *Quaternary Science Reviews* , 89 , 70–84. <https://doi.org/10.1016/j.quascirev.2014.02.007>

- Foster, D. R., Knight, D. H., & Franklin, J. F. (1998). Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* , 1 (6), 497–510. <https://doi.org/10.1007/s100219900046>
- Franklin, J. F., Spies, T. A., Pelt, R. Van, Carey, A. B., Thornburgh, D. A., Berg, D. R., Lindenmayer, D. B., Harmon, M. E., Keeton, W. S., Shaw, D. C., Bible, K., & Chen, J. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* , 155 (1), 399–423. [https://doi.org/10.1016/S0378-1127\(01\)00575-8](https://doi.org/10.1016/S0378-1127(01)00575-8)
- Ghermandi, L., Gonzalez, S., Franzese, J., & Oddi, F. (2015). Effects of volcanic ash deposition on the early recovery of gap vegetation in Northwestern Patagonian steppes. *Journal of Arid Environments* , 122 , 154–160. <https://doi.org/10.1016/j.jaridenv.2015.06.020>
- Gilbert, D., Freundt, A., Kutterolf, S., & Burkert, C. (2014). Post-glacial time series of explosive eruptions and associated changes in the magma plumbing system of Lonquimay volcano, south central Chile. *International Journal of Earth Sciences* , 103 (7), 2043–2062. <https://doi.org/10.1007/s00531-012-0796-x>
- Global Volcanism Program. (2013). *Volcanoes of the World, v. 4.8.2* . Venzke, E (Ed.). Smithsonian Institution.
- Gonzalez, M. E., Cortez, M., Izquierdo, F., Gallo, L. A., Echeverria, C., Bekkesy, S., & Montaldo, P. (2006). *Araucaria araucana*. In C. Donoso (Ed.), *Las especies arboreas de los bosques templados de Chile y Argentina. Autoecologia* (2nd ed., pp. 36–53). Marisa Cuneo Ediciones.
- Henriquez, W. I., Moreno, P. I., Alloway, B. V, & Villarosa, G. (2015). Vegetation and climate change, fire-regime shifts and volcanic disturbance in Chiloe Continental (43 degS) during the last 10,000 years. *Quaternary Science Reviews* , 123 , 158–167. <https://doi.org/10.1016/j.quascirev.2015.06.017>
- Heusser, C. J., Rabassa, J., Brandani, A., & Stuckenrath, R. (1988). Late-Holocene Vegetation of the Andean Araucaria Region, Province of Neuquen, Argentina. *Mountain Research and Development* , 8 (1), 53–63.
- Jenny, B., Wilhelm, D., & Valero-Garces, B. L. (2003). The Southern Westerlies in Central Chile: Holocene precipitation estimates based on a water balance model for Laguna Aculeo (33deg50'S). *Climate Dynamics* , 20 (2–3), 269–280. <https://doi.org/10.1007/s00382-002-0267-3>
- Juggins, S. (2015). rioja: Anlalysis of Quaternary science data. *R Documentation* . <https://doi.org/http://cran.r-project.org/package=rioja2009>.
- Kershaw, P., & Wagstaff, B. (2001). The southern conifer family Araucariaceae: History, Status, and Value for Paleoenvironmental Reconstruction. *Annual Review of Ecological System* , 32 , 397–414.
- Kitzberger, T. (2012). Ecotones as Complex Arenas of Disturbance , Climate , and Human Impacts: The Trans- Andean Forest-Steppe Ecotone of Northern Patagonia. In R. W. Myster (Ed.), *Ecotones Between Forest and Grassland* (pp. 59–88). Springer Science+Business Media. <https://doi.org/10.1007/978-1-4614-3797-0>
- Lamy, F., Hebbeln, D., Rohl, U., & Wefer, G. (2001). Holocene rainfall variability in Southern Chile: A marine record of latitudinal shifts of the Southern Westerlies. *Earth and Planetary Science Letters* , 185 (3–4), 369–382. [https://doi.org/10.1016/S0012-821X\(00\)00381-2](https://doi.org/10.1016/S0012-821X(00)00381-2)
- Loera, I., Ickert-Bond, S. M., & Sosa, V. (2015). Ecological consequences of contrasting dispersal syndromes in New World Ephedra: Higher rates of niche evolution related to dispersal ability. *Ecography* , 38 (12), 1187–1199. <https://doi.org/10.1111/ecog.01264>
- Luebert, F., & Plischoff, P. (2006). *Sinopsis bioclimatica y vegetalional de Chile* . Editorial Universitaria. <https://doi.org/10.4067/S0718-34022008000200008>

- Maher, L. J. (1964). Ephedra Pollen in Sediments of the Great Lakes Region Author ( s ): Louis J . Maher , Jr . Published by : Wiley on behalf of the Ecological Society of America Stable URL : <https://www.jstor.org/stable/1933858> REFERENCES Linked references are available on. *Ecology* , 45 (2), 391–395.
- Matthias, I., Semmler, M. S. S., & Giesecke, T. (2015). Pollen diversity captures landscape structure and diversity. *Journal of Ecology* , 103 (4), 880–890. <https://doi.org/10.1111/1365-2745.12404>
- Montiel, M., Gonzalez, M. E., & Crisafulli, C. M. (2016). Caida de tefra y su influencia sobre la estructura y dinamica de los bosques andinos de Nothofagus en el Parque Nacional Puyehue, Chile. *Anales Del Instituto de La Patagonia* , 44 (3), 5–11. <https://doi.org/10.4067/s0718-686x2016000300001>
- Moreno-Gonzalez, R. (2020). *Holocene Vegetation and Disturbance Dynamics in the Araucaria araucana Forest: a paleoecological contribution for conservation* . University of Gottingen.
- Moreno-Gonzalez, R., Diaz, I. A., Christie, D. A., Coopman, R. E., & Lara, A. (2019). Early vegetation recovery after the 2008-2009 explosive eruption of the Chaiten Volcano. *BioRxiv* .
- Moreno-Gonzalez, R., Giesecke, T., & Fontana, S. L. (2021). Fire and vegetation dynamics of endangered Araucaria araucana communities in the forest-steppe ecotone of northern Patagonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* , 567 , 110276. <https://doi.org/10.1016/j.palaeo.2021.110276>
- Mundo, I. A., Kitzberger, T., Roig Junent, F. A., Villalba, R., Barrera, M. D., Roig Junet, F. A., Villalba, R., & Barrera, M. D. (2013). Fire history in the Araucaria araucana forests of Argentina: Human and climate influences. *International Journal of Wildland Fire* , 194–206. <https://doi.org/10.1071/WF11164>
- Nanavati, W., Whitlock, C., Outes, V., & Villarosa, G. (2020). A Holocene history of monkey puzzle tree (pehuen) in northernmost Patagonia. *Journal of Biogeography* , jbi.14041. <https://doi.org/10.1111/jbi.14041>
- Naranjo, J. A., Moreno, H., Emparan, C., & Murphy, M. (1993). Volcanismo explosivo reciente en la caldera del volcan Sollipulli, Andes del Sur (39° S). *Revista Geologica de Chile* ,20 (2), 167–191.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2017). vegan: Community Ecology Package. In *R package version 2.4-2* (p. <https://CRAN.R-project.org/package=vegan>).
- Raffaele, E., & Veblen, T. T. (1998). Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia, Argentina. *Journal of Vegetation Science* , 9 (5), 693–698. <https://doi.org/10.2307/3237287>
- Roig, F. A. (1998). La vegetacion de la Patagonia. In *Flora Patagonica* (pp. 47–166).
- Rstudio Team. (2016). RStudio: Integrated development for R. RStudio, Inc., Boston MA. In *RStudio* . <https://doi.org/10.1007/978-3-642-20966-6>
- Stern, C. R. (2004). Active Andean volcanism: its geologic and tectonic setting. *Revista Geologica de Chile* . <https://doi.org/10.4067/S0716-02082004000200001>
- Swanson, F. J., & Crisafulli, C. M. (2018). Volcano Ecology: State of the Field and Contributions of Mount St. Helens Research. In *Ecological Responses at Mount St. Helens: Revisited 35 years after the 1980 Eruption* (pp. 305–323). Springer New York. [https://doi.org/10.1007/978-1-4939-7451-1\\_16](https://doi.org/10.1007/978-1-4939-7451-1_16)
- Swanson, F. J., Jones, J. A., Crisafulli, C. M., & Lara, A. (2013). Effects of volcanic and hydrologic processes on forest vegetation: Chaiten Volcano, Chile. *Andean Geology* , 40 (2), 359–391. <https://doi.org/10.5027/andgeov40n2-a10>
- Tognetti, R., Lombardi, F., Lasserre, B., Battipaglia, G., Saurer, M., Cherubini, P., & Marchetti, M. (2012). Tree-ring responses in Araucaria araucana to two major eruptions of Lonquimay Volcano (Chile). *Trees* , 26 (6), 1805–1819. <https://doi.org/10.1007/s00468-012-0749-9>

Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems* , 1 (6), 511–523.

Veblen, T. T., Ashton, D. H., Schlegel, F. M., & Veblen, A. T. (1977). Plant Succession in a Timberline Depressed by Vulcanism in South-Central Chile. *Journal of Biogeography* , 4 (3), 275–294. <https://doi.org/10.2307/3038061>

Veblen, Thomas T. (1982). Regeneration Patterns in Araucaria araucana Forests in Chile. *Journal of Biogeography* , 9 (1), 11. <https://doi.org/10.2307/2844727>

Veblen, Thomas T, Armesto, J. J., Burns, B. R., Kitzberger, T., Lara, A., Leon, B., & Young, K. R. (1995). The ecology of the conifers of southern South America. *Ecology of the Southern Conifers* , JANUARY , 701–725.

Veblen, Thomas T, Gonzalez, M. E., Stewart, G. H., Kitzberger, T., & Brunet, J. (2016). Tectonic ecology of the temperate forests of South America and New Zealand Tectonic ecology of the temperate forests of South America and New Zealand. *New Zealand Journal of Botany* ,54 , 223–246. <https://doi.org/10.1080/0028825X.2015.1130726>

Wilmshurst, J. M., & McGlone, M. S. (1996). Forest disturbance in the central North Island, New Zealand, following the 1850 BP Taupo eruption. *Holocene* , 6 (4), 399–411. <https://doi.org/10.1177/095968369600600402>

Zobel, D. B., & Antos, J. A. (2018). Forest Understory Buried by Volcanic Tephra: Inertia, Resilience, and the Pattern of Community Redevelopment. In *Ecological Responses at Mount St. Helens: Revisited 35 years after the 1980 Eruption* (pp. 113–125). Springer New York. [https://doi.org/10.1007/978-1-4939-7451-1\\_6](https://doi.org/10.1007/978-1-4939-7451-1_6)

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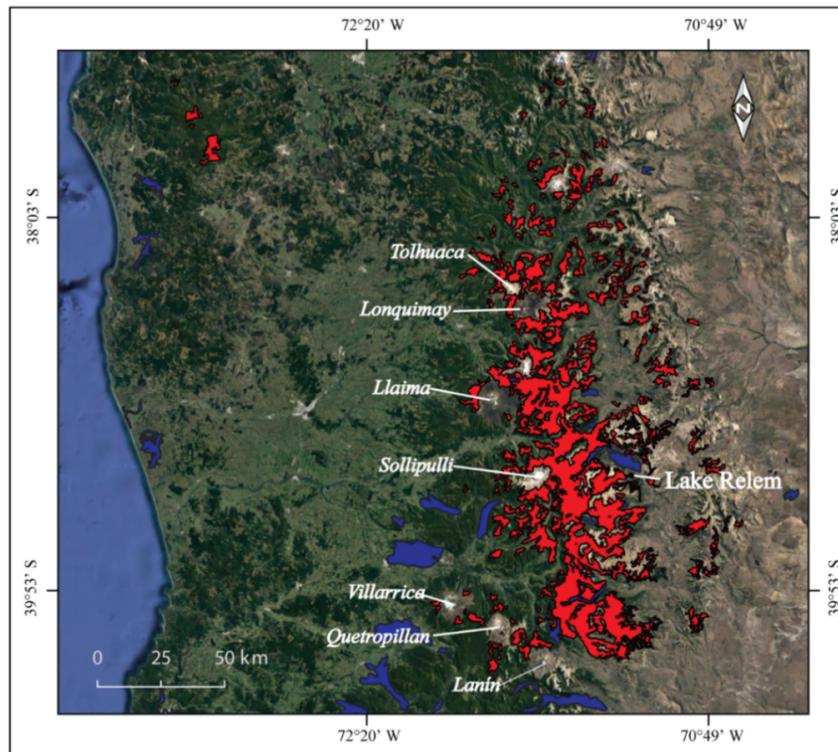


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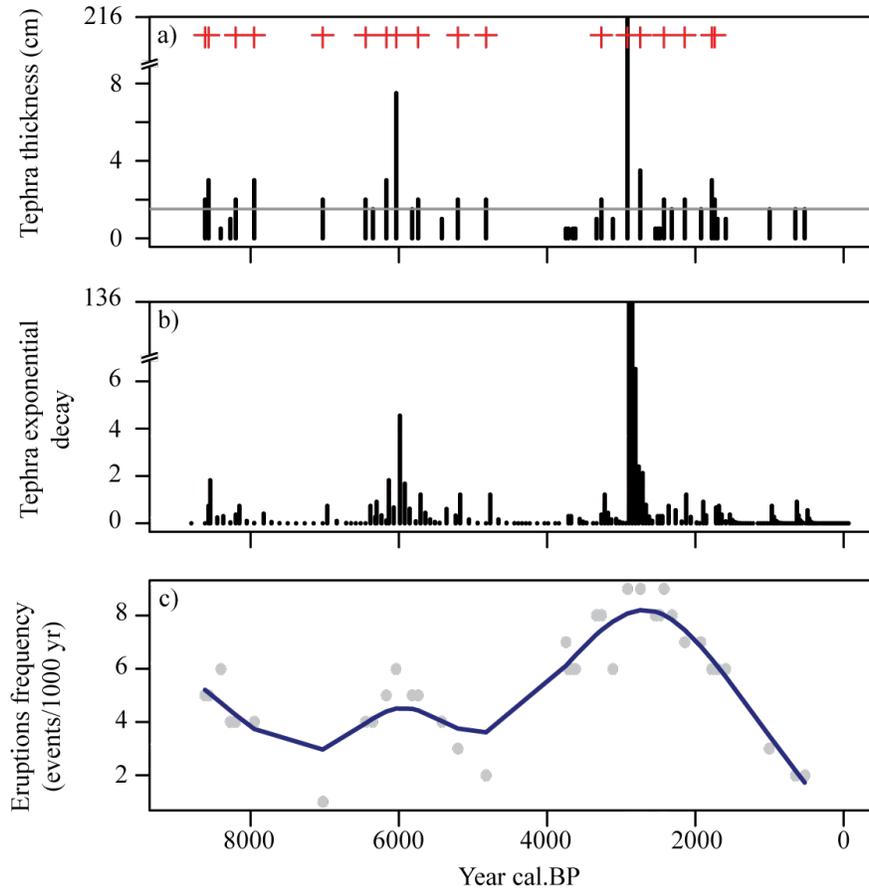


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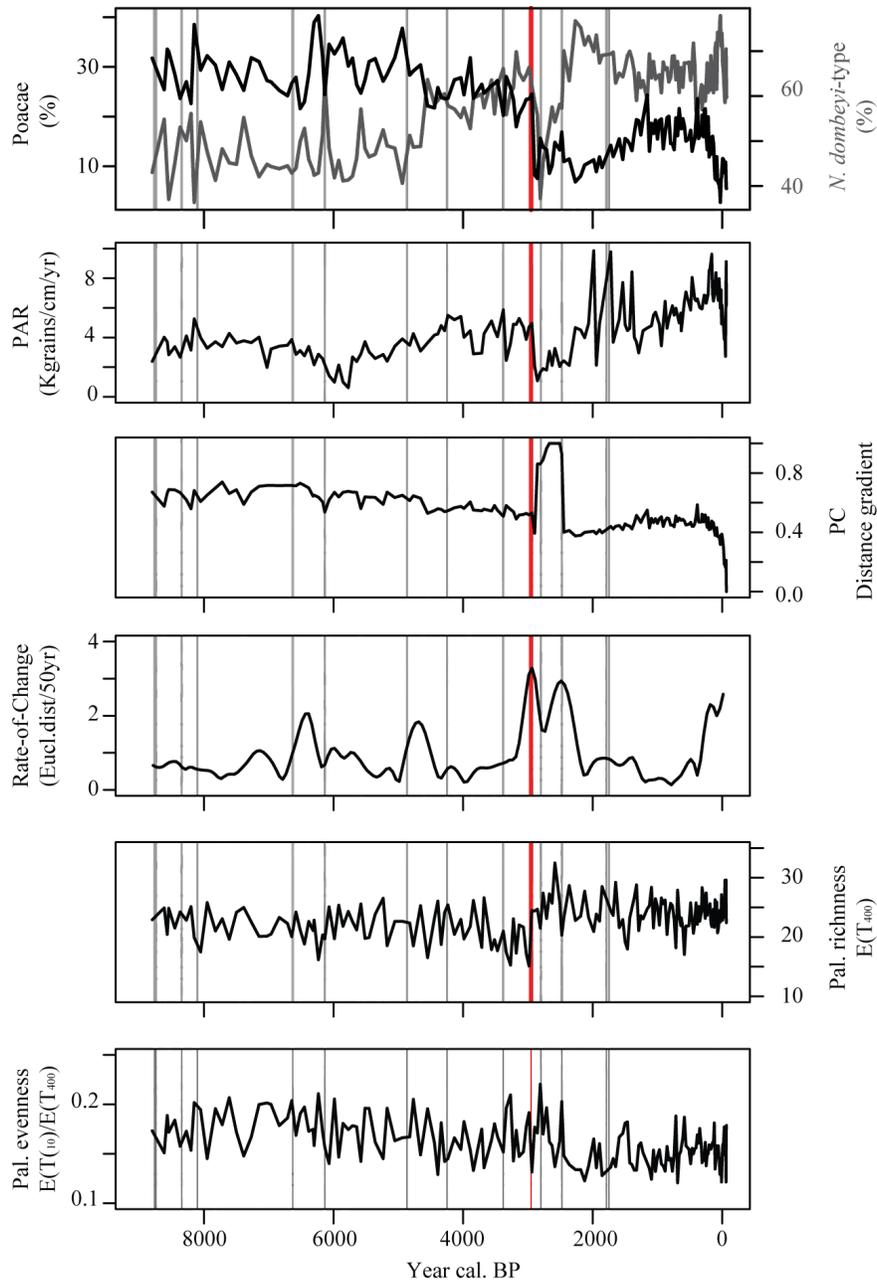


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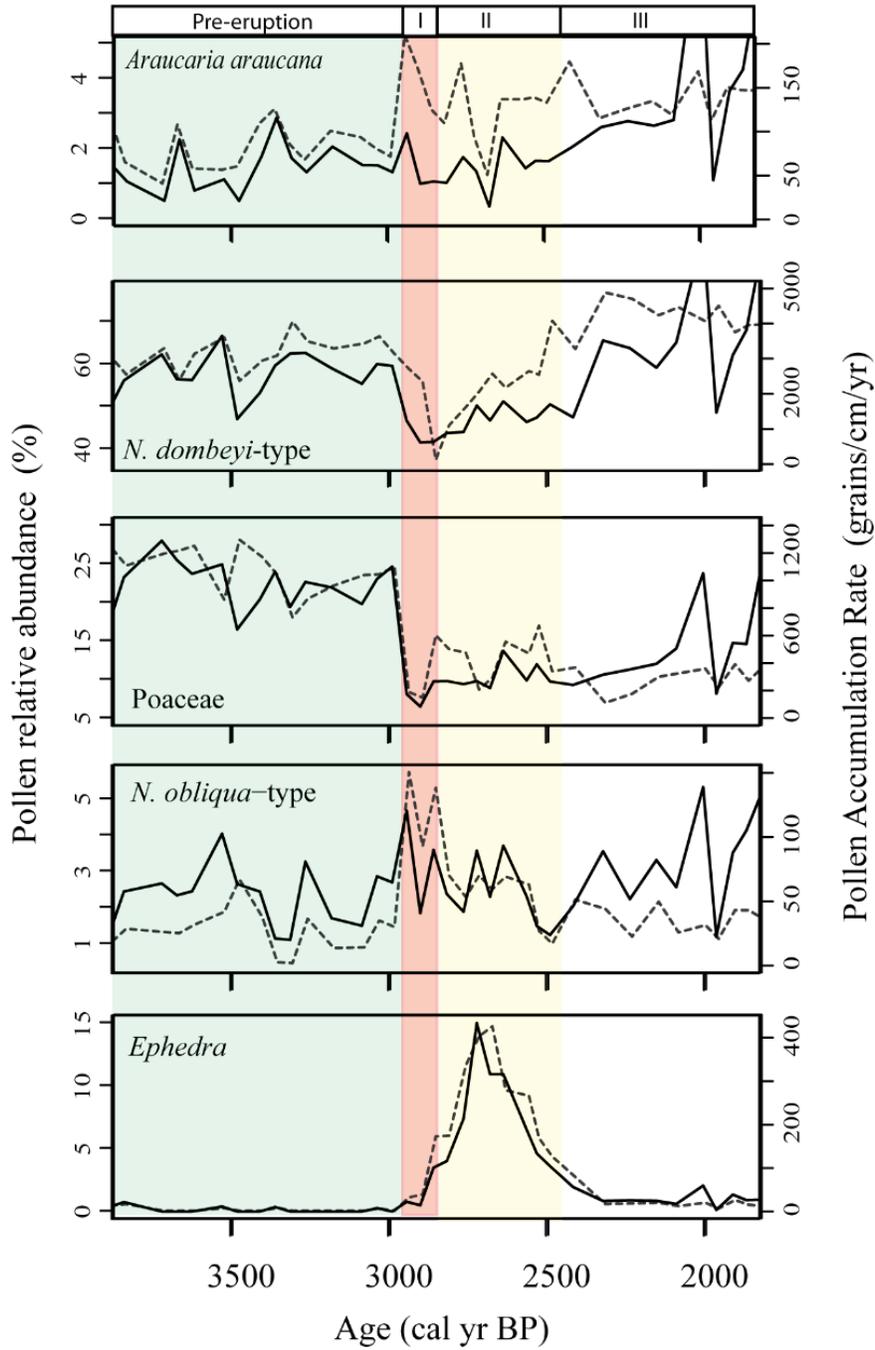


Table 1. Location of potential source volcanoes close to Lake Relem, its frequency (further details for each eruption are found in Fontijn et al., 2014)

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	22	18

Volcano name	Distance and direction from Lake Relem	Total eruptions last 10 ka	Eruptions VEI [?]3
Llaima	64 km; 299° WNW	55	3
Sollipulli	38 km; 270° W	2	2
Villarica	89 km; 236° WS	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 tephras (mainly dacite), probably ejected about 0.01 km<sup>3</sup> 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

Appendix 1. Short pollen diagram of selected taxa. Full pollen diagram is given in Moreno-Gonzalez (2020).

