

Article

Two Thousand Years of Land-Use and Vegetation Evolution in the Andean Highlands of Northern Chile Inferred from Pollen and Charcoal Analyses

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Abstract: The European conquest of the New World produced major socio-environmental reorganization in the Americas, but for many specific regions and ecosystems, we still do not understand how these changes occurred within a broader temporal framework. In this paper, we reconstruct the long-term environmental and vegetation changes experienced by high-altitude wetlands of the southcentral Andes over the last two millennia. Pollen and charcoal analyses of a 5.5-m-long core recovered from the semi-arid puna of northern Chile indicate that while climatic drivers influenced vegetation turnaround, human land use and management strategies significantly affected long-term changes. Our results indicate that the puna vegetation mostly dominated by grasslands and some peatland taxa stabilized during the late Holocene, xerophytic shrubs expanded during extremely dry events, and peatland vegetation persisted in relation to landscape-scale management strategies by Andean pastoralist societies. Environmental changes produced during the post-conquest period included the introduction of exotic taxa, such as clovers, associated with the translocation of exotic herding animals (sheep, cattle, and donkeys) and a deterioration in the management of highland wetlands.

Keywords: Holocene; human impact; environmental change; socio-ecological systems; camelid pastoralism; microcharcoal

1. Introduction

The European conquest of the New World produced major transformations in the socio-environmental systems that evolved in the continent for several millennia [1,2]. Some of the socio-ecological effects that this event produced include demographic collapse, reorganization of the socio-political systems, disruption of previous resource management practices, biodiversity loss, and the translocation of new species of animals and plants [3,4]. Although some regions experienced more direct and dramatic changes than others did, the entire hemisphere experienced significant

socio-ecological reorganization. Paleo-ecological reconstructions have shown an intensification of land use following European settlements in some regions. For example, intense deforestation and land clearing allowed large-scale farming during post-colonial times in the Dominican Republic [5,6], and large forests were burned and logged for pastures for livestock raising in northern and southern Patagonia [7,8].

In the Andes, although we know much about the significant demographic and socio-political changes that the European conquest produced [9,10], only a few studies have addressed the resulting ecological effects. Part of the problem is that very few regional syntheses describe specific trajectories of socio-ecological change (but see [11–13]). For instance, in the Andean highlands, an immediate process occurring after the Spanish conquest was an exponential increase in mining activities that directly produced a significant increase in pollution and deforestation [14,15]. Nevertheless, post-colonial land use also involved the introduction of new domesticated animals including cattle, sheep, goats, pigs, and donkeys, but also the introduction of new cultigens such as wheat, barley, and fava beans, as well as a number of unintentional weeds [14–19]. Although some direct effects of these processes included the replacement of native domesticated camelid herds and cultigens such as maize and quinoa, other direct and indirect effects of this process remain poorly investigated. Moreover, to improve our understanding of the scale and nature of these changes, it is necessary to untangle the long-term trajectories of climatic and socio-ecological change. In this paper, we address the problem of how Andean vegetation responded to the interaction between land-use intensification and extreme climatic events before and after the European conquest. Using data from a pollen record and informed by the archaeological and paleo-ecological records of the area, we evaluated the various transformations that vegetation underwent in the south central Andean of northern Chile and neighboring areas of southern Peru and western Bolivia in the south central Andes.

Paleo-ecological studies suggest that the current distribution and composition of high-Andean ecosystems is the product of both humans and climate change. During the Last Glacial Maximum (LGM), glacier expansion restricted the presence of Andean woodlands above 4000 m above sea level (a.s.l.) causing their migration to protected sites and lower elevations [20–23]. Subsequently, as conditions became warmer and more humid during the glacial-interglacial transition, grasslands and woodlands expanded across the Altiplano [24,25]. During the mid-Holocene, however, aridity prevailed, producing expansion of sclerophyllous shrubs and drying of some lakes and wetlands [26–28]. Loss of woody vegetation was enhanced by anthropogenic disturbance as firewood extraction and landscape transformation intensified, particularly after agro-pastoralism became the main subsistence strategy throughout much of the Andes, starting around 3500 years ago [29–31].

Although human disturbance has played a major role on the present-day distribution and abundance of Andean vegetation, there are still large gaps in information regarding past anthropogenic impacts. Andean people traditionally used, and even actively managed, grasslands and peatlands as grazing areas, and woodlands and shrublands as sources of firewood, building material, and raw material for manufacturing tools [26,32]. Grasslands and woodlands were also important as hunting and gathering places, which occasionally involved using fire [8,33]. Although anthropogenic fire is considered the leading cause of vegetation loss and degradation in the past [30], evidence shows that wild fires were a recurrent event in the central highlands of the Andes, even before human arrival [23,31,34]. For example, in southern Peru and central Bolivia, pollen of the Andean tree *Polylepis* decreased significantly and in correspondence to increased abundance of charcoal related to lightning and drought events, suggesting that although burning inhibited the expansion of woodlands and even produced their local disappearance, it might not have been produced by human agency [20,21,25,35,36].

Several paleo-ecological studies provide relevant information regarding past variation of Andean vegetation, but most of these studies are focused on the eastern slopes of the Andes, with a few exceptions covering the western semi-arid highlands [33,36,37]. In this study, we rely on a paleo-ecological approach to reconstruct past vegetation and fire history of the semi-arid Andes of northern Chile, a region characterized by extreme conditions (freezing night temperatures, high

solar irradiance, and scarce precipitation), by emphasizing anthropogenic effects, such as land-use management practices, as much as the potential effects of climate change. More specifically, to improve our understanding of the long-term history of human impact, we reconstructed past vegetation dynamics by analyzing fossil pollen and charcoal recovered from a sediment core collected on an Andean high-elevation peatland (also known as *bofedal*) located near a *Polylepis tarapacana* forest. An assessment of the role of human societies and the resilience of Andean vegetation to prehistoric and historic disturbance (e.g., fire, grazing) may contribute to a better understanding of the cultural legacy that the modern landscapes incorporate, and, therefore, to more accurately design policies for conservation of native ecosystems and adaptation to ongoing climate change.

2. Materials and Methods

2.1. Study Site

The study site, Cosapilla peatland (17°47'10.62" S, 69°25'46.20" W, 4380 m a.s.l.), is located on the Andean Altiplano of northern Chile (Figure 1). Specifically, the core location was situated in the middle of a *bofedal* associated with a small herding settlement and in the vicinity of a *Polylepis tarapacana* forest patch. The region is situated in a volcanically active region, although most eruptions occur at very long temporal scales [38]. Three stratovolcanoes in the vicinity reach elevations higher than 6000 m: Parinacota (6342 m), Pomerape (6240 m), and Sajama (6452 m).

In the region, semi-arid and cold conditions prevail, with an average mean annual temperature of 4.2 °C and an average total annual precipitation of 300–350 mm⁻¹ [38]. Most of the precipitation (90%) falls during the austral summer, between November and March. The austral winter (April–October) is characterized by little precipitation, night freeze temperatures, high solar irradiance, and low cloud cover. Drastic fluctuations in temperature are experienced during the day; temperature extremes from high to low can be as much as 30 °C. El Niño Southern Oscillation (ENSO) mainly drives the inter-annual climate variability. During ENSO events, dry conditions prevail in the region through the austral summer. In contrast, during the La Niña events, wet conditions are common and snow cover on glaciers persists into the summer in relation to increased cloudiness, lower temperatures, and increased precipitation.

The vegetation of the study area is typical of the dry puna. The landscape is characterized by the presence of Andean peatlands, tussock grasslands dominated by *Festuca orthophylla*, sclerophyllous shrubs of *Baccharis thola* and *Parastrephia* spp., and patches of *Polylepis tarapacana* woodlands [38,39]. Small shrubs such as *Adesmia spinosissima*, *Fabiana densa*, and *Tetraglochin cristatum* are also common in the region. The vegetation of Andean peatlands is typically dominated by hygrophilous forbs (Cyparceae and Juncaceae) and small grasses [40,41]. *Oxychloe andina*, *Distichia muscoides*, and *Plantago tubulosa* form compact cushions that constitute the habitat for several small forbs. Peatlands provide key environmental services, including carbon sequestration, regulation of water influx, soil protection, and habitat for native fauna [42]. Moreover, herders consider Andean peatlands one of the most important grazing areas because they provide forage rich in protein for livestock [43]. Occasionally, saltpans are closely located to peatlands, where saline-tolerant species (*Sarcocornia pulvinata*, *Frankenia triandra*, and *Atriplex nitrophiloides*) are commonly found.

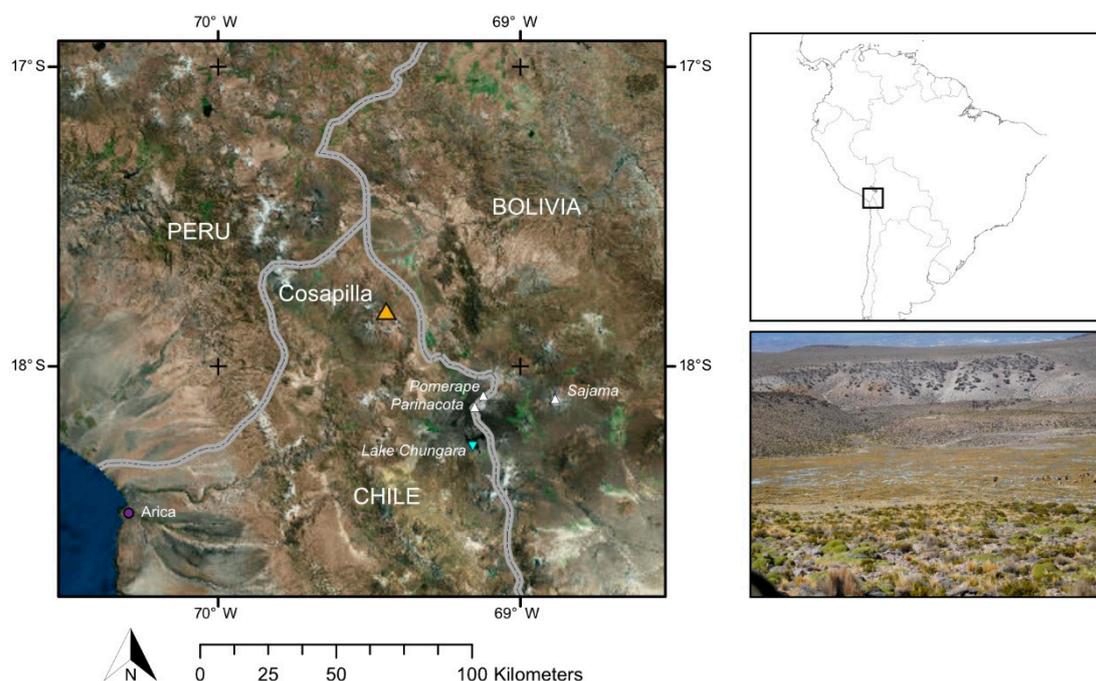


Figure 1. Map of north semi-arid Andes of Chile showing the location of the Cosapilla peatland.

2.2. Sampling and Processing

In 2016, one sediment core was retrieved from an Andean peatland in 50-cm sections with a Russian corer, to a maximum depth of 550 cm. Core sections were packed and transported to the palynology lab at the Centro de Estudios Avanzados en Zonas Áridas (CEAZA) in La Serena, Chile. We characterized the lithology of the sediment cores based on field assessments of the stratigraphy, and later observations derived from X-ray radiographs. We determined the content of organic and inorganic (carbonates and clastic fraction) matter by collecting 1-cm³ sediment subsamples every centimeter and conducting Loss-on-Ignition (LOI) [44,45].

We collected sediment sub-samples every 4–7 cm for pollen and microscopic charcoal analysis (69 samples in total). We added 2 *Lycopodium* tablets to calculate pollen concentration and pollen influx. We used standardized pollen techniques to process soil samples, including HCl, KOH, HF, and acetolysis [46]. Optical microscopy (400×) was used to identify pollen grains. In each sample, we identified a minimum of 300 pollen grains, excluding Cyperaceae and other local aquatic taxa. We identified pollen grains using palynological atlases [47–50], pollen keys, and the pollen reference collections at CEAZA and the Herbario Nacional de Bolivia.

Microcharcoal concentration was determined in the same samples as counted for pollen and spore analysis. We counted microscopic charcoal particles larger than 10 µm size and *Lycopodium* spores on 200 fields of view selected randomly. Microcharcoal particles were categorized either as woody or herbaceous particles based on their morphology. We identified herbaceous charcoal as particles with presence of stomata within epidermal cells and a flat surface, and we considered that they come from grasses or other monocots [51]. We estimated charcoal concentration values by counting the number of *Lycopodium* spores.

We constructed a core chronology by using ¹⁴C accelerator mass spectrometry (AMS) dates on seven bulk organic samples. All samples for radiocarbon dating were analyzed at the DirectAMS radiocarbon lab. We calibrated the radiocarbon dates by using the Southern Hemisphere calibration curve SHCAL13 [52]. We calibrated the samples and generated a Bayesian age–depth model with the Bacon package version 2.2 [53] in R (<https://www.r-project.org/>). The model was built under the assumption that the top of the sequence corresponds to the year of core retrieval (2016 CE).

2.3. Statistical Analysis

We used the pollen sum to calculate relative abundances of each taxon, which was expressed as percentages. We assigned pollen taxa to a vegetation type based on fieldwork and bibliographic references [39,41,50,54]. We created pollen diagrams using pollen percentages with Tilia and Tilia Graph. Pollen zones were determined using the stratigraphically-constrained incremental sum of square clustering (CONISS 1.5.12). The method works by combining the two most similar and stratigraphically adjacent samples [55]. We performed a multivariate analysis to detect differences in the composition of the pollen assemblage between different pollen intervals. A detrended correspondence analysis (DCA) was conducted using all pollen taxa present at abundances higher than 2% and recorded in more than five samples. We performed a DCA to detect major compositional changes and species turnover of dominant taxa through time. The Vegan package of R statistical software (version 3.4.2, R Foundation for Statistical Computing, Vienna, Austria) was used to perform the analysis.

3. Results

3.1. Chronology and Lithological Description

The AMS radiocarbon dates from the sediments provided a consistent chronology with an absence of anomalous dates (Table 1). The earliest date, near the bottom of the core, dates to approximately 7702 calendar year BP. A second date, situated a meter above, dates to 1404 calendar year BP, suggesting a greater compaction in the lowermost meter of deposition, thus a greater temporal resolution in the upper 480 cm. The age-deposition model shows a phase of initial slow sedimentation between ~7700 and ~1400 calendar year BP (0.04 ± 0.013 mm/y), followed by a period of decreased deposition (0.5–1 cm/y) that continued up to 2.3 m (ca. 200 calendar year BP), and a third period of increased deposition rate (0.16 ± 0.08 mm/y) (Figure 2).

The sediment of the core is characterized by the abundance of peat soil, intermixed with layers of higher silt and sand content (Figure 3). The base of the core is composed mainly of fine and compact layers of sand and silt wit. One sandy layer was observed at 350 cm in depth. The loss-on-ignition analysis showed high abundance of inorganic material and carbonates (75–97%) between 550 and 400 cm depth and high content of organic material (75–98%) between 400 cm and the top of the core. The abundance of carbonate was constantly scarce throughout the sediment core (<5%).

Table 1. Radiocarbon ages of the Cosapilla 0016-B core from a peatland in the semi-arid Andes of northern Chile. The modeled ages (mean and standard deviation) are the result of a probabilistic age–depth model.

Lab Code	Core Depth (cm)	¹⁴ C Years BP	Error	Calibrated Age (Calendar Year BP)
D-AMS-028556	48.5	modern		—
D-AMS-028557	116.5	87	28	66 ± 28
D-AMS-028558	228.5	129	26	91 ± 26
D-AMS-028559	297.5	665	32	605 ± 32
D-AMS-028560	356.5	1316	23	1224 ± 23
D-AMS-028561	428.5	1571	22	1404 ± 22
D-AMS-028562	550	6912	25	7702 ± 38

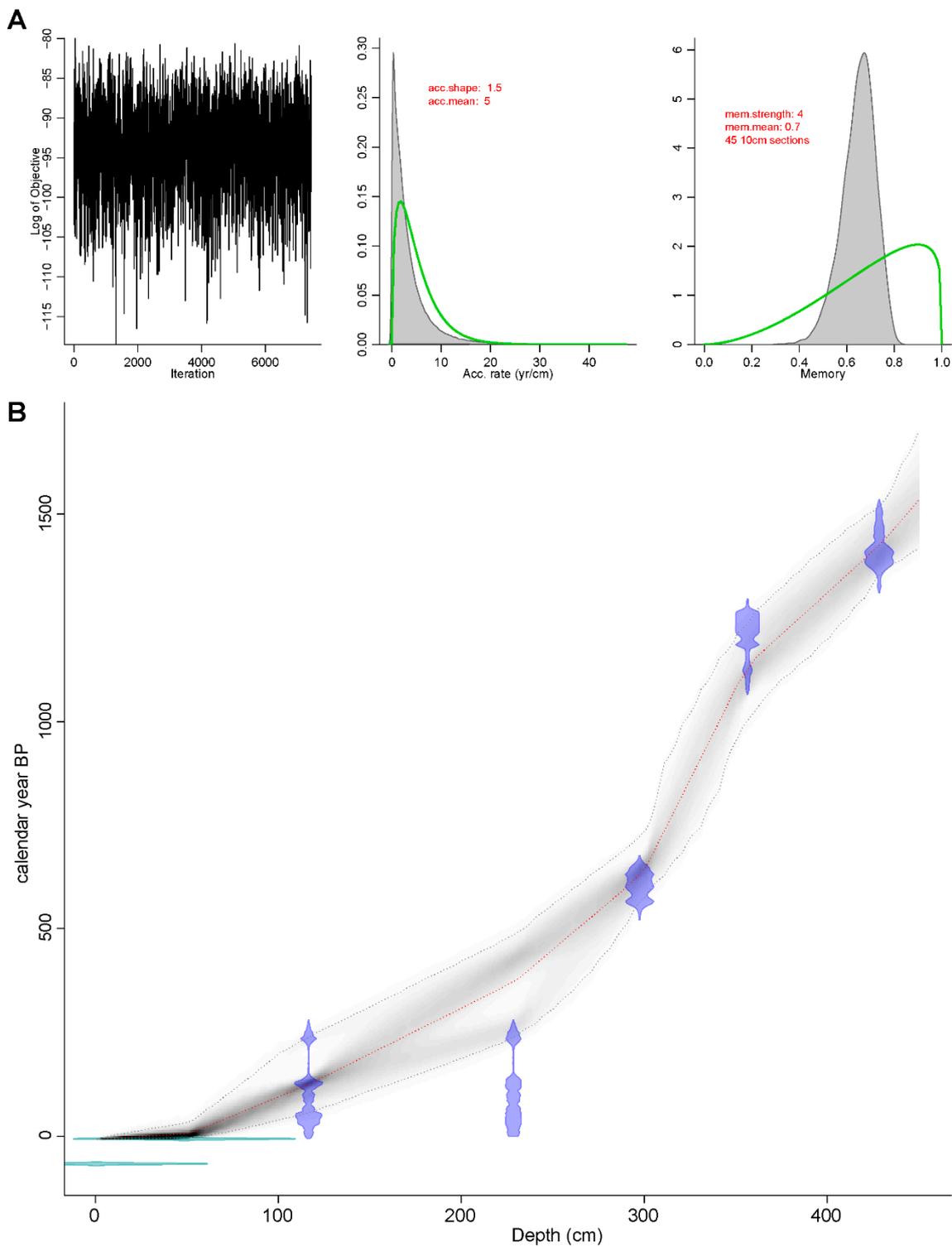


Figure 2. Bacon modeling routine output graph of age–depth model of Cosapilla 0016-B core based on radiocarbon dates. **(A)** Markov chain Monte Carlo iteration, prior (green curves)/posterior (grey histograms) distributions of accumulation rate and memory R of Cosapilla 0016-B core, **(B)** calibrated radiocarbon dates (blue), and age–depth model (dotted grey lines indicate more likely calendar ages; grey dashed lines show 95% confidence intervals, and blue curve shows single “best” model based on the weighted mean age for each depth).

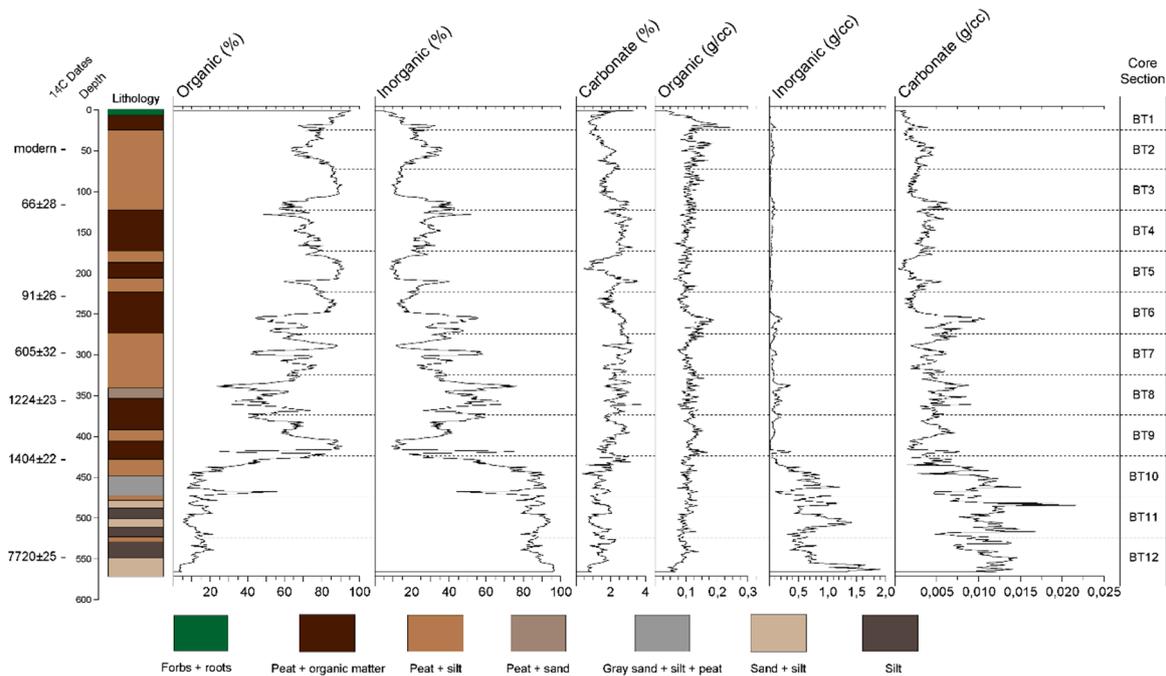


Figure 3. Percentage and concentration of carbonates, inorganics, and organics of Cosapilla 0016-B core from a peatland in the semi-arid Andes of northern Chile, including calibrated radiocarbon dates.

3.2. Microfossil Analysis

Pollen concentration was variable throughout the core, as well as pollen richness, as we identified only 24 distinct pollen types. Pollen preservation was highest at the base of the core, between 550 and 428 cm in depth, with a mean concentration of 57,574.37 grains/cc³. In contrast, the upper core section showed a mean pollen concentration of 22,248.59 grains/cc³, with a peak of at 325 cm of 146,525 grains/cm³. A cluster analysis identified five major zones within the sequence; Z1 and Z2 had a predominance of grassland taxa, whereas Z3–Z5 comprised a higher proportion of peatland vegetation (Figures 4 and 5). Overall, Poaceae was the most dominant taxa, making up nearly 80% of the pollen assemblage and reflecting the dominance of grasslands in the area over time. The second most abundant pollen types were Asteraceae (Asteroideae and Gnaphalidae) and *Baccharis*-type, with abundances ranging between 5% and 60%. *Polylepis* is the only native tree taxon found in the region and its pollen was present in low frequencies. The peatland vegetation was characterized by the presence of *Apium*, Cyperaceae, *Eleocharis*, *Gentiana*, *Myriophyllum*, and *Plantago*. Other pollen types included Amaranthaceae, Caryophyllaceae, *Ephedra*, and Fabaceae. Disturbance taxa included *Trifolium*. Extra-regional taxa included *Alnus*, *Podocarpus*, *Psichotria*, Ulmaceae, Lauraceae, Melastomataceae, Moraceae, Piperaceae, *Sisymbrium*, and *Smilax*. Proxy data suggested five distinct past vegetation communities (Figure 4).

The DCA analysis of Cosapilla records resulted in four ordination axes (Figure 6). The first two axes had eigenvalues of 0.36 and 0.19, respectively. Pollen assemblages were divided based on pollen zones identified by the Cluster Analysis. Samples from pollen zones Z1 and Z5 showed a distinct separation in space, as they rarely overlapped with the other pollen zones, indicating that the species composition is unique. In contrast, pollen zones Z2, Z3, and Z4 showed a larger overlap among each, other indicating that they share the same taxa.

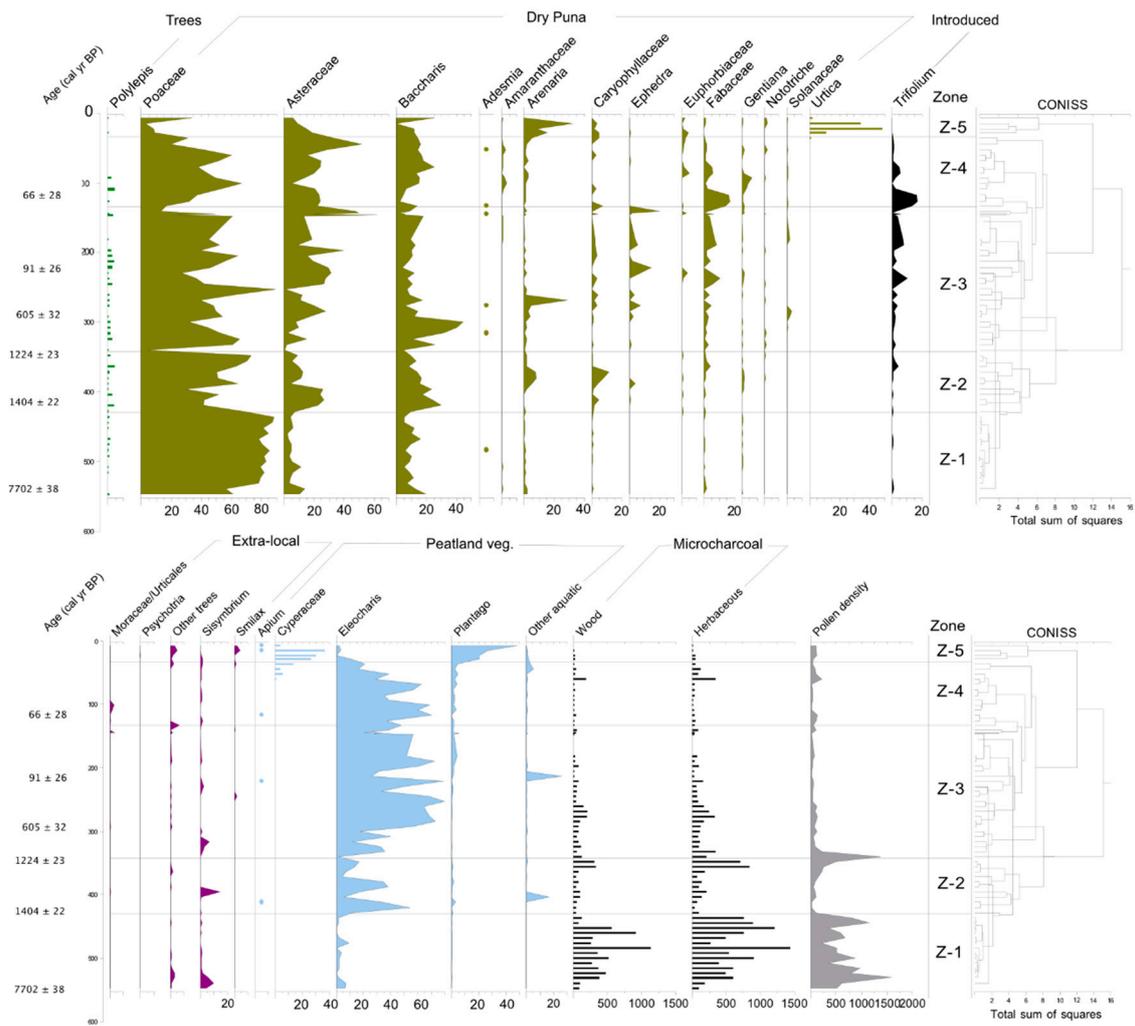


Figure 4. Pollen, palynomorphs, and microcharcoal diagram of Cosapilla 0016-B core from a peatland, northern Chile. Peatland vegetation and ferns were excluded from pollen count.

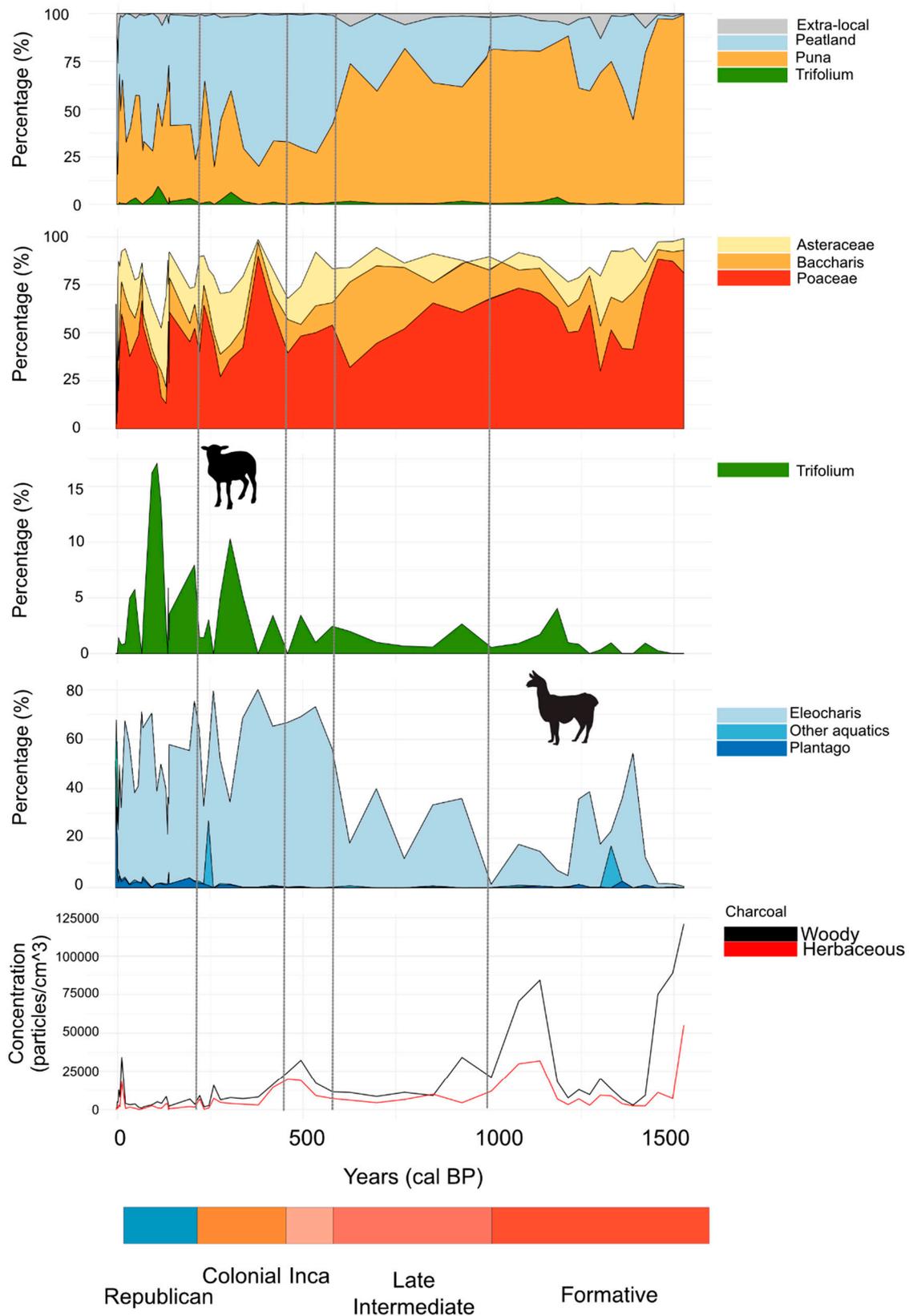


Figure 5. Abbreviated pollen percentage diagram for the last 200 year BP from the Cosapilla 0016-B core from a peatland in the semi-arid Andes of northern Chile.

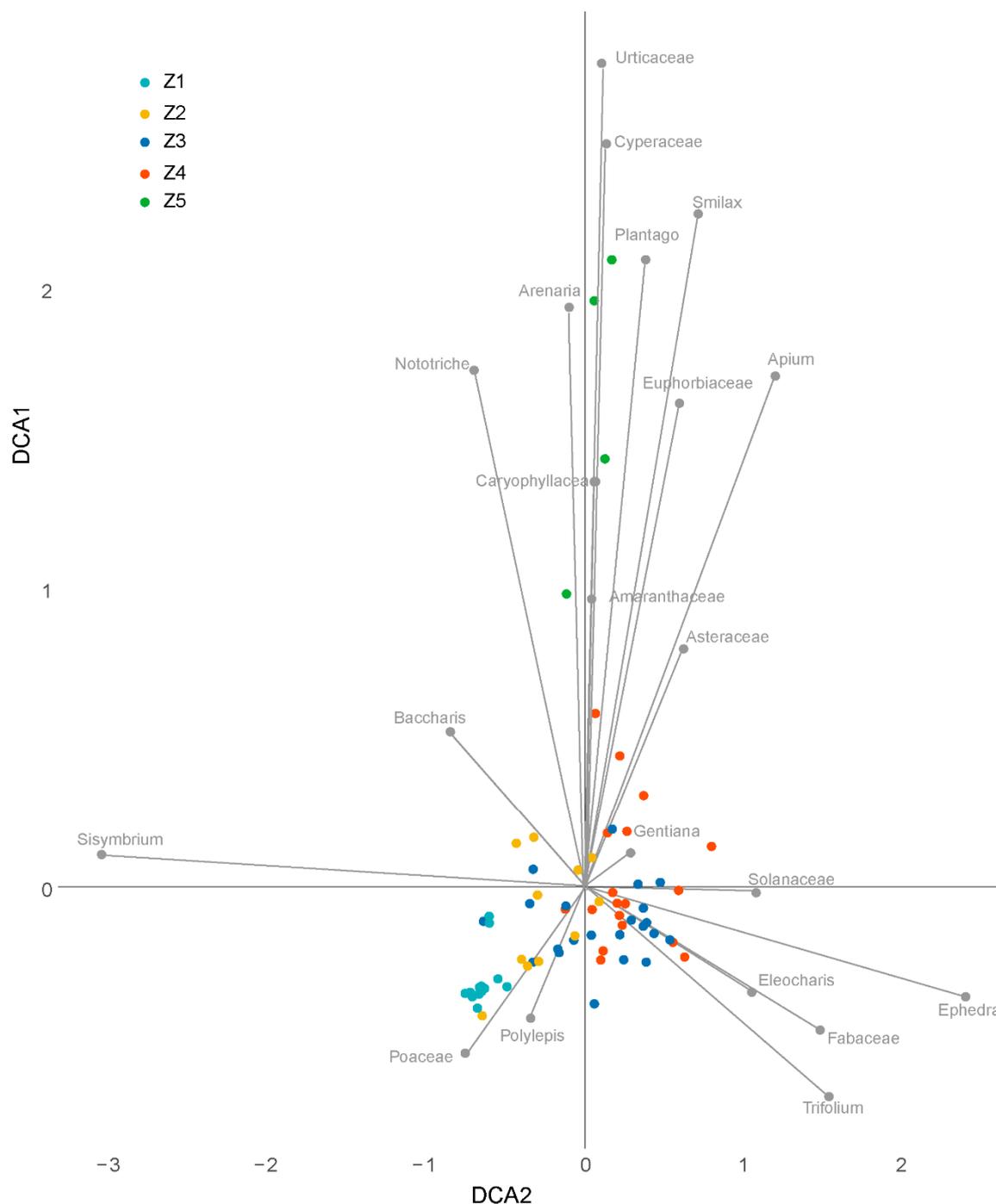


Figure 6. Detrended correspondence analysis (DCA) of pollen zones of Cosapilla 0016-B core from a peatland in the semi-arid Andes of northern Chile.

3.2.1. Pollen Zone Z1 (550–435 cm; 7737–1460 calendar year BP)

Poaceae pollen is by far the most abundant taxon, reaching up to 80%. Asteraceae and *Baccharis*-type are considerably less common, with abundances lower than 20%. Other pollen taxa including peatland vegetation are rare or infrequent. Microcharcoal particles, particularly herbaceous, are extremely abundant through the entire pollen zone (woody = 38.261 particles/cm³, herbaceous = 64,014.86 particles/cm³). This zone suggests moderate humidity and presence of vegetation characteristic of the puna.

3.2.2. Pollen Zone Z2 (350–435 cm; 1460–1250 calendar year BP)

Poaceae is the most abundant pollen taxon as it reaches up to 60%. In contrast, pollen taxa characteristic of shrubland vegetation (Asteraceae and *Baccharis*-type) are less common (~20%). Other high-Andean pollen elements, in particular *Arenaria* (<10%), are also present at very low abundances. *Eleocharis* pollen fluctuates throughout the zone (~10–80%), but its presence signals the establishment of the Andean peatland. Microcharcoal particles fluctuate towards a decrease at the base of the pollen zone (woody = 7941.1 particles/cm³, herbaceous = 18,596.2 particles/cm³). This zone represents the transition from relatively humid grasslands to increasingly dry puna.

3.2.3. Pollen Zone Z3 (150–350 cm; 1250–125 calendar year BP)

Poaceae (5–80%) and Asteraceae (up to 40%) exhibit the highest values. Pollen of *Baccharis*-type is abundant (up to 40%) at the base but decreases in abundance (<20%) towards the end of the pollen zone. Other local pollen taxa include *Arenaria*, Caryophyllaceae, Euphorbiaceae, *Ephedra*, and *Solanaceae*. Pollen of *Trifolium* increases in abundance towards the end of the pollen zone (up to ~15%). *Eleocharis* is the dominant taxon of the peatland, reaching values up to 65%. Microcharcoal particles are comparatively more abundant (woody = 8095.68 particles/cm³, herbaceous = 15,377.54 particles/cm³), particularly near 500 calendar year BP. This zone marks a transition from dominant grasslands to a peatland, likely in relation to increased regional humidity.

3.2.4. Pollen Zone Z4 (30–150 cm; 125–0 calendar year BP)

Poaceae pollen is the most abundant taxon, reaching up to 55%. This zone is also characterized by the abundance of Asteraceae (~5–30%), *Baccharis*-type (~5–40%), and *Eleocharis* (20–70%) pollen. *Polylepis* pollen is in general very low (<5%) and is absent in the record from 30 to 75 cm in depth. Asteraceae pollen is the most abundant at the base of the zone but it decreases over time, while *Poaceae* becomes more abundant.

The remaining local flora include herbaceous and shrub taxa characteristic of the puna belt (4000 m a.s.l.) [39]. Amaranthaceae (including *Gomphrena*), Caryophyllaceae, Euphorbiaceae, *Ephedra*, and *Nototriche* are common elements of the puna vegetation. *Trifolium* pollen is very abundant in the zone, reaching 15% in abundance. The peatland vegetation is characterized by the dominance of *Eleocharis* (up to 80%). Microcharcoal particles, both woody and herbaceous, are found in low abundances (woody = 2438.06 particles/cm³, herbaceous = 6147.76 particles/cm³). The richness of taxa found in this zone seems to be a consequence of a healthy peatland environment as well as adequate taphonomic conditions for the preservation of pollen.

3.2.5. Pollen Zone Z5 (0–30 cm; 0–4 calendar year BP)

This pollen zone is characterized by the abundance of *Baccharis*-type (up to 25%), *Arenaria* (from 16 to 33%), *Plantago* (from 23 to 50%), and Urticaceae (from 3 to 48%). Both Asteraceae and *Poaceae* exhibit varying percentages but *Poaceae* is more abundant at the base of the pollen zone. Abundance of microcharcoal particles was the lowest of the paleorecord (woody = 2212.5 particles/cm³, herbaceous = 5724.8 particles/cm³). This zone reflects the progressive desiccation that the modern peatland in the sample location is currently experiencing.

4. Discussion

The pollen record indicates that grasslands primarily dominated the semi-arid Andean landscape between 7700 and 1400 calendar year BP. This period was followed by a major turnover in the plant community characterized by the emergence of a mixed grassland–shrub community and the formation of a high-altitude peatland. A second major change in the landscape took place around 800 calendar year BP, marked by the retraction of grasslands, the expansion of the peatland, and the appearance of the exotic clover (*Trifolium*). Evidence of burning is documented throughout the record with two

major peaks in fire activity, the largest between 7700 and 1400 calendar year BP and a second around 1200 calendar year BP.

The pollen assemblage shows that the high-Andean steppe was a dominant component of the landscape during the middle Holocene, when arid climatic conditions prevailed in the Andean Altiplano [28,54,56–61]. During this period, precipitation was much lower and variable than today [62–64]. Similar conditions have been documented in Quebrada Puripica [64], Laguna Miscanti [65,66], and Laguna del Negro Francisco [67] towards the south of the study area.

The formation of the Andean wetland occurred approximately around 1400 calendar year BP and reached its maximum extension between 600 calendar year BP and modern times, as indicated by the abundance of *Eleocharis* pollen and organic matter. The establishment of a permanently inundated wetland coincides with an increase in moisture levels during the late Holocene, reported extensively in South America, including the central Altiplano [57], northern and central Chile [67–71], and eastern and northwestern Argentina [72,73].

In Cosapilla, the abundance of xerophytic shrubs fluctuates in time but experiences an increase during 1400–1200 calendar year BP, 800–600 calendar year BP, and 400 calendar year BP–present times. The increase of Asteraceae and *Baccharis* during these periods coincides with events of extreme aridity, in particular the Little Ice Age recorded in the Sajama ice core [74–76]. An expansion of shrubs is associated with drier conditions, linked with a decrease in moisture conditions and precipitation over the Altiplano [77]. However, unlike other semi-arid sites in the puna [37,78], drought-resistant shrubs have remained as a common component of the vegetation in Cosapilla.

Although tree taxa were rare, *Polylepis*, the only tree growing in the region, is present in the paleo-record, albeit in very low frequencies. Moreover, despite the fact that a *P. tarapacana* woodland is closely located to the peatland, pollen abundance was lower than 5%. Previous studies have shown that *Polylepis* pollen tends to travel short distances and that it tends to concentrate within the forest [48]. Several palynological studies highlight the decline in abundance of *Polylepis* in the late Holocene throughout the Andes, a trend that suggests intense deforestation due to increased burning and firewood extraction [79,80]. The evidence recovered in this study, indicates that *Polylepis* pollen likely represents a local signal, and that small woodlands were present on mountain slopes near the peatland during the late Holocene, even at the time of increase in the demand for fuel and growing human population. Analogous pollen records from the region show that *Polylepis* woodlands were a common element of the vegetation, but they were unlikely to have covered large areas [36,37,78].

The paleorecord shows evidence of regional fire during the early and middle Holocene. Fire activity in pollen zones Z1 and Z2 coincide with volcanic eruptions inferred from several tephra layers and high concentrations of Fe in a sediment core from Lake Chungara [61,81]. This overlap suggests that volcanic eruptions were one possible ignition source of regional fires and that charcoal particles were locally transported to the site during events of volcanic eruption. The impact of volcanic eruptions on vegetation is closely associated with the type and quantity of tephra deposited on the surface [82]. The pollen assemblage shows minor fluctuations in time, indicating that the amount of volcanic ash deposited in the site was not significant enough to induce mayor changes in population dynamics and the reconfiguration of the vegetation community. The large abundance of Poaceae and Asteraceae pollen before and after 7000 calendar year BP implies little disturbance on the local vegetation community. However, it is important to note that the slow sedimentation rate until 1400 calendar year BP could have produced the accumulation of charcoal and the temporal variability in sedimentation, challenging our ability to accurately discern the temporal fidelity of total charcoal accumulation as a fire proxy. Thus, these results should be taken with consideration.

Alternatively, the high frequency of wood and herbaceous charcoal could be the result of burning of vegetation by human groups and enhanced by dry conditions. Human groups were present in the highland Andes since approximately 12,000 calendar year BP and played a role in vegetation dynamics in the region [81,83–85]. High-altitude human foragers were particularly mobile between the early and middle Holocene, which could have produced a patchy distribution of temporary residential

and logistical camps [86]. The high density of microcharcoal particles in pollen zones Z1 and Z2 may also suggest that hunter gatherers were using fire for hunting wild camelids (*Vicugna vicugna* and *Lama guanicoe*), taruka deer (*Hippocamelus antisensis*), and lesser rheas (*Rhea pennata*). Although archeological evidence from Hakenasa and other rock shelters in the region suggests decreased occupation intensity during the middle Holocene as a possible response to increased regional aridity [85–87], abundant wood and herbaceous charcoal particles during this period might suggest a more conspicuous presence by human foragers. In this context, it should be noted that Cosapilla is a large wetland in comparison with the Hakenasa surrounding. This suggests that Cosapilla could have acted as an eco-refuge, as defined by Núñez et al. 2013 ([86], see also [71]), for the highlands of Salar de Atacama; meaning that people looked for localized rich environments that contrasted with depleted regional conditions [86]. Field archeological surveys in the study area are needed to test for this alternative explanation.

Fire continues as a common element in the landscape during the Formative period later in the Holocene, as hunter-gatherers were progressively replaced by camelid pastoralists [27,87]. Pastoralism is an economic activity widely distributed in the Andean puna and herders traditionally use grasslands and wetlands as grazing areas for domestic camelids (llamas and alpacas). Herders could have used fire to actively manage pastures for their livestock (Figure 4). The abundance of Poaceae pollen and herbaceous charcoal indicates that grasslands were intentionally burned to promote re-sprouting and to encourage the development of more palatable foraging plants such as *Festuca* and *Deyeuxia* for domestic camelids [83].

A major shift in pollen assemblage is observed around the middle Formative (~1300 calendar year BP) and Late Intermediate period (~800 calendar year BP) (Figure 5). The pollen record shows a decrease in grasslands, with an expansion of sclerophyllous vegetation (Asteraceae and *Baccharis*). Because this shift is correlated to decreased burning, fire suppression could have played an important role on vegetation dynamics. Modern experimental studies in the Argentinian Andes have shown that fire suppression favors establishment of shrubs but limits regeneration of tussock grasses [88]. Carrilla et al. [89] also showed that despite fire reduced aboveground biomass of burned vegetation, it promoted re-sprouting of tussock grasses. Other studies have shown, nevertheless, that burning has a detrimental effect on the overall plant community and biomass productivity [90], suggesting that long-term and comparative studies are needed to understand the magnitude of the effects of burning on Andean ecosystems.

The most significant landscape-modification strategy employed by pastoralists over the last 2000 years was probably increasing the surface of peatlands and wetland as grazing areas. In fact, indigenous groups may have also played an important role on the maintenance and expansion of the Andean wetland in Cosapilla. Ethnographic evidence shows that Andean herders usually managed bofedales by constructing and maintaining irrigated systems that increase water quantity and water availability during the dry and cold season [91,92]. The establishment of the peatland took place during the late Holocene Formative period, when the economy was mostly based on camelid pastoralism and peatlands were important grazing areas, suggesting that herders actively engaged in the development of the wetland in the study site.

The posterior expansion of the peatland coincides with the arrival of the Inca to the region, when climatic conditions were relatively stable. An increase in the area covered by the peatland suggests that it could have been used as a grazing area for a large density of camelids (particularly alpacas). This interpretation is supported by an increase in organic matter concentration, possible related to higher levels of animal excreta. The most common peatland taxa, *Eleocharis*, is commonly consumed by domestic camelids and livestock [93,94] and is able to tolerate high grazing pressures [95]. Furthermore, results suggest a shift in herding strategies, from managing pastures with abundance of highly lignified and short tussock grasses, to managing wetlands characterized by the abundance of moist and succulent herbs available throughout the entire year [96,97].

The evidence of European conquest on the Andes is also present in the pollen record. After the Spanish conquest, peatland pollen continues to be abundant and probably represents the continual effort of the local population to maintain the wetland for grazing of domestic camelids and introduced livestock. Pollen of the exotic clover (*Trifolium*) becomes abundant between 600 and 100 year BP, possibly in relation to the translocation of sheep and cattle herds [7,98]. Currently, Andean pastoralists keep mixed herds of native and exotic animals as a way to diversify their economy [99,100]. While the native camelids might not be as profitable as sheep and cattle, they fair better during droughts and frosts and require less supervision. The environmental impact of cattle and sheep is also considerably higher than llamas and alpacas because the former uproot and trample vegetation and consume more pasture than camelids [91]. It is quite possible that the intensification of livestock raising produced overgrazing and soil erosion, facilitating the establishment of exotic weeds, including *Trifolium* [95,101].

In recent times, the Cosapilla peatland has experienced a mild retraction with an associated expansion of grasslands and shrubs. The appearance of *Plantago* and an abrupt increase of *Trifolium* could suggest a decrease of traditional management and a degradation of the peatland, favoring the establishment of species resistant to trampling and increased herd browsing pressure. Currently, some highland Andean wetlands located near the study area show clear signs of degradation due to climate change and loss of human traditional management practices, which are inducing the reorganization of plant communities. The overall trend suggests that during the last 2000 years, changes in vegetation dynamics were affected by climatic events as much as anthropogenic disturbance [71,102].

Charcoal concentration decreased over time but it remained relatively frequent throughout the record during colonial and republican times. The burning of vegetation by pastoralists can also be related to scaring away predators (foxes and pumas) from camelid herds. This indicates that burning persisted as a common practice, probably associated with camelid herding in the region. Thus, it is likely that burning and grazing simultaneously shaped vegetation structure and plant cover in the semi-arid highlands over millennial scales [89]. Unlike Cosapilla, other paleorecords have shown a marked increase in fire intensity associated with land-use intensification after the European conquest [5–7]. For example, in Huila (Ecuador) and Chachapual Valley (Chile), an intensification of burning took place during the Spanish settlement, probably in relation to land-clearing and land-use intensification [103,104].

The paleoecology of Cosapilla does not evidence land use intensification or large-scale landscape transformation during colonial times. This pattern indicates that the predominant form of land use remained as extensive grazing, in which livestock (both camelids and introduced animals) were fed on forage from natural grasslands and wetlands. Alternatively, it could be attributed to land abandonment due to the demographic collapse and forced relocation of indigenous populations during the colony [71,105–108]. The Altiplano of Tarapacá suffered a second population decline associated with migration waves from the highlands to the coast from 1820 to 1960 [109]. The massive migration was stimulated by economic growth and demand of human labor, but also by a persistent decrease in precipitation in the Andean highlands [77,108].

5. Conclusions

The paleo-ecological record from the Cosapilla peatland in the semi-arid Andes of northern Chile suggests that the environmental impact of anthropogenic activities has been significant over the last several millennia. Throughout time, humans have increasingly managed and modified this landscape, particularly with the emergence of an economic organization dependent on Andean camelid pastoralism. Extensive pastoralism of domesticated camelid herds seems to have involved fire to provide growth of palatable grass species, as much as the construction and management and increase of available peatlands. Camelid pastoralism also expanded the coverture of peatlands and changed the composition of plant communities towards hydrophytic vegetation and tussock grasses. Evidence of the arrival of Europeans to the region is reflected by the appearance of the exotic clover (*Trifolium*), probably connected to the translocation of exotic herding animals. The interaction between

humans and increasing aridity favored the establishment of drought-tolerant vegetation and the reconfiguration of ecological communities in the Andean highlands. Finally, the ongoing changes in human management practices and climatic variability caused by anthropogenic global warming are currently favoring the establishment of drought-tolerant vegetation, a deterioration of wetland systems, and a new reorganization of the ecological communities in the Andes.

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