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Pollen signal of modern vegetation registered in surface soil samples along an elevation gradient from Iztaccíhuatl volcano, central Mexico

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Abstract

Characterising the vegetation-pollen signal is a crucial task for enhancing the interpretation of fossil pollen records. This study analyses 28 surface soil samples collected in the surroundings of Iztaccíhuatl volcano, between 2,650 and 4,024 m asl. Pollen zones and ordination analysis were assessed to establish a qualitative connection between the pollen signal and the distribution of plant communities along the elevation gradient. The results show: (i) the predominant pollen type in the pollen assemblage is *Pinus*; (ii) pollen grains of *Quercus* and *Alnus* are present along the elevation gradient, even at high elevations where the parental plants are not typically found; (iii) samples taken between 2,650 and 3,338 m asl., where fir forests dominate, exhibit higher values of *Abies* pollen compared to samples above 3,405 m asl.; (iv) the locally-dispersed pollen of the hemiparasite *Arceuthobium* results key in identifying the presence of pine forests; and (v) pollen taxa such as Apiaceae, *Eryngium*, Valerianaceae, and Caryophyllaceae are linked to higher elevations, specifically where the plant communities of *Pinus hartwegii* and alpine grassland occur. The study suggests that the pollen signal along the elevation gradient is useful to characterise the main plant communities of the study site (fir forest, pine forest and alpine grassland). Additionally, the percentage variations of *Abies* in the pollen signal below 3,600 m asl. show the reduction of fir forest communities resulting from recent human activities in the area.

Keywords Iztaccíhuatl-Popocatépetl National Park · Modern analogues · Plant communities · Pollen assemblages · Trans Mexican Volcanic Belt · Tropical mountain

Introduction

Modern vegetation-pollen signal studies have long been acknowledged as essential for accurately interpreting fossil pollen records (Birks and Birks 1980; Ortega-Rosas et al. 2008). This understanding helps to infer historical environmental and biotic trends, providing insights to anticipate biotic responses to, for instance, a future greenhouse world (Jackson and Williams 2004). Research has documented a strong connection between the pollen signal and different plant communities, the presence of the parental taxa and/or changes in functional composition (e.g. Gosling et al. 2005; Lu et al. 2008; Niemann et al. 2010; van der Sande et al. 2021; Basumatary et al. 2024). Modern vegetation-pollen signal studies have also registered human impact on vegetation and land use (Franco-Gaviria et al. 2018; Jiménez-Zamora et al. 2024; Shi et al. 2024).

However, the relationship between vegetation and pollen is affected by (i) variability of pollen production between different taxa and from year to year, pollination syndromes, and dispersion capabilities (Bush 1991; Bush and Rivera 1998; Gosling et al. 2009); (ii) deposition and type of analysed samples (Zhang et al. 2020; Fang et al. 2022); and (iii) the landform and elevation of the study sites (Ortega-Rosas

et al. 2008; Castro-López et al. 2021). Therefore, considering these factors of variability in the pollen-vegetation relationships, it is advisable to expand the knowledge worldwide, in order to understand the particularities of each study region. So far, the modern vegetation-pollen signal research has been especially focused on high latitudes (e.g. Minckley et al. 2008; Mishra et al. 2022; Boutahar et al. 2023); however, the Neotropical regions have been patchily covered compared to temperate zones to date. Particularly in Mexico, several studies have examined the vegetation-pollen signal. The first studies focused on using modern pollen signal to enhance palaeoenvironmental reconstructions in specific regions of interest. Notable examples include research in the southeast of Mexico (Islebe et al. 2001; Franco-Gaviria et al. 2018), the central region (Ohngemach and Straka 1983; Correa-Metrio et al. 2012; Chang-Martínez and Domínguez-Vázquez 2013; Lozano García et al. 2014), and the northeast (Ortega-Rosas et al. 2008). In recent years, research has also focused on exploring the quantitative relationship between environmental gradients and the pollen signal (Correa-Metrio et al. 2011), the impact of altitude and climate on the distribution of vegetation in patchy landscapes (Castro-López et al. 2021), and in the context of landscape connectivity and plant diversity conservation (Domínguez-Vázquez et al. 2023).

Within Mexico, the Trans Mexican Volcanic Belt (TMVB) is considered a region of high biodiversity and endemism (Myers et al. 2000; Villaseñor et al. 2006), as well as part of the transition between Neotropical and Nearctic regions (Morrone and Márquez 2001). Considering the biological importance of the region, several studies focusing on biodiversity evolution and late Quaternary trends have been carried out (e.g. Mastretta-Yanes et al. 2015; Caballero-Rodríguez et al. 2017). Additionally, natural protected areas have been established in this region (Toledo 2005; Figueroa and Sánchez-Cordero 2008; Aguilar-Tomasini et al. 2020). Nevertheless, more information is required to understand the drivers that promote high diversity in the zone and create better conservation strategies.

This research presents the analysis of pollen assemblages from surface soil samples collected around the Iztaccíhuatl volcano. These samples were obtained along an altitudinal transect spanning elevations from 2,650 to 4,024 m asl (hereafter referred to as m). The main aim is to analyse the pollen deposition in surface soil samples from the current plant communities. Specifically, this research focuses on: (i) Establishing a qualitative relationship between the pollen signal and the distribution of plant communities along the elevational gradient; (ii) identifying potential indicator taxa and/or taxonomic groups for reconstructing plant communities; (iii) assessing the influence of altitude as a determining factor on the pollen signal, and (iv) evaluating

if the effect of human activities on the plant communities is displayed on the pollen signal. Furthermore, this research will enhance future palaeoecological interpretations serving as a detailed study of modern analogues along an elevation gradient in central Mexico.

Materials and methods

Study site

The study was conducted in the slopes of the Iztaccíhuatl volcano (5,286 m), which is part of the Sierra Nevada Volcanic Range (SNVR), along with Popocatépetl, Tláloc, and Telapón strato-volcanoes (Siebe et al. 2017) (Fig. 1). The SNVR has a north-south trend that separates the basin of Mexico City in the West from the valley of Puebla in the East (Arana-Salinas et al. 2010). The volcanic activity in this zone started around 1.8 Myr and continues until present-day (Nixon 1989; Arana-Salinas et al. 2010; Macías et al. 2012; Siebe et al. 2017). The elevation gradient formed due to volcanic activity in the area (Siebe et al. 2017), creates a significant variation of climates across different altitudes. The average annual temperature decreases linearly with elevation, reducing by approximately 0.5 °C per 100 m (Lauer 1978). The mean annual temperature reported is from ~10 °C at 3,000 to ~2.5 °C at 4,500 m. Around 4,000 m and higher elevations, the diurnal temperature variation can be more extreme than throughout the year (Lauer 1978). Additionally, sporadic winter snowstorms occur, and the snowpack remains for part of the year (Rzedowski 2006). The rainfall is concentrated around the summer monsoon months, with approximately 85% of the precipitation falling from May to October (Almeida-Lenero et al. 2007). The mean annual precipitation is ~1,200 mm at 3,000 m, reaches a maximum of ~1,300 mm at 3,300 m and decreases to ~1,000 mm at 4,000 m (Lauer 1978).

The formation process of soils in the Iztaccíhuatl slopes is strongly influenced by the volcanic activity of the Popocatépetl volcano (Miehlich 1984, 1991; SEMARNAT-CONANP 2013; López-López et al. 2023). Consequently, the most common soils in the area are haplic, umbric and vitric andosols (Cruz-Flores et al. 2020; Chavarin-Pineda et al. 2021; López-López et al. 2023).

The dominant plant communities on Iztaccíhuatl volcano and adjacent areas around the elevations where the samples were taken, are, from low to high altitude, fir forest, pine forest, and alpine grassland (Table 1; Fig. 2). At lower elevations, other plant communities such as mixed, cloud and oak forests also occur. However, these communities are in restricted areas, limited by microclimatic conditions and/or human impact in the zone (Velázquez et al. 2000; Calderón
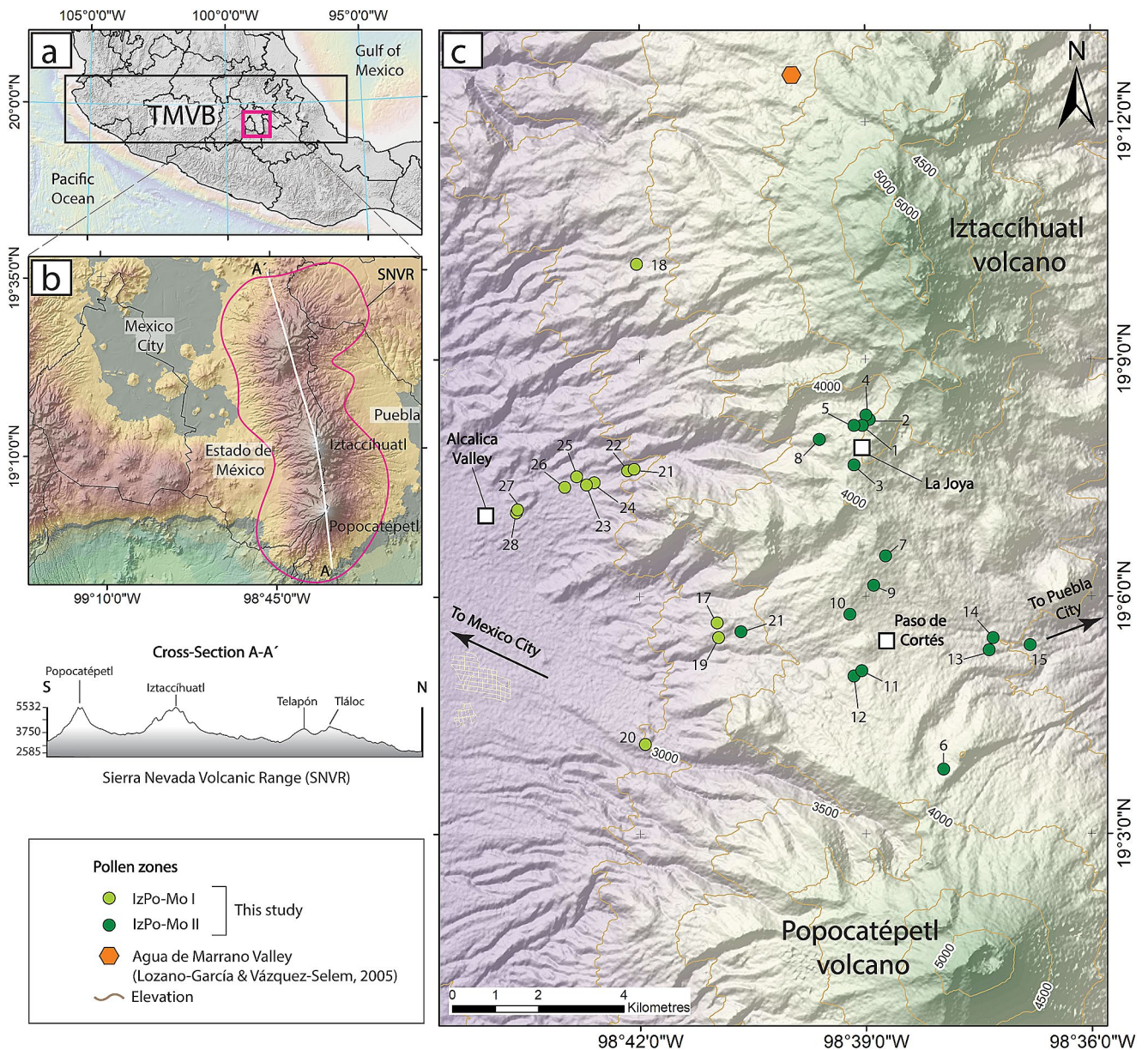
Fig. 1 **a**, Volcanic Belt (TMVB; dark rectangle) and Sierra Nevada Volcanic Range (SNVR; pink rectangle) within Mexico; **b**, Topographic profile of the SNVR; **c**, Iztaccíhuatl volcano's topographic map showing the sampling sites (circles) location and Agua el Marrano Valley (square). The samples are colour-grouped according to the pollen zones established. ESM Table S1 details the numbered labels of the samples. The map was created using arcGIS10.8.1, based on JAXA/ALOS PALSAR-Radiometric Terrain Correction High-Resolution DEM (2014)

de Rzedowski and Rzedowski 2001; Almeida-Lenero et al. 2007).

In the fir forest, located between 2,700 and 3,500 m, *Abies religiosa* is the dominant and often the only tree species in the upper canopy; however, other tree species may occasionally be found (Table 1). Undisturbed fir forests are characterised by dense shrubbery and limited herbaceous growth.

Despite pines can be found between 2,350 and 4,000 m (Calderón de Rzedowski and Rzedowski 2001); plant communities dominated by species of *Pinus* sp. are dominant between 3,500 and 4,000 m (SEMARNAT-CONANP 2013; Acosta Mireles et al. 2014). Various pine species are found around the study site, and the herbaceous and shrubby components of the pine forest are numerous (Table 1). Some of the best-represented families include Asteraceae, Poaceae and Fabaceae (Lauer 1978; Heil et al. 2003; Rzedowski 2006; Caballero Cruz et al. 2022). *Arceuthobium* spp. are among the most frequent hemiparasites of these forests (Rzedowski 2006). Between 3,700 and 4,000 m,

Table 1 List of 12 most common taxa in the three main plant communities of Iztaccíhuatl volcano according to specialised literature (Lauer 1978; Calderón De Rzedowski and Rzedowski 2001; Heil et al. 2003; Steinmann et al. 2021; Caballero Cruz et al. 2022)

Fir forest	Pine forest	Alpine grassland
Abies religiosa (Kunth) Schltdl. et Cham.	*Pinus hartwegii* Lindl.	*Muhlenbergia quadridentata* (Kunth) Trin.
Alnus jorullensis Kunth.	*P. leiophylla* Schiede ex Schltdl. & Cham.	*Calamagrostis orizabae* Steud.
Cupressus lusitanica Mill.	*P. montezumae* Lamb.	*Calamagrostis tolucensis* (Kunth) Trin. ex Steud.
Quercus laurina Bonpl.	*P. ayacahuite* Ehrenb. ex Schltdl.	*Festuca tolucensis* Kunth.
Salix paradoxa Kunth.	*P. pseudostrobus* Lindl.	*Eryngium proteiflorum* F. Delaroche.
Symphoricarpos microphyllus (Humb. & Bonpl. ex Schult.) Kunth.	*P. teocote* Schiede ex Schltdl. & Cham.	*Cirsium nivale* (Kunth) F. Dietr.
Eupatorium glabratum Kunth.	*Festuca* spp.	*Lupinus montanus* Kunth.
Senecio platanifolius Benth.	*Calamagrostis* spp.	*Draba jorullensis* H.B.K.
Senecio barba-johannis DC.	*Ribes ciliatum* Humb. & Bonpl. ex Schult.	*Senecio procumbens* H.B.K.
Brachypodium mexicanum (Roem. & Schult.)	*Lupinus montanus* Kunth.	*Arenaria* spp.
Alchemilla procumbens Rose.	*Acaena elongata* L.	*Juniperus monticola* f. compacta Martínez.
Salvia elegans Vahl.	*Arenaria lycopodioides* Willd. ex D.F.K.Schltdl.	*Berberis alpina* Zamudio.
	Eryngium spp.	
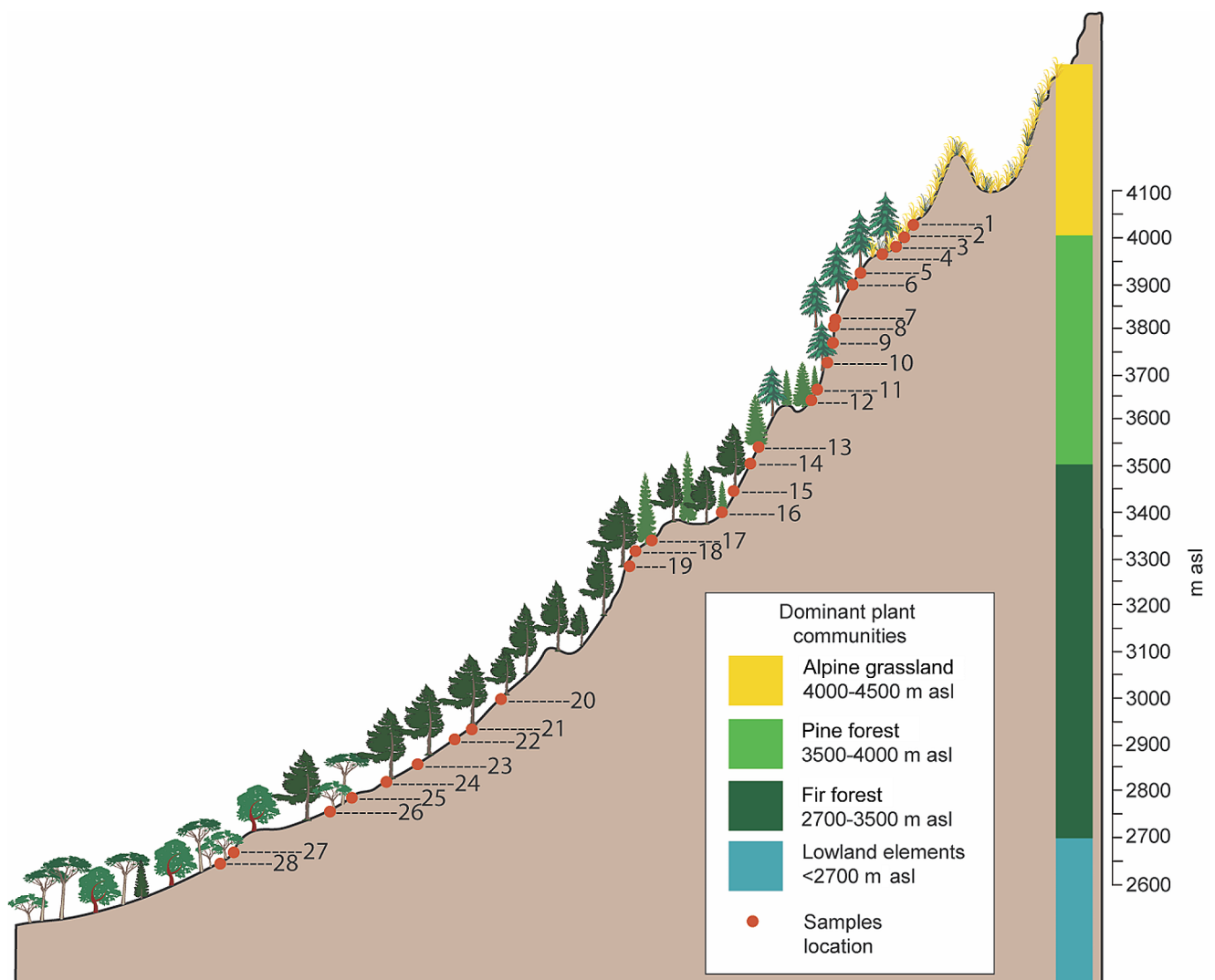
Fig. 2 Sketch of the elevation arrangement of the dominant plant communities (colour bars on the right) defined for the study site. Not to scale. Sample locations are shown (Number on the left, which corresponds to the Id of Table 2)

pine forests are only formed by *P. hartwegii* in the arboreal layer, which forms the timberline around $4,020 \pm 50$ m, although this limit is influenced by cold and dry conditions (Lauer 1978). The herbaceous layer of *P. hartwegii* forest is dominated by several species of bunchgrass (Velázquez et al. 2000).

From the timberline up to 4,500 m, the alpine grassland is dominated by tussock grasses (Velázquez et al. 2000; Almeida-Lenero et al. 2007) (Table 1). On the rocky outcrops and cliffs, it is common to find species such as *Berberis alpina*, *Juniperus monticola* f. *compacta* (Steinmann et al. 2021). The presence of endemic plants such as *Cerastium purpusii*, *Castilleja tolucensis*, *Draba nivicola*, and *Plantago tolucensis* characterises this plant community. Additionally, the Iztaccíhuatl volcano is the only location containing all the endemic alpine species that have been reported in the TMVB (Steimann et al. 2021). From 4,200 to 4,500 m vegetation becomes sparser, and the tussock grasses are replaced by smaller caespitose grasses and low-growing forbs (Steinmann et al. 2021). Near the upper nival border, mosses and lichens dominate (Velázquez et al. 2000), and at about 4,750 m vascular plants cease to grow (Steinmann et al. 2021).

The main human activities in Iztaccíhuatl volcano and surrounding areas are related to the extraction of natural resources and land use change. Most of the settlements around SNVR are currently located below 2,500 m. Agriculture and cattle raising are the primary land uses between 2,300 and 3,000 m. Forestry activities are allowed between 3,000 and 3,600 m (SEMARNAT-CONANP 2013). In 1935, the Iztaccíhuatl-Popocatépetl National Park was established, considering the progressive deterioration of the zone, the intense forest exploitation as well as the recognition of the ecological significance of plant communities (SEMARNAT-CONANP 2013). The lower boundary of the protected area was originally set up at 3,000 m in 1935, then changed to 3,600 m in 1948. In 2011, UNESCO declared the zone as the 'Los Volcanes Biosphere Reserve' (UNESCO 2011).

Despite the conservation efforts, the impact of the local and extensive natural resource extraction, human settlements, and both accidental and provoked fires have been documented, although mainly outside the border of the national park (e.g. Hernández-García and Granados-Sánchez 2006; Osuna et al. 2022). Also, the pressure on natural resources has increased in recent decades due to the proximity of the Mexico City metropolitan area (SEMARNAT-CONANP 2013; Osuna et al. 2022). One documented consequence is the poor soil qualities associated with significant disturbances in different plant communities (Cruz-Flores et al. 2020; Chavarin-Pineda et al. 2021). A reduction in area and the fragmentation of plant communities have

also been recorded (Almeida et al. 1994; Sánchez-González and López-Mata 2003; Caballero Cruz et al. 2022).

Methodology

28 surface soil samples, consisting of the first cm of soil below the litter, were recovered between December 2019 and February 2022. The samples were collected following an elevation range from 2,650 to 4,024 m (Fig. 1; Table 2), with a sampling interval of 100 m. However, due to limited access, no soil samples were collected between 3,000 and 3,200 m. The majority of the samples were acquired from the Alcalica Valley, Paso de Cortés and La Joya areas.

Volumetric subsamples ($2 \, cm^3$) were taken and processed using standard palynological protocols, including KOH, $Na_4P_2O_7$, HCl, HF, and acetolysis treatments (Faegri and Iversen 1989) in the Laboratory of Paleoecology (PALAB) of Geosciences Barcelona (GEO3BCN-CSIC). Exotic *Lycopodium* spores (University of Lund batch #1031; $20,848 \pm 1,546$ spores/tablet) were added to each sample in order to estimate the pollen concentration and as a control (Stockmarr 1971). Samples were mounted in a glycerine medium and pollen counting was conducted until at least 300 pollen grains were reached when possible, excluding Pteridophytes and Cyperaceae. Pollen and spores were identified with the help of pollen and spores atlases (Kapp 1969; Heusser 1971; Moore et al. 1991; Roubik and Moreno Patiño 1991; Reille 1998; Bush and Weng 2006). Pollen percentages were determined using the sum of terrestrial pollen grains, including all the identified taxa and pollen types, except for azonal taxa (Cyperaceae and Polygonaceae) and Pteridophytes spores. The pollen sum varied between 264 and 2,082 (mean = 598) pollen grains.

Pollen diagrams were plotted with Psimpoll 4.27 software (Bennett 2009). All the identified taxa and pollen types with a value ≥ 1% were used to define the pollen zones. Pollen zonation was determined by Optimal Splitting by Information Content (OSIC) method, and the number of significant zones was selected based on the broken stick model test (Bennett 1996). An additional subzone was also identified considering other visible changes in the pollen diagram. Pollen and spores taxa were grouped into trees and shrubs, hemiparasitic plants, herbs, pteridophytes and others according to Calderón de Rzedowski and Rzedowski (2001); Juárez Jaimes et al. (2007); SEMARNAT-CONANP (2013); Espinosa-García and Villaseñor (2017), and Steinmann et al. (2021) (ESM Table 1).

The square root of all pollen percentage data was used to conduct a Principal Component Analysis (PCA), which assisted in examining the similarities between the sampling sites (Legendre and Legendre 2000). Furthermore, a Non-Metric Multidimensional Scaling (NMDS) (Legendre and

Table 2 Coordinates, elevations and in situ observations about current vegetation of the sampling points

Id	Sample name	Coordinates	Altitude (m)	Current vegetation around outcrop
1	IzPo45-22 S	N19º 08.170′, W98º 39.022′	4,024	Alpine grassland
2	IzPo47-22 S	N19º 08.267′, W98º 38.959′	4,004	Alpine grassland
3	IzPo32-20 S	N19º 07.683′, W98º 39.148′	3,972	Alpine grassland
4	IzPo10-22 S	N19º 08.285′, W98º 38.981′	3,967	Alpine grassland
5	IzPo97-22 S	N19º 08.159′, W98º 39.142′	3,927	Alpine grassland
6	IzPo70-22 S	N19º 03.817′, W98º 37.958′	3,889	Ecotone between *Pinus hartwegii* forest and alpine grassland, *P. hartwegii* trees with an infestation of *Arceuthonium* sp., presence of *Eryngium monocephalum*
7	IzPo31-20 S	N19º 06.496′, W98º 38.722′	3,808	Alpine grassland with presence of *E. monocephalum*
8	IzPo85-22 S	N19º 07.990′, W98º 39.611′	3,807	Ecotone between *P. hartwegii* forest and alpine grassland, *P. hartwegii* trees with an infestation of *Arceuthonium* sp., presence of *E. monocephalum*, the soil was frozen during sampling work
9	IzPo30-20 S	N19º 06.143′, W98º 38.894′	3,773	Alpine grassland with presence of *Lupinus montanus*
10	IzPo29-20 S	N19º 05.776′, W98º 39.198′	3,729	Open *P. hartwegii* forest, some *Pinus* sp. trees seem to be from reforestation efforts
11	IzPo42-22 S	N19º 05.064′, W98º 39.057′	3,660	*P. hartwegii* forest with recent colonisation by *Abies religiosa*
12	IzPo43-22 S	N19º 05.007′, W98º 39.164′	3,656	*P. hartwegii* forest with recent colonisation by *A. religiosa*
13	IzPo19-20 S	N19º 05.308′, W98º 37.355′	3,543	*P. hartwegii* forest
14	IzPo21-20 S	N19º 05.473′, W98º 37.292′	3,515	*P. hartwegii* forest, sample taken on the eastern slope of the volcano
15	IzPo64-22 S	N19º 05.367′, W98º 36.802′	3,450	*P. hartwegii* forest, presence of moss with signs of disturbance, sample taken on the eastern slope of the volcano
16	IzPo15-20Sb	N19º 05.539′, W98º 40.652′	3,405	*P. hartwegii* forest, presence of *A. religiosa*, Cupressaceae and other trees, near a place with signs of disturbance
17	IzPo26-20 S	N19º 05.665′, W98º 40.979′	3,338	Fir forest
18	IzPo1-21 S	N19º 10.206′, W98º 42.033′	3,337	Pine forest
19	IzPo69-22 S	N19º 05.469′, W98º 40.949′	3,293	Fir forest
20	IzPo14-20 S	N19º 04.120′, W98º 41.914′	2,993	Fir forest with signs of disturbance
21	IzPo2-19 S	N19º 07.595′, W98º 42.080′	2,934	Fir forest
22	IzPo4-19 S	N19º 07.572′, W98º 42.168′	2,914	Fir forest
23	IzPo52-22 S	N19º 07.411′, W98º 42.690′	2,860	Fir forest with presence of *A. religiosa* and *Pinus* sp.
24	IzPo53-22 S	N19º 07.432′, W98º 42.603′	2,820	Fir forest with presence of *A. religiosa* and *Pinus sp.*
25	IzPo62-22 S	N19º 07.497′, W98º 42.828′	2,788	Fir forest
26	IzPo51-22 S	N19º 07.391′, W98º 42.980′	2,760	Fir forest with presence of *A. religiosa* and *Pinus* spp.
27	IzPo50-22 S	N19º 07.080′, W98º 43.633′	2,654	Presence of *Cupressus* spp., *A. religiosa and Pinus* sp., transition between farmed land and fir forest, signs of disturbance
28	IzPo49-22 S	N19º 07.055′, W98º 43.641′	2,650	Presence of *Cupressus* spp., *A. religiosa* and *Pinus* spp., transition between farmed land and fir forest, signs of disturbance

Legendre 2000) was performed to corroborate the ordering relationship between the sites through a distance matrix using the pollen percentage data and Bray Curtis distance and can be found in the supplementary information (ESM Fig. S3). The relationship between the pollen assemblage obtained and altitude was tested using a Constrained Correspondence Analysis (CCA) (Legendre and Legendre 2000). For this analysis, the dataset used was the square root of pollen percentage data and down weight of the rare taxa. All analyses were performed in RStudio (R Core Team 2021), using the package vegan (Oksanen et al. 2020).

Results

A total of 73 pollen taxa (comprising 30 families and 43 genera) and 27 spore types have been identified (ESM Table S1). The dominant pollen types found in the assemblage are *Pinus*, *Abies*, and Poaceae. The pollen assemblages along the elevation gradient are depicted in both percentage (Fig. 3) and concentration (ESM Fig. S1) values. Two statistically significant pollen zones (named IzPo-Mo I and IzPo-Mo II) have been identified.

Pollen zones

Zone IzPo-Mo I (2,650–3,370 m, 12 samples) is characterised by high values of *Abies*, Cupressaceae, and
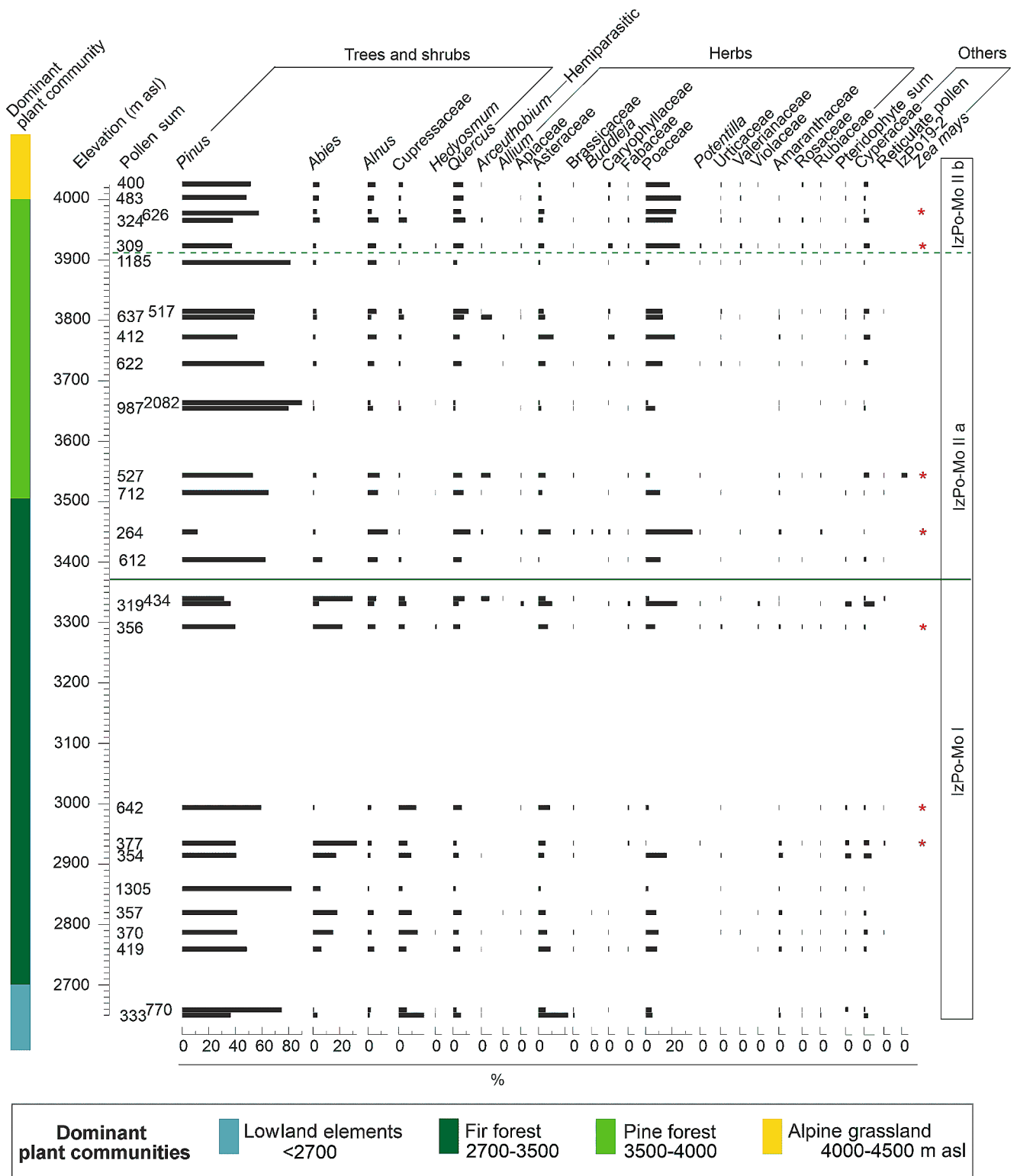
Fig. 3 Pollen diagram of surface soil samples around Iztaccíhuatl volcano expressed in percentages of taxa with values ≥ 1%. Presence of *Zea mays* is shown with single asterisks (*). All the taxa percentages are presented on the same scale and pollen zones and subzones are shown (green lines); plant communities' distributions are also shown (colour bars on the left)

Amaranthaceae (Fig. 3). *Abies* reaches its maximum abundance of 33% and has an average value of 13% through the zone. However, two low values (~0.8%) of this taxon are observed at 2,654 and 2,993 m. Cupressaceae has relatively high values, between 3 and 19%, while Amaranthaceae is particularly present between 2,650 and 2,934 m, reaching values between 0.5 and 3.1%. *Pinus* is present with values ranging from 32 to 82%. In contrast, *Alnus* shows low values (average of 3.4%). *Arceuthobium* is scarce or absent, except for a peak (6%) at 3,338 m. Asteraceae displays a peak (22%) at 2,650 m. Poaceae, one of the major components along the entire diagram, has relatively low values in this zone (average of 7.6%). Other herbaceous elements are present but in low abundances. Isolated pollen grains of *Zea mays* are present from 2,993 to 3,337 m. Pteridophytes show low values in general and present two peaks (~5%) at 2,914 and 3,337 m. Cyperaceae is consistently present throughout the area with an average value of 3% (Fig. 3). Regarding concentration, it is remarkable that *Pinus* values range from 38,769 to 111,845 grains cm^{-3} (ESM Fig. S1). This zone is characterised by high concentrations of *Abies* and Cupressaceae, while Poaceae exhibits an average value of 37,858 grains cm^{-3}. Additionally, the presence of *Fraxinus*, *Salix*, Rutaceae and Violaceae is notable in this zone.

Zone IzPo-Mo II (3,370–4,024 m, 16 samples) is primarily characterised by higher percentages of *Pinus*, *Arceuthobium* and Poaceae than in the previous zone (Fig. 3). On the contrary, *Abies*, Cupressaceae and Pteridophyte spores have lower values than zone IzPo-Mo I. Additionally, the presence of Apocynaceae, Apiaceae, Caryophyllaceae, Lythraceae, and Valerianaceae characterises this zone. The highest concentration values correspond to samples located at 3,660 and 3,972 m (3,053,850 and 1,305,110 grains cm^{-3} respectively). This zone has been subdivided into two subzones.

In subzone IzPo-Mo IIa (3,370–3,889 m), *Pinus* varies between 11 and 90% while Poaceae presents percentages of 12% on average. *Alnus* shows the highest values through the elevational range (10% on average) between 3,405 and 3,543 m. Other remarkable taxa present are *Quercus* (3–8%) and *Abies* (reaching 7% at 3,927 m), with higher and lower abundances respectively than in the previous zone. *Arceuthobium* has two peaks (~8%) at 3,543 and 3,807 m (Fig. 3), but is regularly present through this zone. Isolated pollen grains of *Zea mays* are present around 3,500 m. Regarding pollen concentration, the high values of *Alnus* are noteworthy (39,646 grains cm^{-3} on average) from 3,405 to 3,660 m. Instead, Cupressaceae (7,185 grain cm^{-3} on average) and Poaceae (44,310 cm^{-3} on average) have higher concentration values that in zone IzPo-Mo I. *Pinus* has its maximum value (2,751,402 grains cm^{-3}) at 3,660 m (ESM Fig. S1).

Subzone IzPo-Mo IIb (3,889–4,024 m) is represented by increased Poaceae percentages (22% on average), whereas *Pinus* shows lower values (from 8 to 58%) than in the previous subzone (Fig. 3). *Alnus* and *Quercus* have values between 3 and 8 and 6–9%, respectively. Cupressaceae present two peaks, with values of 6% at 3,967 m and 3% at 4,024 m. *Zea may* is present at 3,927 and 3,972 m. The concentration values of several taxa, such as *Abies*, *Alnus*, *Quercus*, Asteraceae, Poaceae and Cyperaceae, show higher values than in the previous subzone (ESM Fig. S1).

Ordination analyses

The results of the PCA show that the first two axes explain 51% of data variability (Fig. 4 and ESM Fig. S2). Axis 1 (eigenvalue=3.41, proportion explained=0.27) is related to the presence of *Pinus*. Towards the positive values of axis 1, samples with higher *Pinus* values are observed. The sample at 3,660 m, on the right edge, has *Pinus* percentages of 90%. In contrast, the sample at 3,450 m, situated at the lower-left edge of the plot, is characterised by the lowest percentage of *Pinus* (11%), the maximum percentage of Poaceae (35%) and the presence of *Zea mays* pollen. On the second axis (eigenvalue=3.12, proportion explain=0.24), samples characterised by elevated values of *Abies* are positioned on the positive side. Meanwhile, samples with high percentages of Poaceae are on the negative side. The sample at 2,934 m, positioned at the top of the plot, is characterised by the abundance of taxa seldom encountered in the record and present in low percentages. This axis also groups the samples following the two clusters resulted from the OSIC analysis (pollen zones, Fig. 3). Only the sample at 3,337 m shares greater similarity with the samples from higher elevations (>3,500 m), as indicated by negative scores on the second axis. This sample presents low percentages of *Abies* (4%) and high values of Poaceae (24%) (Fig. 4).

The distribution of pollen taxa indicates the presence of four groups, three of which are associated with *Abies*, Poaceae, and *Pinus*, respectively. These are the most abundant taxa and account for a majority portion of the pollen assemblage's variability, as indicated by the pollen zones and PCA analyses (Figs. 3 and 4). The fourth group identified in the PCA consists of taxa that do not exhibit associations with any of the three dominant taxa. In the upper-left square where *Abies* is present, taxa such as Cupressaceae, Asteraceae, Amaranthaceae and Cyperaceae are also displayed. In the lower-left square, Poaceae is associated with taxa such as *Quercus*, *Alnus* and Caryophyllaceae. In the lower-right square, *Pinus*, as well as taxa found in a few samples with low percentages, are presented. It is noteworthy that most of the total taxa have a negative or low relation to *Pinus*. In the upper-right square, herbaceous taxa found in only a few samples are shown. It includes Lamiaceae, Geraniaceae and Solanaceae. Furthermore, the overall configuration of

Fig. 4 Biplot of the first two PCA axes for the pollen assemblage. The first axis explains 0.27 of the variability, and the second 0.24. Elevations of the sampling sites and acronyms of pollen taxa are shown (full name in ESM Table S2). Pollen zones are indicated (colour polygons). A zoom of the graph's centre is available (ESM Fig. S2)
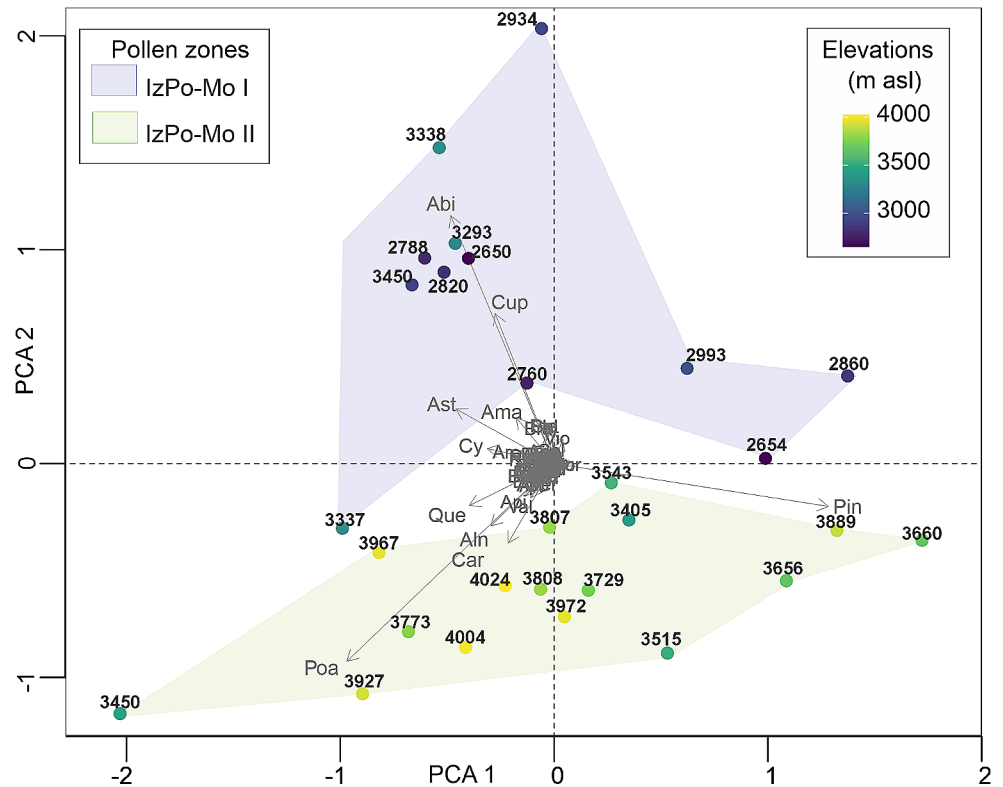
the samples and the most abundant pollen taxa in the PCA closely resembles that of the NMDS analysis (Fig. 2 and ESM Fig. S3). CCA indicates that the elevation gradient variable explains 8% of the data set's variability (eigen-value = 0.068, p-value = 0.001).

Discussion

Pollen signal of the current plant communities

Mid elevation communities: fir forest pollen signal

High pollen percentages of *Abies* identified in zone IzPo-Mo I can be associated with the presence of a fir forest, as previously observed in similar studies. For instance, in Sierra de Cuchumatanes, Guatemala, the highest percent-age of *Abies* recorded was 30% in the *Abies* vegetation zone (Islebe and Hooghiemstra 1995). In the Sierra Madre Occidental, in northwestern Mexico, pollen of *Abies* ranged from 8 to 25% at sites where fir was present (Ortega-Rosas et al. 2008). Besides this abundance in the pollen diagram, the PCA shows that other taxa related to the fir forest are closely located to *Abies* (Fig. 4). Furthermore, the notice-able decrease in *Abies* values in Zone IzPo-Mo II (3,370–4,024 m) can be related to the upper limit of the Fir Forest (~3,500 m). However, it is worth noting that pollen values decrease before reaching the upper limit reported for the

parental plants (3,500 m), possibly due to (i) the impact of human disturbances and (ii) the local dominance of *Pinus* in some of the sampling sites.

High elevation communities: Pine forest and alpine grassland pollen signals

The increase in the average values of *Pinus* and the presence of *Arceuthobium* in subzone IzPo-Mo IIa (3,405–3,889 m) can be associated with the pollen signal of the pine forest plant community. This representation could be particularly relevant for those communities at higher elevations, where pines become more dominant (i.e. the *P. hartweggii* forest, reported at 3,700–4,000 m). Despite the fact that *Pinus* pol-len is present along the entire elevation transect, the higher percentages of this taxa in the subzone IzPo-Mo IIa could indicate a higher proximity of the parental plants, enabling to distinguish the pollen signal of pine forest from fir forest and alpine grassland plant communities. The present pollen record agrees with the modern pollen rain observed in Agua el Marrano Valley study site, located in the northwest side of the Iztaccíhuatl volcano at 3,860 m, where pine forest was documented as the dominant plant community. Pollen signal was dominated in Agua el Marrano Valley by *Pinus* (75%), *Quercus* (10%) and *Alnus* (5%) (Lozano-García and Vázquez-Selem 2005). Moreover, pines are the principal hosts of dwarf-mistletoes (*Arceuthobium* spp.). As a para-site, the pollen dispersion power of this taxon is assumed to

be reduced, providing local evidence of the plant and therefore, of its host (Player 1979; Endara-Agramont et al. 2022). The relation between *Arceuthobium* pollen and pine forests has been previously reported in central Mexico and Guatemala (Ohngemach and Straka 1983; Islebe and Hooghiemstra 1995; Almeida-Lenero et al. 2005).

Despite the challenges of delineating the boundary between pine forests and alpine grassland using pollen assemblages, the higher pollen percentage of Poaceae and the decrease of *Pinus* in subzone IzPo-Mo IIb (3,972–4,004 m) could be related to the limit of the forest and the transition towards more open vegetation at these elevations on Iztaccíhuatl volcano. *P. hartwegii* forests range from moderately dense to open communities, especially near the treeline (Calderón de Rzedowski and Rzedowski 2001), where an ecotone between the forest and the alpine grassland is formed (Almeida-Lenero et al. 2007). Moreover, the similitudes in the pollen signal observed in the ordination analysis in samples from 3,405 to 4,024 m (Fig. 4) evidence the lack of a clear change in the taxa composition and could be explained by several reasons. Firstly, pine forests and alpine grassland in central Mexico share many species and genera that appeared in the pollen record (Apiaceae, Brassicaceae, Poaceae, Rosaceae, Caryophyllaceae and Urticaceae). Secondly, the arrival of extra local pollen is extensively reported in open communities and/or high elevations (Islebe and Hooghiemstra 1995; Connor et al. 2004; Weng et al. 2004; Rull 2006; Olivera et al. 2009; Niemann et al. 2010; Jansen et al. 2013; Hagemans et al. 2019) and can represent up to > 50% of the pollen sum (Islebe and Hooghiemstra 1995; Niemann et al. 2010; Lozano García et al. 2014).

Such a subtle pollen signal around the treeline ecotone has also been found in nearby records. In this sense, in the pollen signal from Popocatépetl volcano above 4,000 m, *Pinus* varied from 10 to 60%, *Alnus* was around 40% and *Quercus* ~ 10–40%. Other characteristic pollen taxa included *Alchemilla*, *Conyza*, *Penstemon*, *Draba*, Brassicaceae, Caryophyllaceae and Poaceae (Lozano García et al. 2014). In a Guatemalan record from above the treeline around 4,000–4,200 m, *Pinus* represented between 50 and 80% and Poaceae reached percentages lower than 20% (Islebe et al. 1995; Islebe and Hooghiemstra 1995). Similarly, Olivera et al. (2009) suggested that wind-dispersed pollen was found overrepresented in the páramo (Andean high elevation grasslands) of Ecuador. This was probably due to the more effective upslope transport of forest pollen into the open grassland (Rull 2006).

Over and under-represent taxa

The wind-pollinated taxa *Pinus*, *Alnus* and *Quercus* are considered over-represented in the pollen signal (e.g. Olivera et al. 2009; Figueroa-Rangel et al. 2010; Niemann et al. 2010; Castro-López et al. 2021). In case of *Pinus*, despite the fact that the increase in the average percentages together with the presence of *Arceuthobium* pollen could be related to the elevations where pine forest occur, the dominance *of Pinus* throughout the pollen assemblage of the Iztaccíhuatl record is remarkable. *Pinus* spp. produces large amounts of pollen grains that are easily transported long distances by wind. This taxon has been also identified as a dominant element in other pollen records of altitudinal transects in Mexico, Guatemala and elsewhere (e.g. Islebe and Hooghiemstra 1995; Lozano-García and Xelhuantzi-López 1997; Lozano-García et al. 2014; Castro-López et al. 2021; Domínguez-Vázquez et al. 2023). In this sense, the *Pinus* pollen signal is typically characterised by broader distribution and less defined boundaries than those established for its parental plants (Islebe and Hooghiemstra 1995; Cañellas-Boltà et al. 2009). Moreover, several species of the genus *Pinus* are dominant or co-dominant elements in different plant communities within the volcano area. Currently, coniferous and pine forests are distributed in the Iztaccíhuatl volcano between 2,350 and 4,000 m (Calderón de Rzedowski and Rzedowski 2001; Rzedowski 2006), covering almost the entire altitudinal transect analysed. This overlap in the altitudinal gradient relates to another common challenge in pollen analysis, that is, the limitation in achieving species-level identification. Mexico holds nearly half of all known *Pinus* spp. (Farjon 1996; Farjon and Styles 1997). However, pollen analysis does not allow for the definition of these species and their elevational distribution and environmental preferences.

Alnus and *Quercus* are also present across the entire elevation transect. Additionally, at the higher elevations of the volcano, where the herbaceous layer dominates, these taxa exhibit some of their highest values and display similar scores to Poaceae and other taxa related to alpine grassland (Figs. 3 and 4). These values suggest that *Alnus* and *Quercus* pollen signals are over-represented at high elevations and should be conservatively used in palaeoecological reconstructions. The over-representation of *Alnus* at high elevations in this record is in agreement with previous studies carried out in tropical mountains (Weng et al. 2004; Rull 2006; Olivera et al. 2009; Niemann et al. 2010; Ortuño et al. 2011; Lozano García et al. 2014). On the one hand, similar to *Pinus* although in narrower elevations, the presence of *Alnus* pollen along the elevation transect could be explained by its widespread occurrence in various plant communities (Calderón de Rzedowski and Rzedowski 2001), as well as the wind-dispersion of its pollen.

In the case of *Quercus*, the low pollen values observed at low and middle elevations (2,650–3,405 m), where the parental plants typically grow, could be attributed to the chosen sampling sites in which the dominance of *Quercus* was not observed (Table 2). Previous research in the northern region of Mexico has reported pollen percentages between 20 and 60% in oak-pine and pine-oak forests where *Quercus* is abundant (Ortega-Rosas et al. 2008). In central Mexico, the Zacapu record indicated that *Quercus* percentages seemed to be particularly high only in patches dominated by the parent taxon (Correa-Metrio et al. 2012). In contrast, *Quercus* percentages up to 5% in samples without oak vegetation have been described as common in Guatemala (Islebe and Hooghiemstra 1995). Also, its pollen has been considered under-represented in mountains and hill landform sites from central Mexico, with *Pinus* as the dominant element (Castro-López et al. 2021).

Additionally, other pollen taxa with low percentages, which in several cases occurred in a small number of samples, were also present. Many of these taxa showed positive values or stay in the lower-right square of the PCA (Fig. 4). The parental taxa of these pollen types are associated mainly with low and mid-elevation distribution and form part of plant communities such as fir, cloud, oak and mixed forests (Calderón de Rzedowski and Rzedowski 2001) (ESM Table S1). The low values and scarce presence of these taxa could be related to: (i) sampling design: cloud, oak and mixed forests have not been properly sampled in the present research, as they were not present in the samples' locations (within the selected altitudinal range). Arboreal taxa like *Hedyosmum*, *Oreopanax*, *Morella*, *Carpinus* and *Ulmus* could be associated with the presence of cloud forest in some areas of the volcano under humid conditions; and/or (ii) pollination syndromes: non-anemophilous pollen taxa are commonly underrepresented in pollen rain studies (Bush 1991; Olivera et al. 2009). In the specific case of central Mexico, research in a temperate forest indicates that 52% of tree species are anemophilous; meanwhile, more than 80% of herbaceous plants and shrubs are pollinated by insects (Cortés-Flores et al. 2015). Herbaceous and shrub taxa such as *Arbutus*, *Buddleia*, *Salvia*, *Solanum*, *Fuchsia*, several species of Caryophyllaceae, Lamiaceae, Campanulaceae, Apiaceae and Apocynaceae are entomophilous or pollinated by other animals (Islebe and Hooghiemstra 1995; Rosas-Guerrero et al. 2014; Cortés-Flores et al. 2015; González et al. 2018). Hence, this pollination syndrome could partly explain why they are underrepresented in this record. On the contrary, anemophilous taxa such as *Hedyosmum* and *Morella* have been previously found in pollen samples even when the parent plants were absent in the local vegetation (Islebe and Hooghiemstra 1995). Based on this evidence, it is suggested

that some dispersion from closer forest patches should not entirely be ruled out yet.

These results are important when considering palaeoenvironmental reconstructions based on fossil pollen data. For instance, some characteristics of the Agua el Marrano Valley record from Iztaccíhuatl volcano, which covers the last 10,900 cal BP, could be emphasised (Lozano-García and Vázquez-Selem 2005), such as: (i) the increase of *Pinus* values together with the most constant presence and higher values of *Arceuthobium* could be a strong evidence of the presence of pine forest near the coring site, as previously interpreted; and (ii) the near constant values of *Quercus* and *Alnus*, especially from 5,000 cal BP onwards should be interpreted with caution due to their possible over-representation at high elevations.

Environmental factors and human impact

The results of the CCA indicated that the elevation gradient is an important determining factor to explain the pollen signal reported. Similarly, despite the differential distribution observed in the diagram and marked by the zonation, the PCA biplot also suggested some relationship between the pollen signal and elevation (Figs. 3 and 4). This partial agreement could be related to the sampling design, pollen production and pollination mechanisms, or the presence of shared taxa and the taxonomic resolution limitation of pollen within the different plant communities sampled for this research.

Elevation has been documented as a key factor explaining the plant communities' distribution (Klinges and Scheffers 2021) due to its relation to temperature (e.g. Rehfeldt et al. 2006; Feeley et al. 2020; Maharjan et al. 2022). Pollen-based data of altitudinal transects have also shown changes in the assemblages found related to the elevation gradient (Weng et al. 2004; Rull 2006; Correa-Metrio et al. 2013; Domínguez-Vázquez et al. 2023). However, other environmental factors are also crucial in explaining plant distributions and diversity. In SNVR vegetation distribution is primarily influenced by the elevation gradient, precipitation, soil properties, insolation and slope (Lauer 1978; Velázquez 1994; Velázquez et al. 2000; Calderón de Rzedowski and Rzedowski 2001; Sánchez-González and López-Mata 2003; Castro-López et al. 2021). However, human disturbance has also played an important role in the distribution and fragmentation of plant communities in the zone, even in the area within the Iztaccíhuatl-Popocatépetl National Park (e.g. Almeida et al. 1994; Sánchez-González and López-Mata 2003; Caballero Cruz et al. 2022).

The low values of *Abies* at different elevations within the fir forest distribution range, together with observations of forest disturbance signals and/or surrounding areas

dominated by agricultural land use and human settlements indicate that human impact on the plant communities of Iztaccíhuatl volcano seems significant in unprotected areas. Fir forests are one of Mexico's most threatened and fragmented forest types (Martínez-Méndez et al. 2016). In the case of SNVR, forestry activities are allowed between 3,000 and 3,600 m, and human impact below the national park boundary (3,600 m) has also been reported (Figueroa and Sánchez-Cordero 2008; SEMARNAT-CONANP 2013; López-García 2019; González-Fernández et al. 2022). Based on the present results, changes in the values of *Abies* pollen could be a tool to record the fragmentation of fir forest in other sites. Similarly, high values of Poaceae, Asteraceae and Amaranthaceae pollen grains between 2,650 and 3,338 m could be related to the fragmentation of the fir forest and other plant communities and the proliferation of agricultural activities at low and mid-elevations. Agricultural activities around the zone, mainly from 2,300 to 3,000 m based on field visits, but also at higher elevations according to the satellite images, have been identified. This activity has been recorded in the pollen signal with the presence of *Zea mays* pollen at different elevations (Fig. 3). Although Asteraceae, Amaranthaceae and Poaceae could be common elements of different plant communities, previous research has shown a close relationship between high values of these pollen taxa and disturbance (Reese and Liu 2005; Olivera et al. 2009; Correa-Metrio et al. 2012; Castro-López et al. 2021; Domínguez-Vázquez et al. 2023). However, additional research is necessary to further develop this hypothesis, due to the low taxonomic resolution based on pollen of these families. Human activities related to population growth, illegal logging and changes in land use and land cover can intensify the impacts of climate change on the distribution and abundance of species (Peterson et al. 1997; González-Espinosa et al. 2012; Steinbauer et al. 2018; Feeley et al. 2020). These negative effects are also reflected in ecosystem functioning and services related to plant communities and species (Steinbauer et al. 2018; Cruz-Flores et al. 2020; Feeley et al. 2020; Bastien-Olvera et al. 2024). This is particularly the case at lower mountain elevations, which tend to be less protected (Elsen et al. 2018) and where fragmentation can have a considerable impact (Peterson et al. 1997).

In Mexico, natural protected areas (NPA) have been designated to maintain the integrity of forest ecosystems and preserve biodiversity while they provide benefits from their ecological services (Toledo 2005). However, an assessment of the success of Mexican NPAs from 1993 to 2002 shows that 46% fail to prevent land-use and land-cover changes effectively (Figueroa and Sánchez-Cordero 2008). Data indicate that a high proportion of endangered species are present in transformed areas, while only < 20% of them occurring in protected areas (Londoño-Murcia and Sánchez-Cordero 2011). The pollen data presented in this research highlight the impact of human activities on plant communities of Iztaccíhuatl volcano, particularly in those below the national park's lower elevation boundary. Therefore, the results underscore the need to re-evaluate the current boundaries of the national park, develop new conservation strategies, and strengthen existing programmes in order to protect these plant communities (Toledo 2005; Martínez-Mendez et al. 2016; López-García 2019). The application of programmes such as the payment for hydrological environmental services (PHES) could be a good tool to conserve and even increase forest cover (Mora Carvajal et al. 2019). This program can also contribute to biodiversity conservation and increased elevational gradient connectivity, enhancing ecological representation and facilitating species range shifts under climate change (Elsen et al. 2018).

Conclusions

The results of this study demonstrate the usefulness of analysing surface soil pollen samples to establish a qualitative relationship between the pollen signal and the distribution of the main modern plant communities along an elevational gradient, removing the limitation of just using natural or artificial pollen traps. This analysis has shown the importance of local variability in the parental distribution, which implies the necessity of incorporating modern analogues as routine in palaeo-studies reconstructing past plant communities based on fossil pollen analysis. High percentages of *Abies* were related to the presence of a fir forest. High values of *Pinus*, together with the presence of the hemi-parasite *Arceuthobium*, were associated with the pine forest plant community. Delineating the boundary between pine forests and alpine grassland is challenging. However, the absence of the locally-dispersed pollen of *Arceuthobium*, high percentages of Poaceae, and the presence of other minor taxa (such as Apiaceae, Brassicaceae, Rosaceae, Caryophyllaceae and Urticaceae) were interpreted as a transition towards alpine grassland plant communities, where the herbaceous layer is dominant. Based on this analysis, *Alnus* and *Quercus* are over-represented taxa in areas where the herbaceous layer is dominated and parental plants are absent; therefore, they should be conservatively used in palaeoecological reconstructions.

The elevation was not found to be a determining factor explaining the pollen signal due to (i) pollen signal presenting limitations related to low taxonomic resolution; (ii) the presence of many taxa with low values and in only few samples; (iii) the influence of the wind-pollinated taxa on the pollen signal; and (iv) the occurrence of taxa

that are common to multiple plant communities within the selected altitudinal gradient. Additionally, it is recommended to increase the number of samples to obtain a more comprehensive understanding of the vegetation in the area, especially related to plant communities located at lower elevations such as oak and cloud forests. The fragmentation of plant communities as a consequence of human activities in the zone, especially in low and mid-elevations, could determine some of the characteristics of the pollen signal. The low values of *Abies*, the peaks of taxa such as Asteraceae, Amaranthaceae and Poaceae, and the presence of *Zea mays* pollen could be related to human impact in the zone. A re-evaluation of the current boundary of the national park and the development of new and better conservation strategies are essential considering the ecosystem functioning and services that the mountain brings to one of the biggest cities in the world and the surrounding areas.

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