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# Changes in vegetation structure during the Pleistocene–Holocene transition in Guanajuato, central Mexico

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## Abstract

To investigate the changes in the structure and composition of the vegetation during the Pleistocene–Holocene transition, pollen and macrocharcoal analyses were carried out on samples of sediments taken from a 14.5 m core from Hoya Rincón de Parangueo, a crater lake (maar) in Guanajuato, Mexico. Fossil pollen data from the core suggest that during the last glacial maximum (LGM) the climate in central Mexico was very wet and cold, and the vegetation was open cloud forest, and fires did not occur. During the Pleistocene–Holocene transition, vegetation diversity was high in the study area, but disturbance to vegetation was observed, indicating an open habitat with fewer trees. There was an abrupt change in the composition of the vegetation during the later Holocene, likely signalling a strong change in climate. During the early Holocene the area remained wet, but there was a trend toward drier conditions that became well established at the end of the middle Holocene and into the late Holocene. As a consequence, the structure of the vegetation changed, with more taxa suggesting dryer environments, lasting until the late Holocene, when human disturbance became an important factor affecting vegetation in the area.

**Keywords** Last glacial maximum · Vegetation · Diversity · Disturbance · Pollen · Cloud forest · Tropical dry forest · Shrubland

## Introduction

Climate change and ecological disturbances are the main driving forces controlling vegetation dynamics. Precipitation and temperature are important climatic factors limiting the distribution of the vegetation and determining its structure and composition. Vegetation structure is defined by the dominant plants in the ecosystem and the structure

of a forest is usually defined by the tree communities within it (Toledo-Aceves et al. 2014). Among the factors affecting the community's structure are disturbances. Whether from a biotic or abiotic origin, a disturbance is a process that removes biomass from an ecosystem (Grime 1977). Disturbances affect diversity, promoting or decreasing species richness according to their intensity and frequency (Kohler et al. 2004).

The main factors promoting disturbances during the Pleistocene–Holocene were grazing by herbivores (Vera 2000; Rule et al. 2012), fire from volcanic eruptions and a dry climate (Torres-Rodríguez et al. 2015). The destructive presence of fire has been determined from charcoal in cores from Chalco, Cuitzeo and Parangueo in Mexico (Istrade-Alcántara et al. 2012; Torres-Rodríguez et al. 2015; Wolbach et al. 2018). A dry climate has been recorded in cores from central Mexico (Lozano-García et al. 1993; Metcalfe et al. 2000). However, herbivory has been ignored as a driver of vegetation change, despite the significant evidence of the presence of a megafauna in México (Arroyo-Cabrales et al. 2007; González et al. 2014, 2015). The megafauna promoted

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the openness of vegetation through grazing and browsing and, when these large animals became extinct, it changed the pattern of distribution and abundance of plants in their absence (Janzen and Martin 1982; Vera et al. 2006; Bar-nosky et al. 2016).

Large lakes, such as Lago Zacapu, Chapala and Cuitzeo, have been extensively studied despite their susceptibility to desiccation and erosion caused by climatic events and active tectonism during the Pleistocene (Correa-Metrio et al. 2012; Israde-Alcántara et al. 2012; Ortega et al. 2010). However, the maar lakes (in craters from explosive volcanic eruptions), present ecological features that make them suitable for palaeoecological reconstructions; these maars could have acted as refugia during events of climatic stress, as they would have had resilience to desiccation and erosion because of the protection by their steep walls from the effect of winds. In this context, the maars present microenvironments that allow the formation of certain vegetation types that give specific pollen signals that facilitate the interpretation of the palaeoecological record.

Most of the long cores recovered from the large lakes of central Mexico have a hiatus during the Pleistocene–Holocene transition (Correa-Metrio et al. 2012; Israde-Alcántara et al. 2010, 2012). Contrasting conclusions have arisen from differing environmental reconstructions of central Mexico for the late Pleistocene. The presence of open woodland has been attributed to dry conditions (Lozano-García et al. 2005). In contrast, other studies indicate wet conditions that allowed the development of wooded and open vegetation, like parkland, which included taxa from the cloud forest, such as *Liquidambar*, *Corylus*, *Betula* and *Alnus* (Bradbury 1997; Robles-Camacho et al. 2009). The Holocene in central Mexico underwent several cycles of wetness and dryness. A core previously taken by Park et al. (2010) at Rincón de Parangueo gave a basal age of 9,600 cal BP and a wet early Holocene, a dryer mid Holocene and a wetter late Holocene were interpreted. However, as with all cores from the late Holocene, it should be noted that the climatic signal recovered is influenced by disturbance from human activities. The Cuitzeo and Alberca cores show a wet early Holocene (10,000–7,000 cal BP) and a climatically variable late Holocene (4,000 cal BP–present) (Istrade-Alcántara et al. 2010; Park et al. 2010; Castro-López 2013). Strong evidence exists that before 4,000 cal BP, dry conditions dominated, whilst wet intervals occurred after 2,500 cal BP (Lozano-García et al. 1993; Metcalfe et al. 2000; Almeida-Leñero et al. 2005; Park et al. 2010).

Today, the Bajío area in central Mexico has been greatly transformed by agriculture, cattle ranching and industrial activities, resulting in the near-disappearance of the original vegetation (Butzer and Butzer 1997; Guevara-Escobar et al. 2008). The original oak forests and seasonal dry forests have given way to shrubland, which is the dominant

vegetation throughout the Bajío today. The origin of this modern shrubland has been attributed to human activities in the area, making the composition of the original vegetation uncertain (Butzer and Butzer 1997). The aim of this work is to provide a climatic history of the Bajío based on the study of its vegetation history.

## Study area

The maar of Valle de Santiago is located in the state of Guanajuato to the south of the city of Salamanca, at the northern limit of the Mexican Volcanic Arc. It is within the Lerma-Santiago watershed, near the border between arid northern Mexico and less arid areas in central and southern Mexico. The weather there is dominated by tropical to subtropical high-pressure climatic systems. The rainfall distribution is controlled in part by the latitudinal seasonal migration of the Intertropical Convergence Zone which brings humid air from the Gulf of Mexico and the Caribbean into contact with westerly winds that carry moisture from the Pacific (Douglas et al. 1993).

The regional climate borders on being semi-arid and can be classified as a Cwa climate, which is semi-warm, sub-humid and temperate (Butzer and Butzer 1997). The annual precipitation of this type of climate ranges from 679 to 1,000 mm, with 90% of it falling between May and October. Significant evaporation occurs between March and May and the mean annual temperature is 19 °C (García 1973).

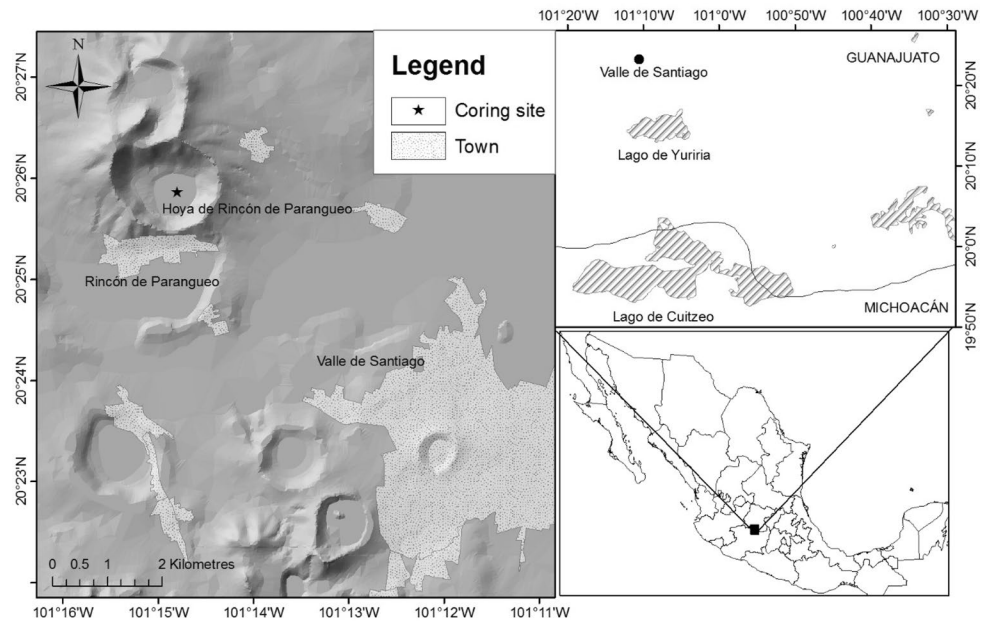
The crater is 1.2 km long and 0.9 km wide and like all the maars in the area, most of the water has been extracted for agriculture and domestic uses, leaving a small pond remaining in the centre. The desiccation of the lake has left a white layer of salt that has become a characteristic of these maars (Fig. 1).

The modern vegetation inside the crater is characterized by a seasonal dry forest dominated by *Bursera*, *Heliocarpus*, *Euphorbia*, *Ipomoea*, *Acacia*, *Conzattia* and various species of Cactaceae. *Prosopis* is very abundant around the edge of the lake. This vegetation type has been destroyed and fragmented and only isolated small areas remain in the Bajío area (Trejo-Vázquez 1998; Carranza-González 2005).

## Coring

In 2011, a 14.5 m core was obtained close to the centre of the maar using a Russian corer. As the Russian corer recovers half tubes 50 cm long, we extracted two sections from every level. Every section was wrapped in plastic film, labelled and taken to the laboratory, where they were kept under refrigeration at 6 °C until analysis. Sediment samples were taken from the sections at regular 5 cm intervals for analyses of pollen and charcoal.

**Fig. 1** Study area. Map of Rincón de Parangueo, Valle de Santiago, Guanajuato, Mexico



## Radiocarbon dating

Seven samples were selected for AMS radiocarbon dating of the organic fraction (Table 1). Organic matter (TOC) was unusually high, the total organic content averaging 3.5%. The samples were treated to isolate the organic matter. AMS analyses were performed at the National Ocean Sciences Accelerator Mass Spectrometry Facility at the Woods Hole Oceanographic Institution and at Beta Analytic, both in the USA. The dates were calibrated using CALIB 7.1 with the IntCal13 curve (Table 1; Stuiver and Reimer 1993). Both radiocarbon ages and corrected calibrated ages are plotted together as age-depth graphs in Fig. 2.

We used a Bayesian analysis to construct an age/depth model, and as we suspected an old carbon effect on the dates, we extrapolated the curve to zero depth, getting a factor

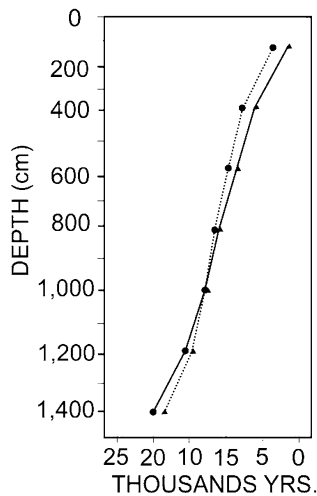
correction of 2,468 years, which means that all the dates were too old by this amount. We applied Bayesian analyses to our dates as outlined in Kennett et al. (2015), with the objective of presenting a robust statistical model that would represent all modelling assumptions and data. Bayesian age-depth modelling is able to calculate millions of possible age models (iterations) and determine the average (weighted mean) and is considered more robust and flexible than other types of analyses (Wolbach et al. 2018).

## Pollen analysis

For pollen analysis, sub-samples of 1 cm<sup>3</sup> of sediment were taken from the core, and routine pollen extraction methods were used (Fægri and Iversen 1989). Five *Lycopodium clavatum* tablets of batch #177745 ( $X = 18,584$  per

**Table 1** List of the sediment samples dated from the Rincón de Parangueo core

Depth (cm)	<sup>14</sup> C-age	Age range (cal BP)					Corrected age
		1 $\sigma$ (68.3%)	Prob dist	2 $\sigma$ (95.4%)	Prob dist	Median probability	
105	3,620 $\pm$ 25	3,895–3,933	0.557	3,851–3,984	0.99	3,929	1,470
		3,940–3,971	0.443	4,054–4,000	0.01		
400	7,840 $\pm$ 40	8,556–8,648	1	8,543–8,762	1	8,620	6,160
		10,884–10,925	0.214	10,792–10,964	0.351		
544	9,670 $\pm$ 45	11,083–11,187	0.786	11,003–11,024	0.018	11,103	8,640
				11,065–11,205	0.631		
				13,194–13,289	1		
997	12,790 $\pm$ 70	15,126–15,335	1	15,036–15,551	1	15,243	12,780
1,176	14,700 $\pm$ 75	17,782–18,000	1	17,7661–18,094	1	17,889	15,430
1,400	18,550 $\pm$ 75	22,353–22,496	1	22,260–22,600	1	22,426	19,970



**Fig. 2** Comparison of radiocarbon age and the modelled calibrated age

tablet,  $\sigma = \pm 1,853$ ) (produced by the University of Lund, Sweden) were added for pollen concentration calculations. The samples were treated successively with solutions of HCl, KOH, HF and by acetolysis. Minimum counts of 300 pollen grains of woody taxa were made for each sample using an Olympus CH30 microscope and 400 $\times$  magnification. The pollen grains were identified using our pollen reference collection based on the flora from the Bajío area and stored at the laboratory of palynology at the University of Michoacán, and a pollen manual from Cuitzeo (Raygadas-Torres 2011). The pollen diagrams were constructed using Tilia version 1.7.16 (Grimm 2011). Pollen zones are based on cluster analysis and observations of major changes in the pollen diagram.

Taxa are grouped, according to their ecological characteristics, into temperate forest taxa, cloud forest taxa, dry tropical forest taxa, riparian forest taxa and shrubland taxa. This classification is based on Carranza-González (2005), Labat (1995) and on our own experience with the vegetation from the area. The pollen grains representing the temperate forest taxa are *Pinus*, *Quercus*, *Abies* and *Alnus*. The cloud forest taxa are represented by *Betula* and *Corylus* (which are plotted as Betulaceae), *Fraxinus*, *Juglans* and *Liquidambar*. The main pollen taxa from the dry tropical forest are *Celtis*, *Condalia*, Fabaceae, Arecaceae, Rutaceae, *Prosopis*, Myrtaceae and Mimosoideae (in which we include *Acacia*). Riparian forests are represented by *Salix* and *Taxodium*. Shrubland taxa are dominated by herbs and shrubs like Asteraceae, Poaceae, Cyperaceae and Euphorbiaceae. Even though we can differentiate *Croton*, *Euphorbia* and *Acalypha*, we decided to plot them together as Euphorbiaceae because they are all associated with open and disturbed habitats.

## Macrocharcoal analysis

Local fires are reflected by high abundances of macrocharcoal. For macrocharcoal analysis, we used a modification of the technique described by Stevenson and Haberle (2005): 1 cm<sup>3</sup> of sediment was placed in a solution of 10% KOH for 12 h, then in a 10% H<sub>2</sub>O<sub>2</sub> solution for 24 h, after which the sample was sieved using a mesh of 120  $\mu$ m. The particles of charcoal trapped in the mesh were rinsed and placed in a petri dish for counting using a Leica LED2000 stereo microscope at 40 $\times$  (Stevenson and Haberle 2005). The results are given in numbers of particles/cm<sup>3</sup>.

## Results

### Radiocarbon dating and zonation

The Paranguero core has an extrapolated basal age of ca. 21,000 cal BP and the age/depth plot has an unusually smooth curve, giving confidence in the quality of the analyses, so we conclude that the chronology of Paranguero is robust. The core covers the period from the late Pleistocene to the whole Holocene. No reversals were observed in the sedimentation (Fig. 2).

The pollen record was zoned using cluster analysis by sum-of-squares (CONISS), which divided the pollen diagram into two pollen assemblage zones, corresponding to late Pleistocene and Holocene. The cluster analysis showed that the end of the late Pleistocene and the early Holocene were related (Figs. 3, 4).

### Pollen zones

#### Zone VI (1,450–1,220 cm, 21,000–16,000 cal BP)

Beginning at the bottom of the core, this zone is dominated by a shrubland where shrubs and herbs oscillated from 50 to 60% with minima of 30% (Figs. 3, 4). Poaceae oscillated around 10% with a peak of 20% at 1,400 cm. Asteraceae input showed marked fluctuations, with some periods reaching 20% and extended periods with 10–15%. *Pinus*, which started with an input of 15%, peaked at 35% at 1,400 cm. *Quercus* was 10% at the bottom of the zone but oscillated between 7 and 5% in the rest of the zone. *Alnus* values were less than 5% throughout the zone. Ulmaceae, in the first 50 cm, had a proportion of 15%, which decreased to 1% before reaching 30% at 1,300 cm, coinciding with a dry forest peak. It peaked several times at 18%, finishing with 5% at the end of the zone.

In this zone, pollen concentrations reached their maximum values with several peaks with more than  $5 \times 10^5$  grains and one spike of  $1.5 \times 10^6$  grains at 1,260 cm, which was

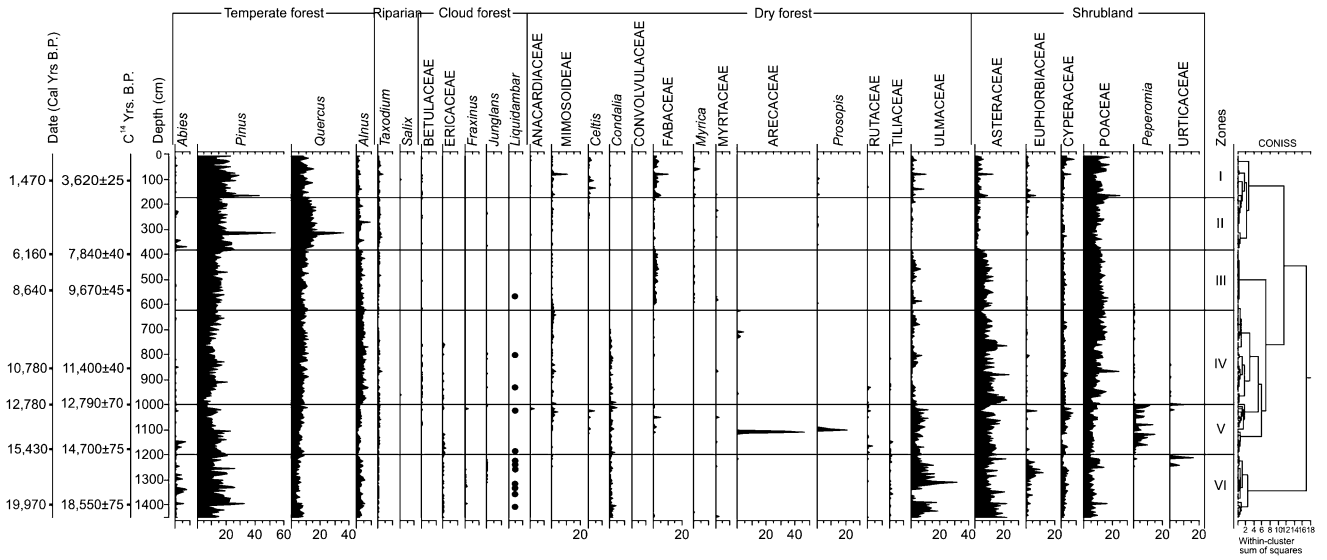


Fig. 3 Pollen diagram with selected taxa from Rincón de Paranguero core

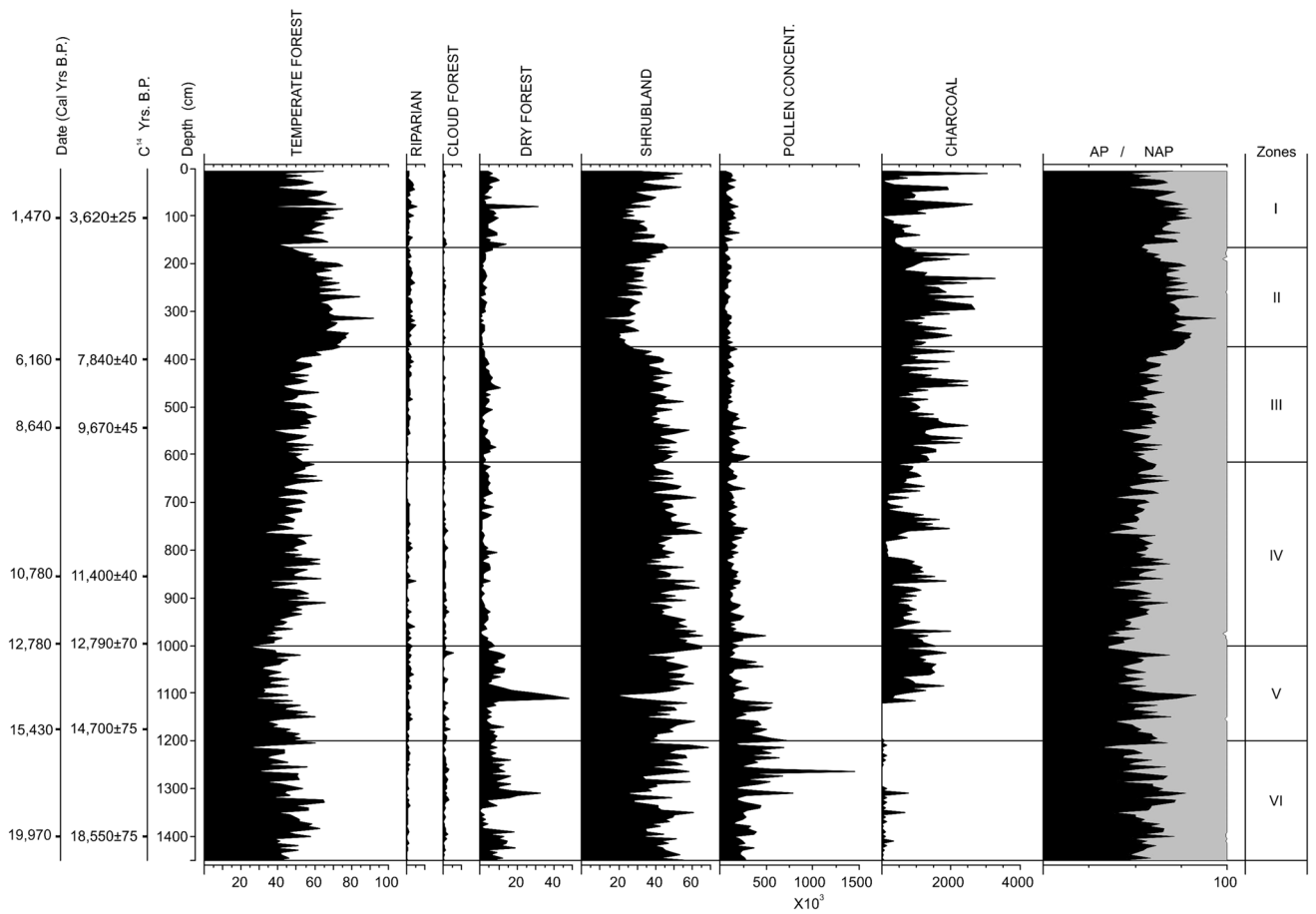


Fig. 4 Pollen summary of vegetation types from Rincón de Paranguero core

the largest peak in the whole core (Fig. 4). Several times, non-arboreal pollen (NAP) was dominant, indicating that the woodland cover was open, with mainly shrubs and herbs rather than trees (Fig. 4).

The concentration of charcoal was low during the Pleistocene. There were two small peaks of 500 particles/cm<sup>3</sup> (p/cm<sup>3</sup>) at 1,350 and 1,320 cm (ca. 18,700 and 18,000 cal BP). After these peaks, signs of fires disappeared from the record until ca. 16,700 cal BP (1,250 cm), when small peaks of charcoal reappeared.

#### Zone V (1,220–1,020 cm, 16,000–12,700 cal BP)

In this zone, the arboreal pollen (AP) increased in importance over NAP. The temperate vegetation showed three peaks at 1,200, 1,150 and 1,025 cm dominated by *Pinus*, which then decreased to 30–20%. *Abies* appeared in low proportions in the zone. *Quercus* maintained values between 10 and 15%. *Alnus* disappeared abruptly at 1,100 cm and remained at 5% in the rest of the zone. The dry forest taxa showed the largest input of the whole core with maxima of *Arecaceae* and *Prosopis* at this level. *Asteraceae* did not exceed 20%. *Poaceae* fluctuated between 15 and 10%, decreasing when *Asteraceae* increased. Total pollen concentration had a maximum of  $6 \times 10^5$  pollen grains/cm<sup>3</sup> (Fig. 4). This zone did not show any fire until 1,120 cm (ca. 14,300 cal BP), when particles of charcoal were recorded with values less than 1,500 p/cm<sup>3</sup>.

#### Zone IV (1,020–600 cm, ca. 12,700–9,000 cal BP)

At the beginning of the zone, there was more NAP than AP. *Pinus* recorded its lowest value for the last 21,000 years. *Alnus* kept a constant input in this zone. Traces of cloud forest taxa were recorded, including *Liquidambar*, *Fraxinus*, *Juglans* and *Taxodium*, while *Mimosoideae* and *Fabaceae* from the tropical forest were also recorded. *Asteraceae* showed an average input of 20%, while *Poaceae* peaked at 25%. Total pollen concentration had a maximum value of  $5 \times 10^5$  pollen grains/cm<sup>3</sup> at 970 cm, after which the concentration decreased ( $2 \times 10^5$  to  $1 \times 10^5$  pollen grains/cm<sup>3</sup>) (Fig. 4). Charcoal concentration at the beginning of the zone averaged 900 p/cm<sup>3</sup>, with three peaks of 2,000 p/cm<sup>3</sup>. Close to the end of the zone, charcoal decreased to 185 p/cm<sup>3</sup>, which was the lowest level recorded for this period.

#### Zone III (600–380 cm, ca. 9,000–5,800 cal BP)

NAP pollen values were greater than AP several times in this zone. Shrubland taxa peaked several times at 60% with a mean proportion of 40%. The taxa from the temperate forest had an increasing trend with maximum peaks of 60%. The increasing trend started with *Pinus*, which peaked several

times at 20%. *Quercus*, *Alnus* and *Abies* had values less than 10%. Elements from the cloud forest *Taxodium* and *Fraxinus* appeared as continuous trace values, while *Liquidambar* and *Juglans* were present on very few occasions. The dry forest taxa *Fabaceae* and *Ulmaceae* were the most important taxa in this zone and had a maximum input of 15%. *Myrica* appeared in this zone and *Condalia*, which had been present before, disappeared. The shrubland taxa peaked at 60% repeatedly, indicating drier conditions than those of the previous zone. However, *Asteraceae* decreased their input from 30% in the last zone to 5–10%. The values of *Poaceae* remained between 12 and 15%. Pollen concentration decreased but with maxima of  $3 \times 10^5$  pollen grains/cm<sup>3</sup> at 610 and 550 cm (Fig. 4). High charcoal concentration was observed. In this zone, fires became more intense, as indicated by large peaks of charcoal with values of over 2,000 p/cm<sup>3</sup> in several places, some of them coinciding with maxima in pollen concentration.

#### Zone II (170–380 cm, ca. 5,800–2,500 cal BP)

In this zone, changes in vegetation became more dynamic as important changes were observed in the pollen signal. The temperate taxa increased significantly, and the shrubland decreased. AP exceeded the NAP, with a *Pinus* peak at 320 cm reaching almost 60%; *Quercus* reached the highest input of the core at 40%; *Abies* peaked at 370 cm, reaching 10%. *Juglans* and *Liquidambar* completely disappeared from the pollen record. The tropical forest taxa like *Fabaceae*, *Mimosoideae*, *Myrica*, *Myrtaceae*, *Prosopis* and *Ulmaceae* were present at trace values. In this zone, the shrubland presented the minimum values of the whole core. *Asteraceae* never exceeded 5% and *Poaceae* 10%. Pollen concentration remained low, without significant peaks and with an average of  $75 \times 10^3$  pollen grains/cm<sup>3</sup> (Fig. 4). Important peaks of charcoal were observed and this zone had the greatest value of charcoal concentration of the whole Holocene, 3,700 p/cm<sup>3</sup>, and there were minor peaks of 2,700 p/cm<sup>3</sup> elsewhere in the zone.

#### Zone I (170–0 cm, ca. 2,500 cal BP–present)

In this zone, the shrubland taxa increased again, peaking at 40% at the base and 55% at the top of the zone. The taxon with the largest contribution was *Poaceae*, which reached 25% at 150 cm and 15% at the end of the zone. *Asteraceae* still had little input, with two small peaks at 10%. *Pinus* peaked repeatedly at 30% with a maximum value of 30% and *Quercus* peaked at 15% at 150 and 75 cm. There was an important increase in the tropical dry forest taxa, with a peak of 35%. There was a slight increase in pollen concentration (Fig. 4), reaching an average of  $1 \times 10^5$  pollen grains/cm<sup>3</sup>. The zone started with a low charcoal concentration, but after

that, fires peaked at 3,000, 2,000 and 3,500 p/cm<sup>3</sup> at the end of the zone. The last of these is the second-most intense charcoal peak recorded in the core.

## Discussion

The composition and structure of the vegetation based on the pollen diagrams from Rincón de Parangueo differed significantly in the Pleistocene from those in the Holocene. In general, the vegetation structure during the Pleistocene was woodland with taxa characteristic of cloud forests. During the Holocene, the vegetation changed to form a forest with a closed canopy of *Pinus* and *Quercus*.

### Climate, vegetation and disturbance during the late Pleistocene

During periods of glaciation, the cold climate allowed the snow line to descend about 500 m in the tropics (Broecker 2000; Lachniet and Vazquez-Selem 2005). The glacial advances and retreats that occurred during the late Pleistocene in Mexico (Vazquez-Selem and Heine 2004) influenced the flora in central Mexico and, more specifically, in Rincón de Parangueo. The vegetation change inferred from the fossil pollen record from this core closely follows glacial development (Vazquez-Selem and Heine 2004), winter precipitation (Bradbury 1997) and orbital forcing connections (Torres-Rodríguez et al. 2015).

In the late Pleistocene at 25,000–10,000 cal BP the climate was cold, caused by the last glacial advances (Lozano-García et al. 2005; Roy et al. 2009). Dry conditions then were inferred from the presence of open woodland with a high proportion of herbaceous vegetation (Lozano-García et al. 2005). In the Rincon de Parangueo fossil pollen record for the Last Glacial Maximum, the main herbaceous taxon is Asteraceae, which is more abundant than Poaceae. This pollen record also indicates that during the late Pleistocene the vegetation represented a cold and wet climate as has been described for Pátzcuaro (Bradbury 1997; Robles-Camacho et al. 2009). The climatic conditions were probably caused by enhanced winter precipitation (Bradbury 1997) or by a minimum spring insolation that decreased the evapotranspiration, increasing the humidity of the air and preventing the occurrence of fires (Torres-Rodríguez et al. 2015). These wet conditions allowed for the development of an analogue of cloud forest, with such mesic taxa as *Liquidambar*, Betulaceae, *Juglans* and *Fraxinus* on the lake shore and *Pinus-Quercus* forest in the hills.

The *Abies* forest, representing colder conditions, expanded for short periods during the late Pleistocene, particularly before 14,000 cal BP (Robles-Camacho et al. 2009). The shrubland dominated all of the late Pleistocene, apart

from at the end of the LGM when it falls to only 25%, which coincides with the peak of the temperate forest. The development of the cloud forest occurs mainly around the full LGM, and the end of the deglaciation is when the cloud forest has its highest value. *Liquidambar*, *Juglans* and *Fraxinus* indicate wet conditions in the area, as is characteristic of cloud forests around the world due to their prolonged immersion in orographic clouds (Luna et al. 1989; Welch et al. 2008).

The most striking feature observed during the LGM in the Rincón de Parangueo results, besides the presence of a cloud forest, is the high pollen concentration, which is related to a diverse and high biomass production ecosystem. Unlike the cores from central Mexico, where low pollen concentration characterized the late Pleistocene sediments (Lozano-García et al. 2005), the dominance of NAP taxa at Rincón de Parangueo is related to a cold and dry climate (Lozano-García et al. 1993; Caballero et al. 1999; Lozano-García and Vázquez-Selem 2005).

The presence of Betulaceae, *Abies* and, sporadically, *Liquidambar* indicate a cool and damp climate. The proportion of NAP during the LGM indicates the prevalence of herbaceous vegetation. The high abundance of taxa from herbaceous habitats, like Poaceae, Asteraceae and Cyperaceae, indicates that, despite the wet conditions, an open tree canopy prevailed in the area (Bradbury 1997; Metcalfe et al. 2007; Robles-Camacho et al. 2009). We assume the presence of a disturbed and open canopy woodland based on the records of modern pollen spectra from pristine temperate forest, where the proportion of NAP never exceeds 20% (Domínguez-Vázquez et al. 2004; Chang-Martínez and Domínguez-Vázquez 2013; Hidalgo-Juárez 2018); in our Rincón de Parangueo core the NAP is 50% most of the time.

Woodlands can have a variety of origins and are not necessarily the consequence of cold and dry climates. Open woodlands in Europe have been connected to the activity of megafauna (Vera 2000; Birks 2005; Corlett 2010). Mexico had a rich variety of megafauna, the remains of which have been found throughout the country in different environments, even associated with activities of early human populations (González et al. 2014, 2015). Our study site has not been the subject of palaeontological studies, but plenty of evidence of megafaunal remains has been found everywhere close to Rincón de Parangueo, mainly in the flood plain of Lago Cuitzeo and Rio Lerma, no more than 20 km away from our site (Marín-Leyva et al. 2015), which make very likely that large fauna like mammoths, mastodons and horses roamed and browsed the vegetation, and in so doing disturbed it (Solow et al. 2006). The structure of the vegetation observed in the pollen assemblage indicates that conditions were favourable for the development of a closed forest. But the constant disturbance by the megafauna is likely to have maintained a patchy environment of open vegetation (Janzen and Martin 1982; Vera 2000; Birks 2005; Johnson 2009;



Robles-Camacho et al. 2009), promoting a higher vegetation diversity than currently exists (Barnosky et al. 2016).

A similar situation may be indicated in Europe, where the presence of *Corylus* and *Quercus* in pollen records was associated with relatively closed woodland. However, this idea was challenged by Vera (2000), who argued that these trees were not able to regenerate in shady conditions and that the presence of megafauna would have prevented the development of a closed canopy (Janzen and Martin 1982; Vera 2000; Birks 2005; Vera et al. 2006; Soepboer and Lotter 2009). Grazing as part of herbivory is considered the main biotic factor affecting the structure and dynamics of vegetation (Kohler et al. 2004). Herbivory changes vegetation at different scales through the selective use of plants, according to herbivore preferences and plant palatability (Janzen and Martin 1982; Gill et al. 2009; Johnson 2009).

The megafauna would have shaped the spatial pattern of plants in the vegetation which relied on them for their dispersion, and causing a significant change in the forest structure after the disappearance of these animals (Janzen and Martin 1982; Barnosky et al. 2016). The distribution of the megafauna has been reported in various vegetation types in Mexico (Arroyo-Cabrales et al. 2007; Robles-Camacho et al. 2009; Marín-Leyva et al. 2015) without considering their effect on the vegetation during the Pleistocene. Despite the impossibility of reconstructing the effects of megafauna on the pattern of distribution and structure of past vegetation, we know from modern studies that herbivores promote diversity through disturbance, creating areas of differing habitats favouring diversity in the landscape (Johnson 2009; Zarekia et al. 2013). The disturbance produced by extant megafauna in the African savannas has been described extensively (van der Waal et al. 2011).

The Pleistocene–Holocene fauna were distributed over a migration corridor of several lake basins. The corridor that occurred along the Valle de Santiago fault enabled a constant movement of megafauna along the hill borders of the volcanoes toward wetter lakeside environments at Lago Cuitzeo, 20 km south of the Rincón de Parangueo crater. Thousands of charred bones of several genera of mega and micro mammals have been found there overlain by an organic charcoal stratum. This black mat lies 2.80 m. under the lake bed of the northeastern border of Lago Cuitzeo and it was dated to 12,800 cal BP (Israde-Alcántara et al. 2012), coinciding with a pulse of high ignition from an airburst impact from the explosion of an incoming meteor (Israde-Alcántara et al. 2012; Wolbach et al. 2018). Evidence of this impact has been found covering megafauna remains at several sites, coinciding with a megafauna decline between 13,000 and 11,000 years ago in South America (Raczka et al. 2017), Asia and North America (Wolbach et al. 2018). The rapid climate change between 13,000 and 11,000 cal BP probably disrupted the abiotic and biotic composition of several

ecological niches with a regional replacement or almost extinction of major species of megafauna in central Mexico.

The disturbance produced in the vegetation by the megafauna ceased with their extinction (Janzen and Martin 1982; Johnson 2009; Corlett 2010). This caused a change in composition and structure of vegetation; arboreal pollen started to dominate NAP. At the end of the Pleistocene, wetness that caused the accumulation of plenty of fuel and prevented the occurrence of fires decreased during the Holocene, and the resulting warmer and drier conditions allowed intense and frequent fires in the area during the Pleistocene–Holocene transition which continued and intensified throughout the Holocene.

### The Holocene in the Bajío area

At the beginning of the Holocene, the forest structure and composition changed as the climate became warmer, mesophilous taxa started to disappear and tropical elements became dominant. This was in accordance with the wet conditions prevailing in the Cariaco basin (Haug et al. 2001), which in central Mexico had a warm climate (Lozano-García et al. 2005; Borejsza and Frederick 2010; Correa-Metrio et al. 2012). According to our results, the last record of *Liquidambar* occurred at 8,500 cal BP. *Quercus*, favoured by the warm and drier conditions, increased in short intervals, which coincides with the findings of Park et al. (2010) in the area. These warmer conditions are also implied by the increase in Mimosoideae and *Alnus*. Asteraceae started to decline while, in accord with the new environmental conditions, Poaceae started to increase and continued to do so throughout the late Holocene.

During the middle Holocene, it is evident that the area became significantly dryer (Park et al. 2010), favouring the presence of a dry forest with pyrophilous taxa like *Pinus*, *Quercus* and Mimosoideae, which are resistant to frequent fires (Domínguez Vázquez and Islebe 2008). Asteraceae decreased, while Poaceae, more resistant to desiccation, were favoured by the frequent fires. Findings at Santa Cruz (Lozano-García et al. 2005) describe similar pollen assemblages to those at Rincón de Parangueo, with an increase in forest taxa, charcoal and a decrease in herbaceous pollen, but with a higher total pollen concentration of herbaceous taxa during the Holocene than during the Pleistocene.

Ca. 6,000 cal BP, with humans already settled in the area (Butzer and Butzer 1997), the vegetation changed. Forest is indicated by the dominance of AP (Park et al. 2010). Close to the lake, there was a tropical forest of Mimosoideae and *Prosopis*, whilst *Pinus* and *Quercus* remained on the rim of the crater and in the hills. Unlike Park et al (2010), we consider that *Pinus* grew locally in the crater. We base our assumption on modern pollen studies in the region (Raygadas-Torres 2011; Chang-Martinez and Domínguez Vázquez

2013), that showed that the *Pinus* pollen proportion is related to the distance of the source. Besides, the local presence of *Pinus* is explained by the dry conditions that were affecting the area and which allowed frequent fires as observed in our Parangueo record. Fires promoted the regeneration of resilient taxa like *Quercus*, Mimosoideae and *Pinus*. *P. oocarpa* Sch. ex Schl. and *P. devoniana* Lindl., which currently grow in the Bajío, regenerate well in burned sites (Rodríguez-Trejo and Fulé 2003). *Pinus* dominance during the middle and late Holocene has also been reported in cores from central-west Mexico, where *Pinus* has been the taxon dominant from 4,200 cal BP (Figueroa-Rangel et al. 2008).

During the last two millennia, the climate has become strongly seasonal, as is observed in short cores from the area (Kienel et al. 2009; Park et al. 2010). Together with cultural activities, the consequences on the vegetation are evident (Oldfield and Dearing 2003; Caballero-Rodríguez et al. 2018), although we did not find pollen grains of *Zea mays*. Park et al. (2010) found evidence of early agriculture at ca. 5,700 cal BP, which coincides with the finding of early agriculture at ca. 6,000 cal BP with large quantities of pollen of *Cucurbita* in a core collected from another maar, La Alberca, 10 km away from Rincón de Parangueo (Castro-López 2013). *Quercus* expanded during the first part of the late Holocene, but as human influence intensified in the area, the distribution of oak increased or decreased according to the level of human activities; *Quercus* is the main wood used for fuel in traditional rural communities. At 1,500 cal BP, short maxima in Mimosoideae, Fabaceae, Asteraceae and *Taxodium* were observed, which can be connected with a short change to wet and warm conditions that coincided with the European medieval warm period (Metcalf et al. 2010).

## Conclusions

In conclusion, our analysis of the pollen from Rincón de Parangueo has demonstrated the significant interaction of climatic fluctuations as an important factor for the expansion and contraction of particular vegetation types. Disturbance, likely caused by the effect of extinct megafauna, was also an important factor in shaping the structure and composition of the vegetation and the promotion of vegetational diversity during the late Pleistocene. We have concluded that environmental conditions during the late Pleistocene were wet and cold. Coolness and moisture were the dominant conditions in the zone until 8,500 cal BP, when *Liquidambar* disappeared. Warm and dry conditions arrived after ca. 6,000 cal BP, with a strong change in pollen assemblage. The climate became warmer and drier in the late Holocene, with wet and dry spells and a strong alteration of the environment by humans.

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