The Holocene

Climatic and anthropogenic influences on vegetation changes during the last 5000 years in a seasonal dry tropical forest at the northern limits of the Neotropics.

Journal:	*The Holocene*
Manuscript ID	HOL-20-0123.R1
Manuscript Type:	Paper
Date Submitted by the Author:	25-Nov-2020
Complete List of Authors:	Lozano-Garcia, Socorro; Universidad Nacional Autonoma de Mexico, Dinámica Terrestre Superficial; Centro Universitario de la Costa Sur, Universidad de Guadalajara, Departamento de Ecología y Recursos Naturales Figueroa-Rangel, Blanca; Universidad de Guadalajara, Department of Ecology and Natural Resources Sosa-Nájera, Susana; Universidad Nacional Autonoma de Mexico, Dinámica Terrestre Superfical Caballero, Margarita; Universidad Nacional Autonoma de Mexico, Laboratorio de Paleolimnología Noren, Anders; University of Minnesota, LRC Metcalfe, Sarah; University of Nottingham, School of Geography Tellez-Valdés, Oswaldo; Universidad Nacional Autónoma de México, Facultad de Estudios Superiores, Campus Iztacala Ortega-Guerrero, Beatriz; Universidad Nacional Autonoma de Mexico, Instituto de Geofísica
Keywords:	palynology,, tropical dry forest, drought, Hill numbers, diversity, western Mexico
Abstract:	Seasonal dry tropical forest (STDF) is a widespread vegetation type in western Mexico. Generally, this type of forest develops in semihumid habitats where lacustrine basins are scarce, preventing documentation of the vegetation history and forest dynamics using a paleoecological approach. Here, we present a palynological record from the Santa Maria del Oro crater lake, located within the distribution area of the STDF and the adjacent dry oak forest which gives insight into the changes in diversity and human impact at this tropical site. Pollen data, in combination with geochemical analysis and microcharcoal data from a lacustrine sequence, are used to discuss vegetation change and diversity in the plant assemblages related to drought or anthropogenic activity over the last 5000 years. Our results show three distinct periods of drought in the basin, from 4200–3850, 3100–2300, 1570–1100, and 300 cal yr BP, with changes in vegetation composition mainly related to a decrease in taxa diversity during these periods. Based on the presence of maize pollen, two periods of human activity (3790–2160 and 280 cal yr BP to present) were detected with an increase in herbaceous pollen used as a surrogate for deforestation. These two disturbance periods, pre-

	Columbian and postcolonial, occurred during wet conditions in the basin. Our results highlight the correlation between El Niño events, drought, and fire with changes in the composition and diversity of STDF.

Climatic and anthropogenic influences on vegetation changes during the last 5000 years in a seasonal dry tropical forest at the northern limits of the Neotropics.

Socorro Lozano-García,[1] Blanca Figueroa-Rangel,[2] Susana Sosa-Nájera,[3] Margarita Caballero,[1] Anders J Noren,[4] Sarah E Metcalfe,[5] Oswaldo Tellez-Valdés,[6] Beatriz Ortega-Guerrero.[2]

[1]Departamento de Dinámica Terrestre Superficial, Instituto de Geología, Universidad Nacional Autónoma de México. (UNAM), Ciudad Universitaria, México

[2]Departamento de Ecología y Recursos Naturales. Centro Universitario de la Costa Sur, Universidad de Guadalajara, Jalisco, México

[3]Laboratorio de Paleolimnología, Instituto de Geofísica, Universidad Nacional Autónoma de México. (UNAM), Ciudad Universitaria, México

[4]LacCore and Continental Scientific Drilling Coordination Office, Department of Earth Sciences, University of Minnesota Twin Cities, Minneapolis, USA

[5]School of Geography, University of Nottingham, UK

[6]Unidad de Biotecnología y Prototipos (UBIPRO), Facultad de Estudios Superiores, Campus Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Los Reyes Iztacala, 54090 Tlalnepantla, Estado de México, México

Abstract

Seasonal dry tropical forest (STDF) is a widespread vegetation type in western Mexico. Generally, this type of forest develops in semihumid habitats where lacustrine basins are scarce, preventing documentation of the vegetation history and forest dynamics using a paleoecological approach. Here, we present a palynological record from the Santa Maria del Oro crater lake, located within the distribution area of the STDF and the adjacent dry oak forest which gives insight into the changes in diversity and human impact at this tropical site. Pollen data, in combination with geochemical analysis and microcharcoal data from a lacustrine sequence, are used to discuss vegetation change and diversity in the plant assemblages related to drought or anthropogenic activity over the last 5000 years. Our results show three distinct periods of drought in the basin, from 4200–3850, 3100–2300, 1570–1100, and 300 cal yr BP, with changes in vegetation composition mainly related to a decrease in taxa diversity during these periods. Based on the presence of maize pollen, two periods of human activity (3790–2160 and 280 cal yr BP to present) were detected with an increase in herbaceous pollen used as a surrogate for deforestation. These two disturbance periods, pre-Columbian and postcolonial, occurred during wet conditions in the basin. Our results highlight the correlation between El Niño events, drought, and fire with changes in the composition and diversity of STDF.

Keywords: palynology, tropical dry forest, drought, Hill numbers, diversity, western Mexico

Introduction

Seasonally dry tropical forests (SDTF) are one of the most diverse and widespread vegetation types in the dry tropics (Pérez-García et al., 2012), inhabited by plant types that are adapted to an extended dry season (4 to 8 months). This vegetation is characteristic of the lowlands (<1400 m a.s.l.) in the northern Neotropics (Rzedowski, 1978), forming an almost continuous band from southern Sonora to central America (Pennington et al., 2000; Rzedowski and Calderon de Rzedowski, 2013). This vegetation generally grows on moderate to steep slopes in warm sub-humid climates, with annual mean precipitation less than 1600 mm/yr, mean annual temperatures between 17 and 27.4 °C (Jansen, 1988; Pennington et al., 2000; Trejo and Dirzo, 2002). It poses high turnover rates, suggesting high local diversification (Rzedowski, 1962, 1991).

According to Rzedowski (1991), SDTF distribution in Mexico encompasses high diversity with 60% of endemic species and 11% of endemic genera. The high diversity can be related to the complex geologic and phytogeographical history of the region (Kohlmann and Sánchez-Colón, 1984). Time-calibrated molecular phylogeny studies of *Bursera*, a dominant member of the STDF, suggest that the establishment of the STDF in western Mexico occurred 30 to 20 Ma, corresponding with the formation of the Trans-Mexican Volcanic Belt (TMVB) and the Sierra Madre Occidental (Becerra, 2005). It has also been suggested that climate changes during the Pleistocene drove fragmentation and expansion processes associated with plant speciation (Pennington et al., 2000; Trejo and Dirzo, 2002). Nonetheless, research on the vegetation history and forest dynamics of SDTF in western Mexico during the Holocene using a paleoecological approach is limited.

One of the reasons for the lack of paleoecological studies related to STDF is the paucity of lacustrine basins with good pollen records and, the use of forest hollows to reconstruct vegetation using fossil pollen, is challenging due to the sub-humid climate habitats where this forest develops.

Lacustrine sediment sequences provide information regarding past landscape changes. These natural terrestrial archives offer information regarding changes in plant communities, hydrological and depositional conditions, and climate change. Due to the complex geological history of the TMVB, many of lakes have formed since the Neogene and efforts have been made to reconstruct the Pleistocene and Holocene environmental history based on the study of sediment cores from lakes in this region. The Holocene palynological records from the central region of the TMVB mainly focused on temperate ecosystems, documenting changes in plant composition and distribution in response to several drivers such as climate variability, (eg, ENSO, droughts), and other disturbances like early agriculture, deforestation, and fires. During early Holocene (11,700–8200 cal yr BP), a trend to low lake levels and saline environments in several lacustrine records of the TMVB have been recognized, this condition has been associated to high summer insolation (Bhattacharya et al., 2017; Del Castillo-Batista et al., 2018; Figueroa-Rangel et al., 2008; Lozano-García and Vázquez-Selem, 2005; Lozano-García et al., 2020); Park et al., 2010). By mid-Holocene (8200–4200 cal yr BP), some records with low lake levels showed a recovery (Caballero et al., 2002; Lozano-García et al., 2013; Vázquez et al., 2017) ; at some sites freshwater conditions were documented although no paleolimnological records are available for the western end of the TMVB. For late Holocene (4200 cal yr BP to the present), a dry period that started at the end of the mid-Holocene, continue until 3000 to 2000 cal yr BP; after this period, a slight recovery in lake levels, is detected. According to the records, another dry period occurs at around 1.5 cal yr BP (AD 600) to 0.8 cal yr BP (AD 1100) that correlates with the demise of Mesoamerican cultures Lozano-Garcia et al., 2020). For the western tropical end of the TMVB, scarce palynological Holocene records are available regarding climate variability and long-term vegetation changes (Brown,1985). A trend towards drier conditions together with the occurrence of agriculture activities are documented from Lago Guzman; pollen data suggests drier conditions and agriculture at 750 cal yr BP (AD 1200) and for Laguna San Pedro pollen record, lying within the STDF zone, shows a period of dry conditions and or agriculture from 3000 yr BP to ca 800 yr BP (1050 BC to AD 1150) although interpretation is problematic due to low resolution in pollen counting (Brown, 1985). The Santa Maria del Oro (SMO) is a crater lake located at the northern limits of the Neotropics, it lies in the western portion of the TMVB, at the intersection of the TMVB and the Sierra Madre Occidental (Figure 1a); it represents a suitable site to study SDTF evolution given its location at the climatic boundary between the northern Mexico arid climates and the temperate sub-humid to humid climates of central Mexico. Previous paleoecological studies of lacustrine sediments in SMO using diatoms and ostracods, along with magnetic mineralogy and inorganic geochemistry, have provided evidence on significant environmental changes during the last 2000 years, particularly those regarding climate change and human impact (Rodríguez-Ramírez et al., 2015; Vázquez-Castro et al., 2008); however, there are no paleoecological records of the tropical plant communities around the basin and their responses to climate variability and human disturbances. Therefore, the main aim of this study was the reconstruction of plant assemblages in SMO in order to answer the following questions: i) based on taxa composition, was the SDTF an stable plant community over the last 5000 years?, ii) is the plant community responding to periods of climate change (droughts) and/or to anthropogenic activity? and iii) what were the main drivers climate change?

Study Site

SMO crater lake is located in west-central Mexico (21°22′N, 104°34′W at 730 m a.s.l.), 65 km from the Pacific coast in the state of Nayarit (Figure 1a). The crater walls are dacitic-rhyolitic in composition with some basaltic flows on the northern slopes. According to Vázquez-Castro et al. (2008), the crater is probably of Pleistocene age based on its alignment with other volcanic cones in the area. The lake inside the crater is almost circular, with an area of 3.7 km^2 and a maximum depth of 65 m (Caballero et al., 2013; Serrano et al., 2002). Most of the lake lacks a shallow littoral zone because the crater walls are very steep down to the bottom of the lake, which is nearly flat (Figure 1b).

Previous paleoenvironmental studies based on magnetic mineralogy, geochemistry, diatoms, and ostracods were undertaken on a littoral core (SMO02V, 880 cm) (Fig. 1b) retrieved from a small shallow (< 20 m) bay in the southwestern part of the lake (Rodríguez-Ramirez, 2015; Vázquez-Castro et al. 2008). Another sediment sequence was retrieved from the central flat area (MOLE SMO03, 894 cm), for which geochemical data have been published for the top 160 cm (Sosa-Nájera et al., 2010) and shown in Figure 1b. The lake is warm monomictic with stable stratification for 9 to 10 months; the water is slightly alkaline with a pH of 8.6 and evidence of evaporative concentration, Ca^{2+} depletion, and Cl^- enrichment of lake waters (Caballero et al., 2013).

The modern climate in SMO is tropical sub-humid with predominantly summer precipitation. Mean annual precipitation is 1214 mm, and the rainy season occurs from June to October responding to the northward migration of the Intertropical Convergence Zone (ITCZ) and the onset of the North America Monsoon (NAM) system. Precipitation in western Mexico is modulated by the ITCZ position and the intensity of NAM (Metcalfe et al., 2015). Summer precipitation is reduced during El Niño events in central and southern Mexico and the Pacific coast of Central America (Castro et al., 2001; Magaña et al., 2003). The dry season lasts between 5 and 8 months. The mean annual temperature is 21°C with monthly mean temperatures ranging from 16.6°C (January and February) to 25°C (June and July) (SMN, 2019, 18005-Cerro Blanco meteorological station).

At present, SMO is surrounded by SDTF, a deciduous community that loses its leaves for 5 to 8 months each year (Figure 1c and 1d). Tree species include *Bursera simaruba* (L) Sarg., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Piscidia piscipula* Sarg., *Pseudobombax ellipticum* (Kunth) Dugand., *Haematoxylum brasiletto* H. Karst., *Parkinsonia praecox* (Ruiz&Pav.) Hawkins, *Lysiloma acapulcense (Kunth)* Benth., *Alvaradoa amorphoides* Liebm., *Diphysa suberosa* S. Watson, and *Guettarda macrosperna* Donn.Sm. Sub-deciduous Tropical forest (SDTF) elements are present in ravines with tree species such as *Acacia polyphylla* DC., *Astronium graveolens* Jacq., *Brosimum alicastrum* Sw., *Ceiba pentandra* (L.) Gaertn., *Cocoloba barbadensis* Jack., *Ficus glabrata* Kunth, *Lonchocarpus hermannii* M Sousa, and *Randia armata* (Sw.) DC.. Numerous vines plants and epiphytes are important elements as well (Tellez, 1995). Oak tropical forest is conspicuous on the steep northern slopes with *Quercus castanea* Née as the dominant species, and common shrubs including *Acaciella angustissima* (Mill.) Britton& Rose, *Acacia tequilana* S. Watson, *Bolanosa coulteri* A.Gray, *Rhamnus palmeri* S. Watson, *Tephrosia sinapou* (Buc´hoz) A. Chev, and *Mimosa somnians* Humb. & Bonpl. Ex Willd. Herbaceous cover is highly diverse with species belonging to the Leguminosae and Asteraceae species such as *Desmodium angustifolium* (Kunth) DC., *D.cinereum,* . Poepp. Ex Grisb. *Eriosema multiflorum* Robinson, *Crotalaria micans* Link, *Tephrosia nicaraguense* Oerst., *Tagetes lucida* Cav., *Verbesina tequilana* J.R. Coleman, as well as numerous graminoids (Tellez, 1995).

Archaeological framework

Some of the earliest human remains in western Mexico belongs to Matanchén bay (Nayarit), dating back to 2200-1730 BC (Williams, 2020) and, according to Mountjoy (2015), there is an archaeological gap between the last Archaic record and the first dates of the Formative period (1500 BC–AD 300). For west Mexico, the first farmer groups of the Middle Formative period (1200 BC arrived into an uncolonized territory (Mountjoy, 2015), while sedentary groups appear to establish during a period of wet conditions (Beekman, 2010). Maize pollen found in lake sediments from Laguna San Pedro in the Nayarit state, indicates agriculture activities at ca. 3000 yr BP to ca 800 yr BP (1050 BC to AD 1150 (Brown, 1985)). During the Classic period (AD 300-900), considered as the cultural blooming of the Maya region and central Mexico civilizations, the western area of Mesoamerica also shows a cultural development; this region played an intermediary role between central and southern Mesoamerica (Williams, 2020). Several records indicate that the late Classic (600–1000 AD) was a period of significant droughts and extreme changes, with the decline of the Teotihuacan city-state (Park et al., 2019). For the western region, there is evidence of decreases in human occupation (Beekman, 2010; Vazquez-Castro et al., 2019). This trend continues during the early Postclassic (1000–1522 AD) with the abandonment of ceremonials sites but with the rise of the Pacific Coast communities, which developed intensive floodplain agriculture and significant technological advances such as metallurgy (Beekman, 2010). Soon after the Spaniards arrival (1532), western Mexico was recognized as a mineral-rich area and a series of roads and bridges were constructed in the XVII century for silver and gold exploitation. During the XVIII century, near the town of Santa Maria del Oro, gold mining was carried out and this activity continues until today.

Material and Methods

Sample collection and Chronology

Sediment cores were taken from the central part of the lake (57 m deep; 21°21.901'N, 104°34.093'W) (Fig. 1) using the Kullenberg coring system from the National Lacustrine Core Facility (LacCore) at the University of Minnesota. Three continuous parallel cores 1A, 1B and 2A, 6.2 m, 7.3 m and 8.2 m deep respectively, and one short core 1BM (71 cm) were retrieved and transported to LacCore for documentation including high-resolution photographs, magnetic susceptibility, and density measurements. A master sequence (MOLE-SMO03, 894 cm long) was constructed by visual comparison of high-resolution photographs and magnetic susceptibility data of the four cores. Sediment sub-sampling for pollen and other proxy analyses was done only down to 868 cm depth at LacCore at approximately 10 to 12 cm intervals.

The chronological model was established based on seven radiocarbon dates (Table 1), assuming that the top of the sequence dates to the year of core collection (i.e., 2003). Samples for age determination were dried and sent to Beta Analytic for AMS radiocarbon dating. Dates were calibrated with IntCal13 (Remier et al., 2013) and an age-depth model was elaborated with the Bacon-v2.3.3 (Blaauw and Christen, 2011) package available in R v3.4.3 (R Development Core Team, 2017) using Bayesian statistics .

Geochemical analysis

The MOLE-SMO03 master sequence sediments down to 761 cm, were analysed using an ITRAX X-ray sediment core scanner at 1 mm resolution at Southampton University, UK. For this study we only selected Ti and Ca data, and the intensities data count per second (cps) were transformed to percentages following the protocol established previously by Sosa-Najera et al. (2010). This transformation was based on a linear regression between the cps data and elemental concentration of selected samples that were analysed using traditional XRF equipment (Siemens SRS 3000) at the Institute of Geology, UNAM (Sosa-Nájera et al., 2010). Titanium is an insoluble element present in minerals of catchment rocks and it was used as a run-off indicator (Metcalfe et al., 2010; Sosa-Nájera et al., 2010). Sources of Ca are the catchment rocks and authigenic carbonates. Previous studies in SMO lake (Rodríguez-Ramírez et al., 2015; Sosa-Nájera et al., 2010) demonstrated that higher Ca concentrations are related to historical droughts; they used Ca normalization against Ti to reduce the detritical input signal in the detection of drought periods.

Pollen and microcharcoal analysis

Samples for pollen extraction were analysed only down to 868 cm depth because of poor preservation in the calcareous laminations at depths > 868 cm in the MOLE-SMO03 master sequence. Sixty-three 0.5 cm^3 sediment samples were processed for pollen extraction according to Batten (1999), including the addition of two *Lycopodium clavatum* spore tablets for pollen concentration calculations. Residues were mounted in glycerin jelly and examined with a Zeiss microscope at 40x and 100x. We counted 400 pollen types, excluding tracer spores, pollen of aquatic taxa, fern spores, microalgae, and testaceae. The pollen assemblage included terrestrial pollen types. Identification was undertaken using comprehensive pollen reference collection from the Laboratorio de Paleoecología, Paleoambientes y Cambio Climático at UNAM which included regional material from a vegetation survey undertaken in the SMO basin in 2004 (Supplementary material). Charcoal particles >100 μm were counted on the pollen slides to calculate concentration (particles/cm3).

Statistical analysis

Tilia software (Grimm, 1991) was used to generate the percentage pollen diagrams and concentration calculations. Four zones were established based on a stratigraphically constrained cluster analysis (CONISS, Grimm, 1987) of the pollen taxa with percentages >1%, and including only trees, herbs, fern spores and pollen types (Figure 3).

Taxa diversity was estimated using four diversity metrics:

a) Hill Numbers (Hill, 1973) were estimated as follow: (a) Hill N0: the number of species (S) found in a sample regardless of their abundance; (b) Hill N1: the exponential of the Shannon-Weaver diversity index represents the number (abundance) of taxa in each sample and weighting each taxon by its relative abundance; (c) Hill N2: the inverse of Simpson's index and representing the number of very abundant (dominant) fossil pollen taxa (Gotelli and Ellison, 2013). Evenness was estimated as the ratio N2/N0, the dominant taxa relative to all taxa.
b) Rate of Change: estimated using the Bray-Curtis dissimilarity index to calculate the dissimilarities between two pairs of samples to record changes over time.

Hill Numbers and rate of change were estimated using the vegan package (Oksanen et al., 2018) available in R-v3.4.3 (R Development Core Team, 2017).

To identify the temporal correlation of anthropogenic activity, drought occurrences, and changes in the plant assemblages of the dry tropical forest, cross-correlation analysis was performed between *Quercus* and *Zea mays* with Ca/Ti as a proxy of high evaporation rate and low precipitation (Rodriguez-Ramírez et al., 2015). Cross-correlation analysis was also carried out between the metrics (N0, N1, and N2) with Ca/Ti, and microcharcoal particles with *Zea mays* and the three-diversity metrics; significant cross-correlation were tested at 95% confidence level. The analyses were developed with the cross-correlation function (CCF) available in R-v3.6.0 (R Development Core Team, 2019).

Results

Core description and age model

According to the age model, the base of the core (894 cm) was determined to be ca. 5000 cal yr BP, with a mean sedimentation rate of ~2 mm/yr and an average pollen sample resolution of ~80 years (Figure 2).

The sediments are characterised by banded to laminated calcareous muds, fine sands, dark organic muds (sapropels), and clayey diatomaceous mud, with characteristic bundles of ~5–30 calcareous laminae separated by 2–8 cm of massive brown silt and fine sands, allowing for correlation between the four cores.

X-Ray Fluorescence (XRF)

Titanium varied along the core from 0.17 to 0.83%, with values generally lower than average (<0.40%) between 761 and 688, 560–410, and 330–110 cm; higher than average values corresponding to 690– 580, 375–320, and 57–45 cm. The Ca/Ti ratio, with an average of 20.8, ranged between 8 and 101; values between 48 to 101 were present from 722–658 cm, 320–240 cm, 27 cm and the top 10 cm (Figure 4).

Pollen record

Pollen composition comprised 88 taxa identified at genera or family level; they included 21 arboreal pollen and 53 non-arboreal pollen (36 herbaceous, 17 fern spores and 14 aquatics-not presented in this work) (Table 2). Besides, 24 taxa were counted as pollen types and 9 taxa as fern spore types. The pollen stratigraphy is presented in percentages showing the downcore changes (Figure 3). Based on the CONISS cluster analysis (Grimm, 1987), the sequence from SMO can be divided into four pollen zones (SMO-1 to SMO-4), one of which is subdivided (Figure 4) into two subzones (SMO-2a and 2b).

SMO-1: 868–656 cm (4940–3800 cal yr BP). Pollen percentages are dominated by *Pinus* (40%), *Quercus* (45%), Moraceae (10%), and *Bursera* (5%), with Poaceae (70%) and Amaranthaceae (8%) as the most important herbaceous pollen. The first occurrence of maize pollen corresponds to the sample at 656 cm (3990 cal yr BP). The highest concentrations of charcoal (1500 particles/cm^3) were recorded at the base of the zone, with a trend towards lower values with fluctuations.

SMO-2: 623–220 cm (3600–1063 cal yr BP) is primarily characterised by a continuous increase in herbaceous pollen percentages. This zone is subdivided into two subzones:

> **Subzone SMO-2a:** 623–321 cm (3593–1797 cal yr BP) is represented by a sudden increase in Moraceae (20%) at the base of the subzone, a reduction in *Quercus* percentages (mostly below 20%), and an increase in Poaceae (52%), Asteraceae (25%), and *Ambrosia* (9 %) with the continuous presence of maize. Higher values in charcoal concentration are reached in the middle and the upper part of this subzone, after a decline at the base.
>
> **Subzone SMO-2b:** 270–220 cm (1450–1063 cal yr BP). Pollen percentage spectra are dominated by *Quercus* (28%), *Pinus* (13%), and Poaceae (44%) together with a decline of Asteraceae (7%), Amaranthaceae (10%), and

Ambrosia (1.7%). The absence of maize differentiates this subzone, and charcoal concentration declines considerably compared to the previous subzone SMO-2a.

SMO-3: 212–78 cm (998–317 cal yr BP). Pollen spectra show a decline in *Quercus* (19%) and herbaceous taxa such as Poaceae, Asteraceae, and Amaranthaceae, while other taxa increase: *Pinus* (16%), Moraceae (12%), *Brosimum* (4%), *Bursera* (3%), *Poulsenia* (4%), and Piperaceae (7%). Maize was only recorded at 176 cm; charcoal concentrations continued with values from 1200 to 7000 particles. *Quercus* and Poaceae increase their percentages in the last two samples.

SMO-4: 69.2 cm (279–3 cal yr BP). A sudden increase in Amaranthaceae (40%) and Asteraceae (20%) and a decline in Poaceae (18%) with the continuous presence of maize characterises this zone. Microcharcoal concentrations are similar to SMO-3.

Taxa diversity

Hill number N0, which expresses the effective number of pollen taxa, varies through the sequence (with a 95% confidence interval) from 28 to 31 taxa; lower numbers (23 and 21 pollen taxa) corresponded to SMO-1 and SMO-2b pollen zones, respectively, and the highest number (43 pollen taxa) was found at SMO-3 (Figure 4).

Both N1 and N2 showed the same pattern of peaks and drops along the sequence; low values (4 to 11 pollen taxa) were observed in all pollen zones, except in SMO-3 where they presented the highest values (10 to 18 pollen taxa). N1, which counts taxa equally in proportion to their abundance, varied slightly from only 8 to 9 taxa; N2, which gives greater weight to the most abundant taxa, oscillated from 5 to 6 taxa (Fig. 4).

Rate of change

The rate of change based on the pollen data was low (<0.1) in SMO-1 and in most of SMO-2a with an increase at 1800 cal yr BP; lower values (0.05) were also present in SMO-2b. An increase in vegetation turnover was recorded in SMO-3, with a maximum (0.3) at 600 yr cal BP. The rate of change decreased in the first section of zone SMO-4 (between 0.1 and 0.2) while an abrupt increase (0.4) was evident in the last section of this zone.

Cross-correlation

Cross-correlation results (Figure 5) revealed a positive correlation between *Quercus* and Ca/Ti at lag 0, indicating that they change together. Correlation between Ca/Ti and the diversity metrics (N0, N1, N2) is negative, so an increase in Ca/Ti coincides with a decrement in N0, N1, and N2. The same pattern of negative correlation was obtained between charcoal concentration with *Zea mays*, N0, N1, and N2 indicating that they shift inversely at the same time. Also, a negative correlation was obtained between *Zea mays* and the Ca/Ti ratio.

Discussion

Vegetation change during the last 5000 years

The 5000 years pollen record of SMO provides historical information on the evolution of the SDTF that grows at the northern limit of the Neotropics and also provides an insights of the evolution of the tropical oak forests adjacent to the SDTF. The fossil pollen assemblage in the small SMO basin was a combination of the SDTF and SCTF represented by a mixture of tropical taxa with relatively low pollen percentages (< 5%) (eg, Bombacaceae, *Heliocarpus*, *Poulsenia)* and the dry tropical oak forest. In many of the tropical taxa pollination is entomophilous, causing these taxa to be poorly represented in the pollen spectra. On the other hand, anemophilous taxa such as *Quercus* and *Pinus* showed the highest percentages in the sedimentary record.

Pollen spectra from ca*.* 4940–3800 cal yr BP have a distinct signal with high percentages (60–70%) of *Quercus* and *Pinus*, while herbaceous pollen such as Asteraceae and Amaranthaceae showed low values; Poaceae had values of 30% except for two peaks. At present, pine forests and mixed pine-oak forests are the dominant vegetation in the highlands of central Mexico. Studies from several lake sequences, reconstructing Pleistocene and Holocene history, report *Pinus* with percentages fluctuating from 60 to 90% (Lozano-García et al., 2005; Park et al., 2010; Ruiz-Córdova et al., 2019; Torres-Rodríguez et al., 2012). In comparison, *Quercus* pollen generally ranged between 10 and 30%. Currently, on the northern slopes of SMO basin, oak groves are dominated by *Quercus castanea.* Therefore, late Holocene fossil pollen spectra in this study point to a larger presence of this plant community at the site. This agrees with evidence on the permanence of a large population of *Q. castanea* in the TMVB since the Pleistocene (Peñaloza-Ramírez et al., 2020).

On the other hand, *Pinus* is absent from the present-day vegetation of the SMO basin, although a few *Pinus* individuals were observed on the eastern slopes outside the SMO basin. Studies involving the floristic composition of oak forests in the state of Nayarit, where SMO lake is located, reported the occasional presence of *Pinus* individuals along with several oak species (Tellez, 1995).

Changes in the pollen spectra between 3800 and 1700 cal yr BP show an increase in non-arboreal pollen, and high values of Poaceae, Asteraceae, Amaranthaceae, and *Ambrosia,* along with the presence of maize pollen (the first record was observed at 3900 cal yr BP). These pollen assemblages evidence that human activities started in the catchment of SMO around this time. We hypothesise that the reduction in the percentages of *Pinus* observed after ca. 4000 cal yr BP in the pollen diagram could be associated with the initiation of human impact in the region that resulted in logging targeting the extraction of wood from the *Pinus* species.

The herbaceous assemblage (*Ambrosia*, Asteraceae, and Poaceae) reduced their percentages between 1500 and 300 cal yr BP. In the first part of this period, between 1500 and 1000 cal yr BP, Poaceae continued with high values and only *Quercus* showed an increase in values. The rate of change was higher from 1000 to 300 cal yr BP) (Fig. 4), Poaceae and *Quercus* percentages showed a reduction, and the taxa belonging to the SDTF such as *Bursera*, and the SCTF taxa as *Brosimum*, *Ficus*, *Poulsenia*, Moraceae, and Piperaceae increased. During this period, maize pollen was only recorded in one sample at 760 cal yr BP (AD 1200).

During the last 300 cal yr BP (since AD1650), an increase of Amaranthaceae and Asteraceae marked a significant change in vegetation coupled with an abrupt rise in the rate of change. Evidence of agriculture, as indicated by the presence of maize pollen, correlates with a significant increase in the non-arboreal assemblage but with low charcoal concentration values.

Correlation between the plant assemblages and periods of drought

The dry tropics have lower diversity in terms of species richness compared to the humid tropics, but in western Mexico, the species richness of the SDTF is very high (Durán et al., 2006). Studies regarding the relationship between diversity and climate parameters such as precipitation and seasonality have shown a positive correlation between the diversity of the Mexican STDF with evapotranspiration (Trejo and Dirzo, 2002).

In the record of SMO, the cross-correlation analysis of *Quercus* and Ca/Ti shows that these two variables shifted together; confirming that *Quercus* is a drought indicator. Based on the combination of the *Quercus* pollen spectra and the Ca/Ti ratio, we inferred four main periods of drought conditions in the SMO basin during the last 5000 years: from ca. 4200–3850 cal yr BP, 3100–2300, 1570–1100 cal yr BP and 300 cal yr BP. (A) During the first drought period, *Quercus* attained values of 50% and the Ca/Ti ratio was high. (B) Throughout the second period, ca*.* 3100–2300 cal yr BP, *Quercus* attained irregular percentages, and there was an increase in Poaceae, possibly related to agricultural practices inferred from the presence of maize pollen. Agriculture probably took place on the slopes near the inlet of the south-western part of the catchment, as it occurs there today. In the other sectors of the crater, the slopes are too steep to carry out agricultural practices. (C) For the third drought period, dated from 1570 to 1000 cal yr BP (AD 380–950), low concentrations of Ti and high values of Ca/Ti suggest severe droughts. Maize pollen was absent in these sediments leaving no evidence of human activity during this period in the basin. This time corresponds to the period of the Classic drought, which has been documented in several paleoecological records in central Mexico (Bhattacharya et al., 2017; Caballero et al., 2002; Metcalfe and Davies, 2007). In SMO, the record is characterised by an increase in *Quercus* percentages, low run-off with low Ti concentrations, and high evaporation, as suggested by the Ca/Ti ratios. Paleoecological evidence for the same period obtained from the littoral core shows low lake levels from 1350–1150 cal yr BP (500 to 1000 AD) and intense evaporation and reduced surface run-off from 600 to 800 AD (Rodríguez-Ramírez et al., 2015). (D) The most recent and intense drought at ca. 300 cal yr BP with an episode of a sudden increase in *Quercus* percentages along with a high Ca/Ti ratio.

Previous high-resolution XRF of Ti and Ca concentration data and magnetic susceptibility for the last 700 yr BP (since AD 1250) in the SMO sequence (top 160 cm), together with historical information and tree-ring chronologies, allowed us to document significant drought events. The drought of 295 cal yr BP (AD1655–1670) was one of the most intense, characterised by an increase in Ca and a reduction in Ti percentages (Sosa-Nájera et al., 2010). According to Stahle et al. (2016), this drought reconstructed on tree-ring chronologies at 1666–1669, was one of the two most extreme of the past 600 years in Mexico. Other analyses, including a combination of magnetic mineralogy, organic and inorganic carbon, and geochemistry have been carried out in a sequence that covers the last 2600 years (SMO02-V) drilled in the littoral zone of SMO lake (Fig. 1b, Vázquez-Castro et al., 2008). Data in this earlier publication shows warmer and drier conditions between 1350 and 810 cal yr BP (AD 600 to 1140) and promoting high pH in the lake and the precipitation of carbonates. Rodríguez-Ramírez et al. (2015) using ostracod and diatom content in combination with magnetic susceptibility, total inorganic carbon, and Ca/Ti concentration values in the same core showed periods of lower lake levels associated with higher Ca/Ti values which were associated with reduced precipitation. The SMO littoral record corroborated that high Ca/Ti values in this lake can be taken as an indicator of high carbonate formation during periods of high evaporation, and therefore lower effective moisture.

Two periods of wetter conditions at SMO can be inferred based on the Ca/Ti record and high percentages of Moraceae pollen. The first event centered at 3700 cal yr BP and the second between 1050– 650 cal yr BP (AD 900–1300). Evenness values /N2/N0 ratio) are high during the periods of more moisture availability.

Anthropogenic activity in the SMO basin

It has been suggested that early agriculture dispersed inland from coastal western Mexico through river basins (Zizumbo-Villareal and Colunga, 2008) and established in various lake basins, such as SMO. In several lacustrine sequences of the TMVB fossil maize is reported after 5000 cal yr BP (Goman and Byrne, 1998; Lozano-García et al., 2010, Lozano-García et al., 2013; Park et al., 2010;

Sluyter and Dominguez-Vázquez, 2006) indicating the expansion of agriculture in central Mexico. Most of the late Holocene paleoecological records from Mexico show evidence of anthropogenic activities, including the presence of agricultural taxa such as maize pollen, reduction in arboreal pollen due to deforestation, increases in charcoal particles pointing to frequent fires, increases in magnetic susceptibility suggesting higher erosion rates, and/or hiatuses in sedimentation (Caballero et al., 2002; Del Castillo-Batista et al., 2018; Figueroa-Rangel et al., 2008; Lozano-García et al., 2013; Park et al., 2010). The pollen record of Tixtla and Huitziltepec karstic lakes, located within the distribution area of the SDTF in southern Mexico (Berrío et al., 2005), shows the evidence of agricultural activities starting at 2700 cal yr BP (750 BC). At Laguna San Pedro near SMO, preliminary pollen analysis suggested that maize agriculture could occur at ca. 3000 yr BP (1050 BC) (Brown, 1985). Maize pollen at SMO was recorded before at 3990 cal yr BP (2040 BC), suggesting an earlier agricultural development for this site.

In the pollen record from SMO, two periods of human disturbance based on the presence of maize pollen were observed, one between 3790 and 2160 cal yr BP (1820 to 190 BC), and the other from 280 cal yr BP to present (ie, 1700 AD to present). The first interval falls within the Formative period (2000 BC to AD 100) and the second corresponds with the postcolonial period starting after the AD 1650 drought. Similarly, the pollen spectra in both periods of disturbance show an increase in non-arboreal pollen suggesting deforestation, but during the first period, Poaceae dominated the herbaceous assemblage, while during the second period, Amaranthaceae was the most abundant pollen taxa.

In several studies, high concentrations of microcharcoal, related to slash and burn agricultural practices have been reported for Mesoamerica (Kennett et al., 2010). However, in the SMO record, the association between the microcharcoal concentration and agriculture is not evident; this is verified by the negative correlation between charcoal and maize in the cross-correlation analysis (Figure 5). The Ca/Ti ratio is used as an indicator of warmer climate and lower precipitation. The cross-correlation analysis between this ratio and *Zea mays,* established a negative correlation which suggests that agricultural activities in the basin may have occurred during wet periods rather than dry periods, an idea consistent with the lower values of Ca/Ti and the high percentages of Moraceae. Archeological data for western Mexico documents an increase in population growth during the late Formative and early Classic periods (300 BC to 600 AD) in the shaft and chamber tomb tradition (Beekman, 2010); however, in the SMO record there is no evidence of agriculture during this period. In the littoral core, some evidence of human presence is inferred during this time ending as the climate became dryer after AD 400 (Rodríguez-Ramírez et al., 2015). Our data suggest the disruption of agriculture by droughts at this site.

Climate, fires, and diversity

Paleoecological studies are useful in assessing the responses on the STDF to natural disturbances such as fires and droughts (Stan et al., 2019). The present study showed changes in diversity in the pollen assemblages over the last 5000 cal yr BP in SDTF in west-central Mexico using different metrics. When looking at N1 and N2 values, the higher diversity in the sequence corresponded to SMO-3 (998–

317 cal yr BP); this zone was characterized by humid conditions as the Ti and Ca/Ti proxies revealed. The resemblance in values and pattern of these two numbers (N1 and N2) exhibit that rare and abundant taxa responded similarly to changes in the environment, but rare taxa dominated the assemblage of the STDF. Also, the higher N2/N0 ratio is presented during the humid periods in the record.

Two drivers for diversity change (climate and human disturbance) intermingle throughout the vegetation history of SMO, both have effects on the pollen taxa diversity and the Ti, Ca/Ti, and charcoal records. Although the dry forests are well-adapted to long periods of dryness (6–8 months), according to our results, the diversity of STDF was affected by droughts throughout the last 5000 years. Actual floristic research in the tropical dry forests of South America and Central America show that species diversity is lower away from the equator and with indications of negative correlation between the number of dry months with diversity and turnover (Golicher et al., 2012). Diversity and turnover decline when dry conditions are established in SMO, this pattern is clearly observed in the record during the period of significant droughts such as during the late Classic and for the AD 1650 drought.

Another disturbance factor related to droughts is fire (Torres-Rodríguez et al., 2015). Fire is an important disturbance factor that can affect diversity in the dry tropics (Rodríguez-Trejo, 2008). The role of fires in the STDF dynamics is poorly studied. Although natural fires are not considered as part of the Neotropics dry forests ecology (Middelton et al., 1997) recent studies in a dry forest in Nicaragua suggest that for this site, the forest is dominated by species that can survive infrequent and low-intensity fires (Otterstrom et al., 2006). More frequent are the anthropogenic fires, when agriculture activity promotes it for field preparation. The cross-correlation results between charcoal concentration and the diversity metrics showed a negative and synchronic correlation, implying that diversity decreases when fire occurrences are high. Our data show two periods of increase in microcharcoal, the first at the end of mid-Holocene with no evidence of agriculture in the record and the second with the presence of maize from 3100 to 1600 cal yr BP. Since the SMO basin is close to the Pacific coast, El Niño events could promote wet-season drought, which could increase the occurrence of fire events in this ecosystem, altering the plant community composition for long-term periods with important changes in diversity. According to a synthesis by Metcalfe et al. (2015) related to Holocene climate change and its consequences in the continental environments of Mexico, the late Holocene climatic pattern is complex, but generally dry conditions are established in most of the lacustrine basins in the TMVB. The main driver for the reduction in summer precipitation seems to be the weakening of the monsoon strength associated with a more southerly mean position of the ITZC. Today, the ITCZ is displaced to the south during El Niño events, reducing summer precipitation in Mexico (Magaña et al., 2003). In the paleorecords, an increase in strength and frequency of El Niño events during the mid to late Holocene is observed in the Pallcacocha record (Moy et al., 2002, Figure 4). Also, in the palynological record of Zirahuen, a temperate site located east of the SMO in the TMVB, a dry event at ca. 4000 cal yr BP was related to an increase in El Niño events. (Lozano-Garcia et al., 2013). Tree-ring analyses of *Mimosa acantholoba*, a pioneer species of the dry tropical forest in southern Mexico, exhibited how large-scale climatic drivers as El Niño, influences tree growth through effects of local climate such as the reduction in rainfall and warmer climates. This research showed that growth was negatively affected by El Niño episodes with a reduction of 37% in growth during El Niño years (Brienen et al., 2010). Although this study referred only to one species, making it difficult to generalize to the tropical dry forest communities, it is evident that climate change affects the survival of the species and modify diversity.

We hypothesised that because SMO is close to the Pacific coast and receives rain during the summer months, El Niño events could promote significant drought conditions, as shown in the Ca/Ti values (Figure 5), which in turn alters the composition of the plant community by decreasing the diversity of its taxa as evidenced in this study.

Conclusions

In this paper, we have explored the history of the SDTF, one of the most widespread tropical vegetation types in Neotropics, and the adjacent oak forest in the SMO basin. Using pollen data and microcharcoal concentration and analysing geochemical proxies from the MOLE-SMO03 lacustrine sediments, past environmental conditions were reconstructed for the last 5000 years. The palynological data show that the main changes in the plant assemblages are represented by a combination of low SDTF pollen percentages and a high representation of the anemophilous *Quercus* and *Pinus* sp. in the fossil pollen spectra. Our data suggest a wider presence of the tropical oak forest at the site. Herbaceous pollen percentages of Poaceae, Amaranthaceae, and Asteraceae correlate with the presence of maize pollen since 3900 cal yr BP.

We found a correlation between the Ca/Ti ratio and *Quercus*, indicating low precipitation, and we used it as a drought indicator for this site. Based on these data, we inferred four main drought events (4200–3850, 3100–2300, 1570–1100, and ca. 300 cal yr BP). The most severe drought occurred during the late Classic (1570–1000 cal yr BP), with no evidence of agriculture at the site. Our results indicate the disruption of agriculture by droughts in SMO. Periods of wet conditions were documented in the sedimentary record based on high values of Moraceae pollen and Ti percentages; during these periods, the presence of maize pollen indicates human activities in the basin. We found a negative correlation between charcoal data and diversity metrics (Hill numbers and palynological richness), suggesting that diversity declined when fire events were high. Although the tropical dry forests are adapted to long periods of dryness, our results indicate that droughts affected the diversity of the STDF. Reduction in summer precipitation seems to be promoted by El Niño events, causing changes in the plant assemblages mainly inferred through changes in the diversity of taxa.

Our data reveal that vegetation of the STDF has mainly responded to climate change rather than human impact in the SMO lake during the last 5000 yrs.

Acknowledgments

We would like to thank those who contributed to the fieldwork in 2003 during the MOLE expedition: Douglas Schnurrenberger, Mark Shapley, Alejandro Ramírez-Rodríguez, Isabel Israde and Sarah Davies. Rodrigo Martinez Abarca Morales helped with the map editing.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This research was founded by UNAM DGAPA-PAPIIT (México grant no. IN203102 and IN110106).

ORDIC iD

Socorro Lozano-García https://orcid.org/0000-0002-3579-175X

References

Batten DJ (1999) Small palynomorphs. In: Jones TP and Rowe NP (eds) *Fossil Plants and Spores Modern Techniques*: The Geological Society, London, pp. 15-19.

Becerra JX (2005) Timing the origin and expansion of the Mexican dry forest. *Proceedings of the National Academy of Sciences* 102(31): 10919-10923.

Beekman CS (2010) Recent Research in western Mexican Archaeology. *Journal of Archaeology Research* 18:41-109.

Berrío JC, Hooghiemstra H, van Geel B, Ludlow-Wiechers B (2006) Environmental history of the dry forest biome of Guerrero, Mexico, and human impact during the last c. 2700 years. The Holocene 16 (1): 63-80.

Bhattacharya T, Chiang JC and Cheng W (2017) Ocean-atmosphere dynamics linked to 800–1050 CE drying in Mesoamerica. *Quaternary Science Reviews* 169: 263-277.

Birks HJB, Felde VA, Bjune AE et al. (2016) Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. *Review of Paleobotany and Palynology* 228: 1-25.

Blaauw M and Christen JA (2011). Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6: 457-474.

Brienen RJW, Lebrija-Trejos E, Zuidema PA et al. (2009) Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. *Global Change Biology* 16: 2001-2012.

Brown RB (1985) A summary of late Quaternary pollen records from Mexico west of the Isthmus of Tehuantepec. In: Bryant VM Jr and Holloway RG (eds) *Pollen Records of Late Quaternary North America Sediments*. America Association of Stratigraphic Palynologists Foundation Dallas TX pp 71-93.

Caballero M, Ortega B, Valadez F, et al. (2002) Sta. Cruz Atizapán: a 22-ka lake level record and climatic implications for the late Holocene human occupation in the Upper Lerma Basin, Central Mexico. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 186, 217-235.

Caballero M, Rodríguez A, Vilaclara G et al. (2013) Hydrochemistry, ostracods and diatoms in a deep, tropical, crater lake in Western Mexico. *Journal of Limnology* 72: 512–523.

Castro CL, Chang HI, Dominquez F et al. (2012) Can a regional climate model improve the ability to forecast the North American Monsoon? *Journal of Climate* 25: 8212-8237.

Del Castillo-Batista AP, Figueroa-Rangel BL, Lozano-García S et al. (2018) 1580 years of human impact and climate change on the dynamics of a Pinus-Quercus-Abies forest in west-central Mexico. *Revista Mexicana de Biodiversidad* 89:208–225.

Durán E, Meave JA, Lott EJ et al. (2006) Structure and diversity patterns at landscape level in a Mexican tropical deciduous forest. *Boletín de la Sociedad Botánica de México*. 79: 43-60.

Figueroa-Rangel BL, Willis KJ, Olvera-Vargas M (2008) 4200 years of pine-dominated upland forest dynamics in west-central Mexico: human or natural legacy? *Ecology* 89:1893–1907.

Goman M and Byrne R (1998) A 5000-year record of agricultural and tropical forest clearance in the Tuxtlas, Veracruz, Mexico. *The Holocene* 8:83–89

Golicher DJ, Cayuela L, Newton AC (2012) Effects of climate change on the potential on the species richness of Mesoamerican forest. *Biotropica* 44 (3): 284-293.

Gotelli NJ and Ellison AM (2013) *A Primer of Ecological Statistics*. second ed. Sinauer, Sunderland

Grimm EC (1991) Tilia and Tiliagraph. Illinois State Museum. Springfield.

Grimm EC (1987) Coniss: a fortrand 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*. 13 (1):13-35.

Hill MO (1973) Diversity and evenness: a unifying notion and its consequences. *Ecology* 54, 427–432.

Janzen D (1988) Tropical dry forest. The most endangered major tropical ecosystems. In: Wilson EO (ed.) *Biodiversity*. National Academy Press, Washington DC pp. 130–137.

Kennett DJ, Piperno DR, Jones JG et al. (2010) Pre-pottery farmers on the Pacific coast of southern Mexico. *Journal of Archaeological Science* 37: 3401-3411.

Kohlman B and Sánchez-Colon S (1984) Estudio aerográfico del género Bursera en México. In: Ezcurra E, Equihua M, Colman B and Sánchez-Colon S (eds) *Métodos cuantitativos en la Biogeografía*. Instituto de Ecología, México.

Lozano-García S and Vázquez-Selem L (2005) A high-elevation Holocene pollen record from Iztaccíhuatl volcano, central Mexico. *The Holocene* 15:329–338.

Lozano-García S, Caballero M, Ortega B et al. (2010) Late Holocene palaeoecology of Lago Verde: evidence of human impact and climate change in the northern limit of the neotropics during the late formative and classic periods. *Vegetation History and Archaeobotany* 19:177–190.

Lozano-García S, Torres-Rodríguez E, Ortega B, et al. (2013) Ecosystem responses to climate and disturbances in western central Mexico during the late Pleistocene and Holocene. *Palaeogoegraphy Palaeoclimatology Palaeoecology* 370:184-195.

Lozano-García S, Caballero M, Ortega-Guerrero B, et al. (2020) Insights into the Holocene Environmental History of the Highlands of Central Mexico. In: Torres-Cano, N, Islebe, G, and Roy, P, (eds.) The Holocene and Anthropocene environmental history of Mexico. Spinger Nature Switzerland, pp.97-114.

Magaña VO, Vázquez JL, Pérez JL, et al. (2003) Impact of El Niño on precipitation in Mexico. *Geofísica Internacional* 42: 313-330.

Metcalfe SE and Davies S (2007) Deciphering recent climate change in central Mexican lake records. *Climatic Change* 83: 169–186.

Metcalfe SE, Barron JA and Davies SJ (2015) The Holocene history of the North American Monsoon: ‘known knows’ and ‘known unknowns’ in understanding its spatial and temporal complexity. *Quaternary Science Reviews* 120: 1-27.

Middelton BA, Sáncez-Rojas E, Suedmeyer B et al. (1997) Fire in a tropical dry forest of central America: a natural part of the disturbance regime? *Biotropica* 29: 515-517.

Mountjoy JB (2015) La colonización del lejano occidente de México por agricultores sedentarios durante el Formativo medio, 1200 a 400 a.C. *Revista Occidente* Junio 1- 18.

Morrone JJ (2019) Regionalización biogeográfica y evolución de la biótica de México: encrucijada de la biodiversidad del nuevo mundo*. Revista Mexicana de Biodiversidad.* 90: e9002980.

Moy CM, Seltzer GO, Rodbell DT et a.l (2002) Variability of El Niño/Southern oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420:162-165.

Oksanen J, Blanchet FG, Friendly M (2018) https://cran. r-project. org/web/packages/vegan/index. Html

Otterstrom, SM, Schwartz MW, Velázquez-Rocha, I (2006) Responses to fire in selected tropical dry forest trees. *Biotropica* 38 (5): 592-598.

Park J, Byrne R, Bohnel H et al. (2010) Holocene climate change and human impact, central Mexico: a record based on maar lake pollen and sediment chemistry. *Quaternary Science Reviews* 29:618–632.

Park J, Byrne R, Bohnel H (2019). Late Holocene change in Central Mexico and the decline of Teotihuacan. *Annals of the American Association of Geographers* 109 (1):104 120.

Pennington RT, Prado DE and Pendry CA (2000) Neotropical seasonally dry forest and Quaternary vegetation changes. *Journal of Biogeography* 27: 261-273.

Peñaloza-Ramírez JM, Rodríguez-Correa H, Gonzales-Rodríguez A et al. (2020) High genetic diversity and stable Pleistocene distributional ranges in the widespread Mexican oak *Quercus castanea* Née (1801) Fagaceae. *Ecology and Evolution* 1-16.

Pérez-García EA, Meave JA and Cevallos-Ferriz SRS (2012) Flora and vegetation of the seasonally dry tropics in Mexico: origin and biogeographical implications. *Acta Botánica Mexicana* 100:149-193.

Reimer PJ, Bard E, Bayliss A et al. (2013) IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon* 55(4): 1869–1887.

R Core Team. (2017). R: A language and environment for statistical computing. Available at: http:// www.R-project.org

Rodríguez-Ramírez A, Caballero M, Roy P et al. (2015) Climatic variability and human impact during the last 2000 years in western Mesoamerica: evidence of late Classic (AD 600-900) and Little Ice Age drought events. *Climates of the Past* 11: 1239-1248.

Rodríguez-Trejo, DA (2008) Fire regimes, fire ecology and fire management in Mexico. *Ambio* 37 (7/8):548-566.

Ruiz-Córdova JP, Lozano-García S, Caballero M et al. (2019) Historia de la vegetación, ambiente y evidencia de actividad humana de los últimos 6,000 años en el lago alpino La Luna, Nevado de Toluca. *Revista Mexicana de Biodiversidad* 90: e902996.

Rzedowski J (1962) Contribuciones a la fitogeografía florística e histórica de México I. Algunas consideraciones acerca del elemento endémico en la flora mexicana. *Boletín de la Sociedad Botánica de México* 27: 52-65.

Rzedowski J (1978) *Vegetación de México*. Ed. Limusa México.

Rzedowski J and Calderón de Rzedowski G (2013) Datos para apreciación de la flora fanerogámica del bosque tropical caducifolio de México. *Acta Botánica Mexicana* 102:1-28.

Rzedowski J (1991) Diversidad y orígenes de la flora fanerogámica de México. *Acta Botánica* 14:3-21.

Serrano D, Filonov A and Tereshchenki I (2002) Dynamic response to valley breeze circulation in Santa Maria del Oro, a volcanic lake in Mexico. *Geophysical Research Letters* 29:1649.

Stahle DW, Cook ER, Burnette DJ et al. (2016) The Mexican drought atlas: Tree-ring reconstructions of the soil moisture balance during the late pre-hispanic, colonial, and modern eras. *Quaternary Science Reviews* 149: 34-60.

Stan K and Sánchez-Azofeifa A (2019) Tropical dry forest diversity, climate response and resilience in a changing climate. *Forests* 10:443.

Tellez O (1995) *Flora, Vegetación y Fitogeografía de Nayarit*. PhD Thesis, Universidad Nacional Autónoma de México, México.

Torres-Rodríguez E, Lozano-García S, Roy P et al. (2015) Last glacial droughts and fire regimes in the central Mexican highlands. *Journal of Quaternary Science* 30(1):88-99.

Trejo I, Dirzo R (2002) Floristic diversity of Mexican seasonally dry tropical forest. *Biodiversity and Conservation* 11:2063-2048.

Serrano D, Filonov A, Tereshchenko I (2002) Dynamic response to valley breeze circulation in Santa Maria del Oro, a volcanic lake in Mexico, *Geophysical Research Letters* 20(13): 1649.

Sluyter A and Dominguez G (2006) Early maize (Zea mays L.) cultivation in Mexico: dating sedimentary pollen records and its implications. *Proceedings of the National Academy of Sciences* 103:1147–1151.

Sosa-Nájera S, Lozano-García S, Roy P et al. 2010. Registro de sequías históricas en el occidente de México con base en el análisis elemental de sedimentos lacustres: El caso del lago de Santa María del Oro. *Boletín de la Sociedad Geológica Mexicana* 62, 437–451.

Stahle DW, Cook, ER, Burnette DJ et al. (2016) The Mexican drought Atlas: Tree-ring reconstructions of soil moisture balance during the late pre-Hispanic, colonial and modern eras. *Quaternary Science Reviews* 149: 34-60.

Torres-Rodríguez E, Lozano-García S, Figueroa-Rangel B et al. (2012) Cambio ambiental y respuestas de la vegetación de los últimos 17,000 años en el centro de México: el registro del lago de Zirahuén. *Revista Mexicana de Ciencias Geológicas* 29(3): 764-778.

Vázquez-Castro G, Ortega-Guerrero B, Rodríguez A (2008) Mineralogía magnética como indicador de sequía en los sedimentos lacustres de los últimos *ca.* 2600 años de Santa María de Oro, occidente de México. *Revista Mexicana de Ciencias Geológicas* 25:21-38.

Williams E (2020) Ancient West Mexico in the Mesoamerican Ecumene, Archaeopress Precolumbian Arachaeology 12: Archaeopress Publising LTD, p. 442.

Zizumbo-Villareal D, Colunga-GarcíaMarin P (2010). Origin of agriculture and plant domestication in West Mesoamerica. *Genetic Resources and Crop Evolution* 57:813-825.

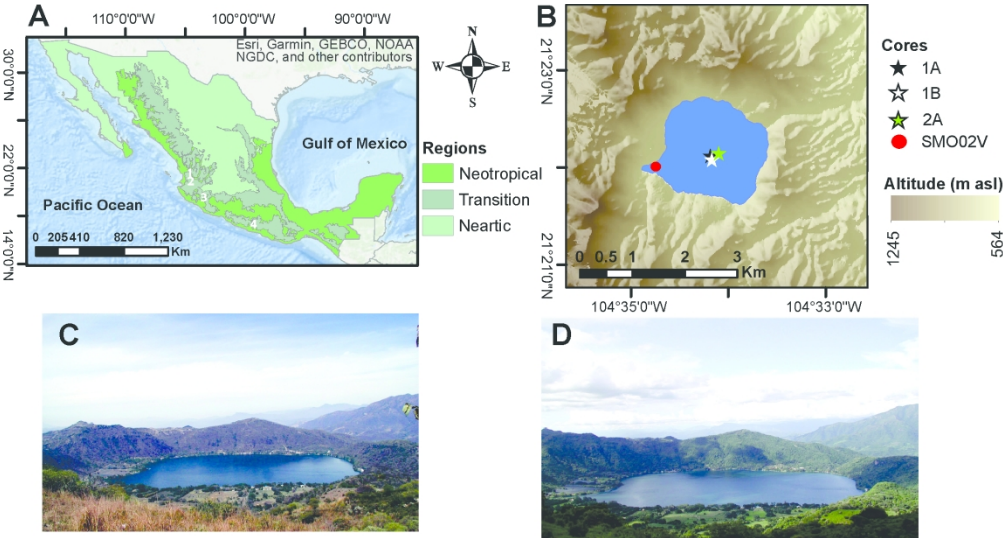

Figure 1. Location of the coring site at Santa Maria del Oro lake (1) at different scales: (A) at country level, showing the Mexican Neotropical region in green, the transition zone in grey and the Nearctic region in light green (Morrone, 2019); other sites mentioned in the text: Laguna San Pedro (2) and Lago Guzman (3) (Brown, 1985), Tixtla and Huitzitlpepec (4) (Berrío et al., 2005). (B) Digital elevation model of Santa Maria del Oro lake and location of the three cores used to reconstruct MOLE-SMO03 (stars) and SMO02V (red circle) (Rodríguez-Ramírez et al., 2015). (C) and (D) represent the marked change in vegetation appearance during the extended dry and the short humid seasons, respectively.

211x113mm (300 x 300 DPI)

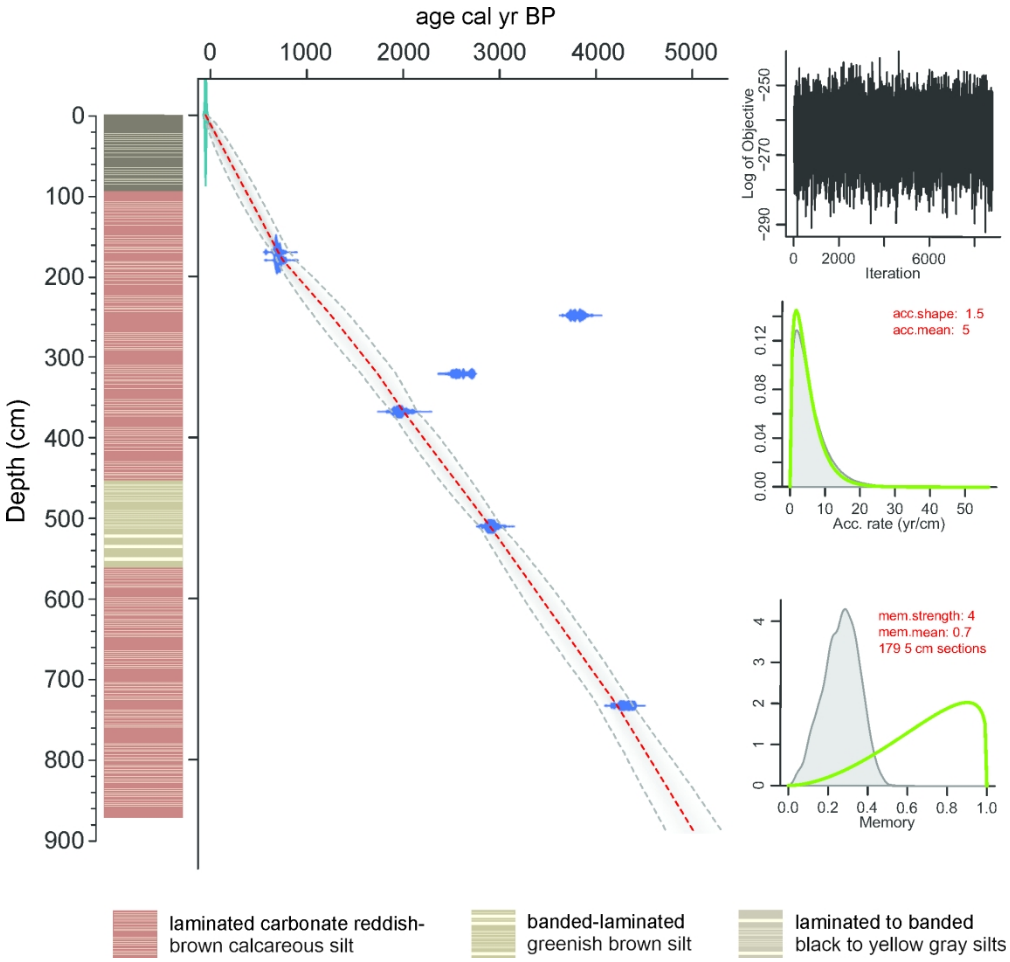

Figure 2. Lithostratigraphy and chronology of the MOLE-SMO03 master sequence in west central Mexico with the calibrated distribution of radiocarbon dates and the Bacon age-depth model; blue symbols represent probability distribution functions; grey stippled lines display 95% confidence intervals; red line is weighted mean maximum probability date for each depth. Details of dates are presented in Table 1.

178x169mm (300 x 300 DPI)

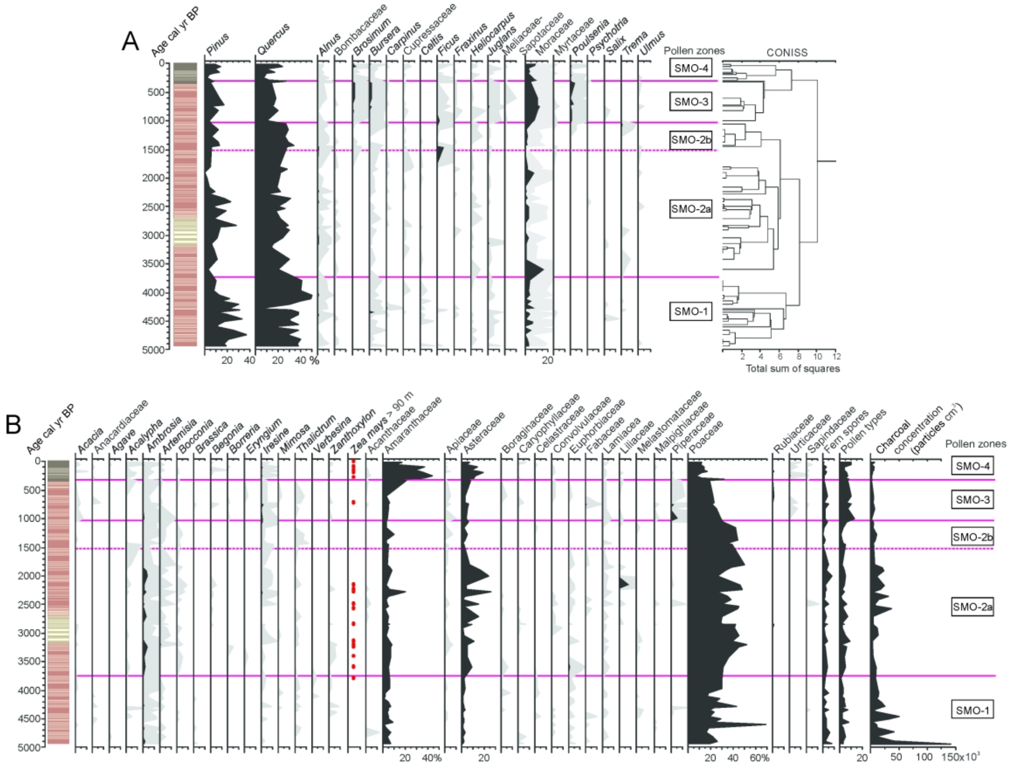

Figure 3. Pollen percentage diagram for the MOLE-SMO03 master sequence. (A) Arboreal pollen. Horizontal pink lines are pollen zones (solid) and subzone (dashed line). (B) Non-arboreal pollen, pollen types, and charcoal concentration (particles/cm3). Gray silhouettes correspond to a 5X exaggeration.

276x209mm (300 x 300 DPI)

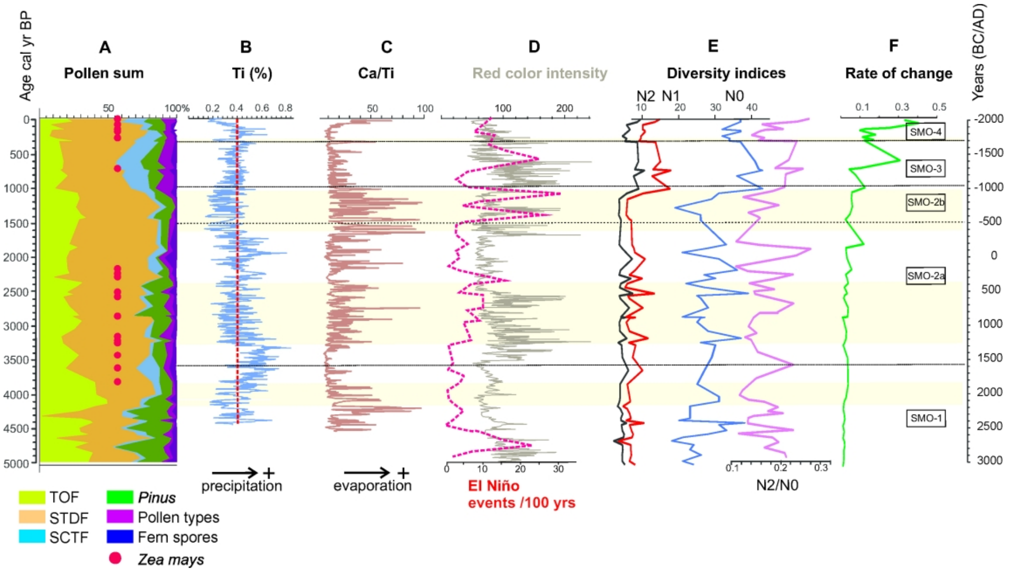

Figure 4. Selected proxies and El Niño record for Santa María del Oro along the last 5000 years. (A) Percentage pollen diagram of the MOLE-SMO03 master sequence showing the Tropical Quercus forest taxa (light green), Seasonal Tropical Dry Forest taxa in orange with maize pollen represented in red dots, Sub-deciduous Tropical Forest taxa in blue, Pinus in dark green, pollen types in violet and fern spores in dark blue, the taxa are listed in Table 2. (B) Titanium (Ti) in percentages values; the red line corresponds to Ti mean value. (C) Calcium/Titanium ratio. (D) ENSO variability record of Laguna Pallcacocha based on red color intensity (blue line) and El Niño events every 100 years from the same site (dotted red line) (Moy et al., 2002). (E) Diversity metrics—black line: N2, red line: N1, blue line: N0, and pink line: N2/N0. (F) Rate of change. Yellow shades indicate periods of dry conditions and pollen zones and subzones in rectangles.

268x151mm (300 x 300 DPI)

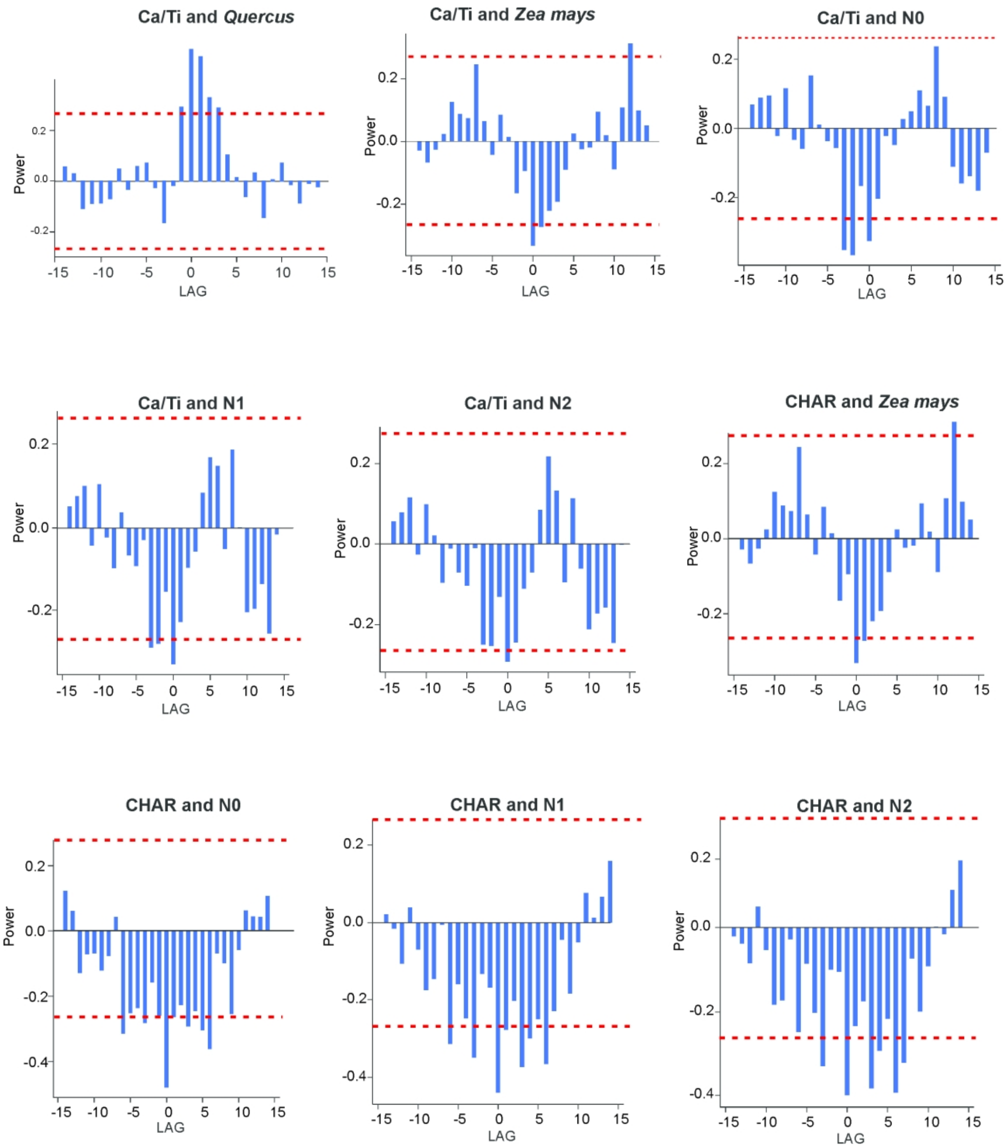

Figure 5. Cross correlations of Ca/Ti and charcoal with the three diversity metrics (N0, N1, N2) and with Quercus and Zea mays. Bars passing through the red dotted line denote significant correlations (p<0.05). Every lag has a sample interval of □80 years. Negative correlations are inverse proportional relationships. Positive lags correspond to delays and shift the series back in time; negative lags correspond to leads and shift the series forward in time. Lag=0 denotes that both variables are synchronous.

198x225mm (300 x 300 DPI)

Table 1. AMS radiocarbon dates of the Santa María del Oro master sequence MOLE-SMO03.

Laboratory ID	Depth (cm)	Radiocarbon ^{14}date (yr BP) and error	Calibrated yr BP (2 σ)	Material dated
Beta 198312	170	750±40	652–739	Bulk sediment organic matter
Beta 227823	180	780±40	666–768	Bulk sediment organic matter
Beta 227824	248	3530±40	3910–3700	Bulk sediment organic matter
Beta 227826	321	2520±40	2740–2470	Bulk sediment organic matter
Beta 198313	368	2010±50	1869–2114	Bulk sediment organic matter
Beta 227825	510	2810±40	27-91–3005	Bulk sediment organic matter
Beta 198315	733	3870±50	4151–4420	Bulk sediment organic matter

Table 2 Identified pollen from lake Santa María del Oro core. Taxa are grouped according to ecological preferences based on the plant survey of SMO basin. Pollen types and fern spores are not listed.

Seasonal tropical dry forest

Acacia
Acalypha
Acanthaceae
Agave
Amaranthaceae
Ambrosia
Anacardiaceae
Asteraceae
Brassica
Bocconia
Bombacaceae
Boraginaceae
Borreira
Bursera
Celastraceae
Celtis
Convolvulaceae
Cuphea
Euphorbiaceae
Fabaceae
Ficus
Heliocarpus
Iresine
Lamiaceae
Malpighiaceae
Meliaceae-Sapotaceae
Mimosa
Myrtaceae
Piperaceae
Poaceae
Psychotria
Rubiaceae
Sapindaceae
Verbesina
Trema
Zanthoxylum

Sub-deciduous tropical forest

Brosimum
Carpinus
Juglans
Liliaceae
Melastomataceae
Moraceae
Poulsenia
Salix
Ulmus
Urticaceae

Tropical Oak forest

Quercus
Alnus
Artemisia
Apiaceae
Begonia
Caryophyllaceae
Cupressaceae
Eryngium
Fraxinus
Thalictrum
Pinus

Human impact indicator

Zea mays

Supplementary material

Species list collected at the Santa María del Oro basin and surroundings.

All names are according to the Plant List and deposited at the Herbario Nacional de México (MEXU).

Family	Species	Author	Habit
Acanthaceae	*Dyschoriste pringlei*	Greenm.	Herb
Adiantaceae	*Hemionitis subcordata*	(D.C. Eaton ex Davenp.) Mickel	Herb
Adiantaceae	*Notholaena jaliscana*	Yatsk. & A.L. Arbeláez A.	Herb
Adiantiaceae	*Adiantum braunii*	Mett. ex Kuhn	Herb
Adiantiaceae	*Cheilanthes lozanoi*	(Maxon) R.M. Tryon & A.F. Tryon	Herb
Anacardiaceae	*Rhus terebinthifolia*	Schltdl. & Cham.	Shrub
Annonaceae	*Annona longiflora*	S.Watson	Tree
Annonaceae	*Annona reticulata*	L.	Tree
Apocynaceae	*Allamanda blanchetii*	A.DC.	Climbing
Apocynaceae	*Dictyanthus pavonii*	Decne.	Climbing
Apocynaceae	*Matelea congesta*	(Decne.) Woodson	Climbing
Apocynaceae	*Stemmadenia tomentosa*	Greenm.	Tree
Araceae	*Anthurium halmoorei*	Croat	Epiphyte
Asparagaceae	*Bessera elegans*	Schult.f.	Herb
Asparagaceae	*Manfreda scabra*	(Ortega) McVaugh	Herb
Basellaceae	*Anredera vesicaria*	(Lam.) C.F.Gaertn.	Climbing
Begoniaceae	*Begonia relicta*	L.B.Sm. & B.G.Schub.	Herb
Bignoniaceae	*Crescentia alata*	Kunth	Tree
Bromeliaceae	*Bromelia pinguin*	L.	Shrub
Bromeliaceae	*Tillandsia achyrostachys*	E.Morren ex Baker	Epiphyte
Burseraceae	*Bursera attenuata*	(Rose) L.Riley	Tree
Burseraceae	*Bursera excelsa*	(Kunth) Engl.	Tree
Burseraceae	*Bursera fagaroides*	(Kunth) Engl.	Tree
Burseraceae	*Bursera penicillata*	(Sessé & Moç. ex DC.) Engl.	Tree
Campanulaceae	*Lobelia cordifolia*	Hook. & Arn.	Herb
Commelinaceae	*Tripogandra amplexicaulis*	(Klotzsch ex C.B.Clarke) Woodson	Herb
Compositae	*Acmella radicans*	(Jacq.) R.K.Jansen	Herb
Compositae	*Adenophyllum porophyllum*	(Cav.) Hemsl.	Herb
Compositae	*Bidens chrysantha*	(L.) DC.	Herb
Compositae	*Bidens riparia*	Kunth	Herb
Compositae	*Brickellia lanata*	(DC.) A.Gray	Herb
Compositae	*Jaumea peduncularis*	(Hook. & Arn.) Benth. & Hook.f. ex Oliv..	Herb
Compositae	*Chloracantha spinosa*	(Benth.) G.L.Nesom	Herb
Compositae	*Chromolaena haenkeana*	(DC.) R.M.King & H.Rob.	Shrub

Compositae	*Cosmos sulphureus*	Cav.	Herb
Compositae	*Elephantopus mollis*	Kunth	Herb
Compositae	*Eupatoriastrum triangulare*	(DC.) B.L.Rob.	Shrub
Compositae	*Guardiola rotundifolia*	B.L.Rob.	Shrub
Compositae	*Lasianthaea ceanothifolia*	(Willd.) K.M.Becker	Shrub
Compositae	*Lasianthaea macrocephala*	(Hook. & Arn.) K.M.Becker	Shrub
Compositae	*Lasianthaea palmeri*	(Greenm.) K.M.Becker	Shrub
Compositae	*Melampodium divaricatum*	(Rich.) DC.	Herb
Compositae	*Melampodium strigosum*	Stuessy	Herb
Compositae	*Milleria quinqueflora*	L.	Herb
Compositae	*Montanoa bipinnatifida*	(Kunth) K.Koch	Shrub
Compositae	*Porophyllum coloratum*	(Kunth) DC.	Herb
Compositae	*Porophyllum pringlei*	B.L.Rob.	Herb
Compositae	*Psacalium pringlei*	(S.Watson) H.Rob. & Brettell	Herb
Compositae	*Sclerocarpus divaricatus*	(Benth.) Benth. & Hook.f. ex Hemsl.	Herb
Compositae	*Sclerocarpus sessilifolius*	Greenm.	Herb
Compositae	*Tagetes erecta*	(L.) Alston	Herb
Compositae	*Tagetes lucida*	Cav.	Herb
Compositae	*Tagetes micrantha*	Cav.	Herb
Compositae	*Tagetes subulata*	Cerv.	Herb
Compositae	*Trixis hyposericea*	S.Watson	Herb
Compositae	*Verbesina sphaerocephala*	A.Gray	Shrub
Compositae	*Verbesina tequilana*	J.R.Coleman	Shrub
Compositae	*Vernonanthura patens*	(Kunth) H.Rob.	Shrub
Compositae	*Vernonanthura serratuloides*	(Kunth) H.Rob.	Shrub
Compositae	*Vernonia coulteri*	(A.Gray) B.L.Turner	Shrub
Cucurbitaceae	*Sechium edule*	(Jacq.) Sw.	Climbing
Cyperaceae	*Bulbostylis funckii*	(Steud.) C.B.Clarke	Herb
Cyperaceae	*Cyperus aggregatus*	(Willd.) Endl.	Herb
Cyperaceae	*Cyperus amabilis*	Vahl	Herb
Cyperaceae	*Cyperus ischnos*	Schltdl.	Herb
Cyperaceae	*Cyperus mutisii*	(Kunth) Andersson	Herb
Cyperaceae	*Kyllinga odorata*	Vahl	Herb
Cyperaceae	*Scleria reticularis*	(Cav. ex Lag.) Hook. & Arn.	Herb
Dioscoreaceae	*Dioscorea carpomaculata*	O. Téllez & B.G. Schub.	Climbing
Dioscoreaceae	*Dioscorea jaliscana*	S. Watson	Climbing
Euphorbiaceae	*Acalypha cincta*	Müll.Arg.	Herb
Euphorbiaceae	*Croton pedicellatus*	Kunth	Herb
Euphorbiaceae	*Croton ynesae*	Croizat	Shrub
Euphorbiaceae	*Euphorbia graminea*	Jacq.	Herb
Euphorbiaceae	*Euphorbia hirta*	L.	Herb
Euphorbiaceae	*Euphorbia multiseta*	Benth.	Herb
Euphorbiaceae	*Euphorbia ocymoidea*	L.	Herb

Euphorbiaceae	*Euphorbia radioloides*	Boiss.	Herb
Euphorbiaceae	*Ricinus communis*	L.	Shrub
Fagaceae	*Quercus resinosa*	Liebm.	Tree
Fagaceae	*Quercus castanea*	Née	
Gesneriaceae	*Achimenes fimbriata*	Rose ex C.V.Morton	Herb
Gesneriaceae	*Achimenes longiflora*	DC.	Herb
Gesneriaceae	*Achimenes patens*	Benth.	Herb
Hydrocharitaceae	*Najas guadalupensis*	(Spreng.) Magnus	Herb
Hydrocharitaceae	*Najas marina*	L.	Herb
Lamiaceae	*Asterohyptis stellulata*	(Benth.) Epling	Shrub
Lamiaceae	*Hyptis albida*	Kunth	Herb
Lamiaceae	*Hyptis rhytidea*	Benth.	Herb
Lamiaceae	*Vitex mollis*	Kunth	Tree
Lauraceae	*Persea hintonii*	C.K. Allen	Tree
Leguminosae	*Acacia farnesiana*	(L.) Willd.	Shrub
Leguminosae	*Acacia pennatula*	(Schltdl. & Cham.) Benth.	Shrub
Leguminosae	*Acacia riparia*	Kunth	Shrub
Leguminosae	*Acaciella angustissima*	(Mill.) Britton & Rose	Shrub
Leguminosae	*Acacia tequilana*	S.Watson	Shrub
Leguminosae	*Aeschynomene americana*	L.	Herb
Leguminosae	*Aeschynomene amorphoides*	(S.Watson) Robinson	Tree
Leguminosae	*Brongniartia inconstans*	S.Watson	Shrub
Leguminosae	*Calliandra grandiflora*	(L'Her.) Benth.	Shrub
Leguminosae	*Calliandra houstoniana*	(Mill.) Standl.	Shrub
Leguminosae	*Calliandra palmeri*	S.Watson	Shrub
Leguminosae	*Calopogonium mucunoides*	Desv.	Climbing
Leguminosae	*Canavalia villosa*	Benth.	Climbing
Leguminosae	*Chamaecrista nictitans*	(L.) Moench	Shrub
Leguminosae	*Chamaecrista rotundifolia*	(Pers.) Greene	Shrub
Leguminosae	*Coursetia caribaea*	(Jacq.) Lavin	Shrub
Leguminosae	*Crotalaria micans*	Link	Herb
Leguminosae	*Crotalaria rotundifolia*	J.F.Gmel.	Herb
Leguminosae	*Crotalaria vitellina*	Ker. Gawl.	Herb
Leguminosae	*Dalea cliffortiana*	Willd.	Herb
Leguminosae	*Dalea tomentosa*	(Cav.) Willd.	Herb
Leguminosae	*Desmodium affine*	Schltdl.	Herb
Leguminosae	*Desmodium angustifolium*	(Kunth) DC.	Herb
Leguminosae	*Desmodium barbatum*	(L.) Benth.	Herb
Leguminosae	*Desmodium guadalajaranum*	S.Watson	Herb
Leguminosae	*Desmodium hartwegianum*	Hemsl.	Herb
Leguminosae	*Desmodium sericophyllum*	Schltdl.	Herb
Leguminosae	*Diphysa suberosa*	S.Watson	Shrub
Leguminosae	*Diphysa thurberi*	(A.Gray) Rydb.	Shrub

Leguminosae	*Enterolobium cyclocarpum*	(Jacq.) Griseb.	Tree
Leguminosae	*Eriosema grandiflorum*	(Schltdl. & Cham.) G.Don	Shrub
Leguminosae	*Eriosema multiflorum*	Robinson	Shrub
Leguminosae	*Eriosema palmeri*	S.Watson	Shrub
Leguminosae	*Eriosema pulchellum*	(Kunth) G.Don	Shrub
Leguminosae	*Erythrina montana*	Rose & Standl.	Tree
Leguminosae	*Eysenhardtia polystachya*	(Ortega) Sarg.	Shrub
Leguminosae	*Indigofera jaliscensis*	Rose	Shrub
Leguminosae	*Macroptilium gibbosifolium*	(Ortega) A.Delgado	Herb
Leguminosae	*Marina diffusa*	(Moric.) Barneby	Herb
Leguminosae	*Marina gracilis*	Liebm.	Herb
Leguminosae	*Marina grammadenia*	Barneby	Herb
Leguminosae	*Marina scopa*	Barneby	Herb
Leguminosae	*Mimosa affinis*	Robinson	Shrub
Leguminosae	*Mimosa tenuiflora*	(Willd.) Poir.	Shrub
Leguminosae	*Mimosa tequilana*	S.Watson	Shrub
Leguminosae	*Phaseolus vulgaris*	L.	Climbing
Leguminosae	*Rhynchosia edulis*	Griseb.	Climbing
Leguminosae	*Senna fruticosa*	(Mill.) H.S.Irwin & Barneby	Shrub
Leguminosae	*Senna obtusifolia*	(L.) H.S.Irwin & Barneby	Shrub
Leguminosae	*Sesbania herbacea*	Radlk.	Herb
Leguminosae	*Tephrosia macrantha*	Pringle	Shrub
Leguminosae	*Tephrosia nicaraguensis*	Oerst.	Shrub
Leguminosae	*Tephrosia rhodantha*	Brandegee	Shrub
Leguminosae	*Tephrosia sinapou*	(Buc'hoz) A.Chev.	Shrub
Leguminosae	*Tephrosia tepicana*	(Standl.) Standl.	Herb
Leguminosae	*Tephrosia vicioides*	Schltdl.	Herb
Leguminosae	*Teramnus uncinatus*	(L.) Sw.	Climbing
Leguminosae	*Vigna speciosa*	(Kunth) Verdc.	Climbing
Leguminosae	*Zapoteca formosa*	(Kunth) H.M.Hern.	Shrub
Liliaceae	*Calochortus hartwegii*	Benth.	Herb
Loranthaceae	*Struthanthus interruptus*	(Kunth) Blume	Hemiparasite
Lythraceae	*Cuphea inflata*	S.A.Graham	Herb
Lythraceae	*Cuphea leptopoda*	Hemsl.	Herb
Lythraceae	*Cuphea llavea*	Lex.	Herb
Lythraceae	*Cuphea rasilis*	S.A.Graham	Herb
Malpighiaceae	*Aspicarpa brevipes*	(Sessé ex DC.) W.R.Anderson	Climbing
Malpighiaceae	*Bunchosia palmeri*	S.Watson	Tree
Malpighiaceae	*Byrsonima crassifolia*	(L.) Kunth	Tree
Malpighiaceae	*Gaudichaudia cycloptera*	(Moç. & Sessé ex DC.) W.R.Anderson	Climbing
Malpighiaceae	*Tetrapterys schiedeana*	Schltdl. & Cham.	Climbing
Malvaceae	*Heliocarpus occidentalis*	Rose	Shrub
Malvaceae	*Heliocarpus palmeri*	S.Watson	Shrub

Malvaceae	*Triumfetta galeottiana*	Turcz.	Shrub
Malvaceae	*Triumfetta heliocarpoides*	Bullock	Shrub
Malvaceae	*Triumfetta polyandra*	Sessé & Moc. ex DC.	Shrub
Martyniaceae	*Martynia annua*	L.	Herb
Menispermaceae	*Cissampelos pareira*	L.	Climbing
Moraceae	*Ficus insipida*	Willd.	Tree
Moraceae	*Ficus maxima*	Mill.	Tree
Moraceae	*Ficus pertusa*	L.f.	Tree
Moraceae	*Ficus petiolaris*	Kunth	Tree
Myrtaceae	*Syzygium jambos*	(Ruiz & Pav.) Holub	Tree
Nyctaginaceae	*Salpianthus purpurascens*	L.	Herb
Onagraceae	*Lopezia lopezioides*	(Hook. & Arn.) Plitmann, P.H. Raven & Breedlove	Herb
Onagraceae	*Lopezia semeiandra*	Plitmann, P.H. Raven & Breedlove	Herb
Onagraceae	*Ludwigia octovalvis*	(Jacq.) P.H.Raven	Herb
Opiliaceae	*Agonandra racemosa*	(DC.) Standl.	Tree
Orobanchaceae	*Buchnera pusilla*	Kunth	Herb
Orobanchaceae	*Castilleja tenuiflora*	Benth.	Shrub
Passifloraceae	*Passiflora edulis*	Sims	Climbing
Phyllanthaceae	*Phyllanthus tequilensis*	B.L.Rob. & Greenm.	Shrub
Pinaceae	*Pinus devoniana*	Lindl.	Tree
Pinaceae	*Pinus oocarpa*	Schiede	Tree
Pinaceae	*Pinus patula*	Schiede ex Schltdl. & Cham.	Tree
Pinaceae	*Pinus praetermissa*	Styles & McVaugh	Tree
Plantaginaceae	*Bacopa monnieri*	(L.) Wettst.	Herb
Poaceae	*Aristida ternipes*	Cav.	Herb
Poaceae	*Axonopus compressus*	(Sw.) P.Beauv.	Herb
Poaceae	*Bothriochloa hirtifolia*	(J.Presl) Henrard	Herb
Poaceae	*Bouteloua radicosa*	(E.Fourn.) Griffiths	Herb
Poaceae	*Bouteloua repens*	(Kunth) Scribn. & Merr.	Herb
Poaceae	*Bouteloua williamsii*	Swallen	Herb
Poaceae	*Digitaria argillacea*	(Hitchc. & Chase) Fernald	Herb
Poaceae	*Digitaria bicornis*	(Lam.) Roem. & Schult.	Herb
Poaceae	*Echinochloa colona*	(L.) Link	Herb
Poaceae	*Echinochloa crus-pavonis*	(Kunth) Schult.	Herb
Poaceae	*Eleusine indica*	(L.) Gaertn.	Herb
Poaceae	*Imperata brevifolia*	Vasey	Herb
Poaceae	*Lasiacis procerrima*	(Hack.) Hitchc. ex Chase	Herb
Poaceae	*Lasiacis ruscifolia*	(Kunth) Hitchc. ex Chase	Herb
Poaceae	*Leptochloa aquatica*	Scribn. & Merr.	Herb
Poaceae	*Melinis minutiflora*	P.Beauv.	Herb
Poaceae	*Melinis repens*	(Willd.) Zizka	Herb
Poaceae	*Muhlenbergia grandis*	Vasey	Herb
Poaceae	*Muhlenbergia tenella*	(Kunth) Trin.	Herb

Poaceae	*Oplismenus burmannii*	(Retz.) P.Beauv.	Herb
Poaceae	*Panicum parcum*	Hitchc. & Chase	Herb
Poaceae	*Panicum trichoides*	Sw.	Herb
Poaceae	*Paspalum convexum*	Flüggé	Herb
Poaceae	*Paspalum langei*	(E.Fourn.) Nash	Herb
Poaceae	*Paspalum notatum*	Flüggé	Herb
Poaceae	*Paspalum paniculatum*	L.	Herb
Poaceae	*Setaria parviflora*	(Poir.) M.Kerguelen	Herb
Poaceae	*Tripsacum dactyloides*	(L.) L.	Herb
Poaceae	*Tripsacum laxum*	Nash	Herb
Poaceae	*Tripsacum maizar*	Hern.-Xol. & Randolph	Herb
Pontederiaceae	*Heteranthera rotundifolia*	(Kunth) Griseb.	Herb
Potamogetonaceae	*Stuckenia pectinata*	(L.) Börner	Herb
Potamogetonaceae	*Stuckenia striata*	(Kunth) Blume	Herb
Primulaceae	*Ardisia revoluta*	Kunth	Tree
Ranunculaceae	*Clematis acapulcensis*	Hook. & Arn.	Climbing
Rhamnaceae	*Gouania lupuloides*	(L.) Urb.	Climbing
Rubiaceae	*Arachnothryx leucophylla*	(Kunth) Planch.	Shrub
Rutaceae	*Zanthoxylum fagara*	(L.) Sarg.	Shrub
Santalaceae	*Phoradendron quadrangulare*	(Kunth) Griseb.	Hemiparasite
Sapindaceae	*Serjania racemosa*	Schumach.	Climbing
Sapindaceae	*Serjania triquetra*	Schumach.	Climbing
Sapindaceae	*Thouinia acuminata*	S. Watson	Shrub
Sapindaceae	*Thouinia serrata*	Radlk.	Shrub
Schizaeaceae	*Lygodium venustum*	Sw.	Climbing
Scrophulariaceae	*Lamourouxia viscosa*	Kunth	Shrub
Selaginellacaeae	*Selaginella pallescens*	(C. Presl) Spring	Herb
Solanaceae	*Solanum candidum*	Lindl.	Herb
Thelypteridaceae	*Thelypteris hispidula*	(Decne.) C.F. Reed	Herb
Typhaceae	*Typha domingensis*	Pers.	Herb
Vitaceae	*Parthenocissus quinquefolia*	(L.) Planch.	Climbing
Woodsiaceae	*Athyrium skinneri*	(Baker) C. Chr.	Herb
Woodsiaceae	*Woodsia mollis*	(Kaulf.) J. Sm.	Shrub