



A critical review of Late Pleistocene human-megafaunal interactions in Mexico

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ABSTRACT

The timing and cause(s) of megafaunal (animals with body mass >44 kg) extinctions during the Late Pleistocene remain a topic of significant multidisciplinary interest. Determining the ecological and evolutionary history of megafaunal communities requires a detailed study of chronology, climate change, environment, and human impact. While some regions of North America are well-studied in this regard, others, such as Mexico, have been more neglected. This is despite the fact that, by the end of the Pleistocene, the region had witnessed the extinction of fourteen families (Chlamyphoridae, Megalonychidae, Mylodontidae, Felidae, Canidae, Ursidae, Tapiridae, Antilocapridae, Bovidae, Cervidae, Gomphotheriidae, Mammutidae, Toxodontidae, Macrauchenidae) and the regional extirpation of a further four (Equidae, Camelidae, Elephantidae and Megatheriidae). Moreover, this region is located at a biotic crossroads and has yielded some of the earliest dates for human occupation across the Americas. This makes Mexico an important study region to explore the effects of human presence and climate change on a variety of megafaunal species. However, research has been hindered by an uneven balance of research, preservation issues, lack of chronological control, and limited synthesis of the available data. In this paper, we provide a critical review of the available records of Late Pleistocene megafauna in Mexico and their relationship to human populations. We evaluate the quality of dates and stratigraphic contexts of recorded megafauna on a site-by-site basis while also exploring available information on human presence and impact on megafauna. We highlight that currently, the human impact on the decline of these populations is far from clear and that more multidisciplinary excavations of well-dated sites are needed. Nevertheless, we contend that current evidence suggests that human hunting of megafauna occurred across most of the Mexican territory in a variety of habitats, with some evidence in the south that these hunts were complemented by significant acquisition of small game, aquatic species and plant foods.

1. Introduction

The causes of the dramatic global loss of megafauna animals weighing up to 44 kg (Koch and Barnosky, 2006), have been the focus of multidisciplinary research involving palaeontology, ecology, archaeology and geology. Across North America alone, thirty-eight genera of mammalian megafauna did not survive into the Holocene, with one order becoming worldwide extinct (Notoungulata) and two others no longer occurring in the Americas (Perissodactyla, Proboscidea) (Arroyo-Cabrales et al., 2007; Meltzer, 2020). Four families have been extirpated (Equidae, Camelidae, Elephantidae and Megatheriidae), though numerous species were lost from within the surviving genera (Arroyo-Cabrales et al., 2010, 2016). It has been of particular interest

that these extinctions took place at the end of the Last Glacial Period (MIS2), coinciding with the time when environments were rapidly changing and when humans were entering the Americas (Chatters et al., 2014; Waters and Stafford, 2013; Waters, 2019; Prates, et al., 2020; Willerslev and Meltzer, 2021). This has led to much debate regarding the role of our species (e.g. through direct hunting or modification of the environment) and/or changing climate in the demise of these megafauna (Bergman et al., 2023). The debate has been particularly intense given the relevance of research looking at the decline of megafaunal biodiversity in understanding the loss of megafauna in the 21st century, which some have described as the sixth mass extinction event (Dirzo et al., 2014; Kidwell, 2015; Ceballos and Ehrlich, 2023). Nevertheless, as in other parts of the world, such studies have often proposed broad,

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sweeping, either/or arguments for extinction drivers in North America, neglecting the significance of local/regional-based variability, particularly in terms of ecosystem responses to climate change, and specific ecological adaptations and behaviours of individual species (Price et al., 2018; Hocknull et al., 2020).

Recent research has provided new evidence refining what we know about the peopling of North America (Jenkins et al., 2012; Gruhn, 2020; Waters et al., 2020; Stewart et al., 2021; Willerslev and Meltzer, 2021; O'Keefe et al., 2023). Traditionally, human arrival around 16,000 cal yr BP had been associated with the rapid dispersals of hunter-gatherer groups with specialized weaponry (i.e. Clovis points) for hunting large game (Martin, 1966; Waters et al., 2018; Waters, 2019). However, new dating efforts and the emergence of novel sites have shown that foraging groups with expedient technology and generalized foraging patterns were already present during the Last Glacial Maximum (LGM) (~26–19 ka ago) (Ardelean et al., 2020; Bennett et al., 2021; Gruhn, 2023). Potential variations in temporal overlap between humans and megafauna in different parts of North America, as well as limited direct evidence for human-megafauna interactions (i.e. anthropogenic modification such as butchery marks), have led to discussion as to the extent to which humans may have been involved in the demise of different taxa. Similarly, there are also debates relating to the degree to which fauna responded to late Quaternary abrupt climate changes in the form of catastrophes, ecosystem dynamics, and even changes to the carbon cycle (Barnosky, 1989; Berzaghi et al., 2018; Stewart et al., 2021). More nuanced explanations highlight the interplay of anthropogenic and climatic factors in megafauna extinctions (Haynes, 2002; Broughton and Weitzel, 2018; O'Keefe et al., 2023). To date, however, much of these discussions have focused on the temperate and subarctic regions of Canada and the United States of America (Haynes, 2002; Goebel et al., 2008; Potter et al., 2018; Meltzer, 2020; Murchie et al., 2021), where there has been a longer history and better records of dated archaeological and paleontological sites.

By contrast, the North American tropics remain remarkably neglected despite evidence for major extinctions in this region (Borrero, 2009; Cione et al., 2009; Barnosky and Lindsey, 2010). Mexico is not only home to some of the earliest alleged evidence of *Homo sapiens* on the continent (González et al., 2003; Ardelean et al., 2020), but also hosted species common to temperate and tropical ecosystems such as horses (*Equus conversidens*), proboscideans (*Cuvieronius* sp., *Mammuthus* sp. and *Mammot* sp.), tapirs (*Tapirus haysii*), llamas (*Hemiauchenia* sp.), ground sloths (*Paramylodon harlani*, *Nothrotheriops* sp., *Eremotherium* sp.), glyptodonts (*Glyptotherium* cf. *floridanum*), saber-tooth cat (*Smilodon fatalis*), short-faced bear (*Arctodus simus*), and American lion (*Panthera leo atrox*), among others (Ferrusquía-Villafranca et al., 2010; Arroyo-Cabrales et al., 2010). This makes it a particularly interesting region to study different environmental responses to Pleistocene climatic changes. Towards the end of the Pleistocene and Early Holocene, fourteen families were extinct in Mexico (Chlamyphoridae, Megalonychidae, Mylodontidae, Felidae, Canidae, Ursidae, Tapiridae, Antilocapridae, Bovidae, Cervidae, Gomphotheriidae, Mammutidae, Toxodontidae, Macrauchenidae) but extant outside this country (Equidae, Camelidae, Elephantidae and Megatheriidae). Moreover, during the latest Pleistocene glaciation, landscape and ecological changes accompanied several terrestrial mammal migrations, including *Homo sapiens*, and major interchange events from both Eurasia and South America (Graham, 1979; Schubert et al., 2019). Given its location at a biotic crossroads, the age of the evidence for the presence of prehistoric human groups and the great diversity of cultures that later settled in this part of the Americas, Mexico provides the ideal setting for exploring the regional impacts of human presence and climatic change on different taxa.

This paper aims to contribute to studying megafaunal extinction in the Americas by compiling and examining available evidence for human-megafauna interactions during the Late Pleistocene in Mexico. We seek to lay the foundations for a comprehensive evaluation of the zooarchaeological record across the modern Mexican territory by

providing a detailed review of available data on megafaunal remains at several archaeological key sites. By carefully documenting and synthesising the distribution of these interactions, we also formulate hypotheses relating to different subsistence strategies by forager groups during periods of changing climatic conditions. We aim to explore the process of megafaunal extinction in this part of tropical North America by undertaking a comparative, detailed local and regional assessment of chronology, climatic and environmental change, and human presence and interaction. We summarise information from the available literature by describing, tabulating, quantifying and plotting data from all relevant studies. This allows the creation of a dataset for comparison with other parts of the Americas to assess the presence of concrete evidence for human-megafaunal interactions. Existing palaeoenvironmental data directly related to the megafauna and from the sites studied are discussed, together with reported archaeological evidence and radiocarbon dates where available. To provide a more detailed analysis, we decided not to include findings that indicate the presence of prehistoric humans in Mexico without an alleged association with faunal remains. (e.g. prehistoric human remains, isolated hearths and/or lithic tools) and overlay our data with the biogeography of Mexican Pleistocene mammals proposed by Ferrusquía-Villafranca et al. (2010).

1.1. Studies of past human-megafauna interactions in Mexico: zooarchaeology, palaeontology and recent multidisciplinary studies

Mexico is located in the southern part of North America, in the transition zone between the Neotropical and the Nearctic regions, extending from approximately 16° to 32°N and 82° to 115°W at its widest points. Within its borders are various environments, from tropical rainforests in the southern lowlands to deserts in the north, with cool pine forests in the highlands and ice-capped volcanoes in the Trans-Mexican Volcanic Belt. High mountain ranges along the Pacific coast act as a partial barrier to the east-west movement of terrestrial mammals, channelling species north-south (Ferrusquía-Villafranca, 1998; Ferrusquía-Villafranca et al., 2010; Schubert et al., 2019). Apart from the influence of elevation, the climate of the Neotropics is largely determined by the amount and seasonal distribution of precipitation, rather than by changes in temperature (Roberts et al., 2021). Palaeoenvironmental reconstructions suggest that conditions in the Pleistocene were very different from those of today (Cruz et al., 2016, 2023; Tomas-Mosso et al., 2024; Vázquez-Selem and Heine, 2011). The climate was on average 7 °C colder and overall drier and temperate pine-oak forest prevailed in the high areas, with mesophyll rainforest in the wetter regions of the Gulf of Mexico slope (Metcalf et al., 2000). The driest regions of the Pacific and the Yucatan Peninsula were dominated by deciduous forests, bushes and grasslands (Piperno and Pearsall, 1998; Metcalf et al., 2000; Ferrusquía-Villafranca et al., 2010). The heterogeneous and complex distribution of biota favoured the development of specific ecosystems capable of supporting a wide range of mammals of diverse origins, some of which are now extinct. For example, microhabitats are thought to have existed within localities, as evidenced by the co-occurrence of at least three Late Pleistocene horse species (*Equus* sp.), despite allopatric speciation being the rule in the distribution of equids (Alberdi et al., 2014).

Early explorations by the 'Comission Scientifique du Mexique' revealed fossil deposits of extinct Quaternary fauna along with stone tools such as arrowheads and hand axes in various layers containing the remains of extinct animals from the Late Pleistocene. Although these pioneering investigations shed light on early human presence in the area studied (Guillermin-Tarayre, 1867; Hamy, 1878, 1884), information on those fossil accumulations is limited. In some cases, only a minimal and general identification of the fauna represented is available, without details of the stratigraphy. They are generally described as a series of overlapping assemblages (palimpsests) in which the materials are mixed. Based on the spatial association alone, and in line with studies of their time in Europe, specialists interpreted these findings as evidence of

prehistoric hunting of extinct large game (Aveleyra Arroyo de Anda, 1967). Despite the lack of compelling evidence to support those interpretations, these early works played a crucial role in kickstarting Quaternary research in Mexico, and eventually led to widespread interest among Mexican scientists in exploring the early occupation of the study area, focusing on chronology, as well as prompting multidisciplinary debates on the interactions between the first settlers and the extinct fauna of the Late Pleistocene in Mexico (Orozco and Berra, 1880; Chavero, 1881; Barcena, 1882; Cope, 1884; Herrera, 1893; Felix and Lenk, 1899; Freudenberg, 1910; Furlong, 1925; Arellano, 1946; De Terra, 1947, 1959; Aveleyra Arroyo de Anda and Maldonado-Koerdell, 1953; Aveleyra Arroyo de Anda, 1955, 1956, 1961, 1962, 1964, 1965, 1967; Armenta Camacho, 1959, 1978; Romano, 1963; Álvarez, 1969; García Cook, 1973, 1974; Lorenzo and Mirambell, 1981, 1986, 1986a, 1999; Solórzano, 1989; Pichardo, 1997, 1999, 2000, 2001; López-Oliva et al., 2001).

Recent discoveries at Chalchihuite Cave suggest that the first human groups were present in north-central Mexico during the LGM. However, the only human skeletons that have been directly dated using radiometric methods, confirming the presence of human populations in the country at the end of the Pleistocene, date back to around 12.5 ka (González et al., 2003; Chatters et al., 2014). This evidence comes from locations more than 1000 km apart, with an altitudinal difference of just over 2000 m, specifically from the lake basins of the volcanic highlands in central Mexico and the submerged caves along the eastern coast of the Yucatán Peninsula (Gonzalez et al., 2015; Chatters et al., 2014). In the first case, the fossil deposits from this region are characterised by fauna typical of the Late Rancholabrean age, which is mainly distinguished by the presence of the genus *Bison*, indicative of a grassland ecosystem. At least 271 of these sites have yielded large numbers of plain mammoth (*Mammuthus columbi*) remains, of which only six are considered reliable to support these interactions, based on taphonomic studies, detailed assessment of stratigraphy and the use of radiometric dating techniques (Arroyo-Cabrales et al., 2006). Among the best documented is the Tocuila site, where the remains of seven plain mammoths have been found together, some of them with breakage patterns suggestive of intentional fracture for the manufacture of cores and blanks for tool production (Johnson et al., 2012). Meanwhile, from the Yucatan Peninsula, the occurrence of extinct fauna and humans has been reported in the submerged caves and the dry Loltún cave; technical divers have discovered eight partial human skeletons and an extant peccary (*Pecari tajacu*) dentary that shows evidence of human modification (Stinnesbeck et al., 2017b; Schubert et al., 2021). The mammal record found in these caves consists of tropical species like various ground sloths, tapirs, sabertooth cats, cougars, gomphotheres, and canids, as well as temperate species such as horses, Pleistocene wolves, bears, and bison.

Ongoing research looking at various palaeoecological proxies is providing insights into early hunter-gatherer subsistence economies and ultimately their interactions with megafauna. Research conducted in the southwest of the country, specifically in the cave of Santa Marta, Chiapas, indicates that the earliest settlers in Middle America played a significant role in the early modification of tropical ecosystems through anthropogenic-caused burning of areas (Acosta et al., 2018). This led to an increase in the number of plants with known human uses, such as *Physalis* sp. (green tomato), *Zea mays* (teosinte), and *Theobroma cacao* (cacao) between 12 and 9.8 thousand years ago (Acosta et al., 2018; Solís-Torres et al., 2021). The possibility of early plant management in the tropical regions of southeastern Mexico provides new insights into the behaviour of early settlers and indirectly broadens the debate on megafaunal-human interactions, particularly when assessing whether these groups were “large-game specialists” or “generalized foragers” (Solís-Torres et al., 2020). Furthermore, the study of technological complexes and prey selection in the region reveals intensive hunting of small and medium-sized game, complemented by the exploitation of aquatic species such as freshwater snails and swamp turtles. This

suggests a wider cultural and economic variability among early settlers that is not discussed in this paper but is important to note.

2. Method

We analysed the Pleistocene zooarchaeological record of Mexico across time and space in three ways: i) by reviewing the existing record of extinct megafauna from archaeological contexts ii) by evaluating evidence of anthropogenic modifications or artefact association with megafauna remains, and iii) by critically evaluating the existing age assignments. In the case of ii) it was necessary to define alleged interactions between extinct Pleistocene megafauna and human activity at Mexican sites based on the spatiotemporal associations of artefacts and faunal records and where there is clear evidence of butchering (e.g. taphonomic indicators such as bone surface modifications or spiral fractures). These records of human-megafauna interactions were derived from exhaustive searching of published scientific sources, including articles, books and book chapters, conference proceedings, publicly available academic theses, and archaeo-paleontological reports in both English and Spanish. These were retrieved through academic search engines (e.g. Web of Science, Scopus, PubMed and Scielo). In the online searches, we used the following keywords: “zooarchaeology”, “human-megafauna interaction”, “late Quaternary extinction”, “megafauna”, “megafauna exploitation”, “megafauna butchering”, “megafauna extinction”, “megafauna hunting”, “Mexico megafauna hunting”, “Mexican prehistory”, and “Mexican Quaternary”. We selected all articles on Mexican archaeological sites with any information on human-megafauna interactions. We also referred to other sources, such as FAUNMAP (FAUNMAP Working Group, 1996) and a database of Mexican Quaternary mammals (QMMDb) by Arroyo-Cabrales et al. (2007), which lists all mammals known in Mexico just before and at the time of the appearance of humans, as well as previous reviews focusing on evidence of human presence in the Americas, such as that by Guadalupe Sánchez (2016).

To make the records accessible, we created a database (fully available in the Supplementary Information) of the sites where human-megafauna interactions have been reported (direct/indirect), the species assigned to the faunal remains, and the types of materials and the archaeological evidence reported, including provenance data (site location and radiocarbon dates when available). For spatial analysis and comparisons between the palaeoecological indicators and the records of the human-megafauna interaction, we plotted our data collection on a morphotectonic provincial map of Mexico, following the scheme delineated and fully characterised by Ferrusquía-Villafraña (1993, 1998), which corresponds to broad regional patterns with meaningful biotic physiogeographic boundaries, and the chronological framework used by Bell et al. (2000). The integration of this information provides a better understanding of the type of environment in which these interactions occurred and fills an important geographical gap in the global literature reviews of archaeological evidence for the exploitation of now-extinct megafaunal populations.

2.1. The geographic framework

Morphotectonic provinces (MP) are practical spatial frameworks for objectively and systematically describing large areas, including their soils, vegetation (cover), fauna, flora, and biota, both recent or fossil (Ferrusquía-Villafraña et al., 2010). For a more detailed account of local ecological adaptations and the type of environments in which interactions took place, the analysis of our results has been compared across the following Morphotectonic Provinces (MP) (Fig. 1): BCP, Baja California Peninsula; NW, Northwestern Plains and Sierras; SMOc, Sierra Madre Occidental; CH-CO, Chihuahua-Coahuila Plateaus and Ranges; GCP, Gulf Coastal Plain; SMO, Sierra Madre Oriental; CeP, Central Plateau; TMVB, Trans-Mexican Volcanic Belt; SMS, Sierra Madre del Sur; CHI, Sierra Madre de Chiapas; and YPL, Yucatan Platform.

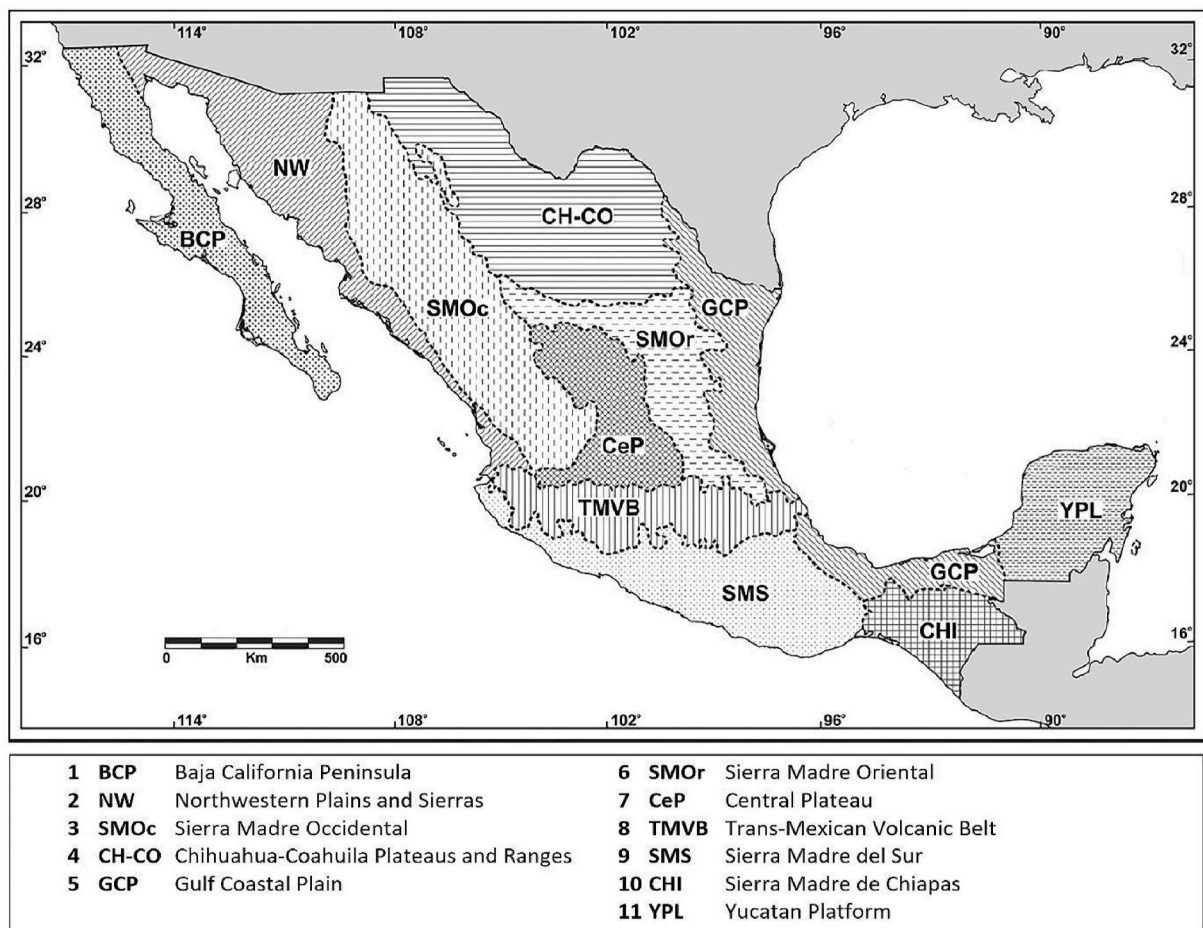


Fig. 1. Morphotectonic provinces of Mexico (modified from Ferrusquia et al., 2010).

Previous research used these MP for biogeographic studies in Mexico (Ferrusquía-Villafranca and Ruiz-González, 2015). These provinces are not only helpful for identifying areas of fossil occurrence but also serve as a standard for similar studies in the country and enable comparisons to be made between different areas.

3. Results

We summarise the evidence for human-megafauna interactions on a site-by-site basis, highlighting the regional characteristics of each during the Late Pleistocene. A total of 216 publications were assessed for this review, including articles published in peer-reviewed journals, theses, reports and other books and book chapters in digital form. The results are summarised as follows: Of the eleven provinces, four had no evidence of human-megafauna interaction (BCP, CeP, CH-CO and SMOc). There is only one documented case in the NW and CHI provinces. Two sites are reported north of the GCP, and two more are recorded in the SMS. The majority of records are concentrated in the TMVB, which contains fifteen records, followed by five for the SMOr and four for the YPL (see Fig. 2). Families are listed by number of occurrences by locality from highest to lowest: Elephantidae (14), Camelidae (3), Gomphotheriidae (3), Equidae (2), Bovidae (1), Megatheriidae (1), Ursidae (1), and Antilocapridae (1). Nevertheless, some studies have reported evidence of human presence in palimpsest contexts with remains of different taxa and have not been considered in the previous count (see SI). In addition to the fact that many previous identifications of specific species require more detailed approaches to taxonomic identification and megafaunal ecology (Schubert et al., 2019). This is particularly the case as major palaeoclimatic and palaeoenvironmental changes have

been documented in this part of the Americas during the Late Pleistocene and Holocene (Ceballos et al., 2010; Ferrusquia-Villafranca et al., 2010). Furthermore, the Pleistocene mammal record of Mexico is mainly biochronologically dated because few radioisotope and paleomagnetic calibrated dates exist (Pichardo, 2000; Arroyo-Cabrales et al., 2003; Mead et al., 2006). Thirty localities are presented here as sites with probable evidence of human interaction with the megafauna. These are divided into two categories according to their type of interaction: direct (18), where taphonomic traits were analysed and attributed to anthropogenic origin (e.g. cut marks, polish, intentional fractures, etc) or/and in association with archaeological evidence; and indirect (12), in contexts where the stratigraphic control is scarce or comes from palimpsest-type contexts where different taxa are represented, in most of these cases the association based on original observations and reports. Of the total, only five have yielded direct radiometric dates on bones Chalchihuite Cave, Tlapacoya, Tocuila, Hoyo Negro and Las Palmas. The rest yielded dates from charcoal, shell, obsidian and soil samples from the units containing the fossil materials. In the case of the Basin of Mexico, maximum and minimum ages are commonly derived from the volcanic layers that seal the fossil deposits, others are not dated at all. (See Table 1). The list of families reported at each site is presented below.

3.1. Large herbivores

Equidae: SMOr (La Morita and El Cedral), TMVB (Valsequillo), CHI (Los Grifos), and YPL (Loltún). The most significant evidence of interaction comes from the Los Grifos site in Chiapas, where horse remains have been found alongside abundant lithic material in excavated

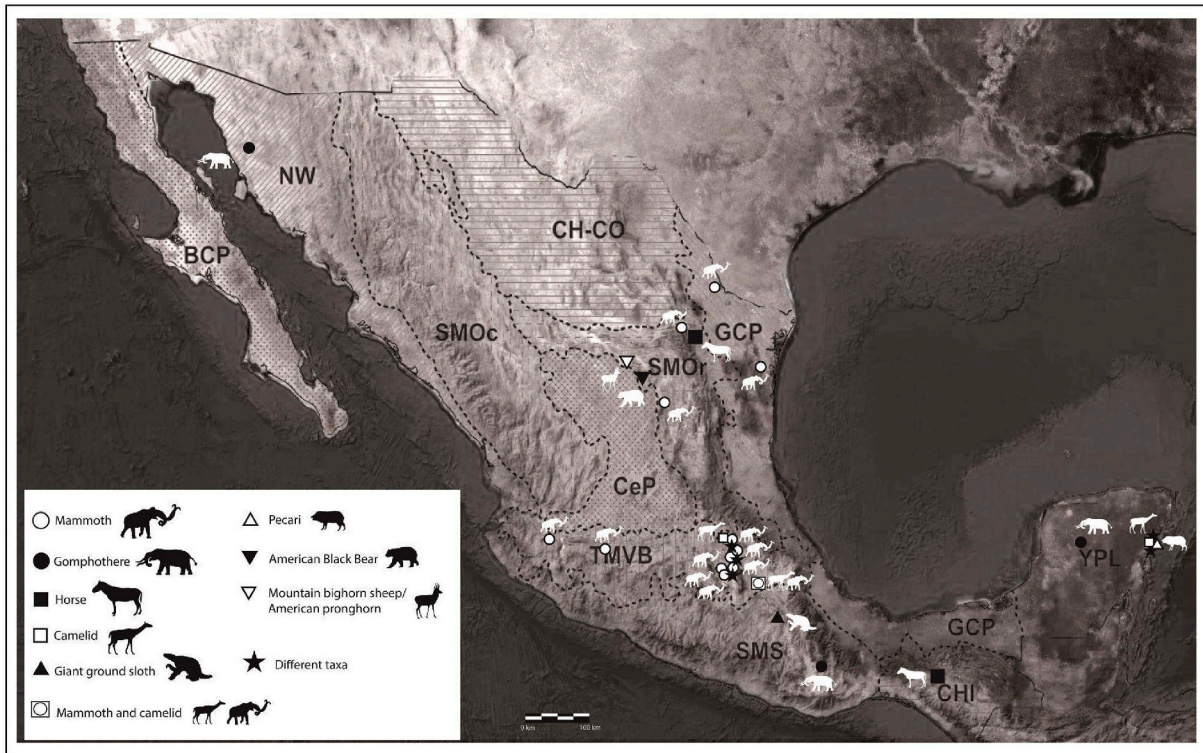


Fig. 2. Location within the MPs of the human-megafauna interactions in Mexico during the Late Pleistocene.

stratigraphic units. In the location of El Cedral, numerous ash and carbon lenses, interpreted as 'hearths', have been reported scattered among horse and other animal remains, of particular interest is a coal concentration surrounded by mammoth patellas. In addition, three different species of horse were identified using morphometric analyses. Archaeological evidence included a circular chert flake scraper and evidence of human modification on a horse tibia. The systematic excavations of levels with lithic materials at Loltun Cave have yielded a large number of extinct horse remains. However, this case has no reliable record of the stratigraphy and horizontal plane findings.

Tapiridae: SMOr (El Cedral) and YPL (Hoyo Negro). In both cases, the remains are found mixed with other extinct faunal remains in units with evidence of human presence.

Elephantidae: TMVB (El Cedral, Zacapú, Chapala-Zacoalco lakes, Los Reyes la Paz y Los Reyes Acozac, Snta. Lucía, San Bartolo, Tlapacoya, Tepexpan, La Villa de Guadalupe, and Chimalhuapan), SMOr (El Cedral), SMOr (La Estanzuela), GCP (A. Chorreras y A. Arenillas) and TMVB (Chapala). The best documented and studied interaction between humans and megafauna is that of mammoths. At El Cedral the earliest reported presence of this interaction, although debated, is possible evidence of human groups during the LGM. Despite the controversy over its antiquity, it is clear that during the Late Pleistocene humans exploited the marshy conditions around Lake Texcoco to hunt proboscideans trapped in the mud or to exploit individuals killed in these natural traps or by other carnivores, although direct or indirect access to prey has received little or no study. Intentional bone surface modifications indicate that humans consumed the meat and used the skeletal remains for tool making.

Gomphotheriidae: NW (El fin del Mundo), SMS (El Pocito), and YPL (Loltún). Evidence of hunting through the direct association of Clovis artefacts with the remains of two gomphotheres was reported at the Fin del Mundo site, despite the eroded stratigraphy of the site, the discovery was made in systematic excavations. The presence of Clovis technology and the ages obtained confirm the presence of a cultural affinity in northern Mexico with those of temperate climates.

Camelidae: SMOr (El Cedral), TMVB (Tlapacoya, Valsequillo), and YPL (La Chimenea). In Tlapacoya, El Cedral and La Chimenea, the evidence is associated with hearths and, in the case of El Cedral in occurrence with lithic tools and a very early date. Unfortunately, in all cases, there is no detailed taphonomic study of these remains. At the site of La Chimenea, the remains were reported since their discovery as possibly having been burnt in a submerged context; however, no subsequent analysis was carried out to confirm this evidence, nor to study the intentional fractures mentioned.

Antilocapridae: TMVB (Valsequillo) and SMOr (Sima de las Golondrinas). The most reliable evidence comes from the Sima de las Golondrinas site, in the form of cut marks and intentional modifications on leg bones, tibia and phalanges, the latest, with ages dating to the end of the LGM, reported as some of the oldest forms of art in the Americas. In Valsequillo, the remains come from a palimpsest context, associated with lithic materials and remains of other extinct species.

Bovidae: SMOr (Sima de las Golondrinas and El Cedral), TMVB (San Vicente Chicoloapan, Tlapacoya, Valsequillo) and YPL (Loltún). Most of the records correspond to *Bison* sp., except for the mountain-adapted bighorn sheep, *Ovis canadensis*, recovered from the Sima de las Golondrinas and showing cut marks in a time preceding the Bølling-Allerød. In contrast to the northern latitudes of the Americas, interaction with genus *Bison* is very scarce and limited to the association of remains of these animals with archaeological material, without any evidence of intentional bone surface modifications.

Chlamyphoridae: TMVB (Valsequillo). The only locality in which this probable interaction is reported is Valsequillo; however, it is a palimpsest site in which the horizontal location of cultural materials and glyptodon remains are not reported, and no other evidence is reported for this family.

Megatheriidae: SMS (Chazumba) and YPL (Hoyo Negro). Evidence from the Chazumba site exists in the form of cut marks on the pelvis of a Giant ground sloth claw (*Eremotherium*) which have been recorded by electron microscopy and come from a recent systematic excavation. It is worth noting that in the south of the Americas, there is compelling

Table 1
Mexican records of paleoarchaeological sites containing human and megafauna remains, along with their associated radiometric dating.

Site	Zone	Location	Taxa	Type of interaction	Date	Type of material
El Fin del Mundo	NW	Sonoran Desert	<i>Cuvieronis</i> sp.	Direct: Clovis points and flakes are scattered in and around two bone concentrations.	11,560 yr BP (13,390 cal yr BP (AA-100181A) (Sanchez et al., 2014)	Charcoal
La Morita	SMOr	Nuevo Leon	<i>Equus</i> sp.	Direct: Polished bones, and burned molars of a horse.	9230 ± 45 yr BP (OxA-17377) and 8935 ± 66 yr BP (Valadez-Moreno, 2006).	Charcoal
Chalchihuite cave	SMOr	Astillero, Mountains, Zacatecas	American black bear (<i>Ursus americanus</i>).	Direct: Three limestone flakes, presumably human-made, were found by sieving, in the same layer as a bear baculum and burnt phytolites, hypothetically brought by people to the cave.	27,830 ± 150 yr BP (Beta-345055) (Ardelean et al., 2020)	Bone
Sima de las Golondrinas	SMOr	Zuloaga mountains, Zacatecas.	Mountain bighorn sheep (<i>Ovis canadensis</i>), American pronghorn (<i>Antilocapra americana</i>).	Direct: Some specimens present butchery-related cut marks, but also engravings possibly related to early symbolic behaviours.	13,435 ± 30 (UCIAMS-233328) (16369-12981 yr cal BP) and 12,948 30 (LEMA-1579) 15687-15265 yr cal BP (Ardelean et al., 2023)	Charcoal
El Cedral	SMOr	Rancho La Amapola, San Luis Potosí	<i>Mammuthus</i> sp.	Direct: Stone artefacts and hearths lined with mammoth leg bones.	37,694 ± 1963 yr BP (INAH-305) and 25,682 ± 1418 BP (INAH-303) (Mirambell, 1994, 2012; Lorenzo and Mirambell, 1999)	Charcoal, soil and preserved wood
Lake Texcoco Mammoth	TMVB	Edo. México	Mammoth	Indirect: Two obsidian flakes and one basalt flake were associated with the bones.	12,600 yr BP (Arroyo-Cabrales et al., 2010)	Obsidian
Los Reyes la Paz	TMVB	Los Reyes la Paz, Edo. Mexico	Mammoth	Indirect: Two bone artefacts were recovered that were associated stratigraphically with mammoth and other extinct animals.	18,280 ± 160 yr BP (García Cook, 1974).	Charcoal
Los Reyes Acozac Mammoth	TMVB	Los Reyes Acozac, Edo. Mexico	Mammoth	Indirect: Two flakes, one of basalt and the other of obsidian, were found in the excavation area.	10,400 yr BP (Arroyo-Cabrales et al., 2010)	Obsidian
Santa Lucia I	TMVB	Air Force Base No. 1 in Santa Lucia, Edo. México	Mammoth	Indirect: One obsidian flake and two andesite flakes were found in the same excavation area.	23,900 ± 600 yr BP (I-10.427), 26,300 ± 880 yr BP (GX-6.628) (Lorenzo and Mirambell, 1986a)	Soil
San Bartolo Atepehuacan	TMVB	San Bartolo Atepehuacan, Edo. Mexico,	Mammoth	Direct: A concentration of 59 flakes and chips of obsidian and fine-grained basalt were found in association with the articulated vertebrae of a mammoth.	9670 ± 400 yr BP. (M-774) (Arroyo-Cabrales et al., 2006)	Charcoal
Santa Isabel Iztapan I and II	TMVB	Santa Isabel Iztapan, Edo. Mexico	Mammoth	Direct: A projectile point and five more artefacts were found lodged between two mammoth ribs.	9900 to 8300 yr BP (Aveleyra Arroyo de Anda, L., 1964)	Charcoal
San Vicente Chicoloapan	TMVB	San Vicente Chicoloapan, Edo. Mexico	<i>Bison priscus</i> , <i>Camelops</i> sp. And <i>Mammuthus</i> sp.	Indirect: Extinct fauna associated with human remains. Fireplace, reddened stones and rock artefacts such as grinding stones, metates and manos.	5600 (23-2) and 7000 yr BP (23-3) (Friedman and Smith, 1960)	Obsidian
Tlapacoya	TMVB	Cerro Tlapacoya, Edo. Mexico	<i>B. latifrons</i> , <i>Camelops hesternus</i> , <i>O. halli</i> , <i>Ursus americanus</i>	Indirect: Association of hearth and lithic with extinct fauna in the same excavation area.	A) 10,200 ± 65 yr BP (OxA-10225) (González et al., 2003), B) 24,000 ± 4000 (A-794b) and 21,700 ± 500 (I-4449) (Haynes, 1967)	A) Human bone, B) Humic soil extracts and charcoal
Tocuila	TMVB	Tocuila, Edo. Mexico	Mammoth	Direct: Several pieces of mammoth bone have been interpreted as “clearly” modified by humans.	A) 11,100 ± 80 yr BP (OxA-7746), B) 11,277 ± 139 INAH-1658 (Morett et al., 2003)	A) Bone, B) Charcoal
Valsequillo	TMVB	Puebla	Mammoth and Camelid	Direct: humanly modified bones (butchered and engraved) and stone artefacts associated with megafaunal remains.	20,000 ± 1500 yr BP (21,850 ± 850 cal yr BP) (M-B-6) (Szabo et al., 1969)	Shell
Chazumba	SMS	Chazumba, Oaxaca	Giant ground sloth (<i>Eremotherium laurillardii</i>)	Direct: Cut mark detected on one of the bones of <i>Eremotherium</i> .	23,420 ± 90 yr BP (27,720 - 27,500 cal BP, 2s CI) (Viñas-Vallverdú et al., 2017)	Charcoal
Los Grifos	CHI	Central Depression of Chiapas	<i>Equus</i> sp.	Direct: The association of lithic artefacts, such as scrapers with lateral spurs and a chert projectile point, with horse remains (<i>Equus</i> sp.).	8930 ± 150 yr BP (I-10760) and 9460 ± 150 yr BP (I-10760) (García-Bárcena and Santamaría, 1982)	Charcoal
Loltún	YPL	Oxkutzcab, Yucatan	<i>Cuvieronius</i> sp.	Indirect: Lithics were found near Pleistocene fauna remains.	12,790 ± 40 yr BP. (Beta-157084) (Morales-Mejía et al., 2009)	Charcoal
Hoyo Negro	YPL	Tulum, Quintana Roo	Different taxa	Indirect: Human remains and extinct fauna are in contextual association.	10,970 ± 25 yr cal BP (UCIAMS- 119438) and 10,985 ± 30 yr (UCIAMS- 123541) (Chatters et al., 2014)	Human bone
Las Palmas	YPL	Tulum, Quintana Roo	Different taxa (unidentified)	Indirect: Human and extinct fauna remains in contextual association.	A) 6941 ± 39 yr BP (INAH-2123) and B) 8050 ± 130 yr BP (UGA-6828) (González-González et al., 2008)	A) Charcoal B) Human bone

evidence of the exploitation of extinct genera of ground sloth carcasses.

3.2. Large omnivores and carnivores

Tayassuidae: YPL (Muknal Cave). The only site where this interaction is reported is the submerged cave of Muknal, the identification of the species is still controversial, however, the atrophic modification is reliable. Based on the characteristics of the fossil and the location of the find, it is dated to the Late Pleistocene.

Felidae: TMVB (Santa Lucía) and YPL (Hoyo Negro). In the Santa Lucia site, the remains of a sabre-tooth cat were recovered from the same stratigraphic unit as other Pleistocene faunal remains, along with lithic material. Similarly, in overlapping assemblages, human and canid skeletons (*Procyon troglodytes*) were found in the submerged cave of Hoyo Negro.

Ursidae: TMVB (Tlapacoya), SMOr (Chalchihuite cave) and YPL (Hoyo Negro and Loltún). In the cases of the Chalchihuite Cave and Tlapacoya, the evidence comes from the associated remains of black bear (*Ursus americanus*) with stone artefacts. In Chalchihuite Cave a baculum (penis bone) has been used to date a layer with lithic materials that have been classified as a previously unseen industry used by forager groups during the LMG. Ancient environmental DNA results show the highest abundance of this species occurs in a period when the cave was occupied by human groups. In Hoyo Negro, the remains of an extinct genus of the Pleistocene short-faced bears (*Arctotherium wingei*), previously restricted to South America, extend the record to the north and are found in a palimpsest context with Late Pleistocene human remains.

4. Discussion

Our analysis of the available records shows that American artiodactyl populations must have been valuable prey during the terminal Pleistocene, in terms of food or exploitation of carcasses. This is consistent with the large geographical range of the interaction between humans and the families Bovidae (*Ovis canadensis* and *Bison* sp.) and Camelidae (*Camelops hesternus* and *Hemiauchenia macrocephala*). However, the widest spatial range involves interactions with Equidae in two MPs in very distant latitudes, such as La Morita and Los Grifos. The interactions with megabaric carnivores of the families Felidae (*Smilodon* sp.) and Ursidae (*Ursus americanus* and *Arctodus simus*) are interesting as they may have involved cave (Hoyo Negro and Chalchihuite Cave) and open space interactions (Santa Lucia I and Tlapacoya). In both cases, there is no evidence of direct interaction or competition for carcasses. Instead, evidence of human presence and faunal remains occur in the same context (Hoyo Negro), or the same stratigraphic layer (Chalchihuite Cave, Tlapacoya and Santa Lucia 1). Any kind of human encounter with these large carnivores forces us to consider the subsistence and sheltering strategies of the first hominins in the Americas and the competition for access to natural resources. This debate is furthered by the large fossil record of carnivores from some localities, such as Hoyo Negro, El Cedral and Valsequillo, which suggest the importance that these interactions must have had, but which unfortunately have been left aside for preservation reasons. Records of bighorn sheep (*Ovis canadensis*) and pronghorn (*Antilocapra americana*) are noted here as extirpated species from the province from which they are reported (TMVB and SMOr). Regarding the proboscideans, only the genera *Cuvieronius* and *Mammuthus* are represented, Notably, the NW has the only record of human gomphothere association in North America. In contrast, evidence of mammoths is abundant, primarily concentrated in the northeast region of Mexico, extending into the TMVB. During the Late Pleistocene, the TMVB was likely a significant resource hub and a transit point on the routes for human populations and megafaunal migrations of that period. The large number of interactions between humans and mammoths have been evaluated in detail by Arroyo-Cabrales et al. (2006). It is here crucial to highlight that the available evidence for these ecological interactions is geographically limited,

primarily spanning the northern regions of the continent extending towards this MP. In particular, the Rancho La Brea site in the southwestern US has provided remarkable insights through recent findings that utilize high-resolution chronological control of the animal entrapment, combined with an extensive palaeoclimatic record. These discoveries have unveiled a synchronous pattern of local extirpations among various taxa, including *Smilodon*, *Aenocyon*, *Panthera*, *Equus*, and *Bison antiquus*. This comprehensive study offers a compelling overview suggesting that both climatic shifts and anthropogenic factors were pivotal in driving this extinction event. Notably, these extirpations occurred just before the onset of the Younger Dryas, and well ahead of the broader continental loss of North American megafauna. Furthermore, the evidence points to even earlier local extinctions, as seen with the camels and sloths during the Bølling–Allerød Interstadial (14.69–12.89 ka), illustrating a complex mosaic of interrelated biological and environmental changes throughout this period. Similar cases of human impact on the landscape and local fauna have been reported in Australia, New Zealand and Panama, among other regions (O’Keefe et al., 2023). Beyond nuanced views, recent studies conducted in both hemispheres of the Americas support Martin’s proposal regarding the rapid spread of big-game hunters using fluted points throughout the continent. These studies reinforce the idea that humans played a significant role in the extinction of megafauna (Prates et al., 2020; Prates and Perez, 2021; Chatters et al., 2024). However, uncertainty still exists, and it may not yet be possible to resolve the overkill debate as proposed by Stewart et al. (2021, 2022) and Cooper et al. (2015).

To expand our understanding of the changes in mammalian biodiversity during the Late Pleistocene, which has been the focus of previous studies by Arroyo-Cabrales et al. (2010) and Ferrusquia et al. (2010), and ongoing scientific database projects (<https://www.neotomadb.org/> and FAUNMAP), and to provide a more detailed analysis to complement previous compilations of the early human presence in Mexico (Sanchez, 2001; Pichardo, 2003; González et al., 2001; Gonzalez and Huddart, 2008; Ardelean et al., 2019), we present the first overall critical review of human-megafaunal interactions in Mexico. This research allows us to gain a more detailed and clearer picture of how our species might have interacted with different megafauna species in the Late Pleistocene. At the same time, it highlights the limitations of our understanding of the timing, seasonality, and nature of these interactions. This article focuses on the faunal remains found in archaeological contexts that allow for a direct assessment of the species selected by human groups. We have not included evidence of Late Pleistocene human groups dependent on aquatic resources, such as shell middens in the Peninsula of Baja California, characterised by temporary campsites (Fujita and Ainis, 2018), neither isolated points that are often discovered fortuitously and out of context, or those found during archaeological projects that do not report the presence of megafauna across various sites in northern Mexico, the Baja California peninsula (Gutiérrez and Hyland, 1994; 1998), the central valleys of Oaxaca (Winter et al., 2008), Sinaloa (Guevara-Sánchez, 1989), Durango (Lorenzo, 1953), Tlaxcala (García Cook, 1973), and Nuevo León (Valadez-Moreno, 2006). We specifically address human bones that are directly or indirectly associated with Pleistocene megafauna. However, the discovery of a significant number of human skeletons in submerged contexts along the east coast of the Yucatán Peninsula suggests that there was a large human population existing contemporaneous to these large bodied animals. In the area of Tulum, Quintana Roo, remains of at least ten individuals, dated to the Pleistocene-Holocene transition (13,000 to 8000 cal BP), have been identified (Chatters et al., 2014; Hubbe et al., 2020; Stinesbeck et al., 2020). Moreover, four direct radiocarbon dates on five prehistoric samples from central Mexico are among the earliest in the Americas, dating back to approximately 12,617 cal years BP (IntCal20) (González et al., 2003).

We confirm the variability of coverage across Mexico, with the TMVB being one of the most studied regions in the Americas in terms of different aspects of the Pleistocene such as sediments, palaeosols,

mountain glaciers, climate change, diatoms, and vertebrates, among others (Metcalfe et al., 2000). This province has a larger number of 25 fossil mammal localities, more than any other and sampling is heavily biased towards the latest Rancholabrean (Ferrusquia et al., 2010). Here we have identified fifteen of these as potentially having a direct or indirect relationship with human activity. In contrast, there are no records for the north-western provinces (BCP, SMOc and CH-CO) and CeP. Several mammoth finds have been reported from the TMVB, but they have not been thoroughly investigated or research is in progress. Surprisingly, in the TMVB, no Clovis points have been found, especially given the number of interactions reported.

From the information analysed, it is clear that the greatest evidence of human-megafaunal interaction is concentrated in the TMVB, followed by the SMOr and the YPL. This is remarkable when compared to the biogeography of Mexican Pleistocene mammals. Both TMVB and YPL, represent geographical and geological conditions associated with highly endemic species, likely acting as Pleistocene refugia (Ceballos et al., 2010). For example, new species have been described from faunal assemblages recovered in the submerged caves on the northeastern Yucatan, including three endemic megalonychids (McDonald et al., 2017; Stinnesbeck et al., 2017, 2017a), one peccary (Stinnesbeck et al., 2017b) and a felid (Stinnesbeck et al., 2018) providing evidence for the area's ecological isolation from the rest of Mexico during the Pleistocene. This allows certain conclusions to be drawn about how human populations have adapted to shape different biotas. In the case of the TMVB, we can observe human groups that have settled at altitudes higher than two thousand meters, mainly by exploiting fluvial-lacustrine landscapes and open-woodland environments (Metcalfe et al., 2000; Perez-Crespo et al., 2010; Chávez-Lara et al., 2022). Meanwhile, human populations in the YPL inhabited a mix of tropical environments, from canopy forests to grasslands. Palaeoecological data from the YPL indicate dry conditions for the Late Pleistocene and early Holocene. Lake levels were low and strongly influenced by glacial sea levels (Metcalfe et al., 2000); water availability appears to have been constrained by groundwater within complex subterranean environments accessed through caves and natural sinkholes created by the collapse of the limestone bedrock, requiring the ability to explore the interior of a large system of caves in search of this and other resources (Chatters et al., 2014; González-González et al., 2014; Brandt et al., 2020). However, the record is biased and reflects a lack of standardization in the conduct of research, highlighting the TMVB as the province with the highest density of prehistoric archaeological finds, in line with the abundance of Pleistocene mammal records (Ferrusquia et al., 2010). An important issue to consider is the differential preservation in the material record due to taphonomic factors. The preservation of the YPL is mainly due to the gradual flooding of the caves, creating a submerged environment that is difficult to access. The TMVB finds have been aided by a large number of chance discoveries due to the urban growth of Mexico City and the sealing of contexts by Pleistocene volcanic activity. It is difficult to determine whether the paucity of evidence in the surrounding provinces (e.g. CeP, SMOc, GCP) is due to the absence of factors contributing to the loss and deterioration of records or correlates with the dispersal routes and settlement patterns of the first foragers' groups to inhabit Mexico.

Previous studies have proposed the presence of a cultural diversity that existed during the Late Pleistocene. Indeed, evidence points to early human populations exploiting different ecological settings, here defined mainly by three morphotectonic provinces. Thus, the exploitation of megafauna and relative reliance on other resources likely varied in terms of prey target and ecological factors across different regions and through periods of abrupt climate change. In the TMVB, the patterns of predation indicate a focus on proboscideans. The larger size of these herds in open spaces may have allowed humans to concentrate their subsistence efforts on just a few species, employing specific hunting strategies. This assumption underlies optimal-foraging models, which suggest that hunter-gatherer mobility is closely related to the

availability of food sources in a given environment. In this context, the effective resource accessibility of game, specifically the time and effort required to exploit these large herbivores, is increased by the facilities for monitoring large gregarious animals in open grassland ecotones and becomes a crucial consideration to determine an extensive logistical mobility of groups (Binford, 1980; Winterhalder and Smith, 1981). Meanwhile, in the SMOr and the YPL, hunters seem to have relied on a high diversity of taxa from closed and semi-open habitats including smaller animals like peccary, as well as bighorn sheep, camelids and horses, among other medium and small-sized species represented in the natural traps as observed in the accumulation in Hoyo Negro. This indicates that the hunting practices and subsistence economies associated with the early settlement of the current region of Mexico were most likely determined, or strongly influenced by, the convergence of geophysical and environmental factors such as latitude, water availability, soils, fauna, flora, and biota, as well as perhaps also cultural diversity. However, except for a few exceptions such as Tocuila, El Cedral, or Hueyatlaco, the evidence does not allow us to recognize settlement patterns or define the nature of human occupations at different sites. Nor are there any detailed taphonomic studies that would allow us to evaluate whether deposits represent primary or secondary access to the prey. In this sense, detailed taphonomic studies using new technologies and methods such as scalar microscopy are necessary, as well as detailed site-based analyses of the seasonality of hunting and the age of selected prey species. The use of morphotectonic provinces could help to avoid uniform characterizations of Pleistocene features, as in the case of faunal provinces such as the Mexican Rancholabrean, based on very large extensions of territories or inferences based on the individual evaluations of the archaeological evidence for early human occupations. By using a more objective and coherent framework, it is possible to identify local/regional trends that allow us to learn more about the first settlers of the Americas. We argue that, on the basis of the current evidence, the TMVB, SMOr and YPL may have had a longer and more consistent occupation than other regions, acting as a vertex of human occupation. In line with the geomorphic corridors detected by Ferrusquia-Villafraña et al. (2010), the evidence for human-megafauna interactions around these MPs could correspond to the natural passage of human groups along the faunal dispersal routes. In contrast, the central highlands of Mexico may have acted as a natural barrier, limiting the movement of both megafauna and early humans.

5. Concluding remarks

Our current review aims to present a detailed critical survey of Mexico's Pleistocene human-fauna interactions, although we acknowledge that it could be improved with similar reviews at more refined regional levels or taking each MP as a unit of analysis. The zooarchaeological evidence for these interactions available today comes from sites that have scarce or altogether lacking geological/stratigraphic control/information because many collections were done using accidental discoveries, not in the context of research projects, thus leading to possible mixing of chronologically/ecologically different faunal elements. About 20 (66.6%) of the 30 reported localities have geochronometrical dating, although only 5 (17%) were obtained from direct bone dating. The palaeoenvironmental indicators have very few radiometric and paleomagnetic calibrated dates, making the reconstruction of the ecological context of the first human occupations is quite approximate. Most excavations of archaeological sites in Mexico that contain evidence of Pleistocene fauna were conducted before the 1990s. However, many of these early excavations were characterized by a lack of rigorous stratigraphic control, which is crucial for accurately understanding the context and chronology of the findings. It is important to note that this paper does not aim to evaluate the methodologies used in these earlier excavations, but it is noteworthy that a significant shift has occurred since the 2000s. In recent years, researchers have begun to adopt more sophisticated techniques, including the utilization of

databases integrated with Geographic Information Systems (GIS) to systematically recover the materials and examine context during excavations. This modern approach not only enhances data management but also facilitates a deeper analysis of spatial relationships between archaeo-paleontological findings. Alongside this advancement, there has been a concerted effort to develop chronological models that incorporate various dating methods, including alternative techniques to Accelerator Mass Spectrometry (AMS) such as Liquid Scintillation Spectrometry (Acosta et al., 2018), to improve the accuracy of dating sites. Several notable projects exemplify these advancements. For instance, Gonzalez et al. (2015) conducted a study in the Basin of Mexico that successfully provided direct dating for sites excavated in previous decades, which had previously lacked proper chronological assessments. Similarly, efforts by Feinberg et al. (2009) in Valsequillo, Puebla, involved a thorough revision of stratigraphy, which is essential for reconstructing the sequence of geological and archaeological events. Despite these improvements, researchers still face challenges due to the taphonomic effects associated with Mexico's subtropical and tropical climates. These environmental factors often compromise the preservation of organic materials like bones and teeth, making it difficult to obtain direct radiocarbon results or other analytical data. Consequently, while the methodologies and technologies have advanced significantly, the influence of climate on preservation continues to pose challenges for archaeologists studying human-megafauna interactions in Mexico. However, some general inferences can be drawn, but the indicators provide partial and sometimes contradictory information, with the accuracy of the correlations suggested by palaeoenvironmental proxies between the reconstructed environments and those experienced by humans varying significantly in their resolution. In the chronological framework to which they refer, they never fully correspond to the period of occupation by human groups. More local studies are needed with high chronological resolution and the study of preferred proxies directly related to human activity such as malacological materials and bone remains with clear evidence of human manipulation. Based on the available information, it is not currently possible to determine the impact of human presence on the decline of megafauna. However, it is important to consider human activity in the context of other ecological factors. A clearer picture could be provided through detailed analysis of existing collections using traditional zooarchaeological methods, along with taphonomic techniques including cutting-edge microscopy and radioisotope dating of extinct species. New archaeo-paleontological excavations are also necessary, incorporating advanced survey techniques and the use of fine-scale chronological controls on palaeoenvironmental proxies. Together, this will provide a more accurate picture of the interactions between the megafaunal populations and human groups, as well as refine the current palaeoclimatic reconstructions of Late Pleistocene sites, allowing for regional-to-global comparisons in quantifiable terms. A detailed understanding of the causes of megafaunal extinctions in Mexico is essential to explain this phenomenon on a continental scale, given its geographical location as a transit zone between hemispheres, but also to contribute to the ongoing debate about the human impact on global biodiversity over time.

CRediT authorship contribution statement

Óscar R. Solís-Torres: All authors have made substantial contribution to the submission, Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing. **Joaquín Arroyo-Cabrales:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. **Patrick Roberts:** Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Supervision, Writing – review & editing. **Noel Amano:** Data curation, Methodology, Project administration, Supervision, Visualization, Writing – review & editing.

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Declaration of competing interest

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Data availability

All data and/or code is contained within the submission.

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