



Effects of Pleistocene environmental changes on the distribution and community structure of the mammalian fauna of Mexico

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ABSTRACT

Biological communities in Mexico experienced profound changes in species composition and structure as a consequence of the environmental fluctuations during the Pleistocene. Based on the recent and fossil Mexican mammal checklists, we determine the distribution, composition, diversity, and community structure of late Pleistocene mammalian faunas, and analyze extinction patterns and response of individual species to environmental changes. We conclude that (1) differential extinctions occurred at family, genus, and species level, with a major impact on species heavier than 100 kg, including the extinction all proboscideans and several ruminants; (2) Pleistocene mammal communities in Mexico were more diverse than recent ones; and (3) the current assemblages of species are relatively young. Furthermore, Pleistocene relicts support the presence of biogeographic corridors; important refugia existed as well as centers of speciation in isolated regions. We identified seven corridors: eastern USA–Sierra Madre Oriental corridor, Rocky Mountains–Sierra Madre Occidental corridor, Central United States–Northern Mexico corridor, Transvolcanic Belt–Sierra Madre del Sur corridor, western USA–Baja California corridor, Tamaulipas–Central America gulf lowlands corridor, and Sonora–Central America Pacific lowlands corridor. Our study suggests that present mammalian assemblages are very different than the ones in the late Pleistocene.

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Introduction

Mammals responded in different ways to the extensive climatic fluctuations that characterized the Pleistocene and early Holocene (e.g., Martin and Klein, 1984; Graham, 1986; Graham and Mead, 1987; Markova et al., 1995; FAUNMAP Working Group, 1996; Wooding and Ward, 1997; Barnosky et al., 2003). As a consequence of the environmental fluctuations, biological communities experienced major changes (Martin and Klein, 1984; Wilson, 1996; Barnosky, 2008). Temperate species were displaced into southern Florida, Mexico, and Central America during cold periods. During interglacial events, they re-invaded the barren land left by the retreat of ice masses (Van Devender, 1977; Graham, 1985; Harris, 1985).

Evidence from fossil deposits, palynological profiles, fossil pack-rat middens, and other proxy data documented the changes in the arid, temperate, and tropical communities in the USA, Mexico, and Guatemala (Van Devender and Bradley, 1990; McDonald, 1993; Barnosky et al., 2004b). During the Wisconsin glacial period, pinyon-oak vegetation was depressed to lower latitudes and altitudes. Typical desert vegetation had more limited distribution, and many typical desert plants survived in isolated areas or coexisted with more mesic plant communities

(Wells, 1974; Van Devender and Burgess, 1985). Tropical rain forests were displaced to southern latitudes and to areas exposed by the changes in sea level (Toledo, 1982). Extensive areas presently covered by tropical rain forest supported very different communities at 12 ka, with species typical of rain forest mixed with species from other vegetation types (Van der Hammen, 1972; Toledo, 1982; Leyden, 1984). The transition to more present-day plant communities occurred sometime between 10 and 8 ka (Van Devender, 1990).

The distribution of mammals and other animals greatly varied during the Pleistocene, and the structure and composition of mammal communities were very different—especially in the extinction of large-bodied species (Kurtén and Anderson, 1980; Martin and Klein, 1984; Alroy, 1999; Barnosky et al., 2004a). Other species were displaced following corridors of suitable climate and vegetation (Martin, 1960), and many of them reached geographic areas where they no longer exist (Harris, 1974; Graham and Mead, 1987). With the retreat of the ice masses and the overall change in climate, populations of some species with continuous geographic ranges became isolated. The present disjunct distributions of boreal mammals and the presence of relict species in southwestern USA and northern Mexico were explained as a result of Pleistocene events (e.g., Martin, 1955, 1960; Martin and Harrell, 1957; Brown, 1971; Patterson, 1980).

The description of the effects of the Pleistocene climatic fluctuations on the distribution of mammals in Mexico is fragmentary and a detailed analysis is lacking to understand the general framework and

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its impacts on the composition and structure of its modern mammalian fauna (Martin, 1955, 1960; Martin and Harrell, 1957; Harris, 1974; Graham, 1985; Van Devender and Bradley, 1990; Arroyo-Cabralles et al., 2007). Therefore, we have analyzed and summarized in this paper the effects of Pleistocene environmental changes on the distribution and community structure of the mammals from Mexico. We address the following questions: (1) What was the composition and diversity of Pleistocene mammalian communities compared to modern communities?; (2) Are any consistent patterns evident in the response of individual species to environmental changes?; (3) Can we reconstruct formation or dissolution of dispersal corridors?; and (4) With available information, can we generate a general framework that will serve as a basis for generating a better understanding of the past for the current species-extinction crises?

Methods

A checklist was compiled of the Pleistocene and present mammals from Mexico from published information. For Pleistocene mammals, we relied on Arroyo-Cabralles et al. (2007) for species occurrences, and for specific state localities. Alvarez (1965), Kurtén and Anderson (1980), and Barrios Rivera (1994) were used as basic references, but such works were complemented with many additional recent studies (Montellano-Ballesteros, 1992; Arroyo-Cabralles and Johnson, 2003; Carranza-Castañeda and Miller, 2004; Mead et al., 2007). We followed the names proposed by Arroyo-Cabralles et al. (2007) as well as unpublished data from the same authors that were proposed during the development of the project titled “Mammal fauna from the late Quaternary of Mexico” (G-012), sponsored by the National Commission for the Knowledge and Use of the Biodiversity (CONABIO, Mexico; see <http://www.conabio.gob.mx/institucion/proyectos/resultados/InfG012.pdf>). The checklist of extant mammals was based on Ceballos and Oliva (2005). The species composition and species richness of the Pleistocene–early Holocene and modern mammalian faunas were compared. A basic assumption was that all species present in modern faunas were present somewhere at least during the late Pleistocene and early Holocene, but not necessarily where they occur today.

All species were characterized by their body mass and feeding habits. Information about body mass was not readily available for many species, so three very broad categories were used: small (<10 kg), medium (10 to 100 kg), and large (>100 kg). Data on body mass and feeding habits of Pleistocene species were obtained or inferred from Kurtén and Anderson (1980). For modern species, we used the data provided by Ceballos and Oliva (2005). The number of extinct species, their body mass, and their feeding habits were used to evaluate the patterns and ecological correlates of extinctions during the Pleistocene and early Holocene.

Extralimital and disjunct geographic ranges of living species of mammals were analyzed to evaluate the possible effects of the Pleistocene environmental fluctuations on the distribution of mammals, especially of montane temperate species. Ceballos and Oliva (2005) and Hall (1981) were used as the basic references for the modern distribution of mammals in Mexico. The presence of continuous temperate forest corridors during the late Pleistocene was tentatively reconstructed by the presence of relict populations and species. Special emphasis was placed on isolated “mountain island” habitats (sensu Brown, 1971).

Results

Pleistocene mammalian faunas

Relatively few Pleistocene sites with fossil mammals have been studied extensively in Mexico, and most of them are from temperate regions (Alvarez, 1969; Mooser and Dalquest, 1975; Reppening, 1983;

Arroyo-Cabralles et al., 2002, 2007; Carranza-Castañeda and Miller, 2004; Mead et al., 2007). Among the sites that have provided more information regarding the past faunal composition are San Josecito Cave, Nuevo León (Wisconsinan and Holocene); El Cedral, San Luis Potosí (late Pleistocene); Cedazo, Aguascalientes (post-Illinoian); Chapala, Jalisco (late Pleistocene); Tequiquiac (late Pleistocene?) and Tlapacoya, State of Mexico (Wisconsinan and Holocene); Valsequillo, Puebla (late Pleistocene); and the most important in the tropical region of Mexico, Loltún Cave in the Yucatán Peninsula (Wisconsinan and Holocene; Arroyo-Cabralles et al., 2007).

Pleistocene mammal fossil remains belong to 12 orders, 44 families, 144 genera, and 273 species (excluding orders Sirenia and Cetacea, and families Otariidae and Phocidae because few explorations have been directed toward the study of these groups, but see Barnes, 2002). The order with the higher number of fossil species is Rodentia, followed by Chiroptera and Carnivora. Among extant taxa, fossil records have been found for all families and orders, but only 186 species (38.8%) still are found in Mexico. During the Pleistocene and early Holocene, the mammalian faunas from Mexico had more diversity at family and order levels (Table 1).

Most of the fossil records (187) were small species; medium-sized and large mammals were represented by 27 and 59 species, respectively. Although similar trends have been observed in present mammalian species, it was clear that profound differences existed with Pleistocene faunas, especially in the number of large species (Fig. 1). Only eight large species (*Bison bison*, *Odocoileus hemionus*, *O. virginianus*, *Ovis canadensis*, *Cervus elaphus*, *Panthera onca*, *Ursus americanus*, *Tapirus bairdii*) are represented in modern faunas while at least 59 species were present in the Pleistocene. Large herbivores were quite common in Central and Northern Mexico, and fossil deposits at San Josecito Cave, Cedazo, Tequiquiac, and Tlapacoya had rich herbivore faunas. For example in Cedazo, central Mexico, at least 23 large species of herbivores were present at different times during the Pleistocene. Remains of large carnivores were less abundant in any particular site, but as a whole, many species were present, and a few sites such as San Josecito and Tlapacoya had rich carnivore faunas.

Extinctions

One of the most remarkable features of the Pleistocene is the extinction of many mammals. Three major patterns have emerged from our data: 1) global extinctions; 2) regional extinctions; and 3) local extinctions. Both regional and local extinctions represent what is termed extralimital distributions, where a taxon has survived on a geographic range that is different from its Pleistocene geographic distribution. In *regional extinctions*, taxa disappear from Mexico but survived in other countries. In *local extinctions*, taxa disappear from a

Table 1

Composition and diversity of Pleistocene (left) and modern (right) mammalian faunas found in Mexico, excluding orders Sirenia and Cetacea, and families Phocidae and Otariidae.

Order	Family	Genera	Species
Rodentia	8/8	36/46	96/235
Chiroptera	7/9	34/66	49/137
Carnivora	6/6	23/22	37/34
Artiodactyla	5/4	18/7	34/10
Xenarthra	6/2	11/4	14/4
Lagomorpha	1/1	5/3	13/15
Perissodactyla	2/1	2/1	7/1
Didelphimorphia	3/3	5/7	7/8
Soricomorpha	1/2	3/6	7/32
Proboscidea	3/0	4/0	5/0
Primates	1/1	2/2	3/3
Notoungulata	1/0	1/0	1/0
12/10	44/37	144/163	273/479

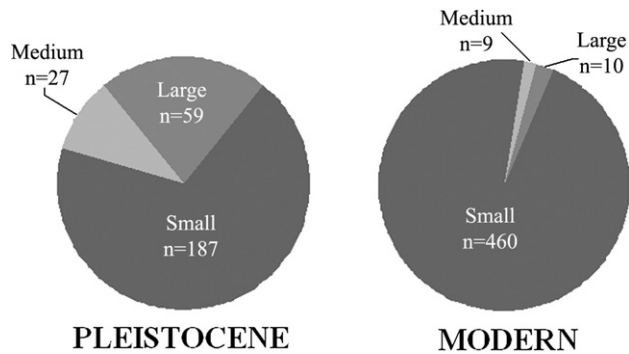


Figure 1. Corporal size of Pleistocene and modern mammalian faunas found in Mexico: small (<10 kg); medium (10 to 100 kg); large (>100 kg).

region but survived in other regions in the country. We discuss in this section the patterns of global extinctions and in the following section the regional and local extinctions.

By the end of the Pleistocene, one order (Notoungulata), six families, 29 genera, and 78 species found in Mexico become extinct globally. Most orders experienced extinctions, except for Soricomorpha and Primates (Fig. 2). Extinctions were distributed unevenly at different hierarchical levels, and represented from none to 100% of all taxa within orders, families, and genera. For example, the order Proboscidea lost two of three families, and almost all genera and species, whereas the order Soricomorpha did not lose any species. While 32 families such as Soricidae did not experience any global extinction, others such as Antilocapridae, Bovidae, and Equidae lost most of their species.

Most of the extinct species (50) had large body mass. Medium and small body mass species were represented by fewer taxa, with 8 and 20 extinct species, respectively. Most (62) were herbivores, followed by carnivores (9), omnivores (5), and sanguivores (2) (Fig. 3). Previous to the extinction phenomena, 178 herbivore species, 66 carnivores, 25 omnivores, and 4 sanguivores occurred. Certainly, herbivore and large animals had the largest extinction percentage, probably related to the impoverishment of environmental conditions at the end of the Pleistocene that most affected the largest species.

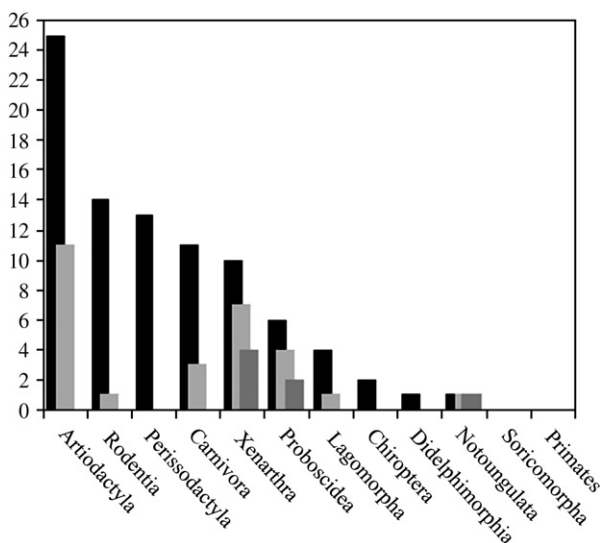


Figure 2. Taxa found in Mexico that became globally extinct by the end of Pleistocene. Species (black); genera (light gray); and family (dark gray).

Extralimital distributions

Extralimital distributions were a common response of mammals to Pleistocene environmental changes. We recorded extralimital distributions at all hierarchical levels, from order to species. Extralimital distributions that represent *regional extinctions* included 10 species (Table 2). Although all the Pleistocene species of proboscideans found in Mexico (represented by mammoths, mastodonts, and gomphotheriids) became extinct, other species belonging to this order such as Elephantidae survived in Africa and Asia. Other families such as Equidae (horses) survived in Asia and Africa; Hydrochoeridae (capybaras) in South America; Camelidae (camels and guanacos) in South America, Africa and Asia; Megalonychidae (two-toed sloths) in Central America and throughout northern South America; and Herpestidae (mongooses) mainly in Africa, but also in Asia and southern Europe.

Some species, such as the dholes (*Cuon alpinus*) that survived in Asia or the spectacle bear (genus *Tremarctos*) from South America, are presently found tens of thousands of kilometers away from their Pleistocene range in Mexico. Others, such as the yellow-bellied marmot (*Marmota flaviventris*) and the southern bog lemming (*Synaptomys cooperi*), are found in North America far north of the fossil beds at San Josecito Cave. Presently, the nearest populations of these species to San Josecito are found in the USA, separated by 1300 km to the northwest (New Mexico) and 1600 km to the northeast (Arkansas). Similarly, recent records of the black-footed ferret are from New Mexico, approximately 700 km north of Jiménez, Chihuahua (not taking into account the recently re-introduced specimens in Janos, northern Chihuahua; Pacheco et al., 2002). Fewer examples occur of tropical species with extralimital distributions, but they support similar trends. For example, Pleistocene records from the giant anteater (*Myrmecophaga tridactyla*) have been found in northern Sonora, more than 1800 km from the nearest modern populations in Belize and Honduras (Fig. 4).

Extralimital distributions that represent *local extinctions* included 23 species (Table 2). Most were temperate taxa. Species such as the North American porcupine (*Erethizon dorsatum*), meadow vole (*Microtus pennsylvanicus*), black-tailed and Mexican prairie dogs (*Cynomys ludovicianus* and *C. mexicanus*), and bighorn sheep (*Ovis canadensis*) had Pleistocene distributions that reached lower latitudes in Mexico. *Erethizon dorsatum* was recorded in Pleistocene fossil beds from Cedazo (Aguascalientes), approximately 700 km from the nearest surviving populations in Nuevo León, *Microtus pennsylvanicus* was found in San Luis Potosi and Durango, approximately 600 km from the nearest populations in Chihuahua, and *C. mexicanus* was recorded recently from Valsequillo, Puebla, more than 500 km south from its current distribution (Cruz-Muñoz et al., 2009). *Ovis canadensis* survives in northern Mexico and fossil records support their presence in central Mexico, approximately 1800 km from the current distribution (Fig. 5). Records from Loltún Cave, in the Yucatán Peninsula, included the bobcat (*Lynx rufus*) and wolf (*Canis lupus*) that are found in temperate regions hundreds or thousands of kilometers to the north.

In San Josecito Cave, several species such as *Orthogeomys onerosus*, *Desmodus stocki*, and *Cryptotis mexicana* of tropical affinities have been recorded. Presently, *Cryptotis mexicana* and species of *Orthogeomys* and *Desmodus* are confined to southern or eastern tropical areas.

Disharmonius faunas

Some Mexican faunas such as San Josecito Cave fauna have Pleistocene disharmonius faunas, where temperate (like vagrant shrew, marmots, and bog lemming) and tropical (spiny pocket mice, tropical pocket gopher) mammals were found mixed. Also, Valsequillo fauna has shown animals from grassland (Mexican prairie dog), and alpine forest (volcano rabbit) mixed in the deposit.

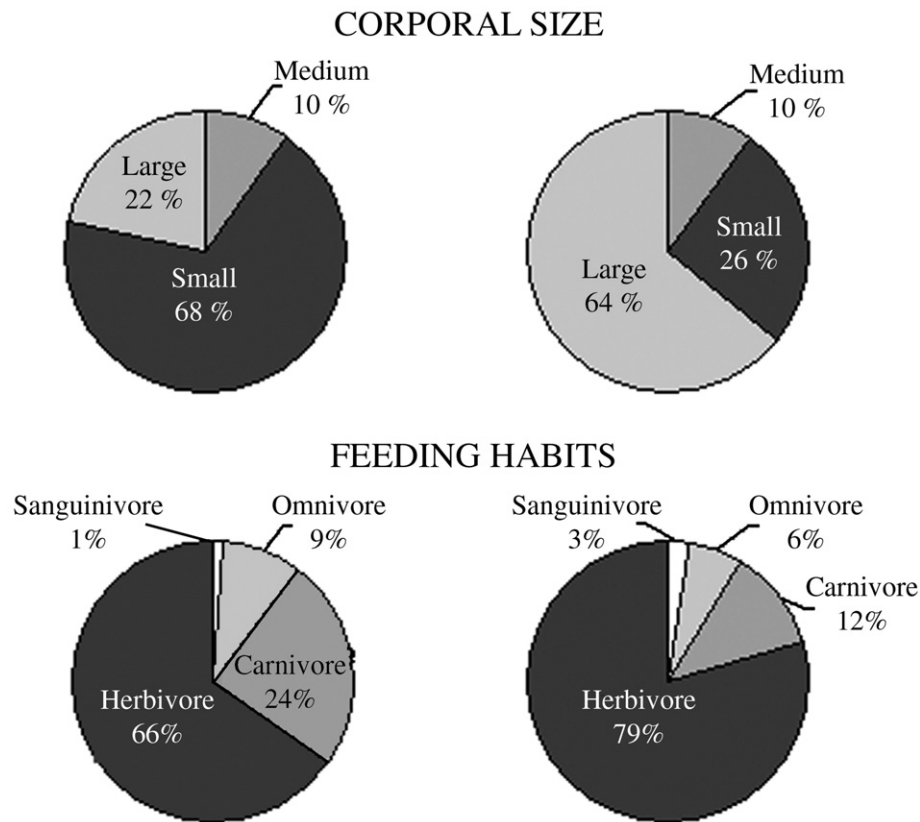


Figure 3. Corporal size and feeding habits of species living during the Pleistocene (left) in Mexico and those that became extinct by the end of the Pleistocene (right).

Disjunct distributions and speciation

Many populations of temperate Mexican mammals survived on “islands” of suitable habitat surrounded by “seas” of drier or moister vegetation. Extant temperate species with disjunct and relict distributions are common, but few tropical species exhibit such a type of distribution. Real islands represent the best example of disjunct

distributions leading to speciation. Presently, 47 species are endemic to “islands habitats”, with close mainland relatives. All island endemics have small body masses and most (71%) are rodents, but lagomorphs and insectivores are also represented (Table 3).

Among species found in “island” habitats are the Sierra Madre mantled ground squirrel (*Spermophilus madrensis*), Douglas squirrel (*Tamiasciurus douglasii*), and Mexican prairie dog (*Cynomys mexicanus*).

Table 2

Extralimital geographic range of living species during the Pleistocene. Regional extinctions represent species that became extinct in Mexico while they survive in other countries. Local extinctions represent species that were distributed in Mexico during the Pleistocene in regions where no longer exist.

Species	Current distribution	Pleistocene region in Mexico (separated by km)
REGIONAL EXTINCTIONS		
<i>Myrmecophaga tridactyla</i>	Central America	Northwestern (1800 km N)
<i>Sorex cinereus</i>	Northern USA and Canada	Northeastern (1500 km S)
<i>Canis rufus</i>	Southeastern USA	Central (850 km S)
<i>Cuon alpinus</i>	Southeastern Asia	Northeastern (1000 s km)
<i>Mustela nigripens</i>	USA–Mexico	Northwestern (700 km S)
<i>Cervus elaphus</i>	Northern USA,	Central (1900 km S)
<i>Marmota flaviventris</i>	Northwestern USA	Northeastern (1200 km S)
<i>Synaptomys cooperi</i>	Northeastern USA	Northeastern (1200 km S)
<i>Neotoma cinerea</i>	USA and southern Canada	Northwestern (700 km S)
<i>Neotoma floridana</i>	Southeastern USA	Northwestern (1200 km S)
LOCAL EXTINCTIONS		
<i>Didelphis marsupialis</i>		<i>Cratogeomys castanops</i>
<i>Marmosa mexicana</i>		<i>Sciurus variegatoides</i>
<i>Cabassous centralis</i>		<i>Chaetodipus penicillatus</i>
<i>Balantiopteryx io</i>		<i>Microtus pennsylvanicus</i>
<i>Macrotus californicus</i>		<i>Hodomys alleni</i>
<i>Alouatta palliata</i>		<i>Neotoma lepida</i>
<i>Spilogale putorius</i>		<i>Neotoma albigula</i>
<i>Tapirus bairdii</i>		<i>Neotoma phenax</i>
<i>Ovis canadensis</i>		<i>Oryzomys melanotis</i>
<i>Odocoileus hemionus</i>		<i>Peromyscus truei</i>
<i>Bison bison</i>		<i>Erethizon dorsatum</i>
<i>Cynomys ludovicianus</i>		

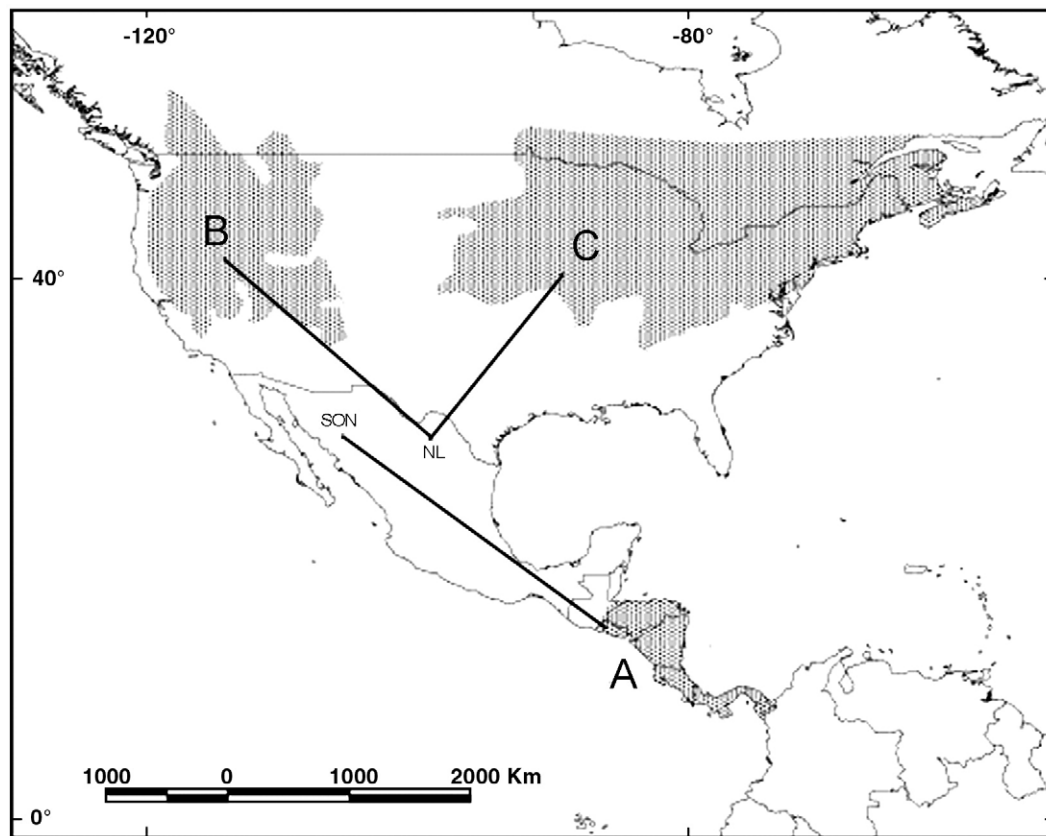


Figure 4. Regional extinctions. Pleistocene fossil records in Mexico are found thousands of kilometers away from current distribution (shaded area). A) Giant anteater (*Myrmecophaga trydactyla*), B) Yellow-bellied marmot (*Marmota flaviventris*), and C) Southern bog lemming (*Synaptomys cooperi*).

Populations of *S. madrensis* from the Sierra Madre Oriental (Chihuahua and Durango), and its closest relative the golden-mantled ground squirrel (*S. lateralis*) from southern USA, are separated by at least 450 km. *T. douglasii* in California and *T. mearnsi* in the Sierra de San Pedro Martir, Baja California, are separated by 750 km. Finally, *C. mexicanus* in Coahuila, and its close relative *C. ludovicianus* in Chihuahua, are separated by approximately 600 km, but not by that much in the late Pleistocene.

Several isolated mountain ranges are unique centers of either relict survival or speciation of endemic species and subspecies. Few species have available genetic information to determine if these were centers of speciation or reflect a longer legacy. The following localities are among the most important examples (number of endemic species/subspecies in parenthesis): the Sierra de San Pedro Martir, Baja California (3/1), Sierra del Carmen, Coahuila (1/1), Cerro Potosí, Nuevo León (1/1), Pinal de Amoles, Querétaro (1/4), Omilteme, Guerrero (1/2), Zempoaltepec and Vista Hermosa, Oaxaca (5/4), and San Cristóbal de las Casas, Chiapas (2/3). The origin of relicts can be explained by three different, mutually exclusive, hypotheses: 1) modern accidental arrivals (i.e., high dispersal and vagility); 2) arrival with isolation during late Tertiary aridity; and 3) Pleistocene arrival and post-glacial isolation (e.g., Martin, 1960). Our data indicate that in Mexico most species were isolated during the Pleistocene (i.e., supporting the third hypothesis).

Pleistocene biogeographic corridors

From the information about extralimital, disjunct and relict distributions of mammals in Mexico, the topographic and potential vegetation map (Rzedowski, 1990), we reconstructed seven major corridors for the dispersal of temperate and tropical species of mammals during the Pleistocene (Fig. 6). The temperate corridors were: 1) eastern USA–Sierra Madre Oriental; 2) western USA–Baja

California; 3) Rocky Mountains–Sierra Madre Occidental (and Sierra de Baja California); 4) central USA–northern Mexico; and 5) Transvolcanic Belt–Sierra Madre del Sur (and central America). The tropical corridors were: 1) Sonora–Central America Pacific lowlands; and 2) Tamaulipas–Central America Gulf lowlands.

The interchange of mammalian faunas in the eastern USA–Sierra Madre Oriental corridor is supported by isolated distributions of *Glaucomys volans*, *Microtus* (*Pytimys*) *quasiater*, *Sorex milleri* (related to *S. cinereus*), and *Scalopus aquaticus* in Mexico. Other widely distributed species apparently dispersed in either direction following this corridor (Table 4).

The eastern USA–Baja California corridor is supported by the faunas of the Sierra de San Pedro Martir and Sierra de La Laguna. The number of endemic species was smaller in the Sierra de La Laguna that is more isolated. Typical species supporting this corridor were *Tamiasciurus mearnsi*, *Sorex ornatus*, *Scapanus latimanus*, *Sciurus griseus*, and *Tamias obscurus*. The relatively large number of relict and isolated populations provided strong support to the Rocky Mountains–Sierra Madre Occidental corridor. Mexican species colonized mountains in Arizona and other locations in the southwestern USA, and several species from the USA penetrated to the mountains of Sonora, Chihuahua, and Durango (Table 4).

The number of species of temperate affinities that survive in the mountains of southern Mexico is relatively small. Most of these species have affinities to the mammals of the Transvolcanic Belt. However, the flying squirrel (*Glaucomys volans*), a species with affinities to eastern USA, has penetrated to Central America. The central USA–northern Mexico corridor is supported by the presence of prairie dogs (*C. mexicanus* and *C. ludovicianus*), *Peromyscus nasutus*, and other species widely distributed (Table 4).

Tropical corridors are located along the lowlands of the Pacific and Gulf of Mexico coasts. The Sonora–Central Pacific lowlands corridor is

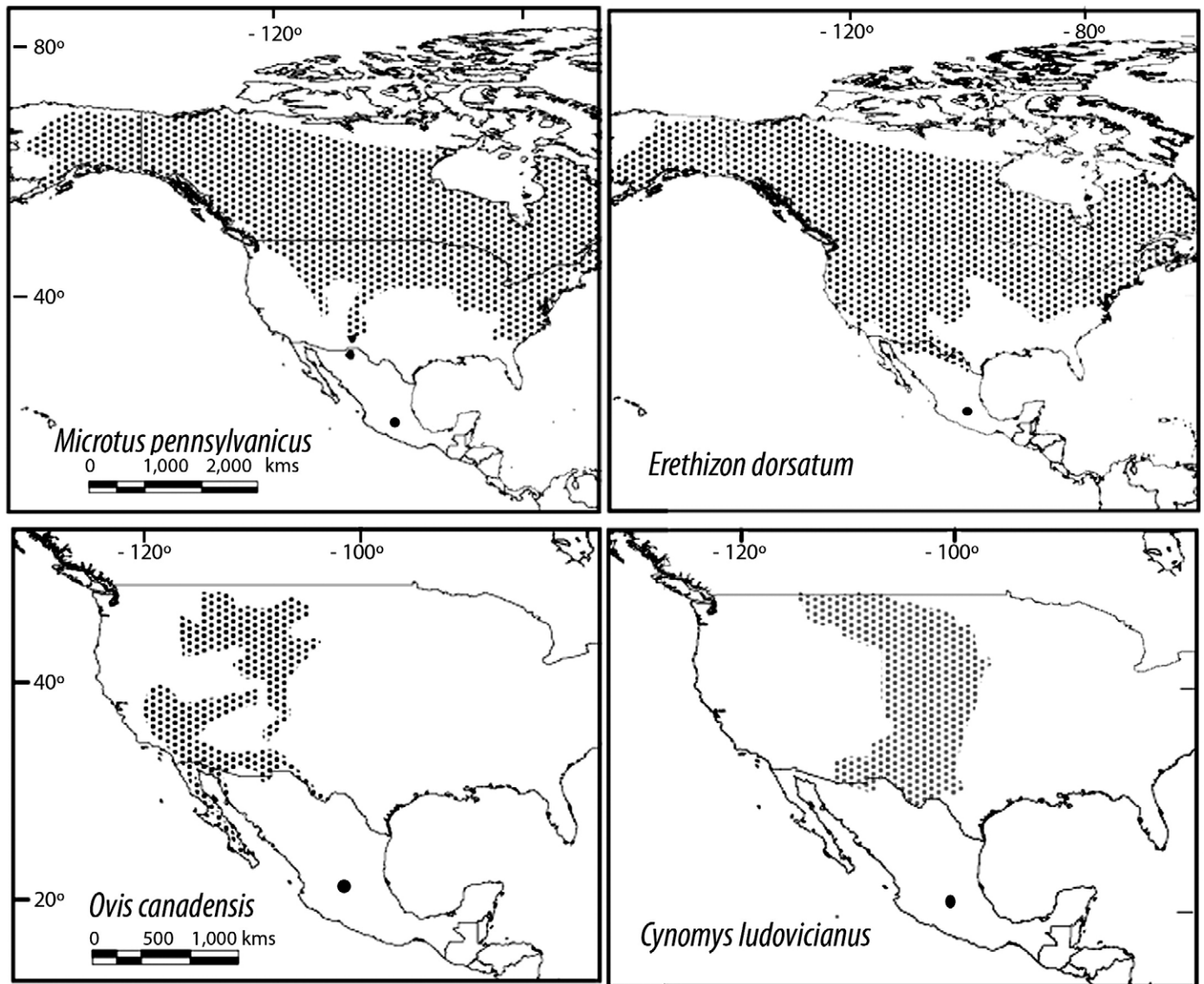


Figure 5. Local extinctions. Pleistocene fossils from central Mexico of northern porcupine (*Erethizon dorsatum*), bighorn sheep (*Ovis canadensis*), meadow vole (*Microtus pennsylvanicus*), and black-tailed prairie dog (*C. ludovicianus*) demonstrate the lower latitudes they reached on the past (●).

supported by the presence of *Myrmecophaga tetradactyla* and isolated populations of species like tayra (*Tayra barbara*). On the other hand, the Tamaulipas–Central America corridor is supported by *Cuniculus paca* and *Potos flavus*.

Discussion

Pleistocene environmental changes had important effects on the distribution of temperate and tropical biotas in Mexico (e.g., Martin, 1955, 1960; Toledo, 1982). Expansions and contractions in the geographic ranges of plant communities, associated with glacial and interglacial climatic changes, causes dramatic changes in the distribution of mammals (and other organisms). The present mammal communities are geologically young and faunistically depauperated (Martin and Klein, 1984; Graham, 1985). The ecological effects of the defauna on community structure and function are unknown. However, present-day defauna has major effects on complex ecological traits such as predator–prey and plant–herbivore interactions (e.g., Dirzo and Miranda, 1990; Terborgh, 1988).

Pleistocene mammal communities in Mexico are apparently more diverse than modern ones. However, in order to compare the

diversity and composition of Pleistocene and modern mammalian faunas properly, an adequate chronology of the sites is imperative. Unfortunately, early studies of San Josecito Cave and other Pleistocene sites in Mexico are not properly dated so it is likely that their faunas were heterochronous (Arroyo-Cabral and Johnson, 2008). Therefore, it is difficult to evaluate their diversity. Further studies may provide additional information about the diversity of Pleistocene mammalian communities in Mexico that may allow better comparisons. Nevertheless, it is evident that at least certain mammalian groups (e.g., large herbivores and carnivores) and communities were more diverse than modern communities during the Pleistocene (see also Martin, 1967; Mooser and Dalquest, 1975; Kurtén and Anderson, 1980; Graham and Lundelius, 1984; Graham, 1985, 1986; Alroy, 1999).

Extinctions were common throughout the Pleistocene. Most of the extinct mammals were large species (Martin, 1973; Kurtén and Anderson, 1980; Lundelius et al., 1983). Of the 44 mammalian families represented in the Pleistocene in North America, extinctions occurred in 80%, of which 30% completely vanished (data from Kurtén and Anderson, 1980). Extinctions in Mexico followed similar trends. Several hypotheses were advanced to explain the Pleistocene extinctions; for example, Kurtén and Anderson (1980) mentioned

Table 3

Species endemic to “island habitats” in Mexico (left) and the closest relative population and species (right). The number indicates the distance between the two taxa in kilometers. An asterisk (*) denotes separated populations of same species with no apparent connection.

<i>Cryptotis magna</i>	<i>C. aticola</i>	200	<i>Dipodomys gravipes</i>	<i>D. stephensi</i>	450
<i>Cryptotis nelsoni</i>	<i>C. mexicana</i>	100	<i>Microtus umbrinus</i>	<i>M. quasiater</i>	80
<i>Cryptotis peregrina</i>	<i>C. obscura</i>	500	<i>Habromys chinanteco</i>	<i>H. simulatus</i>	150
<i>Cryptotis phillipsii</i>	<i>C. mexicana</i>	50	<i>Habromys delicatulus</i>	<i>H. simulatus</i>	200
<i>Notiosorex villai</i>	<i>N. crawfordi</i>	80	<i>Habromys ixtlani</i>	<i>H. simulatus</i>	150
<i>Sorex macrodon</i>	<i>S. milleri</i>	650	<i>Habromys lepturus</i>	<i>H. simulatus</i>	150
<i>Sorex ornatus</i> *		750	<i>Megadonthomys cryophilus</i>	<i>M. nelsoni</i>	180
<i>Sorex sclateri</i>	<i>S. macrodon</i>	200	<i>Megadonthomys thomasi</i>	<i>M. nelsoni</i>	300
<i>Scalopus anthonyi</i>	<i>S. latimanus</i>	100	<i>Neotoma angustapalata</i>	<i>N. goldmani</i>	80
<i>Myotis peninsularis</i>	<i>M. velifer</i>	1000	<i>Neotoma nelsoni</i>	<i>N. micropus</i>	280
<i>Cynomys mexicanus</i>	<i>C. ludovicianus</i>	600	<i>Neotoma palatina</i>	<i>N. albigula</i>	400
<i>Spermophilus atricapillus</i>	<i>S. beecheyi</i>	350	<i>Peromyscus bullatus</i>	<i>P. pectoralis</i>	220
<i>Spermophilus madrensis</i>	<i>S. lateralis</i>	450	<i>Peromyscus mekistrurus</i>	<i>P. pectoralis</i>	220
<i>Spermophilus perotensis</i>	<i>S. spilosoma</i>	350	<i>Peromyscus melanocarpus</i>	<i>P. melanotis</i>	150
<i>Tamiasciurus mearnsi</i>	<i>T. douglasii</i>	750	<i>Peromyscus melanurus</i>	<i>P. melanotis</i>	250
<i>Tamias bulleri</i>	<i>T. durangae</i>	100	<i>Peromyscus ochraventer</i>	<i>P. nasutus</i>	280
<i>Tamias durangae</i>	<i>T. bulleri</i>	100	<i>Peromyscus sagax</i>	<i>P. boylii</i>	105
<i>Cratogeomys fumosus</i>	<i>C. gymnurus</i>	70	<i>Peromyscus winkelmanni</i>	<i>P. spicilegus</i>	90
<i>Cratogeomys gymnurus</i> *	<i>C. gymnurus</i>	250	<i>Reithrodontomys bakeri</i>	<i>R. zacatecae</i>	250
<i>Cratogeomys neglectus</i>	<i>C. zinseri</i>	150	<i>Reithrodontomys hirsutus</i>	<i>R. megalotis</i>	50
<i>Cratogeomys zinseri</i>	<i>C. neglectus</i>	150	<i>Reithrodontomys microdon</i> *		150
<i>Geomys tropicalis</i>	<i>G. personatus</i>	400	<i>Lepus flavigularis</i>	<i>L. callotis</i>	100
<i>Orthogeomys lanius</i>	<i>O. grandis</i>	90	<i>Romerolagus dazi</i> *		40
<i>Dipodomys gravipes</i>	<i>D. stephensi</i>	450	<i>Sylvilagus insonus</i>	<i>S. brasiliensis</i>	350

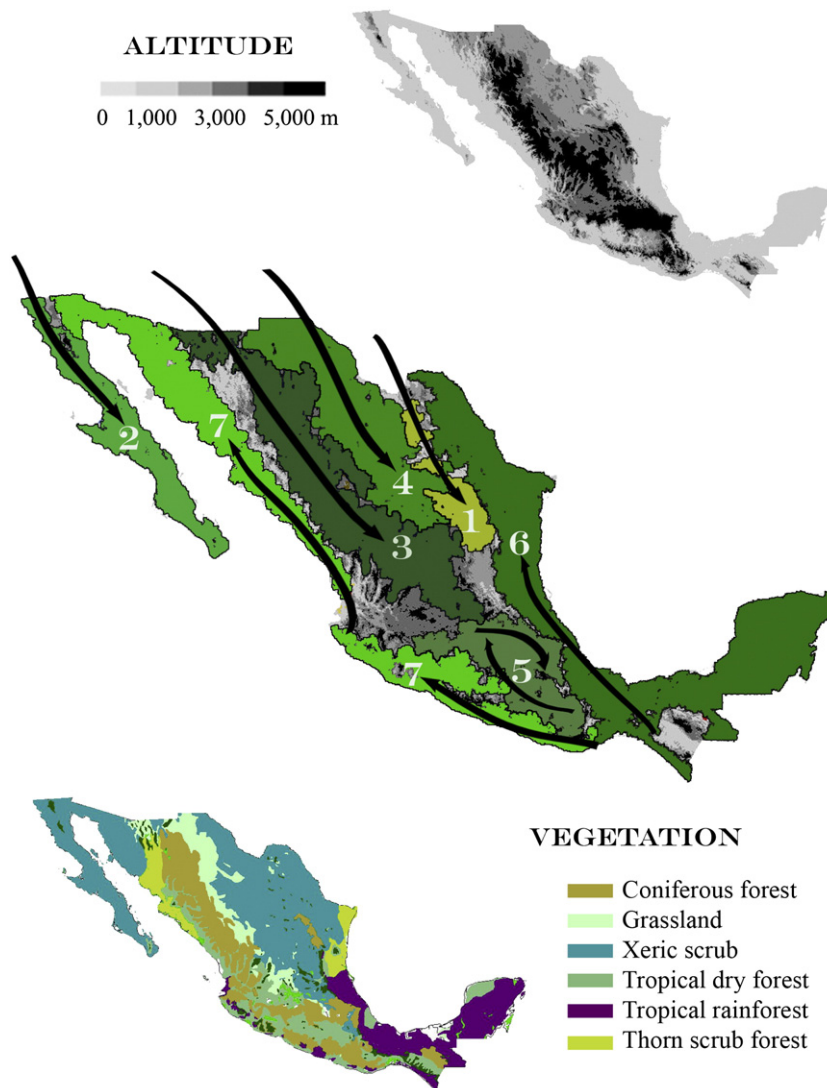


Figure 6. Major biogeographic corridors supporting the dispersal of mammals during the Pleistocene in Mexico. Topographic and potential vegetation map support the presence of these corridors. Temperate corridors: 1. Eastern US – Sierra Madre Oriental, 2. Western US – Baja California, 3. Rocky Mountains – Sierra Madre Occidental, 4. Central US – Northern Mexico, 5. Transvolcanic Belt – Sierra Madre del Sur. Tropical corridors: 6. Tamaulipas – Central America Gulf Lowlands, and 7. Sonora – Central America Pacific lowlands.

Table 4

Extant mammals with extralimital, disjunct or relict distribution supporting the presence of biogeographic corridors during the Pleistocene.

Central USA–Northern Mexico	Western USA–Baja California
<i>Cynomys mexicanus</i>	<i>Scapanus latimanus</i>
<i>Bison bison</i>	<i>Tamias obscurus</i>
<i>Spermophilus spilosoma</i>	<i>Sciurus griseus</i>
<i>Peromyscus nasutus</i>	<i>Sorex ornatus</i>
<i>Dipodomys ordii</i>	<i>Chaetodpus rudinoris</i>
<i>Neotoma mexicana</i>	<i>Peromyscus truei</i>
<i>Peromyscus difficilis</i>	<i>Tamiasciurus mearnsi</i>
Eastern USA–Sierra Madre Oriental	Rocky Mountains–Sierra Madre Occidental
<i>Baiomys taylori</i>	<i>Sigmodon fulviventer</i>
<i>Peromyscus leucopus</i>	<i>Sciurus arizonensis</i>
<i>Onychomys leucogaster</i>	<i>Dipodomys spectabilis</i>
<i>Neotoma micropus</i>	<i>Sciurus nayaritensis</i>
<i>Microtus quasiater</i>	<i>Sciurus aberti</i>
<i>Sciurus niger</i>	<i>Tamias dorsalis</i>
<i>Glaucomys volans</i>	<i>Spermophilus madrensis</i>
<i>Scalopus aquaticus</i>	<i>Microtus pennsylvanicus</i>
<i>Ursus americanus</i>	
Transvolcanic Belt–Sierra Madre del Sur	Sonora–Central America Pacific lowlands
<i>Sorex saussurei</i>	<i>Orthogeomys grandis</i>
<i>Reithrodontomys microdon</i>	<i>Myrmecophaga tetradactyla</i>
<i>Reithrodontomys sumichrasti</i>	<i>Liomys pictus</i>
<i>Glaucomys volans</i>	<i>Tayra barbara</i>
Tamaulipas–Central America Gulf lowlands	
<i>Marmosa mexicana</i>	
<i>Didelphis marsupialis</i>	
<i>Tamandua mexicana</i>	
<i>Eira barbara</i>	
<i>Potos flavus</i>	
<i>Cuniculus paca</i>	

86 different hypotheses. Martin (1967, 1973, 1984) proposed that most of the large mammals survived until the end of the Pleistocene, only to be exterminated by the waves of immigrating people. In contrast, Graham and Lundelius (1984) suggested that the Pleistocene extinctions were caused by a “coevolutionary disequilibrium” in their biotic interactions. Plant–animal and animal–animal interactions were disrupted by the profound environmental changes that occur in the Pleistocene. More recently, Alroy (1999) and Koch and Barnosky (2006) discussed in depth the Pleistocene extinctions and proposed several scenarios.

The scale of the extinctions and the complex environmental changes that occur during the Pleistocene seem to indicate that, very likely, the factors that caused the Pleistocene extinctions were quite varied. In Mexico, it seems that large herbivores were exterminated at least partially by prehistoric hunters; many remains of large herbivores have been found in association with human artifacts (e.g., Alvarez, 1969). On the other hand, the extensive climatic and vegetation changes also have a profound effect (e.g., San Josecito cave fauna). The response of each species to Pleistocene climatic changes is individualistic; each species responded to its own abilities and constraints. Graham (1985) has found a similar pattern in North America. This “Gleasonian” response has important implications to the understanding of both evolutionary and ecological problems.

As previously mentioned, many populations of temperate Mexican mammals survived in isolated “islands” of suitable habitat surrounded by “seas” of drier or moister vegetation. Poor dispersal abilities and relatively small body sizes (i.e., <3 kg) characterize a large percentage of these species. For instance, few species of bats have isolated distributions, probably because bats have better dispersal abilities compared to other small mammals. Isolated distributions may reflect reductions in the original geographic ranges caused by the contraction of suitable habitats (i.e., vicariance) during the late Pleistocene and early Holocene (e.g., Martin, 1960; Brown, 1971; Patterson, 1980). Species with larger body sizes do not have disjunct distribution

because they are: 1) better dispersers; or 2) not able to maintain sustaining populations in small geographic ranges.

How did species with poor dispersal abilities achieve their present disjunct distributions? Disjunctions can be attributed to vicariance or dispersal abilities. Without more complete fossil records it is difficult to assess the factors shaping some distributions. However, some patterns are evident when analyzing disjunct distributions of Mexican mammals. Their distribution can be explained by three different, mutually exclusive, hypotheses: 1) modern accidental arrivals (i.e., high dispersal and vagility); 2) arrival with isolation during late Tertiary aridity; and 3) Pleistocene arrival and post-glacial isolation (e.g., Martin, 1960). The first hypothesis is not supported by available data, because most mammals, if not all, with isolated populations are small species, practically unable to disperse throughout unsuitable habitats. Such populations are usually isolated in temperate forests surrounded by “seas” of drier (e.g., *Sorex milleri* in northern Mexico) or moister (e.g., *Glaucomys volans* in Chiapas, southern Mexico) environments.

With respect to the second hypothesis, some species in central Mexico seem to have been isolated since long before the Pleistocene. Taxonomically, several populations differentiated to the genus level. The best examples are isolated populations of unique genera and species such as the volcano rabbit (*Romerolagus diazi*), the volcano mouse (*Neotomodon alstoni*), and the Michoacan pocket gopher (*Zygoeomys trichopus*) that survived (and probably evolved) in the mountains of the Transvolcanic Belt in central Mexico. It is likely that these high mountains acted as a refugium during the Pleistocene (Ceballos and Galindo, 1984; Ceballos and Rodríguez, 1993).

Most of the populations of mammals with disjunct populations support the third hypothesis (i.e., that they became isolated in the late Pleistocene and early Holocene). In general, the isolated populations are only differentiated to the species and subspecies level. This situation suggests that they have been isolated for only a few thousand years, and that allopatric speciation may have been promoted by lack of gene flow and genetic drift. Genetic studies will help to have a better understanding of the relationship and age of separation of these species.

Several groups of rodents particularly have been affected by the contraction of suitable habitats. A good example is the pocket gophers (genus *Cratogeomys*). Populations isolated in many small mountain ranges become differentiated to the species or subspecies level (e.g., *C. neglectus* in Pinal de Amoles, Queretaro; *C. zinseri* in Lagos de Moreno, Jalisco; and *C. fumosus* in Colima). Other genera such as *Peromyscus* and *Microtus* show similar trends.

Montane species that colonize Mexico followed well-defined biogeographic corridors. Mexican species that penetrate into the USA used the same corridors, but it is possible that such interchanges were heterochronous (e.g., Martin, 1960). The analysis of species that have relict, isolated distributions was particularly insightful in reconstructing these corridors. Five basic corridors for montane species were reconstructed. These corridors also were supported by extensive data on plants (Toledo, 1982; Van Devender, 1977; Van Devender and Burgess, 1985; Wells, 1974), and other vertebrates (e.g., Martin, 1955, 1960; Harris, 1974; Lundelius et al., 1983). Unfortunately, the lack of fossil records made it almost impossible to date the time of the interchange.

It seems evident that the extent of the interchange was related to the availability of corridors of suitable vegetation. The small number of species that dispersed into Mexico through the eastern USA–Sierra Madre Oriental corridor, reflects the fact that during the Pleistocene, intermediate areas were covered by pine–oak forests. Temperate deciduous forests in the Sierra Madre Oriental have been isolated since the Tertiary (Martin and Harrell, 1957).

It is likely that tropical mammals suffered similar constraints in their distributions in the Pleistocene. The lack of fossils and relict species makes it extremely difficult to assess the extent of those

changes. Nevertheless, the extralimital distribution of several mammals at San Josecito and Loltún caves reveal the possibility of important movements.

Finally, disharmonius faunas can shed light to present-day conservation problems. The concept was created back in the 1970s (Lundelius, 1989) to point out about the faunal complexes formed by remains of animals that currently do not co-occur anywhere in the world (ecological incompatibles), but in the past they coexisted in the same habitat by equable climates (with reduced seasonal extremes) that do not have modern analogs (Graham and Mead, 1987). The San Josecito disharmonious faunas could be either real communities or an artifact where remains may come from different strata (Arroyo-Cabrales and Johnson, 2008). The Valsequillo disharmonius fauna could be due to either the lack of stratigraphic control for some of the reported samples or the mixing of animals from different biomes due to the taphonomic history of the deposit (Cruz-Muñoz et al., 2009). However, there is solid evidence in other North America and world regions that Pleistocene communities differed from present-day communities, with coexisting species that are not longer present in the same habitats because they either were extinct or had extralimital distributions (Graham and Mead, 1987). Careful analyses of such faunas and their composition could be used as a natural experiment to evaluate possible impacts of climate change on present-day mammal communities.

Conclusion

In summary, Pleistocene reconstruction of mammalian distributions in Mexico support the following issues:

- 1) Differential extinctions occurred at the family, genus, and species levels;
- 2) Pleistocene communities were more diverse than modern communities;
- 3) Geographic ranges of species expanded and contracted with changes in climate and vegetation. Trends in the movements of tropical mammals appear to be similar to that of temperate mammals. Each species has responded individually (i.e., it responded to its own abilities and constraints);
- 4) Assemblages of species are relatively young;
- 5) Pleistocene relicts support the presence of general biogeographic corridors;
- 6) Important centers of speciation occur in isolated geographic ranges. Some areas (e.g., Transvolcanic Belt) probably acted as Pleistocene refugia; this situation is reflected in the number of isolated, endemic species; and
- 7) Disharmonius faunas, if evaluated in detail, can provide a natural experiment providing useful information about the impact of climate change in present-day communities.

Many of the ideas presented here are based on a poor fossil record. However, without solid paleontological data, it is almost impossible to reconstruct the geological past. Further work will help to better understand the effects of the Pleistocene climatic fluctuations and its ecological and evolutionary consequences on modern communities of Mexican mammals.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yqres.2010.02.006.

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