Yukon to the Yucatan: Habitat partitioning in North American Late Pleistocene ground sloths (Xenarthra, Pilosa)

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ABSTRACT

McDonald HG 2021. Yukon to the Yucatan: Habitat partitioning in North American Late Pleistocene ground sloths (Xenarthra, Pilosa). Journal of Palaeosciences 70(2021): 237–251.

The late Pleistocene mammalian fauna of North America included seven genera of ground sloth, representing four families. This cohort of megaherbivores had an extensive geographic range in North America from the Yukon in Canada to the Yucatan Peninsula in Mexico and inhabited a variety of biomes. Within this latitudinal range there are taxa with a distribution limited to temperate latitudes while others have a distribution restricted to tropical latitudes. Some taxa are better documented than others and more is known about their palaeoecology and habitat preferences, while our knowledge of the palaeoecology of taxa more recently discovered remains limited. In order to better understand what aspects of their palaeoecology allowed their dispersal from South America, long–term success in North America and ultimately the underlying causes for their extinction at the end of the Pleistocene more information is needed. A summary overview of the differences in the palaeoecology of the late Pleistocene sloths in North America and their preferred habitats is presented based on different data sources.

Key–words—Ground sloth, Pleistocene, Palaeoecology.

INTRODUCTION

GROUND sloths primarily evolved in isolation in South America and were adapted to a wide range of habitats with different vegetation compositions and a variety of local climates. With the dispersal of some taxa northward into North America they would have needed to adapt to plants that evolved in North America with different types of nutrients and anti–herbivory toxins. Likewise, the sloths would have been in competition with the native herbivores for food resources. The dispersal of multiple genera of sloths from different families into Central and North America at different times probably reduced competition between them as they entered habitats composed of different plants living under different climatic conditions. The successful establishment of these exotic invaders in Central and North America from their first appearance in North America in the late Miocene until the Pleistocene extinction event was most likely due to the ability of different taxa to utilize a diversity of the available habitats.

The goal of this paper is to provide a general overview of the types of habitats used by the different late Pleistocene sloth taxa in North America and identify the sources of data that permits the inference of the habitat preference of the different taxa. In the few sites where multiple sloth taxa are present the inference is either an ecotonal situation in which different types of habitat are in close proximity or a time–averaged accumulation in which there has been a change in habitat types over time permitting different taxa to inhabit the region but not simultaneously (McDonald, 1996).

In the late Pleistocene of North America there were seven genera of sloth all of which are monotypic except for one for which three species have been proposed. The first appearance of sloths in North America occurs at different times ranging from the late Miocene (Hemphillian) to the late Pleistocene (Rancholabrean) and represents multiple dispersal events (Woodburne, 2010). While there is a broad overlap in the distribution of the more northern sloth taxa in the late Pleistocene, faunas with multiple sloth taxa are not common
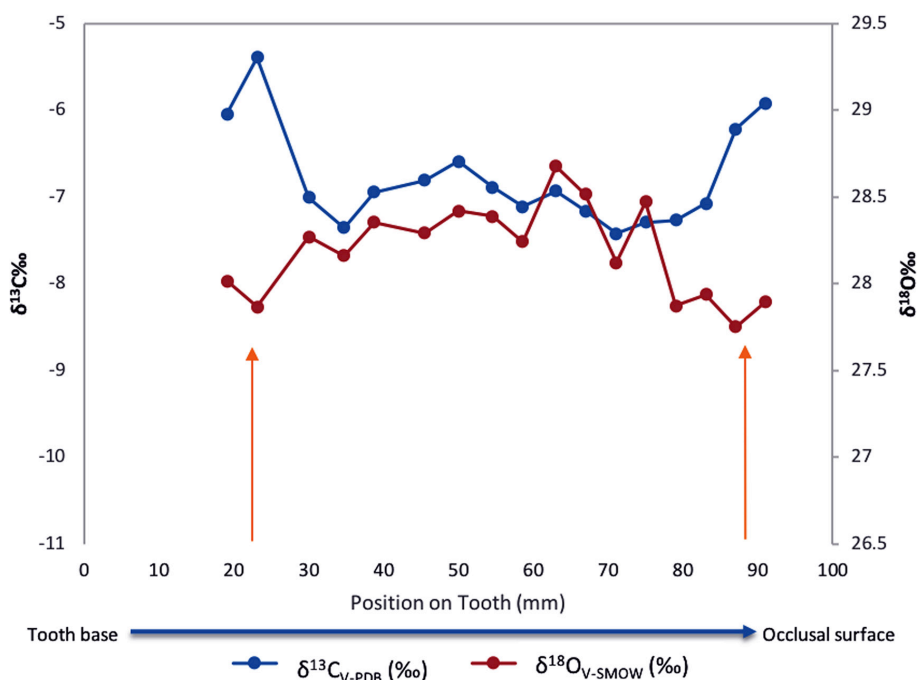
Fig. 1—Results of isotopic analysis of the oxygen and carbon isotopes in the orthodentine of a tooth of *Eremotherium laurillardi* from Belize. Arrows indicate two wet seasons, at ca. 2 and 9 cm (after Larmon *et al*., 2019).

reflecting different habitat preferences by the different taxa. While most faunas may only have a single species of sloth, two different sloths in a fauna are more common than faunas with three sloths and there are no sites in which more than three sloth taxa are present in a fauna. When multiple taxa do co–occur in a fauna generally one taxon is much better represented than the others. Currently the southern taxa are more constrained in their distribution, but this may simply reflect the currently limited number of sites from which they are known. Consequently, their potential for co–occurring in a fauna cannot be determined at this time. Given the wide latitudinal range of the elephant–sized sloth, *Eremotherium* (Table 1), it would be expected that its range would have overlapped with multiple other sloth taxa but often it is the only sloth present in fauna indicating ecological requirements not commonly shared with other sloths. The range of the small sloth, *Nothrotheriops*, extends from the southwestern United States into Belize but while its range overlaps with the southern sloth taxa, again it has not yet been reported from the same sites. The mylodon sloth, *Paramylodon harlani*, is well represented in faunas in temperate North America but while mylodont sloths reported from southern Mexico and northern Central America have been referred to *Paramylodon*, the available material has not been studied in detail and these records may possibly be a different genus or species. Currently the southernmost record of *Megalonyx* only barely extends to within the range of the southern taxa given the record of *Xibalbaonyx* from Jalisco.

The recent recognition of three distinct genera of megalonychid sloths, *Nohochichak*, *Xibalbaonyx* and *Meizonyx*, from southern Mexico indicates the presence of a diversity of sloths in semitropical and tropical North America south into Central America not previously recognized. This suggests either multiple dispersal events restricted to the tropics or the possibility of a local radiation derived from a single ancestor. In either case it is likely that the ecological adaptations of these taxa are quite different from the better known northern temperate adapted sloths.

The palaeoecology of sloths, including their diet and preferred habitat, can be inferred from multiple sources depending on the taphonomy of the site in which a sloth is found. The comparison of multiple sites can provide an idea of the animal's distribution and depending on the nature of the site different components of the sloth's palaeoecology can be inferred as well. Not all sites may preserve or provide the same information, so in most cases our interpretation of the species' ecology is of necessity a composite of data provided by different sources.

PALAEOECOLOGICAL DATA SOURCES

Associated Macrobotanical Remains and Pollen

Many types of deposits may preserve botanical remains along with skeletal material and thus provide direct evidence of the plant associations with the sloths and other associated

herbivores. Besides sedimentary deposits these can include peat bogs, dry caves and asphalt seeps. As each of these types of deposit may be restricted in their distribution due to the specific conditions needed for their formation, they may have a limited geographic distribution so not all are equally available throughout the animal's distribution or may not be present within the range of the different sloths. Consequently, they may be limited in what types of fossil plant remains associated with the sloth may be preserved. Therefore, their contribution to providing information on sloth diet and its associated plant community in a region may be limited as well.

Determination of the preferred habitat for the different sloths cannot always rely on placing them within modern plant assemblages as their preferred habitat. Palaeobotanists have long recognized the individualistic response of plant species to environmental change so some plant taxa may be sympatric at certain limited times when climatic conditions permit and allopatric at others. Consequently, in the late Pleistocene it is necessary to consider the existence of non–analog plant communities formed by the temporary co–occurrence of species in palaeocommunities that today are allopatric (Graham & Grimm, 1990). The difference in composition reflects individual species distributions that change along environmental gradients in different directions, at different rates, and at different time intervals in response to changes in climatic parameters such as seasonal temperatures and rainfall. The individualistic responses of the biota created new community patterns which shifted on the landscape in response to climatic change. The disappearance of these unique vegetational communities due to climate change at the end of the Pleistocene may have contributed to the extinction of megaherbivores. This may indicate a strong fidelity of some sloths to a specific type of habitat while others may have been more labile in their diet and habitat preferences

and able to utilize multiple different habitats. Depending on the fossil record and what is preserved in association with the sloth remains it may not always be possible to identify the specific composition of the associated habitat and only a rough approximation may be possible by placing it within the closest modern equivalent habitat.

Dung Samples

While coprolites are well documented in the fossil record, from the standpoint of the Pleistocene, all known sloth coprolites are from dry cave deposits. The number of known sloth taxa to which the coprolites could be assigned with surety is limited to *Mylodon darwinii* and *Nothrotherium maquinense* in South America, cf. *Megalocnus* from Cuba, and *Nothrotheriops shastensis* in North America (see Hunt & Lucas 2018 for a review and summary). Plant material considered to be from decomposed dung of *Eremotherium laurillardi* has been described from an asphalt deposit in Ecuador (Lindsey *et al*., 2020). While limited in terms of taxonomic diversity these samples do provide the best direct evidence of the types of plants consumed by these sloths and can provide an independent confirmation of their diet based on stable isotope analysis. Confirmation that dung attributed to sloths was in fact produced by a sloth has been provided by ancient DNA analysis for dung of *Nothrotheriops shastensis* (Poinar *et al*., 1998) and on hairs of *Mylodon darwinii* in dung (Clack *et al*., 2012).

Stable Isotopes

Examination of stable isotope values within ancient mammal tissues has proven useful for both identifying dietary and habitat preferences. For mammals, carbon isotope values

Table 1— Latitudinal and elevational ranges of North American Late Pleistocene ground sloths.

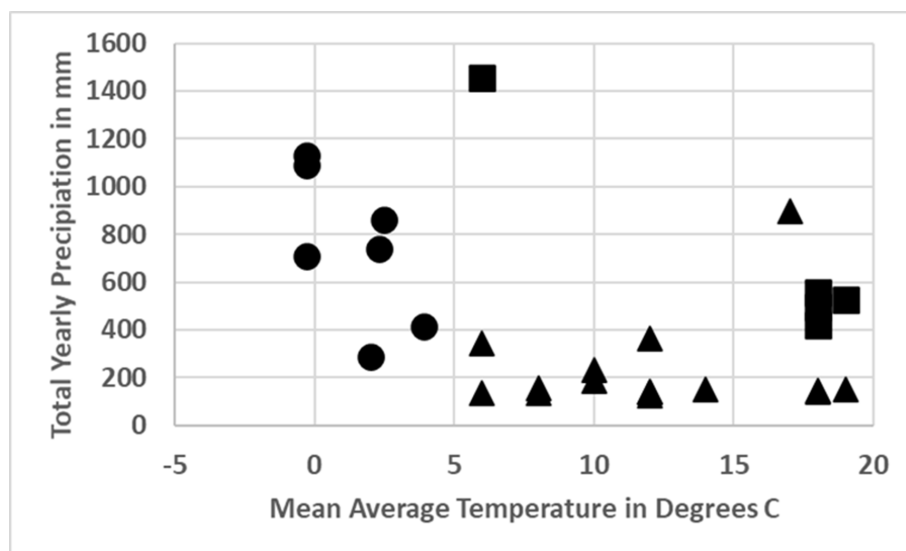| Taxon	Northernmost Record	Southernmost Record	Latitudinal Range	Lowest Elevation	Highest Elevation
Eremotherium laurillardi	40.3° N	–30.51° S	70.81°	0 m	1980
Megalonyx jeffersonii	67.8° N (Sang.) 53.6° N (Wisc.)	18.92° N	48.88°	0 m	2667(Sang.) 2250 (Wisc.)
Paramylodon harlani	48.1 ° N	19.2° N	28.9°	0 m	2375
Nothrotheriops shastensis	40.92° N	17.1° N	23.82°	0 m	2418
Meizonyx salvadorensis	18.12° N	13.75° N	4.37°	687 m	1599
Xibalbaonyx X. oviceps X. microcaninus X. exinferis		20.87° N 20.23° N 20.87° N		10 M 1372 M 10 m	
Nohochichak xibalbahkah		20.32° N		9 m	

Fig. 2—Comparison of Mean Average Temperature and Total Annual Precipitation for multiple sites of *Megalonyx jeffersonii* (circle), *Paramylodon harlani* (square) and *Nothrotheriops shastensis* (triangle). Based on data provided in Tables 2, 3, and 4.

generally reflect differences in the percentages of C3 plants and C4 plants consumed (Koch, 1998; DeNiro & Epstein, 1978a, b). A diet of pure C3 plants in Pleistocene mammals would range from −29‰ to −15‰ in bone collagen, while a diet of pure C4 plants would range from −13‰ to −4‰. Nitrogen isotope values in mammals reflect the isotopic composition in the soil on which the plants they fed grew, the composition in their diet, the metabolism of the particular individual, and the species trophic level. In areas that are warm and dry, $\delta^{15}N$ values in soils will tend to be more positive (Ambrose & DeNiro, 1986, 1987; Ambrose, 1991; Amundson *et al*., 2003). The $\delta^{15}N$ of collagen appears to increase with decreasing precipitation (Heaton *et al*., 1986; Gröcke *et al*., 1997; Koch, 1998; Schwarcz *et al*., 1999; Robinson, 2001).

Changes in the $^{18}O/^{16}O$ ($\delta^{18}O$) concentrations throughout the length of the ever–growing tooth in sloths can be indicative of seasonal changes in the temperature and/or the amount of precipitation. This isotopic data roughly reflects the $\delta^{18}O$ values of water consumed by the animal by both drinking and/or ingested with food (DeSantis *et al.*, 2009; Brookman & Ambrose, 2012). As these values can vary substantially with humidity and water stress, they can provide information on the duration and intensity of the wet and dry seasons. In general, higher $\delta^{18}O$ values in local water can indicate high evaporation and/or low precipitation, often caused by warm and/or dry conditions.

While most stable isotope studies of mammals utilize tooth enamel and sloth teeth lack enamel, the orthodentine of sloth teeth which has not been diagenetically altered can be sampled to provide stable isotope data (Larmon *et al*., 2019). One advantage of sloth teeth is that they are evergrowing (hypselodont) so sampling the entire length of the tooth permits a determination of changes in their diet as well as

climate through different seasons. While carbon isotope values are routinely determined, different researchers may either look at nitrogen isotopes or oxygen isotopes as well. Consequently, different pairings of isotopes are often reported resulting in some inconsistently in the data available and limiting comparisons between regions for one sloth taxon or comparisons between different sloths.

Palaeoclimatic Data Models

Recently Climate Envelope Models (CEMs) have been used to examine the distribution of extant species and infer past and future distribution based on the climatic variables measured at localities across a species' geographic range (Polly & Eronen, 2011). Currently this approach has only been applied to extant taxa for which climatic variables can be directly determined from weather stations within the species range. To determine similar climatic variables for extinct species a Macrophysical Climate Modelling (MCM) can be used to determine many of the climatic parameters used in CEMs to examine similar data for extinct species such as sloths and compare the consistency of the calculated palaeoclimatic parameters for multiple sites. Two primary factors that can be calculated by the MCM that determine vegetation composition of biomes is the Total Annual Precipitation (TAP) and the Mean Average Temperature (MAT) (Whittaker, 1975).

The MCM was developed in the mid–1990s as an alternative to iterative general circulation models (GCMs) (Bryson & Bryson, 1997). The MCM has previously been applied to archaeological sites and has been referred to as archaeoclimatology (Bryson & McEnaney DeWall, 2007). The MCM utilizes a top–down rather than bottom–up approach to model building, based on the following parameters:

orbital forcing, variations in atmospheric transparency, and the principles of synoptic climatology. More comprehensive overviews of the model can be found in Bryson & Bryson (1997, 2000) and Bryson (2005).

Application of Macrophysical Climate Modelling has previously been applied to sites containing specimens with reliable radiocarbon dates of the extinct giant beaver, *Castoroides ohioensis* (McDonald & Bryson, 2010) and the preliminary results of applying this approach to the palaeoecology of *Nothrotheriops* was presented by McDonald (2011). The model permits an examination and comparison of their climatic parameters and the establishment of a rudimentary climatic envelope for an extinct species based on specimens for which there are good radiocarbon dates.

SYNOPSIS OF THE SLOTH GENERA

Eremotherium laurillardi

Eremotherium has been referred to as the Pan–American ground sloth as it has the widest distribution of all sloths, with the range of late Pleistocene species *E. laurillardi* extending from the state of Rio Grande do Sul in southern Brazil to New Jersey in the United States. The genus first appears in the North American fossil record in the middle Pliocene (Blancan) and while it survives in South America until the late Pleistocene. McDonald and Lundelius (2009) proposed that its range started contracting much earlier and *Eremotherium* was absent from the United States by the early Wisconsinan. There was no significant change in body mass of *Eremotherium* from the Blancan to the Rancholabrean. The body mass estimate of *E. laurillardi* for the late Pleistocene is 3961 kg (McDonald, 2005). There are few radiocarbon dates for this species so a precise timing of its range reduction and correlation with climatic change is not possible at this time.

Based on skeletal morphology, it has been suggested that *Eremotherium* was a browser, rather than a mixed feeder (Webb, 1999). However, the higher average δ^{13}C value of −6.8‰ (intermediate between −9 and −2‰) on a specimen from Belize indicates more of a mixed diet and indicates the species was both browsing and grazing. The *Eremotherium* tooth from Belize is from the Last Glacial Maximum (LGM) (26,975 ± 120 calibrated years before present). Stable isotope analysis of the tooth for its entire length for stable carbon and oxygen isotope analysis showed that the tooth recorded two wet seasons separated by one longer dry season and that this sloth was able to adapt its diet to survive the marked seasonality of the LGM (Larmon *et al*., 2019) (Fig. 1). *Eremotherium* likely relied more on C4 or CAM vegetation during the wet season, and C3 plants during the dry season, consistent with their hypothesized adaptive flexibility. Stable isotope analysis of *E. laurillardi* from Sergipe State, northeastern Brazil between 11,084 and 27,690 cal yr BP, indicated it was also a mixed feeder diet utilizing C3/C4 plants based on δ^{13}C values of–7.7 to–3.3 (França *et al*., 2014). They proposed that the meso–megamammals from the late Pleistocene of Sergipe lived in a more closed (presence of C3 plants, like herbs and shrubs) and drier environment than previously occurred in Sergipe between 27 to 11 ky. Omena *et al*. (2020) obtained similar results based on 40 samples for *Eremotherium* from the Brazilian Intertropical Region. The data included 24 new isotopic data which was incorporated with data previously published by Dantas *et al*. (2017), Pansani *et al*. (2019) and Silva *et al*. (2019). The δ^{13}C range was between −11.01‰ and 0.41‰, with a mean value of −5.66 ± 2.60 ‰. They concluded that *Eremotherium* was a generalist species (μBA = 0.76 ± 0.26), feeding more on C4 plants (pi = 53%) than C3 plants (pi = 47%). The δ^{18}O varied between 27.62‰ and 32.77‰, including published data (Dantas *et al*., 2017; Pansani *et al*., 2019; Silva *et al*., 2019). The feeding ecology of *Eremotherium* is interpreted as a mixed–feeder and its diet did not change between 27 and 10 ka, based on associated radiocarbon dates.

Table 2—MCM modelled Mean Average Temperature and Total Annual Precipitation for late Pleistocene localities with *Megalonyx jeffersonii*.

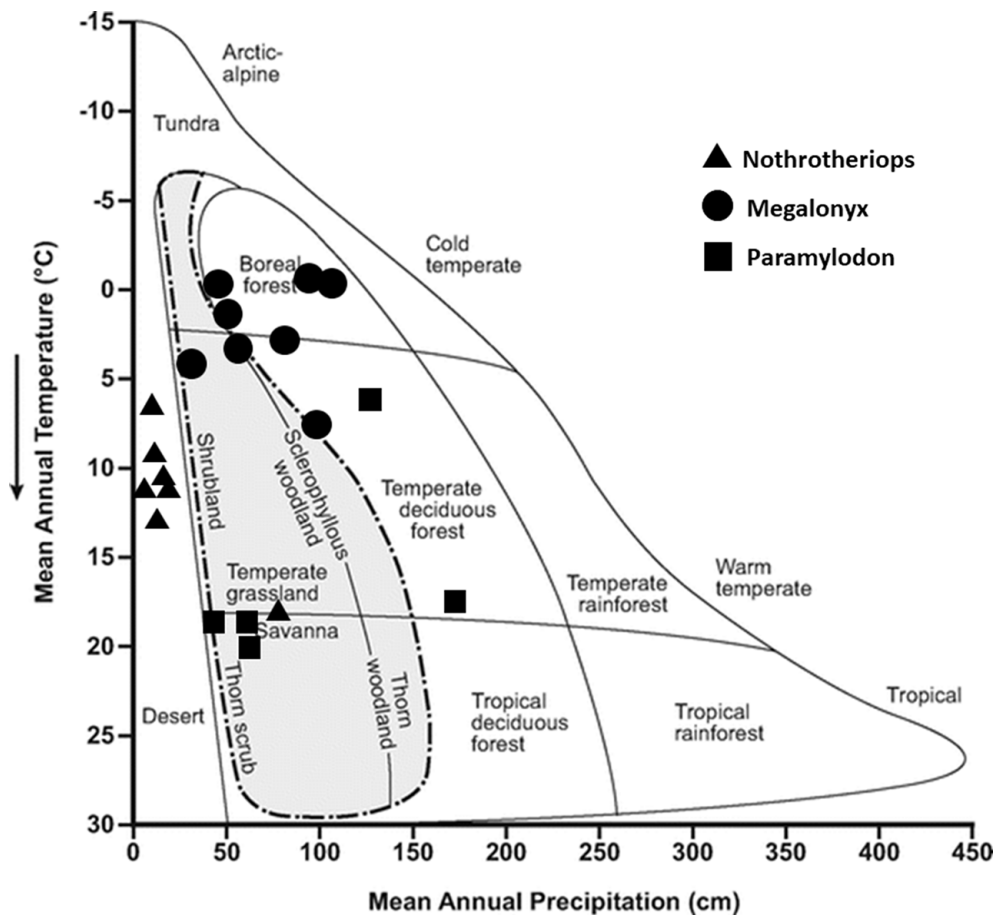| Locality	Age Calendar years	Mean Average Temperature °C	Total Annual Precipitation in mm
Orcas Island WA	13,000	2.3	741
Millersburg OH	13,200	2.5	859
Lange Farm IL	13,400	–0.3	1132
Newburgh NY	13,400	–0.3	1092
North Fairfield OH	13,600	–0.3	711
Haven Site ND	13,800	3.9	413
Bishop Ranch WA	14,200	2.0	286
Average		**1.4**	**748**

Fig. 3—Whittaker Biome Diagram showing difference in modern habitat preference for multiple sites of *Megalonyx jeffersonii* (circle), *Paramylodon harlani* (square) and *Nothrotheriops shastensis* (triangle) based on Mean Average Temperature and Total Annual Precipitation calculated from the MCM.

The isotopic data for *Eremotherium* and other associated mammalian taxa indicates a dry environment with mixed vegetation with a predominance of open savanna, with shrubs and low–density forests suggesting that the area at the time was similar to the current habitat of arid and open areas of shrub savanna. Available oxygen isotopic data from speleothems in northeastern Brazil (Cruz *et al*., 2009) show a decrease of humidity between 27 ka to 21 ka, and an increase of humidity between 21 ka to 10 ka, being, in average, a dry interval in the late Pleistocene. This is complemented by oxygen isotopic data associated with radiocarbon dates from 27–10 ka, which although punctuated also overall show homogeneous dry climatic conditions in this region during the LGM.

In the United States it appears that most of the Rancholabrean records of *Eremotherium* are from the Sangamonian interglacial with possibly one record from the early Wisconsinan (McDonald & Lundelius, 2009). Consequently, there are no good radiocarbon dates for this taxon that would permit the use of the MCM model to calculate temperature and precipitation parameters.

As a generalist feeder having a diverse diet *Eremotherium* appears to have inhabited varied landscapes and was adapted to variable climatic conditions, thus enabling its wide latitudinal distribution (Table 1). While the range of the species is essentially restricted to tropical and subtropical zones it is consistently associated with drier more open habitat and there currently is no evidence to suggest that these giant ground sloths were consuming vegetation in dense forests. The data from South America along with that for *E. laurillardi* in North America is complementary in that the animal primarily inhabited more open environments.

Megalonyx jeffersonii

After *Eremotherium*, *Megalonyx* has the second greatest latitudinal range of the North American late Pleistocene ground sloths extending from the Yukon (McDonald *et al*., 2000) south to central Mexico (Table 1). Changes in its distribution during the Pleistocene reflects changes in climate with the more northern occurrences and presence at higher elevations occurring during the Sangamonian interglacial while during

the Wisconsinan the range contracted to lower latitudes and elevations. The size of *Megalonyx* increased in time from its first appearance in the late Miocene (Hemphillian) until its extinction at the end of the Rancholabrean. The estimated mean body mass of *M. jeffersonii* in the late Pleistocene is 1090 kg although some individuals were markedly larger (McDonald, 2005).

In the eastern United States multiple remains of *Megalonyx* have been recovered from peat bogs which also permit the identification of associated plants based on macrobotanical remains along with pollen. Such a site is the Lang Farm locality in northern Illinois. The late Pleistocene environments of northern Illinois were quite dynamic, exemplified by rapidly fluctuating ice fronts of the Laurentide ice sheet and related changes in the vegetational communities. Comparison of dated pollen data from northern Illinois with that from Lang Farm indicated that these species inhabited a nonanalog environment that was transitional from midlatitude tundra to mixed conifer and deciduous woodland. Although spruce (*Picea* sp.) was dominant, it was less abundant than prior to 12,500 ^{14}C yr B.P. the age of the *Megalonyx* from the site. The presence of black ash (*Fraxinus nigra*) and fir (*Abies* sp.) indicate a wet climate and heavy winter precipitation (Schubert *et al*., 2004). A similar pattern based on pollen was present at a bog site with *Megalonyx* in Darke County, southwestern Ohio and included a double spruce peak that generally characterizes the Bølling–Allerød/Younger Dryas climate fluctuation (Shane, 1976, 1980).

Stable isotope analysis of *Megalonyx* from New York showed a δ^{13}C value for this specimen of −20.5‰ and implies a diet of only C3 plants. The δ^{15}N value was 5.0‰ and is similar to other modern herbivores of New York (McDonald *et al*., 2019). These isotopic values are also similar to values previously obtained for this species from the late Pleistocene Saltville locality, Virginia, and supports the idea that this species was a forest dwelling browser (France *et al*., 2007).

The MAT and TAP for *Megalonyx* from multiple sites of different ages as calculated using the MCM are provided in Table 2. The average MAT of all the sites is 1.4°C indicating *Megalonyx* was more tolerant of colder temperatures than

other North American sloths for which this data can be calculated (Fig. 2). A greater tolerance to colder temperatures, particularly winter temperatures that went below freezing is reflected in its presence at higher latitudes and elevations than the other North American sloths. The average TAP calculated from the MCM is 748 mm with a range from 286 to 1132 mm. In areas with smaller amounts of precipitation *Megalonyx* may have had a more restricted distribution to riparian vegetation along rivers (Hoganson & McDonald, 2007).

Paramylodon harlani

The mylodont *Paramylodon* first appears in North America in the middle Pliocene (Blancan). Mylodonts have typically been interpreted as grazers or at least mixed feeders. *Paramylodon* increased in size from the Pliocene to Pleistocene (Blancan to Rancholabrean) and the estimated body mass of late Pleistocene individuals is 1392 kg (McDonald, 2005). While dung of *Paramylodon* is not known, the dung of a related South American genus, *Mylodon*, is known and predominately includes fragments of grasses and sedges along with other plant species associated with modern cool, wet sedge–grasslands (Moore, 1978). In the late Pleistocene after *Megalonyx jeffersonii P. harlani* had the widest distribution in North America of all the sloths and has been recovered from sites coast to coast and from the United States–Canadian border south into Mexico giving it a wide latitudinal range as well (Table 1).

While originally interpreted as a grazer, based on its skull morphology and dentition Naples (1989) proposed *Paramylodon harlani* (then referred to *Glossotherium*) may have been more of a mixed feeder. Recent stable isotope analysis of *Paramylodon* has provided an independent means to assess the animal's diet. *Paramylodon harlani*, from the Gulf Coast of Texas (Ingleside fauna) showed δ^{13}C values of near–4‰, in the range expected of mixed feeders, but close to the carbon isotopic composition of modern and fossil grazers (Ruez, 2005). Coltrain *et al*. (2004) examined 10 specimens of *Paramylodon* from Rancho La Brea and obtained values with a δ^{13}C range of values between–19.99

Table 3—MCM modelled Mean Average Temperature and Total Annual Precipitation for late Pleistocene localities with *Paramylodon harlani*.

Locality	Age Calendar years	Mean Average Temperature °C	Total Annual Precipitation in mm
Hillsboro OR	14,500	6	1454
Rancho La Brea CA	23,400	18	496
Rancho La Brea CA	24,400	18	559
Rancho La Brea CA	27,500	18	419
Rancho La Brea CA	28,300	19	528
Average		**15.8**	**691**

and–21.49, average–20.99. The δ¹⁵N values ranged from 6.44 to 10.12, average 7.93. Two individuals from the Willamette Valley, Oregon had δ¹³C values of–20.8 and–21 and δ¹⁵N values of 7.4 and 6.6 indicating they were feeding primarily on C3 vegetation in a palaeoenvironment of open grassland and sparse canopy (Gilmour *et al.*, 2015). The inferred diet of *P. harlani* from Valsequillo, Mexico based on δ¹³C indicated that this individual was primarily a grazer (Pérez–Crespo *et al.*, 2014), while two samples from Térapa, Sonora produced quite different δ¹³C values of −6.3 and −0.5 similar to other taxa from the site and supported the interpretation of a mosaic of habitats that supported a variety of herbivores with different dietary preferences. Based on the sloth and other herbivores there is no isotopic evidence to suggest the presence of closed–canopy forests or the strict consumption of C3 plants by any of the mammalian herbivores found at Térapa. Most of the herbivores were exploiting a wide range of vegetation within a tropical dry forest and grassland (Nunez *et al.*, 2010). The sloth had δ¹⁸O values of −6.3 to −4.9 and based on the oxygen isotope values of the other herbivores it does not appear there was any seasonal variation in the δ¹⁸O values (~4‰) compared to modern desert environments of the area which display significant annual variations in δ¹⁸O.

The range of results for stable isotope values obtained from different localities suggests dietary flexibility in *Paramylodon* and that it was able to utilize a variety of different open environments, from grasslands to more wooded areas but did not utilize closed–canopy environments. This is also seen in other localities as well based the reconstruction of the dietary habits of other herbivorous mammals from El Cedral, La Cinta–Portalitos and Villaflores, localities which also include *Paramylodon*, that indicates it lived in areas with heterogenous vegetation dominated by grasslands (Pérez–Crespo *et al.*, 2015; Marín–Leyva *et al.*, 2016; Díaz–Sibaja *et al.*, 2018). The close association of *Paramylodon* with other grazing herbivores was also noted by McDonald and Pelikan (2006).

There are only a small number of radiocarbon dates for *Paramylodon* and most are from Rancho La Brea with one from Oregon (Table 3). Preliminary calculations of MAT and TAP are therefore highly biased and a larger sample throughout the range of the animal is needed to refine what is currently available. The average MAT is 15.8°C with a low of 6°C for the Oregon record suggesting that despite its larger size *Paramylodon* was not as cold tolerant as *Megalonyx*. The TAP is 691 mm with a range of 419 mm to a high of 1454 mm based on the Oregon record so in terms of the TAP broadly overlaps with *Megalonyx*.

Nothrotheriops shastensis

Nothrotheriops first appears in North America in the middle Pleistocene (Irvingtonian) and became extinct at the end of the Pleistocene. While there was a slight increase in size of the genus from the Irvingtonian to the Rancholabrean, the estimated mass of individuals from the late Pleistocene is 463 kg (McDonald, 2005) making this genus the smallest of the late Pleistocene ground sloths in North America.

Nothrotheriops is the most xeric adapted of all the sloths in North America based on multiple localities in the southwestern United States, many of which have preserved soft tissues as well as the animal's dung. This is the only sloth species in North America with preserved dung as confirmed by DNA fingerprinting (Poinar *et al.*, 1998). Analysis of the macrobotanical remains in the dung has permitted a detailed determination of the diversity of plants in its diet (Hansen, 1978). Many of the taxa are restricted to desert environments as indicated by plant taxa including desert globemallow (*Sphaeralcea ambigua*), Nevada Mormon tea (*Ephedra nevadensis*), saltbushes (*Atriplex* spp.), catclaw acacia (*Acacia greggii*), creosote (*Larrea* sp.) and yucca (*Yucca* spp.). There are also many of the other plants with wider distributions that are found in other habitats as well. Examples include common reed (*Phragmites communis*), Utah juniper (*Juniperus utahensis*), cattail (*Typha* sp.), three leaf sumac (*Rhus trilobata*) and gray rabbitbrush (*Ericameria nauseosa* = *Chrysothamnus speciosus*). Similar suites of plants have been identified in the dung of *Nothrotheriops* from Gypsum Cave, Nevada (Laudermilk & Munz, 1934) and Shelter Cave, New Mexico (Thompson *et al.,* 1980).

As the range of *Nothrotheriops* extended beyond the desert southwestern United States, to the west to the coast at Rancho La Brea and into northern California where it is known from three cave sites, Potter Creek, Samwell and Hawver (McDonald & Jefferson, 2008) and south to Belize (DeIuliis *et al.*, 2015) its eclectic diet permitted it to utilize multiple different habitats. Its presence in Belize may have coincided with an arid climatic interval and the presence of more xeric adapted vegetation than exists in the area today.

The vegetation at Rancho La Brea differs significantly from other sites in the southwestern United States with *Nothrotheriops*. Plant macrofossils from Pit 91, the only pit with *Nothrotheriops* that has been radiometrically dated, indicate that between 28–26 ka, the vegetation of the Santa Monica Plain was predominately coastal sage scrub with pines and cypress at slightly higher elevations (Warter, 1976; Shaw & Quinn, 1986). While this vegetation dates younger than the *Nothrotheriops* at 33,000 years, the preserved plant remains at least provide a general overview of the mosaic of different vegetation communities in the area. For example, a chaparral community grew on the slopes of the Santa Monica Mountains along with isolated coast redwood (*Sequoia sempervirens*) and dogwood (*Cornus californica*) in protected canyons with a riparian community that included willow (*Salix lasiolepis*), red cedar (*Juniperus* sp.) and sycamore (*Platanus racemosa*). These plant communities suggest a winter precipitation regime similar to the modern Mediterranean climate of coastal southern California. However, the presence of coast

Table 4—MCM Modelled Mean Average Temperature and Total Annual Precipitation for late Pleistocene localities with *Nothrotheriops shastensis*.

Locality	Age Calendar years	Mean Average Temperature °C	Total Annual Precipitation in mm
Rampart Cave AZ	12,100	12	362
Upper Sloth Cave TX	12,700	10	231
Gypsum Cave NV	13,000	14	152
Gypsum Cave NV	13,300	12	140
Devil Peak NV	13,300	12	124
Shelter Cave NM	13,300	6	137
Lower Sloth Cave TX	13,500	8	157
Gypsum Cave NV	13,700	12	139
Williams Cave TX	14,100	10	186
Rampart Cave AZ	14,700	6	345
Shelter Cave NM	14,700	8	137
Gypsum Cave NV	23,300	18	148
Gypsum Cave NV	25,800	19	151
Gypsum Cave NV	27,600	18	139
Rancho La Brea CA	33,000	17	897
Average		**12**	**230**

redwood, now found 600 km to the north in the summer fog belt indicates a cooler, more mesic and less seasonal climate at terminal OIS 3 than present and corroborates the pollen record. The presence of coast redwood and dogwood in southern California and the Los Angeles Basin suggests the possibility of the existence of no–analog plant communities in the region. While the MAT at Rancho La Brea at 33,000 years is comparable to that of other sites with *Nothrotheriops* there was significantly more annual precipitation as also indicated by the plants (Table 4).

Stable isotope analysis of *Nothrotheriops* from two sites in southern Nevada (Tule Springs and Devil Peak Cave) by Bonde (2013) was consistent with data from the dung that the animal's diet was predominately xeric vegetation. However, analysis of specimens from the northern California cave sites (Potter Creek Cave, Hawver Cave and Samwel Cave) indicated that this species had a much more isotopically diverse diet than previously thought based on the dung samples indicating an enrichment in ^{13}C through life, with a tendency to consume C3 or mixed vegetation in its earlier years and increasing percentages of C4 vegetation as it aged. The δ^{13}C for the Devil Peak individual was–4.1 and–4.7 for the Tule Springs individual while the δ^{18}O was–6.9 for the former and–6.1 for the later. In contrast the δ^{13}C values for Potter Creek Cave were–8.6 and–8.4, Samwell Cave–8.9 and–8.0 and Hawver Cave–11.4 while the δ^{18}O values were–6.9 (Devil Peak),–6.1 (Tule Springs) while the values for the northern

California sites were–5.7 and–5.2 (Potter Creek Cave),–4.7 and–4.3 (Samwell Cave) and–4.2 (Hawver Cave).

There are more available radiocarbon dates for *Nothrotheriops*, than for *Megalonyx* and *Paramylodon* combined (Table 4). The majority of dates were obtained from the dung of *Nothrotheriops* with only a few dates based on bone. This permits a more robust sample for using the MCM to calculate climatic parameters for this sloth, not only from different sites but also from the same site over time. However, it should be noted that as the majority of dates are from dung, they represent only a small part of the range of *Nothrotheriops* since the caves that preserve the dung are restricted to the arid southwestern United States. The average MAT is 12°C with a range of 6–19°C indicating that *Nothrotheriops* was the least cold tolerant of the three sloths in temperate North America and this is reflected by the lower latitudes and elevations for the majority of sites where it has been found and its range extended farther south than either *Megalonyx* or *Paramylodon*. Based on an average TAP of 230 mm with a range of 124 to 897 mm it also seemed more tolerant of drier habitat than any of the other North American sloths.

While *Nothrotheriops* clearly did well in more xeric environments given the larger number of localities of this species in the southwestern United States and south through Mexico to Belize, it clearly utilized other types of habitat as well, which may explain its occasional co–occurrence in faunas with other sloths such as *Megalonyx* and *Paramylodon*

at Rancho La Brea. The abundance of *Paramylodon* at La Brea, the much smaller number of *Nothrotheriops* and rarity of *Megalonyx* (one individual), clearly shows that the habitat was more optimal for *Paramylodon* and probably marginal for the other two sloths.

Meizonyx salvadorensis

Meizonyx salvadorensis is known from the middle Pleistocene of El Salvador and the late Pleistocene of Mexico. The femur, upon which other body mass estimates were made for the other sloths is not known for this sloth so while it is a large taxon based on comparison of skull measurements to other sloths (McDonald *et al*., 2020), there is no estimate of its body mass. Based on the skull it is similar in size to *Megalonyx jeffersonii*.

The distribution of *Meizonyx* in Mexico is limited to two nearby sites in the Sierra Mazateca of the Sierra Madre Oriental del Sur, State of Oaxaca (McDonald *et al*., 2020). The height of the Sierra Mazateca ranges from 500–2800 m, resulting in a high diversity of habitats and the two sites are at 1466 and 1599 masl. The types of plant communities in the mountains are diverse and form a gradient by elevation (Rzedowski, 1983): (1) thorn scrub dominated from 640–800 m (2) tropical semi–deciduous forest from 800–1250 m, (3) old–growth oak–pine forest dominated from1800–1900 m (4) primary oak forest dominated from 2000–2300 m and (5) primary cloud forest dominated from 2200–2700 m. The elevation of caves in which *Meizonyx* was recovered places them in the current transition from tropical semi–deciduous forest to old–growth oak–pine forest zones. During the Pleistocene lower temperatures during glacial intervals resulted in a downslope migration of montane vegetation zones (Lozano–Garcia *et al*., 1993; Metcalf *et al*., 2000; Correa–Metrio *et al*., 2011). These shifts occurred as cycles of expansion and contraction of mountain pinyon, juniper and oak woodlands in the mountains and shifts in their elevational distribution (Toledo, 1982; McDonald, 1993). The δ^{13}C value of–23‰ in *Meizonyx* indicates it was feeding on C3 plants in a reasonably mesic environment so it may have been living in an oak–pine or oak dominated habitat which had shifted downslope. Outside of Mexico the only other record of *Meizonyx* is from a lower elevation, 687 masl, in El Salvador (Webb & Perrigo, 1985). This site is considered middle Pleistocene in age and given the paucity of palaeobotanical data from the site it is difficult to integrate with the Mexican record.

The higher elevation for the current records of *Meizonyx* in Mexico clearly distinguishes it in terms of its habitat from *Nohochichak* and *Xibalbaonyx* from Yucatan at much lower elevation, essentially at sea level. The record of *X. microcaninus* from Jalisco is at 1372 m so approximates that of *Meizonyx*. MCM calculations of the climatic parameters have not been done due to the small sample size.

Nohochichak xibalbahkah

Nohochichak is only known from the late Pleistocene of the Yucatán Peninsula (McDonald *et al.*, 2017). It is about the size of a medium sized *Megalonyx* and an estimate of its body mass based on femur length is 987 kg.

This monotypic genus is currently known only from a single locality, the Hoyo Negro portion of the Sac Actun cave system in the eastern Yucatán Peninsula, Quintana Roo, Mexico. The cave entrance is at 9 masl so during the Last Glacial Maximum with the lowering of sea level and the drop in the local water table the area around the cave system would have been a more arid landscape. The current vegetation on the Yucatán is profoundly affected by the alternating dry and wet seasons, and vegetation zones gradually grade into one another horizontally and lack sharp boundaries due to the lack of any mountain ranges. Tropical dry forests extend across the north central portion while the distribution of tropical forest composed of deciduous semievergreen forests is present in the central, eastern and southern parts of the Yucatán Peninsula (Islebe *et al*., 2015). The pattern of distribution of the vegetation reflects the pattern of rain distribution which ranges from the driest areas in the northeast to the most humid areas in the southwest (Barber *et al.*, 2001). Located in the southeastern portion of the Yucatán Peninsula the vegetation around Actun Sac today is tropical forest.

Knowledge of Pleistocene vegetation on the Yucatán Peninsula during the Pleistocene is based primarily on pollen records from lakes Quexil and Salpeten (Leyden *et al*., 1994; Piperno 2006). They indicate that from the Late Pleistocene to early Holocene the region was dry. In many cases lake levels were strongly influenced by lower glacial sea levels and groundwater levels. By the Last Glacial Maximum, the combination of the extensive Laurentide ice sheet, cool sea surface temperatures over the Gulf of Mexico and Caribbean and lower sea level indicates a collapse of the modern summer rainfall regime (the Mexican monsoon) (Metcalf *et al*., 2000). Lake levels started to rise after 9000 yr BP indicating a wetter climate and generally wet conditions prevailed through the Holocene from about 7000 to 3000 yr BP. after the presumed extinction of the sloth.

Today the most important component of climate variability in the tropical Atlantic is the change in the strength and position of the Intertropical Convergence Zone (ITCZ). During the Pleistocene changes in regional precipitation would have been triggered by shifts in the mean latitudinal position of the Atlantic ITCZ. During periods of cooler sea surface temperatures of the North Atlantic, at time scales ranging from the Little Ice Age to the Younger Dryas to the cold stadials of the last glacial, there was a southward shift in the mean latitudinal position of the ITCZ. In contrast, during warm interstadials and periods of Holocene and deglacial warmth there would have been a northward shift in the position of the ITCZ and its belt of convective rainfall

(Peterson & Haug, 2006). This would have resulted in north south shifts in the different types or vegetation on the Yucatán Peninsula and consequently impacted the distribution of megaherbivores such as sloths, especially if they were closely tied to specific food plants.

Currently, there is no data on plants, either macrobotanical or pollen, associated with the Pleistocene fauna recovered from Actun Sac. Likewise, no stable isotope analysis of *Nohochichak* has yet been done, so inferences as to the specifics of its diet and preferred habitat is not possible. A large stick, which was collected, laying on the mandible of *Nohochichak* produced an AMS radiocarbon date that provides a minimum age for its deposition of 9807 ± 38 radiocarbon years (11,264–11,183 cal yr BP).

Xibalbaonyx (X. oviceps, X. microcaninus, X. exinferis)

While three species have been described for this genus, each is known only from the holotype, so information on the palaeoecology for the genus is more limited compared to other sloth genera. The holotype of *X. oviceps* is an immature animal as indicated by the unfused epiphyses of all the major limb bones and the visible sutures in the skull along with the general lack of rugosity on the bones commonly present in adult sloths (Stinnesbeck *et al.*, 2020). The femur of the holotype is preserved and retains the unfused head, but the distal epiphysis is absent. A very rough estimate of the body mass of this juvenile is 200 kg which given the ontogenetic immaturity of the skeleton would suggest the adult may have been the largest of the North American Pleistocene megalonychids.

There are no radiometric dates for any of the species, but all are presumed to be late Pleistocene in age. The types of *Xibalbaonyx oviceps* and *X. exinferis* were recovered from adjacent cenotes on the Yucatán Peninsula (Stinnesbeck *et al.*, 2017, 2020) while *X. microcaninus* is known from the state of Jalisco. While all three species are from localities that are about the same latitude, there is a significant difference in elevation of the Jalisco specimen (Table 1).

As *Xibalbaonyx oviceps* and *X. exinferis* were recovered from cenotes about 70 km north of Actun Sac the above discussion of palaeoclimate and vegetation for *Nohochichak* is equally applicable. As with *Nohochichak* there are no published data on associated plant material and no stable isotope analysis. The lack of dates prevents any determination as to whether these two genera were contemporaries in the area or if they lived in the area at different times and were tracking different types of vegetation in response to changes in precipitation. Likewise, the lack of a chronology prevents placing any of these animals within a climatic chronology for the region such as that of Metcalf *et al*. (2000) which would provide a general idea of the types of vegetation present when they were alive. Parsing out the ecological differences in the

two genera in the Yucatán requires more data than currently available.

Likewise, little can be said about the palaeoecology, habitat preference or diet of *Xibalbaonyx microcaninus*. While at about the same latitude as the other species of the genus, it is found inland and at a higher elevation (Table 1). Compared to the Yucatán, despite Central Mexico having a larger number of sites and the widest range of palaeoclimatic data in Mexico there is still not a clear picture of the palaeoclimate of that region (Metcalf *et al*., 2000). Early studies indicated that the period around the LGM (ca. 18,000 yr BP) was cool and dry, but more recent work including a better chronology indicates greater variability. Conditions were probably cool and moist (although possibly due to decreased evaporation rather than increased precipitation) up to the LGM, but the late glacial was dry. It appears that like its counterparts in the Yucatán *Xibalbaonyx microcaninus* was adapted to cooler and moister conditions and this most likely would have been reflected in the vegetation as well. Stinnesbeck *et al*. (2018) noted differences in cranial morphology between *X. microcaninus* and *X. oviceps* which they inferred reflected differences in the diets of the two species but did not propose any specifics.

Again, this genus cannot be placed within a climatic chronology for the region as there are no absolute dates for any of the specimens. Like the other species of the genus there is no data on associated plants and no stable isotope data. As there are no radiocarbon dates for any of the species of *Xibalbaonyx*, MCM calculations of the climatic parameters have not been made.

DISCUSSION

Three of the North American Pleistocene sloths, *Megalonyx jeffersonii*, *Paramylodon harlani*, and *Nothrotheriops shastensis*, are known from multiple localities in temperate North America. While their ranges do broadly overlap most localities have only a single sloth in a local fauna, a smaller subset of local faunas have two species of sloth and the presence of all three in a local fauna is rare and usually they are represented in disproportionate numbers with one species dominant and the others relatively rare (McDonald, 1996). Given the differences in the MAT and TAP of these taxa (Fig. 2) their co–occurrence may represent small areas of overlap in these climatic parameters as well as the necessary vegetation for their different dietary needs. Currently we do not have sufficient records for the sloths in semi–to tropical North America to provide the data for a similar analysis.

Megalonyx seemed to track its habitat and responded to climatic change from the Sangamonian interglacial to Wisconsinan glacial. During the Sangamonian it occurred at higher latitudes (Old Crow Basin, Yukon) and elevations (Ziegler Reservoir, Rocky Mountains, Colorado) (Table 1) than during the Wisconsinan. Given its inferred preference

for more boreal habitat the latitude–elevation relationship for modern Appalachian spruce–fir distribution can be used as model for evaluating this relationship. There is an inverse relationship between latitude and the lowest elevation of the spruce–fir/deciduous forest ecotone which decreases from 1,680 m at 35° N to 150 m at 49° N. Linear regressions of this relationship demonstrated a latitude–elevation relationship of −100 m/l° latitude for the spruce–fir/deciduous forest ecotone (Cogbill & White, 1991). The latitude–elevation relationship for mean July temperature (−94 to −121 m/lo latitude) was similar to the slopes of these ecotones so the spruce–fir/deciduous forest ecotone correlated with a mean July temperature of approximately 17 °C but not with the slope for mean annual temperature (−170 to −220 m/l° latitude). Consequently, changes in temperature may have determined the distribution of the preferred habitat of the sloth and therefore indirectly changes in its distribution during the Pleistocene perhaps the sloth's physiology given the low basal metabolism of these animals (McNab, 1985).

The more southern sloths in North America are dominated by members of the Megalonychidae and include three genera, the monotypic *Nohochichak* and *Meizonyx*, and *Xibalbaonyx* with three described species. All of these genera currently have a limited fossil record, which limits our ability to infer their distribution, habitat preferences and differences in diet, compared to other genera known from the region such as *Eremotherium* and *Nothrotheriops* which are known from a more robust fossil record. While it is reasonable to infer significant differences in habitat preference and diet in phylogenetically distinct sloths, the greater diversity of the more closely related megalonychid sloths would suggest more subtle niche partitioning and perhaps more specialized diets. The current limited sample of these taxa restricts the amount of data available but with the recovery and analysis of additional specimens will greatly improve our understanding of the palaeoecology of these animals and what contributed to their phylogenetic diversification in this region.

Use of the MGM palaeoclimatic model to determine MAT and TAP at sites with different species allows us to only broadly identify any differences in the preferred habitats for three of the sloths, *Megalonyx*, *Paramylodon* and *Nothrotheriops*, all from the temperate part of North America on a Whitaker Biome Model (Fig. 3). However, this can only be considered a first approximation as this model only includes modern biomes and does not take into consideration that during the Pleistocene in North America there were plant communities that do not exist today and have no contemporary analog. Recognition of these no–analog floras are best documented in the eastern United States (Williams *et al.*, 2013). Factors that contributed to their existence include insolation and temperatures that were more seasonal than present resulting in climates currently non–existent in North America. This resulted in shifting species–climate relationships for some taxa that probably resulted in changes in each species distribution over time, both floral and faunal. The re–mixing of species into associations with no modern counterpart appears to have been a general phenomenon during the Quaternary and has been documented in a wide range of terrestrial and marine taxa and across both high–latitude and tropical ecosystems (Williams & Jackson, 2007; Williams *et al.*, 2001; Jackson & Overpeck, 2000; Webb, 1987; Edwards *et al.*, 2005).

The establishment of no–analog plant associations was asynchronous and independently occurred in different regions, beginning first in the south–central United States and later at sites in the north–central United States that have been linked to declining megafaunal abundances. Consequently, it seems likely that among terrestrial mammals, including the extinct sloths, throughout the Pleistocene their distribution was impacted either positively with expanding ranges or negatively by reductions in suitable habitat resulting in relict populations. If various species of sloths were primarily adapted to these no–analog habitats any changes in climatic parameters that permitted the existence of this unique vegetation communities could have resulted in their local extirpation and ultimately extinction of the sloth. Another alternative is that climatic conditions that permitted the mixing of plant species to create no–analog plant communities may have provided the right conditions that would have allowed sloths with otherwise distinct adaptations to climatic conditions and different dietary habits to co–exist as part of the local fauna.

In contrast to the idea that some sloths were adapted to no–analog plant communities, it is possible the formation of these communities may have contributed to their extinction. The abundance of spores of the dung fungus *Sporormiella* in pollen samples is used as a proxy for the abundance of megaherbivores on the landscape (Davis, 1987; Davis & Shafer, 2006). It has been shown that at some sites there is a correspondence of the decline in *Sporormiella* abundance with the formation of the no–analog plant communities suggesting that rapid increases in hardwood tree abundances along with the appearance of no–analog vegetation in the upper Midwest was mirrored by declines in end–Pleistocene megafaunal populations and their subsequent extinctions. If the appearance of no–analog plant communities were climatically controlled, then the resulting species composition would have altered the preferred habitats of sloths and other megafauna, resulting in population reduction and the related decline in *Sporormiella*. To resolve this issue multiple sources of information are needed to reconstruct the diet along with the biological and physical attributes of the different habitats utilized by the different sloths. While some species of sloths may have been dependent on no–analog plant communities, other sloths may have been negatively impacted if their preferred habitat was replaced by a no–analog plant community.

SUMMARY

While the different sloths present in North America during the late Pleistocene had different ecological requirements and utilized different types of habitats, the determination of the specific details of the vegetation composition and climatic parameters of those habitats requires more research. The data is more robust for the sloths from temperate North America as they are known from many more records than the more southern sloths in semitropical to tropical North America. It is very likely that some of these extinct sloths depended on plant communities composed of plant species that today do not co–exist and do not even have a close modern analog. Given the long–term presence of the different sloth species in North America it is clear they were capable of adapting to both new environments encountered following their entry into North America and were equally successful in withstanding climatic fluctuations both in temperate and tropical zones, that occurred throughout the Pleistocene and impacted the preferred environment of each species. Currently, we still lack much of the basic information on the specific ecological needs of many of these taxa, especially the recently recognized taxa from currently semitropical and tropical zones.

Ultimately understanding the underlying causes of the extinction for each of these sloth taxa requires a more detailed knowledge of their ecology and the climatic conditions under which they lived. As presented here obtaining this information requires using multiple approaches, but also needs a large sample size over the range of each species in order to examine the consistency of the results. Until this fundamental data is obtained it will not be possible to present plausible explanations for the extinction of sloths at the end of the Pleistocene, not only in North America but South America and the Caribbean as well.

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