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Research

Changes in the diet and body size of a small herbivorous mammal (hispid cotton rat, *Sigmodon hispidus*) following the late Pleistocene megafauna extinction

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The catastrophic loss of large-bodied mammals during the terminal Pleistocene likely led to cascading effects within communities. While the extinction of the top consumers probably expanded the resources available to survivors of all body sizes, little work has focused on the responses of the smallest mammals. Here, we use a detailed fossil record from the southwestern United States to examine the response of the hispid cotton rat *Sigmodon hispidus* to biodiversity loss and climatic change over the late Quaternary. In particular, we focus on changes in diet and body size. We characterize diet through carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis of bone collagen in fossil jaws and body size through measurement of fossil teeth; the abundance of material allows us to examine population level responses at millennial scale for the past 16 ka. *Sigmodon* was not present at the cave during the full glacial, first appearing at ~16 ka after ice sheets were in retreat. It remained relatively rare until ~12 ka when warming temperatures allowed it to expand its species range northward. We find variation in both diet and body size of *Sigmodon hispidus* over time: the average body size of the population varied by ~20% (90–110 g) and mean δ^{13}C and δ^{15}N values ranged between −13.5 to −16.5‰ and 5.5 to 7.4‰ respectively. A state–space model suggested changes in mass were influenced by diet, maximum temperature and community structure, while the modest changes in diet were most influenced by community structure. *Sigmodon* maintained a fairly similar dietary niche over time despite contemporaneous changes in climate and herbivore community composition that followed the megafauna extinction. Broadly, our results suggest that small mammals may be as sensitive to shifts in local biotic interactions within their ecosystem as they are to changes in climate and large-scale biodiversity loss.

Keywords: biodiversity loss, climate change, late Quaternary

Introduction

Large-bodied mammals play a critical role within communities and ecosystems. Either directly or indirectly, they influence soil and vegetation structure and composition, nutrient cycling and other biogeochemical processes, and especially, the distribution

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and abundance of other mammals (Ripple et al. 2015, Malhi et al. 2016, Smith et al. 2016a). The loss of apex consumers can lead to cascading effects, changing community structure and species (Estes et al. 1998, 2011, Schmitz et al. 2000, Shurin et al. 2002, Dirzo et al. 2014, Ripple et al. 2014). For example, experimental removal of large-bodied mammals from plots across a variety of ecosystems has led to increased rodent abundance, likely because of alterations of vegetation abundance and composition (Keesing 1998, Parsons et al. 2013, Galetti et al. 2015). While empirical studies demonstrate rapid responses by the small-bodied mammal community, the ultimate consequences remain unclear, since direct and indirect effects may take decades or longer to be fully realized (Brown and Munger 1985, Smith et al. 1997, Ernest et al. 2000, Brown et al. 2001). Thus, longer-term perspectives are essential for investigating the influence of biodiversity loss and predicting how such events may change the interactions and dynamics within an ecosystem over evolutionarily relevant time scales (Smith et al. 2010, Blois et al. 2013). Moreover, given the precarious state of most megafauna today (Davidson et al. 2009, Ripple et al. 2015, Smith et al. 2016a), such studies are crucial for effective management.

The late Pleistocene megafaunal extinction led to the loss of more than 70 species in North America, including all mammals weighing >600 kg (Martin and Klein 1989, Lyons et al. 2004). The high degree of size-selective extinction was unprecedented in the Cenozoic mammalian record (Alroy 1999, Smith et al. 2018), and likely had significant impacts on the community structure and function of surviving animals (Smith et al. 2018). For example, extinct species had significantly more ecological associations than do modern species today, suggesting a more tightly organized web of species interactions (Smith et al. 2016b). Thus, loss of megafauna at the terminal Pleistocene is a good proxy for examining the consequences of modern losses in biodiversity, which preferentially target Earth's remaining large-bodied mammals (Davidson et al. 2009, Smith et al. 2018). Here, we are particularly interested in the influence of biodiversity loss on surviving smaller-bodied mammals within the community.

Coinciding with the loss of biodiversity at the end of the Pleistocene was a rapidly changing climate associated with the termination of Pleistocene glaciations. While temperatures in the Northern Hemisphere increased from the late Pleistocene to the Holocene, this millennial-scale climate warming was punctuated by several significant temperature fluctuations (Pachauri et al. 2014). These included the Younger Dryas (12.8–11.5 ka) – a cooling and warming event which terminated in a particularly abrupt 7°C temperature increase over as little as several decades, the 8.2 ka cold event – a sudden ~3°C decrease in global temperature that persisted for several centuries, and the mid-Holocene Warm Period or Climatic Optimum (~7–5 ka), which appears to have been concentrated in the Northern Hemisphere (Alley 2000, Rohling and Pälike 2005, Li et al. 2012). These and other climatic changes led to substantial shifts in the composition and distribution of flora and fauna across North America at both regional and continental scales (Prentice et al. 1991, Graham et al. 1996, Whitlock and Bartlein 1997, Lyons 2003, 2005, Blois et al. 2010, Gottfried et al. 2012, Cotton et al. 2016).

Fluctuations in environmental temperature are known to influence the morphology and ecology of species (Bergmann 1847, Brown 1968, Andrewartha and Birch 1986, Gylnn 1993, Smith et al. 1995, Ashton et al. 2000, Stenseth et al. 2002, Walther et al. 2002, Millien et al. 2006). Indeed, the ecogeographic relationship between population and/or species body mass and temperature gradients is so well-characterized it is termed Bergmann's rule; the principle that within a genus, larger species are found in colder climates and smaller species in warmer ones (Bergmann 1847, Mayr 1956). Bergmann's rule is well-supported for most mammals both across time and space, suggesting environmental temperatures have a strong impact on body size evolution (Brown and Lee 1969, Smith et al. 1995, Ashton et al. 2000, Gillooly et al. 2001, Freckleton et al. 2003, Millien et al. 2006, Smith 2008; but see: McNab 1971 and Blackburn et al. 1999). Moreover, changes in body size have consequences because of the allometric scaling of many life history and physiological processes such as metabolism, growth, reproduction, locomotion, home range size and even the degree of consumption of plant fiber (McNab 1980, Peters 1983, Calder 1984, Justice and Smith 1992, Smith 1995). Thus, selection for a larger (or smaller) body size changes how animals interact with and/or are impacted by their ecosystem (Damuth 1981, Peters 1983, Calder 1984). This coupling of climatic change at the late Quaternary with the terminal Pleistocene megafauna extinction likely led to substantial ecosystem alterations for surviving mammals.

We assessed the relative importance of changes in climate, resources and community structure on both diet and body size of *Sigmodon hispidus*, a medium-sized herbivorous rodent, over the past 16 000 years. We employ stable isotope analysis and measurements of fossil molars. We focused on an exceptionally well-stratified and radiocarbon dated fossil record in the Edwards Plateau, Great Plains of Texas. In the late Pleistocene, *S. hispidus*, along with the greater mammal assemblage, lived among a diverse assemblage of megaherbivores, including mammoths, giant ground sloths, mastodons, camels and multiple species of horses and pronghorn. Previous work found that *S. hispidus* overlapped significantly less often than expected based on a null model with several megafauna, forming significant segregations with *Glyptotherium floridanum* (grazer), *Homotherium serum* (carnivore), *Smilodon fatalis* (carnivore), *Tetrameryx shuleri* (browser) and *Tremactos floridanus* (browser) (Smith et al. 2016b). It is difficult to ascribe a mechanism to each of these interactions, but they do suggest that *S. hispidus* may have responded to the loss of the megafauna. Because modern *Sigmodon hispidus* is generally most abundant in grass dominated habitats where it primarily consumes green grass stems (Kincaid and Cameron 1982, Randolph et al. 1991), we hypothesized a response in diet to shifts in resource availability with landscape changes due to climate and the cascading effects of megafaunal removal.

Stable isotope analysis has become a common proxy for characterizing shifts in diet through space and time (Koch 2007), and can provide unique insights into foraging ecology on different time scales depending on the tissues analyzed (Martínez del Rio et al. 2009). Isotope analysis has been used in both paleontological and archaeological contexts to quantify ecological shifts, including the relative use of different plant functional types by consumers, trophic structure (e.g. food-chain length), and niche partitioning that are otherwise difficult to interpret using traditional paleontological approaches (Koch 2007, Koch et al. 2009). Here, we were fortunate that collagen was well-preserved in the fossil bones, allowing measurement of both $\delta^{13}C$ and $\delta^{15}N$ values for fossils spanning the late Pleistocene to Holocene transition.

Earlier studies suggested *Sigmodon hispidus* follows Bergmann's rule (Ashton et al. 2000, Meiri and Dayan 2003); thus, we hypothesized that increased Holocene temperatures likely led to decreased body size (Fig. 1a, path C). Shifts in climate and in the composition of the herbivore community, however, may have had indirect effects through changes in vegetation composition and/or resource availability; these could have led to selection for larger or smaller body size (Fig. 1a, paths AE, AG, DE, DG). Community reorganization might also have directly influenced competitive interactions for resources (Fig. 1a, paths F, H). Decreases in population size or removal of small to medium sized species, particularly dominant ones, have also been shown to lead to habitat and resource expansion within rodent communities (Valone and Brown 1995, Ernest and Brown 2001,
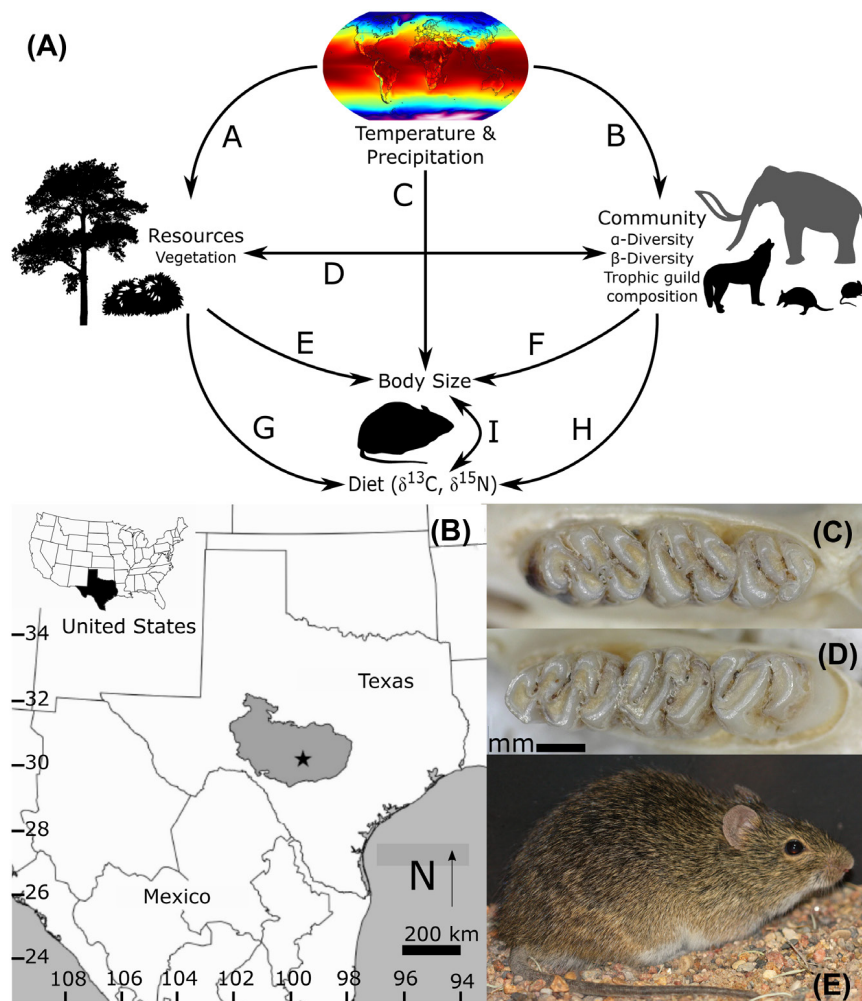

Figure 1. Conceptual diagram, site attributes and study organism. (a) Conceptual diagram of potential abiotic and biotic interactions affecting *Sigmodon hispidus* populations at Hall's Cave over the past 16 000 years. Both extinct (grey) and extant (black) animals occur within the community. Pathways represent potential indirect effects of climate on *Sigmodon* via (A) vegetation, (B) community and direct effects on (C) body size and diet. Potential effects of community variables on *Sigmodon* indirectly through (D) vegetation, or directly on (F) body size and (H) diet. Potential direct effects on vegetation are given by (E) on body size and (G) on diet. Lastly, pathway I represents the potential effects of body size on diet or vice versa. Here our data allow us to test pathways C, F, H and I. (b) Location of Hall's Cave on the Edwards Plateau in Texas. (c) Upper and (d) lower tooth rows of *Sigmodon hispidus* at 50× magnification. (e) Picture of *S. hispidus* (J.N. Stuart, <www.flickr.com/photos/stuartwildlife/5727265600>).

Goheen et al. 2005). Thus, we expect changes in community composition (richness and turnover across trophic guilds) to affect dietary niche space. Because studies of modern megafauna suggest their absence leads to an increased resource base in smaller animals (Keesing 1998, Okullo et al. 2013), we suspected a similar expansion might have occurred in the terminal Pleistocene after the extinction of megafauna. Modern exclusion studies are limited in temporal scope extending from years to decades (Owen-Smith 1988, Okullo et al. 2013) and it is not clear how the absence of megafauna influences vegetation over long time periods.

We note that our study is the first to characterize both population body size and dietary shifts for a single species in a single locality at such fine-grained level for ~16ka. While studies using *Neotoma* paleomiddens and sites such as Porcupine Cave or Lamar Cave have previously yielded insights into body size and biodiversity shifts with climate change at the species and/or community level (Smith et al. 1995, Hadly 1996, Smith and Betancourt 1998, 2003, Barnosky 2004), they have not combined these data with isotope-based analysis of diet shifts over time. Similarly, dietary reconstructions and shifts of both large and small fauna have been studied using stable isotope analysis, without incorporation of morphological responses (Feranec and MacFadden 2000, Yang and Deng 2005, Terry et al. 2017). The substantial amount of fossil material, and the robust and detailed age model provide a unique opportunity to reconstruct the ecology (diet and body size) of *Sigmodon hispidus* in a period marked by intense shifts in both biodiversity and climate.

Material and methods

Study site and data sources

Site, temporal record and natural history
Our study employs a fossil record with high temporal resolution from the southwestern United States. Hall's Cave is located on the Edwards Plateau in Kerrville County, Texas (Fig. 1b). Today, vegetation in the region consists mostly of savanna, shrub and woodland characterized by juniper, mesquite and oak, with both tall and short grasses (Toomey 1993, Joines 2011). Paleontological studies began in the 1960s and have continued to the present, with most excavations of specimens by Toomey et al. (1993). The collection, including unprocessed bulk matrix is housed at the Vertebrate Paleontology Lab of the Texas Memorial Museum (TMM), University of Texas, Austin.

Hall's Cave has a uniquely well-resolved stratigraphic sequence dating back about 22 000 cal BP and a particularly abundant small- and medium-sized mammal record. Past excavations of the site have yielded thousands of mammal and other vertebrate specimens across a range of body sizes and trophic guilds, many of which have already been identified (Toomey 1993). Previous work from the site include reconstructions of both soil erosion (Cooke et al. 2003) and climate using faunal remains (Toomey 1993, Toomey et al.

1993, Joines 2011), magnetic susceptibility of the cave sediments (Ellwood and Gose 2006, Bourne et al. 2016), and the phytolith record of the cave (Joines 2011). Most recently, the community assemblage and species interactions of the Edwards Plateau were characterized across the past 22 thousand years (Smith et al. 2016b).

We developed an age model based on 44 AMS ^{14}C measurements from Hall's Cave materials combined from Cooke et al. (2003), Toomey (1993) and Bourne et al. (2016), with four more AMS ^{14}C measurements from Bourne et al. (2016) being omitted as potential duplicates with specimens from Cooke et al. (2003) and Toomey (1993). Calendar ages (cal BP) were calibrated using OxCal ver. 4.3.2 (Ramsey 1995, 2009, 2017) with the Northern Hemisphere atmospheric curve IntCal13 (Reimer et al. 2013) (Supplementary material Appendix 1 Fig. A1, Table A2). A linear regression of the mean calibrated radiocarbon ages (cal BP) and stratigraphic depth (cm) yielded a robust predictive equation ($Y = 758.82 + 64.57X$; df = 42, p < 0.001, adj. $R^2 = 0.947$). Because elements were originally collected in 5–15 cm intervals, the midpoint of the stratigraphic depth was employed in the regression.

Sigmodon hispidus (80–150 g) currently ranges across the southern United States and Mexico. It is a primary consumer usually found in grass dominated habitats, where it supplements a primary diet of green grass stems of intermediate nutritive value with more nutritious dicot leaves and fruit (Martin 1986, Randolph et al. 1991). Cotton rats in Texas tend to occupy tall grass (i.e. cordgrass, bluestem, beard grass) or shrub habitats that are both a protective cover and a food resource (Cameron and Spencer 1981, Kincaid and Cameron 1985, Schmidly and Bradley 2016). Competition among hispid cotton rats is driven by habitat, with the more aggressive and dominant individuals generally occupying areas of denser vegetation cover, which is thought to be associated with predator avoidance (Roberts and Wolfe 1974, Spencer and Cameron 1983). Interspecific interactions of *Sigmodon* with other Texas rodents include aggressive displacement of pygmy mouse *Baiomys taylori* and competitive exclusion of havest mouse *Reithrodontomys fulvescens* (Raun and Wilks 1964, Cameron 1977).

All *Sigmodon* have highly diagnostic 'S' shaped molars (Fig. 1c–d) readily allowing discrimination from other rodents in the fossil matrix. Here, we follow Toomey (1993) and refer all material to *Sigmodon hispidus* based on geographic and elevational range attributes (Baker and Shump 1978, Cameron and Spencer 1981, Toomey 1993). In addition to specimens previously identified by Toomey (1993), we identified and accessioned 1030 additional individuals from either presorted elements or bulk materials from the fossil matrix. Our final dataset consisted of 1332 individual maxillary or mandibular first molars and jaw elements spanning the past 16 000 years.

Sigmodon fossils are not uniformly present throughout time. *Sigmodon* fossil specimens were not present in the cave sediments from 22 to 16ka cal BP and were comparatively rare from 16 to 12ka cal BP (50 specimens).

Table 1. Summary by time level bin divisions. Age range is the calendar years before present (1950 AD) comprising each interval. N mass and N isotopes show sample sizes for molar measurements and δ13C or δ15N. Only δ15N was found to change significantly over time (ANOVA p<0.01, df=13/306). Temperature and precipitation data from the CCSM3 (Lorenz et al. 2016a, b) are averaged for each time bin. Sorenson to Modern represents similarity in community composition relative to the 0–1500 age range.

Age range (cal BP)	N mass	N isotopes	Mean mass (g) (±SD)	Maximum mass (g)	Mean δ13C (‰) (±SD)	Mean δ15N (‰) (±SD)	Mean temperature (°C) (±SD)	Mean precipitation (mm) (±CV)	Species richness	Sorenson to modern
0–1500	14	12	100.5±21.4	149.9	−15.8±2.7	5.7±1.4	18.7±7.3	545.4±0.4	34	1.00
1500–3100	18	22	109.1±22.5	144.5	−16.5±1.8	5.5±0.8	18.7±7.4	537.2±0.4	36	0.89
3100–5400	13	15	96.1±16	130.6	−15.7±2.7	6.5±1.1	18.6±7.7	554.4±0.4	35	0.81
5400–6100	13	21	89.8±11.2	104.1	−14.9±2.8	5.7±0.8	18.6±8.0	549.8±0.4	31	0.77
6100–6400	13	26	99.5±20.5	146.3	−14.9±2.4	5.9±0.7	18.7±8.1	536.3±0.4	32	0.79
6400–6700	19	9	95.9±19.3	135.7	−15.7±3.6	6±0.4	18.7±8.2	526.8±0.4	33	0.78
6700–7700	16	21	89.5±16.8	120.9	−15.2±2.9	6.2±0.9	18.5±8.5	534.3±0.4	33	0.78
7700–8400	25	21	96.3±22.9	157.4	−13.5±2.5	7.4±1.4	18.4±8.8	532.3±0.4	36	0.71
8400–9000	34	29	90.8±17.6	134.0	−14.7±3.2	7.0±1.3	18.3±8.9	536.1±0.4	35	0.70
9000–9400	15	13	96.6±21.1	130.6	−15.0±2.4	6.7±0.8	18.4±9.0	552.5±0.3	35	0.70
9400–10 000	26	16	89.9±18.6	151.8	−14.5±3.0	6.8±1.4	18.3±9.0	561.6±0.3	39	0.69
10 000–11 000	45	23	94.6±16.6	122.5	−15.6±3.5	6.9±1.1	17.7±8.9	592.5±0.3	35	0.67
11 000–12 700	7	7	100.1±27.3	146.3	−14.1±3.9	7.3±0.8	16.9±9.3	626.6±0.3	53	0.62
12 700–15 800	12	31	96.5±12.9	120.9	−14.5±3.0	6.7±1.0	15.5±10.1	636.6±0.4	74	0.52

Sigmodon hispidus became common in the early-Holocene (852 specimens), and decreased during the mid- (307 specimens) and late-Holocene (123). Thus, to maintain sufficient sample size we binned data into 14 temporal time intervals over the last 16 000 cal BP (Table 1). These intervals were chosen to incorporate important climatic and faunal events while maintaining sufficient sample size. This allowed us to conduct population level analyses using the paleontological record. It is important to note however that both changes in diet and morphology of rodents can occur on much shorter time scales than imposed by our age intervals (Smith et al. 1998, Yom-Tov and Yom-Tov 2004, Eastman et al. 2012, Walsh et al. 2016, Terry et al. 2017). As such, the populations described in each interval will still be subject to a degree of time averaging that may obscure fine level changes occurring through time. However, we note that compared to most paleoecological studies, the resolution we are able to obtain is remarkable.

Community data

Data on community composition were extracted from a compilation by Smith et al (2016b) based largely on Toomey (1993) and the Neotoma Paleoecology Database (2015). Since 2016, updates in the understanding of the evolutionary history of horses in North America have led to the synonomization of two horse species (Winans 1989, Hay et al. 2010, Barron-Ortiz and Theodor 2011, Kefena et al. 2012), necessitating changes in our fossil identifications; ongoing fossil identifications of bulk matrix have also expanded the temporal duration of several species (e.g. *Baiomys taylori* and *Onychomys leucogaster*). Species were assigned to a trophic guild following Smith et al. (2016b). Using this revised species list, we re-calculated α-diversity (richness), β-diversity (Sorenson index) and percent of each trophic guild within the community for each time interval for the entire Edwards Plateau mammal fauna (e.g. small, medium and large mammals) (Table 1, Supplementary material Appendix 1 Table A3). Here β-diversity is calculated using the Sorenson index relative to the most recent time bin (0–1500 cal BP), referred to as modern.

Climatic data

We employed the Community Climate System Model (CCSM3) climate data. This unified dataset of climate simulations for North America extends to 21 000 cal BP in 500-year intervals (Lorenz et al. 2016a, b). The CCSM3 data have 0.5° spatial resolution such that we extracted data for the region surrounding Hall's Cave. Because the CCSM3 combines simulations and interpolates data for all of North America, it represents larger scale climatic events from the terminal Pleistocene onwards. Data obtained from the CCSM3 included mean daily maximum temperature, mean daily minimum temperature and total monthly precipitation. These variables were extracted in 500-year intervals and averaged following the 14-age intervals used for the community data (Table 1).

Analyses

Body size

Of the 1332 fossil *Sigmodon* elements, we obtained body size estimates for 399 using the length of the first upper or lower molar (UM1, LM1), which is a reliable indicator of mass (Damuth and MacFadden 1990) (Fig. 1c–d); the remainder lacked a quantifiable M1. Measurements were taken using Mitutoyo Digital Calipers ser. 500 under a 10× dissecting microscope. Each tooth was measured three times (~1200 measurements total); samples whose means yielded >5% standard error were discarded. These were generally cracked or broken teeth and thus difficult to accurately measure.

Fossil elements employed in our work consisted of loose left or right mandibles and maxillae, generally with only partial toothrows. Because an individual could potentially be represented four times (ULM1, URM1, LLM1 and LRM1), we established a set of criteria to reduce duplicate individuals and calculated the minimum number of individuals (MNI). First, we quantified the amount of natural variation between left versus right, and upper versus lower molars in modern *Sigmodon hispidus*. Using a reference collection of museum specimens from the Museum of Southwestern Biology, we measured upper and lower and right and left molars for 20 individuals ranging in mass from 44 to 206 g (Supplementary material Appendix 1 Table A1). We found that across the 20 specimens examined, modern animals were bilaterally symmetrical; there was less than a 1% difference between left and right molars. However, upper and lower molars varied; upper molars were on average 10% smaller than lower molars (linear model, $p < 0.0001$, $df = 19$, adjusted $r^2 = 0.68$, Supplementary material Appendix 1 Fig. A2).

Because elements (LLM1s, LRM1s, ULM1s and URM1s) were not uniformly found across stratigraphic levels, we employed the LM1 preferably; when upper molar measurements were used, we standardized by adding 10% to the length. To mitigate the likelihood of a single individual being represented twice in a stratigraphic level, we only used a single element unless the standardized measurements were >1% different in size from all other elements in that time bin. Thus, for each unique stratum, we selected the LLM1s and then all LRM1s whose lengths were at least 1% different from those LLM1s. Next, we compared the ULM1s to all LM1s, followed by the URM1s to all other molars already selected for that stratum. A difference >1% was chosen because the variation between left and right molars of either upper or lower elements of modern individuals was below 1% (Supplementary material Appendix 1 Table A4).

Because measurements of first molars were taken on fully erupted molars, no juveniles were included. However, without full toothrows we could not fully assess the ontogenetical development of some animals. Thus, analyses were conducted both with and without putative subadults. Subadults were identified as animals whose estimated body size was lower than 1.5 standard deviations from the mean, as is commonly done in modern studies (Birney et al. 1975, Swihart and Slade 1984).

Our final data set included 270 animals after the removal of potential duplicates and subadults. Body size was computed for lower first molar lengths using the allometric equation (Martin 1990): Log mass (g) = $3.310 \times$ (Log M1 length) + 0.611 ($r^2 = 0.96$, %PE = 15.58, df = 32). We conducted a number of sensitivity analyses to examine the influence of our data manipulations; our analyses were robust regardless of methodology employed (Supplementary material Appendix 1).

Stable isotope analysis

We analyzed stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes from 319 *Sigmodon* maxillary and mandible bones to investigate potential shifts in diet. Carbon isotope values provide insight into what vegetation herbivores are consuming within a system (DeNiro and Epstein 1978). Global average $\delta^{13}C$ values for C_3 and C_4 plants are -26.5‰ and -12.5‰ (Bender 1971, Cerling et al. 1997), respectively, and previous studies have shown that these plant functional groups have similar isotope values in the Great Plains (Derner et al. 2006). $\delta^{13}C$ and $\delta^{15}N$ values of primary consumers like *Sigmodon* mirror that of their diet, but are positively offset due to physiologically mediated processes that discriminate against the light isotope (^{12}C or ^{14}N) during the nutrient assimilation and tissue synthesis; such offsets are often referred to as trophic discrimination factors and for consumer bone collagen are ~2–4‰ for both $\delta^{13}C$ and $\delta^{15}N$ (Koch 2007). Because carbon and nitrogen isotope values vary depending on relative consumption of C_3 and C_4 vegetation and trophic level, $\delta^{13}C$ versus $\delta^{15}N$ isotopic niche space can serve as a proxy for dietary niche space (Newsome et al. 2007). Given the relatively long turnover rate for bone collagen (Hobson and Clark 1992, Koch et al. 2009) and the average life span of six months to one year in wild *Sigmodon* (Rose and Salamone 2017), the isotope measurements represent diet integrated across most of an individual's lifetime.

We subsampled ~150–250 mg of bone from each fossil mandible/maxillary fragment using a low speed Dremel tool. Following sampling, we extracted the organic collagen matrix from the bone by demineralizing with 0.25 N HCl at 3–4°C for 24–48 h depending on initial sample density. Following demineralization, samples were lipid extracted via soaking in 2:1 chloroform/methanol for 72 h, changing the solution every 24-h. Samples were then washed 5–7 times with distilled water and lyophilized. Approximately 0.9–1.0 mg of each dried collagen sample was weighed on a microbalance and packaged into 0.35 mm tin capsules and submitted to the University of New Mexico Center for Stable Isotopes for analysis. $\delta^{13}C$ and $\delta^{15}N$ values of all samples were analyzed using an elemental analyzer interfaced with a isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Isotope values are reported as δ values, where $\delta = 1000[(R_{sample}/R_{standard}) - 1]$ and Rsamp and Rstd are the $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$ ratios of the sample and standard, respectively; units are in parts per thousand, or per mil (‰). The internationally accepted reference

standards are Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N_2 for nitrogen (Fry 2006, Sharp 2017). The standard deviation of organic references within a run was ≤0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. In addition, as a control for the quality of our ancient collagen samples, we measured [C]:[N] ratios. The theoretical weight percent [C]:[N] ratios of unaltered bone collagen falls between 2.8 and 3.5 (Ambrose 1990). Any samples with [C]:[N] ratios >3.5 we considered too diagenetically altered to provide reliable isotope data and were excluded from all analyses.

After removal of potential duplicates and subadults, our final dataset consisted of 384 animals. Of these 266 had isotopes, 270 had mass measurements and 152 had both (Table 1). These sample sizes allowed us to examine changes over time at the population level, largely unprecedented for a paleoecological study where sample size is almost always an issue.

Statistics

Analyses were conducted at two temporal scales using both parametric and non-parametric tests. The first set of analyses sorted body size and isotope data into pre- (12 700–15 800 cal BP) versus post- (0–12 700 cal BP) extinction bins to investigate the impact of the megafauna loss on *Sigmodon*. The second set of analyses were more finely resolved, and employed 14-time intervals over the last ~16 000 years (Table 1).

Sample sizes between the pre- and post-extinction intervals were uneven because *S. hispidus* was less abundant in the older strata. We analyzed body size and isotope variation in the two populations (pre- and post-) using the F-test and Levene's test for homogeneity of variances. Differences in the means and distributions were evaluated using a series of parametric and non-parametric tests to account for non-normal distributions of mass and $\delta^{13}C$ within the post-extinction time bin.

We determined changes in *Sigmodon's* mass and isotopic niche space using ANOVAs, Spearman's rank test and Bayesian ellipse area models. Inconsistences in normal distributions across time bins led us to consider median, first quartile and maximum mass changes within the general population against diet and climate variables using linear models. Here, maximum mass is the mass of the largest individual within a time bin. Isotopic niche space was characterized using Bayesian based standard ellipse areas (SEA_B) of $\delta^{13}C$ and $\delta^{15}N$ using the SIBER based method in the R based SIAR package (Jackson et al. 2011, Parnell and Jackson 2013, <www.r-project.org>). SEA_B were calculated using the posterior estimates for each group (here based on 10 000 draws), with ellipses plotted using 50% coverage in JMP Pro 13 (ver. 13.1) to show shifts in the isotopic niche space of *Sigmodon hispidus* through time. All statistical analyses were performed using R software ver. R ver.3.3.2 (<www.r-project.org>) and RStudio ver. 1.0.136 (RStudio Team 2016).

A state–space model was run to consider whether shifts in mass or diet seen in *Sigmodon* are driven more strongly by each other, by climatic variables (temperature or precipitation) or community changes (α-diversity, β-diversity or changes within the trophic guilds). A state-space model in its simplest form can be thought of as a linear model where each data point gets its own slope and dataset at each time bin. Here, each point has a state of known and unknown components and that state at time t + 1 is a function of that point's state at time t. As such, points will be more similar the closer they are to each other in time. This allows for potential changes in the importance of independent variables on the response variable to be considered at each time bin in order to determine the magnitude of their overall influence. State–space models are therefore useful for data that have variation in the distribution of residuals and the potential for the non-independence of variables to change across a time series (Commandeur and Koopman 2007). State–space models have been employed in ecology to consider changes in population dynamics and biodiversity in a variety of vertebrates (Flowerdew et al. 2017, Leung et al. 2017, Rogers et al. 2017), as well as in economics (Harvey 1990, Kim and Nelson 1999, Durbin and Koopman 2001). We used a stochastic local level and slope model allowing the importance of each explanatory variable to vary at each time point, to account for the fact that each variable may be having larger or smaller effects on the response due to the range and grouping of data values within our time bins. For example, whether climatic variables or community variables are impacting a response in *S. hispidus* more or less may vary in response to a period of higher community turnover (such as the megafauna extinction event) or greater fluxes in temperature and precipitation (e.g. the Younger-Dryas event).

We created separate models to analyze our mass and isotopic variables ($\delta^{13}C$ and $\delta^{15}N$). Our model consisted of a trend constant (μ), and an unknown regression weight (β) for each explanatory variable. Each trend constant and regression weight are determined from the previous time interval ($\mu_{t+1} = \mu_t + \xi_t$ and $\beta_{t+1} = \beta_t + \tau_t$, respectively), where ξ_t and τ_t represent a state or level disturbance. Here, the state disturbances for each are assumed to be independently and normally distributed with zero mean and a variance of σ^2. A $\mu > 0$ indicates a positive correlation to our response and a $\mu < 0$ indicates a negative correlation to our response. β represents the relative strength of each explanatory variable on the response. If we consider our mass model for example, a $\mu > 0$ corresponds to increasing body size, with the β of single explanatory variable giving the relative amount of increase associated with that variable. We ran each model a total of 4000 times, using a Markov chain Monte Carlo (MCMC) algorithm with four chains and 1000 iterations each using the rstan package (Stan Development Team 2018) in the program R. Modelled values fall within the 50% uncertainty interval of the Bayesian framework, such that half of the 50% intervals (2000 of the total 4000 iterations) will contain values falling within the observed values of the data. Our variables and their associated

β's are as follow: body size (BS, β_1), $\delta^{13}C$ (dC, β_2), $\delta^{15}N$ (dN, β_3), mean precipitation (mP, β_4), maximum temperature (mxT, β_5), minimum temperature (mnT, β_6), α-diversity (aDiv, β_7), β-diversity (bDiv, β_8), % browsers (perB, β_9), % carnivores (perC, β_{10}), % frugivores/granivores (perF, β_{11}), % grazers (perG, β_{12}), % insectivores (perI, β_{13}), % omnivores (perO, β_{14}). Model structures are given below with graphs of modelled to raw values for each model available in Supplementary material Appendix 1 Fig. A3:

$$Y_{mass} = \mu_t + \beta_2(dC) + \beta_3(dN) + \beta_4(mP) + \beta_5(mxT) + \beta_6(mnT)$$
$$+ \beta_7(aDiv) + \beta_8(bDiv) + \beta_9(perB) + \beta_{10}(perC) + \beta_{11}(perF)$$
$$+ \beta_{12}(perG) + \beta_{13}(perI) + \beta_{14}(perO)$$

$$Y_{carbon} = \mu_t + \beta_1(BS) + \beta_3(dN) + \beta_4(mP) + \beta_5(mxT) + \beta_6(mnT)$$
$$+ \beta_7(aDiv) + \beta_8(bDiv) + \beta_9(perB) + \beta_{10}(perC) + \beta_{11}(perF)$$
$$+ \beta_{12}(perG) + \beta_{13}(perI) + \beta_{14}(perO)$$

$$Y_{nitrogen} = \mu_t + \beta_1(BS) + \beta_2(dC) + \beta_4(mP) + \beta_5(mxT) + \beta_6(mnT)$$
$$+ \beta_7(aDiv) + \beta_8(bDiv) + \beta_9(perB) + \beta_{10}(perC)$$
$$+ \beta_{11}(perF) + \beta_{12}(perG) + \beta_{13}(perI) + \beta_{14}(perO)$$

Results

Analyses of body mass for pre- and post-extinction time intervals (Fig. 2a) showed no significant change in either variation (F test $p > 0.1$, df = 11/257; Levene test $p > 0.1$, df = 1/268) or distribution (two sample t-test $p > 0.1$, df = 268; Wilcoxon rank sum test $p > 0.1$). Furthermore, mass did not change significantly between individual time bins (ANOVA $p > 0.1$, df = 13/368, Kruskal–Wallis rank sum test $p > 0.1$, df = 13). Mean mass ranged from approximately 90 to 110 g (Fig. 2f). Maximum mass ranged from ~120 to 160 g, with the largest individuals from 7.7 to 8.4 cal BP (Table 1).

No significant differences were found in the variation (F test $p > 0.1$, df = 30/234; Levene test $p > 0.1$, df = 1/264) or distribution (two sample t-test $p > 0.1$, df = 264; Wilcoxon rank sum test $p > 0.1$) of *Sigmodon* $\delta^{13}C$ or $\delta^{15}N$ values from before and after the extinction event (Fig. 2b–c). Mean $\delta^{13}C$ and $\delta^{15}N$ values and associated standard deviations for each time interval are reported in Table 1, Fig. 3. Mean $\delta^{13}C$ values did not significantly change across individual time bins (ANOVA $p > 0.1$, df = 13/306, Kruskal–Wallis rank sum
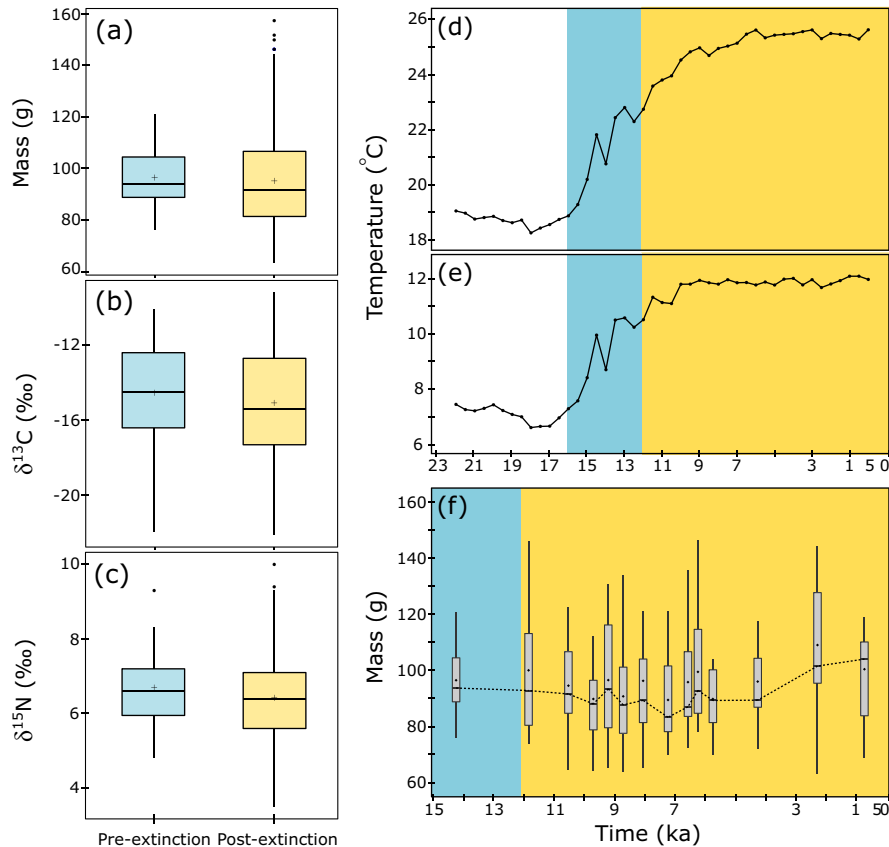

Figure 2. Changes in *Sigmodon hispidus* before and after the megafauna extinction, and in mass over the past 16 ka. Boxplots representing median and interquartile ranges, with means marked by + for (a) Mass, (b) $\delta^{13}C$ and (c) $\delta^{15}N$ distributions of the cotton rat. Pre- and post-extinction intervals are between 12 700–15 800 cal BP and 0–12 700 cal BP, respectively. Changes in (d) maximum and (e) minimum temperature (°C) across the past 23 thousand years for the Hall's Cave community. *Sigmodon* appears in the Hall's Cave fossil record at ~16 ka (blue) and become abundant in the record at ~12 ka (yellow). Temperature data from the CCSM3 (Lorenz et al. 2016a, b) is downloaded at 500-year intervals. Changes in (f) body size are plotted as medians (connected lines), means (diamonds) and interquartile ranges.
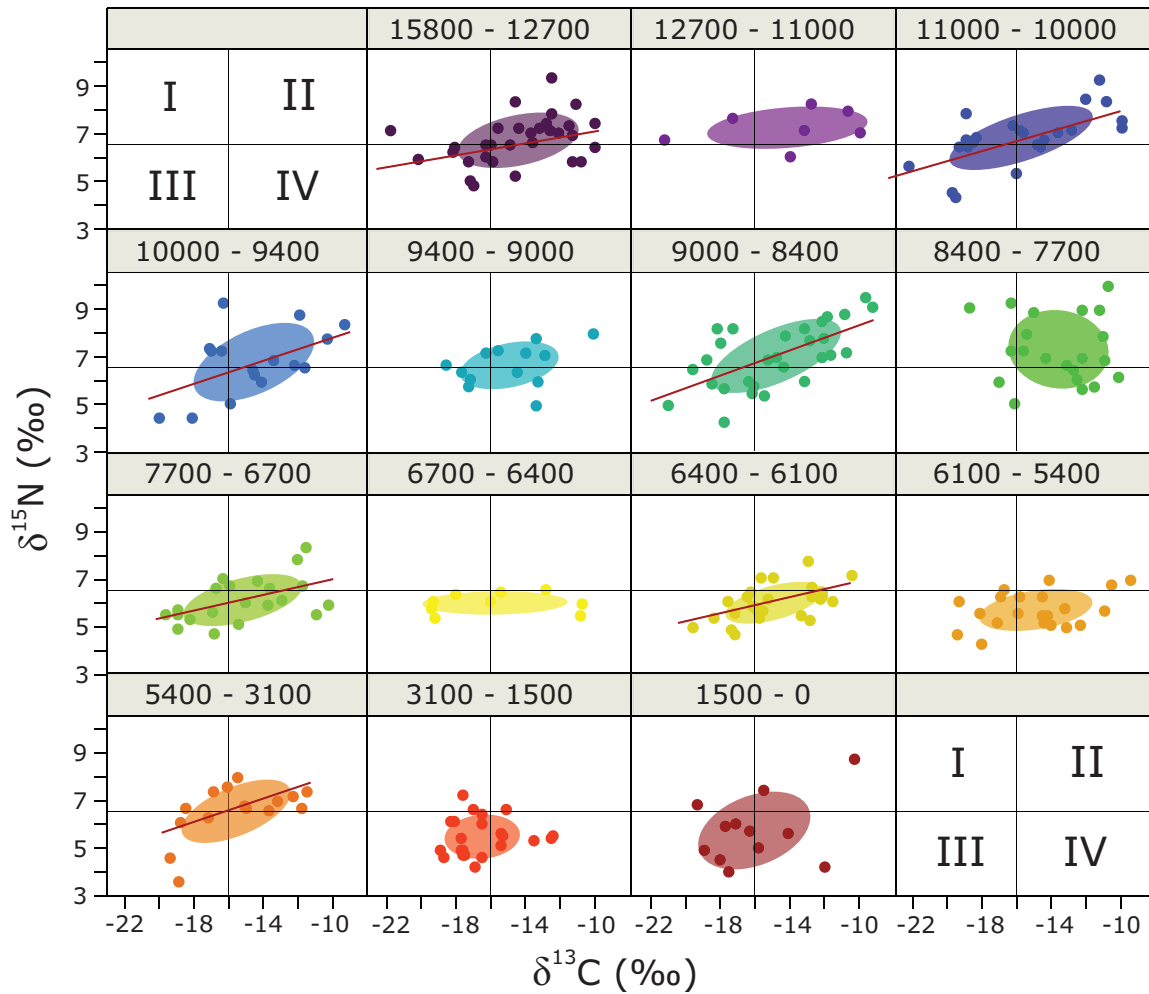
Figure 3. Isotopic niche space of *Sigmodon hispidus* over time. Standard ellipse areas (SEAs) representing where *Sigmodon* populations lie in $\delta^{13}C$ and $\delta^{15}N$ space with 50% coverage of data. Cross (+) within each panel divides isotopic space into four quadrants (I–IV) to help illustrate movement in SEAs over time, with the lines intersecting at $\delta^{13}C = -16‰$ and $\delta^{15}N = 6.5‰$. Red lines indicate a significant relation between $\delta^{13}C$ and $\delta^{15}N$ (linear fit $p < 0.05$, see Supplementary material Appendix 1 Table A6 for details).

test $p > 0.1$, df = 13), but $\delta^{15}N$ values significantly decreased (ANOVA $p < 0.01$, df = 13/306, Kruskal–Wallis rank sum test $p < 0.01$, df = 13, Supplementary material Appendix 1 Table A5 for details). $\delta^{13}C$ and $\delta^{15}N$ values were positively and significantly correlated across several time intervals (Fig. 3, Supplementary material Appendix 1 Table A6). With the exception of the latest time interval (~0–1500 cal BP), Bayesian standard ellipse areas show a trend for a slightly expanded isotopic niche space (4.7–11.1‰², Fig. 3) in the older age intervals from about 7700 to 15 800 cal BP relative to those from the mid- to late Holocene.

Results from our state–space model (Table 2) reflect the slight increase in mass from the oldest (12 700–15 800 cal BP) to the most recent (0–1500 cal BP) time interval (Table 1, Fig. 2f). Higher $\delta^{13}C$, $\delta^{15}N$ values and maximum temperature corresponded to larger body size ($\beta_2 = 1.7$, $\beta_3 = 1.0$, $\beta_5 = 0.9$; ~30, ~17 and 16%, respectively, of positive β values for mass, Table 2). Minimum temperature and the proportion of omnivores in the community were also associated with

increasing body size, but to a smaller degree ($\beta_6 = 0.6$, $\beta_{14} = 0.7$, about 11% and 12%, respectively). Overall, community variables were associated with decreased body mass, with the percent of grazers having the largest impact ($\beta_{12} = -0.9$, ~41% of total negative β values for mass), followed by the percent of insectivores ($\beta_{13} = -0.6$, ~25%), percent browsers ($\beta_{12} = -0.4$, ~19%) and α-diversity ($\beta_{12} = -0.3$, ~14%).

Sigmodon hispidus bone collagen $\delta^{13}C$ values were most positively associated with $\delta^{15}N$ ($\beta_3 = 1.2$ of total 2.9 positive influence on $\delta^{13}C$, or about 40%), in agreement with the correlation of higher $\delta^{13}C$ values with higher $\delta^{15}N$ reported above. $\delta^{13}C$ become more negative (shift towards C_3 vegetation), occupying less area in quadrants II and IV (Fig. 3) from 6700 to 7700 cal BP onwards. This overlaps with the decrease in $\delta^{15}N$, as seen by a shift in the standard ellipse areas into quadrant III and IV (Fig. 3). Higher $\delta^{13}C$ in *Sigmodon* were also associated with increases in both the proportion of granivores and grazers in the community ($\beta_{11} = 0.5$ and $\beta_{12} = 0.5$, ~17% each), followed by β-diversity ($\beta_{13} = 0.4$, ~12%,

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Table 2. Regression weight (β) values as given for each explanatory variable by the three state–space model outputs for mass (Y_{mass}), $\delta^{13}C$ (Y_{carbon}) and $\delta^{15}N$ ($Y_{nitrogen}$). Values in bold have 15% or more of relative positive or negative influence on explanatory variable.

		Y_{mass}	Y_{carbon}	$Y_{nitrogen}$
Main variables				
body size	β_1	~	0.0	0.0
$\delta^{13}C$	β_2	**1.7**	~	0.2
$\delta^{15}N$	β_3	**1.0**	**1.2**	~
Climate variables				
mean precipitation	β_4	0.0	0.0	0.0
maximum temperature	β_5	**0.9**	−0.1	**−0.8**
minimum temperature	β_6	0.6	0.2	**0.6**
Community variables				
α-diversity	β_7	−0.3	**−0.3**	0.0
β-diversity	β_8	0.1	0.4	**−0.6**
% browsers	β_9	**−0.4**	0.2	0.0
% carnivores	β_{10}	0.3	−0.2	0.0
% frugivores/granivores	β_{11}	0.4	**0.5**	**−0.4**
% grazers	β_{12}	**−0.9**	0.5	−0.1
% insectivores	β_{13}	**−0.6**	**−0.8**	**0.3**
% omnivores	β_{14}	0.7	**−0.3**	**0.2**

Table 2). Lower $\delta^{13}C$ values were associated to a greater proportion of insectivores in the community ($\beta_{13} = -0.8$ of total 1.8 negative β values for $\delta^{13}C$, or about 46%), suggesting lower $\delta^{13}C$ values indicative of greater use of C_3 resources when more mammalian insectivores are on the landscape (Table 2). Lower $\delta^{13}C$ values in *Sigmodon* were also associated with α-diversity ($\beta_{12} = -0.3$, ~18%) and the percent of omnivores in the mammalian community ($\beta_{14} = -0.3$, ~18%).

Sigmodon hispidus bone collagen $\delta^{15}N$ values were negatively correlated with maximum temperature ($\beta_5 = -0.8$ of total 1.9 negative β values for $\delta^{15}N$, or ~41%), β-diversity ($\beta_{13} = -0.6$, ~34%) and the proportion of granivores present in the mammalian community ($\beta_{11} = -0.4$, ~19%, Table 2). Higher $\delta^{15}N$ values in *Sigmodon* were associated with minimum temperature ($\beta_6 = 0.6$ of overall 1.4 positive β values for $\delta^{15}N$, or about 47%), and the proportion of insectivores and omnivores in the community ($\beta_{13} = 0.3$ and $\beta_{13} = 0.2$, about 21% and 18%, respectively). Overall, our results suggest that *S. hispidus* is being influenced by both climatic and community variables over time, likely through a combination of direct and indirect effects, but that the combination of these effects is not driving a strong shift in body size and/or diet.

Discussion

The combination of climate change and biodiversity loss at the terminal Pleistocene did influence the ecology of *Sigmodon hispidus* in the Edwards Plateau ecosystem. *Sigmodon* have not been found in the Hall's Cave record from ~22 to 16 ka, likely because temperatures in the region were too low. *Sigmodon* remained relatively rare until ~12 ka when rising temperatures at the end of the Pleistocene (Fig. 2d–e) allowed the species to expand its range northward (Dunaway and Kaye 1961, Fleharty et al. 1972, Cameron and Spencer 1981, Slade et al. 1984, Sauer 1985, Graham et al. 1996,

Eifler and Slade 1998). While the late Pleistocene megafaunal extinction did not mark a simple binary shift in *Sigmodon* body size and diet, changes due to the community restructuring that occurred throughout the Holocene as a consequence of the extinction (Smith et al. 2016b) had varying effects on *Sigmodon's* ecology. Concurrently occurring changes in diet and body size suggest a push and pull dynamic between these traits as *Sigmodon* dealt with changes in environmental and ecological conditions.

We find variation in both body mass and the isotopic niche space of *Sigmodon* at Hall's Cave over time. Overall, body mass fluctuated by more than 20% over the past 16 ka, with substantial variation over time (SD: 11.2–27.3 g, Table 1, Fig. 2f). By far the most important factor influencing body mass was diet. Relative consumption of more C_4 resources led to larger body mass (Table 2, Fig. 1a, path I); $\delta^{13}C$ values were two times more important than any other climatic or community variable in our state space model (Table 2, Fig. 1a). Interestingly, warmer temperatures had a positive influence on mass (Table 2, Fig. 1a, path C) contrary to our expectation based on Bergmann's rule. This suggests that body size changes are more strongly influenced by shifts in available resources than by temperature directly.

Larger body size in *Sigmodon* may have provided access to different resources due to varying metabolic rate or digestive abilities (McNab 1980, Hammond and Wunder 1991, Nagy 2005). Greater consumption of lower quality resources, such as grasses, require larger and/or more complex digestive systems (i.e. greater gut capacity) to account for the faster food passage rates of rodents (Batzli and Cole 1979, Gross et al. 1985, Justice and Smith 1992, Veloso and Bozinovic 1993, Smith 1995). Thus, larger body size in *Sigmodon* may be associated with a higher consumption of C_4 grass on the Edwards Plateau. Moreover, larger body size may provide *Sigmodon* with a compeitive advantage within the community (Martin 1986, Glass and Slade 1980, Kincaid and Cameron 1982),

while alternatively smaller body size and increased numbers of grazer, insectivore and browser species (Table 2) may then have led to changes in the resources available to *S. hispidus* due to competition.

The influence of diet on changes in body size may have been associated with changes in resource availablility. *Sigmodon* showed variation in both $\delta^{13}C$ (SD: 1.8–3.9‰) and to a lesser extent $\delta^{15}N$ (SD: 0.4–1.4‰) values (Table 1, Fig. 3) across time. Modern *Sigmodon* are highly selective of grass habitats, and (C_3 or C_4) grasses can account for ~80% of their diet, but this species consumes higher quality dicots when available (Petersen 1973, Kincaid and Cameron 1982, Kincaid et al. 1983, Randolph et al. 1991, Cameron and Eshelman 1996). Historically, *Sigmodon hispidus* has been found to utilize a mix of C_3 and C_4 resources across the Great Plains, with regions of greater C_4 abundance being associated with higher $\delta^{13}C$ values in *Sigmodon* (Haveles et al. 2019). The observed variation in $\delta^{13}C$ values suggests that *Sigmodon* is not constrained to only consume C_4 grasses (Fig. 3), with shifts potentially reflecting changes in the abundance of C_3 versus C_4 (Fig. 1b, path GI) and expansion and/or contraction of its preferred grassland habitat over time (Fig. 1b, path E). For example, the majority of individuals at 7700–8400 cal BP were within quadrants II and IV (Fig. 3), and had $\delta^{13}C$ values higher than −13‰ suggesting that C_4 resources dominated their diet if average $\delta^{13}C$ values for regional C_3 and C_4 plants are assumed to be −26.5‰ and −12.5‰ (Cerling et al. 1997, Derner et al. 2006). In contrast, the diet of most individuals at 1500–3100 cal BP had $\delta^{13}C$ values lower than −16‰, corresponding to a diet dominated by C_3 resources after accounting for trophic discrimination. Note that changes in isotopic niche space (Fig. 3) are not associated with differences in time-averaging or sample sizes (Table 1) between time intervals, suggesting that the variation in $\delta^{13}C$ and $\delta^{15}N$ likely represent ecological responses through time. Previous small mammal studies have found higher than expected variation in resource use for single dietary specialist species across space and time corresponding to environmental conditions and climate driven vegetational changes (Smiley et al. 2016, Terry et al. 2017, Terry 2018). Pollen records from the region show a shift in the vegetation of the Edwards Plateau from a more mesic deciduous/coniferous forest during the Post Glacial period to a grassland and oak savanna landscape in the Holocene (Bryant and Holloway 1985, Toomey et al. 1993). Prior to ~12 000 cal BP, most grasses were C_3, but beginning ~11 000 cal BP C_4 grasses become dominant and have remained so (Cordova and Johnson 2019). Interestingly, we do not see greater use of C_3 by *Sigmodon* prior to 11 000 cal BP, suggesting that cotton rats were already foraging on C_4 grasses despite their relative scarceness on the landscape (Fig. 3). The period from 2500 to 5700 cal BP is marked by fluctuations in the mesic and xeric vegetation on the Edwards Plateau, and higher levels of C_3 grasses around Hall's Cave (Bryant and Holloway 1985, Toomey et al. 1993, Cordova and Johnson 2019). Here, we do observe a decrease in the use of C_4 resources by

Sigmodon, which may suggest that they are making use of the higher amount of C_3 grasses available (Supplementary material Appendix 1 Fig. A4). These observed shifts in *Sigmodon* diet were likely the result of vegetation change across the Holocene due to shifting climate (Nordt et al. 1994, Fox and Koch 2003, Cotton et al. 2016).

As habitat and resources changed over 16 ka, competitive interactions with other mammals may have caused *Sigmodon* to adapt to new life history strategies. Changes in vegetation composition and resource availability resulting from the removal of large-bodied herbivores can lead to shifts in the abundance of small mammals, which in turn may affect predator presence, small mammal biodiversity and associated intraguild competition (Owen-Smith 1988, Keesing 1998, McCauley et al. 2006, Okullo et al. 2013). The influence of community changes on both the body size (Fig. 1a, path F) and diet of *Sigmodon* (Table 2, Fig. 1b–c, path H) suggests that post-extinction shifts in both resource availability and biotic interactions influenced *Sigmodon's* ecology. Specifically, higher percentages of grazers and granivores in the herbivore community after the extinction, which are expected to have fallen within quadrants IV and III in isotopic space respectively (Fig. 3), were associated with higher consumption of C_4 grasses by *Sigmodon*. While a greater proportion of grazers may have resulted in increased competition within quadrant IV, these results likely reflect the importance megaherbivores, 67% of which were grazers (Smith et al. 2016b), played in the ecosystem before the extinction. The presence of large-bodied herbivores can help maintain grassland ecosystems, reduce woody encroachment and maintain grass species diversity (Laws et al. 1975, Owen-Smith 1988, Bakker et al. 2006, Asner et al. 2009, Smith et al. 2016a). Furthermore, other small mammal grazers in our community include various species of *Microtus*, which are generally outcompeted for habitat and resources by *Sigmodon hispidus* within modern communities (Terman 1974, Smith et al. 2016b). As such, the increased proportion of C_4 grasses in *Sigmodon's* diet when existing in a community with more grazers could have been due to an increased production or diversity of grasses in the region (Fig. 1a, path DE).

Dietary shifts may have corresponded not only to vegetation changes, but could have been related to increased omnivory as modern *Sigmodon* populations are known to opportunistically consume insects, though consumption of this resource is generally limited to <5% of diet composition (Kincaid and Cameron 1982, Schetter et al. 1998). The significant decrease in $\delta^{15}N$ values over time could be due to either a decrease in trophic level or a baseline shift in plant nitrogen isotope values in response to changing environmental conditions (DeNiro and Epstein 1981, Amundson et al. 2003). Plant $\delta^{15}N$ varies in relation to the source(s) of inorganic nitrogen, the physiological mechanism used to uptake nitrogen and environmental conditions (precipitation and temperature) that influence soil $\delta^{15}N$ values via a variety of microbially mediated processes like (de)nitrification and nitrogen fixation (Peterson and Fry 1987, Dawson et al.

2002, Amundson et al. 2003, Murphy and Bowman 2006). In general, plants in environments with lower precipitation and higher temperatures tend to have higher $\delta^{15}N$ values relative to more mesic environments (Ambrose 1991, Austin and Vitousek 1998, Amundson et al. 2003). Our state space model, however, does not find evidence for a correlation between *Sigmodon* $\delta^{15}N$ and precipitation, and $\delta^{15}N$ values actually show a negative relation with increasing maximum temperature in the region (Table 2). Thus, further investigation is required to determine whether the observed shifts in $\delta^{15}N$ of *Sigmodon* are driven by shifts in trophic level versus baseline nitrogen isotope composition of plants, such as a comparison of bone collagen $\delta^{15}N$ values among taxa that have similar functional roles (e.g. herbivores) from the Hall's Cave site, or the analysis of $\delta^{15}N$ values in individual amino acids (Schwartz-Narbonne et al. 2015).

A shift in trophic level would suggest that *Sigmodon* competed with different species for resources over time. A higher proportion of insectivores in the mammalian community is associated with lower $\delta^{13}C$ values in *Sigmodon* (Table 2), or a decreasing proportion of C_4 in *Sigmodon's* diet. Insectivores in the southern Plains are expected to occupy quadrant II (Fig. 3), with higher $\delta^{15}N$ values reflecting higher trophic level, and relatively high $\delta^{13}C$ values corresponding to C_4-based insect herbivores, e.g. grasshoppers, which are one of the most abundant insects in grassland and savannah environments on the Edwards Plateau (DeVisser et al. 2008, Bergstrom 2013). Thus, the negative relationship between *Sigmodon* $\delta^{13}C$ values and the proportion of insectivores in the community may represent competitive exclusion from habitat in quadrant II into quadrant III (towards C_3 resources) or resources in quadrant IV (towards a lower trophic level) (Fig. 3). The significant positive correlations between $\delta^{13}C$ and $\delta^{15}N$ values observed in some time intervals (Fig. 3, Supplementary material Appendix 1 Table A4) could have resulted from *Sigmodon* consuming more insects, essentially filling the niche of an omnivore or insectivore in quadrant II when fewer insectivorous mammals are present in the community. While the relatively low variation in $\delta^{15}N$ (Table 2) suggests *Sigmodon* was primarily herbivorous, its presence in both quadrants II and IV in some time intervals may be the result of shifts in trophic level. Furthermore, the combined interactions of body mass and diet with shifting climate and community structure suggest tradeoffs in *Sigmodon* to cope with environmental and ecological changes across this time span.

Overall, *Sigmodon* responded to a combination of direct and indirect effects of both climate and mammalian community changes through the Holocene, with no single variable driving a dramatic change in cotton rat morphology or ecology. The influence of mammalian community composition on both mass and diet may suggest an indirect effect of the megafauna extinction that led to a large-scale restructuring of the mammalian community in this region (Smith et al. 2016b). Variation in $\delta^{13}C$ and $\delta^{15}N$ values associated with shifts in C_3 versus C_4 resource use and trophic level, were

likely shaped by intraguild competition and changes in vegetation composition that occurred with changing climate conditions and/or the loss of the large herbivores during the extinction (Owen-Smith 1988, Keesing 1998, Okullo et al. 2013). Because climate and community composition were changing together during this period, there may have been tension between potential drivers that result in contrasting effects on *Sigmodon* populations (Blois et al. 2013). The overall stability we see in the body size and diet of *Sigmodon* suggests a high level of adaptability to community and ecosystem restructuring.

Understanding the response of *Sigmodon* to the late Pleistocene megafaunal extinction in North America provides useful insights into the potential responses of small mammals to changes in community structure and ongoing environmental perturbations. The current rate of climate change has led to rapidly rising temperatures over the past 100 years (Pachauri et al. 2014) with continued warming and anthropogenic pressures predicted to have increasing effects on fauna globally (Barnosky et al. 2003). Studies have already shown distribution shifts (Parmesan and Yohe 2003, Moritz et al. 2008) and local extirpations (Munday 2004) across many plant and animal taxa. Work towards conserving biodiversity across the world highlights the importance of the conservation not of a single species but of entire assemblages (Grayson 2007). In the wake of the modern loss in biodiversity, specifically large-bodied species, a combination of ancient and modern studies of generalist species such as *Sigmodon hispidus* may provide a better understanding of the consequences of species removals and provide some insights into how future communities may respond to a combination of abiotic and biotic factors.

Data availability statement

Data are available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.q2bvq83fk> (Tomé et al. 2019).

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