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Unraveling the consequences of the terminal Pleistocene megafauna extinction on mammal community assembly

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Abstract

Recent studies connecting the decline of large predators and consumers with the disintegration of ecosystems often overlook that this natural experiment already occurred. As recently as 14 ka, tens of millions of large-bodied mammals were widespread across the American continents. Within 1000 yr of the arrival of humans, ~80% were extinct including all >600 kg. While the cause of the late Pleistocene (LP) extinction remains contentious, largely overlooked are the ecological consequences of the loss of millions of large-bodied animals. Here, we examine the influence of the LP extinction on a local mammal community. Our study site is Hall's Cave in the Great Plains of Texas, which has unparalleled fine-grained temporal resolution over the past 20 ka, allowing characterization of the community before and after the extinction. In step with continental patterns, this community lost 80%

of large-bodied herbivores and 20% of apex predators at the LP extinction. Using tightly constrained temporal windows spanning full glacial to modern time periods and comprehensive faunal lists, we reconstruct mammal associations and body size distributions over time. We find changes in alpha and beta diversity, and in the statistical moments associated with periods of climate change as well as with the LP extinction event. Additionally, there is a fundamental change in the composition of herbivores, with grazers being replaced by frugivores/granivores starting about 15 ka; the only large-bodied grazer remaining today is the bison *Bison bison*. Moreover, the null model program PAIRS reveals interesting temporal patterns in the disassociation or co-occurrence of species through the terminal Pleistocene and Holocene. Extinct species formed more significant associations than modern ones, and formed more aggregated pairs than do modern species. Further, negative species associations were about three times stronger than positive.

A number of recent studies have associated the decline of large-bodied mammals with the 'unraveling' of ecosystems (Estes et al. 2011, McCauley et al. 2015). Yet, this natural experiment already occurred in the recent past; the largest extant species are the smaller congeners of those present in the terminal Pleistocene. As recently as 14 ka, millions of "megamammals" such as mammoth *Mammuthus* sp., mastodon *Mammut americanum*, stag-moose *Cervalces scotti*, glyptodons *Glyptotherium* sp., camels *Camelops hesternus*, llama *Palaeolama mirifica*, saber-tooth cats *Smilodon fatalis*, short-faced bear *Arctodus simus* and giant sloths e.g. *Megalonyx jeffersonii* were widespread across the continents (Kurtén and Anderson 1980). Indeed, the late Pleistocene (LP) mammal assemblage of the New World was more diverse than that found today in Africa (Lyons et al. 2004, Faurby and Svenning 2015). Within a "geological instant" (~1–2 ka, Faith and Surovell 2009), ~80% of these large-bodied mammals were extinct in North America (Martin 1967, Martin and Klein 1984) including all species over 600 kg (Martin 1967, Lyons et al. 2004). The striking size bias of the LP extinction is unique in the mammal fossil record (Alroy 1999); it even extended to lower taxonomic levels with larger species within orders or families selectively eliminated (Lyons et al. 2004).

For decades, scientists have hotly debated the cause of the late Pleistocene megafauna extinction (Martin 1967, 1984, Guthrie 1984, Graham et al. 1996, Alroy 2001, Grayson 2001, 2007, Grayson and Meltzer 2002, Lyons et al. 2004, Surovell et al. 2005). While the issue remains somewhat contentious, many now agree that humans played a pivotal role through a combination of hunting and habitat alteration (Koch and Barnosky 2006, Sandom et al. 2014a, b). What has been

largely overlooked in the debate, however, are the consequences on ecosystems owing to the loss of hundreds of millions of large-bodied animals, perhaps because such an effort requires intense integration across the ecological, geological and climate sciences. Yet, given on-going trophic downgrading (Estes et al. 2011, McCauley et al. 2015), understanding the ecological consequences of this earlier event is crucial. Consequently, there has been a recent surge of interest in studying the aftermath of the LP extinction (Gill et al. 2009, Johnson 2009, Doughty et al. 2013, Sandom et al. 2014a, b, Smith et al. 2015).

Studies demonstrate that mammalian herbivores play a major role in influencing the composition and structure of vegetative communities (Owen-Smith 1992, Bradshaw et al. 2003, Bakker et al. 2006, Gill et al. 2009, 2012, Johnson 2009). For example, by preventing woodland regeneration, elephants help maintain grasslands; rhinoceros and hippopotamus transform grasslands from tall to more nutritious short grass forms (Owen-Smith 1987, 1992). Similarly, large-bodied mammalian herbivores are critical for the effective dispersal of large-seeded plants (Whyte et al. 2003, Western and Maitumo 2004). Because megaherbivores of extremely large size (>1 ton; Owen-Smith 1987) have a disproportionately greater influence on ecosystems (Owen-Smith 1992, Bakker et al. 2006, 2009), such habitat engineering was likely even more important in the past when the continents supported a diverse and abundant large-bodied mammalian fauna (Owen-Smith 1987, 1992, Zimov et al. 1995, Johnson 2009). Indeed, grazing by megaherbivores may have been crucial for maintaining the vast "mammoth steppe" of the Pleistocene (Zimov et al. 1995, Johnson 2009), a biome absent today. And work investigating the ecology and life history characteristics of tropical and temperate plants has proposed that numerous adaptations for dispersal or regrowth arose in response to foraging by now extinct megafauna (Janzen and Martin 1982, Wing and Tiffney 1987, Barlow 2001).

The loss of an entire suite of large-bodied herbivores undoubtedly led to changes in vegetative structure and composition (Owen-Smith 1987, Johnson 2009), but it may also have led to reorganization of ecological communities and shifts in the foraging niches of surviving species (Donlan et al. 2005, 2006). Such changes could have influenced both large and small surviving species through indirect changes in vegetation and direct effects of competition (Bakker et al. 2009). To date, the influence of the terminal Pleistocene extinction on the

surviving small and medium-sized mammals has been largely ignored.

Community ecology theory suggests that many competitive interactions are size based (Brown and Nicoletto 1991, Marquet and Cofre 1999, Bakker and Kelt 2000, Smith et al. 2008, Ernest 2013); larger animals negatively influence the abundance and distribution of smaller-bodied animals. The loss of large-bodied herbivores may result in ecological release of smaller-bodied species and allow the expansion of geographic ranges or increased abundance. Moreover, the shape of the body size distribution has implications in terms of energy flow through the system (Brown and Nicoletto 1991), and abundance is closely related to the body mass of mammals (Damuth 1981). Thus, we anticipate that the removal of the entire tier of apex predators and herbivores during the terminal Pleistocene had a large impact on surviving lineages of both large and small-bodied animals.

Here, we examine the influence of the LP extinction on a mammal community in the southern Great Plains of North America. Our site, Hall's Cave, lies in the center of the Edwards Plateau (**Fig. 1**), a distinct region of the Texas Hill country dominated by juniper–oak or oak–mesquite savanna with an understory of mid- to short grasslands (Toomey 1993). Because of extensive paleontological excavations and comprehensive radiocarbon dating (Toomey 1993, Toomey et al. 1993, Cooke et al. 2003, Stafford unpubl.), this site has produced an extremely well dated (~160 AMS radiocarbon dates) continuous record of mammals over the past 22,000 yr. In the Pleistocene, the Edward's Plateau supported a diverse mammal assemblage with mammoth, horse, camels and many other megaherbivores, as well as many medium- and small-bodied species that still occur in the region today. The terminal Pleistocene extinction resulted in the loss of 80% of the large-bodied herbivores and 20% of the apex predators in the ecosystem (Fig. 1b). Thus, Hall's Cave provides an unparalleled opportunity to quantitatively examine the influence of the LP megafauna extinction on mammal community structure, and moreover, to potentially disentangle the influence of previously recognized fluctuations in late Quaternary climate from biotic interactions such as competition.

We address two major questions. First, does the fundamental structure of the mammal community change after the terminal Pleistocene extinction? Are features of the local body size distribution resilient to large-scale taxonomic shifts? And, second, do particular species associate — or disassociate — more often than predicted by chance?

Methods

We reconstructed the fossil mammal community at 16 key time intervals over the past 22 ka and examined changes in the composition and function of the surviving mammalian assemblage in relation to the presence or absence of megaherbivores and major climatic fluctuations. Specifically, we characterized alpha and beta diversity, the shape and statistical moments of the overall body size distribution (which reflect energy flow), and the associations of species through time at the site.

Reconstructing mammal paleocommunities

Our mammal communities are based on Hall's Cave and the ~20 nearby fossil sites on the Edward's Plateau of Texas (**Fig. 1**; Supplementary material Appendix 1, Table A1). In the Pleistocene, this region supported an open grassland ecosystem (Joines 2011). Today, it consists of a juniper–oak/mesquite–acacia savanna with an understory of short grasses; both rainfall and temperature is intermediate between dry grasslands/savanna eco-regions (Collins et al. 1990, Toomey 1993, Joines 2011).

Paleontological excavations have occurred at Hall's Cave episodically since 1966, with the most comprehensive in the early 1990s (Toomey 1993). All materials collected during these excavations are archived at the Texas Memorial Museum (TMM) at the University of Texas, Austin. The stratigraphy at Hall's Cave is well-defined with a distinct, horizontal section and with negligible bioturbation; it also has an unparalleled high-resolution chronology based on 162 AMS radiocarbon dates (Stafford unpubl.). There is an incredibly rich fossil record, especially for small mammals, with ~5 g shrews to > 500 kg bison represented.

Because some changes in taxonomy have occurred since the original descriptions of the fossils (Toomey 1993), we updated species identifications as necessary. First, we synonymized species for whom taxonomic revisions have occurred. For example, Harlan's ground sloth has been changed from *Glossotherium harlani* to *Paramylodon harlani* (McAfee 2007) and the American cave lion recently reclassified from *Felis atrox* to *Panthera leo atrox* (Barnett et al. 2009). The most problematic taxonomy was that of horses, which has been grouped into as few as two species (Weinstock et al. 2005) or as many as >12, with
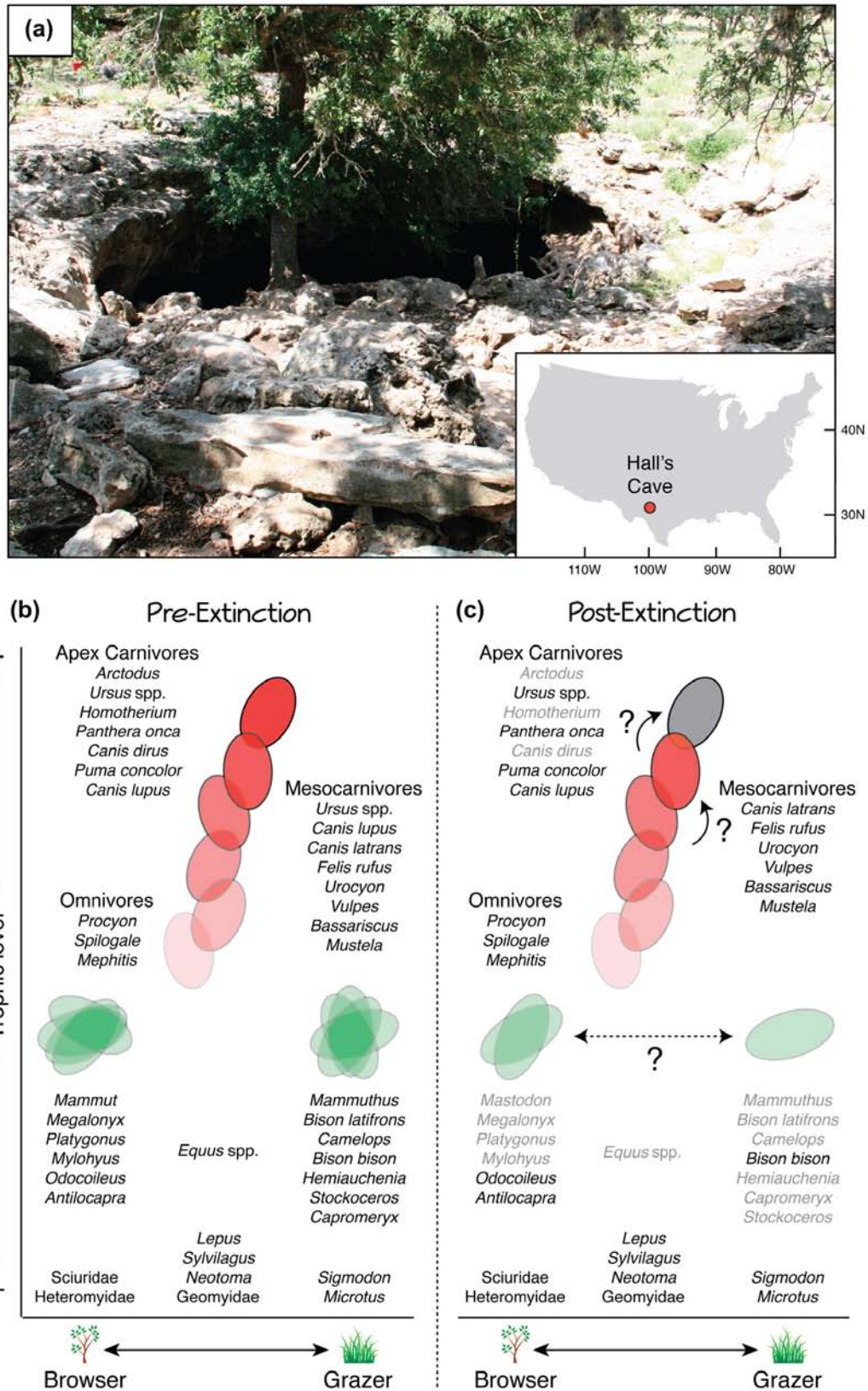
(a)

Hall's Cave

40N

30N

110W   100W   90W   80W

(b) Pre-Extinction

(c) Post-Extinction

Trophic level + —

(b) Pre-Extinction

Apex Carnivores
Arctodus
Ursus spp.
Homotherium
Panthera onca
Canis dirus
Puma concolor
Canis lupus

Mesocarnivores
Ursus spp.
Canis lupus
Canis latrans
Felis rufus
Urocyon
Vulpes
Bassariscus
Mustela

Omnivores
Procyon
Spilogale
Mephitis

Mammut
Megalonyx
Platygonus
Mylohyus
Odocoileus
Antilocapra

Equus spp.

Mammuthus
Bison latifrons
Camelops
Bison bison
Hemiauchenia
Stockoceros
Capromeryx

Lepus
Sylvilagus
Neotoma
Geomyidae

Sigmodon
Microtus

Sciuridae
Heteromyidae

Browser ⟷ Grazer

(c) Post-Extinction

Apex Carnivores
Arctodus
Ursus spp.
Homotherium
Panthera onca
Canis dirus
Puma concolor
Canis lupus

?

?

Mesocarnivores
Canis latrans
Felis rufus
Urocyon
Vulpes
Bassariscus
Mustela

Omnivores
Procyon
Spilogale
Mephitis

?

Mastodon
Megalonyx
Platygonus
Mylohyus
Odocoileus
Antilocapra

Equus spp.

Mammuthus
Bison latifrons
Camelops
Bison bison
Hemiauchenia
Capromeryx
Stockoceros

Lepus
Sylvilagus
Neotoma
Geomyidae

Sigmodon
Microtus

Sciuridae
Heteromyidae

Browser ⟷ Grazer

Figure 1. Hall's Cave, Kerr county, Texas. (a) Picture of the site located at ~30°08′N, 99°32′W at an elevation of ~500 m in an area of modest topographical relief. Mean annual temperature is ~18°C and mean precipitation is ~800 mm (Collins 2004); (b, c) hypothesized trophic relationships between extinct and extant mammal fauna in the community are depicted. The ellipse represents the projected isotopic niche space. Values are approximate; they were taken from the literature and may not be representative of Hall's Cave. Note the large number of grazers present in the pre-extinction panel. Grey text in the "post-extinction" panel represents taxa extirpated by the LP megafauna extinction.

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no clear scientific consensus (< http://fossilworks.org >, Kurtén and Anderson 1980, Winans 1989, Azzaroli 1998, Weinstock et al. 2005). Here, we first identified a candidate list of species using recent literature and personal discussions with experts in the field, (e.g. E. Scott, C. Barron-Ortiz pers. comm.), which resulted in a fairly conservative list of 7 vetted species, six of whom were reported from the Pleistocene of Texas (e.g. *E. conversidens*, *E. complicatus*, *E. giganteus*, *E. scotti*, *E. occidentalis*, *E. laurentius*). Thus, we considered 6 to be the upper limit of species possibly co-occurring within the Edwards Plateau. We synonymized species as appropriate and collapsed all specimens identified as "*Equus* sp." to a single taxon. This reduced the reported diversity of horses, and is likely to represent a reasonable and conservative sampling of the equid community. For some taxa, fossil elements were only classified to the genus level (e.g. *Neotoma*, *Peromyscus*); this results in an underestimate of the species richness of these clades. Given their known distributions and diversity, we estimate we are probably missing < 10 species of small rodents over the 22 ka period of our study.

The taphonomy at Hall's Cave led to the underrepresentation of the largest mammals, which was exacerbated by the lower probability of inclusion because large mammals are less dense on the landscape. Accordingly, we obtained museum and literature records for nearby cave sites within the Edwards Plateau with diverse and abundant large mammal assemblages to obtain a more complete representation of the mammal community. These ranged in distance from Hall's Cave with the farthest (Berclair Terrace) ~282 km away (Supplementary material Appendix 1, Table A1).

Faunal lists and geological coordinates were downloaded for Texas paleontological sites from NEOTOMA (< www.neotomadb.org >).

Using latitude and longitude, we calculated the straight-line distance (*d*) from each paleontological site to Hall's Cave using an online calculator from NOAA (< www.nhc.noaa.gov/gccalc.shtml >). Additional sites were included based on a search of the literature (Evans 1961, Frank 1965, Lundelius 1967, 1979, 1984, 1985, Dalquest et al. 1969, Lundelius and Slaughter 1971, Roth 1972, Graham 1976, Harris 1985, Toomey et al. 1992, 1993, Toomey 1993, 1994). From these, we compiled a comprehensive list of candidate species. To determine if a particular mammal should be included in our "local" community, we determined if either the natal dispersal distance or average home range included Hall's Cave using Euclidean geometry as follows. First, we computed maximum dispersal distance using the species body mass and a guild-specific equation. For carnivores, maximum dispersal distance (D_c, in km) was calculated as:

$$D_c = 40.7 \, M^{0.81} \tag{1}$$

where M = body mass in kg; for herbivores or omnivores ($D_{h/o}$) we used:

$$D_{h/o} = 3.31 \, M^{0.65} \tag{2}$$

based on work by Sutherland et al. (2000). We computed home range for carnivores (HR_c, in km^2) using a comprehensive model developed by Tucker et al. (2014):

$$\log HR_c = 1.19 \log M - 0.29 \tag{3}$$

For herbivores or omnivores, we employed:

$$\log HR_{h/o} = 1.19 \log M - 1.47 \tag{4}$$

(Tucker et al. 2014). Assuming home range was a square, we used the Pythagorean theorem to calculate the hypotenuse of the home range estimate. Both dispersal distance and the hypotenuse of the home range were then compared to the straight-line distance between Hall's Cave and the candidate paleontological site, e.g.

$$d \leq (2HR)^{1/2} \qquad d \leq D \tag{5}$$

to determine if the species should be included as a member of the community assemblage. Thus, species such as the American cave lion *P. leo atrox* were included within our community assemblage because of fossils found at Kincaid Shelter, which is ~85 km away (generic fossils were also found at Hall's Cave). This left us with a list of 90 taxa found over the ~22 ka (Supplementary material Appendix 1, Table A1).

For each species, we derived information on body mass and dietary guild using an updated version of the late Quaternary global mammal database (MOM ver. 4.1, Smith et al. 2003) and a variety of literature sources (Whitaker 1963, Kurtén and Anderson 1980, Linzey 1984, Norrie and Millar 1990, Pinter et al. 1992, McDonald 1996, Barreto et al. 1997, Koch et al. 1998, Martinoli et al. 2001, Rivals and Semprebon 2006, Schmidt 2008, DeSantis et al. 2009, Feranec et al. 2009, Prado et al. 2011, Pérez-Crespo et al. 2012, Ugan and Coltrain 2012, Yeakel et al. 2013, Jasinski and Wallace 2014, Smith et al. 2014, Yann and DeSantis 2014). Note that the frugivore/granivore guild included animals that ate either fruit or seeds. Although body masses are species-specific, they are not spatially explicit. It is likely that some species adapted to climate or ecological shifts in the region over the late Quaternary by morphological changes in body mass (Smith et al. 1995, Smith and Lyons 2011, Smith 2012). However, our analyses were conducted in log space; it is highly improbable that mass shifts would be sufficiently large to influence patterns (Smith et al. 2008).

Temporal windows

We employed 16 temporal windows of ~1.3 ka, which extended from modern to full Glacial conditions (21 ka). Our time span encompassed a number of important climatic and biotic events including (in calendar years before present): essentially modern conditions during the Late Holocene (1–3 ka), a warming during the Middle Holocene (~5–7.0 ka), the Younger Dryas cold episode (11.5–12.8 ka), the Megafauna Extinction Horizon (11.4–13.8 ka; Faith and Surovell 2009), as well as the Full Glacial (~21.0 ka) when ice sheets were at their fullest extent. Species were scored as present or absent for each temporal bin based on the AMS radiocarbon dates associated with the specimen or unit from which they were excavated. While the stratigraphy from Hall's Cave was robust and would have allowed much finer temporal

resolution (Stafford unpubl.), dates for the other sites were not as well characterized, precluding the use of finer temporal units.

Note that our time frame for the extinction is conservative. Our designation of the time period from ~11.4–13.8 ka as the "extinction horizon" is based on the more or less accepted arrival of humans into North America and a conservative estimate of the terminal dates of megafauna (Faith and Surovell 2009, Fiedel 2009). It was probably more constrained than this; the youngest credible dates for megafauna all cluster around 11,000–11,500 ^{14}C yr, or ~12,800 calendar years ago (Fiedel 2009) suggesting that most were extinct shortly thereafter. Archeological evidence from the Edwards Plateau demonstrates that humans were present near Hall's Cave (e.g. Kincaid Shelter) by the late Pleistocene, around ~12 ka (Collins 2004); many artifacts dating to about 8,500 ^{14}C yr (or ~9.5 ka) are reported from the nearby area (Prewitt 1981, 1985). The oldest definitive fossil occurrence of the domestic dog, which can be taken as an indicator of human presence, comes from Schulze Cave at ~7 ka (< www.neotomadb.org >), although bones attributed to dogs or coyotes are present at Hall's Cave earlier (Toomey 1993). Unfortunately, it is not always possible to differentiate between various canid species, making their use as a proxy for human presence less valuable.

Temperature

There is no well-resolved terrestrial temperature record for the past 22 ka for the Great Plains of North America. Thus, we employed an ice core from Greenland as a first approximation of temperature fluctuations over the past 22 ka. While Greenland cores will not capture local or regional fluctuations in climate, they do capture the major climate features (Taylor et al. 1993, Viau et al. 2006). We used the Greenland Ice Sheet Project 2 (EPICA2; Alley 2000, 2004), which has excellent resolution over the late Quaternary. For regression analyses, we averaged all values for 500 yr windows centered on the dates of our community at Hall's Cave. This coarsening of the record means that some high magnitude abrupt events are smoothed out, but binning provides a more appropriate estimate of overall temperature for our communities.

Statistical analyses

We computed presence or absence for each of the 90 species over the 16 time windows, resulting in a 90 × 16 matrix. Alpha and β-diversity and similarity were computed for and/or between each temporal bin. Similarity was characterized using a Sorensen coefficient; β-diversity was calculated as 1 – Sorensen. We also constructed the log-transformed mammal body size distribution for each time period, which provides information on biomass and energy flow through the clade, and computed the statistical moments (mean, median, range, skew, kurtosis) to characterize the shape and mode. Two-sample Kolmogorov–Smirnov tests were performed to determine if body size distributions were significantly different from each other. Because of the large numbers of comparisons made, Bonferroni corrections were applied throughout our analyses. Statistics were performed in R (< www.r-project.org >), ProFit (Quantum software; < www.quansoft. com >), with SPSS statistical software (< www.01.ibm.com/software/ analytics/spss/ >) or computed by hand.

To examine species associations over time, we constructed a 90 × 90 × 16 matrix representing all possible species pair combinations over the 16 temporal windows. Not all species were present at each time. We employed the program PAIRS (Gotelli and Ulrich 2010, Blois et al. 2014) to evaluate overall patterns of species co-occurrence for each time slice. PAIRS is a null model program that uses matrix randomization to determine if species co-occur more or less than would be expected by chance. All species pairs in a matrix are assigned a c-score or co-occurrence score and each pair is assigned to a histogram bin. The matrix is randomized 1000 times to create null assemblages and c-scores are calculated each time. A mean and confidence interval is calculated for the number of species in each histogram bin using the null assemblages. Within each bin, the pairs are ordered by c-score and only pairs with scores higher than the mean expectation are considered further. Each is tested for significance and classified as significantly segregated or aggregated using a Bayes mean criterion. The resultant z-scores represent a measure of interaction strength.

Pairs with significant associations were further analyzed by coding by diet (e.g. carnivore, insectivore, browser, grazer, frugivore/

granivore, or omnivore), the type of likely interaction (predatory–prey, competition, indirect) and the body size differential between pairs. These were then sorted by type of interaction and the absolute value of the body size differential between the two species. Regression analysis was conducted to look at the effect of body size, body size differential between the members of the species pair, trophic level and z-scores (a measure of interaction strength) from the PAIRS analysis. Chi-square was employed to compare the frequency of encountering significant pairs by trophic level and/or body size given the underlying species distributions.

Results

Mammal diversity

Over the 22 ka time period from the late Quaternary to present, some 90 extinct or extant species from 10 taxonomic orders were present within the local community at Hall's Cave (Supplementary material Appendix 1, Table A1). The average number of species present during a time bin was 41.1 (σ = 14.6), with a low of 22 at 17.2 ka to a high of 73 species at 12.9 ka (**Fig. 2**b). Because the diversity at 17.2 ka is so much lower than all other time bins, we suspect that it is likely under sampled and thus view all metrics for this time period with some caution. Alpha diversity was largely invariant over the Holocene with an average of 33.7 (σ = 1.9) species in the community at any given time (Fig. 2b); this was also true of the Full Glacial. As expected, the taxonomic similarity of the community declined over time (Fig. 2c), with

Figure 2. Characteristics of mammal community at Hall's Cave over the past 22 ka. (a) Temperature deviations from modern taken from the GISP2 ice core. The last glacial maximum in North America was ~21 ka, note also the "Younger Dryas," an abrupt cooling/warming event in the late Pleistocene from 12.8–11.5 ka, other well-documented climate events include the 8.2 ka cooling, and warming in the middle Holocene; (b) α-diversity of the community; (c) β-diversity of community between time bins (blue squares) and relative to modern (open squares with dots); (d) body size with maximum (blue), minimum (red), mean (grey) and median (black) indicated for each time bin; and (e) statistical moments of the body size distribution. We plot the midpoint of each time bin; each is approximately 1.3 ka in duration.
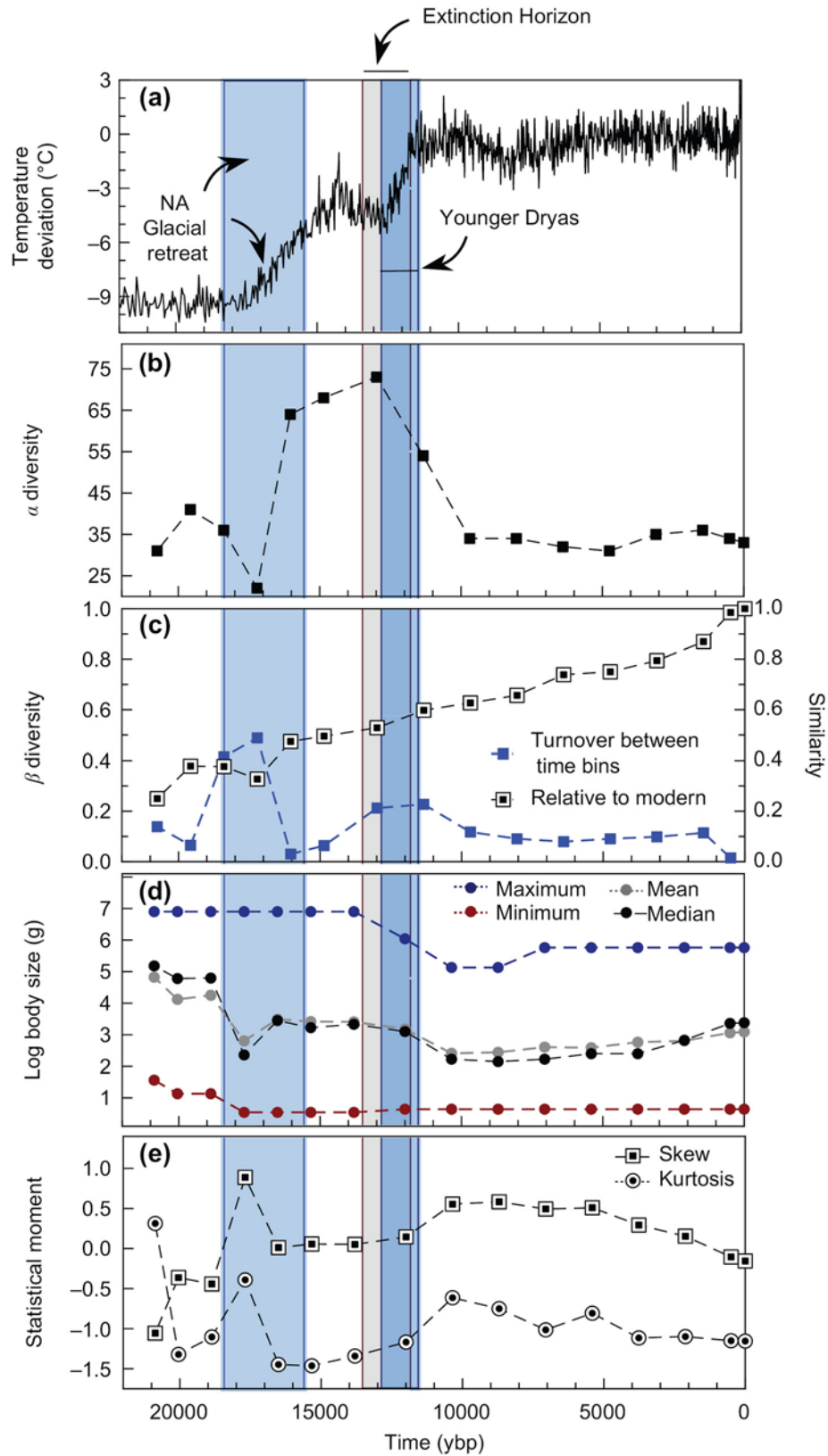
the faunal similarity between the full glacial and the present only 0.25 (**Table 1**). Interestingly, there were several periods of marked turnover in diversity, which corresponded with the retreat of glaciers and warming of the environment (Fig. 2a) as well as the extinction of the megafauna guild. These abrupt changes in beta diversity occurred between 16–18 and ~12–13 ka, the latter coincident with the LP extinction and the beginning of the Younger Dryas (Fig. 2c; Table 1).

Body size distributions of community

Maximum body size was largely invariant through the late Pleistocene, but dropped by ~2 orders of magnitude by the early Holocene (Fig. 2d); it remained largely unchanged until modern. The decrease in body mass was largely driven by extinctions of grazers and browsers, with the average mass of these guilds declining by 2 orders of magnitude at this time; the mean body mass of insectivore, omnivore and frugivore/granivores did not change over the Pleistocene or Holocene. Minimum body size of the community was almost invariant over the entire 22 ka. There were two time periods when the mean/median body size in the community shifted – around 18 ka as climate warmed from the last ice age, and ~12 ka during the extinction event/Younger Dryas climate event. These changes were reflected in differences in the skew and kurtosis (Fig. 2e).

The body size distribution (BSD) also changed over the Pleistocene and Holocene (**Fig. 3**), reflecting shifts in energy flow through the community. This occurred primarily through the loss of the largest species in the community (e.g. mammoths, mastodons, camels, etc.), and not through shifts in the minimum size (Fig. 2d). It led to a fundamental restricting of the shape of the BSD from bimodal to flat, and from right, to left skewed (Fig. 2e, Fig. 3). These shifts were correlated with both climate fluctuations and the LP extinction, with an essentially modern BSD established by the Holocene (Fig. 3, Table 1). The shape of the BSD distribution was significantly different at time periods centered on 10.3, 13.8, 15.3–16.5, and > 18.8 ka (two-sample K–S tests, p < 0.0001; Table 1). This encompassed the terminus of the Younger Dryas cold episode, which was marked by abrupt warming, the onset of the megafauna extinction at 13.8 ka, and the climate changes following the full glacial at 21 ka.

Table 1. Differences in the body size distribution at Hall's Cave over time. Midpoint of time bin is indicated; bins extend ~ 500 yr on either side. Above diagonal are results of two-sample Kolmogorov–Smirnov tests; below are similarity values. Comparisons significant after Bonferroni correction are indicated by blue shading. Discontinuities in similarity indices are indicated by bold.

|	Historic	868	3,763	5,410	7,057	8,704	10,351	11,998	13,805	15,331	16,509	17,688	18,867	20,046	20,870
Modern	D = 0.020, p < 1	D = 0.136, p < 0.90	D = 0.179, p < 0.646	D = 0.255, p < 0.249	D = 0.233, p < 0.341	D = 0.311, p < 0.078	D = 0.340, **p < 0.041**	D = 0.131, p < 0.872	D = 0.210, p < 0.267	D = 0.247, p < 0.132	D = 0.254, p < 0.121	D = 0.303, p < 0.177	D = 0.437, **p < 0.003**	D = 0.421, **p < 0.004**	D = 0.588, **p < 0.0001**
Historic	–	D = 0.118, p < 0.969	D = 0.161, p < 0.766	D = 0.239, p < 0.312	D = 0.217, p < 0.42	D = 0.294, p < 0.106	D = 0.324, p < 0.057	D = 0.134, p < 0.848	D = 0.213, p < 0.243	D = 0.25, p < 0.118	D = 0.257, p < 0.106	D = 0.286, p < 0.224	D = 0.440, **p < 0.002**	D = 0.424, **p < 0.003**	D = 0.592, **p < 0.0001**
868	0.886	–	D = 0.071, p < 1	D = 0.126, p < 0.953	D = 0.120, p < 0.972	D = 0.181, p < 0.613	D = 0.211, p < 0.419	D = 0.167, p < 0.586	D = 0.246, p < 0.109	D = 0.284, **p < 0.045**	D = 0.292, **p < 0.04**	D = 0.172, p < 0.816	D = 0.472, **p < 0.0007**	D = 0.457, **p < 0.0007**	D = 0.626, **p < 0.0001**
3,763	0.812	0.901	–	D = 0.085, p < 0.1	D = 0.100, p < 0.996	D = 0.137, p < 0.903	D = 0.167, p < 0.720	D = 0.137, p < 0.824	D = 0.216, p < 0.221	D = 0.253, p < 0.103	D = 0.261, p < 0.092	D = 0.153, p < 0.909	D = 0.442, **p < 0.002**	D = 0.426, **p < 0.003**	D = 0.595, **p < 0.0001**
5,410	0.769	0.896	0.909	–	D = 0.050, p < 1	D = 0.078, p < 1	D = 0.111, p < 0.988	D = 0.187, p < 0.497	D = 0.241, p < 0.160	D = 0.274, p < 0.082	D = 0.279, p < 0.077	D = 0.150, p < 0.936	D = 0.463, **p < 0.002**	D = 0.448, **p < 0.002**	D = 0.613, **p < 0.0001**
7,057	0.758	0.853	0.836	0.921	–	D = 0.079, p < 1	D = 0.134, p < 0.928	D = 0.185, p < 0.496	D = 0.214, p < 0.262	D = 0.245, p < 0.148	D = 0.25, p < 0.139	D = 0.151, p < 0.929	D = 0.434, **p < 0.003**	D = 0.418, **p < 0.004**	D = 0.589, **p < 0.0001**
8,704	0.676	0.771	0.783	0.831	0.909	–	D = 0.059, p < 1	D = 0.221, p < 0.259	D = 0.276, p < 0.059	D = 0.294, **p < 0.04**	D = 0.308, **p < 0.03**	D = 0.182, p < 0.769	D = 0.490, **p < 0.0005**	D = 0.458, **p < 0.0009**	D = 0.662, **p < 0.0001**
10,351	0.647	0.743	0.754	0.769	0.818	0.882	–	D = 0.249, p < 0.0149	D = 0.319, **p < 0.018**	D = 0.324, **p < 0.017**	D = 0.337, **p < 0.013**	D = 0.182, p < 0.769	D = 0.520, **p < 0.0002**	D = 0.487, **p < 0.0003**	D = 0.692, **p < 0.0001**
11,998	0.614	0.667	0.719	0.659	0.698	0.727	**0.773**	–	D = 0.122,	D = 0.154, p < 0.477	D = 0.170, p < 0.365	D = 0.214, p < 0.473	D = 0.324, **p < 0.021**	D = 0.302, **p < 0.03**	D = 0.483, p < 0.0003
13,805	0.523	0.550	0.593	0.519	0.552	0.579	0.617	**0.787**	–	D = 0.039, p < 1	D = 0.052, p < 1	D = 0.248, p < 0.25	D = 0.240, p < .123	D = 0.222, p < 0.152	D = 0.395, **p < 0.003**
15,331	0.490	0.500	0.544	0.465	0.500	0.529	0.569	0.721	0.936	–	D = 0.025, p < 1	D = 0.245, p < 0.273	D = 0.216, p < 0.224	D = 0.184, p < 0.354	D = 0.368, **p < 0.007**
16,509	0.469	0.480	0.525	0.442	0.458	0.490	0.531	0.695	0.920	0.970	–	D = 0.256, p < 0.235	D = 0.196, p < 0.338	D = 0.177, p < 0.413	D = 0.354, **p < 0.02**
17,688	0.321	0.414	0.421	0.415	0.407	0.429	0.464	0.395	0.463	0.489	**0.512**	– **p < 0.02**	D = 0.412, **p < 0.03**	D = 0.382, **p < 0.0004**	D = 0.579,
18,867	0.371	0.389	0.423	0.358	0.382	0.400	0.400	0.556	0.587	0.635	0.640	**0.586**	–	D = 0.066, p < 1	D = 0.177, p < 0.677
20,046	0.373	0.416	0.447	0.389	0.411	0.427	0.427	0.568	0.632	0.679	0.686	0.603	0.935	–	D = 0.212, p < 0.403
20,870	0.246	0.239	0.273	0.194	0.222	0.246	0.215	0.424	0.500	0.545	0.547	0.377	0.866	0.861	–
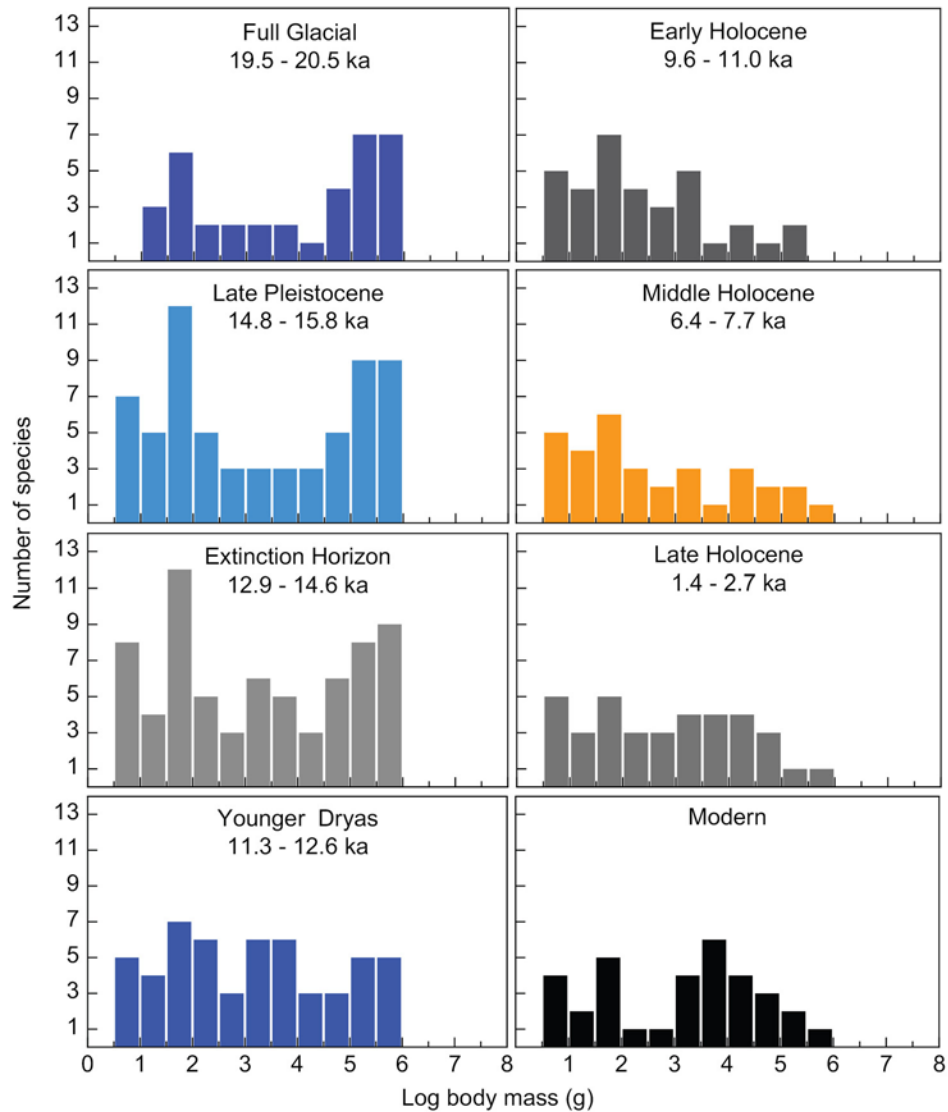
Figure 3. Body size distributions plotted over coarser 8 temporal windows. All analyses were done with the coarse 8 temporal windows as well as the finer 16 windows reported elsewhere; because results are qualitatively similar we only report the statistical results for the later. Note the differences in shape between the Pleistocene (panels on left) and Holocene (panels on right). Two tailed K–S tests of the distributions are presented in Table 1. For each epoch, panels are arranged from oldest to youngest; note that temporal bins shown here do not completely encompass several significant events.

Trophic guilds

There were marked changes in the proportion of species within trophic guilds over time (**Fig. 4**). While some guilds remained relatively constant (e.g. omnivores and insectivores), others changed profoundly over the late Pleistocene (~13–11 ka) as both climate changes and faunal turnover occurred. Interestingly, the proportion of frugivores/granivores and grazers were significantly negatively associated (r = –0.90, DF = 15, p < 0.001; Fig. 4) over the 22 ka. Indeed, there was a marked tradeoff between the proportion of each guild in the community (slope = –0.67). There was also a negative correlation between the proportion of insectivores and carnivores (r = –0.73, DF = 15, p < 0.01). Several of the shifts in trophic guilds were highly
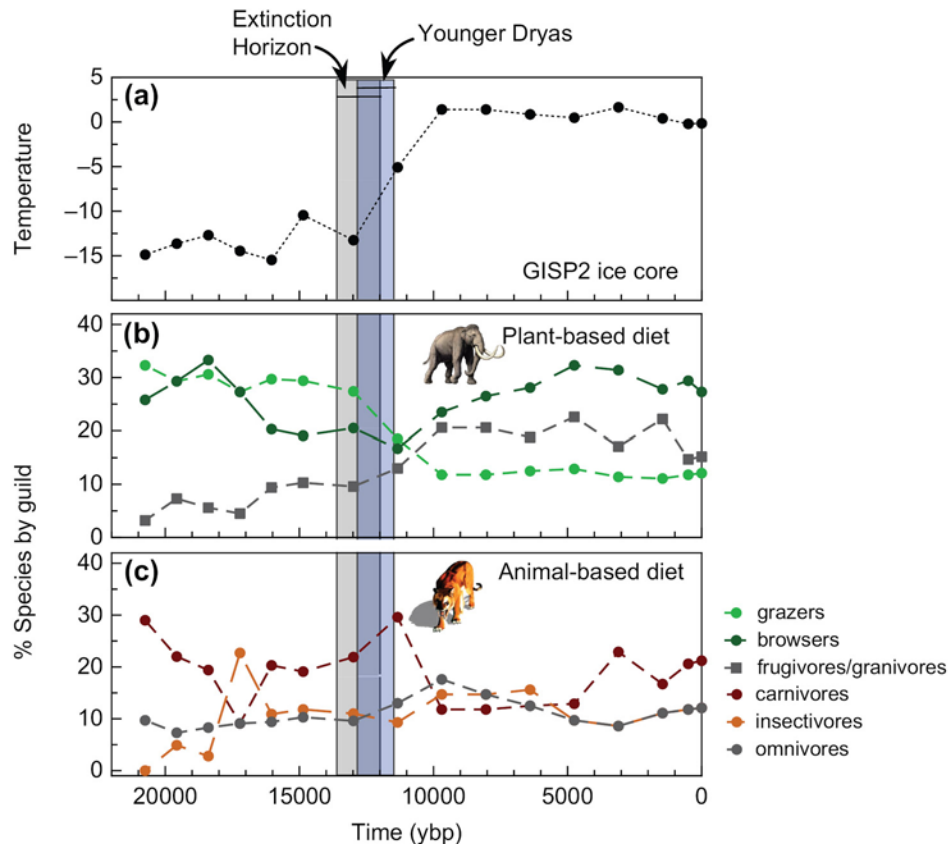

Figure 4. Changes in the proportion of trophic guilds at Hall's Cave over time as compared to temperature. (a) Temperature averaged over 500 yr centered on the radiocarbon date of the assembly at Hall's Cave; data derived from the GISP2 core; (b) percent of various herbivore guilds over time; (c) percent of various animal based diets over time. Other statistics reported in text.

correlated with temperature changes (frugivores/granivores, r = 0.93, DF = 15, p < 0.0001; grazers, r = −0.96, DF = 15, p < 0.0001), but in opposite directions (frugivore/granivores slope = 1.0; grazer slope = −0.78). There was also a positive relationship between temperature and the proportion of omnivores (slope = 1.6; r = 0.61, DF = 15, p < 0.02), but not with other trophic guilds (p > 0.05).

Species associations

Of the possible 4050 unique species pair combinations (e.g. (90 × 90 species)/2), we found a total of 279 that were significant (Supplementary material Appendix 1, Table A1). Negative or segregated associations were twice as common as positive or aggregated associations (194 vs 85, respectively). Of the 90 mammals found at Hall's Cave over the past 22 ka, 77% (69) were involved in one or more positive or negative species interactions (Supplementary material Appendix 1, Table A1). However, the number of significant associations was highly skewed with only 20 species forming 10 or more interactions. Some very common extant species such as the coyote *Canis latrans* or deer *Odocoileus* sp. did not form significant pairs; we interpret this as reflecting a cosmopolitan habitat and generalized ecology, but it could also result from the inability of the PAIRS analysis to identify significant pairs if a species is consistently present in all time bins.

Extinct species formed significantly more species pairs than did extant mammals (two-tailed t-test, t = 4.0413, DF = 88, p < 0.001; **Table 2**). With the exception of the extinct river cat *Felis amnicola*, all extinct mammals identified to species formed one or more associations (Supplementary material Appendix 1, Table A1). For example, the Columbian mammoth *Mammuthus columbi* was part of 8 pairs and the scimitar cat *Homotherium serum* was found in 12. The average number of associations for all extinct taxa (n = 26) was 9.9 (range 0–19 pairs; Table 2). Moreover, these were almost equally split between positive (4.4) and negative (5.5) associations. In contrast, modern mammals (n = 64) formed an average of 4.7 pairs, with most segregated (3.8) rather than aggregated (0.9).

The number of aggregated pairs was influenced by mammalian order (1-way ANOVA, p < 0.001), but the substantial variation within clades (Table 2) led to non-significant results for segregated and overall pairs (1-way ANOVA, p > 0.05). Pilosa, which at our site consisted

Table 2. Results of PAIRS analysis by various categories (trophic guild, status and mammalian order). ANOVA and regression analyses reveal substantial heterogeneity of pair formation with each factor for all 90 species (see text for details).

	Category	Number of species	Mean pairs formed	Median pairs	Standard deviation	Range	Skew	Kurtosis	Mean aggregated pairs	Mean segregated pairs
Trophic guild	Browser	19	8.5	9	8.49	0–28	0.584	−0.662	2.4	6.1
	Grazer	21	7.6	8	4.18	0–17	0.352	0.635	3.7	3.9
	Carnivore	20	3.8	3	4.19	0–13	1.009	−0.089	0.9	3.0
	Frugivore/Granivore	10	5.1	4	4.50	0–14	0.818	−0.320	0.1	5.0
	Insectivore	10	5.1	4.5	3.30	1–14	2.034	5.499	0.9	4.2
	Omnivore	10	6	3	7.55	0–26	2.045	4.630	1.9	4.1
Status	Extinct	26	9.9	9	5.03	0–19	0.117	−0.490	4.4	5.5
	Extant	64	4.7	3.5	5.72	0–28	2.087	5.495	0.9	3.8
Mammalian order	Artiodactyla	11	6.6	6	6.11	0–18	0.594	−0.748	2.5	4.2
	Carnivora	28	5.3	3	6.21	0–26	1.704	3.099	1.0	4.2
	Cingulata	3	10	9	5.35	4–17	0.670	–	3.3	6.7
	Didelphimorphia	1	11	11	–	–	–	–	2.0	9.0
	Insectivora	1	3	3	–	–	–	–	1.0	2.0
	Lagomorpha	4	6.8	6.5	6.76	0–14	0.014	−5.918	0.0	6.8
	Perissodactyla	7	8.6	9	3.99	3–17	1.177	2.758	5.7	2.9
	Pilosa	2	15.5	15.5	3.50	12–19	–	–	8.0	7.5
	Proboscidea	2	10	10	2.00	8–12	–	–	2.5	7.5
	Rodentia	31	5	4	5.55	0–28	2.408	8.437	1.3	3.7

solely of sloths, averaged the highest number of pairs with 15.5, almost evenly split between aggregations and segregations (8.0 vs 7.5, respectively). In contrast, Insectivores formed the least with 3 (1.0 vs 2.0, respectively). Lagomorpha (hares and cottontails) was the only order that formed no aggregated pairs (Table 2). There was a significant interaction between order and guild affiliation for aggregated pairs, but not segregated or overall pairs (2-way ANOVA, $p < 0.05$); both were highly correlated with body mass (order: $p < 0.001$, guild: $p < 0.01$). Sample sizes were too small to examine other levels of the taxonomic hierarchy rigorously, but there was substantial heterogeneity at the family and genus level (Supplementary material Appendix 1, Table A1).

In general, larger animals did not form more associations than smaller ones, even when correcting for differences in species richness between genera or families (regression analyses, $p > 0.05$). In fact, there was a significant decrease in the number of negative associations with increasing body mass for Artiodactyla ($F = 7.29$, m $= −0.79$, $p < 0.05$, DF = 9) and Lagomorpha ($F = 146.1$, m $= −8.15$, $p < 0.01$, DF = 2). However, when trophic guild was incorporated

into the analysis, we found no significant relationships between log body mass and the formation of species pairs. There was, however, an asymmetry in the body size of many species pairs. The difference in mass between the two species in a pair was significantly smaller for aggregated pairs than for segregated ones (t-test, $p < 0.0001$; Mann–Whitney, $p < 0.0001$).

When analyzed by species, pair formation is influenced by trophic level. Browsers form the most pairs (8.5) and carnivores the fewest (3.8, Table 2). While there is no significant pattern overall or for segregated pairs (presumably because of the high variability within groups), we do find a tendency for the total number of aggregated pairs formed to be different for mammals of different trophic guilds (ANOVA, $p < 0.01$). Grazers formed more positive associations than other trophic groups; significantly more so than carnivores or frugivores/granivores (Tukey's HSD, $p < 0.05$). In contrast, carnivores formed 3 times more segregated than aggregated pairs.

Overall, segregations were much stronger associations than were aggregations (2-tailed t-test, $p < 0.001$); mean z-scores, a measure of interaction strength, were ~3 times greater (z-scores of ~3.0 to 6.9 versus –1.8 to –1.5; **Fig. 5**a). Moreover, there was about an order of magnitude more variation in the z-scores for segregated pairs, suggesting less uniformity of the association. The strength of the interactions did not significantly vary between trophic guilds, although the strongest interactions tended to be associated with herbivores, particularly browsers or frugivores/granivores, and the weakest involved omnivores (Fig. 5a). Interactions between carnivores (often thought to be highly competitive) yielded average interaction strengths.

Interestingly, extinct carnivores formed significantly more aggregations than did extant carnivores (t-test, $t = 3.14$, $DF = 15$, $p < 0.01$); virtually all of these were with large-bodied herbivores (**Table 3**). In sharp contrast, among extant carnivores only the short-tailed weasel *Mustela erminea* formed positive associations. In general, extant

Figure 5. Results from PAIRS analysis at Hall's Cave. (a) The strength of aggregated and segregated species pairs ranked by trophic interaction type. Note that green represents interactions involving only herbivores, black represents interactions involving carnivores or insectivores, and grey are interactions involving a mixture of divergent trophic guilds; (b) the rank order of the ratio of observed/expected species pairs by segregated pairs; colors the same as in panel (a); (c) the rank order of the ratio of observed/expected species pairs by aggregations.
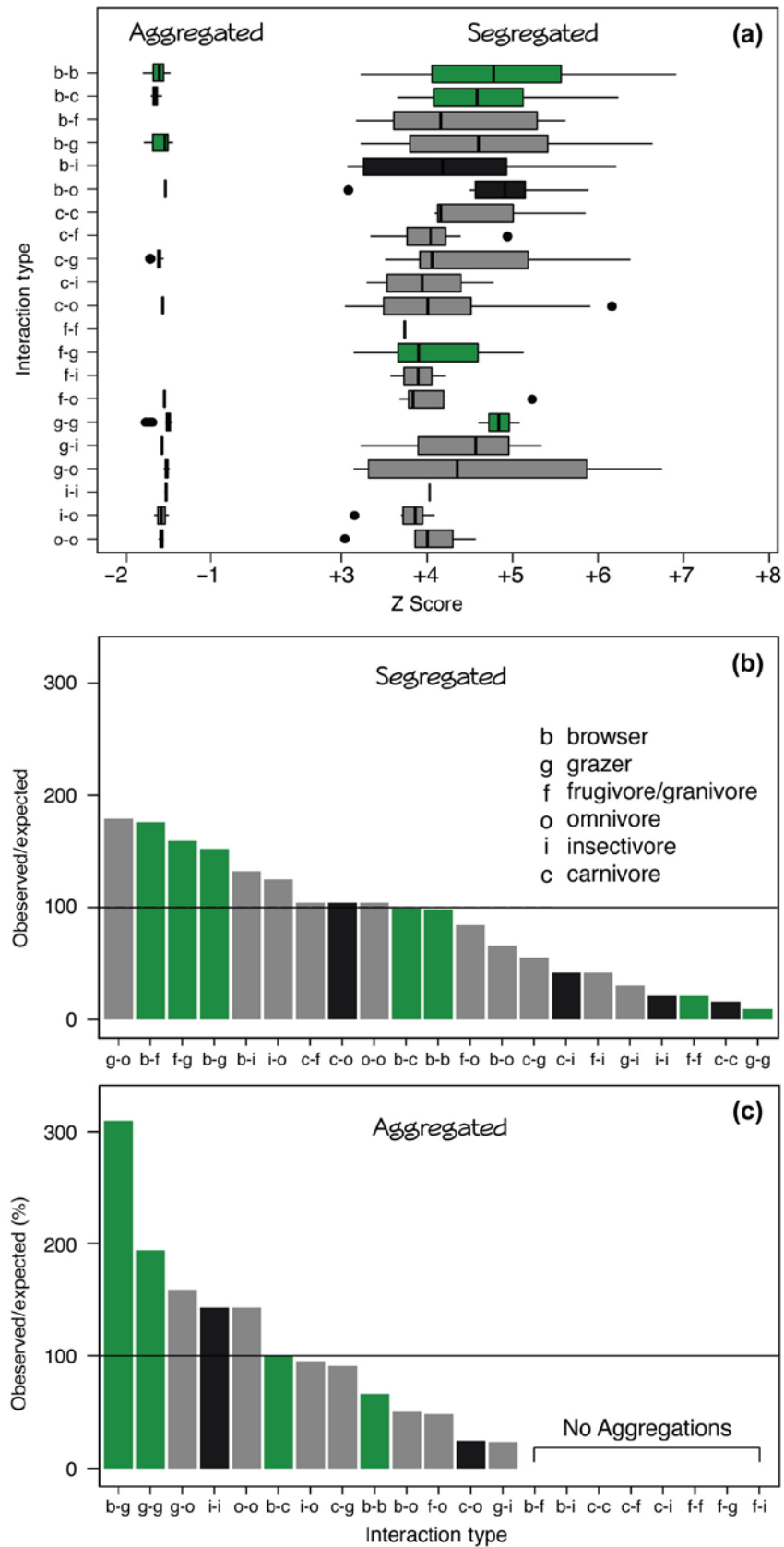
Table 3. Pairs formation among carnivores at Hall's Cave.

Taxon	Status	Number of aggregations	Average Z score of aggregations	Number of segregations	Average Z score of segregations	Total pairs formed	Positive associations formed with:
Arctodus simus	extinct	6	−1.62	4	4.31	10	*Mammut, Megalonyx, Tapirus, Bison, Camelops, Paramylodon*
Canis dirus	extinct	3	−1.67	3	4.34	6	*Megalonyx, Bison, Tapirus*
Homoterium serum	extinct	4	−1.62	7	5.15	11	*Equus, Bison, Megalonyx, Tapirus*
Panthera leo atrox	extinct	2	−1.71	4	4.28	6	*Megalonyx, Bison*
Smilodon fatalis	extinct	0	0.00	8	3.93	8	varied, includes domestic dogs
Felisa amnicola	extinct	0	0.00	0	0.00	0	
Average for extinct species		**2.5**	**−1.32**	**4.3**	**4.40**	**6.8**	
Panthera onca	extant	0		5	3.81	5	
Puma concolor	extant	0		13	4.84	13	10 segregations formed with extinct species (competitive exclusion?)
Canis lupus	extant	0		3	4.13	3	
Canis familiaris	extant	0		4	4.99	4	
Mustela erminea	extant	2	−1.565	1	3.73	3	*Equus*, extant skunk
Urocyon cinereoargenteus	extant	0		3	3.68	3	
Lynx rufus	extant	0		1	4.39	1	
Vulpes vulpes	extant	0		1	4.24	1	
Canis latrans	extant	0		0	0.00	0	
Herpailurus yaguarondi	extant	0		0	0.00	0	
Leopardus wiedii	extant	0		0	0.00	0	
Average for extant species		**0.2**		**2.82**	**3.07**	**3**	

species also formed fewer negative associations than did extinct carnivores, but this difference was not significant. There was a marginal tendency for pair formation to differ between the two groups (t-test, t = 1.97, DF = 15, p = 0.068), with extinct carnivores forming twice as many pairs as extant ones (Table 2).

The frequency of different interaction types within the community (e.g., b-b, b-g, b-m, etc.) was highly skewed, both overall and within either segregated or aggregated pairs (**Fig. 5**). Negative associations that occurred more often than expected virtually always involved herbivores. Indeed, segregations between mixed herbivore types (frugivore/granivores, grazers or browsers) all occurred more than expected. Interestingly, segregations within the same herbivore guild were much less frequent than expected (Fig. 5), perhaps reflecting common habitat selection. However, the most frequent positive

associations were also between herbivores (browsers and grazers, followed by grazer-grazer). There was an interesting difference in the tendency of browsers or frugivore/granivores versus grazers to form pairs; many positive and negative interactions occurring more than expected involved a grazer. In contrast to herbivores, other guilds (e.g., carnivores, omnivores and insectivores) tended to form fewer pairs than expected based on their representation in the community (Fig. 5).

Discussion

We find significant differences in the local mammal community at Hall's Cave over the past 22,000 yr. While some of the changes in shape and structure are clearly related to the terminal Pleistocene megafauna extinction, we also uncover other periods of pronounced change that appear to be related to shifts in climate. The modern mammal assemblage at Hall's Cave varies in many aspects — body size distribution, trophic guild structure, and in the type and strength of species associations — from that present in the Pleistocene (Fig. 3–5). Here, we summarize these changes, identify which can be attributed to the terminal Pleistocene extinction and which likely result from climate shifts, and conclude by discussing what our results might suggest for modern conservation biology.

The alpha diversity at Hall's Cave is relatively invariant except for the period from ~16 to 11 ka, which includes periods of rapid climate shifts (Fig. 2); e.g. the Younger Dryas (YD) interval at 12.8–11.5 ka, and the LP megafauna extinction event at 13.8–11.4 ka. The peak diversity around 16–13 ka may reflect a heterogeneous environment resulting from the retreat of glaciers in North America and resultant warming. A diverse mosaic of habitats likely existed as the area rapidly changed from a mesic grassland/woodland to an arid shrub/grassland (Joines 2011), leading to accelerated faunal turnover (Fig. 2c). These shifts clearly predate the YD interval and overlap with the onset of the extinction event at 13.8 ka. The presence of species known to have divergent habitat requirements, coupled with unusually high alpha diversity (up to 73 species), support the idea that that different "patches" of habitat may have been ephemerally present. Note that certain genera, such as *Microtus*, reached their greatest diversity at

this time with six species, about a third of the total diversity found in all of North America (Hall and Kelson 1981). Today, even in areas of particularly high species richness, it is quite uncommon to find more than three species of *Microtus* within a community (Tamarin 1985, Spaeth 2009) and for most of the record at Hall's Cave there were no more than 2 species present (Supplementary material Appendix 1, Table A1). Interestingly, although there was an abrupt increase in beta diversity at the late Pleistocene (Fig. 2c) coincident with a decrease in the median/mean body mass, neither the minimum nor the maximum body mass changed until 11–12 ka, around the end of the LP extinction event (Fig. 2d). This suggests that warming in North America as the ice sheets retreated and habitats rapidly changed led to the ecological replacement of the largest cold-adapted species with similar-sized congeners. Other shifts in the statistical moments and shape of the body size distribution largely occurred during and just after the extinction, with little change over the Holocene (Fig. 2, 3).

While some changes in the community were clearly the result of the warming climate at the terminal Pleistocene, it is also clear that the loss of 80% of the megaherbivores and 20% of the apex predators (Fig. 1) between 13.8–11.4 ka fundamentally changed the structure of the mammal community at Hall's Cave. In addition to the turnover at 17–18 ka, there is another increase in beta diversity at 12–14 ka coincident with the LP extinction and largely before the YD event (Fig. 2c). This time the increase in beta diversity is accompanied by a 2-order of magnitude reduction in maximum body mass (Fig. 2d). There is also an order of magnitude drop in the median/mean mass (Fig. 2d) as well as changes in the community body size distribution as evidenced by the statistical moments (Fig. 2e, 3). Indeed, the "shape" of the mammal body size distribution (BSD) at Hall's Cave shifted from bimodal to flat by the end of the LP extinction, and from right to left skewed during the Holocene (Fig. 3). These shifts in the BSD are important because proximally they are the result of interspecific interactions, and ultimately, they reflect the flow of energy in the ecosystem (Brown and Nicoletto 1991). Thus, the shape of the BSD is a proxy for the allocation of food and space among co-existing species (Brown and Nicoletto 1991). Since we would expect that species of similar size would tend to be from different trophic guilds unless resources are particularly plentiful, "peaks" consisting of species within a similar trophic guild likely indicate heterogeneous environments or increases

in the availability of resources. Thus, the bimodal BSD distribution (Fig. 3) found at the late Pleistocene could be interpreted to suggest a habitat mosaic. Similarly, the reduction in alpha diversity during the early Holocene, which coincides with the flattening of the BSD, suggests a more homogeneous habitat. While the timing of the changes in the community composition and structure overlap with the rapid cooling and abrupt warming associated with the Younger Dryas episode, our data suggest that the composition of the mammal community was changing before the onset of this climate event.

One of our most intriguing results is the fundamental restructuring of the large herbivore community tightly associated with the LP extinction (Fig. 4). While grazers dominated the community for most of the late Pleistocene record, even during the warming climate associated with the retreat of glaciers in North America (Fig. 4), this abruptly changed with the LP extinction. The proportion of grazers in the system dropped by more than half, with only bison, pronghorn and a few medium- to small-bodied species surviving (Fig. 1). Because large-bodied grazers help maintain grasslands (Owen-Smith 1987, 1992), their absence probably resulted in encroachment of woody vegetation, which may have changed the relative amount of annual C_3 versus C_4 biomass production at the site. Such vegetation changes, coupled with ecological release because of the reduced diversity of grazers, led to a replacement of the grazer guild by other herbivores. While browsers increased in abundance, there was almost a doubling of the percentage of frugivore and granivore species present (Fig. 4). The sensitivity of frugivores and granivores to the extirpation of grazers probably reflected resource competition; they are more likely than browsers to compete with grazers for the same resources. The transition in the herbivores assemblage was complete by the early Holocene, and the overall diversity of each guild remained relatively invariant at Hall's Cave afterward. Note that these changes occurred despite increased precipitation during the Younger Dryas, which should have favored a mesic grassland habitat. Moreover, the turnover in the composition of the herbivore guild (and reduction in average herbivore body mass) was also accompanied by a reduction in the diversity of carnivores at Hall's Cave and a concomitant increase in insectivores (Fig. 4d). Curiously, there was little response among omnivores; the proportion of this guild in the community was almost invariant across the entire 22 ka.

Changes in the structure of the community were also accompanied by significant differences in the associations of mammal species over time at Hall's Cave. We find significant differences in the number of positive (aggregated) versus negative (segregated) species pairs, in the number of associations formed by extinct versus extant species and in the type of pairs formed (Table 2). Moreover, we find considerable heterogeneity among species in terms of their tendency to form pairs, which is related to both body mass and trophic guild, and a difference in the strength of negative versus positive associations (Fig. 5). The significant difference we find in pair formation between modern and extinct mammals (Table 2) suggests that the late Pleistocene mammal assemblage was more tightly structured than the modern community. Indeed, extinct species formed twice as many pairs as those extant today, and these were more evenly spilt between aggregated and segregated associations (Table 2). This finding may reflect the now unoccupied role of 'megaherbivores' in North America communities, which likely served as keystone species (Owen-Smith 1992). Our results also have implications for the types of ecological interactions that existed in the community during the late Quaternary. Aggregated associations can arise because of common niche requirements, a mutualistic interaction or a tightly linked predatory–prey relationship. In contrast, segregations are likely to arise because of habitat filtering and/or competitive interactions (Gotelli and Ulrich 2010). For example, the Perissodacytla, which was mainly composed of horses in the terminal Pleistocene, was one of only two orders with more aggregated than segregated pairs (Table 2). Because many of these associations were with other horse species and bison, we suspect they reflected highly similar resource requirements.

We anticipated that the loss of apex carnivores would lead to a restructuring of the guild. The modern apex carnivores in North America (e.g. jaguar, mountain lion, wolf, grizzly bear) were mesocarnivores in the Pleistocene when saber-tooth and scimitar-toothed cats, dire wolves and the short-faced bear dominated the community (Fig. 1). Because apex carnivores are known to be hyper-carnivorous (Van Valkenburgh et al. 2004), we expected that they would form more positive associations with their prey than their modern counterparts. Indeed, we found this expected pattern (Table 3). Not only did extinct carnivores form many more overall pairs than extant ones (6.8 ± 3.92 vs 3.0 ± 3.74), but they also formed significantly more aggregated

pairs than do modern predators (2.5 ± 2.35 vs 0.2 ± 0.60 for modern). These positive associations included some putative predator–prey relationships that have been suggested by paleontologists. For example, the short-faced bear *Arctodus simus* significantly aggregated with bison, camel, mastodon, tapir and sloths; similarly, the scimitar-toothed cat *Homotherium serum* was positively associated with horses, bison sloth and tapir (Table 3). The almost complete lack of positive pair formation among modern carnivores — even species such as wolves *Canis lupus*, mountain lions *Puma concolor* and jaguar *Panthera onca* — strongly suggests that modern apex consumers do not associate with their prey in the same way as those in the Pleistocene. We suspect this may reflect a loss of the "hyper-carnivore" trophic guild and that modern carnivores, which are smaller than their LP counterparts, are not as tightly tied to a specific prey base. The hyper-carnivores in the Pleistocene may have been highly specialized morphologically (Van Valkenburgh et al. 2004), which may have resulted in the greater number of observed pairs for these taxa. Ultimately, this specialization may have contributed to a higher vulnerability to extinction (Van Valkenburgh et al. 2004).

We suspect that the species involved in the most pairs were those who had strong habitat associations and consequently, whose pair formation reflected environmental filtering. For example, the two species forming the most associations were the pocket gopher *Thomomys* sp. with 28 pairs and the raccoon *Procyon lotor* with 26 (Supplementary material Appendix 1, Table A1). All pairs formed by the pocket gopher were negative associations, generally with large-bodied grazers such as bison, horses, camels and mammoths. This is intriguing because *Thomomys* construct shallower burrows than other species of pocket gophers, averaging just 5–35 cm in depth (Best 1973, Hickman 1977, Vleck 1979). Thus, the negative associations may reflect the inability of this taxa to co-exist with extremely large-bodied mammals whose huge mass (~5–10 tons) likely led to soil compaction (Owen-Smith 1987, 1992). Raccoons are generalist omnivores; while they formed associations with both extinct and extant taxa, most were grassland specialists. Thus, their high number of pairs may also reflect environmental filtering.

We find that negative associations are a stronger force than positive ones in species assembly over time (Fig. 5), especially for extant species (Table 2). This might have been expected given the strong

role competition has been postulated to play in community assembly (Brown 1975, Brown and Heske 1990, Mitchell et al. 1990), but oddly, many of the negative associations we uncover do not appear to be largely driven by competition (Fig. 5). With the exception of those involving frugivore/granivores, most competitive interactions (e.g. those within the same trophic level) occur much less frequently than expected by chance (Fig. 5b, c). We predicted that mammals that were similar in body size and trophic level would be strongly negatively associated, and moreover, that the strength of the interaction would be negatively related to the size differential between the species. However, we found the opposite: aggregated pairs tended to be more similar in body mass than segregated ones. Moreover, with the exception of the frugivore/granivores and browsers, there are fewer intra-guild segregations than for other interactions (Fig. 5). Indeed, the most frequent positive association is between browsers and grazers. Because the majority of our grazers are very large-bodied, this implies that competition between megaherbivores was structured by means other than body mass. Further, it implies "cohesion" between large-bodied grazers, perhaps because of reduced predation in a mixed herd. This finding is in line with observations of African mammals, which suggest that the largest herbivores compete more with mesograzers than each other (Owen-Smith 1992).

Frugivore and granivores disassociate more than expected with all other guilds, including other frugivore/granivores, browsers, grazers, omnivores, carnivores and insectivores (Fig. 5). The strong segregation with these guilds is unexpected. While competition is likely between frugivores/granivores and grazers, or between frugivores/granivores and omnivores, it is highly unlikely to occur with carnivores or insectivores. Some of these disassociations probably reflect habitat filtering, but it is unclear why the remainder occur. We are currently employing stable isotope analysis to characterize the dietary niche of these guilds more quantitatively and may in the future be able to resolve these questions.

Our results have clear implications for modern conservation biology. Today, the majority of large-bodied mammals around the globe are listed as either vulnerable or endangered because of a disastrous combination of environmental and societal factors as well as intrinsic traits such as low fecundity (Cardillo et al. 2005, Schipper et al. 2008, Hoffmann et al. 2011). For example, there has been a >50% decrease

in the population density of the largest mammals in Africa since the 1970s; similar declines are reported in other regions around the globe (Schipper et al. 2008, Craigie et al. 2010). While the loss of such charismatic fauna is of great concern for many reasons, their role in ecosystem function is still unresolved. Our results document a shift in the type and prevalence of aggregated versus segregated pairs related to the extinction; if pair formation can be interpreted as influencing the cohesiveness or structuring of the mammal community, then the loss of megafauna at Hall's Cave clearly led to a less stable mammal assemblage. Indeed, the strong association between grazers suggests a role for co-occurrence of taxa, perhaps to reduce predation risk. Thus, it appears that modern mammal communities in North America may be less connected than ancient ones.

Several other findings are of conservation importance. For example, the fundamental change in the body size structure after the extinction suggests that energy flow through the community was permanently altered at this local site. Moreover, we find strong evidence that the carnivore guild operates differently today than it did in the past; that is, modern terrestrial "apex" consumers are not as hyper-carnivorous as in the late Pleistocene and may be more opportunistic in their dietary choices. Some of these shifts in energy flow such as changes in the relative consumption of browse (C_3 plants) versus grass (C_4) biomass and/or trophic status over time can be further quantified with stable isotope analysis of fossil remains from Hall's Cave. We anticipate that future studies combining isotope-based quantification of diet composition with statistical analysis of community composition and structure (e.g. PAIRS) will provide unique insights into the consequences of the late Pleistocene extinction on mammal communities.

A major theme of conservation biology focuses on developing an understanding of how megafauna loss may impact contemporary ecosystems. Elucidating the role extinct megafauna played in the structure and functioning of North America ecosystems, and how their extinction at the terminal Pleistocene disrupted species associations and community functioning provides insights into the likely consequences of contemporary biodiversity loss. By providing a historic perspective, our project adds significantly to an understanding of the consequences of the current decline in megamammals taking place globally.

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Supplementary material (Appendix 1) follows.

Appendix 1

Table A1. Species list for Hall Cave Mammal Community. Body mass and trophic designations are derived from an updated version of MOM v4.1 (Smith et al. 2003). As described in the main text, the trophic designation 'frugivore/granivore' includes animals primarily foraging on fruit, seeds or nuts; 'carnivore' are those eating any type of animal, including fish; and 'insectivore' are mammals primarily foraging on insect prey.

Order	Family	Genus	Species	Average Body Mass (g)	Status	Trophic Level	Segregated Pairs	Aggregated Pairs	Total Pairs	Sites
Artiodactyla	Antilocapridae	*Antilocapra*	*americana*	46,083	extant	browser	0	0	0	HC; 41; KS; MC
Artiodactyla	Antilocapridae	*Stockoceros*	*sp.*	720,000	extinct	browser	1	8	9	CQ; SC
Artiodactyla	Antilocapridae	*Tetrameryx*	*shuleri*	8	extinct	browser	16	2	18	LC3
Artiodactyla	Bovidae	*Bison*	*antiquus*	1,130	extinct	grazer	6	10	16	HC; KS
Artiodactyla	Bovidae	*Bison*	*bison*	195,718	extant	grazer	0	0	0	HC; 41; EC; FF; KS; MC; CW; FC; Fr; SC; ZC
Artiodactyla	Camelidae	*Camelops*	*hesternus*	579,255	extinct	grazer	6	4	10	BT; Fr; KS; LC2; ZC
Artiodactyla	Camelidae	*Hemiauchenia*	*macrocephala*	14	extinct	grazer	4	2	6	HC; ZC
Artiodactyla	Cervidae	*Navahoceros*	*fricki*	1,100,000	extinct	browser	1	0	1	MS; SC
Artiodactyla	Cervidae	*Odocoileus*	*sp*	65,000	extant	browser	0	0	0	HC; KS; MiC; CW; MS; SC; ZC
Artiodactyla	Tayassuidae	*Pecari*	*tajacu*	17,000	extant	frugivore/ granivore	8	1	9	HC
Artiodactyla	Tayassuidae	*Platygonus*	*compressus*	13,406	extant	grazer	4	0	4	HC; ZC
Carnivora	Canidae	*Canis*	*dirus*	19,892	extinct	carnivore	3	3	6	HC; FR; KS; LC3; ZC

Carnivora	Canidae	Canis	familiaris	32	extant	carnivore	4	0	4	HC; SC
Carnivora	Canidae	Canis	latrans	3,500	extant	carnivore	0	0	0	HC; CW; CS; EC; Fr; KS; LC3; MC; SC; ZC
Carnivora	Canidae	Canis	lupus	5	extant	carnivore	3	0	3	HC; 41; KS; SC
Carnivora	Canidae	Urocyon	cinereoargenteus	1,364	extant	carnivore	3	0	3	HC
Carnivora	Canidae	Vulpes	vulpes	45,000	extant	carnivore	1	0	1	HC; SC; ZC
Carnivora	Felidae	Felis	amnicola	4,204	extinct	carnivore	0	0	0	SC
Carnivora	Felidae	Herpailurus	yaguarondi	2,195	extant	carnivore	0	0	0	HC
Carnivora	Felidae	Homotherium	serum	77	extinct	carnivore	8	4	12	Fr; LC2
Carnivora	Felidae	Leopardus	wiedii	400,000	extant	carnivore	0	0	0	HC
Carnivora	Felidae	Lynx	rufus	465,000	extant	carnivore	1	0	1	HC; CW; KS; SC; ZC
Carnivora	Felidae	Panthera	leo atrox	555,000	extinct	carnivore	4	2	6	HC; KS
Carnivora	Felidae	Panthera	onca	259,000	extant	carnivore	5	0	5	HC; KS; LC1; LC3; SC
Carnivora	Felidae	Puma	concolor	400,000	extant	carnivore	13	0	13	HC; HiC; KS; SC
Carnivora	Felidae	Smilodon	fatalis	465,000	extinct	carnivore	8	0	8	FR
Carnivora	Mustelidae	Conepatus	leuconotus	5,000	extant	insectivore	13	1	14	HC
Carnivora	Mustelidae	Mephitis	macroura	248	extant	omnivore	1	4	5	HC
Carnivora	Mustelidae	Mephitis	mephitis	1,100,000	extant	omnivore	1	2	3	HC
Carnivora	Mustelidae	Mustela	erminea	110,000	extant	carnivore	1	2	3	HC; SC
Carnivora	Mustelidae	Mustela	frenata	9,000	extant	carnivore	0	0	0	HC;SC
Carnivora	Mustelidae	Spilogale	sp	189,000	extant	omnivore	0	3	3	HC

Carnivora	Mustelidae	*Taxidea*	*taxus*	3,250	extant	carnivore	0	0	0	SC
Carnivora	Procyonidae	*Bassariscus*	*astutus*	2,422	extant	carnivore	0	0	0	HC
Carnivora	Procyonidae	*Procyon*	*lotor*	8,904	extant	omnivore	26	0	26	HC
Carnivora	Ursidae	*Arctodus*	*simus*	4,523,800	extinct	carnivore	5	6	11	CQ; Fr; SC
Carnivora	Ursidae	*Tremarctos*	*floridanus*	8,000,000	extinct	browser	15	2	17	LC3
Carnivora	Ursidae	*Ursus*	*americanus*	600,000	extant	omnivore	3	0	3	HC; CW; Fr; MiC; SC; ZC
Carnivora	Ursidae	*Ursus*	*arctos*	801	extant	omnivore	0	0	0	SC
Cingulata	Dasypodidae	*Dasypus*	*bellus*	2,085	extinct	omnivore	1	8	9	HC; 41
Cingulata	Dasypodidae	*Dasypus*	*novemcinctus*	47	extant	insectivore	4	0	4	41
Cingulata	Glyptodontidae	*Glyptotherium*	*floridanum*	35	extinct	grazer	15	2	17	LC3
Didelphimorphia	Didelphidae	*Didelphis*	*virginiana*	36	extant	omnivore	9	2	11	HC
Insectivora	Talpidae	*Scalopus*	*aquaticus*	38	extant	insectivore	2	1	3	HC
Lagomorpha	Leporidae	*Lepus*	*californicus*	37	extant	browser	13	0	13	HC
Lagomorpha	Leporidae	*Sylvilagus*	*aquaticus*	26	extant	browser	14	0	14	HC
Lagomorpha	Leporidae	*Sylvilagus*	*audubonii*	169	extant	browser	0	0	0	HC
Lagomorpha	Leporidae	*Sylvilagus*	*floridanus*	147	extant	browser	0	0	0	HC
Perissodactyla	Equidae	*Equus*	*complicatus*	250,000	extinct	grazer	1	8	9	BT1
Perissodactyla	Equidae	*Equus*	*francisci*	211	extinct	grazer	1	2	3	CQ; SC
Perissodactyla	Equidae	*Equus*	*scotti*	4	extinct	grazer	3	4	7	CQ; SC
Perissodactyla	Equidae	*Equus*	*fraternus*	54,861	extinct	grazer	1	8	9	BT1
Perissodactyla	Equidae	*Equus*	*giganteus*	28	extinct	grazer	1	8	9	BT1
Perissodactyla	Equidae	*Equus*	*sp. 1*	433,200	extinct	grazer	6	0	6	Various
Perissodactyla	Tapiridae	*Tapirus*	*veroensis*	100,000	extinct	browser	7	10	17	MS; Fr
Pilosa	Megalonychidae	*Megalonyx*	*jeffersonii*	252	extinct	browser	7	12	19	Fr; LC3; ZC
Pilosa	Mylodontidae	*Paramylodon*	*harlani*	1,587,000	extinct	grazer	8	4	12	A;KS
Proboscidea	Elephantidae	*Mammuthus*	*columbi*	21,267	extinct	grazer	7	1	8	BT1; Fr;

										SC
Proboscidea	Mammutidae	*Mammut*	*americanum*	9	extinct	browser	8	4	12	A; BT1; CW; Fr
Rodentia	Geomyidae	*Geomys*	*sp*	8	extant	browser	4	0	4	HC
Rodentia	Geomyidae	*Pappogeomys*	*castanops*	36	extant	browser	0	0	0	HC
Rodentia	Geomyidae	*Thomomys*	*sp*	36	extant	browser	28	0	28	HC
Rodentia	Heteromyidae	*Chaetodipus*	*hispidus*	136,000	extant	frugivore/ granivore	0	0	0	HC
Rodentia	Heteromyidae	*Dipodomys*	*elator*	5,525	extant	frugivore/ granivore	4	0	4	HC
Rodentia	Heteromyidae	*Perognathus*	*flavescens*	51,600	extant	frugivore/ granivore	4	0	4	HC
Rodentia	Heteromyidae	*Perognathus*	*flavus*	16	extant	frugivore/ granivore	4	0	4	HC
Rodentia	Muridae	*Baiomys*	*taylori*	91	extant	frugivore/ granivore	11	0	11	HC
Rodentia	Muridae	*Microtus*	*longicaudus*	500	extant	browser	1	8	9	HC
Rodentia	Muridae	*Microtus*	*mexicanus*	92	extant	grazer	1	8	9	HC
Rodentia	Muridae	*Microtus*	*montanus*	400,000	extant	grazer	1	8	9	HC
Rodentia	Muridae	*Microtus*	*ochrogaster*	5	extant	grazer	0	0	0	HC
Rodentia	Muridae	*Microtus*	*pennsylvanicus*	4	extant	grazer	1	8	9	HC
Rodentia	Muridae	*Microtus*	*pinetorum*	4	extant	browser	0	0	0	HC
Rodentia	Muridae	*Neotoma*	*sp*	326	extant	browser	0	0	0	HC
Rodentia	Muridae	*Onychomys*	*leucogaster*	288	extant	insectivore	1	0	1	HC
Rodentia	Muridae	*Peromyscus*	*sp. 1*	53,000	extant	omnivore	0	0	0	HC
Rodentia	Muridae	*Peromyscus*	*sp. 2*	2,136	extant	omnivore	0	0	0	HC
Rodentia	Muridae	*Reithrodontomys*	*sp*	890	extant	frugivore/ granivore	4	0	4	HC

Rodentia	Muridae	*Sigmodon*	*hispidus*	1,173	extant	grazer	5	0	5	HC
Rodentia	Muridae	*Synaptomys*	*cooperi*	32	extant	grazer	5	1	6	HC
Rodentia	Sciuridae	*Cynomys*	*ludovicianus*	275,000	extant	grazer	5	0	5	HC
Rodentia	Sciuridae	*Sciurus*	*sp*	7,108	extant	frugivore/granivore	14	0	14	HC
Rodentia	Sciuridae	*Spermophilus*	*sp.*	60,000	extant	frugivore/granivore	1	0	1	HC
Rodentia	Soricidae	*Blarina*	*carolinensis*	135	extant	insectivore	3	0	3	HC
Rodentia	Soricidae	*Cryptotis*	*parva*	150,000	extant	insectivore	5	0	5	HC
Rodentia	Soricidae	*Notiosorex*	*crawfordi*	3,834	extant	insectivore	4	0	4	HC
Rodentia	Soricidae	*Sorex*	*cinereus*	99,949	extant	insectivore	2	3	5	HC
Rodentia	Soricidae	*Sorex*	*haydeni*	139,441	extant	insectivore	4	2	6	HC
Rodentia	Soricidae	*Sorex*	*longirostris*	6,000	extant	insectivore	4	2	6	HC
Rodentia	Zapodidae	*Zapus*	*hudsonius*	17	extant	frugivore/granivore	0	0	0	HC

* For all included Texas sites the full name and distance from Hall's Cave site are as follows: HC (Hall's Cave) = 0 km; 41(41TG91) = 165 km; A (The Avenue) = 172 km; BT (Barton Road Shelter) = 171 km; BT1 (Berclair Terrace Site 1) = 268 km; CQ (Cueva Quebrada) = 185 km; CW (Cave Without A Name) = 93 km; CS (Coontail Spin) = 178 km; EC (Eagle Cave) = 197 km; FC (Felton Cave) = 104 km; FF (Finis Frost) = 140 km; Fr (Friesenhahn Cave) = 126 km; HiC (Hinds Cave) = 185 km; KS (Kincaid Shelter) = 85 km; LC2 [Inner Space Cavern (Laubach No. 2)] = 192 km; LC3 [Inner Space Cavern (Laubach No. 3)] = 192 km; MC (Murrah Cave) = 178 km; MiC (Miller Cave) = 100 km; MS (Montell Shelter) = 83 km; SC (Schulze Cave) = 34 km; ZC (Zesch Cave) = 74 km.