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LETTERS

Small mammal diversity loss in response to late-Pleistocene climatic change

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Communities have been shaped in numerous ways by past climatic change; this process continues today[1]. At the end of the Pleistocene epoch about 11,700 years ago, North American communities were substantially altered by the interplay of two events. The climate shifted from the cold, arid Last Glacial Maximum to the warm, mesic Holocene interglacial, causing many mammal species to shift their geographic distributions substantially[2,3]. Populations were further stressed as humans arrived on the continent[4]. The resulting megafaunal extinction event, in which 70 of the roughly 220 largest mammals in North America (32%) became extinct[5], has received much attention. However, responses of small mammals to events at the end of the Pleistocene have been much less studied, despite the sensitivity of these animals to current and future environmental change. Here we examine community changes in small mammals in northern California during the last 'natural' global warming event at the Pleistocene–Holocene transition and show that even though no small mammals in the local community became extinct, species losses and gains, combined with changes in abundance, caused declines in both the evenness and richness of communities. Modern mammalian communities are thus depauperate not only as a result of megafaunal extinctions at the end of the Pleistocene but also because of diversity loss among small mammals. Our results suggest that across future landscapes there will be some unanticipated effects of global change on diversity: restructuring of small mammal communities, significant loss of richness, and perhaps the rising dominance of native 'weedy' species.

Mammal communities that reassembled after the end-Pleistocene extinctions now face new threats of species extinction and reorganization because of similar events—intense human influence coupled with a rapidly warming climate. Understanding how these species and communities responded to past environmental change is fundamental to advancing our understanding of responses to future change. Most research on small-mammal response to end-Pleistocene environmental change has focused on the responses of individual species and the resulting formation of no-analogue communities[2,3]. However, changes to the diversity and structure of local communities are also of interest because of their roles in ecosystem function[6]. Discerning prehistoric local community response has been hampered by the paucity of well-dated fossil deposits that continuously span the Pleistocene–Holocene transition to the present and include the entire suite of extant mammalian taxa through that time[7]. Here we present data from a new, well-dated fossil excavation in northern California (Samwell Cave Popcorn Dome (SCPD); Fig. 1, Supplementary Fig. 1 and Supplementary Tables 1–3) and examine the effects of changing climate on the diversity and structure of local small mammal communities since the Last Glacial Maximum (LGM).

Two complementary diversity metrics—evenness and richness—indicate that Holocene small-mammal communities were significantly less diverse than Pleistocene communities, with two turnover pulses in the latest Pleistocene contributing to the diversity decline (Fig. 2). The pattern and timing of diversity loss is clearest in the 26% decrease in evenness (Fig. 2a and Supplementary Table 4). Evenness dropped relatively rapidly 15,000–12,000 calibrated years before present (cal yr BP). Pleistocene communities were significantly more even than Holocene communities, with fewer rare taxa. Evenness is a measure of the relative dominance of different species within a community; because decline in abundance precedes extinction, and evenness metrics incorporate abundance, evenness may be a more sensitive indicator of community change than richness. Further, evenness may confer functional stability on communities, because it has been shown to be a predictor of community persistence under environmental stress[8].

All taxa present at SCPD during the late Pleistocene still exist today in the broader species pool in northern California; the major changes in this system over the past 20,000 years are due to abundance changes within the community rather than to taxonomic loss. Despite this, richness in the local small-mammal community declined from 12 to 8

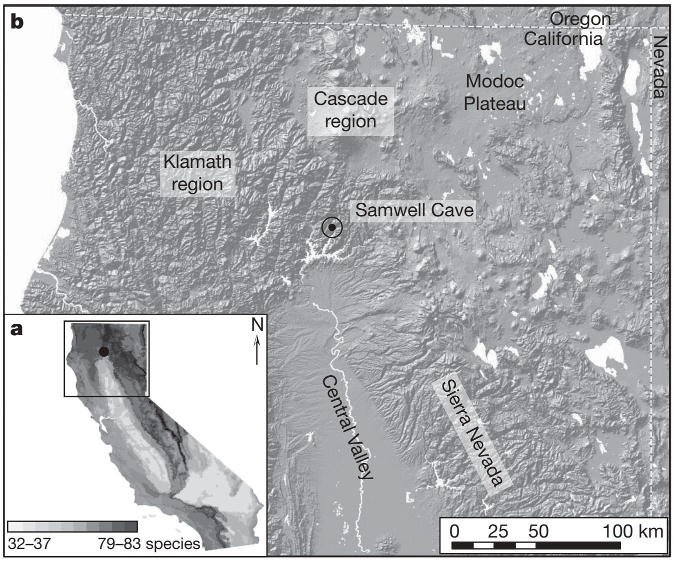

Figure 1 | Location map. a, Modern mammal species richness in California (see the California Department of Fish and Game website, http://www.dfg.ca.gov/biogeodata/cwhr/), with low richness shown in lighter grey and high richness in darker grey. The filled circle indicates the location of Samwell Cave. **b,** Enlarged map of the boxed region in **a** showing the location of Samwell Cave (filled black point) with the approximate collection radius associated with the fossil deposit (Supplementary Discussion) indicated by the open black circle around the point. Major biogeographic regions surrounding the cave are indicated.

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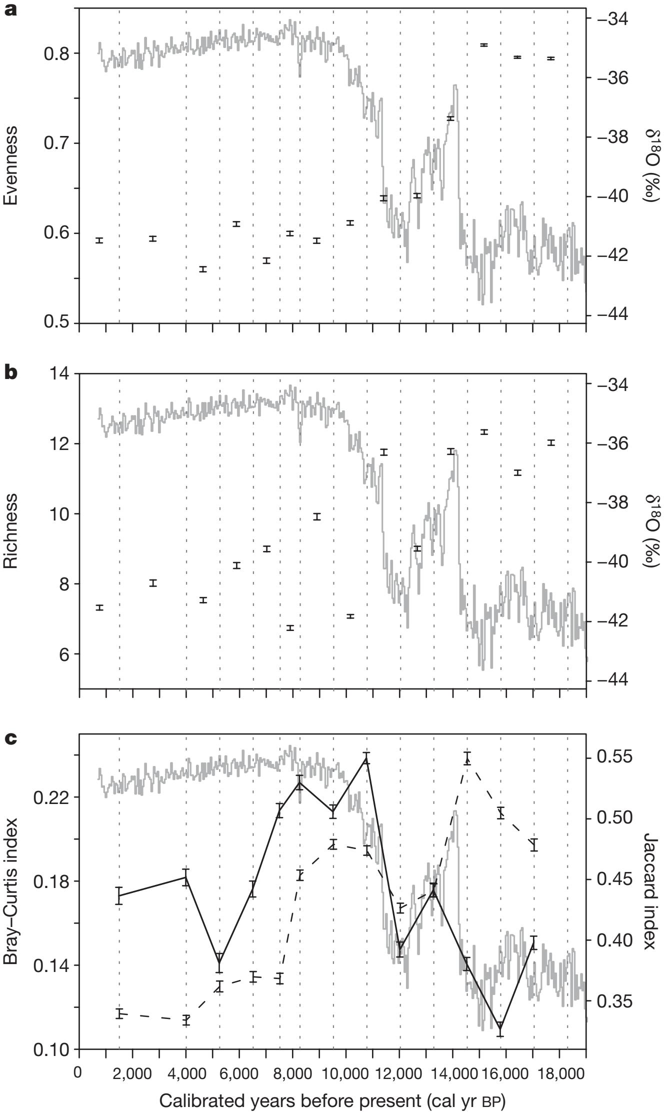

Figure 2 | Diversity through time based on standardized abundance data from 1,000 subsamples at $n = 132$. **a**, Evenness; **b**, richness; **c**, turnover (dotted line, Bray–Curtis index; solid line, Jaccard index). Lines connecting points in **c** are for comparison purposes only. Higher turnover values indicate greater differences between communities over time (Supplementary Discussion). On all figures the light grey curve indicates a temperature proxy, δ^{18}O from the North Greenland Ice Core Project ice-core record[20], expressed in parts per thousand with respect to Vienna Standard Mean Ocean Water. Vertical dotted lines indicate SCPD level boundaries. Error bars indicate 95% confidence intervals.

taxa across the Pleistocene–Holocene transition: a 32% loss (Fig. 2b, Supplementary Table 4 and Supplementary Fig. 2). This was partly due to the local extirpation of two species: *Thomomys* cf. *mazama* and *Aplodontia rufa*. The remainder of the decline in richness was explained by rare taxa (such as *Spermophilus lateralis*, *Tamias* spp. and *Arborimus albipes*), which were persistently present during the late Pleistocene but intermittently present during the Holocene epoch. Significant taxonomic loss from the local community mirrors findings of Holocene small-mammal diversity loss elsewhere in North America[9–11] and across previous glacial–interglacial transitions[12]. Thus, the local SCPD fauna may be broadly representative of small-mammal diversity across this period.

Two pulses of community turnover shaped the ecological transition from Pleistocene to Holocene communities in northern California (Fig. 2c, Supplementary Fig. 3 and Supplementary Discussion). The initial pulse, detected between 15,000 and 14,000 cal yr BP, was characterized primarily by changes in abundances of small mammals rather than local extirpations. A second period of high turnover, from 11,000 to 7,500 cal yr BP, was characterized by both changing abundances and extirpations. Community turnover was exemplified by within-genus faunal turnover in the gophers (*Thomomys*). One species (*Thomomys* cf. *mazama*) was abundant but declining in the late Pleistocene, whereas *Thomomys bottae* showed the opposite trend: it increased in abundance in the early Holocene and now is the only gopher present locally (Supplementary Fig. 2b).

These data demonstrate that local small-mammal communities changed substantially at the Pleistocene–Holocene transition, and effects of these changes linger in contemporary mammal communities. Small mammals are generally perceived to be impervious to extinction risk because of their relatively high fecundities, local densities and population growth rates. However, the magnitude of diversity loss and turnover indicates that although they may be resistant to complete extinction, they are highly sensitive to environmental change in unexpected ways. Perturbations in the small-mammal community may in turn affect ecosystem function because small mammals have important roles within ecosystems[13,14], for example in soil aeration, seed dispersal, mycorrhizal dispersal and as a prey base.

Both the timing and character of faunal changes suggest that climate was the primary driver of the diversity changes. Declines in both evenness and richness are significantly negatively correlated with climatic changes associated with the glacial–interglacial transition (evenness, $r = -0.903$; null interval -0.5696 to 0.5037; richness, $r = -0.7691$; null interval -0.5392 to 0.5207). The small-mammal community was highly even and taxonomically rich during the cold, arid Pleistocene climates but less so during the warmer Holocene climates. Evenness declined sharply with the very rapid warming of the Bølling–Allerød period[15], coincident with the first turnover pulse (Fig. 2). In addition, *Aplodontia rufa* and *Thomomys* cf. *mazama* completely disappeared from the cave deposits during the late Pleistocene and early Holocene. Today, both are found regionally in cooler environs than are present at Samwell Cave, implying they tracked cool climates as the region warmed after the LGM. Finally, turnover within gophers is consistent with the different ecological niches inhabited by the two species. *Thomomys* cf. *mazama*, dominant in the cooler Pleistocene, has a more northerly distribution and locally inhabits higher-elevation localities than *Thomomys bottae*, which persisted through the warmer Holocene.

One intriguing aspect of these small mammal diversity dynamics is the role of deer mice (*Peromyscus* spp.). Much of the decline in evenness during the late Pleistocene was driven by a doubling in *Peromyscus* abundance from 16,000 to 13,000 cal yr BP, leading to their numerical dominance of the modern small mammal community (Supplementary Figs 2a and 3). In general, deer mice are habitat generalists with high reproductive rates and broad climatic tolerances[16]. Among small mammals, they have some of the lowest habitat fidelity and are usually the first species to colonize disturbed areas[17]. That only this animal, the most generalist of North American small mammals, showed such startling increases in abundance during a period of rapid climatic change suggests that species tolerant of rapid habitat change and disturbance may have been favoured across the transition. *Peromyscus* may also be expanding across present landscapes as a result of anthropogenic climatic change[18]. Recent range and abundance shifts are tied to warming climates: a species with a more southerly range increased markedly in abundance, possibly owing to the earlier arrival of spring over the past century. At least two species currently occur in the region surrounding Samwell Cave (Supplementary Table 5), one of which is near its northern range limit, suggesting that similar dynamics might have been operating. An increase in deer mice is thus consistent with both warming and rapid habitat change in the latest Pleistocene (Supplementary Discussion).

How did the Pleistocene–Holocene climatic transition drive changes to small-mammal communities? Our data indicate several complementary mechanisms. Diversity decline may have been a direct effect of the general transition from a cooler glacial to warmer interglacial climate and corresponding habitat change in this area. Mammal diversity is indeed lower in more southerly, warmer climates in this region (for example the Central Valley), counter to continental patterns (Fig. 1). In addition, much of the decline in diversity at SCPD was a consequence of loss of mammals that prefer cool and mesic forests, which were not replaced by mammals from warmer habitats. The absence of small-mammal immigrants from an outside species pool is consistent with the indirect effects of constant or decreasing geographic-range sizes of small mammals since the Pleistocene[19]. Other sites throughout North America also showed lower richness during the Holocene[10], and local signatures of community change are mirrored by regional patterns, which also demonstrate a decline in small mammals since the Pleistocene[11]. Finally, decrease in diversity may have been catalysed by the rapidly oscillating climates at the Pleistocene–Holocene transition[20] such that some species were not able to track the rapid rates of climate and subsequent habitat change and became locally extirpated.

Although it is most parsimonious to attribute the direct and/or indirect effects of climatic change as the driver of diversity loss in small mammals, other factors could have influenced small-mammal communities. For example, extinction of the northern California megafaunal community may have had an impact on the small-mammal community through altered predation pressures[21], species interactions[22] and/or vegetation structure[23]. Final megafaunal extinction in the continental United States occurred between 13,350 and 11,500 cal yr BP (ref. 5), well after evenness started declining sharply at SCPD at about 15,000 cal yr BP. However, megafauna in some parts of North America may have been functionally lost from ecosystems earlier[23], indicating that substantial changes to species interactions were already affecting mammal communities. Small mammals were also probably responding to changes in vegetation, mediated through climatic changes and/or megaherbivore decline. However, in eastern North America, compositionally novel plant communities appeared at about 13,500 cal yr BP, after the megafaunal decline[23]. If the timing of vegetation changes was similar in the west, they occurred after diversity largely declined at SCPD. Human impacts were also unlikely to be driving diversity decline in small mammals. Establishment of human populations south of the Cordilleran ice sheet probably occurred after 16,600 cal yr BP (ref. 4), with founding populations small[24] until closer to 13,000 cal yr BP (ref. 25). All evidence of human use of Samwell Cave and the surrounding area dates to the Holocene[26,27]. Additionally, much of the richness loss was due to the local extirpation of *Aplodontia rufa* and *Thomomys* cf. *mazama*, both of which shifted their geographic distributions in accordance with their habitat and climatic associations; local extirpation of these species therefore cannot be attributed to either megafaunal loss or human impacts. Overall, although these alternative mechanisms remain possible, specific support for each is lacking and all available evidence points instead to the effects of climate on the small-mammal community.

Our data have clear implications for the future of small-mammal communities in the present time of rapidly changing climates. As climate continues to warm globally[28], our historical perspective leads us to predict further decreases in richness, increasing species turnover, and perhaps local increases in the abundance of generalist species in communities that are already more susceptible to perturbation[8]. Further exacerbating these effects are the rapidity of climatic changes, future temperatures that are expected to rise beyond the range of temperatures experienced in the evolutionary lifetimes of most mammal species[28,29], and immigration of non-native species. The synergy of these influences suggests that small-mammal responses will be even more pronounced in the future than has been observed for the past. Overall, although impending species extinctions have occasioned much concern, changes to community structure and function are also important harbingers of imperilled ecosystems.

METHODS SUMMARY

We excavated a new woodrat midden fossil deposit (SCPD) within Samwell Cave along the McCloud River drainage in northern California (Fig. 1). Radiocarbon dating by accelerator mass spectrometry (AMS) on bone collagen from specimens in the deposit (Supplementary Table 1) combined with the best-fit age–depth model indicate that the deposit is characterized by linear deposition with well-resolved temporal resolution and little evidence of bioturbation, and spans at least the past 18,000 years (Supplementary Fig. 1). We identified all mammalian taxa in the deposit, tallying both the number of identified specimens (NISP) and the minimum number of individuals (MNI) of each taxon (Supplementary Table 2). Focusing only on NISP from Lagomorpha, Rodentia and Soricomorpha, we standardized NISP ($\mathrm{NISP_s}$) to account for differences in the temporal duration and sample size of different levels of the deposit (Supplementary Table 3). We used $\mathrm{NISP_s}$ values for each species and each level to calculate evenness, richness and two indices of turnover (Bray–Curtis and Jaccard) for the small-mammal community through time. We examined the impact of individual taxa on each metric by sequentially dropping each taxon from the data set and recalculating the diversity metric (Supplementary Fig. 3). We then used temporal cross-correlation to quantify the relationship between diversity and climate. We relied on the δ^{18}O ice-core record from Greenland[20], averaging the δ^{18}O values for the period encompassed by each level of SCPD so that time-averaging of the climate and diversity records was similar (Supplementary Fig. 4). We assessed the significance of all temporal cross-correlation coefficients by means of a permutation test.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions J.L.B. planned the project, excavated the deposit, identified specimens, analysed the data and wrote the paper. J.L.M. identified *Microtus* spp., performed radiocarbon dating and wrote the paper. E.A.H. planned the project, helped excavate the deposit and wrote the paper.

Author Information Fossil specimens are deposited in the University of California Museum of Paleontology as localities V99822 and V99785. Modern specimens are deposited in the University of California Museum of Vertebrate Zoology under accession number 14590. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to J.L.B. (blois@wisc.edu).

METHODS

Excavation and specimen identification. The SCPD fossil deposit was 70 cm wide and 170 cm long and was excavated to a rock floor at 110 cm (ref. 30). No stratigraphic breaks in the sediment were obvious and there was minimal evidence of bioturbation, so we excavated the deposit in roughly 5-cm intervals. The overall volume of excavated material totalled 1.11 m^3 but decreased substantially below 75 cm. All analyses focused on the top 14 levels (levels e1 to e8b). Sediment was wet-sieved and then dried in the field with a nested series of five mesh sizes to remove organic detritus ($4\ \text{mesh} = 0.635 \times 0.635\ \text{cm}^2$; $8\ \text{mesh} = 0.3175 \times 0.3175\ \text{cm}^2$; $16\ \text{mesh} = 0.159 \times 0.159\ \text{cm}^2$; $20\ \text{mesh} = 0.127 \times 0.127\ \text{cm}^2$; $30\ \text{mesh} = 0.085 \times 0.085\ \text{cm}^2$). We separated all bone from the 4-mesh and 8-mesh samples, and all teeth from the 'e-levels' for the 16-mesh samples.

Radiocarbon dating. We dated six bones from the e-levels of the deposit (Supplementary Table 1). AMS radiocarbon preparation procedures generally followed refs 31 and 32. Samples were decalcified with 0.25 N HCl to obtain collagen, which was then gelatinized at 58 °C for 16 h. Remaining solids were filtered out of the gelatin solution and the solution was then ultrafiltered to remove the 30-kDa fraction. The 30-kDa fraction was freeze-dried and graphitized for AMS analysis. Analyses were conducted at the Lawrence Livermore National Laboratory CAMS facility. Dates were calibrated with OxCal version 4.0 (refs 33, 34), using the IntCal04 (ref. 35) calibration curve.

We determined an age model by assessing the fit of the modal age of the sample with depth, using both linear and exponential models of deposition. Both deposition models provided good fits to the e-level samples (linear model: $\text{age} = 251 \times \text{depth}$, residual standard error $(\text{RSE})_{\text{df}=6} = 2901$, adjusted $R^2 = 0.92$, $P = 0.0001$, Akaike Information Criterion (AIC) = 134.4072; exponential model: $\text{age} = 43 \times \text{depth}^{1.45}$, $\text{RSE}_{\text{df}=5} = 2914$, AIC = 135.19). The linear model was slightly better, so all dates reported in subsequent analyses are based on this model (Supplementary Fig. 1).

Quantifying small-mammal community structure. We identified species to the finest taxonomic resolution possible[30] by using modern and fossil comparative specimens, the literature, ancient DNA techniques for *Thomomys* spp., and geometric morphometric discriminant analysis on lower left first molars for *Microtus* species. Identification to species was difficult because most specimens were isolated teeth; most specimens are identified at least to genus. We determined NISP and MNI for each species by using only dental elements[36] (Supplementary Table 2). MNI was calculated as the maximum number of unique teeth (considering both type and side) in a particular level; the element was not necessarily the same between levels. In all, 97% of the 3,641 specimens were terrestrial small mammals from Lagomorpha, Rodentia and Soricomorpha, so community analyses focused on these Orders only.

All our analyses rely on NISP because it is a less biased estimator of the relative importance of each taxon to the community[37]. However, NISP is correlated with MNI, both in other studies[37,38] and in our data (for example, for *Peromyscus* spp. $r = 0.9589$ and $P < 0.001$; for *Neotoma* spp. $r = 0.7561$ and $P = 0.002$; for *Microtus* spp. $r = 0.8617$ and $P < 0.0001$; for *Thomomys* cf. *mazama* $r = 0.9161$ and $P < 0.001$; and for *Thomomys bottae* $r = 0.7070$ and $P = 0.005$). We standardized the raw NISP data to the lowest sample size (level e5b; $n = 132$) by randomly sampling 132 specimens from each level, in proportion to the original relative abundances of taxa within each level. We repeated the sampling routine 1,000 times and calculated the mean and 95% confidence interval for each statistic below based on the 1,000 subsamples (Supplementary Table 3). Results are similar for standardized and raw data.

We calculated evenness (probability of interspecific encounter (PIE))[39], richness (S) and two indices of turnover[40] (Bray–Curtis and Jaccard). For all diversity metrics we simply examined overlap in the 95% confidence interval of each level to quantify diversity differences between time periods because points within a time series may be serially autocorrelated, thus violating assumptions of independence of errors (autocorrelation was detected for PIE (correlation between the error at time t and at time $t - 1$; $r = 0.5571$, $P = 0.048$) but not for S ($r = -0.5064$, $P = 0.0774$)). We also present averages for each general time period (Supplementary Table 4).

Correlations with climate. To test correlations between climate and diversity, we performed temporal cross-correlation. Because autocorrelation within each series precludes traditional significance testing, we performed a permutation test to calculate a null distribution representing 95% of the correlation values under an expectation of no correlation between the two series. To do this, we held one time series stationary, randomly reshuffled the values in the second time series, and recalculated the cross-correlation coefficient between the two series. We repeated the procedure 1,000 times. Cross-correlation coefficients outside the null interval were considered significant.

We first examined the correlation between the δ^{18}O ice-core record from Greenland[20] and reconstructed sea surface temperatures from a site off the northern California coast that spans the past 14,900 years (ref. 41) by linearly interpolating climate values between sampling points and resampling each curve at the same 100-year intervals. The two climate records were significantly correlated ($r = 0.6386$, null interval -0.1602 to 0.1741), so all subsequent analyses relied on the longer Greenland core. To ensure that time-averaging of the climate and diversity records was similar, we averaged all δ^{18}O values for the period encompassed by each level of SCPD. We also calculated alternative climate values by sampling the δ^{18}O record at the midpoint of each level and then examined how well each method characterized climatic changes over the last 18,000 years (Supplementary Fig. 4). Both data sets adequately characterized the transition from glacial to interglacial conditions. However, the averaged climate data tracked the Bølling–Allerød and Younger Dryas, whereas the sampled climate data only showed general Pleistocene–Holocene warming (Supplementary Fig. 4). We therefore used the averaged climate data for further analyses. We then used temporal cross-correlation to quantify the relationship between climate and diversity (evenness and richness) through time. Strongest correlations between climate and diversity were at a lag of 0. All statistical analyses were performed with R (version 2.9.2 or 2.10.1 (ref. 42)).

Mammal trapping. In 2008 we sampled the modern mammal community by live-trapping at several locations surrounding Samwell Cave to determine species presence and absence (Supplementary Table 5). No attempt to standardize or compare abundance data between the fossil and modern specimens was made. All specimens were handled in accordance with American Society of Mammalogists and Stanford University guidelines.

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