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Exceptional record of mid-Pleistocene vertebrates helps differentiate climatic from anthropogenic ecosystem perturbations



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Abstract

Mid-Pleistocene vertebrates in North America are scarce but important for recognizing the ecological effects of climatic change in the absence of humans. We report on a uniquely rich mid-Pleistocene vertebrate sequence from Porcupine Cave, Colorado, which records at least 127 species and the earliest appearances of 30 mammals and birds. By analyzing >20,000 mammal fossils in relation to modern species and independent climatic proxies, we determined

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how mammal communities reacted to presumed glacial–interglacial transitions between 1,000,000 and 600,000 years ago. We conclude that climatic warming primarily affected mammals of lower trophic and size categories, in contrast to documented human impacts on higher trophic and size categories historically. Despite changes in species composition and minor changes in small-mammal species richness evident at times of climatic change, overall structural stability of mammal communities persisted >600,000 years before human impacts.

Fossil vertebrates dating to the mid-Pleistocene (Irvingtonian Age) of North America are known from <40 sites, compared to thousands of late Pleistocene sites (1–3). This has complicated attempts to understand the response to climatic change of Pleistocene communities in all but the latest slice of Quaternary time, that is, within the last ≈40,000 years (3). Specifically, it has been unclear whether the ecological changes observed at the last glacial–interglacial transition some 10,000 years ago, including decrease in species richness, assembly of contemporary community structure (3), and widespread extinction especially of large mammals (4), were driven by climatic change, introduction of humans, or some combination of both (4–7). Arguments against the influence of climatic change cite absence of pronounced ecological change in earlier glacial–interglacial transitions (4, 8); however, the paucity of fossil deposits demonstrated to span earlier glacial–interglacial transitions have prevented adequate testing of that assumption (6).

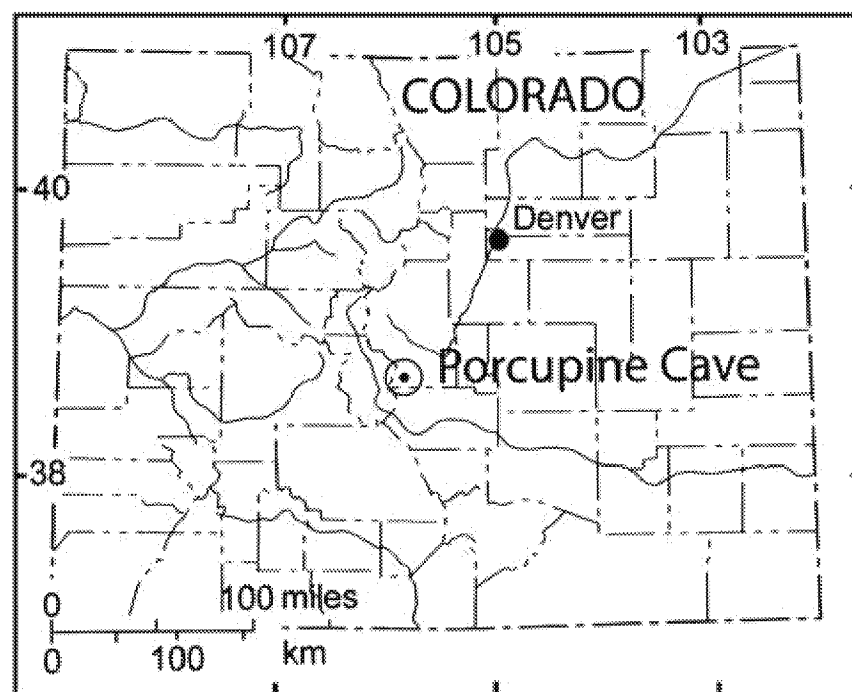
Here we provide relevant information from a richly fossiliferous, mid-Pleistocene vertebrate site, Porcupine Cave, Colorado (**Fig. 1**). We have two goals. First, we address whether mid-Pleistocene communities resembled late Pleistocene ones (3–9) in their adjustments at times of climatic change, as a way to test for the relative influence of humans versus climate in the late Pleistocene. This test is possible because inferred mid-Pleistocene glacial–interglacial transitions at our study site predated human arrival by at least 600,000 years. Second, we compare the mid-Pleistocene and contemporary communities to assess how multiple perturbations through hundreds of thousands of years may have affected community structure. Our metrics for characterizing and comparing communities include taxonomic composition and mammalian species richness within various size and trophic categories.



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Fig. 1.

Location of Porcupine Cave (small black dot) within Colorado. Circle shows 12.5-km radius around the cave. Base map is from ref. 16.

Materials and Methods

Study Site. Porcupine Cave (10–12) is located at 2,900-m elevation in the Colorado Rocky Mountains (**Fig. 1**). We concentrate on fossils from two of the 26 localities known in the cave, the Pit Sequence and the Badger Room.

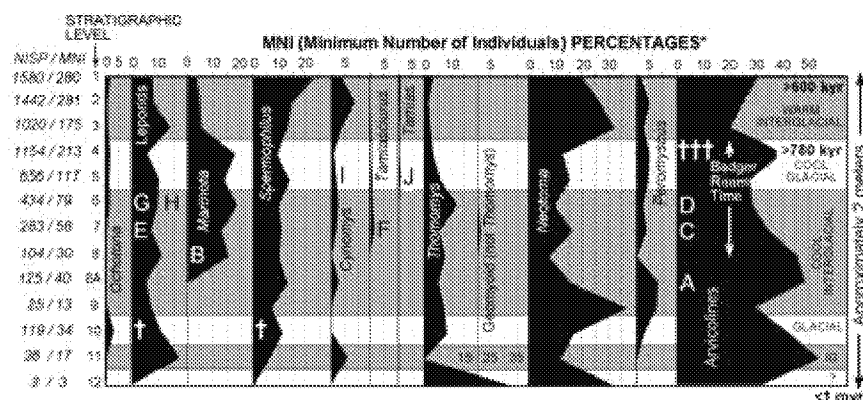
The Pit Sequence (University of California Museum of Paleontology location V93173), diagrammed in **Fig. 2**, is 2 m thick and includes 13 fossiliferous stratigraphic levels inferred to represent two glacial–interglacial transitions. Each level varies in thickness laterally (**11, 12**); for ease of presentation, **Fig. 2** spaces stratigraphic levels at regular intervals. The Pit produced

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7,724 identified fossils representing at least 1,402 individual mammals. Bones accumulated primarily from wood rats (*Neotoma*) dragging in bone-laden raptor pellets and carnivore scat (11, 12).



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Fig. 2.

Relative percentages of small-mammal taxa (rodents and lagomorphs) through the Porcupine Cave Pit Sequence of Irvingtonian age. Inferred immigration events are indicated by letters (A, B, C, etc.), and extinctions are indicated by daggers. Within each genus or subfamily, multiple species are included (ref. 11 and supporting information). See text for names of taxa involved in immigrations and extinctions. The Badger Room locality correlates to somewhere between levels 4 and 8 in the Pit Sequence. Inferred climatic intervals are shown as gray for interglacials and white for glacials. Asterisk indicates the percentage of total MNI per level for all taxa shown on the diagram. Sample sizes per level are listed at the left. NISP, number of identified specimens; MNI, minimum number of individual animals.

The Badger Room locality (University of California Museum of Paleontology location V93176) is a nonstratified sample coeval with some part of the interval represented by levels 4–8 in the Pit (11), and provides a good sample of the larger mammals. It includes >13,000 identified specimens collected by mammalian carnivores such as coyotes and badgers as well as by wood rats (11).

Communities at Different Time Intervals. Fossil deposits were dated by magnetostratigraphy and biochronology (11, 12), which indicated that levels 1–13 in the Pit Sequence maximally span from 600,000 to 1,000,000 years old. Level 4 is at least 780,000 years old, and most likely dates to between 800,000 and 900,000 years old (11). Level 1 is clearly >600,000 years old, with the most robust age interpretation placing it near 800,000 years old (11).

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We combined the fauna from level 4 in the Pit Sequence with the Badger Room fauna for an older community sample (referred to as “Badger Room time”). It would not substantially change results to combine the Badger Room with any of Pit levels 5–8. Level 1 of the Pit Sequence provides a younger mid-Pleistocene community sample. It consists only of small mammals, because the large mammals are under-sampled in level 1. Our paleoclimatic interpretation (see below) assigns Badger Room time to a glacial and Pit level 1 to an interglacial.

We compared the fossil communities with contemporary communities (13) that were present near Porcupine Cave during the late 19th and early 20th centuries: (i) before recent human impacts (the “historic” sample); and (ii) after human-caused extirpations and introductions mostly during the 20th century (the “modern” sample).

Space and Time Averaging. Spatially, the Porcupine Cave fossils represent animals that lived within 8–18 km of the fossil site, inferred from the hunting range of predators that ultimately accumulated the bones and from strontium-isotope analyses of taphonomically similar deposits (11, 12, 14, 15). To obtain comparable contemporary samples, we considered the historic and modern communities to consist of species whose published ranges (13) fell within a 12.5-km radius around Porcupine Cave (Fig. 1).

Time averaging (lumping into the same assemblage animals that lived at different times) of the Porcupine Cave samples is assumed to resemble that of taphonomically similar, well dated deposits of Holocene Lamar Cave, Wyoming (14–16), where most stratigraphic levels represent a few hundred years and all are <5,000 years. We assumed that time averaging does not substantially inflate apparent species richness because, in the well dated Lamar Cave sequences, (i) time-averaging of $\approx 1,000$ years is needed to sample nearly all species in an 8-km radius (15, 16); and (ii) fossil richness values apparently increase slowly with increasingly long time averaging by the relationship $S = 1.76T^{0.27}$ (where S is species richness and T is time) for time averaging ranging up to 1,000 years (16). This means that increasing time averaging from 100 to 1,000 years would increase the small-mammal species count by five. Because in the Lamar Cave study (16) nearly all species within 8 km were represented at 1,000 years, presumably the rate of species gain slows considerably between 1,000 and 10,000 years, given no major environmental changes.

Specimen Counts. Number of identifiable specimens (NISP) and minimum number of individuals (MNI) that the specimens represent were computed by using techniques described in ref. 11. We illustrated relative abundance by using the MNI counts (Fig. 2); using NISP yields similar results.

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Species Richness. The taphonomic setting remains constant through the Pit Sequence (11, 12), and such accumulations sample with fidelity the communities they represent (14, 15). Thus, the primary sampling concern was whether the number of specimens per level was adequate to compare presence–absence data, relative abundance, and diversity across stratigraphic levels. Previous studies (11) applied rarefaction analysis (17) to the Pit Sequence and demonstrated that, for rodents and rabbits, sample size is sufficient if the number of identified specimens (NISP) is ≥ 300 . Accordingly, our conclusions about samples from the Pit Sequence rely primarily on small mammals from levels 1–8A and 10 (Fig. 2). Our conclusions about the large-mammal component draw on data from the Badger Room, where the taphonomic pathway yielded a more adequate sample of large mammals (11).

Trophic and Size Categories. Autecology of relevant species was discussed elsewhere (11) and follows standard references (18, 19). We define size categories as: small, average adult biomass < 0.5 kg; medium, 0.5 – 8.0 kg; large, > 8.0 kg (20).

Results and Discussion

Species Present. At least 127 species of amphibians, reptiles, birds, and mammals are known from Porcupine Cave, including the only occurrence of four mammal species, the earliest known occurrences of 30 species (10 mammals, 20 birds), and the earliest western USA records of four mammals. We discuss all of these in detail in ref. 11 and list them in Table 3, which is published as supporting information on the PNAS web site. Only taxa pertinent to this report are discussed below.

Paleoclimate. Interpretations were based primarily on cave sediments, which provide highly reliable proxies of glacial versus interglacial conditions (21–26). Relative percentages of ecologically sensitive mammals per stratigraphic level were consistent with the interpretations from the sediments (11, 12). The paleoclimatic inferences from Porcupine Cave agreed with those derived independently from a nearby mid-Pleistocene site, Hansen Bluff (27), located ≈ 200 km to the south.

The top of the Pit Sequence (levels 1–3) is a tan, loess-like dust, indicating a very dry time when too little moisture was available to initiate grain-to-grain cementation or deposition of flowstone or other speleothems. Warmth is indicated by the occurrence of a relatively diverse assemblage of reptiles and amphibians (11, 12), including a desert species (*Phrynosoma*, horned lizard) that does not range into the area today. From these observations, we interpret

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levels 1–3 as representing a dry, warm interglacial, and attribute the lack of speleothems to high evaporation relative to yearly precipitation. Lack of speleothem growth during interglacials due to a net precipitation deficit characterizes caves in arid climates (26).

Levels 5, 6, and 10 are composed mainly of dark brown clay pellets and lack speleothems. Formation of the clay pellets required moisture, ultimately derived from groundwater percolating through soils (22, 23), to make the clay sticky enough to accrete into pea- to marble-sized balls. Because some water had to be present as the clays accumulated, the lack of speleothems such as flowstone suggests that (i) water was frozen for much of the year (22, 23, 25), and/or (ii) vegetation cover was sparse (21, 22). Sparse vegetation decreases the amount of root respiration and microbial activity in soils, which in turn reduces CO₂ concentration in carbonate groundwater; when CO₂ in groundwater falls below a critical level, speleothems cannot form (21–23). These considerations suggest that levels 5, 6, and 10 represent relatively cold glacial times, but with more effective moisture than during deposition of inferred interglacial levels 1–3. Badger Room sediments most closely resemble those of Pit levels 5, 6, and 10.

Levels 7, 8, 8A, 9, and 11 contain lenses of flowstone interspersed with silt through pebble-sized clasts that are indurated in some places with calcareous cement. Flowstone and calcareous cement indicate abundant groundwater saturated with CO₂, which can only occur when precipitation exceeds evaporation and temperatures are above freezing for much of the year (22, 23, 25). For these reasons, flowstone deposition typically occurs during interglacials rather than during glacials (21–23, 25), especially in high montane settings (23, 25). We accordingly interpret levels 6–9 and 11 as representing relatively moist interglacial times.

Given the biostratigraphic placement of Pit level 1 near 800,000 years, the most likely correlation to the oxygen-isotope chronology is with parts of interglacial stage 19 or 21 for Pit levels 1–3, and glacial stage 20 or 22 for levels 5 and 6 (11, 28). The Hansen Bluff sequence appears to be the same age as the Porcupine Cave deposits as determined by magnetostratigraphy and biostratigraphy (27). Palynology, invertebrate paleontology, isotopic analyses, and radiometric age control provided secure correlation of Hansen Bluff to oxygen-isotope stages 20 and 21 (27, 28), as well as yielding a variety of paleoclimate proxy data. The Hansen Bluff data indicated differences in effective moisture during middle Pleistocene glacials and interglacials that resembled those we inferred from Porcupine Cave (11, 27).

Ecological Response to Mid-Pleistocene Climate Change. Our analyses focused on mammals to examine the following potential responses: changes in species composition, particularly the assembly or disaggregation of taxa that are allopatric today (so-called “no-analog assemblages”; refs 9), species richness within various higher taxa, body size, or trophic categories, and extinction.

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In the Pit Sequence, species composition changed through time. Local immigration events are probable, with *Microtus meadensis* appearing first in level 8A (A in **Fig. 2**), *Marmota* in level 8 (B in **Fig. 2**), *Microtus paroperarius* in level 7 (C in **Fig. 2**), and *Microtus* characterized by five complete triangles on the lower first molar, probably representing an extant species, in level 6 (D in **Fig. 2**). Additionally, *Brachylagus coloradoensis* and *Tamiasciurus hudsonicus* appear first in level 7 (E and F in **Fig. 2**), and *Sylvilagus* and *Lepus* appear in level 6 (G in **Fig. 2**); it is not clear whether these taxa are local immigrants because sampling issues cloud their first-appearance status in the cave. All of these potential immigration events took place within the same interglacial, but did not cluster at the same time, suggesting that the community assembled as the interglacial progressed. Taxa continued to assemble during the ensuing glacial, with *Cynomys* cf. *Cynomys leucurus* (I in **Fig. 2**) and possibly *Tamias* cf. *Tamias minimus* (J in **Fig. 2**) appearing first in level 5 (a caveat is that sampling issues may be a problem with this taxon).

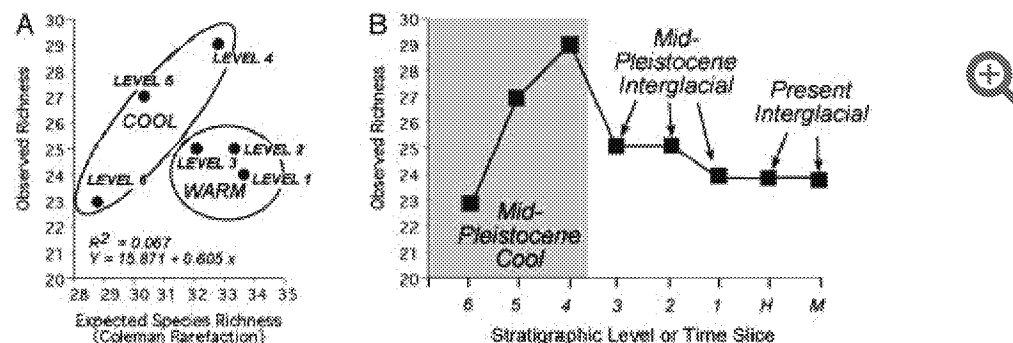
The general character of the glacial and interglacial mid-Pleistocene small-mammal community (**Fig. 2**) appears similar to the contemporary community, in which (i) arvicoline rodents are the most abundant small mammals, (ii) *Spermophilus*, *Marmota*, various leporids, and burrows of *Thomomys* are very commonly seen on the landscape, and (iii) *Cynomys*, *Tamiasciurus*, and *Tamias* are least commonly seen because patchy distribution, low abundance, or life history strategy. The high abundance of fossil *Neotoma* is consistent with expectations because their middens produced the Pit Sequence and modern *Neotoma* is often sighted in the cave. However, a pronounced difference in comparison to the contemporary fauna is the presence throughout the Pit Sequence of *Lemmiscus curtatus* and *Mictomys* sp. of the *Mictomys borealis* lineage. Today, neither of these taxa are found in the vicinity of the cave, and in fact are largely allopatric in distribution (29), with *L. curtatus* restricted primarily to the Great Basin and *M. borealis* to boreal regions. This combination of species constitutes a no-analog association, such as has been reported commonly for late Pleistocene faunas and floras (9). However, in contrast to the late Pleistocene situation, the no-analog pair at Porcupine Cave did not disassociate during either of the mid-Pleistocene glacial to interglacial transitions.

Numbers of species per genus are very similar for the level 1, historic, and modern samples (**Table 1**). Decrease in species richness of some genera occurred across the transition from glacial level 4 to interglacial level 1, the time we interpret as representing the most pronounced warming and drying. Observed richness values per level were plotted against the richness expected from rarefaction (**Fig. 3A**). R^2 for observed versus expected richness in interglacial level 6 and glacial levels 5 and 4 is 0.932. This indicates that what we interpret as a relatively slight climatic cooling at this interglacial to glacial transition had little effect on small-mammal species richness. When the upper interglacial levels 3, 2, and 1 were added to the analysis, the observed values were much lower than expected (r^2 drops to 0.067; **Fig. 3A**). The shift in

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richness from relatively cool, moist times (levels 6, 5, and 4) to the very warm, dry interglacial (levels 3, 2, and 1) is larger than the shift from level 1 to modern values (**Fig. 3B**). Decreases in small-mammal species richness also have been documented for times of late Quaternary aridity in the Bonneville Basin, Utah (30).



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Fig. 3.

Expected and observed species richness. (A) Expected species richness derived from Coleman rarefaction analysis plotted against actual species richness for stratigraphic levels of Porcupine Cave Pit Sequence that had numbers of identifiable specimens >300. The plot is for rodents and lagomorphs only. Each point represents a single stratigraphic level. Levels 6, 5, and 4 represent a climatic interval that is substantially cooler and moister than the interglacial represented by levels 3, 2, and 1. (B) Observed richness graphed as a function of time. Time proceeds from left to right; numbers indicate the stratigraphic level, H indicates historic time, and M indicates modern time as explained in *Materials and Methods*. The drop in richness from cool to interglacial times is particularly dramatic given that sample sizes are so much larger for the interglacial (see text and the sample-size listings in **Fig. 2**).

Table 1.

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Species richness of small mammals in Pit Sequence and existing fauna within 12.5 km (13) of Porcupine Cave

The deleted species that reduce richness from glacial level 4 to interglacial level 3 include three arvicolines (*Allophaiomys pliocaenicus*, *Mimomys virginianus*, *Phenacomys gryci*) plus a geomyid (*Thomomys* aff. *Thomomys bottae*). The rabbit *Aztlanolagus* has its last appearance in interglacial level 2. *Allophaiomys pliocaenicus*, *Mimomys virginianus* and *Phenacomys gryci* represent true extinctions. Likewise, the youngest records anywhere of *Hypolagus* and what is possibly an extinct morphotype of *Spermophilus* (?*Otospermophilus*) sp. (11) occur between levels 10 and 9, which is the lower glacial–interglacial transition in the Pit Sequence.

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Community Structure and Climate Change. To what extent do the faunal changes noted through the Pit Sequence indicate a shift to a new ecosystem state (31) versus minor fluctuations within a long-term dynamic equilibrium? To examine this question, we compared richness, trophic, and size structure of the mammal community during the relatively cool Badger Room time (>780,000 years), interglacial Pit level 1 (>600,000 years), historic time, and modern time. The historic and modern samples represent the interglacial in which we now live.

If ecosystem structure is stable through long periods of time, with climatic changes acting as minor perturbations that fine-tune the system but do not shift it to a new state (31), we expect little difference in richness, size, and trophic patterns between the cool-episode Badger Room time and the ensuing interglacial sample of Pit level 1. Likewise, we expect little structural difference between interglacial level 1 and the present interglacial; in this view, even though species identities change through time and through climatic changes, they fill the same roles within the ecosystem. If any of the glacial–interglacial transitions that occurred since Badger Room time shifted the ecosystem to a new state (31), we would expect clear differences in richness patterns in most taxonomic, size, and trophic levels.

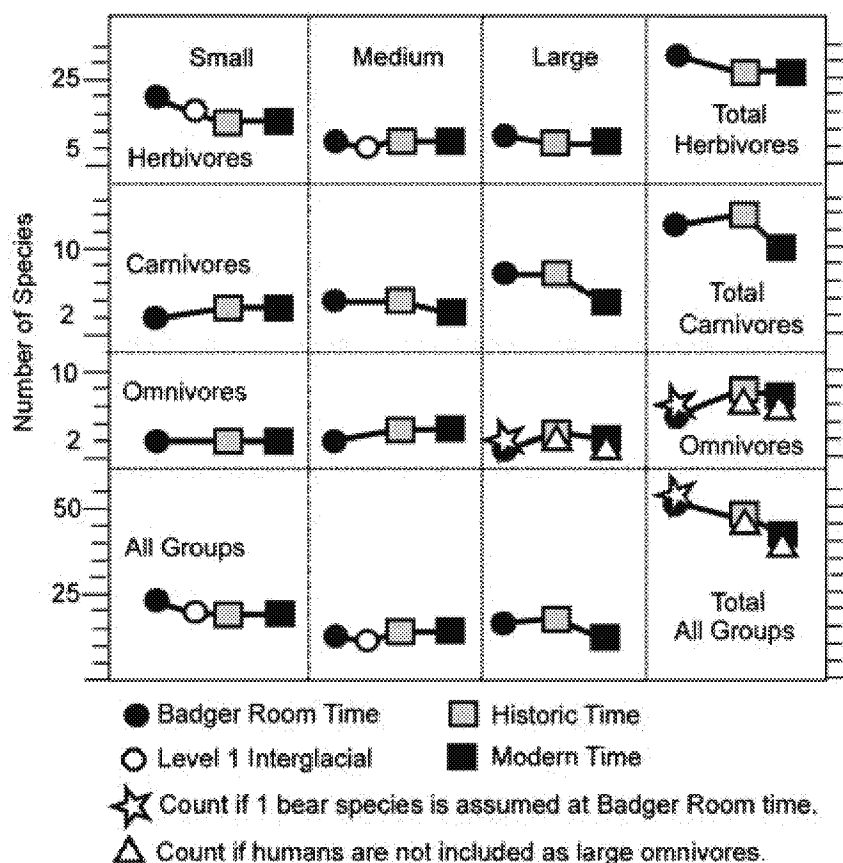
Fig. 4 and **Table 2** summarize species richness changes through time for various trophic, body-size, and taxonomic categories. The biggest change is a reduction in species of small herbivores, from 20 to 16 species, between Badger Room time and interglacial level 1 (**Fig. 4** and **Table 4**, which is published as supporting information on the PNAS web site); this results from decline in rodents and rabbits from 29 to 24 species (**Fig. 3B**). Diversity, trophic, and size patterns of small herbivores are not substantially different in the mid-Pleistocene (level 1) and present interglacials (historic and modern), which are separated by >600,000 years and at least six glacial–interglacial cycles.



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Fig. 4.

Numbers of species (vertical axis) observed in trophic and size categories (along horizontal axis) for various time intervals: Badger Room time, level 1, historic time (late 19th and early 20th centuries), and modern time (late 20th and early 21st centuries). See text for further explanation and Tables 1 and 2, ref. 11, and supporting information for data.

Table 2.

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Taxonomic richness within orders for species, genera, and families in the middle Pleistocene and current faunas

In medium-sized and large mammals, species richness within taxonomic, trophic, and size levels is remarkably similar in Badger Room time and historic time. The similarities evident in **Fig. 4** become even more striking for omnivores when it is taken into account that: (i) bears (large omnivore) are fossilized elsewhere in Porcupine Cave and conceivably were part of the fauna during Badger Room time, (ii) that humans are included in the large omnivore category for the historic and modern counts, and (iii) that procyonids (medium omnivore) are present

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today, but would have a poor chance of preservation given the taphonomy of Porcupine Cave. A notable difference in the large size category is one additional large herbivore order (Xenarthra = ground sloths) in Badger Room time.

The overall pattern suggests that, in warmest interglacials, fewer species of small herbivores are present than in cool episodes, but otherwise community structure differs little between the two climatic states. These data support inherent stability in montane mammal communities (16), with community structure and function persisting for hundreds of thousands of years despite species turnover. Within this context of long-term stability, fine-tuning of species composition and interrelationships occurs from the “bottom up,” at lower trophic and lower size levels, in response to climatic change.

In contrast are changes that percolate from the “top down,” those that occur first at the highest trophic and size levels. Such effects on species richness patterns are apparent in the decrease of medium and large carnivores from 11 historic to seven modern species (Fig. 4), which resulted locally from human activities in the last 100 years or so (11, 13). Globally, over the past century, human hunting has preferentially targeted herbivores and carnivores of largest size classes, as demonstrated by body-size distributions of mammal species on the IUCN threatened and endangered species lists (32). Such top-down changes were not evident across the studied Porcupine Cave glacial–interglacial transition. Although sampling issues still preclude tracing most large mammals through the mid-Pleistocene, the horse *Equus* and the peccary *Platygonus* persisted across mid-Pleistocene glacial–interglacial boundaries in Porcupine Cave (Tables 2 and 3), but became extinct continent-wide in the latest Pleistocene (4, 7).

The large herbivore counts remained relatively stable from mid-Pleistocene, to historic, to modern times (Fig. 4), but only because of pronounced modern human influences that included replacing native large herbivores such as bison and bighorn sheep with domestic cows and sheep. Horses, lost at the end of the Pleistocene, were reintroduced by people in historic time. Taking these domestic large herbivores into account means there has been a net loss of only one species (ground sloths). Ground sloths, like many other large herbivores and carnivores, suffered extinction on a continental scale near the end of the Pleistocene (4–8), but extinction timing is unknown locally.

Also unknown is whether such megafauna as mammoths, which immigrated into North America just slightly earlier than Badger Room time (1) and became extinct there near the end of the Pleistocene (33), were present locally. If so, the local end-Pleistocene loss of large herbivores would be more pronounced than indicated by Fig. 4. In general, such top-down losses defined the late Pleistocene megafauna extinction event (4–8, 34).

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Conclusions

Our conclusions about mammal communities are most applicable to high montane ecosystems like the one we studied. Our data suggest that montane mammal communities are stable over long periods of Quaternary time at the functional and structural levels, agreeing with other work (16). In our record, climatic change stimulated adjustments at lower size and trophic levels in the absence of humans, shown by a slight reduction in species richness and extinction of small-mammal taxa at what we interpret as a particularly pronounced mid-Pleistocene glacial–interglacial transition. However, such changes were apparently minor adjustments within a system that did not fluctuate widely through hundreds of thousands of years in numbers of species or in roles that species filled within the community, although taxonomic composition changed through time. It will be important to see whether similar long-term structural and functional stability characterizes communities in other ecological settings.

Observed 19th and 20th century human impacts seem fundamentally different from those caused by climate in our study area and globally (32, 35). Contemporary humans influence communities from the top down, as shown by loss of large carnivores and herbivores in historic time (13, 32). Climatic change affects lower size and trophic levels widely (exerting a bottom-up influence), as evidenced by our study and by effects of contemporary global warming on biota (35, 36).

Our results have implications for interpreting other past ecosystem changes. All of the bottom-up changes we identified as characteristic of mid-Pleistocene climatic change were also evident at the latest Pleistocene glacial–interglacial transition (36), as was an even more pronounced bottom-up effect: no analog small-mammal assemblages persisted through the mid-Pleistocene glacial–interglacial transitions, but disaggregated at the latest Pleistocene one. This is consistent with much previous work suggesting strong climatic influence on community reorganizations at the late Pleistocene (3, 9). However, in contrast to what we found for the middle Pleistocene, extinction concentrated in high trophic and size categories characterized the late Pleistocene. Whether this implicates humans in late Pleistocene extinctions remains a hotly debated topic (3–9).

The great similarity between the mid-Pleistocene and contemporary mammal communities around Porcupine Cave suggests that even the combined effect of climatic change and human immigration in the late Pleistocene did not permanently change local ecosystem structure from a longer-term baseline. For at least 600,000 years, the mammal community in high-elevation Colorado demonstrated structural stability that was perturbed more by people in the 19th and

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20th centuries than it was by numerous glacial–interglacial transitions. It is unclear whether the initial phases of anthropogenic perturbation began in the latest Pleistocene. The historic perturbation deleted large- and medium-sized carnivores.

Our study has some implications for the future. Global warming could result in rates of climatic change that are higher than any that have characterized the past 60 million years (36). Therefore, accelerated top-down (from ever-increasing human populations) and bottom-up (from global warming) pressures may well prevent the natural equilibration that the Porcupine Cave data and others (16) suggest has been characteristic of montane mammal communities. Should these changes come to pass, we predict they will be recognizable by changes in numbers of species in different trophic and size categories, and by overall changes in species richness that exceed those evident in our study. Thus, monitoring species richness within communities may be a powerful yet simple tool for assessing the health of target ecosystems.

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Footnotes

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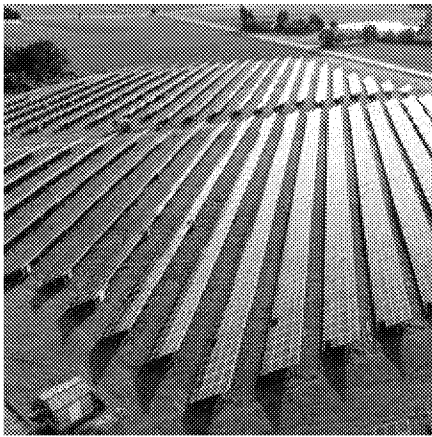
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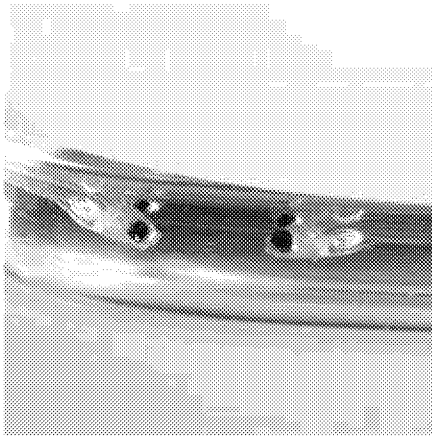
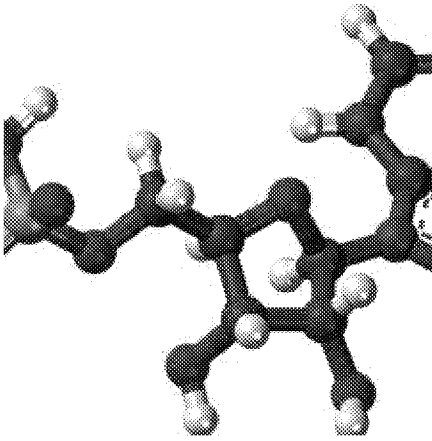
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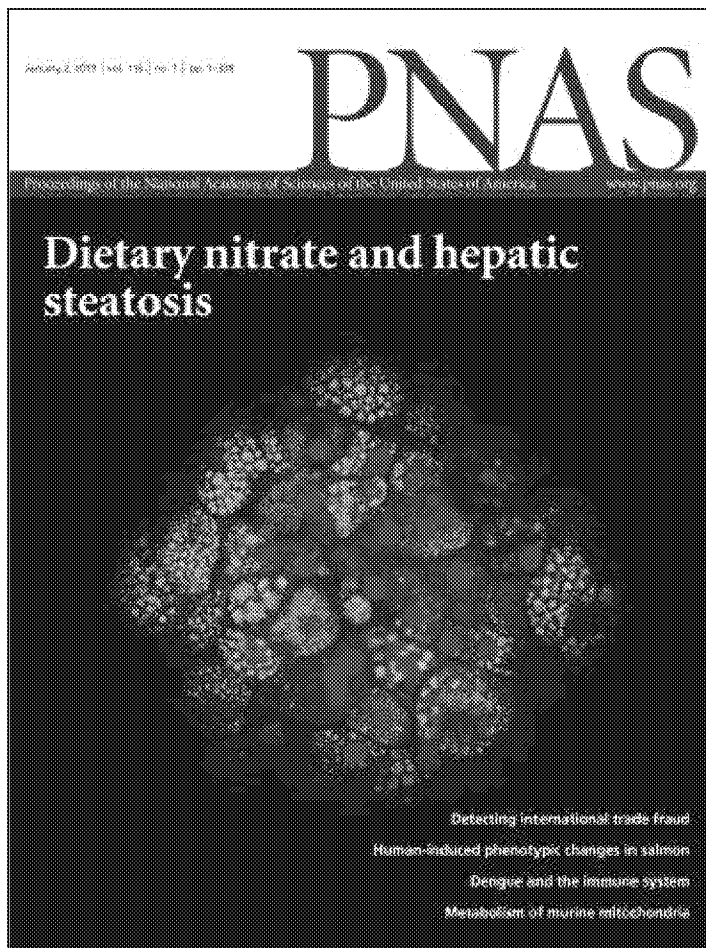
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