Microfauna relative abundance since the Late Pleistocene at Natural Trap Cave, Wyoming, U.S.A

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ABSTRACT

Microvertebrate communities have shifted and adapted to a variety of climate extremes since the Late Pleistocene, which can inform us on how modern communities might respond to similar climatic changes. Here we evaluate the microvertebrate remains from Natural Trap Cave (NTC), Wyoming, in the Western US, as an initial evaluation of how these communities responded to changes in local climate throughout the Late Quaternary. We calculated the number of identified specimens (NISP) and the minimum number of individuals (MNI) to determine relative abundance, richness, and evenness across 3 layers at the site, from the Late Pleistocene, the Middle Holocene, and the Late Holocene. Community composition was largely affected by changes in the abundances of taxa rather than local extinctions or colonizations. Evenness was highest in the arid Late Pleistocene, 23,000 cal BP and Late Holocene, approximately 2,000 to 6,000 cal BP. Shifts in evenness were primarily driven by changes in abundance of *Phrynosoma* with abundances of Lagomorpha and *Thomomys* contributing to changes within the small mammal community. Raw richness was highest in the Middle Holocene when *Cynomys* and *Perognathus* appeared in the region while standardized richness was highest in the Late Pleistocene with these differences being caused by small Late Pleistocene sample sizes. We performed a principal coordinate analysis to compare the small mammal community of NTC to three other caves with well-represented small mammal fauna from the Late Quaternary. NTC grouped closest with Samwell Cave, in California, another cave where small mammal material is collected by packrats. Across all four caves, layers generally grouped based on cave affinity. However, Samwell and NTC layers were grouped by age rather than cave identity. Further comparison between these two caves found that evenness decreased similarly from the Late Pleistocene to the Holocene.

1. Introduction

Throughout time, biotic communities have had to adapt to changing climate or risk local or complete extinction. Since the Last Glacial Maximum (LGM; 21 kya) (Otto-Bliesner et al., 2006), there has been a relatively steady increase in global temperature into the Holocene. The Holocene of North America consisted of periods of cooling at 8.2 ka, and prolonged warming and drying across many mid/low latitude regions across the continent, which has also been documented from South America, the Middle East, China, and Africa at 4.2 ka (Booth et al., 2006; Grayson, 2000; Harbert and Nixon, 2018; Shuman and Marsicek, 2016; Walker et al., 2012). Millennial-scale climate variability during the Holocene in North America is on the order of $\pm 0.2\,^\circ C$ (Viau et al., 2006).

However, anthropogenically-driven climate change has created an even more rapid increase in global mean temperature, outpacing the speeds at which many plants and animals can shift ranges due to slow dispersal speeds and human impacts on landscape connectivity (McGuire et al., 2016; Schloss et al., 2012; Viau et al., 2006). By exploring the fossil record, we can understand how past climate-species dynamics have played out on the landscape, helping to establish effective strategies for preserving species' biodiversity on this rapidly changing planet (Barnosky et al., 2017; Dietl et al., 2015; McGuire and Davis, 2014).

At any given location, climate dynamics affect the identities and abundances of the local species (Monte-Luna et al., 2004; Prugh et al., 2018). Bottom-up and top-down trophic effects can both, directly and indirectly, affect a community, as small effects of climate change

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culminate into broader ecosystem changes (Berteaux et al., 2006). Microvertebrates, such as rodents, lagomorphs, and reptiles, are very closely tied to their environment and are particularly sensitive to local climate changes. These groups have small home ranges and limited dispersal abilities compared to larger megafauna (Sandel et al., 2011; Schloss et al., 2012). However, microvertebrates that can survive environmental changes respond relatively quickly, and *in situ*, due to their short generation times and home range sizes (Samuels and Hopkins, 2017). Increased sensitivity of this group means that they are excellent thermometers of local environmental changes (McGuire, 2010; McGuire and Lauer, 2020; Schap et al., 2021). Patterns of these past community changes are then recorded in the fossil record and can be used to better understand these processes in modern and future communities. Microfauna, and particularly small mammals, play an integral role in their environment influencing vegetation, altering the landscape, and acting as prey for a variety of predators (Sieg, 1987). Any alteration to these groups could cause cascading effects throughout their local ecosystem. Therefore, it is critical to focus on how these communities might respond to modern climate change in an effort to prevent potential ecosystem collapse.

By examining the changing composition of microvertebrate communities, past studies have been able to evaluate important ecological principles. The western United States contains multiple well-sampled fossil cave localities allowing for community comparison across space and time. Previous work has been conducted on how small mammals have responded to events such as the megafaunal extinction and Holocene climate changes (Blois et al., 2010; Grayson, 2000; Terry et al., 2011). For example, an examination of the relative abundances of small mammals at Samwell Cave, California demonstrated a decrease in community evenness and a renewed dominance by generalist species (Blois et al., 2010). This dramatic change in community composition corresponded with the major climate and habitat change that resulted from the last glacial-interglacial (Pleistocene-Holocene) transition (Blois et al., 2010). At Lamar Cave, Wyoming, researchers found that local small mammal community compositions shifted rapidly depending on whether xeric (dry) or mesic (moderate) conditions dominated (Hadly, 1996), indicating that microvertebrate communities are quite sensitive to changing precipitation levels. Likewise, when xeric conditions dominated at sites throughout the Great Basin in the western U.S., granivorous mammals thrived (Terry et al., 2011). Even now, we continue to see changes in small mammal community composition in response to recent changes in precipitation (Terry et al., 2011). In these studies and others, changes in the relative abundances of small mammals characterize community responses to local environmental change rather than extirpations or introductions of new species (Blois et al., 2010; Hadly, 1996; Terry, 2010a, 2010b; Terry et al., 2011; Terry and Rowe, 2015). While there are a handful of well-studied and informative cave localities, they are still relatively rare and each new locality brings a suite of new information on how species respond to environmental changes.

By comparing microvertebrate communities and their responses to environmental changes across caves, we can gain a stronger, more integrated understanding of how these communities change in concert with changing climates across the landscape. Natural Trap Cave (NTC), Wyoming contains an exciting and unique microvertebrate deposit with incredible preservation across well-stratified sediments. NTC also provides the potential to study many aspects of not only the animals of the site but the surrounding environment through pollen analyses, stable isotope geochemistry, and aDNA to incorporate comparisons of local community ecology with environmental change (Grass, this issue; Higgins, this issue; Lovelace et al., this issue; McGuire et al., this issue; Minckley and Clementz, this issue; Mitchell et al., this issue; Redman, this issue; Spencer and Scott, this issue). Here we describe the relative abundances of microvertebrate taxa—including reptiles, mammals, and birds—from approximately 23 ka to 2.5 ka. By using multiple groups of diverse taxa within the community, we can observe the responses of a full set of direct competitors. We then compare the small mammal data to previously studied sites of similar age to place NTC in environmental context, and evaluate whether it experiences similar types of shifts in richness, evenness, and composition of taxa as observed at other rich cave sites of North America. It is predicted that during more arid periods, there will be an increase in evenness of the community, as has been seen in past communities (Blois et al., 2010) and modern communities following drought events (Prugh et al., 2018).

2. Regional setting

Natural Trap Cave is a 24.5 m (80 ft) deep karst-sinkhole, with a 7.6 × 4 m (25 × 13 ft) diameter cave entrance, located at the base of the Bighorn Mountain range in Big Horn County, north-central Wyoming (Meachen et al., 2016; Wang, 1988; Wang and Martin, 1993). As the cave is on a plateau, it acted as a natural trap for larger animals who could not see the cave entrance. However, the accumulation of fossils from small animals are mostly the result of packrat middens (McGuire et al., this issue). Located south of the corridor between the Cordilleran and Laurentide ice sheets, the cave is able to record mammal movements from Beringia into the continental United States (Heintzman et al., 2017; Meachen et al., 2016; Shapiro et al., 2004; Wang et al., 2021) during the Late Pleistocene, providing a unique understanding of these events. Excavation of the site began in the 1970s to the 80s and then picked up again in 2014–2017 (Meachen et al., In Review). Fossils in the cave date back roughly 130,000 ka to the present with a gap in sedimentation spanning part of the Late Pleistocene to the Middle Holocene from approximately 20,000 to 8,000 ka (Lovelace et al., this issue). The cave has preserved complex, but well-defined strata with varying types of matrix (Lovelace et al., this issue; Martin and Gilbert, 1978). Strata containing the densest concentrations of microfossils are discrete from those described elsewhere, as they formed primarily as the result of packrat midden accumulation, being located just below a high ledge containing a long-standing packrat nest (McGuire et al., this issue).

Previous examination of the Late Pleistocene microvertebrates, including pika, and cursorial, arid, open-habitat-adapted large mammal fauna, like horses and the American lion, of the site, has pointed to NTC having been located within a steppe tundra (Martin and Gilbert, 1978; Meachen et al., 2016; Redman, this issue). Most work at NTC has been done examining the large mammals of the site and highlighted how important NTC is in understanding the migration of these groups as well as the relatedness of these fossil species to their modern descendants (Chorn et al., 1988; Martin and Gilbert, 1978; Meachen et al., 2016; Redman, this issue; Wang, 1988). However, some work has been done to identify some of the small mammals at the cave and what their presence means for the local environment at the time or across their distribution (Hafner, 1993; Martin et al., 1979) and evaluating the taphonomy of the cave (McGuire et al., this issue). With the abundance of microfaunal remains, there are still many questions about the site to be answered, with this study focusing on how the diversity of the microvertebrate community changed over the last 20,000 years. All microvertebrates identified from the cave thus far are extant today, making NTC a useful and informative site to study potential similarities between how these groups shifted in response to climate, and how they might respond in the future.

3. Material and methods

Fossils used in this study were excavated during the 2014 field season. The north wall of the cave was excavated in one-foot (0.3 m) increments resulting in layers we call "1 foot down", "2 foot down", and "3 foot down". Sediment is composed of a brown (5 YR 5/4) clay-rich silt containing some highly weathered pebble-to medium-gravel-sized breakdown blocks with a chalky appearance. Sediment was screen washed at the site using stacked sieves of 10 and 20 mesh. Microfossils were then picked and sorted at Georgia Institute of Technology in part

through a citizen science effort called "Fossil Fridays" and by experts, including the authors of this paper and a previous lab technician. Material from the finer screen size has not yet been fully sorted and therefore is not analyzed in this study, but will be used in future studies. As a result, two Chiropteran teeth and a Soricidae dentary and upper fourth premolar (P4) found within the finer screen material were excluded from this study. Several anuran limbs and pelvic bones and myriad fish bones were also excluded from this study because they were most likely brought in by birds and were not part of the local community.

3.1. Radiocarbon dating of layers

Eight fossils from the three layers were radiocarbon dated at Lawrence Livermore National Laboratory CAMS facility (LLNL; following Brown et al., 1988; Ramsey et al., 2004) and calibrated using OxCal v.4.4.3 using the IntCal20 calibration curve (Ramsey, 2009; Reimer, 2020) at the 95% confidence interval. For the 1-foot-down layer, cranial and indeterminant bone fragments were sampled to determine these ages. Femur, humerus, and rib fragments were sampled to determine 2-foot-down layer ages. A femur fragment and a *Panthera atrox* metacarpal V, which was run for mtDNA, were used to determine 3-foot-down layer ages. For more information on radiocarbon dating methods see Lovelace et al. (this issue). An estimated age range for each layer was created by taking the youngest calibrated radiocarbon date and subtracting the uncertainty and taking the oldest calibrated radiocarbon date and adding the uncertainty.

3.2. Paleoclimate

We compiled local paleoclimate corresponding to each layer using a combination of medium-resolution Hadley Centre coupled model, version 3 (HadCM3) climate simulations over the last 120,000 years, and high-resolution Hadley Centre global atmospheric model (HadAM3H) simulations over the last 24,000 years at 0.5 × 0.5-degree resolution at NTC (Beyer et al., 2020). Climate variables examined include mean annual temperature and mean annual precipitation. We extracted local climate values from the global circulation model every 1,000 years for the 1 foot down and 2-foot-down layers and 2,000 years for the 3-foot-down layer based on the available temporal resolution of the dataset, and averaged temperatures and precipitations across each stratigraphic layer, as determined by the calibrated radiocarbon dates (Table 1).

3.3. MNI comparisons across NTC strata

Given differential bone and tooth numbers in reptiles, birds, and mammals, Number of Identified Specimens (NISP) values necessarily compare an unequal number of elements (e.g., two dentaries for reptiles compared to 12 or more individual teeth for small mammals). Therefore, we used the Minimum Number of Individuals (MNI) instead of NISP for analyses of the full communities of NTC (Fig. 1a and b; Tables S1 and S2). We used a single tooth, sided either right or left, to determine the MNI of each small mammal group. If the same tooth was not found for that group across layers, a different tooth was used. Additionally, if there were two options for teeth to count in a taxon, the option with the higher

Table 1
Mean Annual Temperate and Mean Annual Precipitation estimates for each layer of NTC using HadCM3 and HadAM3H paleoclimate data.

	Mean Annual	Mean Annual	Mean Annual	Mean Annual
	Temp (°C)	Temp Std	Precip (mm)	Precip Std
1 foot down	6.56	0.20	230.36	23.09
2 foot down	6.23	0.10	210.24	15.11
3 foot down	−4.27	0.23	145.69	48.19

number was counted. Therefore, the tooth used may differ between layers. For lagomorphs, we use the lower third premolar (p3) or upper second premolar (P2). *Lemmiscus* was determined using upper third molars (M3). We identify *Microtus*, *Neotoma*, and *Peromyscus* from lower first molars (m1) except for the 2-foot-down layer, where *Neotoma* was determined from the upper first molar (M1). *Thomomys* was determined from the lower fourth premolar (p4). Sciurids (*Marmota*, *Tamias*, and *Cynomys*) were determined from P4s or p4s in the 1-foot-down layer, M1s or M3s in the 2-foot-down layer, and M3s from the 3-foot-down layer. For reptiles, we used a single side of the dentary, depending on which had a larger sample size. Aves were counted with right or left tibiotarsi. A full list of field numbers for all specimens used can be found in the appendix.

To account for differences in sample size and time averaging between layers, we standardized MNI to the layer with the smallest sample size, which was the 3-foot-down layer. The MNI of our 3-foot-down layer was 29 individuals. This standardization follows methods in Blois et al. (2010). We resampled each community for 1,000 iterations. Standardized values were used in all analyses.

Community diversity was examined by evaluating changes in evenness and richness of taxonomic groups across the three layers (Table 2). For each layer, richness was calculated as the total number of taxonomic groups per layer, and evenness was calculated using Shannon evenness: Shannon Diversity Index divided by the log of the species richness. This was calculated using raw MNI values at each layer and then also using standardized MNI which can be found in Table 2.

3.4. Comparisons with other caves

To place NTC communities in a broader context, we compared the small mammal community to those of Samwell Cave, Homestead Cave, and Two Ledges Chamber (Fig. S1). We used only the NISP of the small mammal community because these data were reported consistently across these sites (Blois et al., 2010; Terry et al., 2011). Samwell Cave is located in California in a dense forest on the edge of Lake Shasta in the McCloud Limestone at 460 m elevation. The sedimentation of the cave consists of breccia overlain by flowstone and covered in gravel with a thin layer of reddish clay on top (Feranec et al., 2007). Two Ledges Chamber is located in Nevada at 1244 m in elevation, and Homestead Cave is located in Utah at 1406 m in elevation. Both caves are in desert shrub habitats of the Great Basin in the Western United States and were formed through wave action of Pleistocene pluvial lakes that later became roosts for owls (Terry et al., 2011). NISP values were standardized to the layer with the smallest sample size within each cave, following the methods for our MNI values (33 specimens for NTC, 60 specimens for Two Ledges Chamber, 154 specimens for Homestead Cave, and 132 specimens for Samwell Cave). We excluded non-mammals and any mammal actively excluded from one of the caves, notably bats and shrews (or chiropterans and soricids), and used genus level identifications so that they were uniform across caves. We used the total number of identifiable teeth to determine NISP for small mammals. Deciduous teeth, incisors, and fragmented teeth were excluded from analyses.

Richness and evenness were compiled for each published layer from Samwell Cave, Homestead Cave, and Two Ledges Chamber for comparison with NTC richness and evenness (Blois et al., 2010; Terry et al., 2011). Additionally, a principal coordinate analysis (PCoA) using the Bray-Curtis Dissimilarity metric was performed to gain a visual representation of which small mammal communities across the caves were most similar (Fig. 2). Since Homestead Cave and Two Ledges Chamber only reported taxa <500 g due to size biases from owl pellet collection of small mammal taxa (Terry et al., 2011; Terry and Rowe, 2015), we excluded taxa >500 g from NTC and Samwell Cave for the PCoA analysis. The changes in richness and evenness were then compared for NTC and Samwell Cave, which were most similar (Fig. 3). Since comparisons were not being made to Homestead Cave and Two Ledges Chamber for
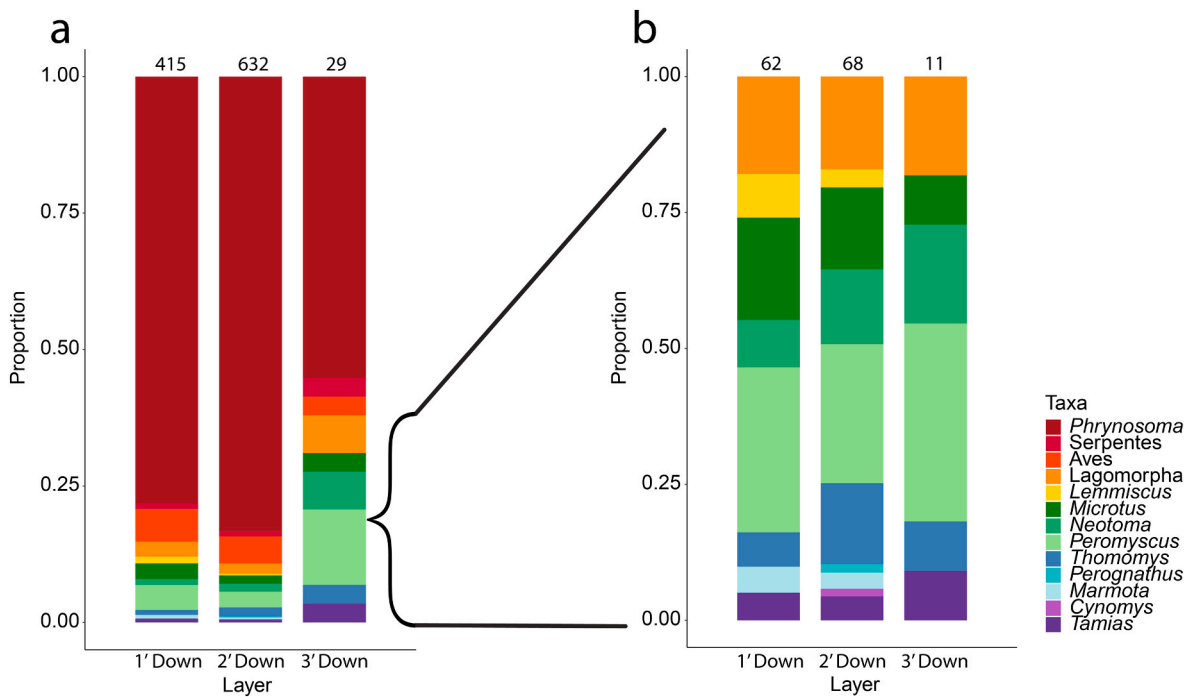
Fig. 1. Relative abundance of the MNI per group in the microvertebrate community for each layer of Natural Trap Cave with the total number of specimens used for each layer above the columns (a). MNI per group in the small mammal community for each layer of Natural Trap Cave with the total number of specimens used for each layer above the columns (b).

Table 2
Richness and evenness of the microvertebrate and small mammal communities of Natural Trap Cave using standardized MNI values for richness and evenness with raw values listed below in parentheses. Small mammal richness and evenness from NISP values used in comparison with Samwell Cave are listed in the two rightmost columns.

	Microvertebrate Richness (MNI)	Microvertebrate Evenness (MNI)	Small Mammal Richness (MNI)	Small Mammal Evenness (MNI)	Small Mammal Richness (NISP)	Small Mammal Evenness (NISP)
1 foot down	5.296 ± 1.3 (11)	0.492 ± 0.09 (0.404)	5.574 ± 1 (8)	0.915 ± 0.05 (0.896)	6.603 ± 0.76 (8)	0.827 ± 0.06 (0.800)
2 foot down	4.505 ± 1.3 (13)	0.424 ± 0.09 (0.310)	5.77 ± 1 (10)	0.925 ± 0.04 (0.851)	6.692 ± 0.97 (10)	0.820 ± 0.06 (0.728)
3 foot down	9	0.706	6	0.916	6	0.896

this comparison of richness and evenness, taxa >500 g were included. Midpoints, older, and younger age estimates for each layer within Samwell Cave were collected from the Neotoma Paleoecology Database (neotomadb.org) using the SCPD vertebrate dataset associated with Samwell Cave. Richness and evenness metrics were again standardized by resampling each layer to the smallest sample size and iterating 1,000 times. We calculated both richness and evenness for each iteration and reported the mean and standard deviation of the iterations for each layer. We also calculated the rarefaction curves for the three NTC layers to assess collection biases among the layers (Fig. S2).

4. Results

4.1. Radiocarbon dating of layers

Our three layers have non-overlapping dates from the Holocene and Pleistocene. Radiocarbon dates from the 1-foot-down layer include $2,460 \pm 35$ BP, $3,270 \pm 35$ BP, and $5,045 \pm 30$ BP. Radiocarbon dates from the 2-foot-down layer include $6,880 \pm 40$ BP, $7,125 \pm 35$ BP, and $7,215 \pm 35$ BP. Radiocarbon dates from the 3-foot-down layer include $19,600 \pm 70$ BP and $19,680 \pm 60$ BP. These dates were then calibrated with resultant dates from the 1-foot-down layer to be $2,608 \pm 171$ cal BP, $3,556 \pm 84$ cal BP, and $5,856 \pm 120$ cal BP, falling within the Late

Holocene. This gives an estimated age range of 2,437–5,976 cal BP. Calibrated dates from 2 foot down include $7,795 \pm 105$ cal BP, $8,013 \pm 74$ cal BP, and $8,128 \pm 112$ cal BP, putting this layer in the Middle Holocene with an estimated age range of 7,690–8,240 cal BP. Calibrated dates from 3 foot down include $23,651 \pm 234$ cal BP and $23,693 \pm 224$ cal BP, which is the Late Pleistocene with an estimated age range of 23,417–23,917 cal BP. Holocene boundaries follow designations from Walker et al. (2018) of 8.2 years before 2000 as the early to Middle Holocene boundary and 4.2 years before 2000 as the middle to Late Holocene boundary.

4.2. Paleoclimate

According to paleoclimate models (Beyer et al., 2020), paleoclimate estimates of mean annual temperature increased from $-4.3\ °C$ at 3 foot down in the Late Pleistocene to $6.2\ °C$ at 2 foot down in the Middle Holocene and remained relatively constant at $6.6\ °C$ at 1 foot down in the Late Holocene (Table 1). Mean annual precipitation increased from 146 mm in the Late Pleistocene to 210 mm in the Middle Holocene and increased to 230 mm in the Late Holocene (Table 1). Isotopic analyses from NTC estimate mean annual precipitation in the Late Pleistocene to have been around 150 mm $\pm$ 200 mm (Kohn and McKay, 2012), which is just slightly higher than the 146 mm estimates from general circulation
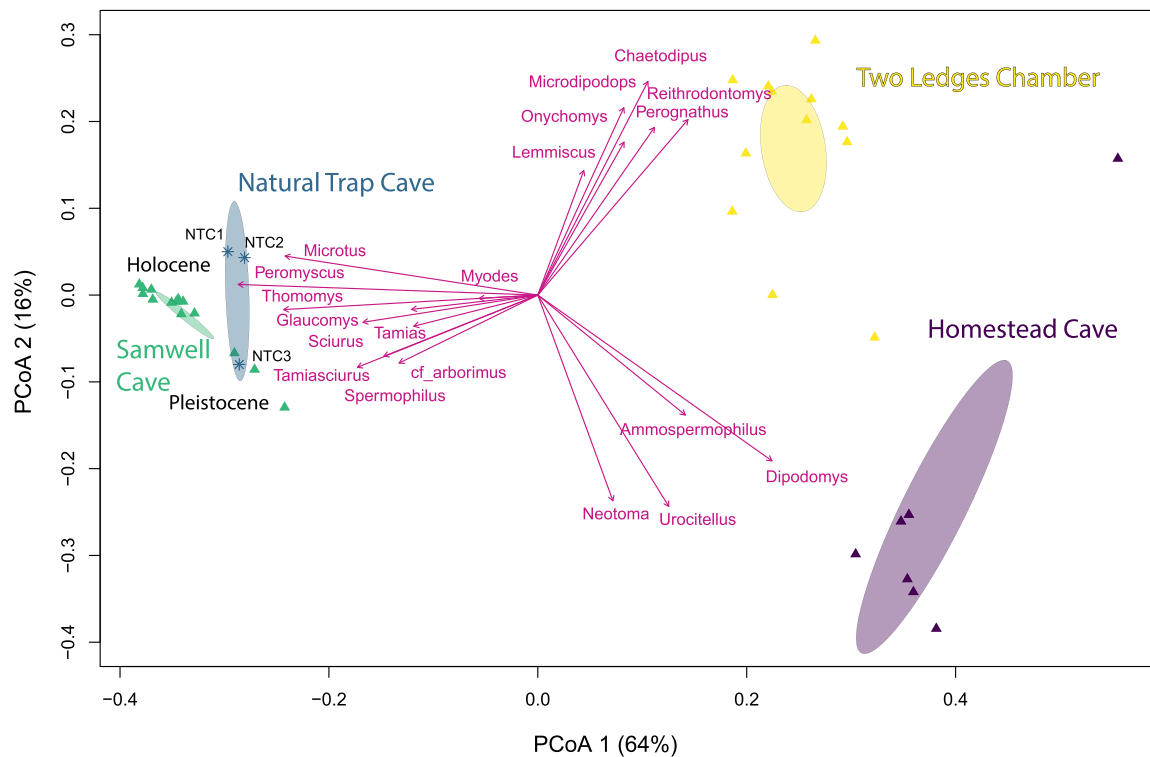
Fig. 2. PCoA using Bray-Curtis Dissimilarity matrix for Homestead Cave (purple), Natural Trap Cave (blue), Samwell Cave (green), and Two Ledges Chamber (yellow). PCoA 1 explained 64% of the variance and PCoA 2 explained 16% of the variance. Layers of Natural Trap Cave and Samwell Cave from the Holocene and Pleistocene clustered together and are labeled. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

model (GCM) data.

4.3. Comparisons across NTC strata

A total of 1,278 fossils from at least 415 individuals comprise the microvertebrate community of the 1-foot-down layer. These were standardized to 29 individuals for comparison with the 3-foot-down layer. Jaws classified as *Phrynosoma* (pers. comm. C. Bell) made up the highest percentage of MNI at the 1-foot-down layer, at 78%, while the small mammals made up 15% (Table S1; Fig. 1a). At the 2-foot-down layer, 1,649 fossils from 632 individuals were sampled. Jaws of *Phrynosoma* once again accounted for the majority of the MNI at 83%. Small mammals made up a smaller portion with 11% (Fig. 1a; Table S1). Smaller sample sizes were available from the 3-foot-down layer, with only 63 fossils analyzed from 29 individuals. Jaws of *Phrynosoma* accounted for 55% of the community. Small mammals made up 38% (Fig. 1a; Table S1). A full list of both raw and standardized MNI and the standard deviations of the standardized layers for the entire microvertebrate community can be found in Table S1.

When considering only the small mammal community at NTC, *Peromyscus* made up 30%, *Microtus* made up 19%, and Lagomorpha made up 18% of the 1-foot-down layer (Fig. 1b; Table S2). At 2 foot down, the three most abundant groups were *Peromyscus* at 25.5%, Lagomorpha at 17%, and *Microtus* at 15% (Fig. 1b; Table S2). The 3-foot-down layer was dominated by *Peromyscus* at 36%, and Lagomorpha and *Neotoma* both at 18% (Fig. 1b; Table S2). A full list of raw and standardized MNI of the small mammal community can be found in Table S2.

Richness and evenness were also analyzed for the entire microvertebrate community as well as among just the small mammal community. Microvertebrate richness increased from 9 at the 3-foot-down layer to 4.5 ± 1.3 at the 2-foot-down layer and then increased to 5.3 ± 1.3 at the 1-foot-down layer (Table 2). Small mammal community

richness showed a different trend decreasing from 6 at the 3-foot-down layer to 5.8 ± 1 at the 2-foot-down layer and then decreasing to 5.6 ± 1 at the 1-foot-down layer (Table 2). No taxa were present in the Late Pleistocene that did not also appear in the Middle Holocene, but there were new taxa found in the Middle Holocene including *Cynomys*, *Marmota*, *Perognathus*, and *Lemmiscus* (Fig. 1a and b; Tables S1 and S2). Microvertebrate evenness decreased from 0.71 at 3 foot down to 0.4 ± 0.09 at 2 foot down, and then increasing to 0.5 ± 0.09 at 1 foot down. Small mammal evenness increased slightly from 0.92 at 3 foot down to 0.93 ± 0.04 at 2 foot down and then decreased to 0.92 ± 0.05 at 1 foot down (Table 2).

For non-mammalian groups, from the Late Pleistocene to the Middle Holocene, there was an increase in relative abundance of birds and lizards and a decrease in relative abundance of snakes (Fig. 1b; Table S1). When examining the small mammal community, there was a decrease in the relative abundance of *Tamias*, *Peromyscus*, *Neotoma*, and an increase in *Thomomys* and *Microtus* (Fig. 1b; Table S2). The Order Lagomorpha remained roughly constant in relative abundance. Changes in community composition from the Middle Holocene to Late Holocene include increases in birds, decreases in lizards, and snakes remaining the same. In just looking within the small mammal community, Lagomorpha remains at the same relative abundance across these two time bins, increases are seen in *Lemmiscus*, *Tamias*, *Peromyscus, Marmota*, and *Microtus* while decreases are found in *Thomomys* and *Neotoma*. *Cynomys* and *Perognathus* were not found from the Late Holocene (Fig. 1b; Table S2).

4.4. Comparisons with other caves

Results from the PCoA showed 3 clusters of cave layers (Fig. 2). Almost every layer from each cave clustered closer to each other than to the other caves. Homestead Cave layers all clustered together except for
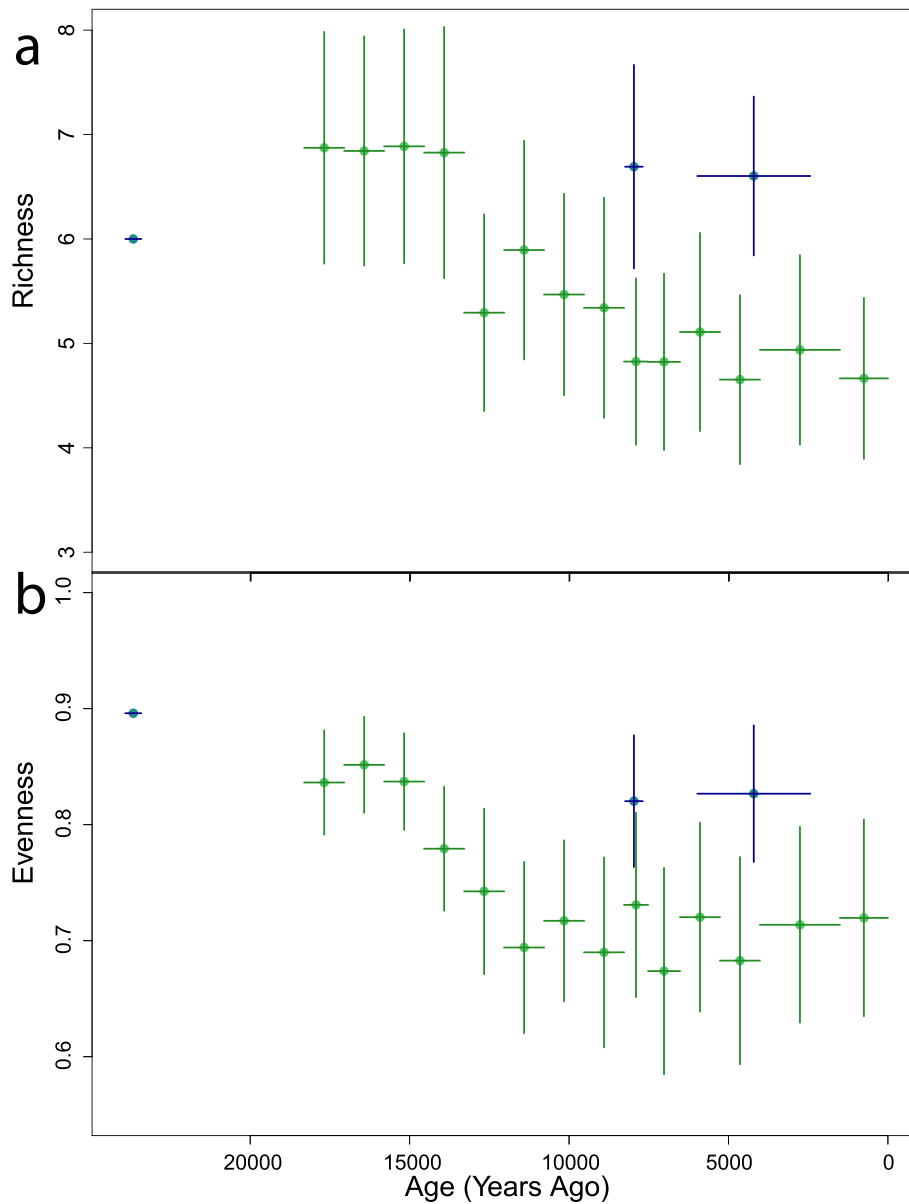
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Fig. 3. Richness (a) and evenness (b) of each layer in Natural Trap Cave (blue) and Samwell Cave (green) through time using the NISP of small mammals. Vertical error bars show standard deviation across the 1,000 iterations run. Horizontal error bars show temporal uncertainty of that layer. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the most recent layer, a modern layer, which plotted by itself away from other layers. NTC 1-foot-down and 2-foot-down layers clustered together close to Samwell Cave's Holocene layers. The 3-foot-down layer also clustered with Samwell Cave, but this layer was directly adjacent to three Pleistocene layers from Samwell Cave (Fig. 2).

Because Samwell Cave was the most similar to Natural Trap Cave, we compared the richness (Fig. 3a) and evenness (Fig. 3b) changes, based on NISP values, that occurred at each of these two sites. Richness slowly decreased through time from the Pleistocene to the modern at Samwell Cave, while richness at NTC slightly increased from the Pleistocene, 6, to the Holocene, 6.7 ± 0.97 at the Middle Holocene and 6.6 ± 0.76 at the Late Pleistocene layer (Fig. 3a). At layers of contemporaneous time periods during the Holocene, NTC had slightly higher richness levels than Samwell Cave. NISP trends of evenness showed values with highest evenness at the 3-foot-down layer, 0.9, decreasing to 0.82 ± 0.06 in the Middle Holocene, and slightly increasing to 0.83 ± 0.06 in the Late Holocene. This overall trend in evenness was found at both caves (Fig. 3b). NTC had a higher level of evenness during the Pleistocene than

Samwell. At contemporaneous times during the Holocene, NTC had slightly higher evenness values (Fig. 3b).

5. Discussion

5.1. Trends through time at NTC

NTC microvertebrates explored in this paper come from three, time-resolved, non-overlapping strata from the Late Pleistocene, Middle Holocene, and Late Holocene. By assessing the community compositions of these layers in conjunction with climate trends, and in comparison to other North American cave sites, we can begin to get a sense of how communities responded to environmental changes over this timeframe. Much like what has been noted from Samwell Cave, changes in the community from NTC were mostly due to changes in abundances of taxa rather than local extinctions or colonizations (Blois et al., 2010). The most consistent trend that we see at NTC is a change in community evenness through time, with higher evenness during the arid Late

Pleistocene. Shifts in evenness in the overall microvertebrate community are the result of shifts in abundance in the dominant taxa, *Phrynosoma*, which remained over 50% of the community across all three time periods. A large increase in the abundance of *Phrynosoma* from the Late Pleistocene to the Middle Holocene layer, continuing somewhat to a lesser extent in the Late Holocene, primarily drove these shifts in evenness. The microhabitat around NTC, semiarid with scattered vegetation, is ideal for short-horned lizard populations to thrive. It is likely that almost every carnivore or omnivore in the area was consuming *Phrynosoma*, including various rodents (Powell et al., 2017; Sherbrooke, 1991). A 2017 study suggested that the skulls of short-horned lizards, such as *P. hernandesi*, the species found around NTC today, have been altered in size and density to protect the orbits and braincase from attacks commonly shown by rodents and other predators (Powell et al., 2017). With the existence of many potential predators at the site and alterations for a denser skull, as opposed to defense from various dermatocranial horn arrays found in longer-horned species (Bergmann and Berk, 2012; Sherbrooke, 1991), it would follow that these often consumed and dense, more easily preserved bones would preserve, and be collected, en masse.

For small mammals, the Late Pleistocene community had fewer Lagomorphs, leading to higher NISP evenness than the Holocene, where the group made up roughly 42% of the community. A decrease in *Thomomys* from the Middle Holocene to the Late Holocene explains the increase at that time. However, a large number of Lagomorphs from both layers cause the increase in evenness to be slightly lower than the Late Pleistocene community. However, evenness of MNI values showed a slight increase from the Late Pleistocene to the Middle Holocene and a slight decrease into the Late Holocene. All values of evenness are within one standard deviation of each other and show that small mammal evenness has remained relatively constantly high through time staying above 0.9. Changes in richness between layers resulted from an absence of *Perognathus* and *Cynomys* at 1 foot down and *Lemmiscus, Perognathus*, and *Cynomys* at 3 foot down, all found in low relative abundances within the layers where they are present (Tables S1 and S2). MNI richness showed a slight decrease from the Late Pleistocene to the Holocene. Similar to evenness, all richness values were within one standard deviation of each other. Low abundances of some groups, as well as differences between MNI and NISP trends, implies that inconsistences in richness and evenness may be the result of poor sampling in the Pleistocene layer, as is supported by small mammal rarefaction curves (Fig. S2). Larger sample sizes for standardization methods will help in interpreting these trends better and having a better idea of the community composition of the site. Changes in community composition may be understood better with respect to a more thorough evaluation of local climate shifts from the LGM throughout the Late Holocene.

On average, global temperature and precipitation have increased since the end of the LGM throughout the Holocene (Grayson, 2000; Harbert and Nixon, 2018; Shuman and Marsicek, 2016). A study of plant fossils from North America found mean annual temperatures increased roughly 5 °C since the LGM, reaching a peak around 6ka, followed by slight cooling of about 2 °C from 5-4ka, a 2 °C increase from 4-3ka, and another slight cooling from 2ka (Harbert and Nixon, 2018). Looking locally at paleoclimate reconstructions around NTC, we identify a total temperature increase of approximately 10 °C. However, we do not observe a change in temperature between the Middle Holocene and Late Holocene. Local temperature, therefore, exhibits more stability than continental temperatures as a whole during the Holocene. Both isotope analyses and GCM data agree that precipitation increased after the end of the LGM into the warmer, wetter Holocene (Kohn and McKay, 2012). Carbon isotope discrimination factors of plants from NTC also found values indicating arid conditions during the Pleistocene and with precipitation increasing but remaining moderately arid throughout the Mid-to-Late Holocene, though analyses do not differentiate between these time periods (Minckley and Clementz, this issue). Mean annual precipitation today at NTC is slightly lower than the mid-Holocene,

roughly 200 mm (Kohn and McKay, 2010). Shifts from C3 to C4 plant diets and vegetation structure models of North America are consistent with an open, arid environment near NTC during the LGM and that has slowly increased in annual precipitation, but is still relatively arid (Cowling, 1999; Kohn and McKay, 2012; Wang and Martin, 1993).

The cold and dry climate of the Late Pleistocene corresponded with the highest richness and evenness, in the microvertebrate community and the lowest richness and highest evenness in the small mammal community (Table 2). The small mammal community evenness, as previously mentioned, always remained relatively high across all three time periods. A lower percentage of *Phrynosoma* and fewer groups found in low abundances accounted for higher evenness in the Late Pleistocene compared to the Holocene layers of the microvertebrate community (Table 2). Evenness is a predictor of community persistence under environmental stress, and it is also a more sensitive indicator of community change than richness since species will decrease in abundance before going extinct (Blois et al., 2010; Wittebolle et al., 2009). No small mammal taxa became locally extinct from the Late Pleistocene to the Holocene, perhaps in part owing to the high evenness seen during the Late Pleistocene (Tables 2, S1, S2) and showing that these groups could persist for long periods of time during variable climatic conditions (Table S1). It is also important to note that the 3-foot-down layer was from before the megafaunal extinction, which may also help to explain the increase in the small mammal community richness after this event.

The warmer and wetter Middle Holocene corresponded with the lowest richness and lowest evenness in the overall microvertebrate and the highest richness and lowest evenness in the small mammal community (Table 2). The warm and slightly wetter Late Holocene had a slight increase in richness in the microvertebrate and a slight decrease in richness in the small mammal community, and a slight increase in evenness in the microvertebrate and small mammal community. It has been hypothesized that periodic drought events may play a role in the abundance of rare and common species on a local scale. A study examining community structure after recent droughts in California saw an increase in relative abundance of locally rare species and a decrease in locally abundant species after the drought event (Prugh et al., 2018). Since we find higher evenness in the Late Pleistocene with lower precipitation, we could be seeing this same trend play out on a deeper, broader time scale. The biggest changes in abundances from the middle to the Late Holocene were a decrease in *Phrynosoma* and *Thomomys* and an increase in *Peromyscus*. As the temperature remained relatively constant between the middle and Late Holocene, the relationship between these groups and their reliance on precipitation should be further examined.

5.2. Cross cave comparisons

Results from the PCoA showed that variance in small mammal community composition is influenced more strongly by cave identity and taxonomy than by time period except for the modern layer from Homestead Cave (Fig. 2). This is expected when considering the role the local environment and taphonomy play on species composition (Andrews, 1990; Monte-Luna et al., 2004; Prugh et al., 2018). NTC fell closer to Samwell Cave than Homestead Cave or Two Ledges Chamber. Surprisingly, Natural Trap Cave's Late Pleistocene layer clustered closely with Samwell Cave's Pleistocene layers, and the Holocene layers from NTC clustered with Samwell's Holocene layers. These are the two instances of layers clustering closer to each other based on age (Fig. 2). It would be unexpected for communities to cluster by time considering that climate changes are not uniform across landscapes through time, and ecosystems are also not uniform across the landscapes making the clustering of NTC and Samwell interesting. A variety of sieve sizes were used in screen-washing among caves. Samwell Cave small mammals were collected from 4, 8, and 16 sieves, NTC were collected from 10 to 20 sieves, and Homestead Cave and Two Ledges Chamber were collected from 1/4″ and 1/8″ sieves. Screen size may play a role in which species

were collected, but the body size range of species within all caves was similar despite sieve sizes. Both Samwell Cave and NTC small mammal communities are accumulated by packrat middens (Blois et al., 2010; McGuire et al., this issue) while Two Ledges Chamber and Homestead Cave communities are a product of owl pellets (Blois et al., 2010; Terry et al., 2011). Owls, like raptors, are prey-selective and can also only consume animals of a certain size, creating a size bias in what they leave behind (Andrews, 1990; Redpath et al., 2001; Terry, 2010c; Terry et al., 2011; Viteri et al., 2021), whereas packrats are secondary collectors of any remains within 100 m of their nests (Betancourt et al., 1990; Hadly, 1999). These different means of collection can play a role in the identity of the taxa found at the site despite their differences in climate and habitat (Andrews, 1990).

Standardized NISP richness and evenness values from Samwell and NTC show that NTC had a more stable community in regards to richness and evenness since the Late Pleistocene. NTC had higher evenness across all time periods and a higher richness in the Holocene than Samwell Cave. The Pleistocene layer at NTC had lower richness than all but one Samwell Cave Pleistocene layer (Fig. 3a). As mentioned previously, according to rarefaction curves, the low richness of the Late Pleistocene at NTC is likely a product of a small sample size. It would therefore not be indicative of the true richness at that time period, rather than representing a richness trend counter to those found across North America (Fig. S2) (Blois et al., 2010; Carrasco et al., 2009; Graham, 1976; Grayson, 2000). Given the small sample size, species that were smaller or less common at the time may have not been found from the 3-foot-down layer yet. Rarefaction curves leveled off for both NTC Holocene layers and therefore richness values are not expected to change with more sampling. As a result, NTC may end up being even more constant through time. However, the Late Pleistocene layer from NTC is roughly 6,000 years older than the oldest layer at Samwell Cave. This gap may account for this trend since any changes between those two layers of NTC are missing. Middle and Late Holocene layers are more contemporaneous between the two caves and show similar trends in changes in evenness. For NTC, the small mammal community had fewer rare species, and therefore more even communities during the layer with low precipitation, the Late Pleistocene (Tables S1 and S2). Communities were also most even at Samwell Cave during the arid Pleistocene, decreasing into the Early Holocene, and fluctuating with a general increase into the modern (Blois et al., 2010). Local climate from Samwell Cave could help in finer-scale determination if changes in evenness throughout the Holocene align with periods of drought, or if the more forested environment made communities more resilient to these climatic changes with evenness being driven by another force.

5.3. Potential biases and future directions

Within the analyses, there are groups identified to different taxonomic levels from Aves, identified broadly to class, and small mammal groups, identified to order or genus. We expect that this will lead to changes in conclusions made as we refine our taxonomic identifications in future studies. Increased identification of groups to lower taxonomic levels will also help give a more refined response to climate and which, if any, species are more sensitive to changes than others within their genus. Processing of material from finer mesh screens will also allow for a more complete examination of sampled layers. As rarefaction curves showed, increasing the sample size of our Pleistocene material is critical for a better understanding and interpretation of trends through time in the cave.

Additional radiocarbon dates and processing of the finer stratigraphic sections from 2015, 2017, and ongoing excavations, could also clarify community changes through time. Differences in time averaging occurred between the three layers studied in this paper and greater time averaging can result in apparent increases or decreases in diversity, as multiple communities are being analyzed together (Behrensmeyer et al., 2000). However, the layer with the largest time averaging (1 foot down)

did not contain the largest sample size, and layers were subsampled to account for these differences. Additionally, many short- and long-term changes in climate have been noted throughout the Holocene (Booth et al., 2006; Shuman and Marsicek, 2016), and finer sampling has narrowed down stratigraphic levels in the cave and will aid in better capturing the effects of these events on communities. Our higher temporal resolution material will be critical for evaluating responses to discrete climate events, such as the megadrought around 4.7 ka. This finer stratigraphic resolution could also provide more information on where the tipping point for different taxa is and how long they can withstand changes in temperature and precipitation before going locally extinct.

5.4. Conclusion

Over the last 20,000 years, the microvertebrate community of NTC has shifted through changes in relative abundance, richness, and particularly evenness in response to environmental changes, driven largely by changes in *Phrynosoma* populations with richness and evenness decreasing from the Late Pleistocene into the Holocene. Natural Trap Cave helps add new information to previous cave studies on how small mammal communities have shifted through time, with peaks in evenness during the arid Late Pleistocene but remaining relatively constant through time. Studies such as this are useful for examining more minute changes to communities rather than just examining extirpations or colonizations. Smaller community interactions are affected by changes in abundances between taxa and can lead to larger ecosystem disturbances, which is why studies of relative abundances are crucial in aiding our understanding of at-risk communities.

Author contributions

Julia A. Schap: Conceptualization; Data curation; Formal analysis; Investigation; Visualization; Writing – original draft. **Jenny L. McGuire:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Project administration; Resources; Supervision; Visualization; Writing – review & editing. **Julie A. Meachen:** Data curation; Funding acquisition; Investigation; Project administration; Resources; Writing – review & editing.

Data availability

Field numbers for all specimens used in this study are listed in the supplements. Specimens will be reposited at the University of Wyoming Geological Museum and will be available via their database and for in-person evaluation once processing is complete. Taxon list and NISP/MNI are available in Tables S1 and S2. Any other data are available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2021.11.018.

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