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Comparison of *Neotoma* (packrat) feces to associated sediments from Paisley Caves, Oregon, U.S.A

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ABSTRACT

Paisley 5 Mile Point Caves, Oregon, U.S.A. offer a unique perspective on Native Americans living in the Great Basin during the Younger Dryas. The cave sediments are mixed with abundant, disaggregated, packrat coprolites. We developed a technique for processing these packrat coprolites. Using this technique, this study analyses fifteen packrat coprolite samples separated from sediments collected from the sidewall of a test unit within Paisley Caves #2. The results were then used to create a paleoenvironmental reconstruction of the region. This reconstruction was then compared to a previous reconstruction based on the fossil pollen in the sediment from the same site. The reconstructions were similar. However, we found that the packrat coprolites were prone to dietary biases that could mask the true paleovegetation of the area. By studying the differences and similarities of these two sample sets, we obtained a better understanding of how each set reflects the local environment.

KEYWORDS

Paisley Caves; Great Basin, U.S.A.; paleoenvironment; wood rat; archaeology; pollen analysis

1. Introduction

In 2012, Jenkins et al. published data from an archaeological site, the Paisley 5 Mile Point Caves, Oregon, U.S.A., showing evidence supporting human habitation at the site dating as far back as 14,000 years ago (cal BP) (Figure 1), While additional studies from Paisley Caves have confirmed and supported the evidence, the site features unique qualities. Various radiocarbon-dated samples have provided evidence that the sediments appear to be chronologically intact (Table 1).

Additionally, preliminary analysis of those sediments indicates that there is still much more to be learned concerning the complex taphonomy within the site (Shillito et al. 2018). In a previous study, Beck et al. (2018) separated the cave sediments from the plant matter, packrat coprolites, and roof spall. This was done because analyzing the sediment would provide the clearest representation of the paleoenvironment. The remaining desiccated packrat feces provided an opportunity to understand the dietary and behavioral idiosyncrasies of these cave-dwelling rodents and to determine how reliably these animals' fecal remains reflect the paleoenvironment.

In this study we discuss various species of *Neotoma*, which are known by many names, including 'goatters', 'trade rats' (Cole 1990), 'wood rats' (Hemmes et al. 2002), 'woodrats' (Hall 1997), 'packrats' (Van Devender and Hall 1994), 'packrats' (Baker 2000), 'pack rats', 'brush rats', and 'brush-rats' (Gander 1929). For our purpose, we refer to them only as 'packrats' unless directly quoting an individual or previous publication.

The nest-building behavior of packrats has long been recognized to be not only exceptionally localized, but also impressively inclusive of many plant taxa (Gander 1929). The limited collection range and diversity of nest contents led researchers, such as Wells and Jorgensen (1964), to consider the use of packrat-midden contents for paleoenvironmental interpretations. This, coupled with the application of radiocarbon dating, began the study of packrat behavior, which culminated in the book, *Packrat Middens: The Last 40,000 Years of Biotic Change* (Betancourt et al. 1990).

Today, plant remains from packrat middens are being used to reconstruct localized paleovegetation shifts in arid regions of North America. Studies of pollen and other remains found within packrat middens also show potential as descriptive elements, further defining the ecology and environmental composition of various areas in which they are found (Hall et al. 1988; Van Devender and Hall 1994). However, questions have been raised as to how accurately the contents of an ancient packrat midden can reflect the vegetation of past environments (Dial and Czaplewski 1990; Mehringer and Wigand 1990; Hall 1997; Hall and Riskind 2010). Researchers like Hall and Riskind (2010) concluded that the contents of packrat middens indicate dietary preference. However, by increasing the number of middens analyzed in each region (five instead of one), Dial and Czaplewski (1990) reported that they could create a fairly accurate reconstruction of about 75% of the total local plant species.

While macro-remains from intact packrat middens are often used for paleoenvironmental reconstructions, intact middens are not present at Paisley and are therefore unavailable for analysis. However, because of the unique composition of the sediments from the Paisley Caves, where

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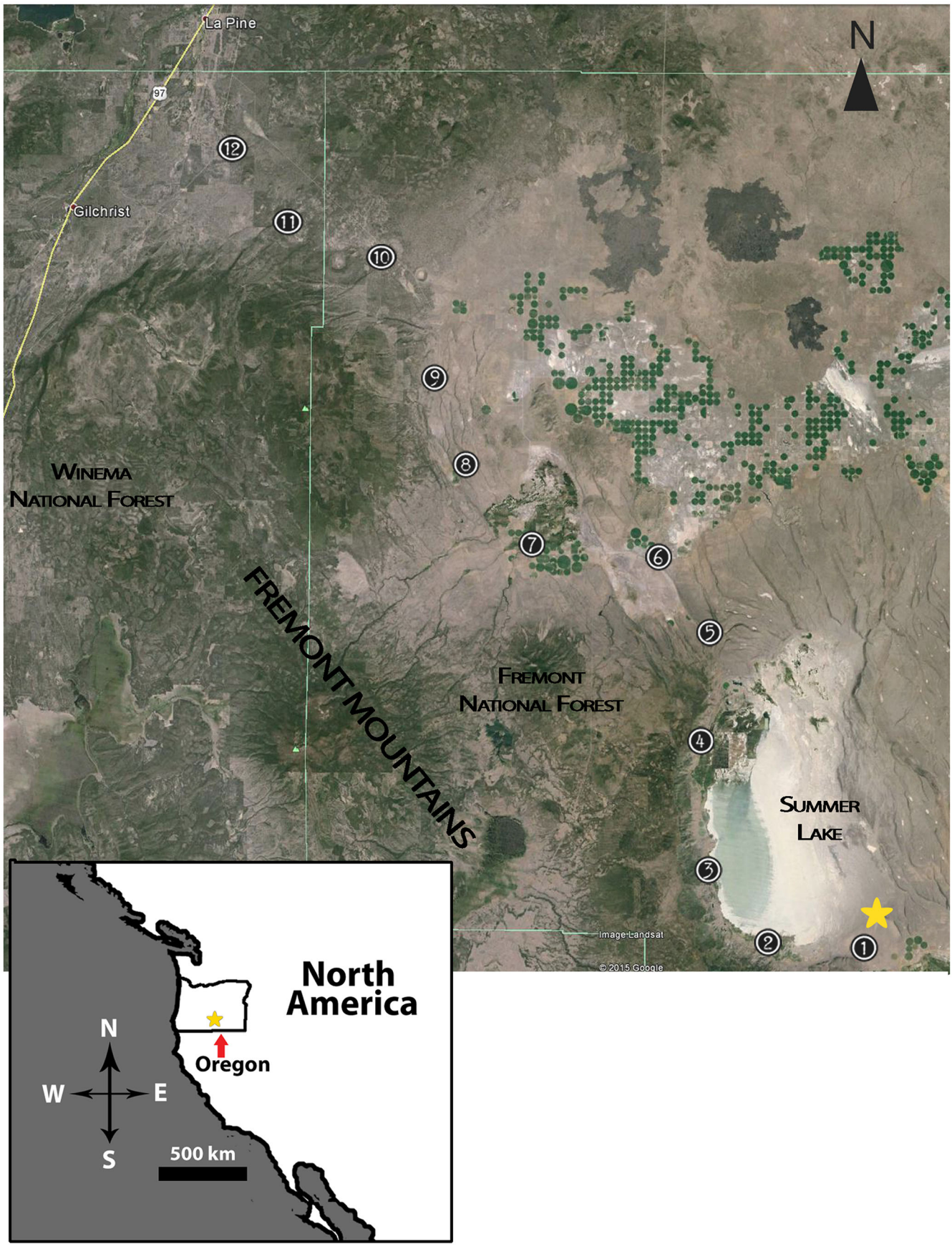

Figure 1. Map showing the location of the study site (star) and the approximate sampling locations of the surface samples. Satellite image provided by Google. Reprinted with permission from Beck et al. (2018).

Table 1. Radiocarbon Dates from 2/4 C South, reprinted from Beck et al. 2018.

Elevation	Lithic unit	Specimen no.	14C Lab. sample, no.	Conventional 14C date	Calib. date BP at 1σ (Cal Pal)	Material	Corresponding sediment sample #
1366.48	3	2009PC-162	UCIAMS-68046	6790 ± 15	7621 (7640) 7658	BAT GUANO	38
1366.35	3	1830-PC-2/4C-34-101	UCIAMS-79704	7490 ± 20	8313 (8338) 8360	HUMAN COPROLITE	33
1366.35	3	1830-PC-2/4C-34-101	UCIAMS-79705	7605 ± 20	8397 (8406) 8414	HUMAN COPROLITE	33
1366.19	3	2009PC-169	UCIAMS-76192	8180 ± 15	9056 (9094) 9131	COPROLITE	27
1365.85	3	2009PC-166	UCIAMS-68045	9480 ± 20	10,706 (10,725) 10,744	ATRIPLEX TWIG	13
1365.85	3	2009PC-165	UCIAMS-68044	9565 ± 20	10,806 (10,922) 11,038	INSOLUBLE RESIDUE	13
1365.6	2	1829-PC-2/4C-49	UCIAMS-76191	10,980 ± 20	12,803 (12,896) 12,989	HUMAN COPROLITE	4
1365.6	2	1829-PC-2/4C-49	UCIAMS-77100	11,090 ± 30	12,880 (12,977) 13,073	HUMAN COPROLITE (WATER SOLUBLE)	4
1365.53	2	1830-PC-2/4C-51-101	UCIAMS-77103	11,270 ± 30	13,085 (13,174) 13,262	HUMAN COPROLITE (MACRO)	3
1365.53	2	2009PC-167	UCIAMS-68047	11,560 ± 40	13,339 (13,448) 13,557	INSOLUBLE RESIDUE	3
1365.52	2	1830-PC-2/4C-51-102	UCIAMS-77104	11,625 ± 35	13,386 (13,510) 13,633	HUMAN COPROLITE (MACRO)	3
1365.5	2	1829-PC-2/4C-51-11	UCIAMS-79658	11,790 ± 35	13,582 (13,698) 13,795	LARGE MAMMAL BONE	2
1365.48	2	2009PC-168	UCIAMS-68018	11,830 ± 25	13,613 (13,735) 13,857	RODENT BONE	2
1365.48	2	1829-PC-2/4C-52a	UCIAMS-79659	12,025 ± 30	13,806 (14,003) 14,200	LARGE MAMMAL BONE (LIGHT)	2
1365.48	2	2009PC-168	UCIAMS-68016	12,190 ± 30	14,001 (14,222) 14,442	RODENT BONE	2
1365.48	2	1829-PC-2/4C-52b	UCIAMS-79660	12,275 ± 30	14,087 (14,360) 14,633	LARGE MAMMAL BONE (DARK)	2
1365.4	2	1829-PC-2/4C-54-101	UCIAMS-79663	12,320 ± 35	14,136 (14,469) 14,801	RODENT RAMUS	1

sediments are mixed with packrat coprolites, we sought to compare the pollen from the packrat coprolites with the pollen in the associated sediments. By doing so, we hoped to determine whether there are elements of disagreement between the two. If disagreement existed between the two sources of information, we sought to identify a pattern and wanted to find a way to quantify the degree of disagreement. We hoped to then conclude if this disagreement reflected in the pollen profiles could be ascribed to the collection behavior or the dietary biases of packrats. Finally, we sought to determine if the pollen data from the packrat feces could be used as a predictor of local vegetation/environment. Specifically, we hoped to learn whether both sources of information, packrat feces pollen and sediment pollen, would lead to the same conclusions concerning the local vegetation.

There has been considerable debate over the intactness and conditions of the stratigraphic sediments at Paisley Caves (Poinar et al. 2009; Shillito et al. 2018). It is a serious topic that we choose to leave to those more specialized and qualified. However, it is an issue that must be resolved before the discoveries made at the Paisley Caves will gain wider acceptance. Based on the remarks of Jenkins (Jenkins 2007, p. 61–65), we proceeded from the position that the sediments and stratigraphy at the site are chronologically intact, undisturbed, and of considerable value for analysis. We recognize that no site is perfect. However, we fear that were we to wait for a ruling or consensus before performing our analysis, one might never arrive. If future research shows that stratigraphic integrity is not present at the site or in some way deficient, we look forward to revisiting the topic of this study.

Cave systems are complex (Hunt et al. 2015) and any pollen data obtained from cave sediments can be considered to be equally complex (Beck 2019). Additionally, human use of caves adds another factor that complicates interpretation. Animals are known to introduce pollen into caves and humans are perhaps a better exemplar of this than they are an exception (Horowitz 1992, Hunt et al. 2015). Packrats, also, play a large role in the introduction of foreign material into caves (Finley 1990, p. 31, Vaughan 1990). Finally, the interaction of these two cave inhabitants serves to further complicate attempts at interpretation of sites. We hope that the contents of this article serve to, in some small way, begin to address the inter-related systems that must be addressed when attempting to address archaeological material, taphonomic processes, and the biases that these multiple influences introduce.

1.1. Packrat middens

There are 21 known species of packrats. All are dietary specialists, each focusing on a narrow range of available plants. Living in fairly dry climates, all generally derive their water from the food that they eat (Vaughan 1990). Packrats also live in a constant state of chronic energy stress (McClure and Randolph 1980), and this has been suggested as a partial reason for their habit of den building (Vaughan 1990). This foraging behavior became the basis of all packrat-midden reconstructions of paleoenvironmental data (Gander 1929; Dial and Czaplewski 1990).

Packrat middens are described as, 'nondescript masses, gray to dark brown in color' (Spaulding et al. 1990) or 'hard, dark, organic deposits preserved in dry rock shelters' (Van Devender and Bradley 1990). Today, packrats continue to construct dens and middens much as they did during the Pleistocene. Referred to as 'paleomiddens', they can show the accumulation of contents through time (Spaulding et al. 1990).

Many archaeological studies using packrat-midden data have focused on the macrofossils that are present in the amberat (solid packrat midden mass) once it is dissolved and separated (Wells and Jorgensen 1964; Van Devender and Bradley 1990; Rhode 2001; Lyford et al. 2004). In a midden, macrofossil remains would be elements (not exclusively botanical) brought into a nest by the packrat or elements present in the nest prior to nest building (Thompson 1982). Macrofossil remains are rarely transported into packrat dens or middens by other means (Gander 1929; Dial and Czaplewski 1990).

1.2. Criticisms of Packrat-Midden analysis

In his review and critique of the book *Packrat Middens: The Last 40,000 Years of Biotic Change*, Stephen Hall (1992) offered this quote:

> *… the potential for new insights on plant community dynamics through time is exciting. The characterization of plant abundances in middens and their relationship to abundances in the woodrat home-range plant community is a topic of recurring interest to midden analysts […] woodrats can be highly selective in the plants they eat and bring to their dens; as a result, middens may reflect woodrat diet rather than local plant abundances, and changing plant records may signal species turnover of woodrats rather than climate change.*

Hall (1997) referred to the selective foraging behavior exhibited by packrats as the 'Woodrat Filter Effect', as it results in only partial representation of the local paleoflora within midden contents. Procedural methodologies for the analysis of packrat-midden materials call for the separation of fecal remains from the main body of the midden sediments prior to plant matter sorting and identification (Spaulding et al. 1990).

1.3. *Local* Neotoma *species at Paisley Caves*

There are two species of packrats with habitation ranges covering the Paisley Caves region today. They are the bushy-tailed woodrat (*Neotoma cinerea*) and the desert woodrat (*Neotoma lepida*). (Smith 1997; Verts and Carraway 2002). Both are known to consume prickly pear (*Opuntia* spp.), shadscale (*Atriplex confertifolia*), juniper (*Juniperus osteosperma, Juniperus californica*), sagebrush (*Artemisia tridentata*), and vetch (*Astragalus* spp., *Vicia* spp.). Additionally, *Neotoma lepida* packrats have been observed eating shrub live oak (*Quercus turbinella*), creosote bush (*Larrea divaricata*), teddy bear cholla (*Opuntia bigelovii*), and other flora. *Neotoma cinerea* collect aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), rabbitbrush (*Crysothamnus* spp.), spruce (*Picea* spp.), pine (*Pinus* spp.), and other vegetation. Due to the consumption of these taxa by local packrat populations, we would expect the pollen of these species to be higher than background pollen levels for the same taxa. *Neotoma lepida* is referred to as a dietary specialist, concentrating on relatively few species, but they are also described as an opportunistic feeder, varying their diet widely across the geographic range in which they are found (Verts and Carraway 2002). Like the desert woodrat, the bushy-tailed woodrat (*N. cinerea*) is described as having a broad and flexible diet (Smith 1997). These characteristics, having a broad and flexible diet while being able to specialize their diet to a small number of available plants, coupled with their habits of den building and food collecting, allow these species to adapt to a wider array of vegetation zones, thus enabling them to maintain a larger habitable range than otherwise would be possible (Vaughan 1990, p. 16–17).

Paisley Caves is theorized to have been terribly unsanitary in the prehistoric past, with the added problems of parasitic infestations and lack of water. Due to the large amounts of terrestrial invertebrates found in the sediments, Jenkins and et al. (2016, p. 175–176) believe the botanical layer must have "appeared 'alive' with their movement at times" We do not know what role packrats at Paisley played in disease transmission if any. However, we know from a well-researched theory of Reinhard and Araujo (2015) that they might have played a significant part in the perpetuation and transmission of Chagas Disease in the Lower Pecos Canyonlands of Texas. Contributing to the nidi of infection along with triatomines, packrats might have significantly increased transmission of Chagas Disease due to prehistoric people's reliance on earth ovens and, as a result, subsequent production of burned rock middens. Similarly, today many North American species of packrats have been linked to various diseases that have great potential to harm humans including Lyme Disease (Maupin et al. 1994), Human Granulocytic Ehrlichiosis (Zeidner et al. 2000), Leishmaniasis (González et al. 2010), Whitewater Arroyo Virus (Fulhorst et al. 2001), Colorado Tick Fever (Hubálek and Rudolf 2010), and Sin Nombre Virus, a hantavirus (Dearing et al. 1998).

2. Materials and methods

Thirty-eight sediment samples were collected from a continuous profile from test unit 4C in Cave 2 of Paisley Caves (Figure 2). Of these samples, 35 were labeled as containing probable wood-rat-midden material. The remaining three samples have no provided description. Four of the samples also noted 'rat coprolites' among their observed components. Most packrat middens appear as solid masses of sticks, plant material, and feces held together by dried amberat; however, the packrat middens and sediments in Paisley Cave 2 are unconsolidated and mixed with the cave sediments.

Samples were collected at three-inch (≈7.62-cm) intervals and cover a span of 45 inches (≈114.3 cm) from a single column. Samples were collected starting from sediments dated to approximately 14,469 cal BP and ended with the Mazama

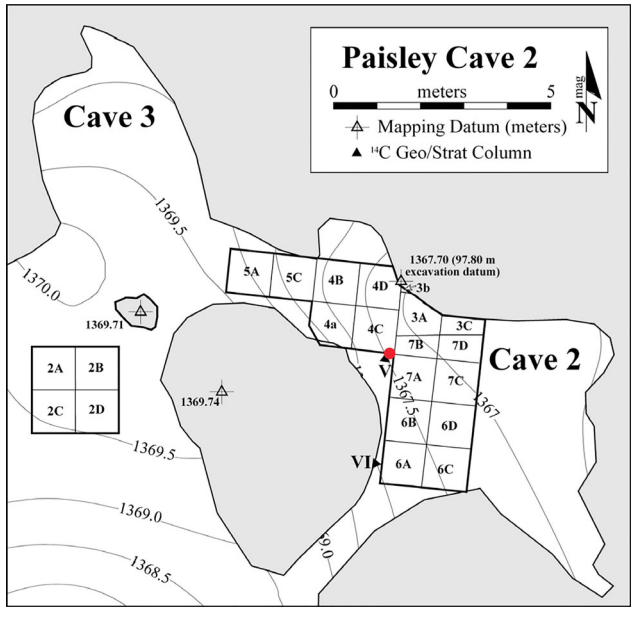

Figure 2. Plan view map of Paisley Cave 2 showing the sampling location for the sediment samples (red dot). Reprinted with permission from Beck et al. (2018).

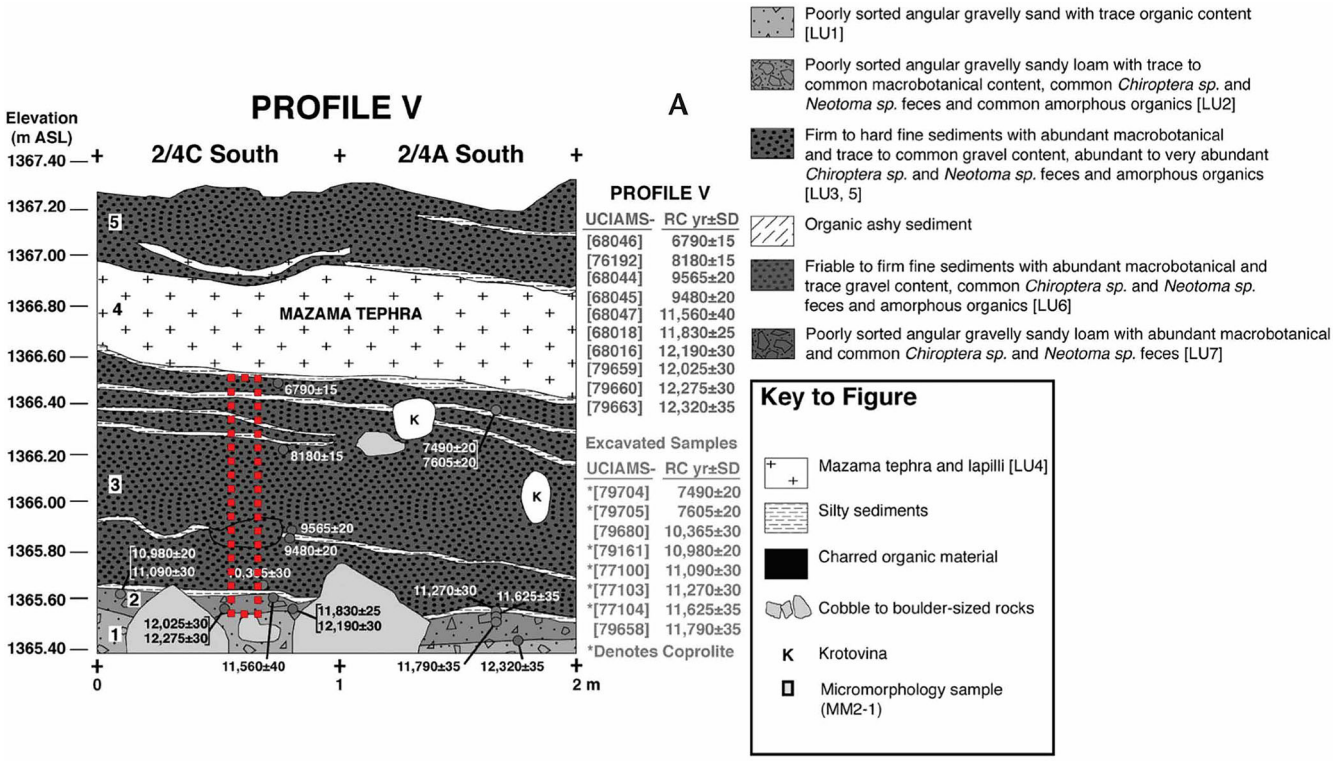

Figure 3. Profile map showing sediment sampling column (area within dashed line). Reprinted with permission from Beck et al. (2018).

Table 2. Surface sampling locations and data, reprinted with permission from Beck et al. 2018.

Surface sample No.	GPS coordinate	Location	Vegetation type	Elevation above sea level (in meters)	Nearby plant communities
#1	N 42° 36.29.9 W 120° 25.42.9	≈16 km South of Paisley	Artemisia Grassland	1312	8 km to Cedar scrub
#2	N 42° 43.44.1 W 120° 32.54.9	Near Paisley Cave on Hwy 31	Artemisia Steppe	1331	9.7 km to Juniper in mountains
#3	N 42° 45.43.1 W 120° 33.14.3	≈16 km North of Paisley on Hwy 31	Artemisia Grassland	1374	
#4	N 42° 35.20.2 W 120° 22.02.5	≈32 km North of Paisley on Hwy 31	Artemisia Grassland	1314	16 km to Juniper
#5	N 42° 16.31.1 W 120° 21.12.4	≈48 km North of Paisley on Hwy 31	Artemisia Grassland, Juniper present	1489	1.6 km to Pine
#6	N 42° 43.55.0 W 120° 44.11.8	≈64 km North of Paisley, North end of Summer Lake on Hwy 31	Grass abundant, Farm with Pine, Willow, and Oak nearby	1316	Pine close by
#7	N 42° 52.04.5 W 120° 48.24.9	≈80 km North of Paisley on Hwy 31	Some Cedar and Grass	1293	Pine within 91 meters.
#8	N 43° 00.50.6 W 120° 46.20.6	≈97 km North of Paisley, North end of Summer Lake on Hwy 31	Grass, Artemisia, Cedar, and Asteraceae	1358	Pine within 46 meters
#9	N 43° 06.33.6 W 120° 51.16.3	≈113 km North of Paisley on Hwy 31	Grass, Asteraceae, and small Cedars	1322	no visible Pine, large Juniper 8 km away
#10	N 43° 08.13.8 W 121° 04.39.4	≈129 km North of Paisley on Hwy 31	Asteraceae and Grasses	1341	Junipers .8 km distant
#11	N 43° 15.39.8 W 121° 09.34.3	≈145 km North of Paisley on Hwy 31	Asteraceae, Grasses, Artemisia, and small wildflowers	1401	Pine and Juniper 6 km distant
#12	N 43° 24.46.1 W 121° 14.51.6	≈161 km North of Paisley on Hwy 31	Pine, Grasses, and unidentified bushes	1420	

tephra layer, from which a sample dating to 6,790 cal BP was obtained (Figure 3). The location of the sampling column was chosen specifically because it contained intact sediments uninterrupted by krotovinas. Bryant collected the samples. These cave sediments and their fossil-pollen content were analyzed and discussed in a previous paper (Beck et al. 2018). The samples were dated by correlating the depths from which they were collected with radiocarbon-dated samples from similar strata in the site (Table 2).

The dates, performed by Stafford, are taken from previously published material (Jenkins et al. 2013). The sediments were initially sieved through a 500 μm mesh screen to separate visible coprolites from the soil samples.

For the current study, fifteen samples of the packrat coprolites were selected for analysis. Once sieved and separated from the other sediments, the feces samples were chemically processed to recover the pollen. We processed 0.25 grams (approximately 57 coprolites) of packrat coprolites for each

sample. Before processing, we tested two methods of disaggregation. One method involved placing a sample in a 10% aqueous solution of potassium hydroxide (KOH), and heating it in a heating block, at 80° C, for approximately ten minutes. Another method involved the use of room temperature, 0.5%, aqueous solution of trisodium phosphate ($Na_5P_3O_{10}$), a common treatment used in the rehydration of human coprolites. Human coprolites in trisodium phosphate can take several days, or even weeks, to fully hydrate (Callen and Cameron 1960). We expected, packrat coprolites, being small, would take a considerably shorter amount of time, but they did not. The first method seemed to yield the best results in the shortest amount of time; therefore, the 15 packrat-coprolite samples were prepared using the KOH method. We later discovered that King and Van Devender had used the same method to analyze packrat coprolites in 1976.

The 15 samples were next filtered through a 250 μm mesh screen and then through a 150-μm mesh screen. The larger fraction was saved for macrofossil analysis. All liquid passing through the 150-μm mesh screen was then processed first using the KOH method and then acetolysis (Erdtman 1960) using a solution of 9:1 acetic anhydride and sulfuric acid, heating them in a heating block for 10 minutes at 80° C. If a large amount of siliceous material was present after acetolysis, then the samples were left overnight in 49% HF. The final steps for all samples were to stain them and then transfer each to 2-ml vials. Glycerin was used as a mounting medium.

Two separate slides were prepared for each of the 15 samples of the processed material. Bryant and Beck conducted separate 200-grain pollen counts for each sample using Nikon compound light microscopes. The two counts were combined into single 400+ grain analyses for each packrat sample. An attached Nikon camera was used to photograph images of pollen types. Pollen reference slides from our collection of modern types and keys were used to assist in the identification of unknown types.

Analyzing compositional data can be challenging and can lead to mistakes if not properly addressed (Aitchison 2005). We selected principal components analysis (PCA) and a modification of stratigraphically constrained cluster analysis by the method of incremental sum of squares (CONISS) as the best means for determining the relatedness of the samples (Martín-Fernández et al. 1998). The PCA analysis was performed using the proportions of the pollen grains in each sample. For PCA, two elbow plots were constructed to determine the proper number of groups into which the samples could be placed. One elbow plot contained non-transformed data. The other used a centered log ratio transformation to compensate for the large number of zeros that are present in the datasets. CONISS has long been a standard for pollen analysis and is even included in the premier pollen graphing software, TiliaGraph (Grimm 1987; Bennet 1999). However, these analyses were performed using R software. A plugin called Rioja is often used to perform CONISS analysis in R. In this case, instead of stratigraphically constraining the data, the analysis allowed for any similar samples to group together, making this cluster analysis. This method was selected so as to determine the similarity of the packrat samples to the sediment samples. Cluster analysis using the modern sediment samples also indicated the modern vegetation zones with which the packrat samples were most similar. The modern samples were collected previously and discussed in detail in Beck et al. (2018). These were surface soil samples collected along Oregon Highway 31 at approximately 16-km intervals beginning at Paisley Caves and ending near La Pine, Oregon. Samples were collected using the pinch method described by Adam and Mehringer (1975). Descriptions of the modern sample collection sites are provided in Table 2.

3. Results

3.1. Macrofossils

A cursory examination of the large fraction recovered from the packrat coprolites reveal insect parts mixed among the expected plant fibers. We made no effort at identification as the main purposes for our study were pollen comparison, dietary bias and paleoenvironment reconstruction.

3.2. Microfossils

This study's packrat pollen counts are shown in Figure 4. In a few places, the packrat-pollen profile diverges from the ancient sediment pollen profile in the amounts of pollen they display for a few taxa. To better illustrate the differences, we prepared an additional figure (Figure 5) of the seven most common pollen taxa found at the site and arranged them by sample number and taxa. The samples that exhibit the most visible disagreement are numbers 4, 6, 8, 10, and 37. Samples 4, 6, 8, and 10 are all found in sediments correlating to the Younger Dryas. Sample 37 is at the other end of the sediment column, very near the Mazama ash layer.

Additionally, the packrat samples display a greater variety of rare taxa. Examples of this are found in the presence of the pollen identified as insect-pollinated *Phlox* spp., and the algal spore *Pediastrum* sp. (Figure 4). Raw counts of the packrat-coprolite samples (Appendix, Table A1), sediment samples (Appendix, Table A2), and modern samples (Appendix, Table A3) are included.

While counting the packrat samples we occasionally encountered clumps of pollen. Each clump was counted only as a single pollen grain to prevent skewing our counts, if the clump pollen identity was clear. Because some of the clumps were so large, attempting to estimate and include the total grains encountered in our counts would have prevented accurate recording and masked the presence of many taxa in the samples. This situation closely matches Hall's Woodrat Filter Effect where large amounts of material from a single taxon swamp material contributions of other taxa. These clumps were not overly abundant but displayed great variability in size. Some of the larger clumps contained over a hundred pollen grains, and in one case we estimated that a single clump contained a thousand individual grains (Figure 6).

While certain, smaller clumps were clearly composed of pollen from the Amaranthaceae, the pollen of other clumps

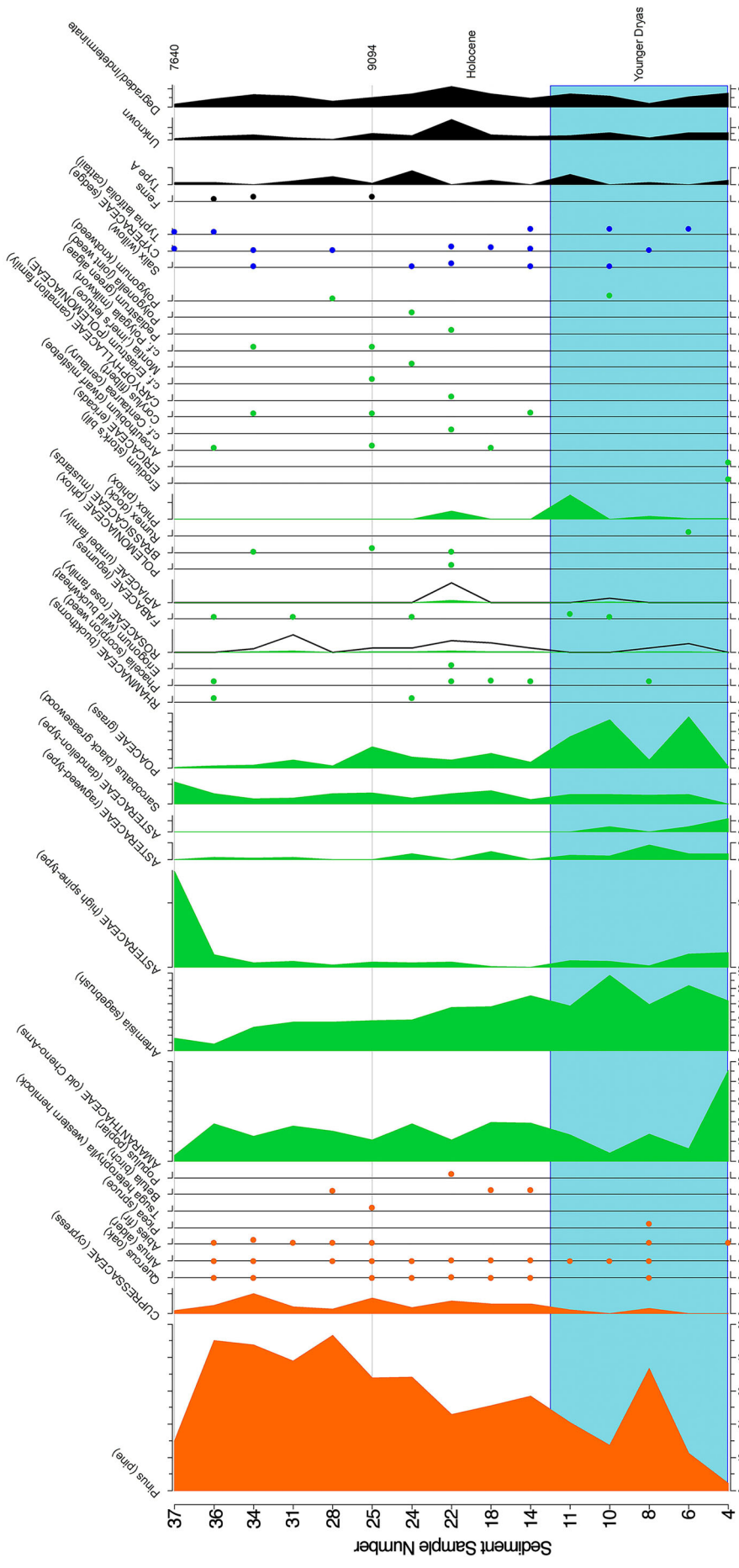

Figure 4. Pollen chart of packrat coprolite samples from Paisley Caves. Black outlines indicate 10 times exaggeration of pollen percentages. Dots represent taxa that were never present at higher than 1% throughout the samples analyzed.

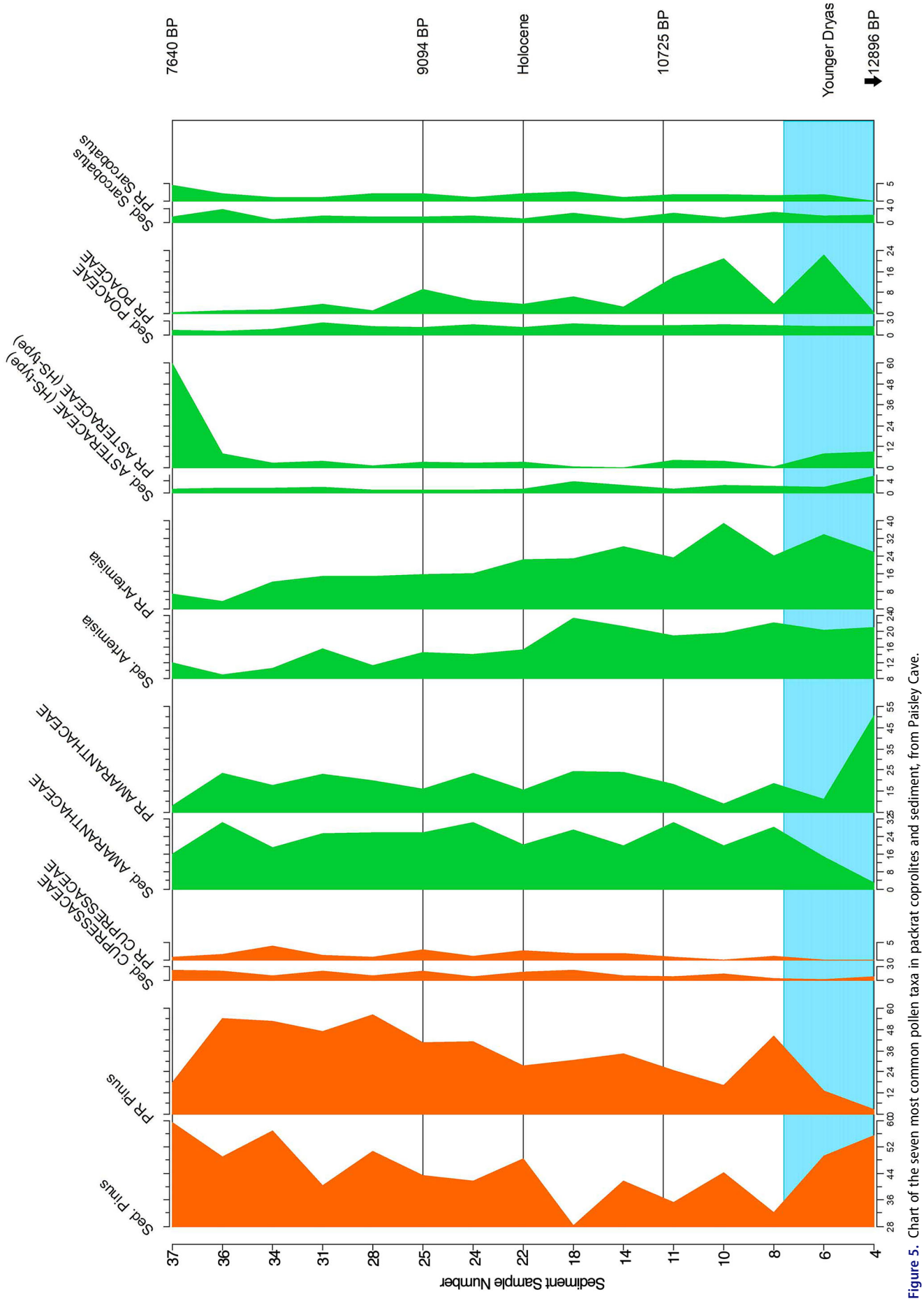

Figure 5. Chart of the seven most common pollen taxa in packrat coprolites and sediment, from Paisley Cave.

were difficult to identify. We used a Tescan Vega 3 environmental scanning electron microscope (ESEM) to attempt to identify the taxa of the pollen clumps (Figure 7).

The pollen values from the modern sediments (Beck et al. 2018) are provided for reference (Figure 8). The figures show the ratio of plant taxa pollen in the packrat coprolites. The pollen ratios of Figures 4 and 8 seem to agree in most respects. For instance, the amount of pine pollen in the modern samples matches closely with the proportions in both the packrats and sediment samples.

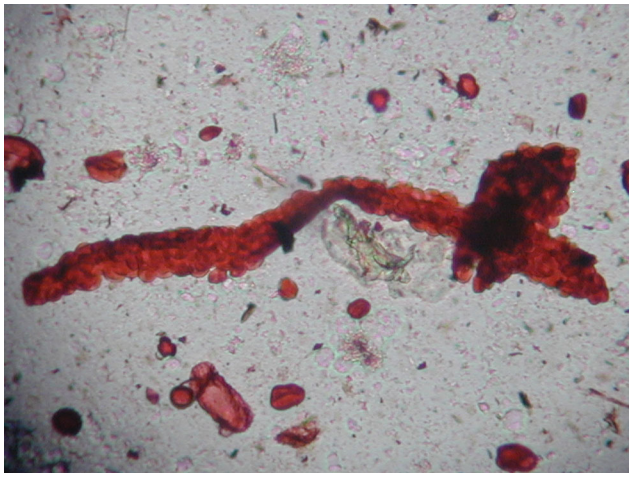

Figure 6. Light microscope image of a pollen clump encountered in packrat coprolites.

3.3. Quantitative analysis

When performing PCA we were unable to fully differentiate the packrat samples from the sediment samples (Figure 9). Cluster analysis was also used for determining the similarities between groups of samples.

When performing the cluster analysis, the first step was to determine the potential number of groups into which the samples could be separated. The transformed elbow plot (Figure 10) suggests that the ideal number of groups for all three data sets lies between two and five. Organizing the samples into five groups provided the clearest picture. Table 3 shows how the three sample sets separate into the five cluster analysis groupings. The modern samples have the most variability, separating into four of the five groups.

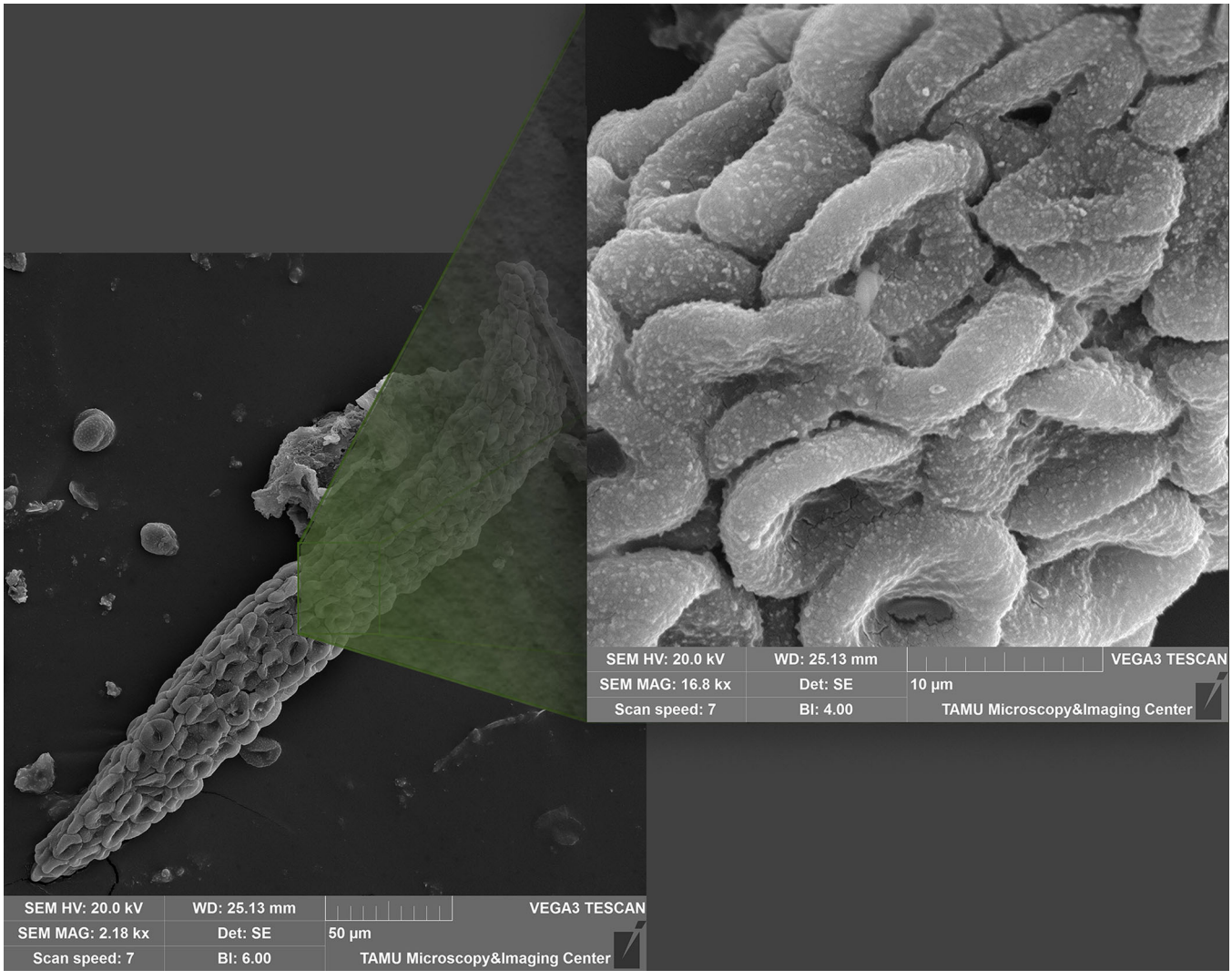

Figure 7. SEM image of a pollen clump encountered in a packrat coprolite. Image photographed using a Tescan Vega 3 under high vacuum.

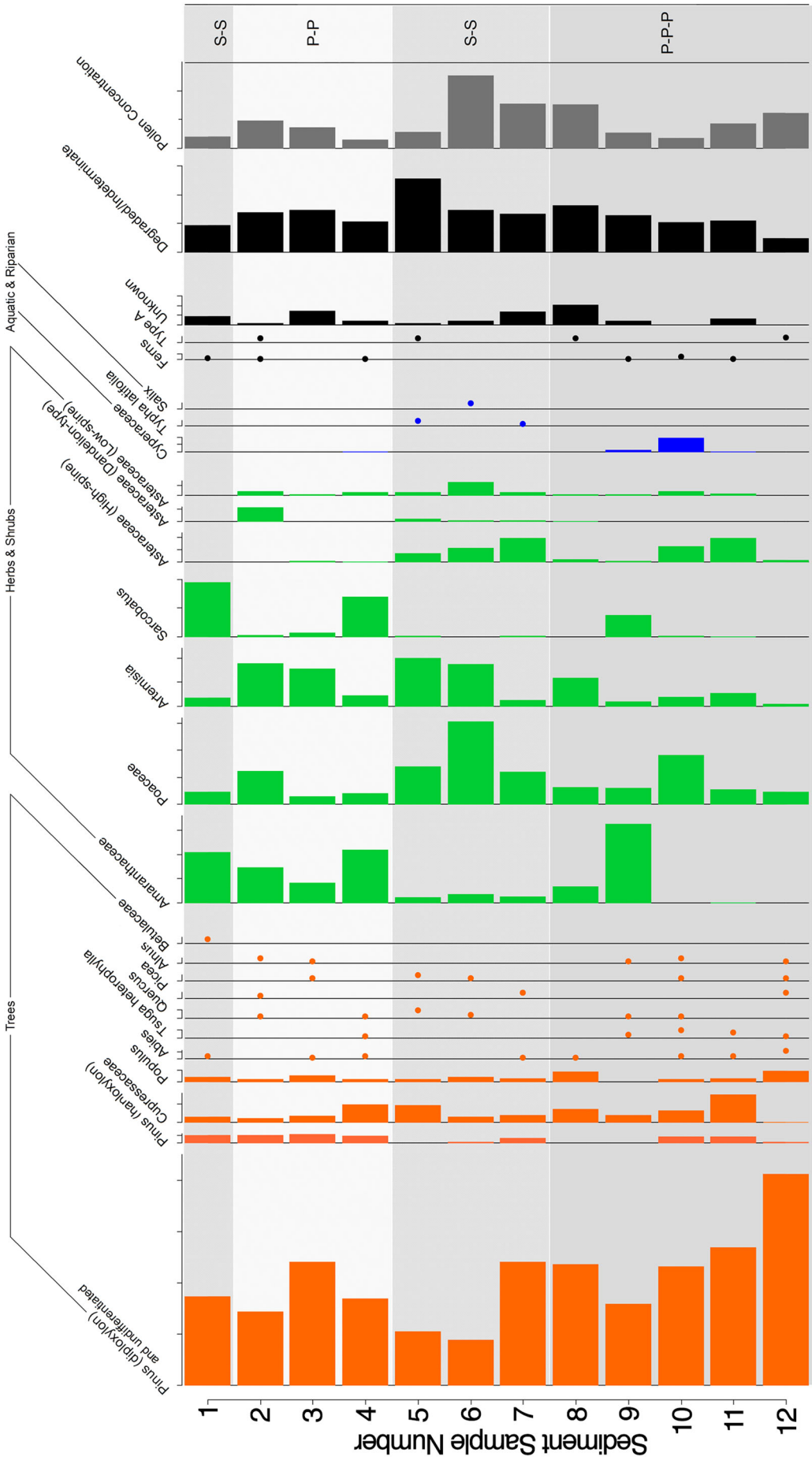

Figure 8. Pollen chart of modern sediment pollen collected in the immediate area of Paisley Caves. Reprinted with permission from Beck et al. (2018).

The packrat samples fall into three groups, and the sediment samples separate into two groups. In the analysis, group three contained ten packrat samples, 37 sediment samples, and modern samples 3 and 8.

The PCA showed that the contents of the 38 sediment samples generally clustered closer together than that of the 15 packrat samples. However, the PCA could not differentiate the two sample sets from one another statistically (Figure 9).

Nevertheless, the clustering of the sediment samples was distinct from the 12 modern samples. Only one of the 38 sediment samples, 1, is in the modern sample cluster. By contrast, four of the 15 packrat samples share similarities with the modern sample cluster. These packrat samples are 6, 10, 18, and 25. This is likely due to both sample sets displaying high values for the same five taxa: *Pinus*, Amaranthaceae, *Artemisia*, Poaceae, and *Sarcobatus*.

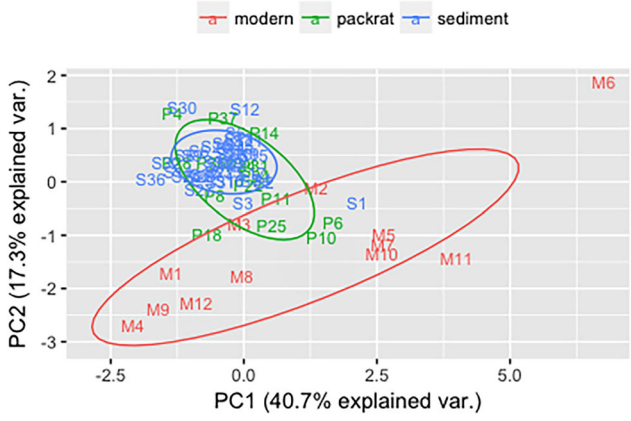

Figure 9. PCA of modern, packrat, and sediment samples.

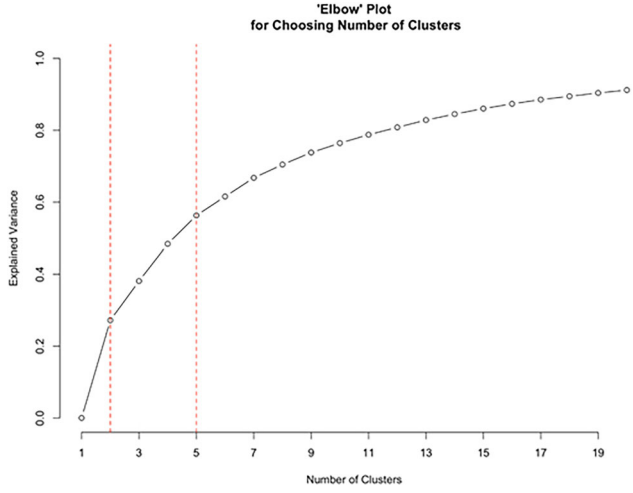

Figure 10. Elbow plot of packrat, modern, and sediment data using centered log ratio transformation.

In the cluster analysis (Table 3), Group 1 contained only two samples, packrat samples 4 and 37. These were the samples that had extreme values for Amaranthaceae (4) and high-spine Asteraceae (37). Neither statistical analysis separated samples correlating to the Younger Dryas (11, 10, 8, 6, and 4) into separate categories. This was true for both packrat and sediment samples.

4. Discussion

4.1. Macrofossil remains

The presence of insect parts in the packrat feces was unexpected as packrats are described in multiple sources as herbivores (Lee 1963; Dial and Czaplewski 1990; Vaughn 1990; Smith 1997; Verts and Carraway 2002). This is important to note as these insects could be a potential source of additional pollen found within the coprolite samples. It is possible that ingestion occurred during the packrats' regular grooming behavior in an attempt to remove ectoparasites (Hemmes et al. 2002). The bushy-tailed woodrat (*Neotoma cinerea*) has been observed eating fleas and lice arthropods during grooming (Johnson and Hansen 1979). While unidentified, we suspect the insect parts we found are ectoparasites, ingested by the packrats during grooming and were later eliminated in feces. Numerous plant fibers were also present in the packrat coprolite material. A more rigorous attempt at identification and quantification of the insect remains and plant fibers offer potential as avenues for further study.

4.2. Microfossil remains

The high levels of pine and high-spine Asteraceae pollen in the packrat coprolites suggest that the bushy-tailed woodrat (*Neotoma cinerea*) is the most likely inhabitant at the site. We cannot rule out, however, long-distance transport of pine pollen to the site where it was then deposited on foods selected by the packrats or from background pollen picked up on the fur of the animals and then ingested during grooming. A few pine-nut shells and cone scales are listed among the plant macrofossils identified at the site from an adjacent cave (Jenkins et al. 2013). We suspect the pine macrofossils recovered at the site were brought from distant sources by humans, rather than coming from local pine trees growing at the site. Additionally, the level of pine pollen is similar to what is currently found in the region (Appendix, Tables A1, A2 and A3). There is no pine growth at the site today nor within the estimated collection range of any packrats still living there. Analyses of faunal remains from the site

Table 3. Cluster analysis groupings of pollen samples.

Group	Packrat sample number	Sediment sample number	Modern sample number
1	4, 37		
2	6, 10, 11	1	2, 5, 7, 10, 11
3	8, 14, 18, 22, 24, 25, 28, 31, 34, 36	2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15,16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31,32, 33, 34, 35, 36, 37, 38	3, 8
4			1, 4, 9, 12
5			6

have not been specific enough to confirm our species identification. Often analyses of microfauna from Paisley list only "rodent" or "*Neotoma*" (Jenkins et al. 2013). Future studies might provide more conclusive identification of the rodent remains recovered there.

The grass values in packrat samples 10 and 6 are consistent with those values found in some of the modern sediments (Appendix, Table A3). While one may conclude that the early packrat feces reflect increased food use of local grasses, which might have been more plentiful in the region than previously documented, we believe that it is too early to make such claims. It is possible that examining additional packrat-feces samples from close intervals might strengthen this theory. Thus, with the exception of samples 4 and 37, the packrat coprolites indicate an environment that is nearly identical to what is found in the area today when comparisons of samples are limited to grass values.

Samples 4 and 37 indicate unusual pollen values. Number 4 contains a high concentration of Amaranthaceae pollen (50.48%). While the percentage of Amaranthaceae pollen was generally high among most of the samples, the next highest occurrence of it in the packrat samples is only one-half that amount at 24.38% in sample 18. Packrat sample 37 had a high concentration of high-spine (insect-pollinated) Asteraceae pollen (59.43%) yet the next highest percentage of this pollen type from the packrat samples is only 9.13%, in sample 4. Throughout the packrat, modern, and sediment samples, high-spine Asteraceae pollen regularly appears in low percentages. The highest occurrence across all samples is in modern sample 11 (10.26%).

The high occurrence of Amaranthaceae pollen in sample 4 and the high occurrence of high-spine Asteraceae in sample 37 (Figure 4, Table 3) are both probably remnants of specific meals eaten by packrats. The presence of pollen clumps in the coprolites supports this conclusion. While some of the smaller clumps were easily identifiable as Amaranthaceae, some of the larger clumps appeared to be grass anthers. As previously mentioned, in some cases, they were difficult to distinguish. By using the SEM, we concluded that some of the clumps of pollen grains were likely to be a low-spine (wind-pollinated) Asteraceae, while others appeared to be species of *Artemisia*. Still, some of the larger clumps remained unidentified. The presence of these clumps suggests the consumption of anthers or whole flowers by the packrats. We believe the pollen clumps, found in packrat coprolites, seen in Figures 6 and 7, are such anther fragments.

While there are many articles and studies on packrats (McClure and Randolph 1980; Hemmes et al. 2002; Schmitt and Lupo 2012), or studies of their middens (Wells and Jorgensen 1964; Cole 1990; Hall 1997; Lyford et al. 2004; Jackson et al. 2005; Hall and Riskind 2010) and their coprolites (Smith et al. 1995; Smith and Betancourt 1998, 2006), there are few articles that discuss pollen representation in packrat coprolites (Van Devender and King 1971; Thompson 1985).

One unexpected discovery, during our analysis, was the presence of the algae *Pediastrum* spp. in the packrat feces (Figure 4; Appendix, Table A1). Packrats can acquire all necessary water needs through diet alone (Linsdale and Tevis 1951, p. 293). Today, there are no known sources of water near Paisley Caves that would be within the foraging range of packrats. *Pediastrum* algal species prefer large bodies of water with few exceptions (Jankovská and Komárek 2000). We also agree with the conclusion about the algae *Botryococcus*, which Mehringer and Wigand (1990) encountered in their study of packrat middens from Diamond Craters. In their case and ours, we believe the *Pediastrum* and *Botryococcus* remains can be attributed to the recycling of dust from floors of ephemeral ponds and seasonally dry marsh margins.

4.3. Quantitative analysis

When visually comparing the packrat samples to sediment samples already analyzed (Appendix, Table A2), we found several similarities as well as a few differences. Not all of these differences can be explained by dietary preference. Based on the shared groupings, the cluster analysis suggests that the environment represented by modern samples 3 and 8 is the most like the environment represented by those packrat and sediment samples. In the cluster analysis, Group 2 contained three packrat samples, five modern samples and one sediment sample. This would suggest that the environment indicated by the packrat and sediment samples in group 2 is possibly most like the environment represented by our modern samples 2, 5, 7, 10, and 11. This is noteworthy because sediment sample 1 is the deepest and therefore oldest sample we examined from Paisley Caves. Groups 4 and 5 only contained modern samples (1, 6, 9, and, 12). Additionally, because the modern samples fall into more groups than the packrat and sediment samples, we can conclude that there is probably more vegetation variation in the region today than occurred in the Paisley Caves region during the pre-Mazama period spanning nearly 5,000-7,000 years. Fossil pollen data and a climate reconstruction based on nearby Dead Horse Lake sediments suggest that region was about 3 °C lower during the coldest months and between 1-3 °C higher during the warmest months of the Younger Dryas (Minckley et al. 2007). While the fossil pollen from the sediment and packrat samples suggest little environmental change, we suspect Minckley's temperature reconstruction could also be applied to the Paisley Caves area. Other pollen data from sites near Paisley Caves support the conclusion that the area around the Paisley Caves was likely a shrub steppe throughout the time periods covered by our sediment and packrat samples (Minckley et al. 2008).

5. Conclusions

We believe the analysis of pollen and other materials derived from packrat coprolites can be a useful addition to the more common and traditional analysis of packrat middens as well as being a valuable component of archaeological site interpretation when available. Middens show which plant materials packrats were collecting, but not exclusively what they were eating. Instead, middens can contain material collected for protection in addition to material collected specifically for

dietary purposes (Smith 1997; Hemmes et al. 2002; Verts and Carraway 2002). Similarly, cave site sediments can contain pollen borne by natural processes, such as wind or by aspects related to human habitation. The specificity of packrat coprolites can serve to enhance our understanding of these methods by showcasing exactly which plants in the local environments these animals chose to eat.

The statistical analyses show that the packrat data and the sediment data are similar, with a few exceptions. If this similarity is not merely a product of contamination of the sediment by the packrat coprolites, then the pollen evidence suggests that the packrat coprolites provide additional indications of the local environment but also provide a potential for over-representation of pollen from packrat dietary staples. Perhaps the best way to gain more certainty concerning the possibility of sediment and coprolite mixing at the Paisley Caves would be to gather additional samples. The inclusion of a third data set originating from a nearby depositional environment (i.e., lake or bog) to compare to both the packrat and sediment pollen data sets would provide greater clarity to the issue. This environmental sample, likely collected as a sediment core, would need to be contemporaneous with samples from Paisley Caves, spanning the period from about 17,000-5,000 cal yr B.P. The sediments would likely reflect pollen deposited by wind and water sources, limiting biotic contributions. This core sample should provide a pollen record with minimal influence from human or packrat activity.

In our previous paper, we concluded that pine trees were not part of the paleovegetation growing locally at Paisley Caves (Beck et al. 2018). This conclusion was based on comparing the ratios of pine pollen found in the prehistoric sediments with those pine ratios found in the region today. We believe our assumption is correct and conclude that the pine pollen found in both the cave sediments and the packrat coprolites came from long-distance transport sources. Pines produce large amounts of pollen that travel long distances, often allowing the pollen to become over-represented in areas where pollen production by local plants is relatively low (Mack and Bryant 1974; Jackson and Lyford 1999). If macrobotanical analyses of the site were to reveal large amounts of pine material we would be forced to re-evaluate our pollen-based conclusions. In undertaking this study, we were expecting the packrat coprolite values to be dissimilar from the sediment values. Without statistical analyses, we might have concluded that both the sediment samples and the packrat coprolites were quite distinct. However, the use of PCA and cluster statistics reveal that there are some differences, yet each dataset did not prove unique.

However, despite the similarities of the sediment and packrat pollen samples indicated by PCA and cluster analysis, when compared to the pollen record of the sediments, the packrat record shows more variability than the sediment samples. This suggests that the packrat coprolites are in some cases reflecting specific meal choices and that any one packrat coprolite might over-represent specific plant taxa in the environment and thus should not alone be considered a representation of past or present plant communities. This dietary assumption is confirmed by the presence of pollen clumps and anthers in the packrat-coprolite samples.

Our study used the composite pollen data from 0.25 g of coprolites, which averaged about 57 individual coprolites. Even though the composite approach we used blurs the data from individual coprolites, we believe it gave us a better overall view of average diets than we would have found by examining only one coprolite at a time. A potential future packrat-coprolite study could examine each separate coprolite from a closely-related deposit. That study might show diet variation of individual packrats or similar dietary habits.

5.1. Future research

This study was undertaken to determine the practicality and methods of packrat-coprolite processing and analysis. We have demonstrated that this type of analysis is possible, practical for understanding packrat diets, and offers insights that reflect local environments. Additional studies of pollen in packrat coprolites, particularly as they relate to their midden contents are needed to continue to search for potential biases and variations. These steps are necessary to begin the process of disentangling the formation processes of complex archaeological cave sites.

Reinhard and Araujo (2015) mentioned the relationship between packrats, kissing bugs (Triatominae), and the spread of Chagas Disease (*Trypanosoma cruzi*) in prehistoric North America. Triatomine species are unrecorded in Oregon today (Bern et al. 2011) and we did not attempt to identify any insect parts found in the packrat feces. However, it would be valuable to attempt to do so in the future, particularly in regions with strong archaeological evidence of Chagas Disease.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix

Table A1. Raw counts of packrat coprolite samples.

Paisley Cave packrat samples															
Sample Number	4	6	8	10	11	14	18	22	24	25	28	31	34	36	37
Plant Taxa															
Abies (fir)	1	0	1	0	0	0	0	0	X	1	1	1	3	1	X
Alnus (alder)	0	0	2	1	1	4	4	5	1	1	2	0	1	1	0
AMARANTHACEAE (old Cheno-Ams)	210	47	76	38	75	102	99	73	101	73	87	98	83	104	36
APIACEAE (umbel family)	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0
Arceuthobium (dwarf mistletoe)	0	0	0	0	0	0	1	0	0	2	0	0	0	1	0
Artemisia (sagebrush)	107	140	98	165	96	120	92	105	68	72	64	64	57	15	30
ASTERACEAE (HS-type)	38	34	3	15	17	0	2	16	11	14	5	15	12	34	271
ASTERACEAE (dandelion-type)	10	4	0	4	0	0	0	0	0	0	0	0	0	0	0
ASTERACEAE (ragweed-type)	3	3	7	2	2	0	4	X	3	0	0	1	1	1	0
Betula	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
BRASSICACEAE (mustards)	0	0	0	0	0	0	0	1	0	4	0	0	1	0	0
CARYOPHYLLACEAE (carnation family)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
cf. Centaurea	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Corylus (filbert)	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
CYPERACEAE (sedge)	0	0	1	0	0	2	3	4	0	0	1	0	1	0	2
cf. Elymus cinereus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cf. Eriastrum (POLEMONIACEAE)	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
ERICACEAE (ericads)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriogonum (wild buckwheat)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Erodium (stork's bill)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FABACEAE (legumes)	0	0	0	1	2	0	0	0	1	0	0	1	0	1	0
Ferns	0	X	X	X	0	X	0	0	X	2	X	0	2	1	0
Juniperus (juniper)	0	0	4	0	3	8	8	12	5	14	4	6	19	7	3
Montia	0	0	0	0	0	0	X	0	1	0	0	0	0	0	0
Myriophyllum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ONAGRACEAE	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0
Pediastrum	0	0	0	0	0	0	0	1	X	0	0	0	0	0	0
Phacelia (scorpion weed)	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0
Phlox (phlox)	1	1	3	0	24	0	0	9	0	0	0	0	0	0	X
Picea (spruce)	0	0	1	0	0	0	0	0	0	0	X	0	X	X	0
Pinus (combined)	11	55.5	181	69	102	145	124	129	175	188	244	201	247	238	82
POACEAE (grass)	2	93	15	89	57	11	26	16	21	43	4	15	6	4	2
c.f. Polygala	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
POLEMONIACEAE	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Polygonella (joint weed)	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Polygonum coarctum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0
Populus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pseudotsuga (Douglas fir)	0	0	X	0	0	0	0	X	0	0	0	0	0	0	0
Quercus (oak)	0	0	1	0	0	3	2	5	1	2	0	0	2	2	0
RHAMNACEAE (buckthorns)	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
ROSACEAE (rose family)	0	2	1	0	0	1	2	3	1	1	0	4	1	0	0
Rumex (dock)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix (willow)	0	0	0	1	0	1	0	3	1	0	0	0	1	0	0
Sarcobatus (black greasewood)	0	8	7	8	8	4	11	10	5	10	9	5	5	9	20
SCROPHULARIACEAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tsuga heterophylla (Western Hemlock)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Typha latifolia (cattail)	0	2	X	2	0	2	0	X	0	0	0	0	0	1	1
Type A	2	0	1	0	5	0	2	0	7	1	4	2	0	1	1
Unknown	13	13	4	13	7	6	8	39	8	13	1	4	10	7	3
Degraded/Indeterminate	16	12	4	13	15	10	15	26	15	12	7	13	16	10	4
TOTAL	416	415.5	411	424	414	424	406	470	428	463	435	430	470	440	456

"X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts.

Table A2. Raw counts of archaeological samples.

Sediment sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Abies	2	3	4	3	2	3	3	1	1	1	0	1	3	1	X	X	3	1	1
Alnus	5	2	0	0	0	1	1	1	1	2	1	3	0	1	4	2	1	1	2
APIACEAE	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	4	0	0	2
Artemisia	29	67	60	84	77	83	59	90	71	83	77	77	69	89	82	90	64	97	85
ASTERACEAE (dandelion-type)	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
ASTERACEAE (high spine-type)	35	23	15	23	21	8	10	9	8	11	5	10	18	10	17	9	15	16	21
ASTERACEAE (low spine-type)	9	2	1	1	4	6	2	5	1	0	2	0	3	4	5	1	3	4	0
Betula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
BRASSICACEAE	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	2	0	0	0
POLEMONIACEAE	0	1	0	0	3	0	2	0	0	0	0	0	1	0	0	1	0	0	0
AMARANTHACEAE	16	30	31	12	21	60	67	114	92	84	124	137	123	83	95	89	65	113	108
Corylus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
CYPERACEAE	0	0	0	0	1	1	2	1	2	3	1	3	4	1	3	2	1	0	0
Dalea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eriogonum	9	2	2	1	0	1	1	0	0	0	0	2	4	1	0	0	2	0	1
FABACEAE	0	0	1	0	0	0	0	0	2	1	0	1	0	1	2	1	1	0	1
Ferns	1	2	1	0	1	1	0	0	1	1	1	2	3	2	1	3	2	1	3
CUPRESSACEAE	0	2	0	3	1	1	0	2	1	6	3	2	3	4	6	11	6	9	7
ONAGRACEAE	0	1	1	0	0	0	0	0	0	0	0	X	X	1	X	0	0	1	2
Phacelia	0	2	3	0	0	1	1	9	1	0	8	1	3	1	0	0	1	1	2
Phlox	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Picea	1	1	0	1	0	3	2	1	0	1	2	X	X	1	X	0	0	0	0
Pinus (diploxylon)	204	180	214	186	227	186	231	119	156	183	131	112	140	169	159	127	189	104	124
Pinus (haploxylon)	2	8	14	37	18	17	7	12	16	5	13	7	2	6	6	8	16	14	12
POACEAE	20	17	7	7	4	7	8	8	9	9	8	8	11	8	13	11	12	10	12
Populus	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Pseudotsuga	5	0	0	0	1	0	0	0	0	0	0	0	X	X	X	X	1	0	0
Quercus	1	0	0	0	0	0	1	1	1	3	0	3	1	1	1	6	2	1	0
RHAMNACEAE	0	6	1	0	0	2	0	1	3	0	1	0	5	4	6	4	7	3	0
ROSACEAE	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	2
Rumex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Salix	0	3	7	1	1	1	2	0	2	2	0	1	1	2	0	2	0	0	0
Sarcobatus	2	8	11	9	6	8	5	12	9	6	11	2	5	5	5	8	6	11	7
Tsuga	1	1	0	0	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Typha latifolia	0	3	0	0	0	1	0	2	0	0	3	0	2	0	0	0	2	1	1
Type A	0	0	0	0	0	2	4	0	2	2	0	5	0	3	1	3	2	0	1
Unknown	0	13	6	0	8	4	0	0	5	13	0	2	1	6	8	2	4	0	1
Degraded/Indeterminate	87	24	31	32	16	13	16	19	23	8	16	24	25	12	17	24	14	27	25
Total	429	404	413	401	415	411	424	407	410	424	409	404	431	420	432	421	422	417	421
Lycopodium	86	26	13	7	9	5	3	10	4	7	4	11	8	6	10	33	7	8	4.69
Concentration value	9,270	29,663	59,326	137,817	85,693	152,000	262,654	75,637	190,486	258,772	190,021	68,254	100,121	129,699	104,535	94,835	114,790	96,869	166,711

Sediment Sample Number	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Abies	0	2	0	0	0	X	1	2	0	2	1	1	2	0	0	4	1	5	2
Alnus	3	1	0	1	2	1	3	1	0	3	0	1	1	1	3	0	0	0	1
APIACEAE	0	0	1	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0
Artemisia	49	84	65	52	60	58	44	35	53	57	59	67	55	52	47	41	37	49	49
ASTERACEAE (dandelion-type)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASTERACEAE (high spine-type)	13	9	5	15	4	4	8	2	5	9	10	8	3	9	7	6	6	5	10
ASTERACEAE (low spine-type)	2	2	0	0	1	3	6	0	2	0	1	7	1	1	2	0	2	1	2
Betula	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
BRASSICACEAE	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0
POLEMONIACEAE	0	0	2	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
AMARANTHACEAE	98	64	86	97	128	102	134	94	121	97	79	108	101	101	83	94	126	65	82

(*continued*)

Corylus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
CYPERACEAE	1	2	3	1	0	1	1	1	1	0	1	1	0	0	0	2	0	2	1
Dalea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriogonum	1	3	0	1	0	0	2	0	0	0	0	1	0	0	0	1	0	0	0
FABACEAE	0	0	0	0	1	0	1	0	0	0	1	4	0	0	0	0	0	1	1
Ferns	1	3	3	3	0	1	1	2	1	1	2	1	0	0	2	3	0	2	0
CUPRESSACEAE	6	4	8	6	3	8	3	3	5	9	7	9	13	11	4	11	8	9	8
ONAGRACEAE	1	1	0	1	0	0	1	X	1	0	0	1	0	0	0	0	0	1	0
Phacelia	0	0	1	1	0	0	0	0	1	1	0	0	3	0	0	0	0	0	0
Phlox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picea	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Pinus (diploxylon)	209	219	202	193	165	166	164	237	208	187	207	167	197	178	244	214	188	238	202
Pinus (haploxylon)	9	6	3	6	11	8	6	8	30	4	7	7	5	8	6	5	15	3	10
POACEAE	7	7	7	8	9	6	7	8	8	7	1	11	2	5	5	6	3	4	5
Populus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudotsuga	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0
Quercus	0	1	4	1	2	3	1	0	0	1	2	0	1	0	1	0	0	1	0
RHAMNACEAE	7	2	0	2	1	1	1	2	3	2	1	5	0	2	2	0	0	0	3
ROSACEAE	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1
Rumex	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix	0	0	1	0	1	2	1	0	0	3	0	1	0	0	0	0	0	0	0
Sarcobatus	5	3	5	5	8	6	4	4	7	5	5	8	7	3	3	4	16	6	6
Tsuga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Typha latifolia	1	1	0	0	0	2	1	1	1	2	1	0	0	0	0	1	0	0	0
Type A	6	2	2	2	4	1	2	1	6	3	1	4	2	5	3	0	1	0	1
Unknown	1	3	10	3	3	13	4	5	4	3	1	3	8	1	4	1	0	3	3
Degraded/Indeterminate	19	25	13	17	17	13	25	15	10	25	15	13	15	34	24	27	11	8	23
Total	439	445	422	418	422	400	423	422	470	424	404	430	418	413	440	420	415	406	410
Lycopodium	5	6	3	4	6	12	5	5	4	2	5	2	5	4	5	8	4	3	15
Concentration value	163,539	137,831	261,415	194,203	130,707	61,947	157,221	156,849	218,362	393,981	150,159	399,556	155,362	192,344	163,539	97,566	192,809	251,503	50,796

"X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts. Reprinted with permission from Beck et al. 2018.

Table A3. Raw counts of modern samples.

Modern sample number	1	2	3	4	5	6	7	8	9	10	11	12
Abies	2	X	1	2	X	X	1	1	X	2	2	5
Alnus	0	0	1	0	2	1	0	0	0	1	0	1
APIACEAE	0	0	0	0	4	1	1	0	0	0	0	0
Artemisia	16	75	63	19	84	73	12	50	9	17	24	5
ASTERACEAE (dandelion-type)	0	25	0	0	5	3	2	1	0	0	0	0
ASTERACEAE (high spine-type)	0	0	3	1	15	25	43	5	2	27	43	4
ASTERACEAE (low spine-type)	0	4	1	3	3	12	3	1	1	4	2	0
Betula	1	0	0	0	0	0	0	0	0	0	0	0
BRASSICACEAE	0	0	0	0	0	0	4	1	0	0	0	0
AMARANTHACEAE	90	62	34	89	11	16	12	29	135	0	1	0
Corylus	0	0	0	0	1	0	0	0	0	0	0	0
CYPERACEAE	0	0	0	1	0	0	0	0	3	16	1	0
Eriogonum	3	1	2	0	1	1	3	2	0	0	2	0
Erodium	0	0	0	0	0	0	3	0	1	0	0	0
FABACEAE	0	0	0	0	0	0	1	0	0	1	0	0
Ferns	1	0	0	1	0	1	0	0	1	2	1	0
CUPRESSACEAE	7	5	8	20	20	7	9	16	9	14	33	1
ONAGRACEAE	0	0	0	0	X	0	0	0	0	0	0	0
Phacelia	0	0	0	0	0	0	0	0	0	0	0	0
Phlox	0	0	0	0	1	0	0	0	0	1	1	0
Picea	X	1	X	0	0	0	2	X	X	X	X	2
Pinus (diploxylon)	148	121	195	136	88	74	203	197	131	190	226	335
Pinus (haploxylon)	5	5	5	4	0	1	3	0	0	4	4	1
POACEAE	21	52	13	17	59	127	51	27	26	75	24	20
Populus	4	2	5	2	2	4	3	8	0	2	3	8
Pseudotsuga	X	2	1	0	X	X	X	X	1	2	X	1
Quercus	0	1	0	1	4	2	0	0	1	1	0	0
RHAMNACEAE	0	0	0	2	1	0	0	0	0	0	0	3
ROSACEAE	0	0	0	0	0	0	0	0	1	0	0	2
Rumex	0	0	0	0	0	0	0	0	0	2	0	0
Salix	0	0	0	0	0	2	0	0	0	0	0	0
Sarcobatus	81	3	6	57	2	0	2	0	32	2	1	0
Tsuga	X	x	X	1	X	X	X	X	2	4	3	1
Typha latifolia	0	0	0	0	2	0	1	0	0	0	0	0
Type A	0	1	0	0	1	0	0	1	0	0	0	1
Unknown	4	1	6	2	1	2	6	9	2	0	3	0
Degraded/Indeterminate	41	59	60	44	106	61	57	69	54	43	47	20
Total	424	420	403	401	413	413	421	416	411	409	419	406
Lycopodium	18	8	10	24	13	3	5	5	14	20	9	6
Concentration value	43,776	97,566	74,894	31,051	59,040	255,840	156,477	154,619	54,557	38,004	86,512	125,752

"X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts. Reprinted with permission from Beck et al. 2017.