DEVELOPING NEW TECHNIQUES IN COPROLITE ANALYSIS: PACKRAT FECES FROM PAISLEY CAVES AND HUMAN COPROLITES FROM HINDS CAVE

A Dissertation

by

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ABSTRACT

The Paisley Caves (35LK3400) are a system of rockshelters in the Summer Lake sub-basin of Oregon. Excavations of these caves resulted in the discovery of 14,300-year-old coprolites yielding ancient human DNA. Pollen analysis from Paisley Cave 2 has produced a record of climate change affecting the Summer Lake Sub-basin during a 7,000-year time period spanning between ~14,500 and 7,600 cal BP. The sediments of the Paisley Caves provide an opportunity to examine questions concerning human-environmental interaction at the end of the Pleistocene Epoch, during the Younger Dryas climatic event. The cave sediments are mixed with abundant, disaggregated, packrat coprolites. A study of pollen records in Cave 2 deposits shows a relatively unchanging environment that combines predominantly xeric conditions with subalpine and marsh communities nearby as well as little evidence of culturally-significant use of any specific plant species. I developed a technique for processing the packrat coprolites. Using this technique, I analyzed fifteen packrat coprolite samples separated from sediments collected from the sidewall of a test unit within Paisley Caves 2. The results were then compared to the previous study based on the fossil pollen in the sediment from the same site. They were similar. However, I found that the packrat coprolites were prone to dietary biases that could mask the true paleovegetation of the area. Methods of processing and sampling human coprolites have changed since the early days of analysis. However, rather than standardizing sampling size and sampling location, practices for collecting material have become specialized by preference and research focus. When sampling a human coprolite for pollen data, sample size and sampling location affect the conclusions of a study. By subsampling five coprolites from Hinds Cave, five times, in five different locations on each coprolite, I was able to compare the pollen ratios from each subsample. I conclude that not only is pollen distribution within a single coprolite

heterogeneous, but this lack of homogeneity can result in different interpretations of the coprolites' contents. These different interpretations can affect conclusions concerning the diets of ancient inhabitants and conclusions concerning the paleoenvironments of the associated archaeological sites.

DEDICATION

To my Father, Kim W. Beck, who always encouraged me.

In faeces veritas est.

Etaion Shrdlu

κοπροφορεω.

Herakles

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The work contained herein may not be my highest academic achievement, but it does represent my highest academic achievement up to this point. It would be impossible for me to arrive here were it not for the efforts of my advisory committee. Particularly, Dr. Bryant has always motivated me to do better than I thought myself capable. Dr. David Carlson performed invaluable analyses of the Hinds Cave coprolite samples. Dr. Ted Goebel has been essential in helping me think about site taphonomy in the Great Basin. Dr. Anne Raymond has helped me consider the ways environmental effects will be reflected by fossil remains across time.

I also must acknowledge the works of those that came before. Chantel Saban's Master's Thesis on the pollen from Paisley Caves inspired my own efforts in that arena. Tim Riley began looking at packrat coprolites, also from Paisley, but was unable to complete that project before completing his studies and accepting a position elsewhere. Additionally, all of the people who have devoted their lives and studies to understanding human coprolite composition and determining all the information we can extract from what otherwise might be overlooked as merely waste. While there are more than can be mentioned here, I would specifically like to acknowledge the efforts of Glenna Dean, Kristen Sobolik, Karl Reinhard, and Sarah Tennison, all without whom, my work would not be possible.

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NOMENCLATURE

BP	Before Present
MASL	Meters Above Sea Level
UO	University of Oregon
DNA	Deoxyribonucleic Acid
aDNA	Ancient DNA
YD	Younger Dryas
PYD	Post Younger Dryas
Pre-YD	Pre-Younger Dryas
HCl	Hydrochloric Acid
HF	Hydrofluoric Acid
SEM	Scanning Electron Microscope
ESEM	Environmental Scanning Electron Microscope
KOH	Potassium Hydroxide
C	Celsius
PCA	Principle Component Analysis
CONISS	Stratigraphically Constrained Cluster Analysis by the Method of Incremental Sum of Squares
BiG Lab	Bioarchaeology and Genomics Laboratory
TrEnD Lab	Trace and Environmental DNA Laboratory
PCV	Pollen Concentration Value

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CHAPTER I

INTRODUCTION

The questions about early human inhabitants of North America that we return to again and again involve how they lived, what they ate, and what their world was like. There are nearly as many ways to go about finding answers to these questions as there are people interested in asking them. For the purposes of this dissertation, however, I used palynology as a well-understood method for pursuing answers to these questions. Pollen is a particularly useful source for answering these questions due to a number of unique characteristics. It is ubiquitous, due to the constant pollen rain. It is resilient to degradation in sediment. Finally, because it is often purposefully or incidentally ingested, it is frequently found in association with archaeological sites and artifacts.

By putting the habitation at Paisley into a clearer environmental context I present a basis of comparison for earlier, contemporary, and later human habitation sites in the region. The importance of this project is partially in developing a high-resolution, paleohistory of the Paisley Caves site. One of the confounding factors at the site, an abundance of packrat feces, needed to be addressed. While pollen and macrofossils from dens, burrows, or middens are useful for paleoenvironmental reconstruction in arid environments (Horowitz 1992:69-78), actual fecal remains of packrats are often discarded prior to analysis.

While desiccated packrat feces (packrat coprolites) might have gone overlooked in the past, desiccated human feces (human coprolites) have a long history of study

(Bryant and Reinhard 2012). However, due to the many researchers and research questions answered by human coprolite analysis, not all methods of coprolite analysis are equal. In an effort to begin some standardization, and to call into question some recent recommendations for human coprolite analysis (Wood and Wilmshurst 2016), I conducted a small study aimed at identifying and quantifying the amount of pollen variability within a coprolite. While pollen is a constant theme in these studies, they also have other unifying characteristics.

Caves and Arid Environments

The Paisley Caves archaeological site is a series of shallow caves (Jenkins 2007). Hinds Cave is a rockshelter among a series of rockshelters (Williams-Dean 1978). Caves and rockshelters can be particularly useful for palynological study in arid regions where other sources of paleoenvironmental pollen data are scarce (Dimbleby 1985:126). Complete desiccation of pollen grains (due to conditions common in arid environments) could prevent deterioration (Wodehouse 1935). Protection from oxidation and UV radiation (like that offered by the roof of a cave or rockshelter) may be just as important. However, despite these potential benefits, the problems that can affect cave pollen deposits are not as well understood as those associated with open-sites (Carrión et al. 1999).

It is necessary to individually assess caves for suitability prior to sampling for palynological data (Horowitz 1992:122). Dry caves are generally good repositories of pollen sequences. Taphonomic factors that can potentially affect fossil pollen cave data are: 1) where the pollen originates; 2) where the pollen becomes deposited in the cave

sediments; and 3) the preserved pollen's ability to reflect the original, regional vegetation (Coles et al. 1989). These factors are complex, interrelated, and must be assessed when interpreting cave pollen profiles (Hunt et al. 2015). Any pollen found in a cave was likely carried to the site from its point of origin by one or more vectors. Cave roofs and walls present a physical barrier to pollen intrusion preventing some from entering. Air transport, waterborne transport, and biotic transport (including humans) are the most common means of pollen introduction into a cave (Horowitz 1992, p.120; Hunt et al. 2015). Other sources of pollen and microscopic particles can come from dissolved minerals entering caves through the percolation of water, dissolving material from the roofs of caves (Coles et al. 1989; Lauritzen et al. 1990), or through graviturbation, specifically the mass-wasting of nearby slopes and the movement of liquefied materials across and into the floor of the cave (Waters 1992, p. 301).

Due to their arid settings, it is unlikely that waterborne transport was a major contributor to the pollen at the Paisley Caves or Hinds Cave. However, there is evidence that, on rare occasions, high winds caused rainwater intrusion into the Paisley Caves. These were 'instantaneous' events (Jenkins et al. 2012; 2013). Had these wet conditions happened frequently, over extended periods of time, pollen destruction, due to alternating sequences of wetting and drying, would have been a major factor in these deposits (Campbell and Campbell 1994). Additionally, the coprolites and perishable artifacts at the site would not have been preserved for later recovery (Jenkins et al. 2012; 2013). The deposits were formed in a semiarid environment and were over-whelmingly protected from wetting by the cave (Hansen 1947b; Allison 1982). The aridity of the

deposits at both Hinds and the Paisley Caves discouraged fossil pollen destruction due to microbial activity (Havinga 1984; Bryant and Hall 1993).

Coprolites

Packrat middens, while containing an abundance of macrofossil remains, also include a large amount of packrat feces. These feces can provide direct evidence of packrat dietary choices. By comparing the packrat feces pollen to sediment pollen from the same site, it becomes possible to observe and quantify the degree of packrat dietary bias at a site, through time. Like the packrat feces composition question, there is no consensus for human coprolite sampling procedure when it comes to amount or which portion of the coprolite to sample. This is true whether performing pollen, macrofossil, or any number of the other analyses common in coprolite studies. Additionally, many make the mistake of assuming that a single sample can fully represent the contents of a coprolite. In some of the early human coprolite analyses, the whole coprolite was processed (Callen and Cameron 1960). Today, multiple methods are employed, depending on the research question being addressed and researcher preference. These sampling methods include one-end-sampling (Reinhard et al. 1991), center-sampling (Wood and Wilmshurst 2016), and half-sampling (Bryant 1974; Wigand and Mehringer 1985). Despite the different sampling methods, these methods all rely on the contents of the coprolites being homogeneous. While limited in scope, early research in this area has demonstrated that homogeneity of pollen within a coprolite cannot be assumed (Martin 1965, Kelso 1976, Williams-Dean 1978).

Initially, I had no plans to perform a detailed sediment analysis of the Paisley Caves site. However, with the completion of Saban's work, and her suspect conclusions (2015), it became necessary to publish an account to attempt to correct her story. Because the Paisley Caves site offered stratigraphically intact sediments mixed with packrat feces, it provided a unique chance to compare both and identify areas of potential disagreement. By processing both types of material from their associated strata, I could conduct a direct comparison. While a visual comparison provided insight into how well they matched, some simple quantitative analyses helped confirm and clarify their similarities. Finally, pollen variation within human coprolites had been observed in studies that were now decades old (Martin and Sharrock 1964, Kelso 1976, Williams-Dean 1978). Because pollen variation was not the main purpose of those studies, there had been no real attempt to quantify that variation. An exploration of that topic was long overdue. It was past time to revisit the topic and clarify details that had previously gone overlooked.

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CHAPTER II

ANALYSIS OF YOUNGER DRYAS-EARLY HOLOCENE POLLEN IN SEDIMENTS OF PAISLEY CAVE 2, SOUTH-CENTRAL OREGON*

Introduction

Located in the Basin and Range physiographic region of southcentral Oregon, the Paisley Caves are found at an elevation of 1369.7 m above sea level near Summer Lake in the shrub steppe vegetation zone in North America (Figures II-1 and II-2; Franklin and Dyrness 1988) Human coprolites (fecal material) found in undisturbed layers of sediment at this site date to just over 14,500 cal BP and provide evidence that humans occupied that area of North America before the arrival of the Clovis technological culture (Jenkins et al. 2013). Like most of the pre-Clovis sites in the Americas, the Paisley Caves are subject to skepticism from some scientists although the tide of acceptance of these early sites is gaining momentum (see Poinar et al. 2009; Goldberg et al. 2009; Sistiaga et al. 2014; Wheat 2012; Graf et al. 2013). For this reason, gaining a better understanding of the cultural history, archaeological evidence, and environmental setting in the Paisley Caves region is important.

The Paisley Caves are in a basalt ridge on the southeastern end of the Summer Lake basin in Oregon (Figure II-2; Allison 1945). Today, Summer Lake is a remnant of the much larger Pluvial Lake Chewaucan that once covered nearly 800 square kilometers of the Great Basin in south-central Oregon and at its maximum was estimated to be

nearly 122 meters deep (Allison 1982). The present environment around Summer Lake is semiarid with little rainfall (ca. 300 mm) or runoff; therefore, the main water source continues to come from the Ana River that originates in the northwest side of the 32-kilometer-long Summer Lake basin. The lacustrine beds of the lake and the remnants of the lake's ancient shorelines provide a good record of the paleoenvironment as well as capturing evidence of the volcanic pumice eruptions of both Glacier Peak and Mount Mazama volcanoes (Hansen 1947b). The caves were formed first by wave erosion of softer layers of volcanic breccia and basalt, filling the lowermost levels with lakeshore rounded sands and gravels before the pluvial lake receded leaving a broad grassland plain surrounding the reduced Summer Lake near the Paisley Caves. These ideal conditions must have been attractive for both late Pleistocene mammals and human groups searching for food and shelter around 14,000 years ago (Jenkins et al. 2012).

Interest in the archaeology of the Paisley Caves began with Luther Cressman's long term 'Lakes Project' beginning the summer of 1934 and continuing into the 1940s. Cressman conducted excavations in several caves in the Northern Great Basin of Oregon (Cressman et al. 1940). Following excavations in Catlow Valley he tested the Paisley Caves, which contained evidence of human activity above and below a layer of Mt. Mazama pumice although the origin of this pumice was at the time still under debate (Grayson 2011, p. 252-253).

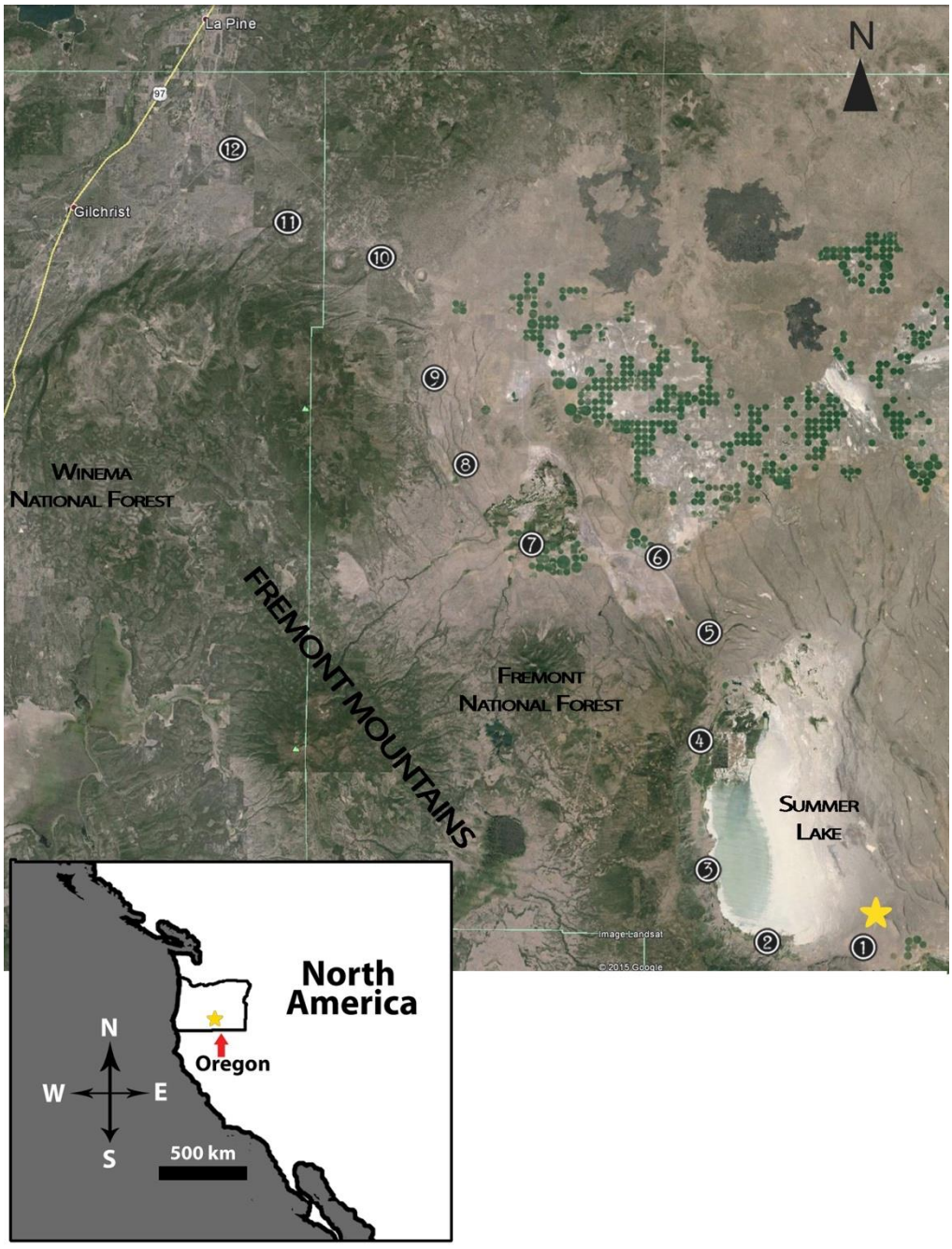

Figure II-1: Map showing the location of the study site (star) and the approximate sampling locations of the surface samples. Satellite image provided by Google. Reprinted with permission from Beck, Bryant, and Jenkins (2018).

Between 1938 and 1939, Cressman found not only lithic and perishable artifacts below this ash layer, but also the remains of late Pleistocene megafauna (Smith 2009). Based on these findings, and with the help of geologist Howel Williams, Cressman concluded that humans had inhabited this region much longer than prevailing theories on the origins of New World peoples allowed (Cressman et al. 1940). Beginning in 2002 and continuing until 2011, Dennis Jenkins and the University of Oregon (UO) archaeological field school renewed excavations at the Paisley Caves hoping to resolve the question regarding the true antiquity of human occupations. Using excavation techniques and analytical methods unavailable during Cressman's time, Jenkins documented evidence of human occupation beginning as early as 14,500 years ago (Aikens et al. 2011, p. 51). Combining extensive radiocarbon (N=241 ^{14}C dates) and obsidian hydration (N=487) dating with ancient DNA, chemical, protein, and hair analysis of human coprolites, Jenkins accomplished what Cressman could not: demonstrating the high probability that humans inhabited the site during the late Pleistocene. This was accomplished through several means, including: correlating radiocarbon dates from organic, extinct megafaunal remains with human coprolites; direct radiocarbon dating of coprolites analyzed for DNA (Gilbert et al. 2008); direct radiocarbon dating of another set of coprolites examined for microscopic and chemical contents (Cummings et al. 2007); and, finally, correlation from various strata with artifacts found at the site (Jenkins et al. 2012, 2013). Although Jenkins' interpretations of early human presence at the Paisley Caves has been challenged (Goldberg et al. 2009; Poinar et al. 2009; Sistiaga et al. 2014), continued study of the site and its contents will

hopefully resolve the question regarding the maximum antiquity of human habitation at the Paisley Caves. What has not been adequately documented is the paleoenvironment to which the earliest inhabitants had to adapt.

Present Vegetation

The present shrub-steppe vegetation of the Northern Great Basin is created in part by the arid 'rain shadow' on the eastern side of the nearby Cascade Mountain Range. The resulting effect is a climate with hot, dry summers, cold winters, and a short growing season. The major vegetation consists of various bunch grasses such as *Festuca idahoensis*, *Poa secunda* and *Pseudoregneria spicata* mixed with three main species of sagebrush including *A. arbuscula, A. rigida, and Artemisia tridentata*. Much of the area has exposed soils (Figure 2).

Figure II-2: Photograph of local vegetation and Paisley Caves archaeological dig from below. Reprinted with permission from Beck, Bryant, and Jenkins (2018).

Immediately to the west of Paisley Caves, and within sight of the caves, lies the physiognomic region of the forested Pinus Ponderosa Zone called the Pumice Region (Franklin & Dyrness 1988). Today, that region of the Fremont National Forest is characterized by *Pinus ponderosa* forests that form a mosaic distribution as they grade downslope into the lower steppe and shrub-steppe communities. The main understory vegetation consists of shrubs such as the ericad greenleaf manzanita (*Arctostaphylos patula),* snowbrush ceanothus (*Ceanothus velutinus),* and antelope bitterbrush (*Purshia tridentata*), which become more common at the lower elevations where ponderosa pine (*Pinus ponderosa*) forests grade into the Shrub-Steppe Zone. Numerous forbs dot the understory of the Pinus Ponderosa Zone including nine leaf biscuitroot (*Lomatium triternatum*), varileaf phacelia (*Phacelia heterophylla*), tail cup lupine (*Lupinus caudatus*), slender *phlox* (*Phlox gracilis*), fireweed (*Chamerion angustifolium*), and lambs tongue ragwort (*Senecio integerrimus*), (Franklin and Dyrness 1988, p.168-183).

Cave Palynology

Caves present ideal locations for conducting archaeological studies of past cultures because humans worldwide often used caves for protection, shelter, religious ceremonies, latrines, and burial of their dead. Palynologists are often asked to collect and analyze cave sediments and human coprolites in hopes of learning more about past environments, cultural habits, human health, and ancient human diets (Bryant and Reinhard 2012).

Fiacconi and Hunt (2015), in their reexamination of pollen deposits in Shanidar Cave, Iraq, noted that unless a cave has a large opening and free passage of air and water, pollen transport and deposition mechanisms may be skewed and therefore the pollen record must be considered accordingly. The same holds true for the pollen recovered from the Paisley Caves deposits. Previous studies have concluded that pollen profiles from inside caves may closely resemble the pollen from the local environment found outside the cave under certain circumstances (Lauritzen et al. 1990; Hunt and Rushworth 2005). However, we are cognizant that we may never be positive that the fossil pollen data from the Paisley Caves provides unbiased clues to the paleoenvironment.

Paisley Caves

The Paisley Caves are located at an average elevation of approximately 1377.70 meters (4520 feet) above sea level. Our study focuses on the fossil pollen record recovered from Cave 2. Cave 2 is approximately 7 m deep by 6 m wide. A large roof fall, dated at ca. 2000 cal BP, spans most of the southwest-facing cave entrance (Figure II-3). UO excavations reached a maximum depth of 240 centimeters at the bottom of Cave 2. The sediments used for the current pollen study were collected by Bryant from a continuous column at the southeast corner of Unit 2/4C (Figure II-4). No visible krotovinas were present in the sediment from which the column was collected.

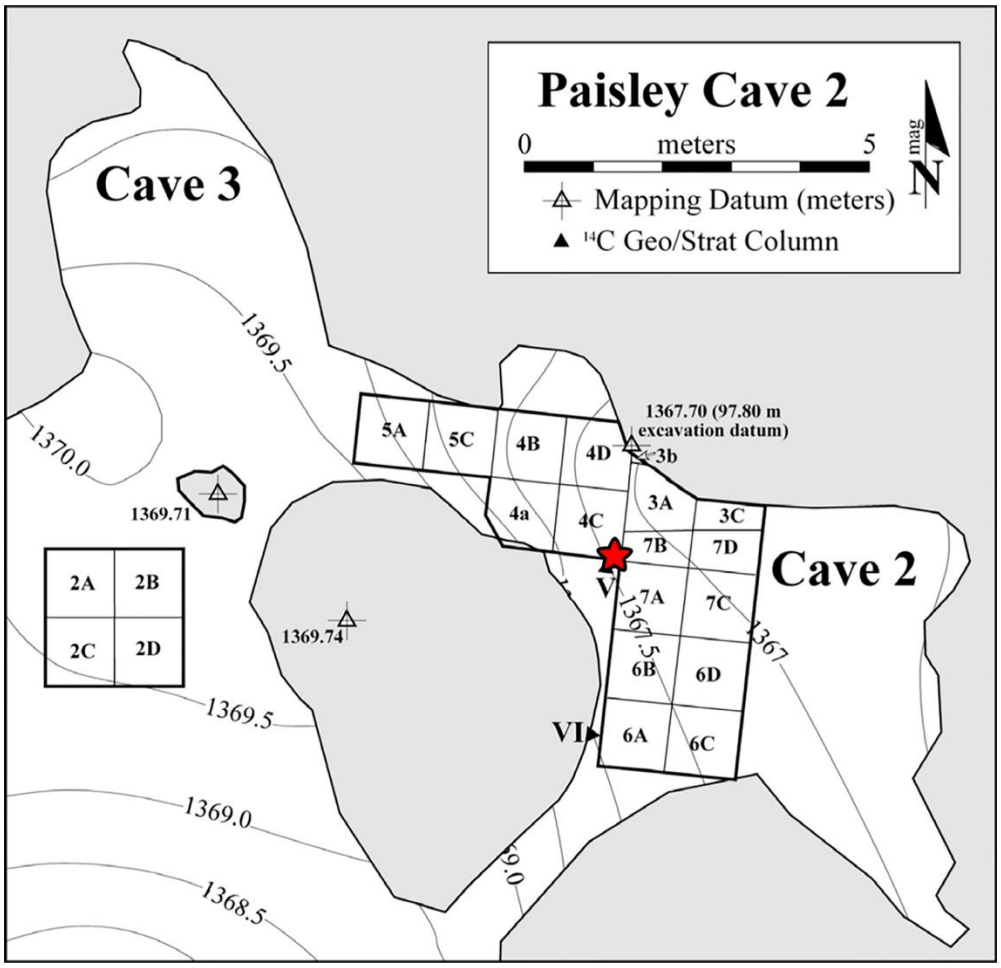

Figure II-3: Plan view map of Paisley Cave 2 showing the sampling location for the sediment samples (star). Reprinted with permission from Beck, Bryant, and Jenkins (2018).

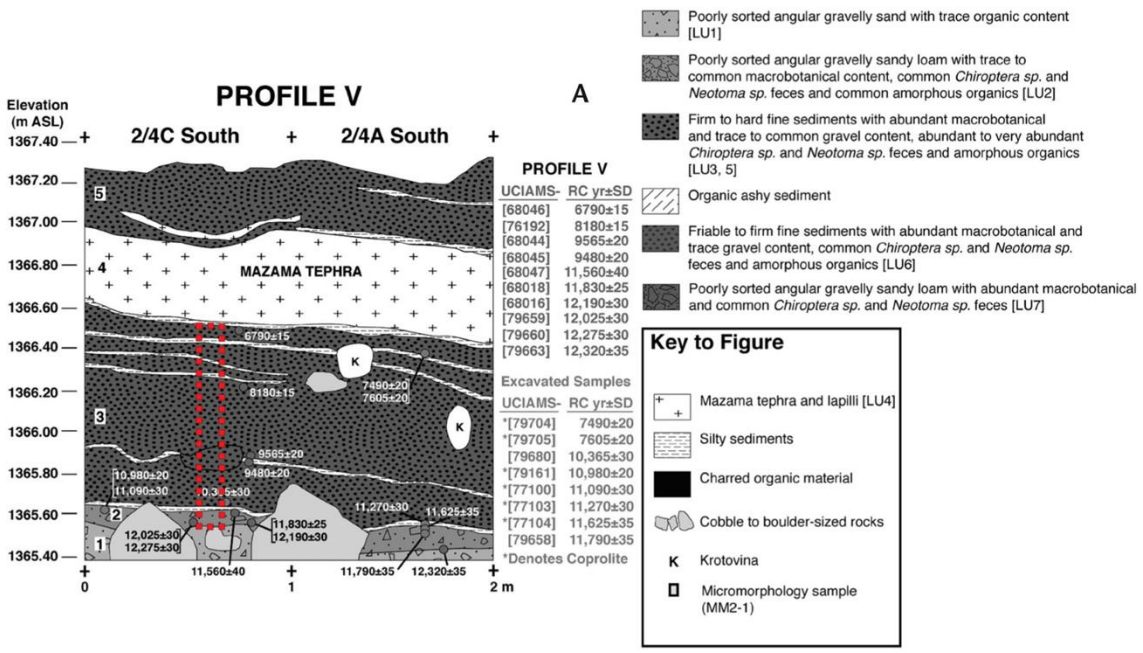

Figure II-4: Profile map showing sediment sampling column (area within dashed line). Reprinted with permission from Beck, Bryant, and Jenkins (2018).

The 38 fossil pollen samples of this study were taken in a continuous profile beginning at bedrock and ending at the base of the Mazama Ash layer, Stratum LU4 dated at ca. 7640 cal BP (Bacon 1983; Jenkins et al. 2012, p. 226). Before sampling, the face of the profile was shaved with a trowel to limit modern pollen contamination. Beginning at bedrock and moving up the profile, each sample was collected using a trowel that was thoroughly cleaned with distilled water between samplings. Each sample was placed in a separate, sterile Ziploc® plastic bag numbered with the provenience of the sample in the column and the sample depth. Each sample consisted of approximately 3 cm of deposits in the profile, which varied from fine grained sand and silt deposits

containing small fragments of angular roof fall, to silty deposits of shredded plant material mixed with *Chiroptera* and *Neotoma* feces (Jenkins et al. 2012).

The chronology of the pollen profile was established by reference to 79 ^{14}C dates, most of which have been previously reported (Jenkins et al. 2012). Those ^{14}C dates from the same test unit were correlated with our sampling column by comparing related elevations within the stratigraphic profile with our sediment samples (Table II-1).

To compare the late Pleistocene paleoecology with the modern environment we collected 12 widely separated surface soil samples from areas beginning close to Paisley Caves and then extending the sampling to off-road areas along Oregon Highway 31 (Figure II-2; Table II-2). The samples were collected at roughly 16-kilometer intervals for comparing modern surface pollen spectra from known vegetational associations with the fossil pollen record recovered from the Paisley Caves. By collecting multiple surface soil samples at varying distances, we could acquire samples from several different elevations and modern plant communities. At each sampling location we collected a soil sample using the 'pinch method' recommended by Adam and Mehringer (1975). We selected sites at least 100 meters away from the highway and sampled throughout an area of about 50 m^2. We tried to select sampling areas that were level and contained the representative vegetation assemblage common at that location. We used sterile plastic spoons to collect the top few millimeters of sediment at each of more than 20 individual locations within the sampling area. All samples were placed in sterile, plastic Ziploc© bags and labeled with the number of the sampling location.

Table II-1: Radiocarbon Dates from 2/4C South. Reprinted with permission from Beck, Bryant, and Jenkins (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[11]	8313 (8338) 8360	HUMAN COPROLITE	33
1366.35	3	1830-PC-2/4C-34-101	UCIAMS-79705	7605±20[11]	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[7]	12,803 (12,896) 12,989	HUMAN COPROLITE	4
1365.6	2	1829-PC-2/4C-49	UCIAMS-77100	11,090±30[7]	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

Once sampling was completed at a location, the sealed sample bag was vigorously mixed to homogenize the sample. At each sampling location we also recorded the vegetational assemblage using the six categories recommended by Daubenmire (1959, see also Table II-2).

Modern Surface Samples

To compare the late Pleistocene paleoecology with the modern environment we collected 12 widely separated surface soil samples from areas beginning close to Paisley Caves and then extending the sampling to off-road areas along Oregon Highway 31 (Figure II-2; Table II-2). The samples were collected at roughly 16-kilometer intervals for comparing modern surface pollen spectra from known vegetational associations with the fossil pollen record recovered from the Paisley Caves. By collecting multiple surface soil samples at varying distances, we could acquire samples from several different elevations and modern plant communities. At each sampling location we collected a soil sample using the 'pinch method' recommended by Adam and Mehringer (1975). We selected sites at least 100 meters away from the highway and sampled throughout an area of about 50 m^2. We tried to select sampling areas that were level and contained the representative vegetation assemblage common at that location. We used sterile plastic spoons to collect the top few millimeters of sediment at each of more than 20 individual locations within the sampling area. All samples were placed in sterile, plastic Ziploc© bags and labeled with the number of the sampling location.

Table II-2: Surface Sampling Locations and Data. Reprinted with permission from Beck, Bryant, and Jenkins 2018.

Sample	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	

Once sampling was completed at a location, the sealed sample bag was vigorously mixed to homogenize the sample. At each sampling location we also recorded the vegetational assemblage using the six categories recommended by Daubenmire (1959, see also Table II-2).

Materials and Methods

Processing

Modern and paleo-sediment samples were first screened through a stainless-steel screen with diagonal openings of 1 mm to remove large debris, coarse sand grains, small rocks, fibrous plant material, rodent feces, and small animal bones. Our goal was to recover a subsample of 10 g of screened sediment from each sample for processing. Only samples 15 (3.89 g) and 16 (2.5 g) did not provide 10 g of sediment. For these exceptions, we recorded the weights and made the necessary adjustments to our calculations. Each sample was placed in a 400 ml plastic beaker to which we added tracer spores that consisted of one tablet (177745 [18,584 ± 829 spores]) of *Lycopodium clavatum* C. Linnaeus.

Chemical extraction began with a rinse using 15% HCl followed by water washes to remove dissolved calcium ions before adding 48% HF to remove silicates. Cellulose and most other organic materials were reduced using acetolysis (9:1 mixture of acetic anhydride and sulfuric acid; Erdtman 1960). The pollen residue was stained with safranin-0 and stored in glycerine until the analysis could be performed.

The amount of recovered fossil pollen in each sediment sample greatly exceeded our initial expectations. A small drop from each sample was spread on a microscope slide using a sterile toothpick to prevent the 'edge effect'.

Pollen Analyses

We prepared two separate slides for each of the 38 archaeological samples and 12 surface samples. Bryant and Beck then counted at least 200 pollen grains for each of the samples by viewing different slides. The counts by each person for each sample were then combined to provide a 400+ grain analysis for all of the paleo-sediment and modern surface samples. Combined count values of the archaeological samples and the surface samples have been included in the Appendix (see Appendix A, tables 0-11 and 0-12, respectively). Throughout the paper we refer to plant and animal taxa variously by their scientific and common names. Additionally, there are some palynological naming conventions that can cause further confusion. We have included a table of names in the Appendix to aid the reader (See Appendix A, Table 0-4). We also scanned slides and noted the presence of important conifer taxa in each sample such as *Abies*, *Picea*, *Pseudotsuga*, and *Tsuga*.

Lycopodium spores were counted but they were not included in the pollen sum for each sample. Pollen concentration values (PCV), the number of taxa in each sample, and the relative pollen percentages were calculated. Pollen concentration values per gram of sediment for each sample were calculated by computing the ratio of marker spores added to the marker spores counted while completing the pollen sum for each sample using the following formula:

$$\frac{\text{(pollen grains counted)(} \textit{Lycopodium} \text{ spores added)}}{\text{(} \textit{Lycopodium} \text{ counted)(grams of soil in sample)}}$$

Pollen Types

Pollen identification was accomplished by identifying standard morphological features of the grains. All fossil pollen identifications were based on comparative modern pollen reference slides stored in the Texas A&M Palynology Laboratory. The fossil pollen grains in each sample were identified, counted, and photographed using a NIKON compound light microscope with an attached NIKON camera. Images were taken for all samples and then viewed by us to ensure the correct identification of pollen types, especially conifer species, unidentified pollen grains, and the questionable identification of degraded pollen. Uneo (1958) recognized two groups of pine (*Pinus* spp.) pollen which were first termed 'diploxylon' (verrucae absent) and 'haploxylon' (verrucae present). We determined that bisaccate conifer pollen grains with at least one bladder attached would be counted as a whole grain. If both bladders were missing the pollen grain body was not counted. Individual detached bladders were each counted as ½ grain. We do not view this as 'overcounting' the pine pollen since if a bladder was attached it was counted with the body as a whole grain, whereas detached bladders were counted as 1/2 grain. Most detached bladders mechanically degrade rapidly, and we only counted detached bladders that were whole; we ignored bladder fragments. When *Pinus* pollen grains could not be verified as being haploxylon or diploxylon, they were included as a diploxylon type because most of the pines growing near the Paisley Caves

are diploxylon types. Therefore, our diploxylon category is labeled as 'Pinus diploxylon and undifferentiated' in our diagrams.

We followed the pollen terminology proposed by Martin (1963) for pollen of the composite family (Asteraceae). He suggested it could be divided into a few major categories such as 'low spine' types, that are wind-pollinated, with surface ornamentation containing tiny spines shorter than 2.5 mm; and the 'high spine' group, including pollen types that are insect-pollinated, with surface spines longer than 2.5 mm. Other groups of composites that Martin separated included the types with fenestrate surface ornamentation (dandelion group) and the sagebrush group (Artemisia). Highly distorted and altered pollen grains that could not be identified with any degree of certainty were placed in the 'degraded,' category. Unknown pollen types that could potentially be identified are listed in the 'unknown' category.

Results

Pine pollen dominated all of the ancient site sediment and modern surface samples examined for this study. We found that some of the pine fossil pollen grains were missing one or both bladders, and sometimes both bladders were collapsed or folded over the germinal furrow making a correct identification of haploxylon vs. diploxylon types impossible.

In both the sediment and surface samples there were only sporadic occurrences of *Tsuga heterophylla* pollen, which could be identified even when they were broken or degraded. However, we did not feel confident in trying to identify *T. mertensiana* pollen

and therefore, all hemlock pollen listed in our report reflects only the presence of *T. heterophylla*.

Cupressaceae tend to rupture easily, especially during changes in humidity or when the pollen contact with water. Once ruptured, the grains often continue to degrade and soon become unrecognizable. Those factors, combined with additional degradation caused by recycling and unfavorable soil preservation, may account for the low recovery of this pollen type in our samples.

We recovered grass pollen in all samples but only in low amounts. Additionally, Amaranthaceae periporate grains, which Martin (1963) called 'Cheno-Am', were abundant in all of our samples. Only small amounts of greasewood (*Sarcobatus*) pollen were found in most of the Paisley Cave sediment samples and in most of the modern surface samples. Of the remaining pollen types identified, none occurs in large numbers; instead, most occur as intermittent examples in both the fossil and modern record. None of the types occurs in a percentage that would provide reliable information about the environment or cultural use patterns.

The fossil pollen concentration estimates in the sediments from the Paisley Caves were higher than expected and show some notable variations (Table II-3, Figure II-5). However, we are not sure whether those variations in pollen concentration values result from dramatic changes in pollen deposition at the site. Dimbleby (1985 p. 130) remarked that, except in cases of frequent human habitation, pollen frequencies in caves are characteristically low. In addition, much of our experience examining pollen from archaeological cave sites in Texas (Bryant 1969; Dering 1979) suggests that pollen

concentration values at Paisley Caves should have been low. However, as we discovered and as noted in Table II-3 and Figure II-5, estimated pollen concentrations at Paisley Caves were quite high. Mayer (1981) has shown that errors can occur in pollen concentration values when total pollen concentrations exceed a ratio of 2:1 (pollen to tracer spores) in a sample. Thus, that error may have led to overestimation and created the irregularities in the pollen concentration values we obtained.

Paleoecology

One way of interpreting the potential reliability of the fossil pollen record from the Paisley Caves is to compare it to other paleoenvironmental studies conducted in the Great Basin with a specific emphasis on those fossil records nearest to the Paisley Caves. Similar pollen records for the Younger Dryas (YD) and later Holocene period come from Hansen's pollen studies and proposed chronology in the Northern Great Basin (Hansen 1947a). He concluded that from 15,000 to 8000 years ago there was a period of gradual warming and drying in the region. Even though Hansen believed the Mount Mazama pumice layer he found in his sediment cores dated to 10,000 BP, his incorrect dates are less important than is his description of the ecological succession revealed by his pollen data. Hansen recognized a western white pine (*Pinus monticola*) predominance and maximum expansion during the period that correlates to the YD.

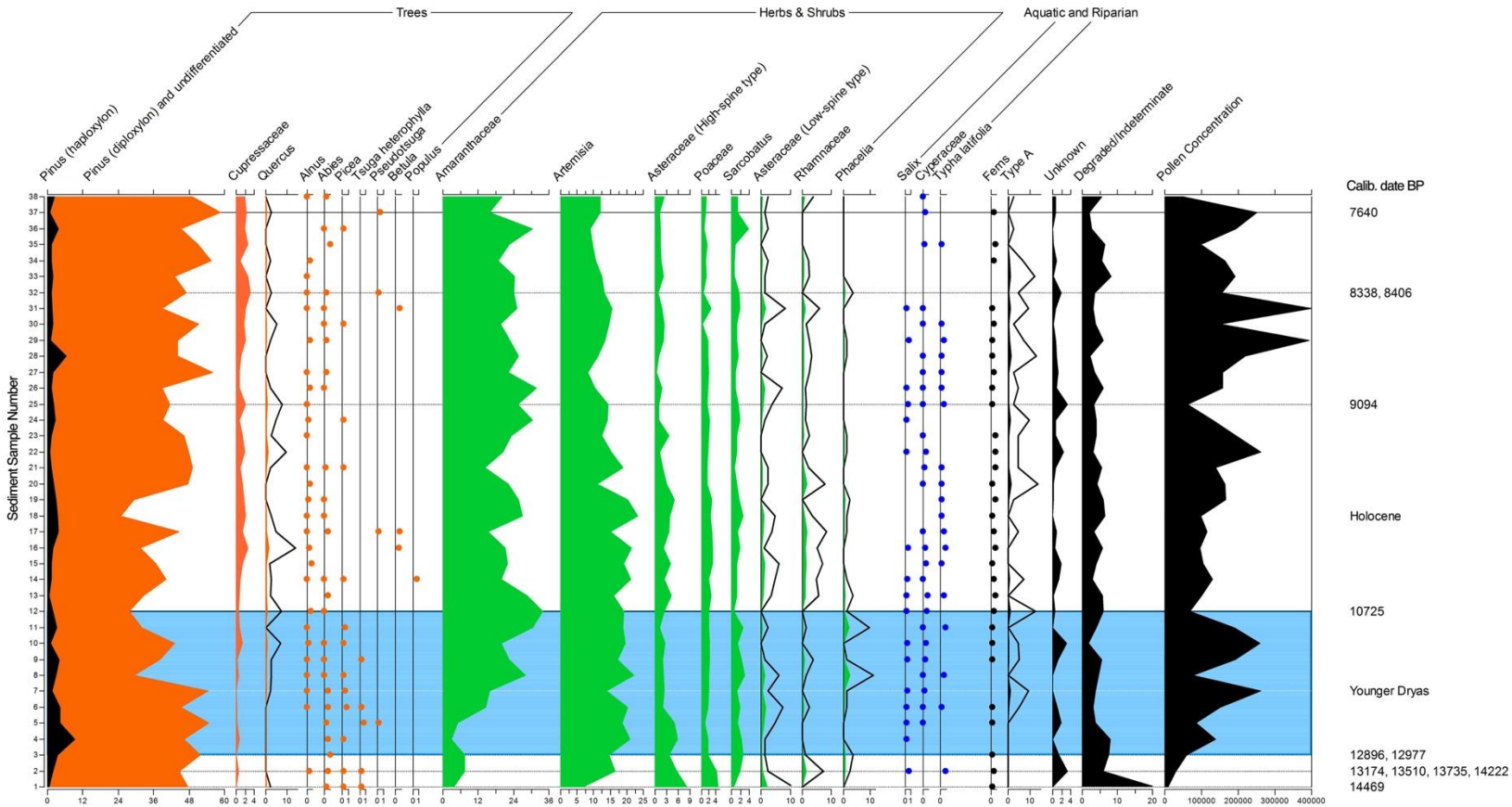

Figure II-5: Pollen chart of archaeological sediment from Paisley Caves. Black outlines indicate ten times exaggeration of pollen percentages. Dots represent taxa that were never present at higher than 1% throughout the samples analyzed. Reprinted with permission from Beck, Bryant, and Jenkins 2018.

This interpretation suggests that the forested areas east of the Cascades in Oregon were at their largest area of expansion and that the steppe regions were smaller in area than during the Post Younger Dryas (PYD) period. According to Hansen, the YD period of forest expansion was then followed by the retreat of conifer forests and the rapid expansion of grasslands and steppes around 12,000 BP characterized by increases in the fossil record of Amaranthaceae and Asteraceae pollen (Hansen 1947a). Our samples show a decrease in pines around the halfway mark of the YD (Figure II-5). However, our data do not confirm an increase in grass, Amaranthaceae or Asteraceae after the YD.

The Minckley and colleagues (2007) fossil pollen study of Eastern Oregon also recognized the same apparent expansion of pines around 14,000 cal BP. Their study included their own sediment core samples as well as summaries of previous cores (eight sites in total). The closest site that they examined near Paisley Caves is a core sample from Dead Horse Lake located approximately 35 km northeast of Paisley Caves at an elevation of 2,248 m, or about 1,000 m higher than the Paisley Caves. Minckley and colleagues (2007) concluded that during the YD the areas around Dead Horse Lake were dominated by a western white pine (*Pinus monticola*) forest with subalpine fir (*Abies lasiocarpa*) present. They also believed that low and high elevation grasslands expanded and covered a larger area between 11,000 and 7,000 BP than at present.

Discussion

Minckley and colleagues (2008) compiled a study of 1,884 modern pollen samples throughout the Western US. By focusing on 14 pollen taxa, they created a system for

recognizing various vegetation types including (among others) grasslands, sagebrush steppes and western pine forests. Additionally, they provided average values for potential pollen types that are representative in each vegetation region as well as notes on their variability and usefulness in typifying the vegetation types in which they are found. For example, Minckley and colleagues (2008) determined that while pine pollen percentages were highly variable, the values were useful in identifying two out of the twelve recognized vegetation types: northern mixed forest and western pine forest. Additionally, they found pine pollen estimates greater than 30% to be highly indicative of forested areas in all but the temperate forest vegetation type.

Such a detailed and diverse study is useful to us in determining prehistoric vegetation pattern changes in the area immediately surrounding the Paisley Caves. Applying Minckley and colleague's (2008) method we could eliminate several vegetation types from consideration, including many forested regions. However, a final determination became complex when the pollen estimations observed in the Paisley archaeological sediments varied distinctly from every modern vegetation type presented by Minckley and colleagues (2008). We note that pine pollen percentages in our samples were high enough to conclude that the area around the caves was forested as per Minckley and colleagues (2008).

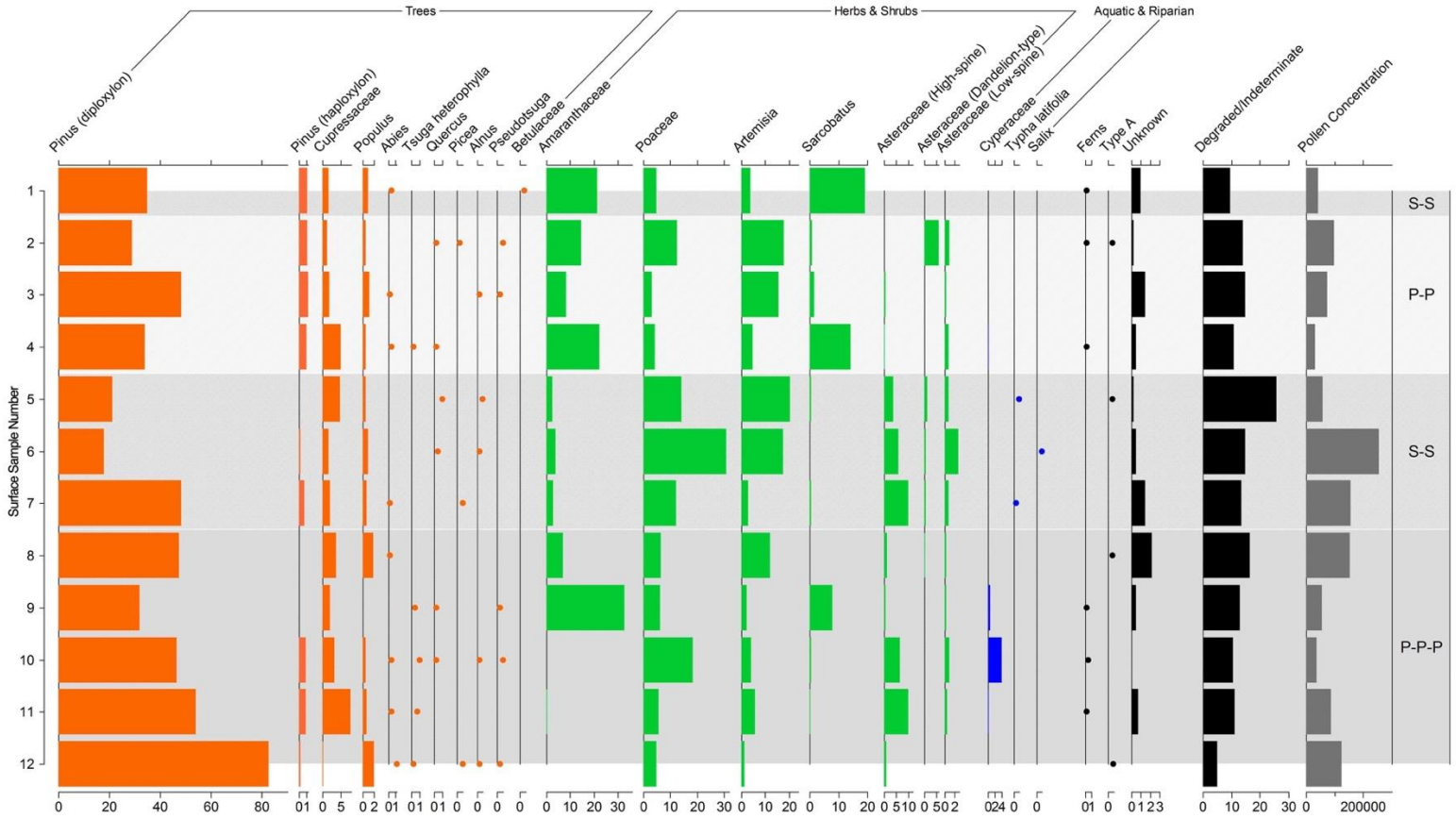

Figure II-6: Pollen chart of modern sediment gather from three ecological zones in the immediate area of Paisley Cave. Dots represent taxa that were never present at higher than 1% throughout the samples analyzed. Reprinted with permission from Beck, Bryant, and Jenkins 2018.

Table II-3: Characteristics of Sediment Pollen Samples. Reprinted with permission from Beck, Bryant, and Jenkins 2018.

Sample Number	Total Number of Pollen Counted	Percentage of Degraded/ Indeterminate Grains	Number of Observed Taxa	Number of Pollen Grains/ Gram of Sediment
1	429	20%	16	9,270
2	415	6%	25	29,663
3	415	7%	19	59,326
4	402	8%	14	137,817
5	415	4%	16	85,693
6	411	3%	21	152,000
7	424	4%	19	262,654
8	407	5%	17	75,637
9	410	6%	23	190,486
10	424	2%	18	258,772
11	409	4%	18	190,021
12	404	6%	21	68,254
13	431	6%	24	100,121
14	420	3%	25	129,699
17	422	3%	24	114,790
18	417	6%	19	96,869
19	421	6%	21	166,711
20	440	4%	20	163,539
21	445	6%	20	137,831
22	422	3%	20	261,415
23	418	4%	22	194,203
24	422	4%	17	130,707
25	400	3%	20	61,947
26	423	6%	24	157,221
27	422	4%	18	156,849
28	470	2%	18	218,362
29	424	6%	22	393,981
30	404	4%	19	150,159
31	430	3%	21	399,556
32	418	4%	17	155,362
33	414	8%	17	192,344
34	440	5%	14	163,539
35	420	6%	15	97,566
36	415	3%	12	192,809
37	406	2%	17	251,503
38	410	6%	17	50,796

However, when comparing those with our own modern surface samples from the Paisley region, we found that estimates of pine pollen in excess of 30% were common even when pines were distant or not visible upon the landscape (surface samples 1, 2, 4, 9, 10, and 11). This determination departs from the conclusions of Minckley and colleagues (2008) but agrees with earlier studies by Mack and Bryant (1974). Additionally, the abundance of pine pollen that we observed during the YD (and throughout our samples) likely reflects mostly long-distance transport of pollen from pine forests some distance from Paisley Caves rather than the presence of local pines.

In arid situations where the local flora consists of low-pollen producers from limited types of wind-pollinated plants and many insect-pollinated taxa - such as grasses, buckthorns, Asteraceae, forbs (herbaceous, non-graminoid, flowering plants), and sagebrush - pine pollen from distant sources can often dominate the local pollen rain (Mack and Bryant 1974; Mack et al. 1978). Pine pollen domination of the local pollen rain of that type can provide the false impression that pine trees are growing locally as suggested by Jenkins and colleagues (2013) and Saban (2015). Those conclusions were based on pollen percentages rather than pine macrofossil remains in the site. There was a paucity of *Pinus* macrofossils at the Paisley Caves site sediments although a few pine nut shells and cone scales were recovered from PYD sediments (Jenkins et al. 2013).

Paleoclimate

The fossil record from Paisley Caves shows that *Artemisia* pollen, as well as species of insect-pollinated types of Asteraceae (i.e., *Chrysothamnus*) are stable during the YD (12,800 to 11,700 cal BP). *Pinus* pollen, while high, seems to decrease dramatically towards the end of the YD. Finally, Amaranthaceae begins at low recorded levels but rises steadily throughout the YD (Figure II-5). The higher proportion of *Pinus* pollen to Amaranthaceae pollen during the YD most probably reflects a cooler and slightly wetter period than in the PYD, when conditions deteriorated, leading to a fairly barren landscape of exposed soils and clumps of grasses mixed with low scrub vegetation consisting of sagebrush and rabbitbrush. Plant macrofossils recovered in Paisley Caves from deposits dated to immediately after the YD period include a few pine nut shells and cones scales. Those macrofossils, dated at 10,010 ±30 (UCIAMS98930; 11,371-11,644 cal BP), 10,165 ±25 (UCIAMS98930; 11,719-11,968 cal BP), and 10,195 ±25 (UCIAMS102111; 11,776-12,014 cal BP), come from deposits in caves 1, 2, and 5. From this evidence, Jenkins and colleagues (2013) concluded that early human occupants were collecting and using resources from local pine trees. The question 'How distant were those pine tree resources?' remains, however. The absence of pine needles from Paisley cave deposits suggests that only a few pine cones and pine nuts may have been collected, which could have been carried to the site from distant pine forests on Winter Rim to the west of the Paisley Caves. The pine pollen records from the same pinecone- and pine nut bearing strata do not suggest pine trees were growing locally. Had pine trees been a component of the local flora at Paisley Caves, we believe that pine

pollen would have dominated the fossil pollen spectra in those early cave strata; however, that did not occur. When pine trees are locally present, we would expect pine pollen percentages like what we recovered in surface sample 12 (>80%) (Figure II-6), collected in a pine forest near La Pine, Oregon. Taxa of forbs and shrubs that were never present in any sample at greater than 1% were omitted from Figures II-5 and II-6 for the sake of space and readability. They have been included in Table II-4.

Other pollen types found in the Paisley Caves sediments from the YD period indicate there were scattered forbs and shrubs in the local vegetation, such as buckthorns (*Ceanothus*), antelope bitterbrush (*Purshia*), greasewood (*Sarcobatus*), willows (*Salix*), and wild buckwheat (*Eriogonum*).

Abies pollen is present in 100% of the Pre-Younger Dryas (Pre-YD) samples and 90% of YD samples, but only 73% of PYD samples. *Picea* pollen occurs in 100% of Pre-YD samples, 70% of the YD samples, but only 26% of the PYD samples. *Pseudotsuga* pollen is present in 50% of Pre-YD samples, 10% of YD samples, and 26% of PYD samples. *Tsuga* is in 100% of the Pre-YD samples, 30% of YD samples and 0% of the PYD samples. Based on our values, these taxa all decreased from the Pre-YD through the YD and into the PYD with the single exception of *Pseudotsuga*.

Table II-4: Herb & Shrub Taxa appearing at less than 1%, numbers indicate the number of samples in which they appeared, percentage values indicate the percentage of total samples in which they appeared in that particular category (*Asteraceae [Dandelion-type] appears in the modern samples at higher than 1%). Reprinted with permission from Beck, Bryant, and Jenkins 2018.

Shrub and Forb Taxa	Younger Dryas	Post-Younger Dryas	Total Occurrences in Archaeological Samples	Modern
Rosaceae	7 (87.5%)	12 (40%)	19 (50%)	2 (16.7%)
Eriogonum	5 (62.5%)	11 (36.7%)	16 (42.1%)	8 (66.7%)
Fabaceae	1 (12.5%)	14 (46.7%)	15 (39.5%)	2 (16.7%)
Onagraceae	2 (25%)	10 (33.3%)	12 (31.6%)	0
Apiaceae	1 (12.5%)	8 (26.7%)	9 (23.7%)	0
Polemoniaceae	3 (37.5%)	6 (20%)	9 (23.7%)	0
Brassicaceae	1 (12.5%)	7 (23.3%)	8 (21.1%)	2 (16.7%)
Asteraceae (Dandelion-type)	1 (12.5%)	4 (13.3%)	5 (13.2%)	5 (41.7%)*
Rumex	0	4 (13.3%)	4 (10.5%)	1 (8.3%)
Phlox	2 (25%)	1 (3.3%)	3 (7.9%)	3 (25%)
Corylus	0	3 (10%)	3 (7.9%)	2 (16.7%)
Dalea	0	1 (3.3%)	1 (2.6%)	0

Abies, *Picea*, *Pseudotsuga*, and *Tsuga* pollen are only weakly represented in the sediments of the Paisley Caves, often occurring at percentages ranging from 2% to <1%. This could be due to the rapid sinking speed of these pollen grains coupled with the high likelihood that those trees were never growing close to the Paisley Caves. While the percentage of *Abies* was low, it was present in thirty out of thirty-eight archaeological samples. *Picea* was found in sixteen archaeological samples. *Pseudotsuga* was present in nine archaeological samples. Finally, *Tsuga* pollen was only present in five out of thirty-

eight archaeological samples. Because of the low values, these pollen types only occur as rare elements in the regional rain. The pollen of those taxa in the archaeological samples can be attributed to long distance transport from sources west of the Paisley Caves in the foothills of the Cascades and/or from the mountains in the Upper Klamath Lake region. According to Burns and Honkala (1990), those conifer species that are still present in the Pacific Northwest region today require abundant moisture and cooler temperatures. Nevertheless, even as weakly defined traces, the pollen of these important cold- and moist-loving conifers is still more prevalent in the YD deposits than those of the later Holocene. These data imply that perhaps those conifer species grew closer to the Paisley Caves during the YD and then retreated upslope when the PYD climate warmed.

Conifer pollen of all types was more prominent in the sediments of Paisley Caves during the YD than after that period. Based on those data we can conclude that, during the YD, conditions were probably cooler and wetter than during the PYD or even today. However, those conifer species were most probably growing at elevations west of Lake Chewaucan rather than on the flood plain of the lake or in the area directly below the Paisley Caves. The more frequent occurrence of these conifer pollen types during the YD age samples is not dramatic, but their presence is still important.

In a previous study of sediments in Paisley Caves, completed as a thesis, Saban (2015) recorded much higher percentages of fir pollen (*Abies* spp.) in many of her samples. Saban's percentages of fir pollen fell between 10% and 40%. Due to the pollen sedimentation rate of fir, values such as these should be found only within a fir forest or

in a location where large amounts of fir pollen had been redeposited (Jackson and Lyford 1999, Minckley 2008). Saban (2015) also heavily weighted the occurrence of a few pollen grains from the Hippiduraceae family. Our column of sediment samples was collected from a nearby test pit in the same cave, yet we found only sporadic occurrences of fir pollen; therefore, our study does not support her findings or conclusions.

The end of the YD is marked in the fossil pollen record from Paisley Caves by a decrease in Amaranthaceae pollen, and an increase in high-spine Asteraceae. There does not appear to be any major change in the percentages of sagebrush or grass pollen either near the end of the YD or after it. The decrease in Amaranthaceae pollen is unexpected because we suspect that changes in the climate would have created new habitats that favored the weedy varieties of plants in the Amaranthaceae, which often grow quickly in disturbed and saline habitats and disperse large numbers of pollen grains. As the size of Lake Chewaucan began to shrink, it should have created favored habitats for the growth of Amaranthaceae plants. Likewise, with the warmer and drier climate after the YD, pines would have retreated upslope west of the Paisley Caves and that is reflected in our data by lower pine percentages. However, the fossil profile at Paisley Caves later indicates an increase in pine pollen around an estimated 9800 cal BP. After that period, pine pollen remains the dominant type in the fossil record until the eruption of Mt. Mazama around 7600 cal BP.

We believe the difference between the grass pollen percentages in the archaeological sediments and the grass percentages in our modern surface samples could

reflect either lower amounts of grass growing in the immediate area during earlier periods prior to the Mt. Mazama eruption, or the typically poor distributional pattern of grass pollen, which is often dispersed close to the ground and may not have been recycled into the caves located at higher elevations.

Conclusion

We examined a total of 50 sediment samples for pollen content (38 ancient cave sediment samples and 12 surface samples). The pollen preservation overall was good and the pollen concentrations per sample were high. Data from our study and others suggest that the YD did not affect all areas of the Great Basin in the same manner. Goebel and colleagues (2011) conclude that the region around Paisley Caves was probably cooler and by inference perhaps wetter during the YD based on lower evapotranspiration rates. Grayson (1993) suggests that temperatures during the YD were cooler as indicated by Lake Chewaucan reaching its maximum depth by 11,930-12,500 yr. ago, but shortly after that the YD ended and temperatures rose quickly. The lowered lake levels resulted in an arid regional ecosystem. The fossil pollen data from the Paisley Caves confirm the previous pollen data from the region (Hansen 1947a; Minckley et al. 2007). A climate reconstruction based on nearby Dead Horse Lake pollen cores suggests the region was about 5°C cooler during the YD, which we suspect also applied for the Paisley Caves area. Additionally, pollen data from many surface sites supports the conclusion that the area around Paisley Caves was likely a shrub steppe throughout the time periods covered by our samples (Minckley et al. 2008).

In both the paleo sediment samples from Paisley Caves and the surface samples, there were isolated and random appearances of a few pollen grains from conifers associated with cooler and wetter conditions, such as hemlock, spruce, fir, and Douglas fir. From these data, we conclude that those pollen grains in the past and today are the result of long-distance transport from sources most probably at higher elevations to the west of the Paisley Caves. The generally higher percentages of pine pollen during the YD can be attributed to cooler temperatures and perhaps wetter conditions than existed until the end of the PYD period. We suspect the higher pine pollen presence during the YD was the result of an increase in the density of distant pine trees or a movement of pines further downslope into the steppe grasslands of eastern Oregon. The presence of small amounts of non-pine conifer pollen grains in the YD age sediment samples also suggests the climate was cooler and possibly wetter during the YD than it is today. Finally, an important feature of the fossil pollen record from Paisley Caves is that the PYD period shows little evidence of any major climatic changes in that region of the northern Great Basin during the early Holocene. Overall, it is possible some of the minor pollen types found in our sediment samples may be related to the cultural use of plants by the cave's inhabitants. However, even if some of the fossil pollen might reflect economic uses of key plants at the Paisley Caves, we believe that much of the pollen came from natural, non-cultural sources.

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CHAPTER III

COMPARISON OF *NEOTOMA* (PACKRAT) FECES TO ASSOCIATED SEDIMENTS FROM PAISLEY CAVES, OREGON, U.S.A.

Introduction

In 2012, Jenkins and colleagues published data from an archaeological site, the Paisley 5 Mile Point Caves, Oregon, showing evidence supporting human habitation at the site dating as far back as 14,000 years ago (cal BP) (Figure II-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 (Jenkins et al. 2012, 2013). 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, Bryant, and Jenkins (2017) 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, Alvarado, and Hart 2002), 'woodrats' (Hall 1997), 'packrats' (Van Devender and Hall 1994), 'pack-rats' (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, Van Devender, and Martin 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, Van Devender, and Olson 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; Hall 1997; Hall and Riskind 2010; Mehringer and Wigand 1990). 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 three-fourths of the total local plant species.

Because of the unique composition of the sediments from the Paisley Caves, where 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. Finally, 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.

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 and colleagues (Jenkins et al. 2007:61-65), 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.

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).

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).

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. *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).

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 colleagues (2016:175-176) 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. 2010), Colorado Tick Fever (Hubálek and Rudolf 2010), and Sin Nombre Virus, a hantavirus (Dearing et al. 1998).

Materials and Methods

Thirty-eight sediment samples were collected from a continuous profile from test unit 4C in Cave 2 of Paisley Caves (Figure II-3). Of these samples, 35 were labelled 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 tephra layer, from which a sample dating to 6,790 cal BP was obtained (Figure II-4). 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, Bryant, and Jenkins 2017). The samples were dated by correlating the depths from which they were collected with radiocarbon-dated samples from similar strata in the site (Table II-1). 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^o 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 media.

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, Barceló-Vidal, and Pawlowsky-Glahn 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 1986; 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, Bryant, and Jenkins (2017). 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 II-2.

Results

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.

Microfossils

This study's packrat pollen counts are shown in Figure III-1.
The pollen values from the modern sediments (analyzed in a previous study) are provided for reference (Figure II-5). The figure shows the ratio of plant taxa pollen in the packrat coprolites. The pollen ratios of figures III-1 and II-5 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. However, 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 (Fig. III-2) 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. (Fig. III-1). Raw counts of the packrat-coprolite samples (0-5), sediment samples (0-1 and 0-2), and modern samples (0-3) are included in appendices A and B.

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 taxa 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 III-3).

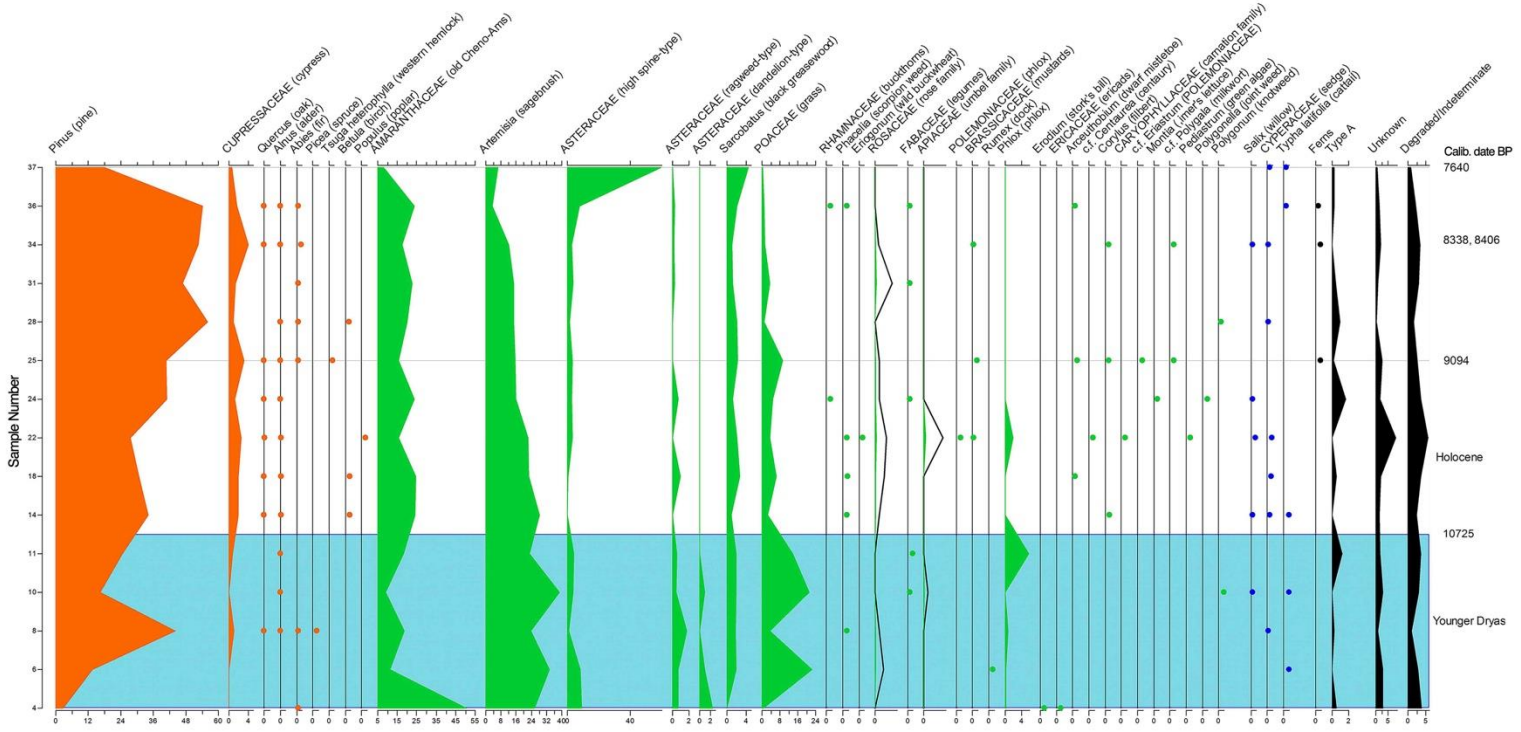

Figure III-1: Pollen chart of packrat coprolite samples from Paisley Caves. Black outlines indicate 10 times exaggeration of pollen percentages. Dots represent taxa that were never present at higher than 1% throughout the samples analyzed.

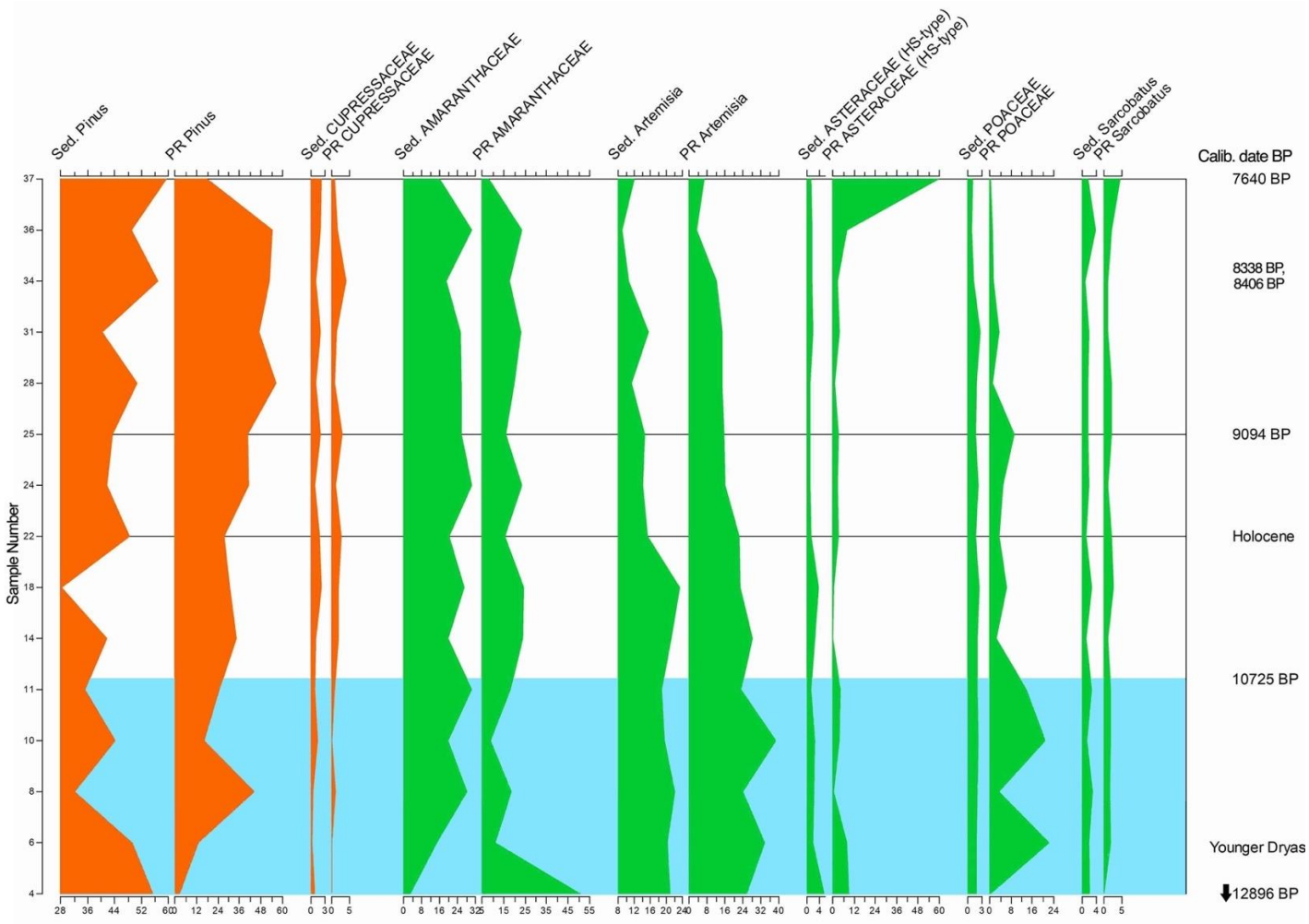

Figure III-1: Chart of the seven most common pollen taxa in packrat coprolites and sediment, from Paisley Cave.

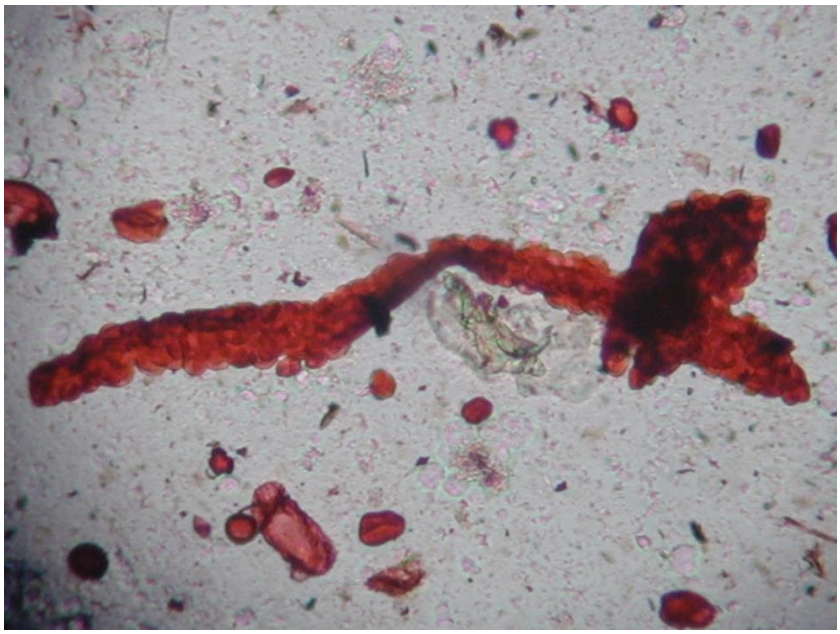

Figure I-2: Light microscope image of a pollen clump encountered in packrat coprolites.

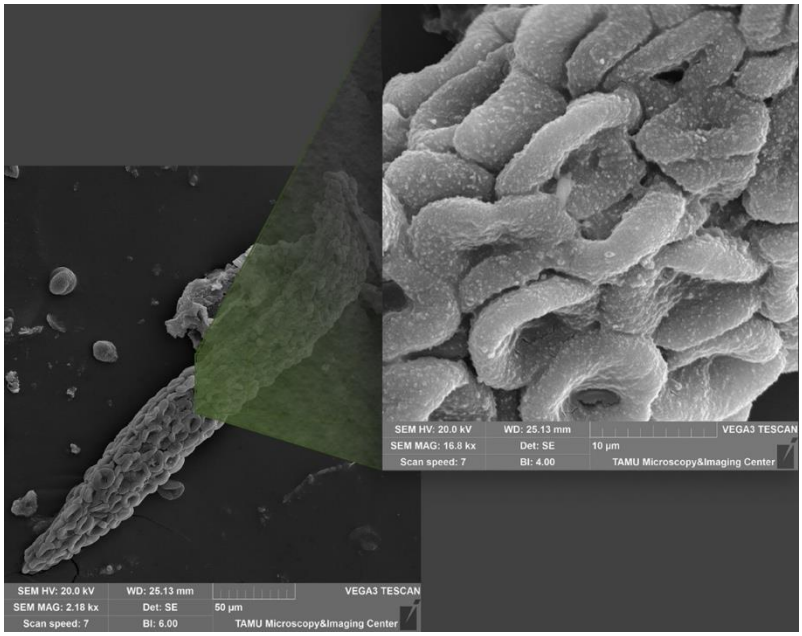

Figure I-3: SEM image of a pollen clump encountered in a packrat coprolite. Image photographed using a Tescan Vega 3 under high vacuum.

While certain, smaller clumps were clearly composed of pollen from the Amaranthaceae, the pollen of other clumps 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 III-4).

Quantitative Analysis

We used TiliaGraph and CONISS for some preliminary visualization of the data, however chose instead to use C2 to display the graphs of the pollen. Additionally, the other quantitative methods proved more useful to accomplishing our research goals and depicting and interpreting the data. When performing PCA we were unable to fully differentiate the packrat samples from the sediment samples (Figure III-5). 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 III-6) 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

III-1 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.

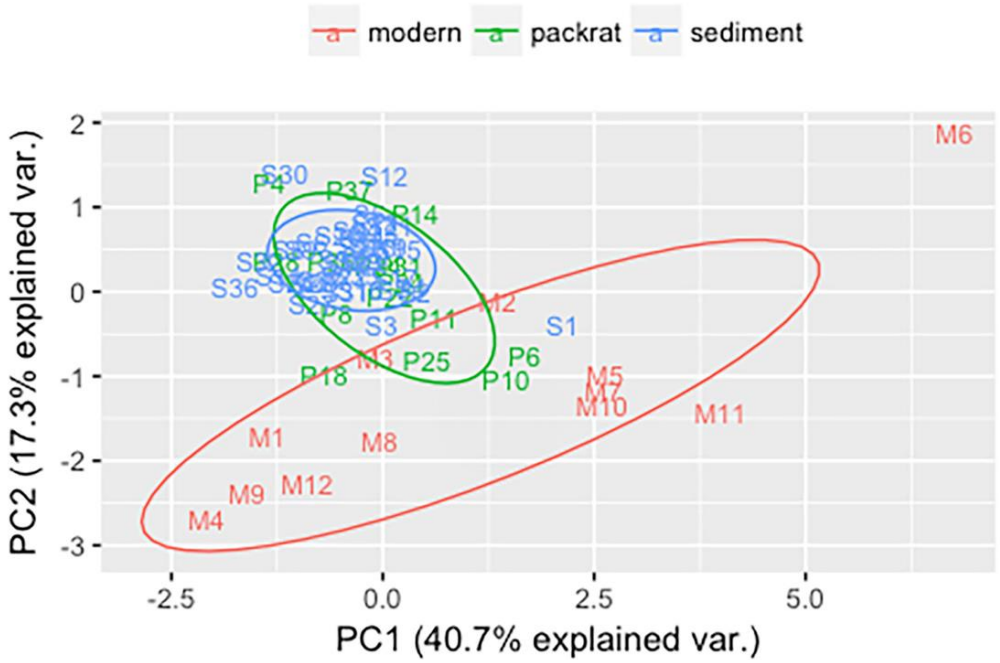

Figure I-4: PCA of modern, packrat, and sediment samples.

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 III-5).

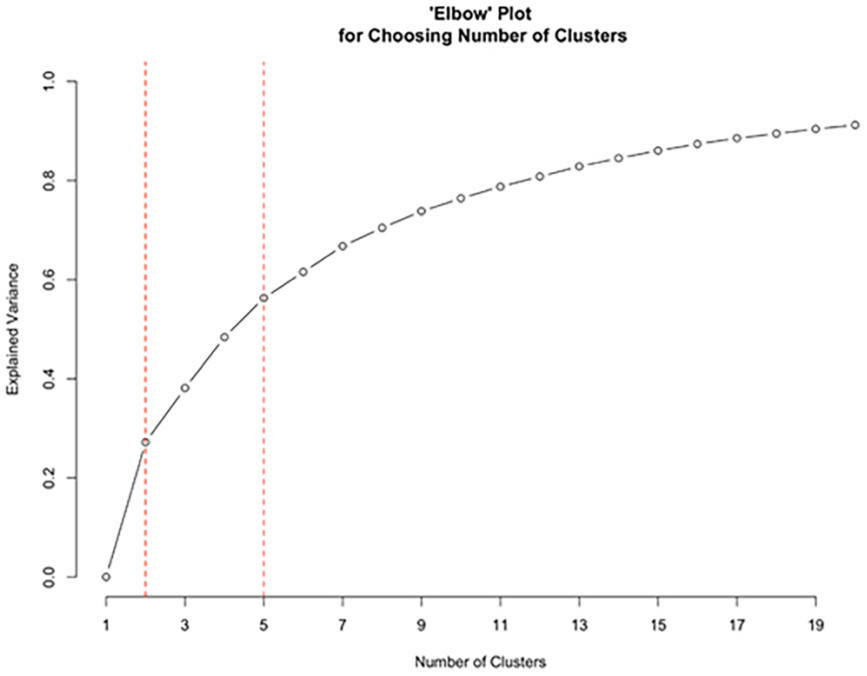

Figure I-5: Elbow plot of packrat, modern, and sediment data using centered log ratio transformation.

Table I-1: 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

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 *Sarcobatu*s.

In the cluster analysis (Table III-1), 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.

Discussion

Macrofossil Remains

The presence of insect parts in the packrat feces was unexpected as packrats are described in multiple sources as herbivores (Dial and Czaplewski 1990; Lee 1963; Smith 1997; Vaughn 1990; 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, Alvarado, and Hart 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.

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 A, Tables 0-1, 0-2 and 0-3). 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 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 A, Table 0-3). 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, except for samples 4 and 37, the packrat coprolites indicate an environment that is nearly identical to what is found in the area today.

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 III-1 (Table III-1) 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 III-3 and III-4, are such anther fragments.

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

One unexpected discovery, during our analysis, was the presence of the algae *Pediastrum* spp. in the packrat feces (Figure III-1; Appendix B, Table 0-5). Packrats can acquire all necessary water needs through diet alone (Linsdale and Tevis 1951:293). 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.

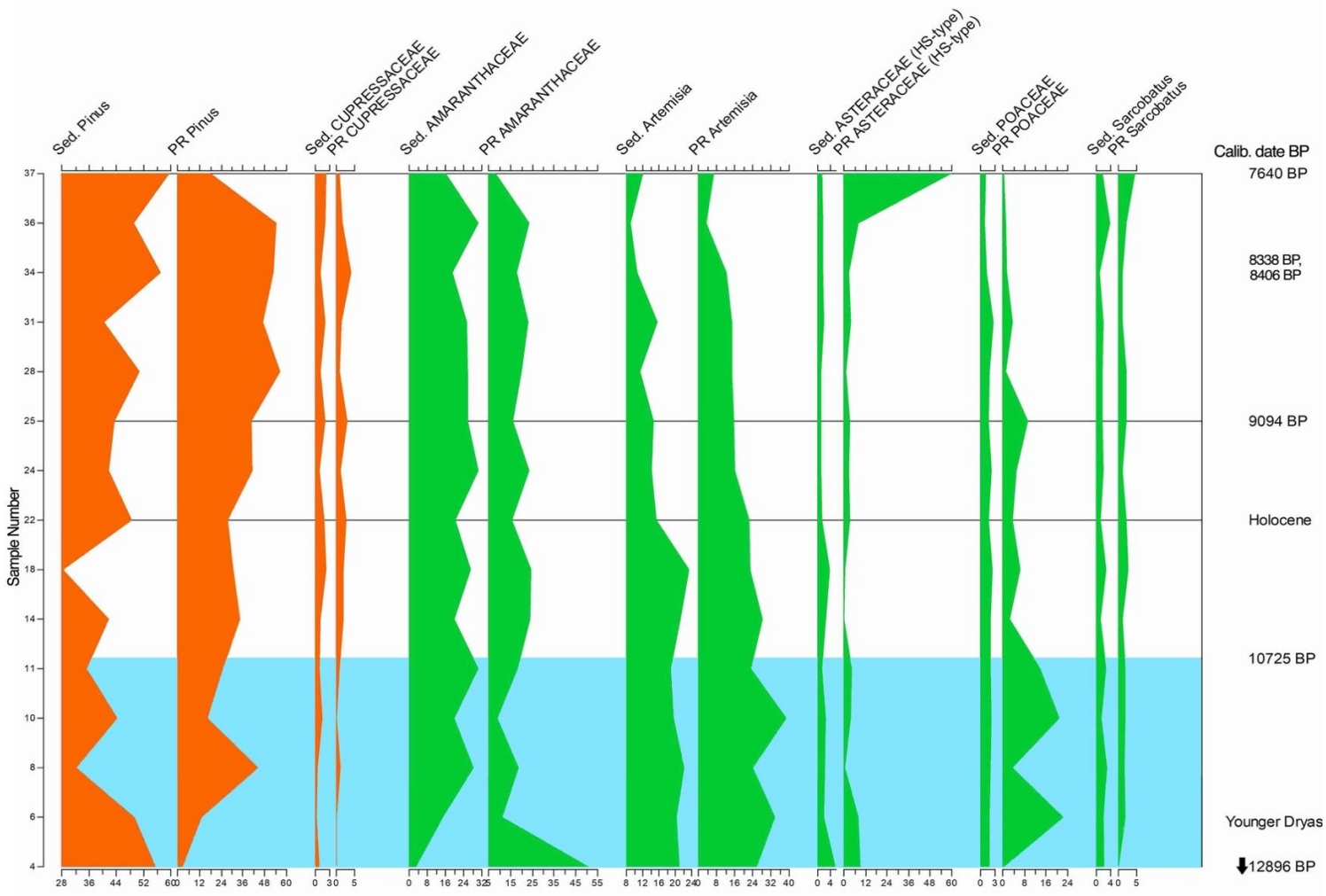

Figure I-6: Chart of the seven most common pollen taxa in packrat coprolites and sediment, from Paisley Caves.

Quantitative Analysis

When visually comparing the packrat samples to sediment samples already analyzed (Table 0-2), 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^{o}C lower during the coldest months and between 1-3^{o}C higher during the warmest months of the Younger Dryas (Minckley, Whitlock, and Bartlein 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).

Conclusion

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, Alvarado, and Hart 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, Bryant, and Jenkins 2017). 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.

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.

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CHAPTER IV

EVIDENCE FOR NON-RANDOM DISTRIBUTION OF POLLEN IN HUMAN COPROLITES

Introduction

Coprolites are one of the most direct sources of dietary evidence available in the archaeological record (Bryant 1974; Bryant and Williams-Dean 1975; Bryant and Holloway 1983; Heizer and Napton 1969; Reinhard and Bryant 1992). Coprolites encapsulate a remarkable breadth of data, including phytolith, botanical, intestinal parasite, other pathogens, isotopes, faunal remains, steroid, and DNA components, all of which reflect the individual's diet, health, and environment (Bryant and Reinhard 2012). However, there does not yet exist a standard sampling procedure for coprolites. Instead, coprolite sampling has been approached in a variety of ways; some researchers process the entire coprolite (Callen and Cameron 1960), others sample one end (Reinhard and Hevly 1991), the center (Wood and Wilmshurst 2016), or cut the specimen in half (Bryant 1974; Stock 1983; Wigand and Mehringer 1985). All of these methods assume homogeneity of coprolite contents, but research has raised questions concerning the validity of such assumptions (Martin and Sharrock 1964; Kelso 1976; Kelso and Solomon 2006; Williams-Dean 1978; Dean 2006). To properly assess the contents of human coprolites, we must begin by understanding the effects of human digestive taphonomy (O'Meara 2014).

One of the earliest attempts to study variability of pollen distribution was conducted by Martin and Sharrock (1964). Their contribution consists solely of the

comparison of three extractions from one coprolite, two from one end of the coprolite and one from the opposite end. Their results, while tentative, were enough to suggest, "a significant change in pollen proportions within a single specimen of dung" (pg. 171). Another attempt to understand coprolites was the modern experimental work conducted by Kelso (1976) and Kelso and Solomon (2006). Kelso spiked food with pollen grains and fed it to test subjects. Then, he measured the distribution of pollen in the collected human feces. Kelso found that ingested pollen first appears in low frequencies in the center or trailing end of a stool rather than the beginning. Kelso observed that the stools produced displayed frequent mixing of pollen from separate meals. He also concluded that pollen can persist in feces well after the meal in which it was consumed. The main conclusion of his study was that small samples from a coprolite fail to provide the entire picture of what was consumed.

Kelso's 1976 study is difficult to interpret for the sole reason that Kelso seems to have been testing many variables simultaneously (rate of travel, relative vs. absolute pollen frequencies, etc.). Additionally, the work of Williams-Dean (1978) suggests that Kelso may have ended his study prematurely when he concluded that all ingested pollen had been passed after nine days. Thanks to elaborate, well-documented, and extensive experimental work, Williams-Dean established much of our current understanding of pollen persistence in coprolites today. While her work was detailed and broad in scope, she did not address the topic of pollen distribution within a single specimen (Williams-Dean 1978). Instead, Williams-Dean attempted to avoid the problem by processing half of each coprolite studied. Neither Kelso nor Williams-Dean ever attempted to determine

if pollen distribution within a coprolite could vary across the width of the specimen; however, Williams-Dean (1978) does mention the possibility of such variation. This would seem a necessary concern due to the amorphous nature of many collected coprolites. Much later, Tennison (2005) set out to refine some of Williams-Dean's conclusions and in the process demonstrated that inhaled pollen could be mistaken for purposefully ingested pollen, thus challenging Sobolik's (1988) 100,000 grains/gram threshold on intentional ingestion of economic pollen.

Some work on variability and flow of particles through the digestive system has been done by non-archaeologists as well. Martin (1965) measured the flow of colored, glass beads and grass seeds through the human digestive system as an analogue for the flow of parasite eggs. He observed significant mixing of beads from separate groups. By the time of excretion, beads had lost their group identity, no longer exhibiting the discontinuity nor arrangement in bead distribution that had existed at ingestion. While informative, the glass beads were much larger (2 mm) than pollen grains (~10-100 μm) and likely had a specific gravity of about 2.5 (Onada and Liniger 1990; Bixler and Rappe 1970), which is different from pollen's specific gravity of 1.45-1.52 (Pearsall 2010:293) and other digesta, around 1.0 (Cummings et al. 1976). Still, Martin demonstrated that some beads were retained by test subjects up to 10 days post-ingestion.

There is also some relevant work concerning non-coprolite solutions to pollen variability. When focusing on settlements and open areas, Adam and Mehringer (1975) recognized a problem with variability in surface pollen representation stemming from,

then standard, methods of pollen collection. They determined how to avoid the mistake of collecting unique samples that result from the uneven distribution of pollen across the landscape. To prevent the large amount of variation observed when collecting surface samples, they recommended increasing the number of samples from an area to between ten and fifteen and then mixing them prior to taking a subsample for processing. By using a large number of samples and combining them, they minimized variability and maximized representation of the local pollen rain. This collection technique came to be colloquially referred to as the "pinch method".

Cully adopted a similar approach when she attempted to study the pollen distribution in Pueblo buildings at Chaco Canyon National Monument. By dividing the ancient room into grids and sampling from each unit, Cully demonstrated that different areas of habitations were used for different tasks (1979). She also demonstrated that pollen "variability within a room" could be "extremely high" (pg. 98). Scott Cummings used this same approach in her master's thesis in 1983 showing that variation of pollen concentrations could be linked to type of structure, time period, and location within the structure (Scott 1983, Scott Cummings 1998). By performing this work, Scott Cummings hoped to maximize information retrieved from a minimum number of samples, speeding up the work.

Despite all we know thanks to previous studies, there is still a great need for experimental archaeology to understand the effects of digestion and representation in human coprolites (O'Meara 2014). In the absence of that modern experimental analysis, we can rely upon the vast store of museum collections material. The numerous coprolites

from Hinds Cave, for example, present an opportunity for such a study, as their microfossil and macrobotanical contents have been the subject of extensive work leading to a firm understanding of site chronology and the subsistence of its occupants (Shafer and Bryant 1977; Belknap 2011).

In our present study, palynological analysis of high-resolution subsamples extracted from Hinds Cave coprolites is conducted to determine the amount of natural variation present within ancient human coprolites. This study advances our understanding of coprolite composition and informs future sampling methods.

Site Description

All coprolite samples came from the Hinds Cave assemblage currently housed in the Archaeological Research Collections at Texas A&M University. Hinds Cave (41VV456), Val Verde County, Texas is one of the largest known reservoirs of desiccated human feces, with thousands of collected specimens spanning a range of ~9,000 years (Belknap 2011, Riley 2008). Hinds Cave rockshelter is located in the wall of a small side canyon about 1.5 km from the Pecos River within a semiarid desert setting common throughout much of southwestern Texas. The material components of coprolites from this site have been extensively studied, providing the basis for a variety of master's theses, graduate dissertations, and academic articles (Williams-Dean 1977; 1978; Stock 1983; Dean 1984; 2006; Edwards 1990; Poinar et al. 2001; Riley 2008; 2012; Belknap 2011). Thus, the coprolites from this site are well understood.

Riley's articles in 2008 and 2012 incorporated microbotanical remains to determine the range of plants eaten at the site. For his study, he chose thirty coprolites,

ten each from three lenses. This study showed the presence of three distinct meals or menus at the site:

1. Nopales (*Opuntia* spp.), as a major component, although not exclusively, eaten in the late spring. This menu was primarily consumed when other resources were not readily available and may be considered a dependable but undesirable meal (Cotton 1996:132).
2. Pit-baked lecheguilla (*Agave lechuguilla*) and sotol (*Dasylirion* spp.), common throughout all seasons. This menu entails high processing costs but provides a reliable caloric return.
3. A monolithic reliance on *Opuntia* tunas and prickly pears pads (*Opuntia* spp.) during the summer. The ease of harvest and consumption is reflected in the seasonal dominance of this resource.

Riley concluded that these patterns of dietary consumption extend back eight thousand years. Prickly pear cactus were important dietary staples all year: nopales (young cactus pads) in the cooler months, prickly pear fruit in the summer, and cactus pads throughout the year. Onions were also a primary resource. Although the diet was varied, staples were always available when there was a scarcity of food (Riley 2008; 2012).

Materials and Methods

The number of coprolites analyzed for this study is affected by two limiting factors: the total number of specimens available for analysis and the amount of time/money required to complete the study (Reinhard 1988). In any analysis, the

question being asked is also of great importance. The question we ask is how to determine the degree of variation within a coprolite. We settled upon five coprolites and believe it should be sufficient to determine the existence of variability within a coprolite as each coprolite will yield multiple samples for analysis. Additionally, the sampling for this research took place in conjunction with sampling of the same coprolites for DNA analysis. The two types of analysis, pollen and DNA, should complement each other and allow for greater understanding of the contents of the coprolites. The current article limits its conclusions to pollen data within the coprolites.

Coprolite selection followed a few specific criteria. Namely, we sought unfragmented coprolites of sufficient size to yield multiple subsamples. Because we were testing pollen variation within a single coprolite, we preferred complete and unbroken specimens. Additionally, we sought coprolites each with a mass greater than 50 grams to ensure that there would be enough material to collect each subsample once the specimens had been prepared. Recently, Wood and Wilmshurst (2016) suggested a microscopic analysis, including pollen, sample size of .6 g (Wood and Wilmshurst). Dean and Bryant had shown that coprolite subsamples as small as 1.0 g were sufficient for pollen analysis (Williams-Dean 1978). We selected the 1.0 g subsample size as sufficient for our purposes knowing that we would need five subsamples from each coprolite as well as enough room between the subsamples to allow us to accurately distinguish different regions of the coprolite.

Coprolite description followed Jouy-Avantin et al. (Jouy-Avantin et al. 2003). After recording external details and characteristics, the north and south axes were

assigned to each coprolite. It was determined that the best way to accomplish subsampling of these coprolites was to assign each subsample to a cardinal direction from a map or compass and include another subsample, taken from the center of the coprolite. It was also necessary to collect an additional subsample, collected from the center for aDNA analysis. Thus, each coprolite has a north, south, east, west, and center subsample for pollen analysis and an additional center subsample for aDNA analysis. North and south were assigned to each coprolite arbitrarily but opposite each other. East and west were then determined from the extremes of an imaginary line running perpendicular to the north/south line and forming 90° angles. The center subsample was collected from the imaginary point where those lines crossed. To aid in subsampling, the north point of each coprolite was marked with a red-tipped toothpick, driven into the coprolite at the appropriate location. South was also marked in a similar way using a natural-colored toothpick (See fig. 13).

Figure IV-1: Example coprolite (Coprolite 4) prior to subsampling. Note the toothpicks marking arbitrary cardinal directions of north and south to aid in subsampling. The distance between the toothpicks is approximately 10 cm.

After visual inspection, sample selection, and documentation, one millimeter of surface material was removed from the exterior of each coprolite specimen. This procedure took place in the Bioarchaeology and Genomics Laboratory (BiG Lab) in the Department of Anthropology at Texas A&M University. It is a clean lab, maintaining an environment capable of DNA extraction techniques with a minimal risk of contamination. Once the surface was removed, subsamples were collected from the north, south, east, west, and center quadrants of the coprolite. Each sample weighed one gram, totaling six grams of material extracted from each coprolite. One center sample

from each coprolite was reserved for aDNA amplification and analysis. The genetic analysis was performed by Taryn Johnson, with supervision by Anna Linderholm (BiG Lab) and Mike Bunce (TrEnD Lab). The remaining north, south, east, west, and single center samples were reserved for processing in the Texas A&M Palynology Research Laboratory. This subsampling method was modelled after sampling strategies developed by Adams and Mehringer (1975) for surface pollen, and by Cully (1979) for her study of pueblo floors. A total of 25 subsamples were collected and analyzed for pollen. Each subsample was assigned a random number to protect against bias during counting. Subsamples were placed in airtight containers filled with enough 0.5% solution of trisodium phosphate to completely cover the specimen. Samples were left in this solution for a minimum of one week to ensure complete softening and disaggregation of the coprolites (Pearsall 2010:297). Once complete, the color and smell of each solution was recorded.

The solution and softened specimen were put through a 250 μm mesh screen and then a 150 μm mesh screen (Bryant 1974; Pearsall 2010:297). Any remaining, larger material was broken up to encourage the release of pollen grains. All material larger than the sieve size was collected as the "coarse fraction" and saved for future study. The fine fraction (<150 μm) from each sample, including the trisodium phosphate solution in which the coprolite specimen was originally soaked, was concentrated through centrifugation and decanted. The concentrated residue from below the screen (the fine fraction) was used for pollen processing and analysis (Pearsall 2010:297-298).

One tablet of marker spores (*Lycopodium*) was added to each sample to track recovery rates throughout processing and to facilitate quantification (Batch number 1031; 20,848 ± 691/tablet). The marker spores are necessary for determining concentration values of the pollen per gram of sediment for each sample. This value is calculated by computing the ratio of marker spores added to the marker spores counted while completing the pollen sum for each sample. The formula is as follows:

$$\frac{\text{(pollen grains counted)(} \textit{Lycopodium} \text{ spores added)}}{\text(\textit{Lycopodium} \text{ spores counted)(grams of soil in sample)}}$$

Additional processing followed the procedure for pollen analysis of human coprolites outlined by Pearsall (2010:294-311). This included soaking the samples in Hydrofluoric Acid (HF). Then, treatment with hydrochloric acid (HCl) to remove residual fluorosilicates and any remaining carbonates, and treatment with acetolysis solution at a 9/1 ratio of acetic anhydride ($C_4H_6O_3$) to sulfuric acid (H_2SO_4). Heavy density separation was also employed to disperse any remaining soil particles in any samples found to contain high amounts of non-organic material (Pearsall 2010:422-434). Finally, samples were stained with Safranin O, and mixed with glycerin for slide preparation.

Once the samples were prepared, glass slides were made, and 200-grain counts were conducted for each of the subsamples. In pollen analysis, 200-300 grain counts are generally employed due to time constraints (Barkley 1934, Traverse 1988). However,

greater resolution, and interpretation, of any pollen present, can be improved by increasing counts to 500-1000+ grains (Bryant and Hall 1993). Counts were performed on a Nikon Eclipse E200 microscope, and photographs were taken using a Nikon DS-Fi2, with attached Nikon touchscreen (Digital Sight DS-L3), to aid in identification. After counting, photographing and identification, the resulting counts were compared to the other subsamples from the same coprolite to determine agreement and degrees of variation among the samples. These comparisons were aided by tables and graphs created using Microsoft Excel (2016; 2018), C2 (2014), and R (2014).

Quantitative methods were employed to determine the degree of variation among the subsamples collected from a single coprolite. The method we chose was to take the data from the five counts performed for each coprolite and create five individual databases based on the values. These databases were then used to construct 1000+ random samples of 200+ grain pollen counts. The values of these 1000+ counts for each of the five coprolites could then be compared with our counts. Deviation in values from the 1000+ randomly generated samples from our actual counts would be good indications of variability of distribution of pollen within the actual coprolites. We applied a significance level of .05, to our data (i.e. percentages outside of this range should only occur 5% of the time).

Results

Size, shape, mass, and weight were all recorded for each coprolite prior to sampling as well as other pertinent information (Table IV-1).

Table 0-1: Metadata information recorded prior to subsampling and processing.

Provenience	External Color of Coprolite	State of Preservation	Weight (g)	Volume	Extremity 1	Extremity 2	Minimal width (mm)	Maximal width (mm)	Length (mm)	Taphonomical Modifications	Inclusions	Hardness
B-BL IV	10YR 8/1	The Coprolite is Entire	52.99	Flat, Conical	Round	Sharp-pointed	20.1	68.9	118.8	Gallery-hole	Fibers	Hard
BN-18x Area B 1976 B-Block North N. wall profile clean-up ARC 2010.1.5 Bag 1 of 2	5YR 4/2	The Coprolite is Entire	102.93	Flat	Round	Round	77.1	104.7	109.7	Fissure	Fibers, Stones	Hard
Area C 1976 C-South 3 lens 4 C5 3-5x ARC. 2010.1.200	5YR 6/1	The Coprolite is Entire	53.25	Flat	Round	Round	81.4	84.9	87.1	Fissure	Fibers	Hard
Area C 1976 C-South 4 lens 4 C5 3-5x ARC. 2010.1.201	5YR 6/1	The Coprolite Consists of an Isolated Fragment	116.30	Flat, Conical	Round	Broken	11.1	80.2	119.3	Gallery-hole, Fissure	Fibers	Hard
Unit D-2 level 6 "Plotted Coprolites July 23, 1975 1 of 2 bags" ARC.2010.1.161 from bag 1 of 7	10YR 7/4	The Coprolite is Entire	91.68	Flat, Conical	Round	Round	70.3	86.7	89.6	Gallery-hole, Fissure	Fibers, Charcoals	Hard

Because subsamples were randomized for processing and analysis in an attempt to minimize counting and identification biases, we include a list of the subsample numbers assigned to each one as well as their coprolite of origin. During processing, the color of the liquid for each sample was also recorded. We have included this information as well as the sample numbers and pollen concentration values from each sample (Table IV-2).

Table 0-2: Processing details for each subsample including coprolite of origin.

Sample	Coordinates	Liquid Color (After Hydration)	Screening Observations	Heavy Density Separation	Pollen Concentration Value (per gram)
1	4E	5YR 2.5/1		X	14107
2	4N	2.5YR 2.5/2		X	24343
3	4C	2.5YR 2.5/2			14038
4	4S	5YR 2.5/1			19971
5	4W	5YR 3/2		X	24627
6	2E	5YR 2.5/1			41696
7	5S	2.5YR 2.5/2	dark (charcoal?)	X	18103
8	3W	10YR 2.5/1	lots of plant matter		5676
9	1W	10YR 2.5/1			12122
10	2N	2.5YR 3/2	dark (charcoal?)		32851
11	1S	5YR 3/1			5156
12	5E	2.5YR 4/4			36572
13	3N	5YR 2.5/1			9937
14	1N	10YR 2.5/1			14014
15	2C	2.5YR 3/2			34692
16	3C	2.5YR 3/4			96256
17	1E	10YR 2.5/1			7872
18	3S	10YR 2.5/2			11749
19	2S	2.5YR 3/2			48645
20	5W	2.5YR 3/4		X	25040
21	2W	2.5YR 2.5/2			54891
22	5N	2.5YR 2.5/2		X	16869
23	3E	5YR 2.5/1			18611
24	5C	5YR 2.5/1		X	20848
25	1C	10YR 2.5/1			23280

Additionally, graphs showing the proportions of pollen grains in percentage values were created for each subsample by coprolite (Figs. IV-2, IV-3, IV-4, IV-5, and IV-6).

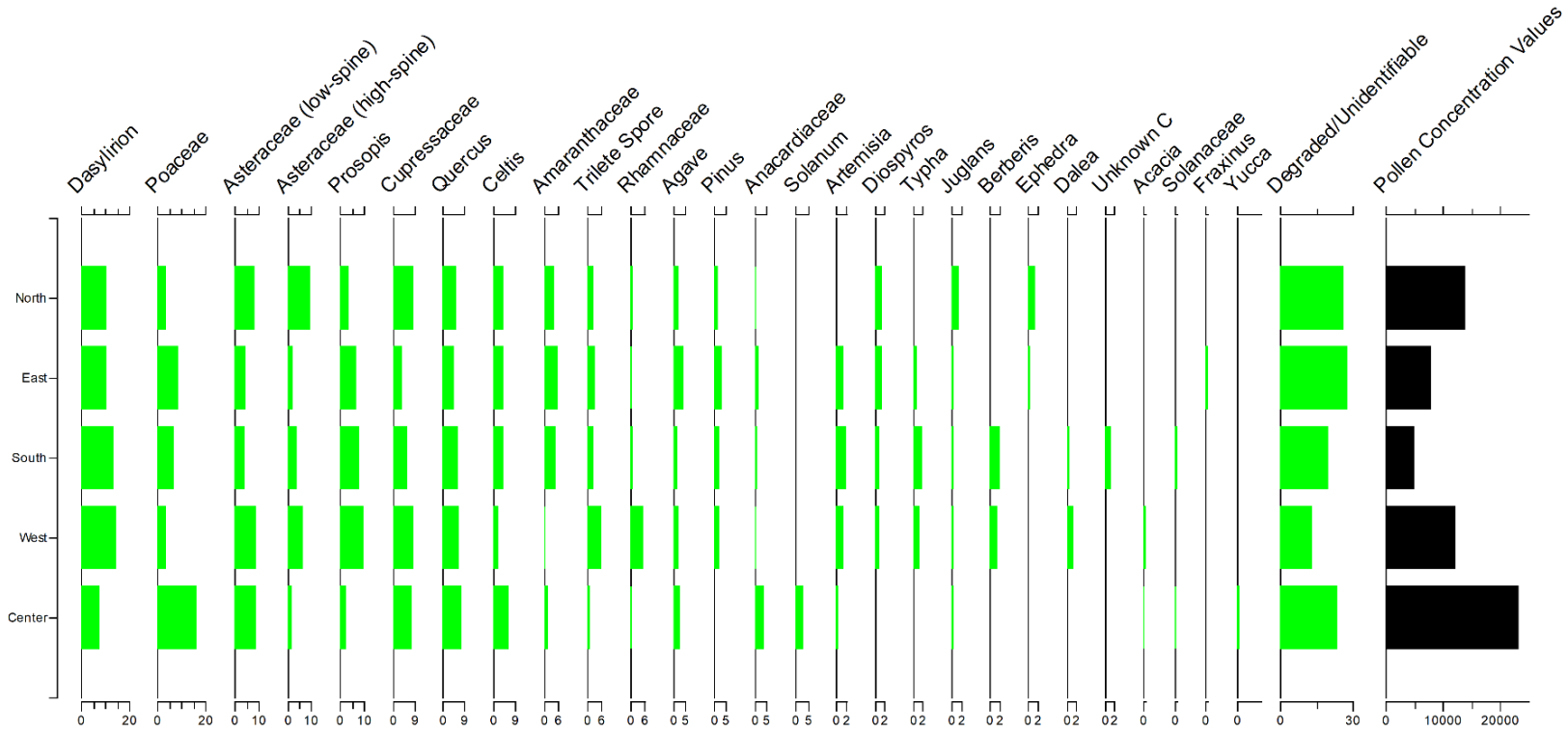

Figure 0-1: Pollen ratios of the five subsamples from Coprolite 1.

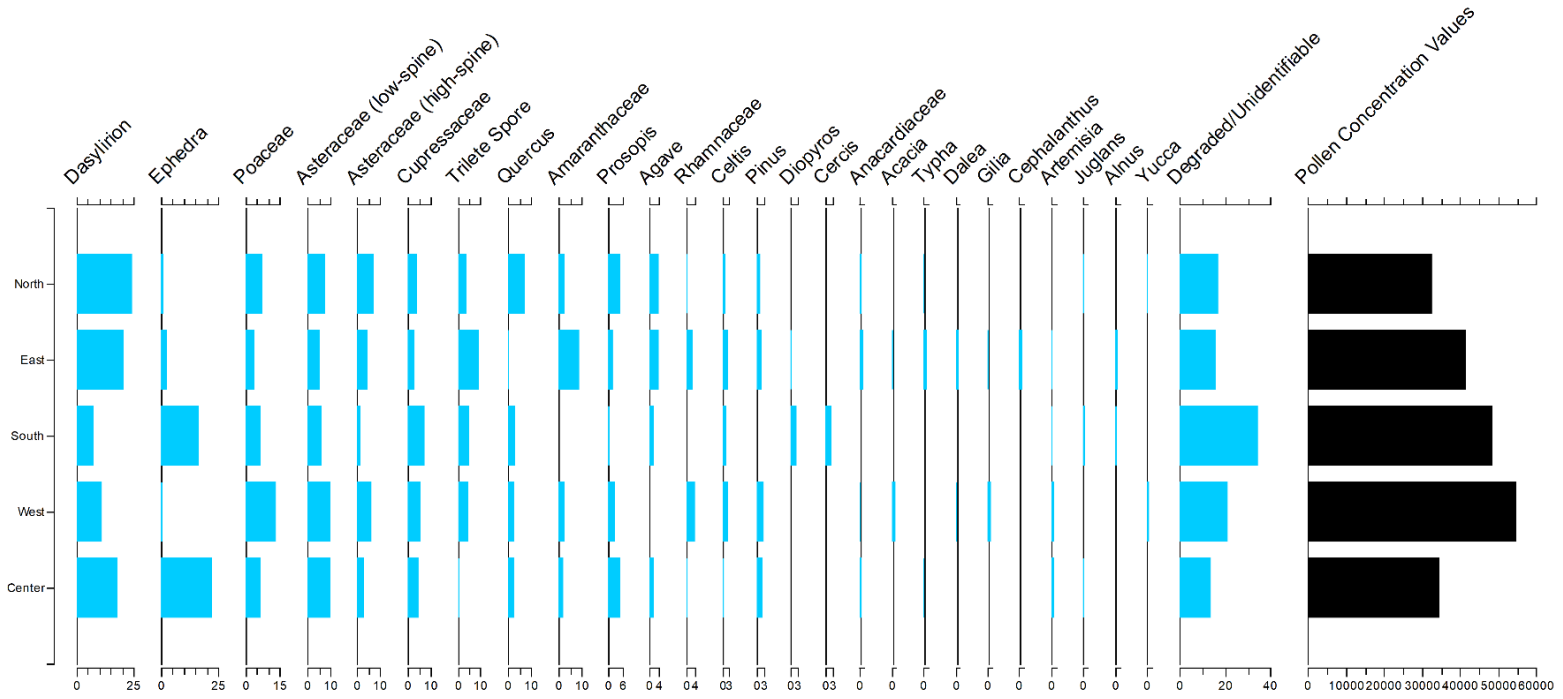

Figure 0-2: Pollen ratios of the five subsamples from Coprolite 2.

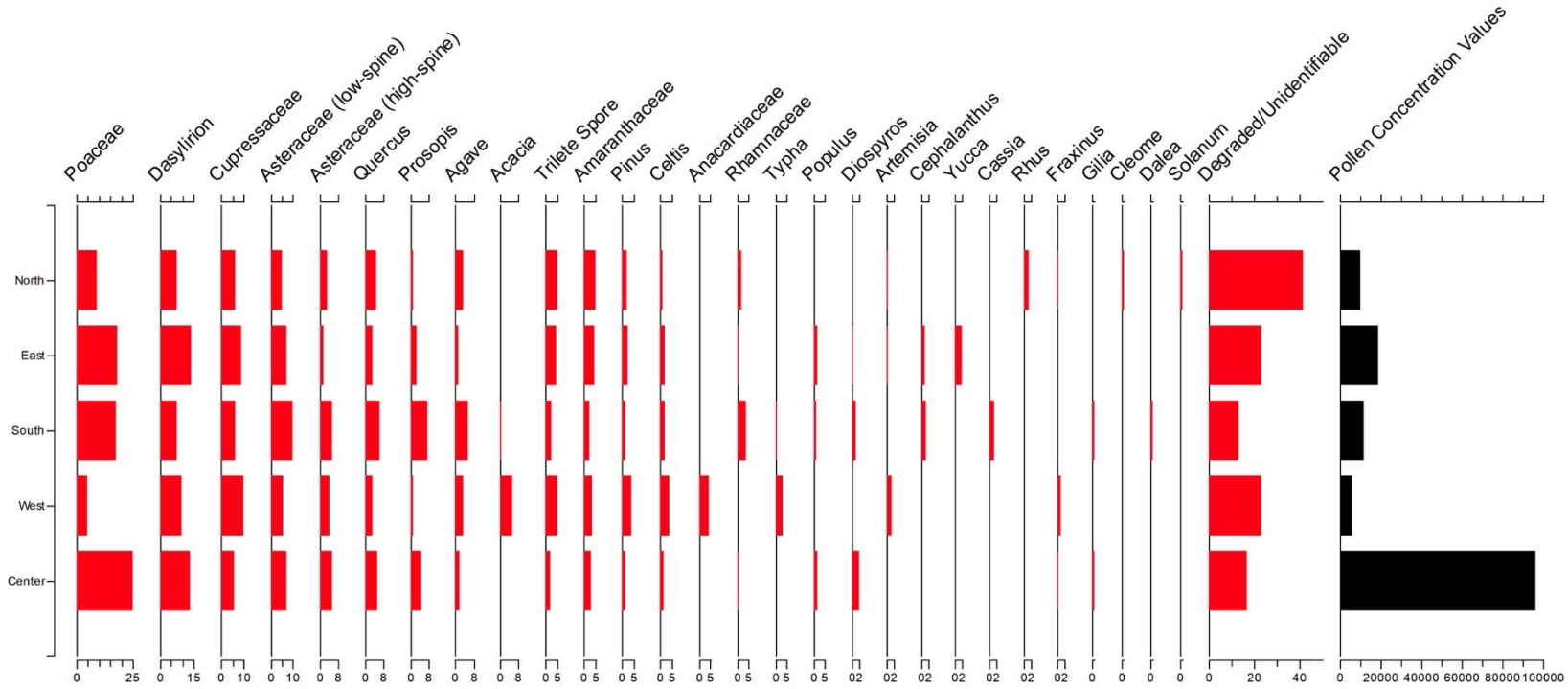

Figure 0-3: Pollen ratios of the five subsamples from Coprolite 3.

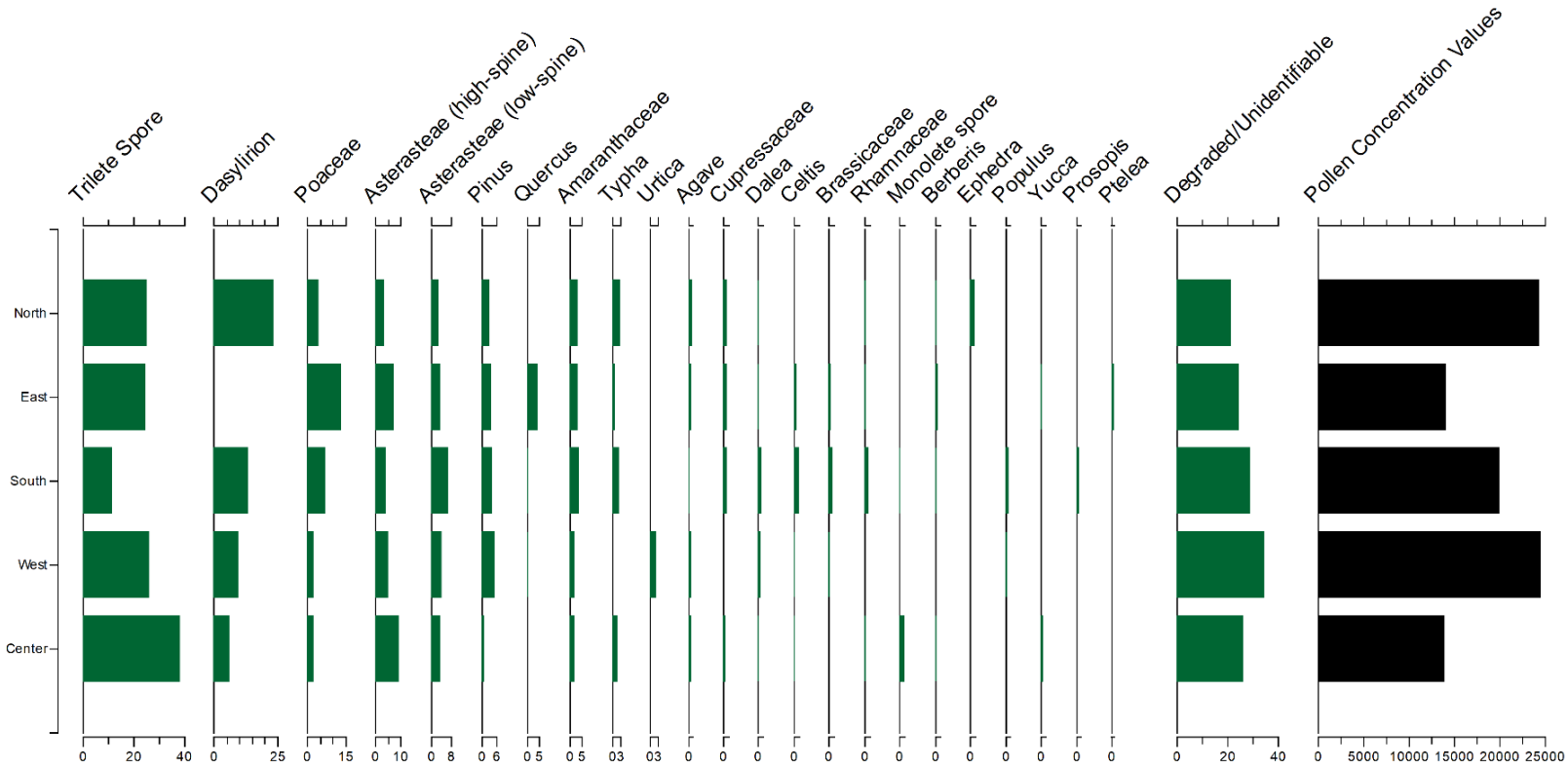

Figure 0-4: Pollen ratios of the five subsamples from Coprolite 4.

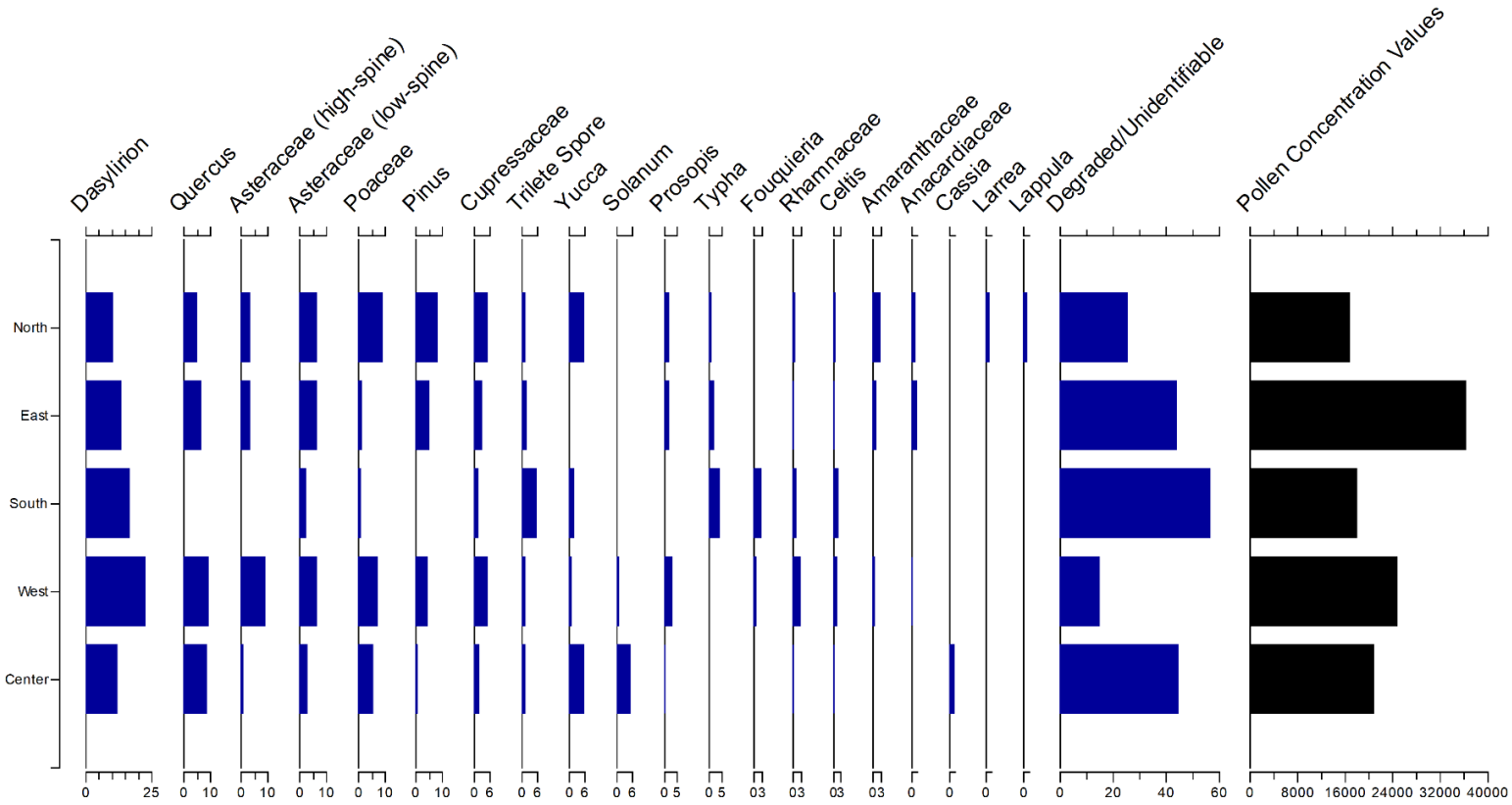

Figure 0-5: Pollen ratios of the five subsamples from Coprolite 5.

Pollen grains that appeared below 1% were excluded from the graphs for the sake of space and readability; they have been included in table IV-3.

Table 0-3: Pollen taxa that occurred below 1%. Letters indicate subsamples in which they appeared. Blank squares indicate those taxa were not observed in any of the five subsamples for that coprolite. Black boxes indicate taxa that appeared greater than 1% in at least one subsample from that coprolite.

	Coprolite 1	Coprolite 2	Coprolite 3	Coprolite 4	Coprolite 5
Acacia	W, C	E, W			
Agave					S, W, C
Alnus		E, S	E	S	
Anacardiaceae		N, E, W, C		S, W	N, E, W
Artemisia	E, S, W, C	E, S, W, C	N, E, W	N, E, S, W	N, E, S, W
Berberis	S, W	S, W		N, E, S, C	
Betula	S	W			
Brassicaceae	N			E, S, W	
Cactaceae				S	
Carex			E	E	N
Carya		N			
Cassia	S	N	S		
Cephalanthus	W	E	E, S		
Cercis	S	S		E	
Cleome	N		N		
Dalea	S, W	E, W	S	N, E, S, W, C	E
Diospyros	N, E, S, W	E, S	E, S, C	N, S, W,	N, E
Ephedra	N, E		S, W	N	N, W
Ericaceae		W			
Eriogonum				E	
Eryngium	E				
Fouquieria		N, E		W	
Fraxinus	E	N, C	N, W, C	S	
Geranium				C	
Gilia	N	E, W	S, C		
Jatropha				E	

Table IV-3 Continued

Juglans	N, E, S, W, C	N, S, C	N		N, E, W
	Coprolite 1	Coprolite 2	Coprolite 3	Coprolite 4	Coprolite 5
Lappula					N
Larrea		W			N
Leucophyllum	W				
Mammalaria		W			
Monolete spore		N		S, C	
Myrica	S				
Oenothera				N	
Opuntia		E		E	W
Phacelia			C		
Picea			C		
Polygonaceae			W	N	
Populus		C	E, S, C	S	W
Prosopis				S	
Ptelea				E	
Salix	N				
Solanaceae	S, C	S	W	E	C
Solanum	C	C	N		
Sophora		E		E	
Taxodium			S	C	
Trifolium	S				
Typha	E, S, W	N, E, C	S, W		
Ulmus			W	E	
Unknown A	S			C	
Urtica				W	
Vitis		W			
Yucca	C	N, W	E	E, C	

We categorized an unexpectedly high proportion of grains in each sample as "Degraded/Indeterminate" (Appendix C, Tables 0-5 and 0-6; see also Figures IV-2, IV-3, IV-4, IV-5 and IV-6). This category is reserved for grains that were so poorly preserved or otherwise obscured as to make identification impossible through the means

available to us. This large proportion of unidentified grains would be problematic if our objective was to extrapolate human diet or local environment from the coprolite contents; however, this category is still useful to us for the purposes of this study. When compared with the quantiles generated from our randomly generated samples (Appendix C, tables 0-8, 0-9, 0-10, 0-11, and 0-12) we were able to determine that the number of "Degraded/Indeterminate" grains varied highly not only across the five coprolites, but also within each coprolite (Fig. 19). These values, while important, are not included in summaries by taxa listed below because Degraded or Indeterminate grains are unlikely to represent a singular taxon. Additionally, we saw a relationship between the percent of degraded grains and the number of taxa. As the percent of degraded grains increased in a subsample, the number of identified taxa decreased. This relationship has been previously observed in surface pollen samples (Bryant et al. 1994) This variation often fell outside of what would be expected given random distribution of pollen grains in the sample (Table IV-4).

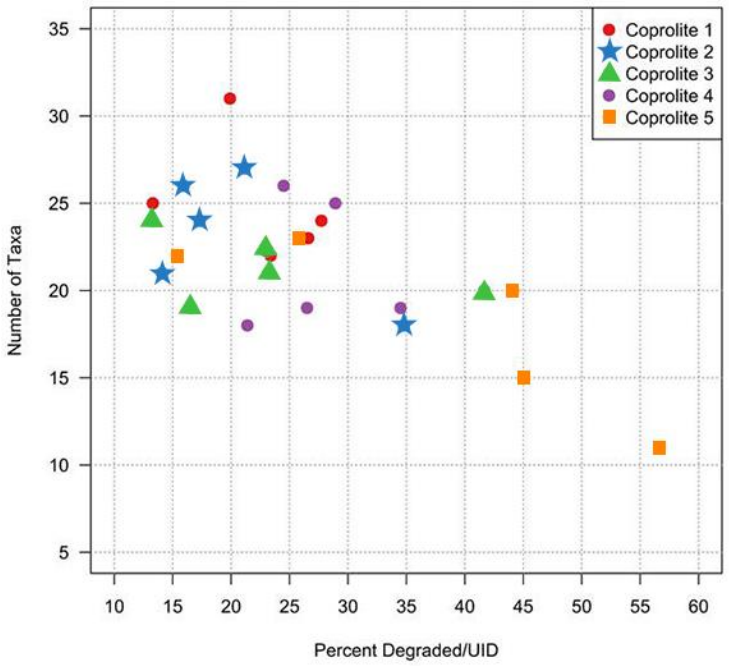

Figure 0-6: Graph of Number of Taxa by Percent Degraded/Unidentified.

Using the 1000+ randomly generated pollen counts for each coprolite, we constructed quantiles based on the likelihood of occurrence of values for every taxa observed for their respective coprolites. The upper and lower limits of the quantiles contain values outside of the 5% and 1% significance levels (Appendix C, tables 0-8, 0-9, 0-10, 0-11 and 0-12).

Every subsample from every coprolite in the study exhibited at least one variation outside of the 5% range, or the range that would be expected given even distribution of pollen within each coprolite. We have listed the number of taxa present in each subsample as well as the total number of taxa identified when combining the five subsamples from each coprolite (Table IV-5).

Table 0-4: Taxa, arranged by coprolite, that fell outside of the expected ranges. Black boxes represent values greater than 1% predicted range. Dark grey boxes fell below the predicted range by 1%. Boxes where the values have been bolded designate values that were within the expected ranges based on the 1000+ randomly generated samples for each coprolite. Boxes with greyed-out numbers depict values that fell within the expected range.

Coprolite 1	North	East	South	West	Center
Anacardiacae	0.49	1.49	0.97	0.49	**4.06**
Aster_hs	9.80	1.98	3.86	6.40	1.52
Amaranthaceae	4.41	4.46	4.35	**0.49**	1.52
Poaceae	**3.43**	8.91	6.76	**3.45**	16.24
Prosopis	3.92	**6.93**	**7.73**	9.85	2.54
Rhamnaceae	0.98	0.50	0.97	5.42	0.51
Solanum	0.00	0.00	0.00	0.00	3.05
Trilete Spore	2.94	3.47	2.90	**5.91**	1.02
Degraded/UnID	26.47	**27.72**	19.81	13.30	23.86

Coprolite 2	North	East	South	West	Center
Amaranthaceae	2.40	9.18	0.00	2.40	1.88
Dasylirion	24.52	20.77	7.62	11.06	18.31
Diospyros	0.00	0.48	2.38	0.00	0.00
Ephedra	0.96	2.90	16.67	0.48	22.54
Poaceae	7.69	**3.86**	6.19	**13.46**	6.57
Prosopis	**4.81**	1.93	0.48	2.88	**5.16**
Quercus	**7.21**	0.48	3.33	2.88	2.82
Rhamnaceae	0.48	2.90	0.00	**4.33**	0.47
Trilete Spore	3.85	**9.66**	4.76	4.33	0.47
Degraded/UnID	17.31	15.94	34.76	21.15	**14.08**

Coprolite 3	North	East	South	West	Center
Acacia	0.00	0.00	0.49	5.45	0.00
Anacardiacae	0.00	0.00	0.00	4.46	0.00
Poaceae	**8.82**	17.87	17.65	4.95	24.88
Prosopis	**0.98**	2.42	7.35	0.99	4.61
Rhamnaceae	1.47	0.48	3.92	0.00	0.46
Typha	0.00	0.00	0.49	3.47	0.00
Yucca	0.00	1.93	0.00	0.00	0.00
Degraded/UnID	41.67	23.19	13.24	23.27	**16.59**

Table IV-4 Continued

Coprolite 4	North	East	South	West	Center
Aster_hs	3.48	7.50	4.41	5.00	**9.50**
Dasylirion	23.38	0.00	13.73	10.00	**6.00**
Ephedra	1.99	0.00	0.00	0.00	0.00
Monolete Sprore	0.00	0.00	0.49	0.00	**2.00**
Pinus	3.48	4.00	4.41	5.50	**1.00**
Poaceae	4.48	13.50	7.35	**2.50**	**2.50**
Quercus	0.00	4.50	0.49	0.50	0.00
Trilete Spore	25.37	24.50	11.76	26.50	38.50
Urtica	0.00	0.00	0.00	2.50	0.00
Degraded/UnID	21.39	24.50	28.92	**34.50**	26.50

Coprolite 5	North	East	South	West	Center
Aster_hs	3.90	3.92	0.00	9.50	0.94
Cassia	0.00	0.00	0.00	0.00	2.82
Dasylirion	**10.73**	13.73	17.24	23.08	12.21
Fouquieria	0.00	0.00	3.45	0.90	0.00
Cupressaceae	5.37	3.43	**1.48**	5.43	2.35
Pinus	8.29	5.39	0.00	4.98	**0.94**
Poaceae	**9.27**	**1.47**	0.99	7.24	5.63
Quercus	5.37	6.86	0.00	**9.50**	8.92
Rhamnaceae	0.98	0.49	1.48	**3.17**	0.47
Solanum	0.00	0.00	0.00	0.90	5.63
Trilete Spore	1.46	2.45	6.90	1.81	1.41
Typha	0.98	1.96	4.43	0.00	0.00
Yucca	5.85	0.00	1.97	0.90	**9.39**
Degraded/UnID	25.85	**44.12**	56.65	15.38	**44.60**

Table 0-5: Number of identified taxa observed in each count by location and coprolite. "Combined" is the number of total unique taxa observed when all observations from that coprolite are combined.

	Coprolite 1	Coprolite 2	Coprolite 3	Coprolite 4	Coprolite 5
North	22	24	19	18	23
East	22	26	20	26	20
South	29	18	24	25	11
West	24	27	21	19	22
Center	20	21	19	19	15
Combined	41	44	38	41	31

The north sample from Coprolite 5 achieved the highest representation at 74% of total taxa found, while the south sample from Coprolite 5 yielded the lowest representation at 35% of total taxa found. Individual 200-grain-count subsamples from Coprolite 1 yielded a total taxa representation range of 22%. Subsamples from Coprolite 2 yielded a range of 20%, with its west subsample reaching its highest yield (61%) of total taxa identified. Coprolite 3 exhibited the smallest range of all at 13%, with the highest subsample, of that coprolite, being the south subsample, representing 63% of the total taxa found. Coprolite 4 had its highest taxa yield in the east subsample (63%), with a range of 20%. Coprolite 5 exhibited a total taxa representation range of 39%.

Coprolite 1 had eight taxa with higher or lower than expected values. Coprolites 2 and 4 had nine taxa each, displaying higher and lower than expected values. Coprolite 3 had the lowest number of taxa, displaying unexpected values at seven taxa. Coprolite 5 had the highest number of taxa, with unexpectedly high and low values at thirteen.

Poaceae counts were both higher and lower than expected due to random distribution of pollen within a coprolite across all five coprolites studied. Rhamnaceae and trilete spores displayed unexpected values in four of the coprolites. High-spine Asteraceae, *Prosopis*, *Dasylirion*, and *Quercus* departed from expected values in three of the coprolites. Anacardiaceae, Amaranthaceae, *Solanum*, *Ephedra*, *Typha*, and *Yucca* stood out as having unexpected values in two coprolites. *Diospyros*, *Acacia*, Monolete spores, *Urtica*, *Cassia*, *Fourquieria*, and Cupressaceae all had unexpected values, when compared to the 1000+ computer-generated samples, assuming random distribution of pollen in a coprolite, in one of the five coprolites in the study. Five figures showing the departure from the norm have been generated for each coprolite (Figs. IV-8, IV-9, IV-10, IV-11, and IV-12). A table is also provided for clarity (Table IV-4). Pollen concentration values (PCV) showed some variation across all five coprolites (Appendix C, Tables 0-6 and 0-7; Figure IV-13).

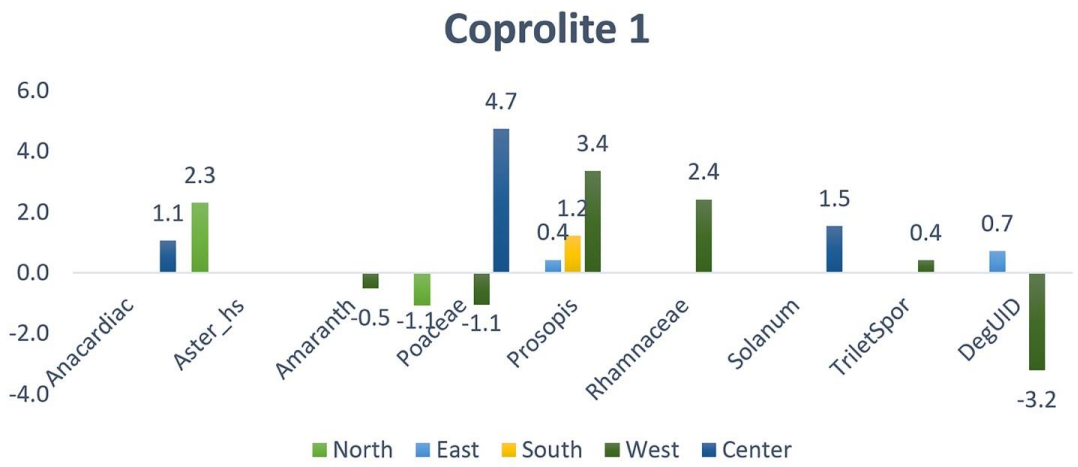

Figure 0-7: Variation outside of expected values for Coprolite 1. All values that fell inside of the expected range have been set to 0. Only taxa with values outside of their expected have been included.

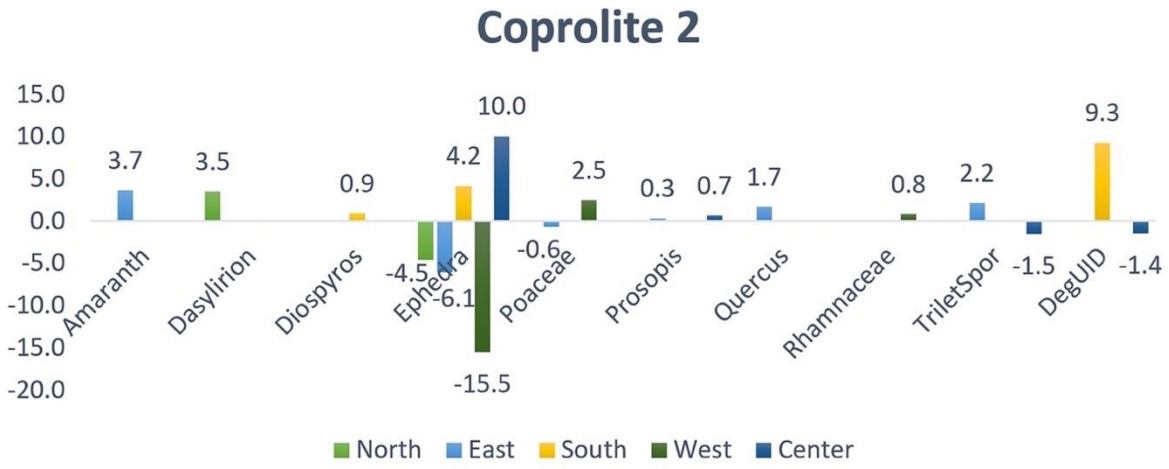

Figure 0-8: Variation outside of expected values for Coprolite 2. All values that fell inside of the expected range have been set to 0. Only taxa with values outside of their expected have been included.

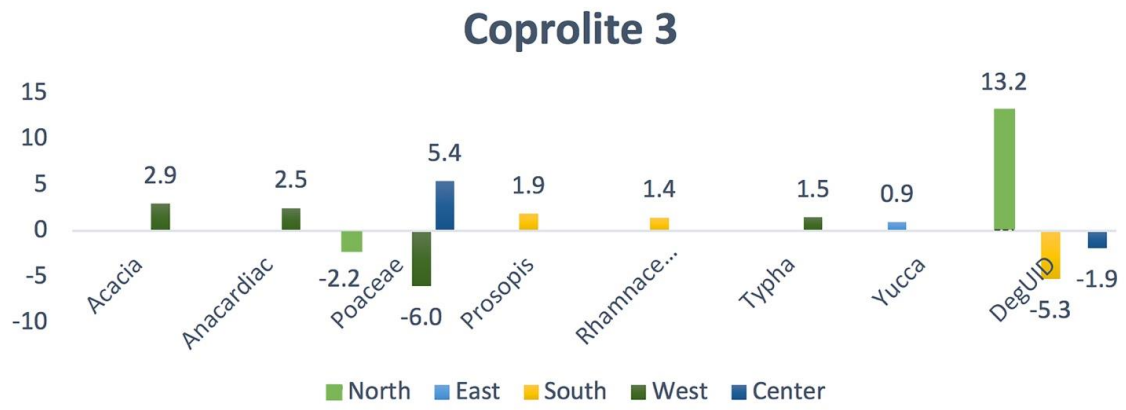

Figure 0-9: Variation outside of expected values for Coprolite 3. All values that fell inside of the expected range have been set to 0. Only taxa with values outside of their expected have been included.

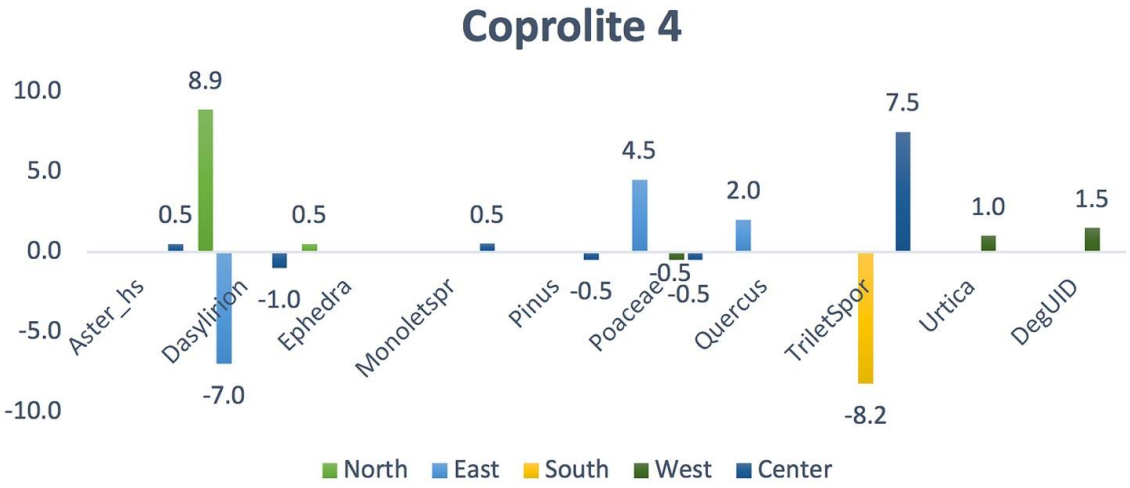

Figure 0-10: Variation outside of expected values for Coprolite 4. All values that fell inside of the expected range have been set to 0. Only taxa with values outside of their expected have been included.

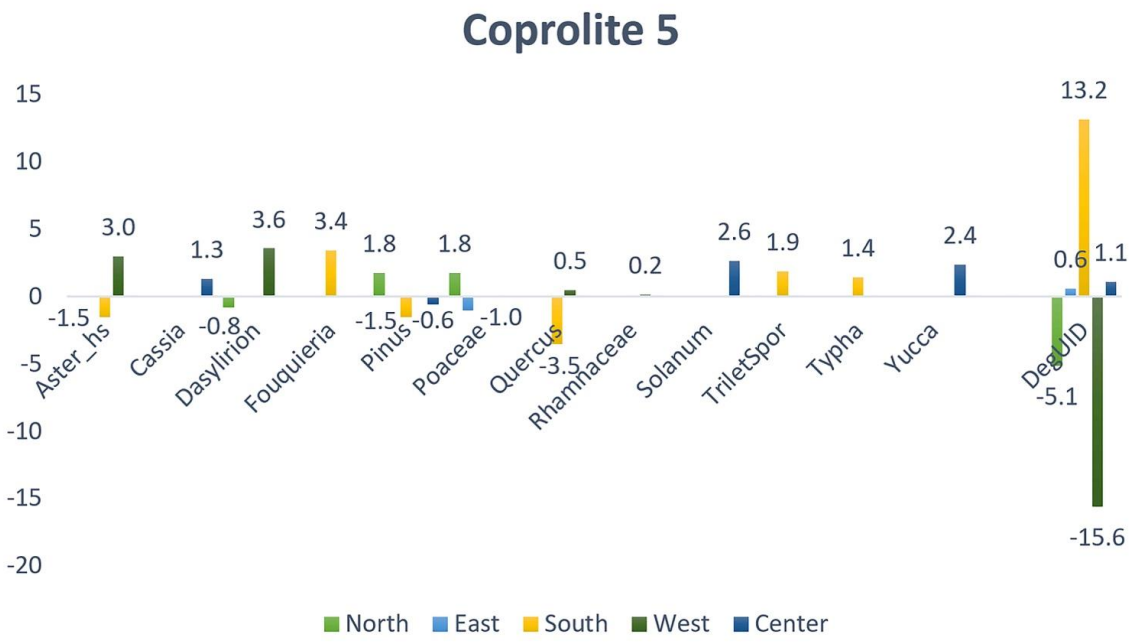

Figure 0-11: Variation outside of expected values for Coprolite 5. All values that fell inside of the expected range have been set to 0. Only taxa with values outside of their expected have been included.

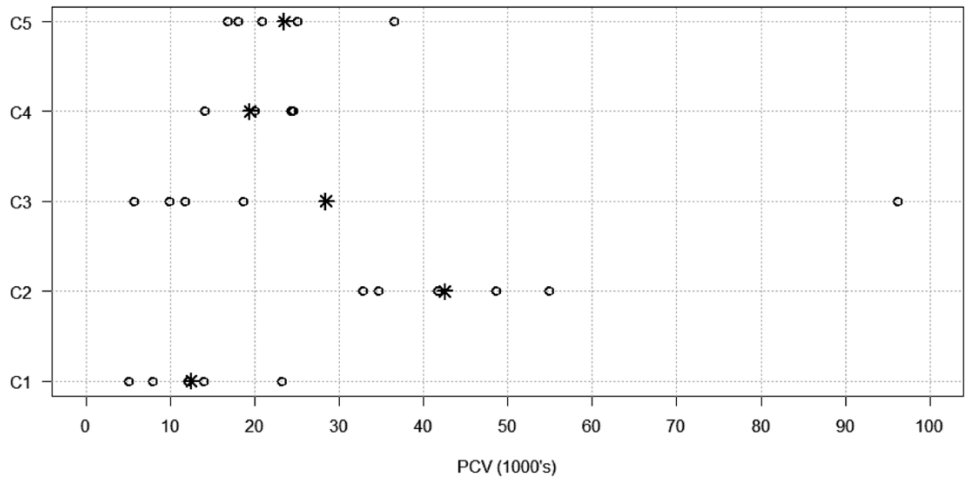

Figure 0-12: Range of pollen concentration values by coprolite, means are indicated by asterisks.

None of the pollen taxa in the subsamples in this study reached the minimum threshold (100,000 grains/gram) to indicate immediate intentional consumption of plants of economic value (Sobolik 1988). However, Dean (1993, 2006) convincingly argued that PCVs could obscure dietary pollen values. Dean showed that pollen analyses of coprolitic material for determining diet should rely on PCV in conjunction with pollen percentages and take into consideration "the dispersal mode of the pollen type(s) in question" (Dean 2006:73). The PCV range for Coprolite 1 was 18,125 grains/gram of sediment. The PCV range for Coprolite 2 was 22,040 grains/gram of sediment. Coprolite 3 had the widest the PCV range of all five coprolites at 90,580 grains/gram of sediment. The PCV range for Coprolite 4 was the smallest of the five coprolites at 10,590 grains/gram of sediment. Finally, Coprolite 5 had a PCV range of 19,703 grains/gram of sediment. As indicated by the graph, the large range observed in Coprolite 3 is due mostly to a single sample with a PCV far higher than the other Coprolite 3 subsamples. If we were to exclude that one outlier, the range of Coprolite 3 would fall between the ranges of the other four coprolites.

Discussion

Across all coprolites, each 200-grain-count poorly represented the total taxa identified within each coprolite (Table IV-5). While the representation of observed pollen taxa in the individual subsamples can be attributed to the differences expected between a 200-grain count and a 1000-grain count, it also illustrates the inherent biases of basing a study on a small, single-point subsample from a single section of a coprolite.

All subsamples in the study exhibited significant variation from homogeneity. However, variation of pollen, statistically significant or not, is not important if the interpretations based on the data remain unaffected. For many taxa, a variation of 1-2% would not make much of a difference when extrapolating diet. Certain airborne taxa, known for their dietary and medicinal applications, in this study fell outside the range by over 10-15% (Poaceae and *Ephedra* - Figures IV-2, IV-3, IV-4, IV-5, and IV-6, Table IV-7, and Appendix C Tables 0-6 and 0-7). Even when a coprolite subsample yielded taxa values well above or below what the random samples estimated, other subsamples from the same coprolite indicated values that fell within the predicted ranges. In some cases, only one or two of the five subsamples reflected over- or under-representation of the total grains found. Due to this, it is likely that a single sample of 1 gram from a coprolite would not indicate the actual values. Based on the evidence here, the amount of variation in pollen values observed in these subsamples almost guarantees that using Wood and Wilmshurst's (2016) recommendation of one, .6 g sample, for pollen analysis of a coprolite would yield incomplete and potentially misleading data.

In Sobolik's 1988 paper on ancient diets in the Trans-Pecos region, she identified seven plants of probable economic value. Five of the seven plants Sobolik (1988) identified as having economic value for subsistence and medicinal need (*Dasylirion*, *Ephedra*, High-spine Asteraceae, Poaceae, and *Typha*) varied from the values expected given random distribution in our samples. Bryant (1975) makes a distinction between economic pollen, background pollen, and "special economic pollen"; "special economic pollen" being those grains from anemophilous (wind-pollinated plants) sources which

appear in high enough proportions to suggest economic usage, for example; some taxa in the Asteraceae or Amaranthaceae. *Ephedra* would also fall into Bryant's "special economic pollen" category. While it is true that some of these economic pollen taxa and "special economic pollen" taxa appeared in our subsamples at lower than expected proportions, many of the same taxa also appeared in higher proportions than expected in other subsamples of the same coprolite. Additionally, these taxa display some of the highest variation in values of all the taxa observed. Bryant suggests that economic pollen grains appearing above 10% likely represent direct ingestion. Bryant reasoned that "special economic pollen", being naturally more abundant, must reach a percentage "in excess of approximately 40%" (pg. 91). *Dasylirion*, being insect-pollinated and therefore an economic pollen grain, meets Bryant's threshold in all five coprolites analyzed in this study. Additionally, in four of those five coprolites, at least one subsample fell below that 10% value. If only one, 1.0-gram subsample were collected from those four coprolites, the potential exists for *Dasylirion* to go unrecognized as a purposefully ingested grain.

High-spine Asteraceae, an economic pollen grain, was observed to be highly variable in three of the five coprolites but never rose to Bryant's 10% requirement. Poaceae, *Typha*, and *Ephedra* being anemophilous and thus "special economic pollen" taxa were present and highly variable but never reached Bryant's minimum threshold of 40%. The variability of these taxa within coprolites is great enough that their presence could be missed entirely if only a single point sample is taken. Based on Riley's conclusions, we should also look for evidence of *Agave* and *Opuntia* pollen. *Agave* pollen was present in

low percentages in all. *Opuntia* pollen was present in only a few of the coprolites studied and absent from many of the subsamples in those coprolites in which the pollen was present. *Agave* pollen percentages met Bryant's minimum threshold (5%) for plants dependent on pollinators in one subsample from Coprolite 3 and came close to meeting that minimum in Coprolites 1 and 2. *Opuntia* pollen never met Byrant's minimum threshold.

Dietary Interpretation

None of the samples had high enough pollen concentration values to meet Sobolik's threshold for intentional ingestion of plants of economic value (Sobolik 1988). However, many pollen grain values in the subsamples did exceed those observed in pollen from sediment collected nearby (Shafer and Bryant 1977). Sotol seems to be a high contributor to pollen in most of the coprolite subsamples. Amaranth (*Amaranthus* sp.), grasses (Poaceae), joint-fir (*Ephedra*), Agave (*Agave lechugilla*) and high-spine Asteraceae could have been contributors to diet as well. While there is ample evidence of prickly-pear cactus consumption at Hinds cave in the form of nopales and tuna (Riley 2012), the five coprolites chosen for this study lack sufficient pollen evidence to indicate such use.

Ephedra pollen was unexpectedly high in some samples, ranging from zero to over 8000 grains/gram of coprolite material. These values exceed those reported by Dean (2006). We do however, admit that there is only scant macrofossil evidence of joint-fir usage at Hinds Cave (Dering 1979; Stock 1983). Reinhard and ccolleagues (1991:127-128) argue that the method in which joint-fir is prepared for consumption

minimizes macrofossil evidence. However, Dean (1993) provides a counter to that by showing that background PCV levels of joint-fir pollen can rise that high or higher at times of pollen release. While pollen analyses of coprolites can provide insight into the diet, range, and seasonality of ancient Americans, we must also emphasize that dietary and environmental analyses of coprolites are greatly improved when pollen analyses are accompanied by macrofossil analyses (Dering 1979; Tennison 2005). Despite Riley's conclusion of dietary constancy (2012), we believe Hinds Cave coprolite subsamples reveal significant diet variation based on the palynological variation we observed.

Conclusion

These results strongly support our hypothesis that pollen is unevenly distributed in a coprolite and that this variability is significant enough to affect interpretations drawn from a single, 1-gram sample. Though compelling, this study is limited by a small sample size. We feel that this exploratory study has raised more questions than it has answered. We have analyzed only a small number of coprolites from a single site. We selected large, complete coprolites and limited ourselves to pollen counts of approximately 200 grains. If this study were to be replicated with smaller or even incomplete coprolites using larger counts, the conclusions might be different. While our subsamples might seem deliberately small, they closely match sample sizes currently recommended for analysis and being employed by researchers (Wood and Wilmshurst 2016). We feel it necessary to encourage further study of coprolite heterogeneity focused on coprolites from other sites, where diets might be drastically different. Variation in coprolite size, shape, and completeness could also affect outcomes. While we believe

additional tests on the distribution of other microfossil coprolite contents, such as starches or phytoliths might yield similar results, we are not certain that will be the case. Additionally, we cannot guarantee the same will hold true for macrobotanical or faunal remains contained within coprolites.

It is possible that subsampling half of a coprolite for pollen analysis would alleviate some of the worst effects we observed due to pollen variation within a coprolite. We recommend that dividing coprolites across the longest axis and analyzing one half for dietary investigations is the best practice until further studies refine the level of pollen variation across coprolite widths. We also reiterate that pollen analyses must be done in conjunction with macrobotanical analyses, particularly when performing dietary studies. We cannot, at this time, recommend the homogenization of fecal material before subsampling for pollen, like that practiced by Tennison (2005:15). While similar to Adam and Mehringer's (1975) "pinch" method and practical for Tennison's study, we maintain that such practices would be unnecessarily destructive and could even prevent the homogenized material from being available for later means of analysis, like aDNA sampling. Tennison concluded that the pollen found within human coprolites, while useful in tying a person to a location, could not reliably be linked to a specific diet nor could a single sample be expected to tie a person to a single location or environment. Macrobotanical and other macrofossil remains found within a coprolite are better indicators of diet than pollen alone (Tennison 2005:42).

By implementing the steps we advised, we hope to offer some standardization to these analytical practices. However, as long as people continue to analyze the pollen of

human coprolites, they should be aware of not only the limitations these data present, but also the probability for misrepresentation due to lack of pollen homogeneity within a coprolite. Finally, it might be necessary to revisit previous archaeological interpretations based on pollen from small samples taken from coprolites from other sites and sources.

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CHAPTER V

CONCLUSIONS

In conclusion, I further discuss some observations made concerning working on the projects, as well as the developing results of those studies.

Bias

Biases can seep into many aspects of analysis when examining samples. When preparing slides, pollen samples can suffer from a 'Drift' effect, where smaller pollen grains tend to migrate to the edges of the coverslip (Brookes and Thomas 1967). This can affect counts recorded from such slides. In addition to analysis bias, inadvertently introduced through improper slide preparation, two other analytical biases may occur. Examining sediment cores or sample series extending back into glacial periods may unconsciously introduce an 'expectation' to see higher percentages of pollen taxa representing cold-loving plants in the earliest levels. Thus, there is a tendency to sometimes 'over identify' some taxa or some partly degraded fossil pollen into categories expected in cold environments. Likewise, when counting pollen cores or sediment series from the same location there is a tendency to become more familiar with the recovered taxa and thus be able to make better identifications of fossil and degraded taxa as the number of sediment samples examined increases. Thus, if pollen samples are examined in sequential series the analyst is making better identifications of some difficult taxa and partly degraded taxa at the top or bottom of the column. Such a bias could alter the overall interpretations due to less accurate identifications at the beginning of the counted sequence. The effects of such problems can be minimized by assigning

the samples with an arbitrary numbering system and counting samples in a random rather than continuous sequence. Random sampling was used during both the Paisley and Hinds Cave counts. In the case of the Hinds Cave coprolite samples, the subsample numbers were randomly assigned by a second party and all counts were completed without any knowledge of the actual order of the subsamples. In the case of the Paisley sediment and packrat samples, we had two researchers perform pollen counts on each sample, confirming values and identifications; limiting, although not entirely eliminating, sampling biases. In some cases, it is often enough just to be aware of possible areas where bias might impact results.

Archaeology, and to the same extent all scientific pursuits, are not generally embarked upon with the determination to prove one's peers wrong. Rather, those in the discipline seek more often to refine and clarify previous theories or to make their own theories fit within what has already been established. When previous work had determined the paleoclimate of Paisley Caves, the reliability of packrat midden contents for interpreting local vegetation, or the usefulness of pollen in human coprolites to indicate diet; we did not embark upon our research questions with the intention of disproving them, but rather to add to those works. While these types of analyses might not demand grant money, win awards, or gain the attention of a large public audience; they are, nevertheless, essential parts of the scientific process. Like most research, they build upon the previous work of others to lead to more careful and considered conclusions that benefit scientific-based interpretations.

Barriers to Acceptance

Of the article chapters contained in this dissertation, only the pollen analysis of Paisley has been published. I cannot predict the impact of either the Paisley Cave packrat or the Hinds Cave studies. I can, however, discuss my current impression of the impact of the pollen analysis of Paisley Caves. I have received good feedback from a few individuals concerning the rigor, detail, and intention of the work. Still, others have chosen to embrace the conclusions of Saban's Master's Thesis (2015). During the writing of our article of Paisley Caves' paleoenvironment, I contacted Saban to attempt to address the perception that I might be attacking her work. I know, from my own experience in preparing my master's thesis, during my time as East Tennessee State University, that it can be a long and difficult process. Additionally, not all theses contain the most well-researched and robust conclusions. While there are many aspects of my master's thesis that I find impressive, there are also many parts of it that make it a poor candidate for publication. I am appreciative to Saban for her work. Without her foundational attempt, I would not have felt it necessary to embark upon my study of the site. However, I am disappointed that some have chosen to continue to adhere to the conclusions contained within her study. I do not know if this choice is a result of holding on to theories in which one is invested. However, I hope that when the subsequent chapters of this dissertation become published they will not face the same resistance before becoming accepted.

Future Work

At one time I entertained the notion of finding an intact pollen record of the vegetation region around the Paisley Caves area during the time that corresponds to human habitation at the caves. I even went so far as to visit the area and scout out potential sites for coring. I researched Dr. Henry Hansen's personal papers and notes in the library collections at Oregon State University. I met with Dr. Jenkins to discuss potential locations. I wrote, submitted, and received a departmental grant to do the work. I also enlisted the help of Bill Cannon from the Bureau of Land Management in the region and fellow Texas A&M University graduate student Morgan Smith to identify likely areas of sediment preservation using topographical and satellite maps coupled with GIS. Sadly, the work never progressed further than that. I still harbor hopes of finding a decent pollen core with which to compare the data from the cave sediment and packrat coprolites. I feel that this would be the best way to measure the influence of the packrat coprolites on the sediment at the site. While I could blame poor cooperation from land representatives, inability to wrangle resources, and poor familiarity with the area, I believe the failure of this project rests on my shoulders alone. I was afraid: afraid of being unable to find the intact sediments (with good preservation), afraid that I might collect the cores improperly, afraid to dedicate that much time and money to a project with so much uncertainty, and (more generally) afraid of failure. If I had to make a prediction, I believe that pollen data from an intact core of the region will show that some of the sediment samples from Paisley Caves will mirror the packrat coprolites completely in a few strata and that this mirroring would depart significantly from the

environmental data. However, at this point, that is still unknown.

Now that I have completed the sampling and analysis of material from five coprolites, myriad new questions present themselves for the further study of material distribution within human coprolites. However, in many cases, these questions are more academic than practical in nature. Only those studies that have the potential to actually affect the common and useful analysis and conclusions of human coprolites are in need of further exploration. Before I settled on the study of sampling locations, I was going to test how variations in samples sizes from human coprolites can affect pollen results. Human coprolite sample size still needs to be explored. Additionally, human coprolites are found in a variety of sizes, shapes, and intactness. We do not yet know how each of those conditions affect subsampling results.

Final Analysis

Inevitably, whether through my own work or the works of others, the material contained herein will become dated, shown to be wrong, or demonstrated to be inaccurate in some way. I welcome such circumstances. If this work inspires others to explore these topics and seek to confirm, refute, or add to these conclusions; it will only serve to increase the available knowledge in these subjects, thus improving all our work and our efforts to better understand the world around us.

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APPENDIX A

PAISLEY POLLEN COUNTS

Table 0-1: Raw Counts of Archaeological samples. "X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts

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

Table 0-1 Continued

Sediment Sample Number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
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**

Table 0-2: Second Half of Raw Counts of Archaeological samples. "X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts

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
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

Table 0-2 Continued

Sediment Sample Number	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**
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**

Table 0-3: Raw Counts of Modern samples. "X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts

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

Table 0-3 Continued

Modern Sample Number	1	2	3	4	5	6	7	8	9	10	11	12
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**

Table 0-4: Taxa referred to in the text

	Family	Genus	Common	Palynological
Trees				
	Betulaceae	*Alnus*		
	Betulaceae	*Betula*		Betula, Betula-Corylus
	Betulaceae	*Corylus*		Corylus, Betula-Corylus
	Cupressaceae			
	Fagaceae	*Quercus*		
	Pinaceae	*Abies*	fir	
	Pinaceae	*Abies lasiocarpa*	subalpine fir	
	Pinaceae	*Larix*		
	Pinaceae	*Picea*	spruce	
	Pinaceae	*Pinus*	pine	haploxylon
	Pinaceae	*Pinus*	pine	diploxylon
	Pinaceae	*Pinusmontico la*	western white pine	
	Pinaceae	*Pinus ponderosa*	ponderosa pine	
	Pinaceae	*Pseudotsuga*		
	Pinaceae	*Tsuga heterophylla*		
	Pinaceae	*Tsuga mertensiana*		
	Rosaceae	*Cercocarpus*		

Table 0-4 Continued

Shrubs, Grasses, and Herbs

Family	Genus	Common	Palynological
Amaranthaceae			Cheno-am(s)
Apiaceae	*Lomatium triternatum*	nineleaf biscuitroot	
Asteraceae	*Artemisia*		no-spine
Asteraceae	*Artemisia tridentata*	Great Basin sagebrush	
Asteraceae	*Artemisia arbuscula*	low sagebrush	
Asteraceae	*Artemisia rigida*	scabland sagebrush	
Asteraceae	*Chrysothamnus*		high-spine
Asteraceae			low-spine
Asteraceae		dandelion-type	fenestrate
Asteraceae	*Senecio integerrimus*	lambs tongue ragwort	
Boraginaceae	*Phacelia heterophylla*	varileaf phacelia	
Brassicaceae			
Ericaceae	*Arctostaphyl os patula*	greenleaf manzanita	
Fabaceae			
Fabaceae	*Lupinus caudatus*	tail cup lupine	
Fabaceae	*Dalea*		
Onagraceae			
Onagraceae	*Chamaenerion angustifolium*	fireweed	
Poaceae	*Pseudoroegn eria spicata*	bluebunch wheatgrass	
Poaceae	*Festuca idahoensis*	Idaho fescue, blue bunchgrass	
Poaceae	*Poa secunda*	Sandberg bluegrass	
Polemoniaceae	*Phlox gracilis*	slender phlox	

Table 0-4 Continued

Shrubs, Grasses, and Herbs				
	Family	Genus	Common	Palynological
	Polygonaceae	*Eriogonum*	wild buckwheat	
	Polygonaceae	*Rumex*		
	Rhamnaceae	*Ceanothus*	buckthorn	
	Rhamnaceae	*Ceanothus velutinus*	snowbrush ceanothus, varnishleaf ceanothus	
	Rosaceae			
	Rosaceae	*Purshia tridentata*	antelope bitterbrush	
	Santalaceae	*Arceuthobium*		
	Sarcobataceae	*Sarcobatus*	greasewood, saltbush	
Aquatic and Riparian	Cyperaceae			
	Salicaceae	*Salix*		
	Typhaceae	*Typha latifolia*		
Chiroptera			bat(s)	
Neotoma			packrat(s), woodrat(s)	
Pteridophytes			fern(s)	
Lycopodiales	Lycopodiaceae	*Lycopodium clavatum*		tracer spores

APPENDIX B

PACKRAT COUNTS

Table 0-5: Raw Counts of Packrat coprolite samples. "X"s indicate pollen that was present on the slide but not found during either of the 200 grain counts

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

Table 0-5 Continued

Paisley Cave Packrat Samples															
Sample Number	**4**	**6**	**8**	**10**	**11**	**14**	**18**	**22**	**24**	**25**	**28**	**31**	**34**	**36**	**37**
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

APPENDIX C

HINDS CAVE COPROLITE COUNTS

Pollen count data for the Hinds Cave subsamples can be found at:

https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/POTEYB

Quantile Data for the Hinds Cave subsamples can be found at:

https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/J8KVIY&version=DRAFT

Table 0-6: Pollen counts from three coprolites

Location	North	East	South	West	Center	North	East	South	West	Center	North	East	South	West	Center
Sample	14	17	11	9	25	10	6	19	21	15	13	23	18	8	16
Coprolite Pollen Concentration Value	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3
	14014	7872	5156	12122	23280	32851	41696	48645	54891	34692	9937	18611	11749	5676	96256
Acacia				2	1		2		4				1	11	
Agave	5	9	4	4	5	8	9	4		4	7	3	11	7	4
Alnus							2	1				1			
Amaranthaceae	9	12	10	1	3	5	19		5	4	9	8	5	7	7
Anacardiaceae	1	3	3	1	8	2	3		2	2	3			9	
Artemisia		3	5	3	1		1	1	2	2	1	1		3	
Asterasteae (high-spine)	20	4	8	13	3	15	10	3	13	7	6	3	11	9	11
Asterasteae (low-spine)	17	10	9	18	18	16	11	13	21	22	10	15	20	11	16
Berberis			4	3				1	1						
Betula			1						1						
Brassicaceae	1														
Cactaceae															
Carex												1			
Carya						1									
Cassia			1			1							3		
Celtis	9	9	9	4	13	3	5	4	5	1	2	4	4	8	3
Cephalanthus				1			3					2	3		
Cercis			1					5							
Cleome	1										2				
Cupressaceae	17	8	12	17	27	9	6		12	10	13	19	13	20	13
Dalea			1	3			3		1				2		
Dasylirion	21	21	28	30	20	51	43	16	23	39	15	29	15	20	29
Diospyros	2	3	1	2			1	5				1	2		4
Ephedra	3	1				2	6	35	1	48			1	1	
Ericaceae									1						
Eriogonum															
Eryngium		1													

Table 0-6 Continued

Location	North	East	South	West	Center		North	East	South	West	Center		North	East	South	West	Center	
Fouquieria							1	1										
Fraxinus		2					1				1		1			2	1	
Geranium																		
Gilia	1							1		3					2		2	
Jatropha																		
Juglans	3	1	1	1	1		1		2		1		1					
Lappula																		
Larrea										1								
Leucophyllum				1														
Maclura	1	3	6	12	1		4		1	1			2		1			
Mammalaria										1								
Monolete spore							1											
Myrica			1															
Oenothera																		
Opuntia								1										
Phacelia																		1
Picea																		2
Pinus	3	7	5	5			3	4		6	5		4	5	3	8	3	
Poaceae	7	18	14	7	32		16	8	13	28	14		18	37	36	10	54	
Polygonaceae																1		
Populus											2			4	2		4	
Prosopis	7	11	10	8	4		6	4		5	11			5	14	2	10	
Ptelea																		
	12	10	13	14	16		15	1	7	6	6		10	7	13	7	12	
Rhamnaceae	2	1	2	11	1		1	6		9	1		3	1	8		1	
Salix	1																	
Solanaceae			2		1				1							1		
Solanum					6						1		2					
Sophora								1										
Taxodium															1			
Trifolium			1															

Table 0-6 Continued

Location	North	East	South	West	Center	North	East	South	West	Center	North	East	South	West	Center
Trilete Spore	6	7	6	12	2	8	20	10	9	1	10	9	5	10	4
Typha		2	4	3		1	3			1			1	7	
Ulmus														1	
Unknown A			3												
Urtica								15							
Vitis									1						
Yucca					2	1			2			4			
Degraded/ Unidentifiable	54	56	41	27	47	36	33	73	44	30	85	48	27	47	36
Totals	203	202	206	203	212	208	207	210	208	213	204	207	204	202	217
COUNT	22	22	28	24	20	24	26	18	26	21	19	20	24	21	19

Table 0-7: Pollen counts from two coprolites

Location	North	East	South	West	Center	North	East	South	West	Center
Sample	2	1	4	5	3	22	12	7	20	24
Coprolite	4	4	4	4	4	5	5	5	5	5
Pollen Concentration Value	24343	14107	19971	24627	14038	16869	36572	18103	25040	20848
Acacia										
Agave	4	3	2	3	2	2	2		1	
Alnus			1	1						
Amaranthaceae	7	7	8	4	4	6	3		2	
Anacardiaceae			1	1		3	4		1	
Artemisia	1	1	1	1		2	2	1	2	
Asterasteae (hig spine)	7	15	9	10	19	8	8		21	2
Asterasteae (lov	6	7	14	9	7	14	14	5	15	7
Berberis	1	2	1		1					
Betula										
Brassicaceae		2	3	1						
Cactaceae			1							
Carex		1				1				
Carya										
Cassia										6
Celtis		2	4	1	1	2	1	5	4	1
Cephalanthus										
Cercis		1								

Table 0-7 Continued

Location	North	East	South	West	Center	North	East	South	West	Center
Cleome										
Cupressaceae	3	3	3		2	11	7	3	12	5
Dalea	1	1	3	2	1		1			
Dasylirion	47		28	20	12	22	28	35	51	26
Diospyros	1		1	1		1	1			
Ephedra	4					2			2	
Ericaceae										
Eriogonum		1								
Eryngium										
Fouquieria				1				7	2	
Fraxinus			1							
Geranium					1					
Gilia										
Jatropha		1								
Juglans						1	1		1	
Lappula						3				
Larrea						3				
Leucophyllum										
Maclura							1			
Mammalaria										
Monolete spore			1		4					
Myrica										
Oenothera	1									
Opuntia		1							2	
Phacelia										
Picea										
Pinus	7	8	9	11	2	17	11		11	2

Table 0-7 Continued

Location	North	East	South	West	Center	North	East	South	West	Center
Poaceae	9	27	15	5	5	19	3	2	16	12
Polygonaceae	1									
Populus			3	1					1	
Prosopis			3			5	3		7	1
Ptelea		2								
Quercus		9	1	1		11	14		21	19
Rhamnaceae	1	1	3		1	2	1	3	7	1
Salix										
Solanaceae		2								1
Solanum									2	12
Sophora		1								
Taxodium					1					
Trifolium										
Trilete Spore	51	49	24	53	77	3	5	14	4	2
Typha	6	2	5		4	2	4	9		
Ulmus		1								
Unknown A					1					
Urtica				5						
Vitis										
Yucca		1			2	12		4	2	20
Degraded/ Unidentifiable	43	49	59	69	53	53	90	115	34	96
Totals	201	200	204	200	200	205	204	203	221	213
COUNT	18	26	25	19	19	23	20	11	22	15

Table 0-8: Quantiles generated from randomly sampling counts from coprolite 1

Quantiles: Coprolite 1	0%	2.50%	50%	97.50%	100%
Acacia	0	0	0	1	1.5
Agave	0	1	2.5	5	6.5
Alnus	0	0	0	0	0
Amaranthac	0	0	0.5	1	2
Anacardiac	0	0	1.5	3.5	5
Artemisia	0	0	1	2.5	3.5
Aster_hs	1	2.5	4.5	7.5	9.5
Aster_ls	1.5	4	7	10.5	12
Berberis	0	0	0.5	2	3
Betula	0	0	0	0.5	0.5
Brassicace	0	0	0	0.5	0.5
Cactaceae	0	0	0	0	0
Carex	0	0	0	0	0
Carya	0	0	0	0	0
Cassia	0	0	0	0.5	0.5
Celtis	0.5	2	4.5	7	8
Cephalnths	0	0	0	0.5	0.5
Cercis	0	0	0	0.5	0.5
ChenoAm	0	1	3	5.0125	7
Cleome	0	0	0	0.5	0.5
Dalea	0	0	0.5	1	2
Dasylirion	5	8	12	16	19
Diospyros	0	0	1	2	2.5
Ephedra	0	0	0.5	1.0125	2
Ericaceae	0	0	0	0	0
Eriogonum	0	0	0	0	0
Eryngium	0	0	0	0.5	0.5
Fouquieria	0	0	0	0	0
Fraxinus	0	0	0	1	1
Geranium	0	0	0	0	0
Gilia	0	0	0	0.5	0.5
Jatropha	0	0	0	0	0
Juglans	0	0	0.5	2	2.5

Table 0-8 Continued

Quantiles: Coprolite 1	0%	2.50%	50%	97.50%	100%
Juniperus.C	2	3	5.5	8.5	10
Lappula	0	0	0	0	0
Larrea	0	0	0	0	0
Leucphyllm	0	0	0	0.5	0.5
Maclura	0	0.5	2.5	4.5	5.5
Mammalaria	0	0	0	0	0
Monoletspr	0	0	0	0	0
Myrica	0	0	0	0.5	0.5
Oenothera	0	0	0	0	0
Opuntia	0	0	0	0	0
Phacelia	0	0	0	0	0
Picea	0	0	0	0	0
Pinus	0	0.5	2	4	5.5
Poaceae	3	4.5	7.5	11.5	13.5
Polygonace	0	0	0	0	0
Populus	0	0	1	2.5	4
Prosopis	0.5	1.5	4	6.5	9
Ptelea	0	0	0	0	0
Quercus	2.5	3.5	6	9.5	12
Rhamnaceae	0	0.5	1.5	3	4.5
Salix	0	0	0	0.5	0.5
Solanaceae	0	0	0	1	1.5
Solanum	0	0	0.5	1.5	2.5
Sophora	0	0	0	0	0
Taxodium	0	0	0	0	0
Trifolium	0	0	0	0.5	0.5
TriletSpor	0.5	1	3	5.5	8
Typha	0	0	1	2	3
Ulmus	0	0	0	0	0
UnkG71x25m	0	0	0	1	1.5
Urtica	0	0	0	0	0
Vitis	0	0	0	0	0
Yucca	0	0	0	1	1
DegUID	14.5	16.5	22	27	31

Table 0-9: Quantiles generated from randomly sampling counts from coprolite 2

Quantiles: Coprolite 2	0%	2.50%	50%	97.50%	100%
Acacia	0	0	0.5	1.5	2.5
Agave	0	0.5	2.5	4.5	5.5
Alnus	0	0	0	1	1.5
Amaranthac	0	0	0	0	0
Anacardiac	0	0	0.5	2.5	3.5
Artemisia	0	0	0.5	1.5	2
Aster_hs	1	2	4.5	7.5	9
Aster_ls	3	4.5	8	11.5	13.5
Berberis	0	0	0	1	1
Betula	0	0	0	0.5	0.5
Brassicace	0	0	0	0	0
Cactaceae	0	0	0	0	0
Carex	0	0	0	0	0
Carya	0	0	0	0.5	0.5
Cassia	0	0	0	0.5	0.5
Celtis	0	0	1.5	3.5	4.5
Cephalnths	0	0	0	1	1.5
Cercis	0	0	0.5	1.5	2.5
ChenoAm	0	1	3	5.5	6.5
Cleome	0	0	0	0	0
Dalea	0	0	0.5	1	2
Dasylirion	7.5	12	16.5	21	24
Diospyros	0	0	0.5	1.5	2.5
Ephedra	3	5.5	9	12.5	16
Ericaceae	0	0	0	0.5	0.5
Eriogonum	0	0	0	0	0
Eryngium	0	0	0	0	0
Fouquieria	0	0	0	1	1
Fraxinus	0	0	0	0.5125	1
Geranium	0	0	0	0	0

Table 0-9 Continued

Quantiles: Coprolite 2	0%	2.50%	50%	97.50%	100%
Gilia	0	0	0.5	1.0125	1.5
Jatropha	0	0	0	0	0
Juglans	0	0	0.5	1.0125	2
Juniperus.C	0.5	1.5	3.5	6	7.5
Lappula	0	0	0	0	0
Larrea	0	0	0	0.5	0.5
Leucphyllm	0	0	0	0	0
Maclura	0	0	0.5	1.5	2
Mammalaria	0	0	0	0.5	0.5
Monoletspr	0	0	0	0.5	0.5
Myrica	0	0	0	0	0
Oenothera	0	0	0	0	0
Opuntia	0	0	0	0.5	0.5
Phacelia	0	0	0	0	0
Picea	0	0	0	0	0
Pinus	0	0.5	1.5	3.5	4.5
Poaceae	3	4.5	7.5	11	13.5
Polygonace	0	0	0	0	0
Populus	0	0	0	1	1
Prosopis	0	0.5	2.5	4.5	6
Ptelea	0	0	0	0	0
Quercus	0	1.5	3.5	5.5	7.5
Rhamnaceae	0	0.5	1.5	3.5	4.5
Salix	0	0	0	0	0
Solanaceae	0	0	0	0.5	0.5
Solanum	0	0	0	0.5	0.5
Sophora	0	0	0	0.5	0.5
Taxodium	0	0	0	0	0
Trifolium	0	0	0	0	0
TriletSpor	1	2	4.5	7.5	10
Typha	0	0	0.5	1.5	2.5
Ulmus	0	0	0	0	0
UnkG71x25m	0	0	0	0	0
Urtica	0	0	1.5	3	4.5
Vitis	0	0	0	0.5	0.5
Yucca	0	0	0	1	1.5
DegUID	13	15.5	20.5	25.5	27.5

Table 0-10: Quantiles generated from randomly sampling counts from coprolite 3

Quantiles: Coprolite 3	0%	2.50%	50%	97.50%	100%
Acacia	0	0	1	2.5	3.5
Agave	0.5	1	3	5.5	7.5
Alnus	0	0	0	0.5	0.5
Amaranthac	0	0	0	1	1
Anacardiac	0	0	1	3	5
Artemisia	0	0	0.5	1.5	2
Aster_hs	0.5	1.5	4	6.5	8.5
Aster_ls	2.5	4	7	10.5	13
Berberis	0	0	0	0	0
Betula	0	0	0	0	0
Brassicace	0	0	0	0	0
Cactaceae	0	0	0	0	0
Carex	0	0	0	0.5	0.5
Carya	0	0	0	0	0
Cassia	0	0	0	1	1.5
Celtis	0	0.5	2	3.5125	6.5
Cephalnths	0	0	0.5	1.5	2
Cercis	0	0	0	0	0
ChenoAm	0	1	3.5	5.5	8
Cleome	0	0	0	1	1
Dalea	0	0	0	1	1
Dasylirion	4.5	7	10.5	14	17
Diospyros	0	0	0.5	2	2.5
Ephedra	0	0	0	1	1
Ericaceae	0	0	0	0	0
Eriogonum	0	0	0	0	0
Eryngium	0	0	0	0	0
Fouquieria	0	0	0	0	0
Fraxinus	0	0	0.5	1.5	2
Geranium	0	0	0	0	0

Table 0-10 Continued

Quantiles: Coprolite 3	0%	2.50%	50%	97.50%	100%
Gilia	0	0	0.5	1.5	2
Jatropha	0	0	0	0	0
Juglans	0	0	0	0.5	0.5
Juniperus.C	2.5	4	7.5	11	13.5
Lappula	0	0	0	0	0
Larrea	0	0	0	0	0
Leucphyllm	0	0	0	0	0
Maclura	0	0	0	1	1.5
Mammalaria	0	0	0	0	0
Monoletspr	0	0	0	0	0
Myrica	0	0	0	0	0
Oenothera	0	0	0	0	0
Opuntia	0	0	0	0	0
Phacelia	0	0	0	0.5	0.5
Picea	0	0	0	1	1
Pinus	0	0.5	2	4	5.5
Poaceae	8.5	11	15	19.5	22.5
Polygonace	0	0	0	0.5	0.5
Populus	0	0	1	2.5	4
Prosopis	0	1	3	5.5	7
Ptelea	0	0	0	0	0
Quercus	0.5	2	4.5	7.5	10.5
Rhamnaceae	0	0	1	2.5	3.5
Salix	0	0	0	0	0
Solanaceae	0	0	0	0.5	0.5
Solanum	0	0	0	1	1
Sophora	0	0	0	0	0
Taxodium	0	0	0	0.5	0.5
Trifolium	0	0	0	0	0
TriletSpor	0.5	1.5	3.5	6	7.5
Typha	0	0	0.5	2	3
Ulmus	0	0	0	0.5	0.5
UnkG71x25m	0	0	0	0	0
Urtica	0	0	0	0	0
Vitis	0	0	0	0	0
Yucca	0	0	0.5	1	1.5

Table 0-10 Continued

Quantiles:

Coprolite 3	0%	2.50%	50%	97.50%	100%
DegUID	15.5	18.5	23.5	28.5	33.5

Table 0-11: Quantiles generated from randomly sampling counts from coprolite 4

Quantiles: Coprolite 4	0%	2.50%	50%	97.50%	100%
Acacia	0	0	0	0	0
Agave	0	0	1.5	3	4
Alnus	0	0	0	1	1
Amaranthac	0	0	0	0	0
Anacardiac	0	0	0	1	1
Artemisia	0	0	0.5	1.5	2
Aster_hs	1.5	3	6	9.0125	11
Aster_ls	1	2	4	7	8.5
Berberis	0	0	0.5	1.5	2
Betula	0	0	0	0	0
Brassicace	0	0	0.5	1.5	2.5
Cactaceae	0	0	0	0.5	0.5
Carex	0	0	0	0.5	0.5
Carya	0	0	0	0	0
Cassia	0	0	0	0	0
Celtis	0	0	1	2	2.5
Cephalnths	0	0	0	0	0
Cercis	0	0	0	0.5	0.5
ChenoAm	0	1	3	5	6.5
Cleome	0	0	0	0	0
Dalea	0	0	0.5	2	3
Dasylirion	5	7	10.5	14.5	18
Diospyros	0	0	0.5	1	1.5
Ephedra	0	0	0.5	1.5	1.5
Ericaceae	0	0	0	0	0
Eriogonum	0	0	0	0.5	0.5
Eryngium	0	0	0	0	0
Fouquieria	0	0	0	0.5	0.5
Fraxinus	0	0	0	0.5	0.5
Geranium	0	0	0	0.5	0.5
Gilia	0	0	0	0	0
Jatropha	0	0	0	0.5	0.5
Juglans	0	0	0	0	0
Juniperus.C	0	0	1	2.5	3.5
Lappula	0	0	0	0	0

Table 0-11 Continued

Quantiles:

Coprolite 4	0%	2.50%	50%	97.50%	100%
Larrea	0	0	0	0	0
Leucphyllm	0	0	0	0	0
Maclura	0	0	0	0	0
Mammalaria	0	0	0	0	0
Monoletspr	0	0	0.5	1.5	2.5
Myrica	0	0	0	0	0
Oenothera	0	0	0	0.5	0.5
Opuntia	0	0	0	0.5	0.5
Phacelia	0	0	0	0	0
Picea	0	0	0	0	0
Pinus	0.5	1.5	3.5	6	8
Poaceae	1	3	6	9	11
Polygonace	0	0	0	0.5	0.5
Populus	0	0	0.5	1	2
Prosopis	0	0	0	1	1.5
Ptelea	0	0	0	1	1
Quercus	0	0	1	2.5	4
Rhamnaceae	0	0	0.5	1.5	2.5
Sabal	0	0	0	0	0
Salix	0	0	0	0	0
Solanaceae	0	0	0	1	1
Solanum	0	0	0	0	0
Sophora	0	0	0	0.5	0.5
Taxodium	0	0	0	0.5	0.5
Trifolium	0	0	0	0	0
TriletSpor	16	20	25.5	31	34.5
Typha	0	0	1.5	3.5	4.5
Ulmus	0	0	0	0.5	0.5
UnkG71x25m	0	0	0	0.5	0.5
Urtica	0	0	0.5	1.5	2
Vitis	0	0	0	0	0
Yucca	0	0	0	1	1.5
DegUID	19	21.5	27	33	36.5

Table 0-12: Quantiles generated from randomly sampling counts from coprolite 5

Quantiles: Coprolite 5	0%	2.50%	50%	97.50%	100%
Acacia	0	0	0	0	0
Agave	0	0	0.5	1.5	2
Alnus	0	0	0	0	0
Amaranthac	0	0	0	0	0
Anacardiac	0	0	0.5	2	3
Artemisia	0	0	0.5	1.5	2.5
Aster_hs	0.5	1.5	3.5	6.5	9
Aster_ls	1	2.5	5	8	10
Berberis	0	0	0	0	0
Betula	0	0	0	0	0
Brassicace	0	0	0	0	0
Cactaceae	0	0	0	0	0
Carex	0	0	0	0.5	0.5
Carya	0	0	0	0	0
Cassia	0	0	0.5	1.5	2.5
Celtis	0	0	1	2.5125	3.5
Cephalnths	0	0	0	0	0
Cercis	0	0	0	0	0
ChenoAm	0	0	1	2.5	3.5
Cleome	0	0	0	0	0
Dalea	0	0	0	0.5	0.5
Dasylirion	9	11.5	15.5	19.5	22.5
Diospyros	0	0	0	1	1
Ephedra	0	0	0.5	1	1.5
Ericaceae	0	0	0	0	0
Eriogonum	0	0	0	0	0
Eryngium	0	0	0	0	0
Fouquieria	0	0	1	2	3
Fraxinus	0	0	0	0	0
Geranium	0	0	0	0	0
Gilia	0	0	0	0	0
Jatropha	0	0	0	0	0
Juglans	0	0	0	1	1.5
Juniperus.C	0.5	1.5	3.5	6	7.5
Lappula	0	0	0	1	1.5

Table 0-12 Continued

Quantiles: Coprolite 5	0%	2.50%	50%	97.50%	100%
Larrea	0	0	0	1	1.5
Leucphyllm	0	0	0	0	0
Maclura	0	0	0	0.5	0.5
Mammalaria	0	0	0	0	0
Monoletspr	0	0	0	0	0
Myrica	0	0	0	0	0
Oenothera	0	0	0	0	0
Opuntia	0	0	0	1	1
Phacelia	0	0	0	0	0
Picea	0	0	0	0	0
Pinus	0.5	1.5	4	6.5	7.5
Poaceae	1	2.5	5	7.5	9.5
Polygonace	0	0	0	0	0
Populus	0	0	0	0.5	0.5
Prosopis	0	0	1.5	3	4
Ptelea	0	0	0	0	0
Quercus	1.5	3.5	6	9	10.5
Rhamnaceae	0	0	1	3	4
Salix	0	0	0	0	0
Solanaceae	0	0	0	0.5	0.5
Solanum	0	0	1	3	4.5
Sophora	0	0	0	0	0
Taxodium	0	0	0	0	0
Trifolium	0	0	0	0	0
TriletSpor	0	1	2.5	5	6
Typha	0	0	1.5	3	4
Ulmus	0	0	0	0	0
UnkG71x25m	0	0	0	0	0
Urtica	0	0	0	0	0
Vitis	0	0	0	0	0
Yucca	0	1	3.5	7	11.5
DegUID	27.5	31	37	43.5	46.5