

ANTHROPOGENIC AND NON-ANTHROPOGENIC CONTRIBUTIONS TO
END-PLEISTOCENE MEGAFUNAL EXTINCTIONS
IN THE AMERICAN WEST

by

LEONARD FINKELMAN

A THESIS

Presented to the Department of Earth Sciences
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

June 2019

THESIS APPROVAL PAGE

Student: Leonard Finkelman

Title: Anthropogenic and Non-Anthropogenic Contributions to End-Pleistocene Megafaunal Extinctions in the American West

This thesis has been accepted and approved in partial fulfillment of the requirements for the Master of Science degree in the Department of Earth Sciences by:

Gregory Retallack	Chairperson
Edward Byrd Davis	Member
Samantha Hopkins	Member
Daniel Gavin	Member

and

Janet Woodruff-Borden Vice Provost and Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

Degree awarded June 2019

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THESIS ABSTRACT

Leonard Finkelman

Master of Science

Department of Earth Sciences

June 2019

Title: Anthropogenic and Non-Anthropogenic Contributions to End-Pleistocene Megafaunal Extinctions in the American West

Widespread extinctions of mammalian megafauna at the end of the Pleistocene epoch remain insufficiently explained. In North America, approximately sixty megafaunal species disappeared in a window between 13 and 11 ka that is coincident both with large-scale climate changes and with human arrival on the continent.

Analytical methods may distinguish these factors' relative contributions to megafaunal extinctions. Here I give one such analysis for megafaunal taxa from the American west. I compiled a comprehensive chronology of fossil occurrences for eight taxa and used the Gaussian-resampled, inverse-weighted method to infer their likely true extinction dates; these inferences were then compared with human occupation, temperature, and palynological data from sites west of the North American continental divide. Results suggest that human activity, climate shifts, and vegetation change made distinct contributions to megafaunal extinctions. Ecological state shifts offer a unified account of the causal contributions of all three factors.

CURRICULUM VITAE

NAME OF AUTHOR: Leonard Finkelman

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
City University of New York Graduate Center, New York
University of Virginia, Charlottesville

DEGREES AWARDED:

Master of Science, Earth Science, 2019, University of Oregon
Doctor of Philosophy, Philosophy, 2013, CUNY Graduate Center
Master of Philosophy, Philosophy, 2008, CUNY Graduate Center
Bachelor of Arts, Philosophy, 2003, University of Virginia

AREAS OF SPECIAL INTEREST:

Vertebrate Paleontology
Philosophy of Science
History of Paleontology

PROFESSIONAL EXPERIENCE:

Assistant professor, Linfield College, 2014–Present

Full-time lecturer, Lehman College, 2012–2014

GRANTS, AWARDS, AND HONORS:

Student-Faculty Collaborative Research Grant, “Natural History of the Willamette Valley: Research, Education, and Outreach,” Linfield College, 2019

Juan Young Trust Youth Education and Outreach Grant, “Pleistocene Megafauna Fossil and Trace Excavation on the Yamhill River,” Linfield College, 2018

Faculty Development Grant, “Toward a New Philosophy of Paleontology,” Linfield College, 2017

CURRICULUM VITAE (CONTINUED)

PUBLICATIONS:

- Finkelman, L. (Forthcoming). Betting and hierarchy in paleontology. *Philosophy and Theory in Biology*.
- Finkelman, L. (2019). Crossed tracks: *Mesolimulus*, *Archaeopteryx*, and the nature of fossils. *Biology and Philosophy* 34(28): 1-16.
- Finkelman, L. (2018). De-extinction and the conception of species. *Biology and Philosophy* 33(32): 1-18.
- Pigliucci, M. & Finkelman, L. (2014). The extended (evolutionary) synthesis debate: Where science meets philosophy. *BioScience* 64(6): 511-516.
- Pigliucci, M. & Finkelman, L. (2014). The value of public philosophy to philosophers. *Essays in Philosophy* 15(1): 86-102.
- Siipi, H. & Finkelman, L. (2017). The extinction and de-extinction of species. *Philosophy & Technology* 30(4): 427-441.

ACKNOWLEDGMENTS

I wish to express sincere thanks to Professors Retallack and Gavin for their assistance in the preparation of this manuscript. Special thanks are due to Professor Hopkins, who offered special accommodations and challenging debate throughout my paleontological education and in the development of this project. I also thank members of the Hopkins Lab for their insights, with particular recognition of contributions made by Paul Barrett, Dylan Carlini, Holley Flora, Win McLaughlin, Genevieve Perdue, Dana Reuter, and Kellum Tate. Thanks are also due to Professors Ray Weldon and Matthew Polizzotto for their support and encouragement.

Additionally, I am indebted to Ashley Hart, Bronwyn Boyd, and Colleen Johnson for their assistance in data collection. Dr. Yanna Weisberg also provided valuable help in coding to produce the figures in this document.

Friends and family have provided support throughout my education. In this most recent endeavor I owe my deepest gratitude to my parents, Neal and Phyllis Finkelman, and to my wife, Shannon McClean. Their compassion and assistance very literally kept me alive during long days of study. I also wish to thank Marco Trauzzi, who convinced me to pursue a degree in the earth sciences; his tireless work ethic always serves as an inspiration.

Finally, I offer my deepest gratitude to Professor Davis, whose advice and guidance through this project is just one among many examples of his exemplary care for student achievement, intellectual development, and overall well-being.

This investigation was materially supported in part by a Faculty Development Grant from Linfield College.

To Shay, with no take-backsies

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CHAPTER I

INTRODUCTION

Approximately sixty megafaunal (>44 kg) mammal species disappeared from North America at the end of the Pleistocene epoch between 13 and 11 ka (Barnosky et al., 2016). The rate of megafaunal extinction in this timeframe rose significantly above background levels for mammals; the narrow timeframe and taxonomically selective nature of the extinctions has led researchers to seek for potential causes (Carrasco et al. 2009). Causal responsibility for megafaunal disappearances remains controversial because multiple explanations adequately account for available evidence (Pielou, 1991; Barnosky et al., 2004; Koch and Barnosky, 2006; Doughty, et al, 2010; Lindsey et al., 2015; Saltré et al., 2015; Barnosky et al., 2016; Villavicencio et al., 2016; Emery-Wetherell et al., 2017). Current estimates of extinction dates for megafaunal taxa may correlate both with climate shifts and with human arrival on the continent (Barnosky et al., 2016; *cf.* Grayson and Meltzer, 2002; Emery-Wetherell et al., 2017). If both of these causes may explain the data then there can be no principled way to choose one explanation over the other, thus perpetuating the current debate (Cleland, 2002; *cf.* Turner, 2005).

Distinguishing the causal contributions of climate and human activity to megafaunal extinctions may be aided by development of new analytical methods. Marshall et al. (2015) suggest a method for assessing the relative contributions towards megafaunal extinctions made by climate and human activity through

multiple regression of data for extinctions, human occupation, and climate. These data were measured for megafaunal extinctions in the Última Esperanza province of Chile as proof of concept, demonstrating significant independent contributions to megafaunal disappearances from climate and human activity (see also Villavicencio et al., 2016). The Marshall et al. (2015) analysis drew upon high-resolution estimates of extinction dates inferred through the Gaussian-resampled, inverse-weighted McInerny et al. (GRIWM) method developed by McInerny et al. (2006), Bradshaw et al. (2012), and Saltré et al. (2015; *cf.* Rivadaneria et al., 2009; Marshall, 2010). GRIWM intends to calculate a realistic uncertainty envelope surrounding probable megafaunal extinction dates. This is useful for application of the Marshall et al. (2015) model, in which true extinction dates are a primary source of uncertainty (p. 17).

Application of these new methods has thus far been limited. Apart from the Última Esperanza analysis, GRIWM has been used to estimate last appearance dates (LADs) for recently extinct mammal species (Fisher and Blomberg, 2012). An adapted form of the Marshall et al. (2015) method determined synergistic effects between climate change and human activity as the cause of extinction of European cave bears (Mondanaro et al., 2019). There has not been similar analysis for North American megafaunal disappearances.

My objective in this work is to determine whether or not the relative contributions of climate change and human activity towards megafaunal extinctions in North America can be distinguished. The current null hypothesis, then, is that the effects of climate change and human activity on megafaunal extinctions are

indistinguishable. Given the effectiveness of similar assessment in the Última Esperanza province, I adopt the same combination of the method of Marshall et al. (2015), with GRIWM estimation of megafaunal extinction dates. Previous studies that used quantitative models to assess causes of megafaunal extinctions tend not to be spatially explicit (see discussion in Emery-Wetherell et al., 2017; Mondanaro et al., 2019); however, given that late-Pleistocene mammal communities may have responded to climate change and human activity with biogeographic range shifts, this lack of spatial explicitness may fail to recover ecological signals within the relevant data. To address this concern, I focus here on data from sites west of the North American continental divide in the United States of America.

CHAPTER II

METHODS

Quantitative assessment of causal contributions

The model for this assessment of causal contributions to end-Pleistocene megafaunal extinctions was derived from the above-mentioned work by Marshall et al. (2015). In that work, the authors propose a quantitative model that tests for proximate correlation between megafaunal extinction, non-anthropogenic climate change, and human activity. The relative contributions of these factors to extinction are represented by the equation

$$E = a\Delta C + b\Delta H + c\Delta C\Delta H$$

where E represents the number of megafaunal extinctions; ΔC represents non-anthropogenic climate change and a is the parameter that measures the strength of its contribution to megafaunal extinctions; ΔH represents change in human activity and b is the parameter that measures the strength of its contribution to megafaunal extinctions; and $\Delta C \Delta H$ represents synergy between climate change and human activity, with c being the parameter that measures the strength of the contribution of synergistic effects to megafaunal extinctions. Any parameter in the equation that differs significantly from zero indicates some measurable contribution to extinction. The goal of this work, then, is to test this model for difference from zero for all parameters when applied to a dataset from the North American west.

To achieve this goal through application of the given model, extinction, climate, and human data must be sorted into time bins against which quantitative

changes are measured. Following Marshall et al. (2015), I sorted all data into bins that capture 1,000-year intervals with boundaries set at the start of each millennium before present (BP). Each bin includes the number of extinctions, averaged climate data, and number of dated specimens from human-occupied sites (including both human remains, artifacts, and occupation evidence such as charcoal) for the given millennium BP. The temporal length of these bins is a function of the uncertainty surrounding dates for our data points, which tend to be on the order of hundreds of years. Data were also sorted into bins offset by 500 years in order to determine whether or not temporal binning influenced results of the analysis.

The Marshall et al. (2015) method calls for non-linear least squares regression analysis on E , ΔC , and ΔH values. Inferred values of a , b , and c are then compared against one another to determine whether the strength of any one factor is significantly different from the rest. Parameter a differs from zero in the proportion that E correlates with ΔC and ΔC is not correlated with ΔH ; parameter b differs from zero in the proportion that E correlates with ΔH and ΔH is not correlated with ΔC ; parameter c differs from zero in the proportion that ΔC and ΔH are correlated with one another and with E . If any parameter is significantly different from zero, one may infer that the associated factor is a contributor to the associated extinctions (Marshall et al., 2015, p. 3).

The analysis described is run twice—once for millennial bin-sorted data and again for offset bin-sorted data—to test whether or not significant values for strength parameters a , b , and c are artifacts of time binning rather than genuine ecological signals. If parameter values are significant for millennial and offset time

bins alike, then the signal does not depend on the binning of data; if the values are significant only with respect to data in one set of bins or the other, then significance can be attributed to data sorting rather than to an ecological signal.

Marshall et al. (2015) provide R code for the non-linear least squares analysis. The current analysis therefore uses the R statistical software program: specifically R version 3.4.4 (R Core Team, 2013), running in the RStudio shell (version 1.2.1335) in MacOS version 10.14.3 (RStudio Team, 2015). The program ran R code adapted to automate GRIWM analysis of megafaunal data and export of extinction date estimates, climate data, and human activity data into the Marshall et al. (2015) model. My code is included below in Appendix A.

Data collection

Application of the given model requires data for megafaunal extinctions, climate indices, and human occupation of the relevant geographic area. These data are freely available through several online databases. I obtained data for dated megafaunal samples through the Neotoma Paleoecology Database, a centralized compilation of constituent databases (Goring et al., 2015); data for climate indices were downloaded from climate and weather model archives in the World Data Center for Paleoclimatology (Webb et al., 1994) and the Dryad Digital Repository (White et al., 2008); and data for human occupation are from the Paleoindian Database of the Americas (PIDBA; Anderson et al., 2010).

Megafaunal data collection: Precise timing of extinction for relevant taxa is a requirement for successful application of the Marshall et al. model (2015, pp. 12-13). One significant difficulty in determining the timing of extinctions is the Signor-

Lipps effect: since fossilization is generally unlikely, the last members of any taxon are likely to have survived after the taxon's LAD in the fossil record. One therefore cannot reject the possibilities that fossil taxa with different LADs in fact went extinct simultaneously or that taxa with similar fossil LADs have significantly different true extinction dates (Signor et al., 1982). Since uncertainty with respect to a taxon's extinction is a primary source of uncertainty in the Marshall et al. (2015) model, application of the model requires avoiding the Signor-Lipps effect through high-precision estimation of extinction dates. GRIWM is a method for estimating extinction dates in spite of the Signor-Lipps effect (Rivadaneira et al., 2009; Bradshaw et al., 2012; Saltré et al., 2015). Execution of GRIWM requires multiple dated specimens for each taxon (see below). These are the data collected from the Neotoma Paleoecological Database.

To ensure precision of my extinction date estimates, I analyzed only megafaunal occurrences that had been dated directly from fossil material of megafaunal taxa. These data are obtainable through constituents of Neotoma, which include databases for vertebrate fossil occurrences and geochronology data. The latter database includes radiocarbon dates for directly sampled megafaunal specimens; unfortunately, this database cannot currently be cross-referenced with the vertebrate fossil occurrence database. I therefore manually compiled a database of radiocarbon dates sampled directly from North American megafauna (see Appendix B).

To compile the database, I searched taxon-by-taxon through the vertebrate fossil database, starting with a list of megafaunal genera compiled from Pielou

(1991). Neotoma's advanced search form allows specification of taxon and can be constrained by the inclusion of directly dated specimens. Following this search, I searched each resulting fossil site for a correlated geochronology dataset in which radiocarbon dates are specified for relevant taxa. If an extinct taxon was from an extant genus, I conducted my search at the species level; in all other cases, I conducted my search at the genus level. Relevant taxon searches included a species-level search for *Canis dirus*, the extinct dire wolf, *Oreamnos harringtoni*, the extinct southern mountain goat, and *Panthera atrox*, the extinct American lion; for all other taxa, I conducted genus-level searches. My searches yielded 518 radiocarbon dates directly attributable to specimens from fourteen taxa: *C. dirus*; *Arctodus*; *Bison*; *Bootherium*; *Camelops*; *Equus*; *Mammut*; *Mammuthus*; *Nothrotheriops*; *O. harringtoni*; *P. atrox*; *Paramylodon*; *Platygonus*; and *Smilodon*.

To avoid potential differences in calibration standards over time, I retrieved only specimen dates measured in radiocarbon years BP and then calibrated each date through the OxCal Project program (Bronk Ramsey and Lee, 2013). Program settings used the IntCal13 calibration curve (Reimer et al., 2013). After calibrating radiocarbon dates, I rejected all dates with uncertainty in excess of 1000 years, or larger than the time bins for the least-mean-square regression analysis.

To improve the spatial explicitness of this analysis, I included only specimens found in the United States west of the North American continental divide. These included specimens from the American states of Arizona, California, Idaho, Nevada, Oregon, Utah, and Washington. Because the American-Canadian border is an ecologically irrelevant boundary (Carrasco et al., 2009), I also included six

specimens found immediately north of the border in the Canadian province of British Columbia. The resulting dataset included 168 specimens from the taxa *Arctodus*, *Bison*, *Camelops*, *C. dirus*, *Mammuthus*, *Nothrotheriops*, *O. harringtoni*, *P. atrox*, *Paramylodon*, and *Smilodon*.

Finally, I rejected all taxa for which I could not find six or more directly sampled radiocarbon dates from this geographic region. This choice followed from sensitivity analysis performed by Saltré et al. (2015), which indicated that five or fewer radiocarbon dates are insufficient to infer a reasonable extinction date estimate. After eliminating insufficiently sampled taxa, the database included data from eight remaining taxa: *Arctodus*, *Bison*, *C. dirus*, *Mammuthus*, *Nothrotheriops*, *Oreamnos*, *P. atrox*, and *Smilodon*.

Megafauna GRIWM analysis: These data are useful in this analysis towards the goal of generating precise estimates of megafaunal extinction dates, which are themselves the megafauna data points analyzed in the Marshall et al. (2015) model. Extinction dates may be inferred from directly sampled radiocarbon dates by several methods (Rivadaneira et al., 2009; Alroy 2014; Saltré et al., 2015). I chose GRIWM for three reasons:

1. Marshall et al. (2015) and Villavicencio et al. (2016) both assess probable extinction dates using GRIWM. Since those studies served as the model for this one, I aimed for methodological consistency.
2. Rivadaneira et al. (2009) demonstrate that GRIWM is the best available estimation method for minimizing uncertainty (*cf.* Saltré et al., 2015).

Because uncertainty surrounding extinction dates is a principal source of

uncertainty in the Marshall et al. (2015) model, it follows that GRIWM would be the best method for inferring data useful to that model.

3. GRIWM models theoretical and epistemic ambiguities in assessment of more recent extinctions; whatever uncertainty persists through GRIWM is therefore not unique to assessment of extinction in the fossil record. In the recent historical record, extinction is a *post hoc* assessment of population dynamics. Different features of a taxon's population dynamics may factor into different assessments—e.g., ecologists may focus on ecological function whereas taxonomists may focus on population size—and so varying research interests will imply different dates for a taxon's true extinction (Siipi & Finkelman, 2017; Finkelman, 2018). As a means of avoiding these ambiguities, Solow (1993; 2005) recommends inferring a range of probable extinction dates from a taxon's historical sighting record; GRIWM models this method by weighting fossil occurrences through time as Poisson-distributed in the same way as historical sighting records (Marshall, 2010). In this sense, whatever uncertainty remains through GRIWM analysis is theoretically consistent with uncertainty surrounding the extinction of any taxon.

The current analysis therefore infers extinction dates for relevant taxa using GRIWM. In their analyses, Marshall et al. (2015) and Villavicencio et al. (2016) adapted R code developed by Saltré et al. (2015); I use the same code here.

The Saltré et al. (2015) code yields a 95% confidence interval and median value for predicted extinction dates of each taxon. For the purpose of sorting taxon

extinctions into time bins for the Marshall et al. (2015) analysis, the Saltré et al. (2015) code uses the median value. My analysis therefore used the same practice. *Climate data:* To maintain spatial explicitness of this analysis, I analyzed climate data from multiple sites in the American west. I chose sites that included multiple climate proxies that were likely to be representative of different biogeographic provinces (Faith & Surovell, 2009; cf. Carrasco et al., 2009). The two chosen sites are Monterey Bay, California (36.8007°N, 121.9473°W), as representative of coastal biogeographic provinces; and Bear Lake, Idaho (49.0299°N, 111.3322°W), as representative of interior biogeographic provinces. Both sites included multiple records extending back at least 20000 years BP, which encompasses the temporal period of interest.

Palynological records have been a useful proxy for millennial-scale climate change (Cronin, 2010, pp. 129-130). As a record of changes in vegetation, relative abundance of pollen and spores in sediment cores demonstrate a biome's direct response to fluctuations in temperature, precipitation, and atmospheric composition. In this sense, vegetation marks the inflection point between biotic and abiotic components of an ecosystem; therefore, if climate change were to have an effect on megafaunal populations, that effect would likely be mediated through changes in vegetation. I selected the relative abundance of oak (genus *Quercus*) as a climate proxy for two reasons. First, oak abundance is sensitive to changes in temperature and precipitation, indicating warmth and aridity where present (Jiménez-Moreno et al., 2007); second, changes in relative abundance of oak have

been demonstrated to correlate with millennial-scale climate changes through the last several deglaciations in the Quaternary (Lyle et al., 2010).

For the current analysis, I downloaded palynological data for the past 600000 years associated with Monterey Bay, where oak percentages have varied from 5 to 45%, from Lyle et al. (2010); data for the past 225000 years associated with Bear Lake, where oak percentages have varied from 0 to 15%, comes from Jiménez-Moreno et al. (2007). Both datasets are available as text files through the World Data Center for Paleoclimatology (Webb et al., 1994).

Paleoclimate simulations provided by Lorenz et al. (2016) offer an additional measure of climate change. The authors' Earth systems CCSM3 models, inferred from trends in orbital parameters, ice sheet coverage and height, sea level, greenhouse gases, and meltwater pulses in the North Atlantic, produced simulated data for temperature, precipitation, surface radiation, surface pressure, and wind speed for the past 22000 years across North America (*cf.* Liu et al., 2009). One derivative of these data is Growing Degree Days (GDD), or the daily accumulation of warmth above a specified baseline temperature. GDD has proved a useful marker of primary productivity, with minimum and maximum GDD values determined for broad vegetation categories in Quaternary records (Prentice et al., 1992). GDD is therefore a useful value for this analysis for the same reason as pollen abundance: it quantifies a variable in the environment that has a direct effect on biotic response.

Data from Lorenz et al.'s climate simulation are available for download through the Dryad Digital Repository in NetCDF format (White et al., 2008). I processed these data files through Panoply software v.4.10.5, available for

download through giss.nasa.gov. The software allows for collation of multiple plots of multivariate data; I plotted GDD values per month against years BP for each site and exported the resulting datasets as a comma-separated values files.

Human occupation data: PIDBA includes a dataset of all radiocarbon dates associated with human occupation sites in North and South America, updated through 2010. This dataset is available for download as a Microsoft Excel spreadsheet.

I downloaded the PIDBA dataset and modified it to include only radiocarbon dates for material associated with sites in Arizona, British Columbia, California, Idaho, Nevada, Oregon, Utah, and Washington. The resulting dataset of 103 specimens includes dates sampled from human tissue, charcoal, and human-modified organic material, measured in radiocarbon years BP. As with the megafauna dataset, I calibrated all dates through OxCal online using the IntCal13 calibration curve and also rejected all dates with uncertainty exceeding 1000 years for the same reasons noted above (see Appendix C).

CHAPTER III RESULTS

Megafaunal extinction dates

The Marshall et al. (2015) least-squares regression analysis requires high-resolution prediction of true extinction dates for all fossil taxa. GRIWM produces these predictions by sampling from within a Gaussian distribution of uncertainties surrounding measured fossil dates. The current analysis resampled from 10000 simulated distributions to produce 95% confidence intervals for true extinction dates for each taxon (see Table 1).

Taxon	Number of specimens	Lower 95% (years BP)	Median (years BP)	Upper 95% (years BP)
<i>Arctodus</i>	7	12800	12430	11710
<i>Bison</i>	9	12110	11310	10120
<i>C. dirus</i>	35	11780	8000	5320
<i>Mammuthus</i>	16	13690	12930	11570
<i>Nothrotheriops</i>	25	12030	11100	10000
<i>O. harringtoni</i>	29	12350	10200	8180
<i>P. atrox</i>	6	17110	15730	13950
<i>Smilodon</i>	34	13180	12070	11120

Table 1: Summary data for ranges of true extinction dates inferred by GRIWM. Data show median values and 95% confidence intervals for true extinction dates of eight megafaunal taxa from the American west. All dates have been rounded to the nearest decade to reflect the precision of radiocarbon dating. GRIWM-estimated extinction date probability distributions differ from a normal distribution due to the irregularity of radiocarbon calibration (Marshall et al., 2015). GRIWM analysis predicts confidence intervals for *Bison*, *C. dirus*, *Mammuthus*, *Nothrotheriops*, *Oreamnos*, and *Smilodon* that include the Pleistocene-Holocene boundary (approximately 11.65 ka); *Arctodus* and *P. atrox* likely went extinct just before the end of the Pleistocene.

GRIWM predicts some overlap in potential extinction dates for most taxa analyzed, with *P. atrox* (13180–11120 years BP) being the sole exception (see Figure 1).

Relative contributions of climate and human activity

Following high-resolution prediction of megafaunal extinction dates, I applied Marshall et al.'s (2015) model to the data to determine whether or not the causal contributions of climate change and human activity towards megafaunal extinctions could be distinguished. I repeated the analysis twice, first using environmental data from Monterey Bay and again using data from Bear Lake; megafauna and human-associated data remained the same for each analysis. Least-squares regression analyses yielded values given in Table 2 below.

The analysis of the Monterey Bay data showed correlations between megafaunal extinctions and climate changes, human activity, and synergistic effects between the two. Changes in GDD are significantly correlated with megafaunal extinctions both ($p < 0.05$); changes in vegetation are significantly correlated with extinctions ($p < 0.10$); human activity is significantly correlated with extinctions when compared against coastal vegetation change ($p < 0.05$); synergistic effects between human activity and coastal vegetation change are significantly correlated with megafaunal extinctions ($p < 0.05$). Comparison of the relative effects of human activity and vegetation change suggests that human activity (parameter value 0.1071 ± 0.033) had a stronger effect than vegetation change (parameter value 0.076 ± 0.04), while a negative synergistic effect had the weakest effect (parameter value -0.012 ± 0.01).

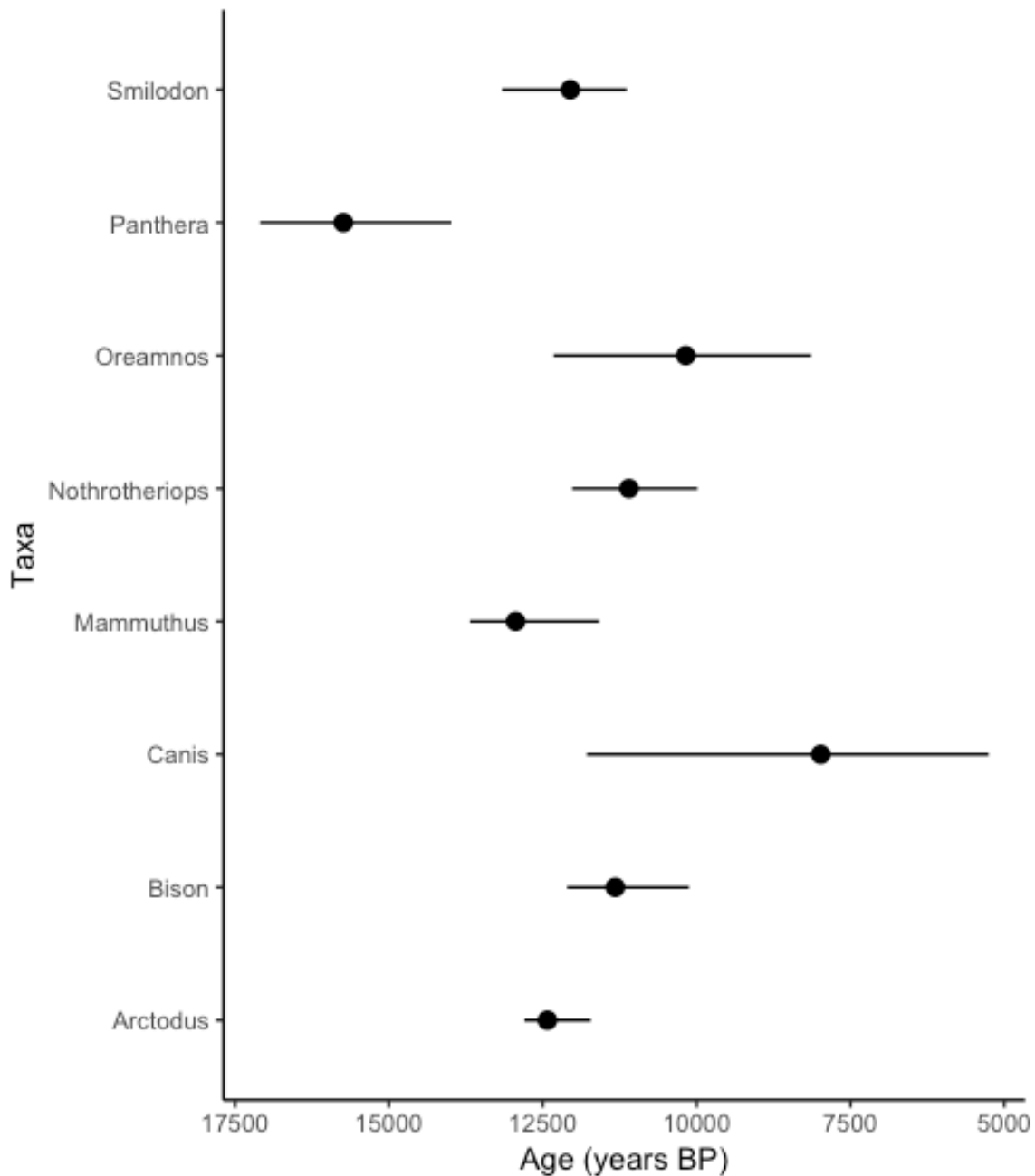


Figure 1: GRIWM predictions of true extinction dates for eight megafaunal taxa in the American west. Dots represent median predicted dates; whiskers represent 95% confidence intervals. The confidence intervals by taxon are: *Arctodus*, 12800–11710 years BP; *Bison*, 12110–10120 years BP; *C. dirus*, 11780–5320 years BP; *Mammuthus*, 13680–11570 years BP; *Nothrotheriops*, 12030–10000 years BP; *Oreamnos*, 12350–8180 years BP; *P. atrox*, 17110–13950 years BP; *Smilodon*, 13180–11120 years BP. Figure generated using R software.

Site	Climate Index	Lag	Parameter	Value	St. Error	p-value
Monterey Bay	GDD	None	<i>a</i>	0.0030	0.0014	0.0418**
			<i>b</i>	0.0118	0.0344	0.7359
			<i>c</i>	0.0005	0.0004	0.2109
		Offset	<i>a</i>	0.0034	0.0012	0.0125**
			<i>b</i>	-0.0034	0.0310	0.9149
			<i>c</i>	-3.9402	0.0004	0.9913
	Pollen	None	<i>a</i>	0.0764	0.0398	0.0712*
			<i>b</i>	0.1071	0.0334	0.0049**
			<i>c</i>	-0.0115	0.0052	0.0407**
		Offset	<i>a</i>	0.0686	0.0355	0.0688*
			<i>b</i>	0.0638	0.0297	0.0459**
			<i>c</i>	-0.0114	0.0046	0.0243**
Bear Lake	GDD	None	<i>a</i>	0.0030	0.0016	0.0799*
			<i>b</i>	0.0458	0.0339	0.1940
			<i>c</i>	-3.9474	0.0004	0.9217
		Offset	<i>a</i>	0.0038	0.0013	0.0118**
			<i>b</i>	0.0101	0.0278	0.7214
			<i>c</i>	-0.0002	0.0003	0.5916
	Pollen	None	<i>a</i>	0.0618	0.0775	0.4376
			<i>b</i>	0.0609	0.0367	0.1174
			<i>c</i>	0.0187	0.0098	0.0756*
		Offset	<i>a</i>	0.1008	0.0695	0.1672
			<i>b</i>	0.0082	0.0329	0.8074
			<i>c</i>	0.0149	0.0088	0.1105

Table 2: Non-linear least squares regression analysis of relative contributions to megafaunal extinctions by climate change (parameter *a*), human agency, (parameter *b*), and synergistic effects (parameter *c*). Values marked with a single asterisk (*) are significance to 90% confidence; values marked with a double asterisk (**) are significant to 95% confidence or more. Analysis suggests that megafaunal extinctions in the western United States correlated with changes in Growing Degree Days (GDD) on the coast (Monterey Bay) and in the continental interior (Bear Lake); with changes in coastal vegetation; with coastal human activity; and with negative synergy between vegetation change and human activity on the coast. See Discussion for more details.

Analysis of the Bear Lake data yielded fewer significant results. As in Monterey Bay, changes in GDD at Bear Lake are correlated with megafaunal extinctions. The effect

is stronger using offset time bins ($p < 0.05$) than it is using millennial time bins ($p < 0.10$), suggesting that data sorting had some influence on the results. The correlation between vegetation change and human activity appears significant ($p < 0.10$) when using millennial time bins, but the apparent effect disappears when using offset time bins. This last result is therefore unlikely to be an ecological signal.

CHAPTER IV

DISCUSSION

The most important epistemic obstacle in resolving the debate over end-Pleistocene megafaunal extinctions is the underdetermination of theory by evidence, or the insufficiency of evidence in deciding between competing hypotheses. This problem is particularly acute in historical sciences such as paleontology wherein decisive evidence may be limited by information-destroying geological processes (Turner, 2005). To date, there has been no “smoking gun” evidence that would decide between the competing hypotheses and explain the end-Pleistocene megafaunal extinctions (Faith & Surovell, 2009; Ericksson et al., 2012; Barnosky et al., 2014; *cf.* Koch & Barnosky, 2006; Guthrie, 2006). The “climate change” and “human agency” hypotheses may both accommodate currently available evidence and so neither can be summarily rejected.

Between the two competing hypotheses, human agency is currently ascendant (Koch & Barnosky, 2009; Bartlett et al., 2016). Even among proponents of human agency, the exact form of extinction-causing human agency remains a matter of dispute (Koch & Barnosky, 2009; Emery-Wetherell et al., 2017); nevertheless, global analyses tend to converge on human agency as a primary driver of megafaunal extinctions (Barnosky et al., 2014; Bartlett et al., 2016). Against this conclusion, proponents of climate change as the primary driver of megafaunal extinctions may dispute the evidence cited by proponents of human agency (Lima-Ribiero & Diniz-Filho, 2013), but the more common response is to argue the

consistency of that evidence with the climate change hypothesis (Braje & Erlandson, 2013; Emery-Wetherell et al., 2017). Instead of seeking an evidential resolution to the debate, then, recent researchers have recommended methodological solutions whereby evidence is interpreted with new analyses (Benton, 2014; Marshall et al., 2015; Bartlett et al., 2016; Emery-Wetherell et al., 2017).

Following Cleland (2002), Currie (2018) recommends an “omnivorous” approach to resolving underdetermination problems in historical sciences. Even though “smoking gun” evidence may not be available, past events leave a wide variety of traces that may collectively lend a preponderance of evidence towards one theory or another (Cleland, 2002); integration of multiple lines of evidence collected through different methodologies may therefore resolve debates such as that between climate change and human agency (Currie, 2018). The strength of analytical methods such as the one recommended by Marshall et al. (2015) is that they formalize the “methodological omnivory” that may be necessary to resolve historical debates in the absence of smoking guns by drawing upon evidence from multiple research programs (e.g., climate modeling, palynology, archaeology, and paleontology).

Of course, the absence of smoking guns may not signal any epistemic deficiency; rather, smoking gun evidence may be absent because there was no shooter, so to speak. The end-Pleistocene megafaunal extinctions may not have had any cause *per se*. Such a view is consistent with early Neo-Darwinian accounts of mass extinction: Dobzhansky (1951), for example, argued that periods of significantly elevated extinction rates ought to be expected from a purely stochastic

process operating over evolutionary timescales (*cf.* Raup, 1992; 1993; Gould 2002). By this view, the unlikelihood of multiple qualitatively similar taxa coincidentally disappearing within the same short timeframe is mitigated by the fact that geological time offers vast timescales through which unlikely events occasionally do in fact occur.

The contrary view—that periods of significantly elevated extinction rates require some causal explanation—has gained recent support due to the success of the “extraterrestrial impact” theory of K-Pg extinctions, but may not be broadly applicable to other extinction events (Benton, 2014; *cf.* Cleland, 2002). Development of this view led Barnosky et al. (2004) to suggest that the end-Pleistocene extinctions may have had multiple independent or synergistic causes; indeed, this is the view endorsed by Villavicencio et al. (2016) in their *Última Esperanza* analysis.

That last analysis demonstrates another strength of the Marshall et al. (2015) model: it may be capable of resolving these debates as well. The model is explicitly designed to distinguish the relative contributions to extinction given by multiple causes. With sufficient statistical power, the model may also distinguish between no-result reflecting insufficient data and no-result reflecting causal inefficacy (*cf.* Saltré et al. 2015).

Presuming that the results given above do have sufficient power (but see “Challenges to this analysis” below), it is possible to disambiguate some factors responsible for the disappearance of megafauna in the American west. The consistency between the Bear Lake and Monterey Bay data alike suggest that climate change may have been a causal factor and human activity seems to have

been a factor in relation to climate changes along the coast; however, further analysis of the coastal data suggests some reason to be skeptical of these findings.

Megafaunal extinctions

Following rejection of inappropriate radiocarbon dates and taxa with insufficient dated material, the current analysis focused on eight megafaunal taxa: the short-faced bear *Arctodus*; the American buffalo *Bison*; the dire wolf *C. dirus*; the proboscidean *Mammuthus*; the ground sloth *Nothrotheriops*; the southern mountain goat *O. harringtoni*; the American lion *P. atrox*; and the saber-toothed cat *Smilodon*. GRIWM analysis suggests that all of these taxa went extinct in the American west in a temporal window spanning 17.1 ka to 5.3 ka; if one removes from the analysis species in genera currently extant in the American west, the window narrows to 13.7–8.1 ka. In both cases the temporal span encompasses the Pleistocene-Holocene boundary and the Younger Dryas event; it is also coincident with an increase in human occupation in North America (see below). This result is consistent with previous analyses that timed megafaunal extinctions to a 5000-year window correlated both with rapid climate change and with human population growth (Faith & Surovell, 2009; Emery-Wetherell et al., 2017).

There is a sharp increase in the number of megafaunal extinctions between 12 ka and 10 ka, i.e., at the Pleistocene-Holocene boundary (see Figure 2).

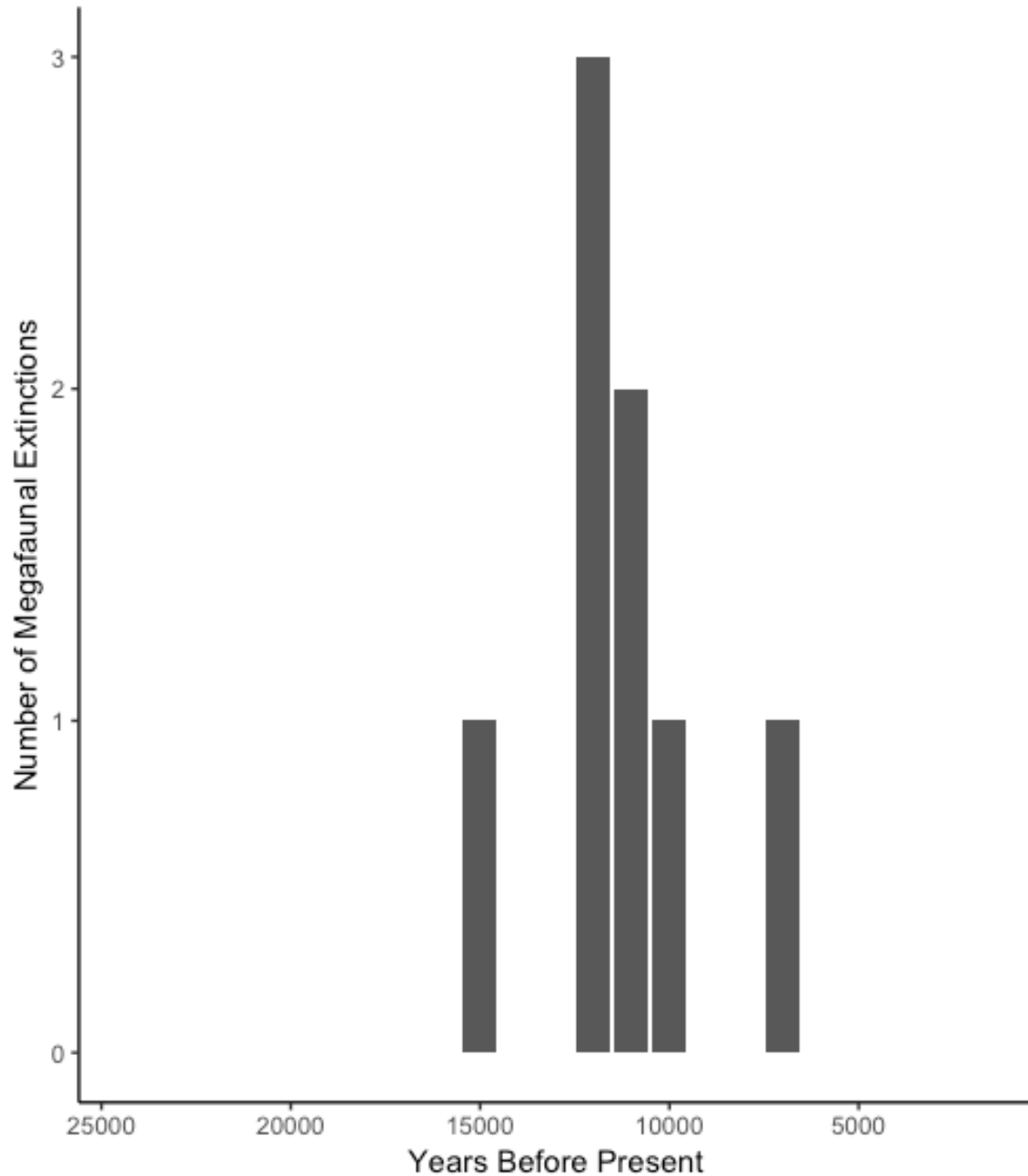


Figure 2: *Number of megafaunal extinctions over time.* Among the eight megafaunal taxa analyzed here, the greatest number of extinctions occurred in the time bins encompassing 11–12 ka (2) and 12–13 ka (3). These data are consistent with a rapid disappearance of megafauna at the end of the Pleistocene epoch. Figure generated using R software.

Faith & Surovell (2009) argue that such a rapid increase in extinction rate is most clearly consistent with the human agency hypothesis; however, Emery-Wetherell et

al. (2017) dispute the sufficiency of human-megafauna overlap in explaining such a pattern.

Among previous analyses that suggested multiple causes of the end-Pleistocene megafaunal extinctions, several suggest that ecological state shifts played a role in at least some of the extinctions (Barnosky et al., 2004; Barnosky et al., 2011; Barnosky et al., 2015). A taxonomically explicit review of the results given here is consistent with this suggestion. *P. atrox* was the first taxon to disappear from the American west; the next were *Mammuthus*, *Smilodon*, and *Arctodus*. Finke & Denno (2004) show that predator diversity correlates inversely with the probability of trophic cascade effects (*cf.* Ripple & Beschta, 2012) while Barnosky et al. (2015) note that the disappearance of ecosystem engineers such as *Mammuthus* should produce ecological state shifts that increase the probability of further extinctions (Eklöf & Ebenman, 2006; Brook et al., 2008; Doughty et al., 2010; Sahasrabudhe & Moller, 2011). Results given above show that the first four megafaunal taxa to disappear in the American west were the three largest predators and a significant ecosystem engineer (Guthrie, 2001; Johnson, 2009), which are precisely the taxa among those analyzed whose disappearances would be likely to trigger ecological state shifts. Explaining the disappearances of these keystone taxa, then, may explain other megafaunal extinctions as well.

While small-bodied mammals (< 2 kg) were not included in this analysis, prior analyses of those taxa also suggest that the American west underwent a large-scale ecological state shift at the end of the Pleistocene. Barnosky et al. (2011) demonstrate that small-bodied mammal taxa were less prone to extinction at the

end of the Pleistocene than larger-bodied taxa, but nevertheless suffered collateral biodiversity loss as a result of biogeographical range shifts (p. 186). As the results in the current analysis also suggest, the collateral biodiversity loss among small-bodied mammals was more acute along the western coast than in the continental interior (Barnosky et al. 2011, p. 185; see also “Assessment of relative causal contributions to megafaunal extinctions” below). If the region underwent such an ecological state shift, a likely cause would be the disappearances of ecological engineers and archpredators (Barnosky et al., 2015).

Human agency

Data analyzed for this analysis include some evidence for direct human interaction with megafauna, including the keystone taxa noted above. Human-modified *Mammuthus* material accounts for four human-associated radiocarbon dates in the analyzed dataset; additionally, the data include three radiocarbon dates sampled from human-modified *Bison* material. Emery-Wetherell et al. (2017) also demonstrate overlap between human occupation and some megafaunal populations in the American west. With respect to human agency in megafaunal extinctions, however, this evidence is purely circumstantial (*cf.* Grayson & Meltzer, 2002). The evidence most directly relevant to this analysis is the trend in human activity or population growth at the end of the Pleistocene (see Figure 3).

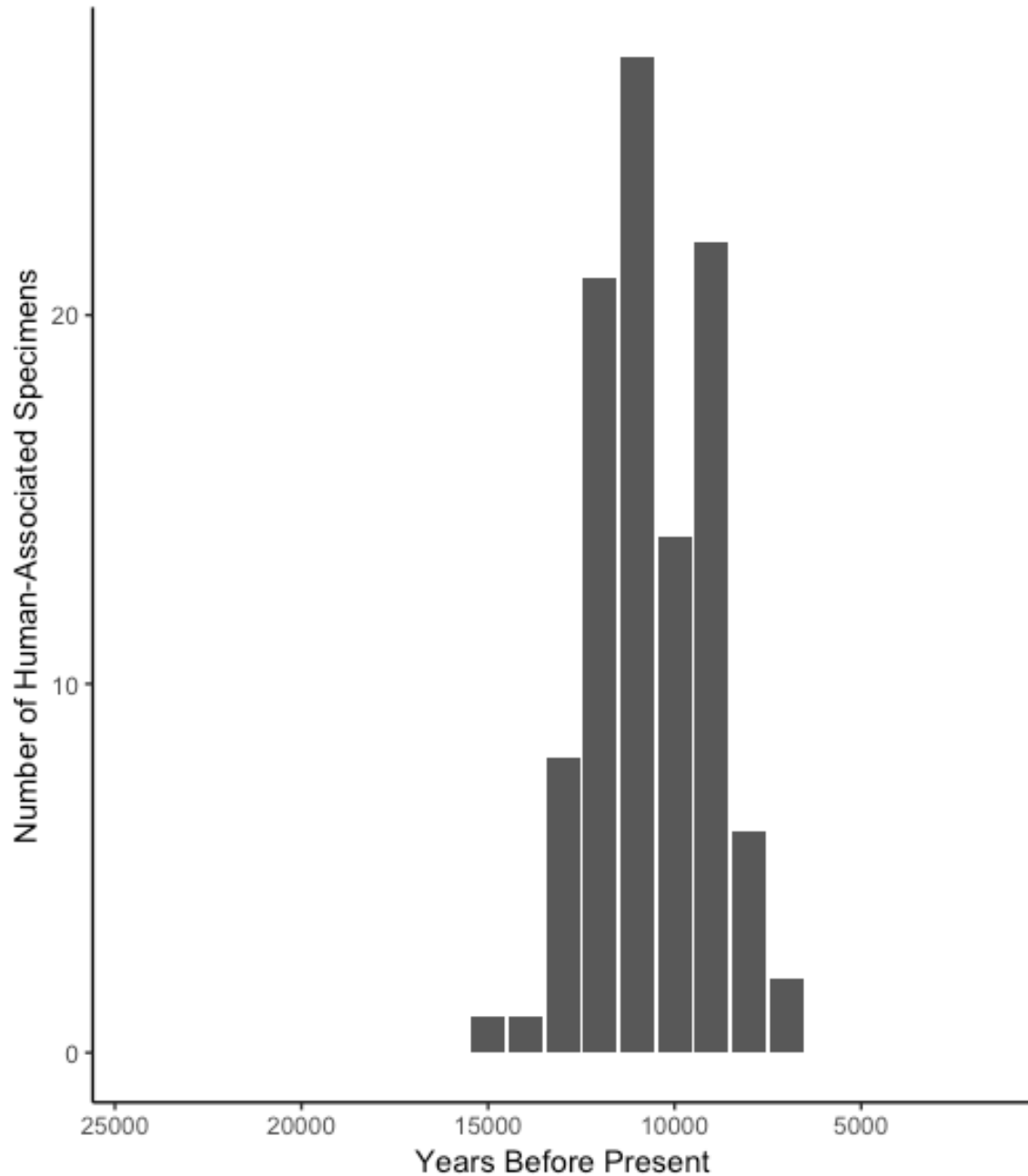


Figure 3: *Number of human-associated specimens over time.* Data show a sharp increase in human activity starting approximately 13 ka. The greatest numbers of human-associated specimens occur in time bins encompassing 11–12 ka (21), 10–11 ka (27), 8–9 ka (22). The first two of those bins correlate with a sharp increase in megafaunal extinctions (see Figure 2). The most recent material in my dataset was dated to 7.8 ka and so the apparent decrease in human activity after 7 ka can be interpreted as an artifact of these data; the apparent decrease in activity in the 9–10 ka time bin may also be due to an edge effect. Figure generated using R software.

The number of human-associated specimens in the analyzed dataset increases starting 12–13 ka, increases even more sharply 11–12 ka, and peaks 10–11 ka. The inferred timeframe of increasing human activity in this analysis therefore corresponds with the greatest number of megafaunal extinctions, which occurred between 10 and 12 ka. This result may be suggestive, but it is not significant *per se*: correlation between megafaunal disappearances and human data does not seem distinguishable from correlation between megafaunal disappearance and other data from Bear Lake (see Table 2).

Nevertheless, human activity does correlate significantly with megafaunal extinctions when compared against climate data from Monterey Bay (see Table 2). This regional disparity may be due to human migration patterns: the first Americans likely migrated down the Pacific coast and into the interior thereafter (Erlandson, 1994; Erlandson et al., 2007; Reich et al., 2012; Erlandson & Braje, 2015; Anderson et al., 2015; *cf.* Emery-Wetherell et al., 2017). One would reasonably infer, then, that the most direct correlation between megafaunal extinctions and human activity would occur along the Pacific coast at points of first regional contact. This expectation is consistent with the result given above: human activity is significantly correlated with megafaunal disappearances in the given coastal analysis, suggesting immediate and sustained interaction. This correlation is also consistent with patterns of biodiversity loss among smaller mammals due to changes in biogeography (Barnosky et al., 2011).

The direction of causal influence between human arrival and megafaunal disappearance in that region of first contact remains ambiguous. On the one hand,

these results may be consistent with Villavicencio et al., (2016) who argue that human activity explains the disappearance of megafaunal predators in Última Esperanza—perhaps through niche exclusion—given that human arrival in that area immediately predates the regional disappearance of *Smilodon* and *Panthera*. On the other hand, these analyzed data do not clearly imply the same conclusion. While *P. atrox* was the first megafaunal taxon to disappear in the American west, current data seem to suggest that human arrival was not the cause of its disappearance. The earliest sympatric human-associated radiocarbon date in the analyzed dataset is 13222 ± 71 calendar years BP (calibrated mean \pm standard deviation), which follows the latest likely extinction of *P. atrox*. If there were a causal connection between megafaunal disappearance and human arrival, it may have been that humans migrated into the coastal region because of the disappearance of a potential predator.

This explanation cannot be eliminated on the basis of the data given here, but some evidence counts against it. The earliest human-associated radiocarbon date from the continental interior in this dataset is 15350 ± 260 calendar years BP (calibrated mean \pm standard deviation), which falls well within the 95% confidence interval for likely extinction dates of *P. atrox*; while this date was not sampled from a coastal site, likely patterns of human migration to the region imply that humans arrived on the Pacific coast well before that date and, therefore, likely before the extinction of *P. atrox* (see “Assessment of relative causal contributions to megafaunal extinctions” below; cf. Jenkins et al., 2012; Erlandson & Braje, 2015).

By contrast, the earliest date of human arrival on the coast, ~13220 years BP, is earlier than the earliest bound on the 95% confidence interval for the disappearance of *Smilodon*, another megafaunal predator. American coastal data therefore follow the same pattern as in Última Esperanza, where human arrival immediately preceded the disappearance of *Smilodon*. Villavicencio et al. (2016) argue that human arrival explains the disappearance of *Smilodon* in the region of their analysis. Absent some ecologically relevant difference between their data and the data presented here—which seem to follow the same pattern—a similar explanation seems appropriate here.

Climate shifts

Results given above also imply a role for climate change. The results indicate a general correlation between megafaunal disappearances and changes in temperature as well as a more specific correlation between megafaunal disappearances and vegetation changes on the coast.

Both Monterey Bay and Bear Lake would have been subject to global climate trends at the end of the Pleistocene, which was marked by a general warming trend following the Last Glacial Maximum abruptly punctuated by the Younger Dryas cooling event that marked the end of the Pleistocene (Cronin, 2010). The post-glacial warming trend that began ~17 ka is evident in GDD models for both sites (see Figure 4), if less acute at Bear Lake (Lorenz et al., 2016).

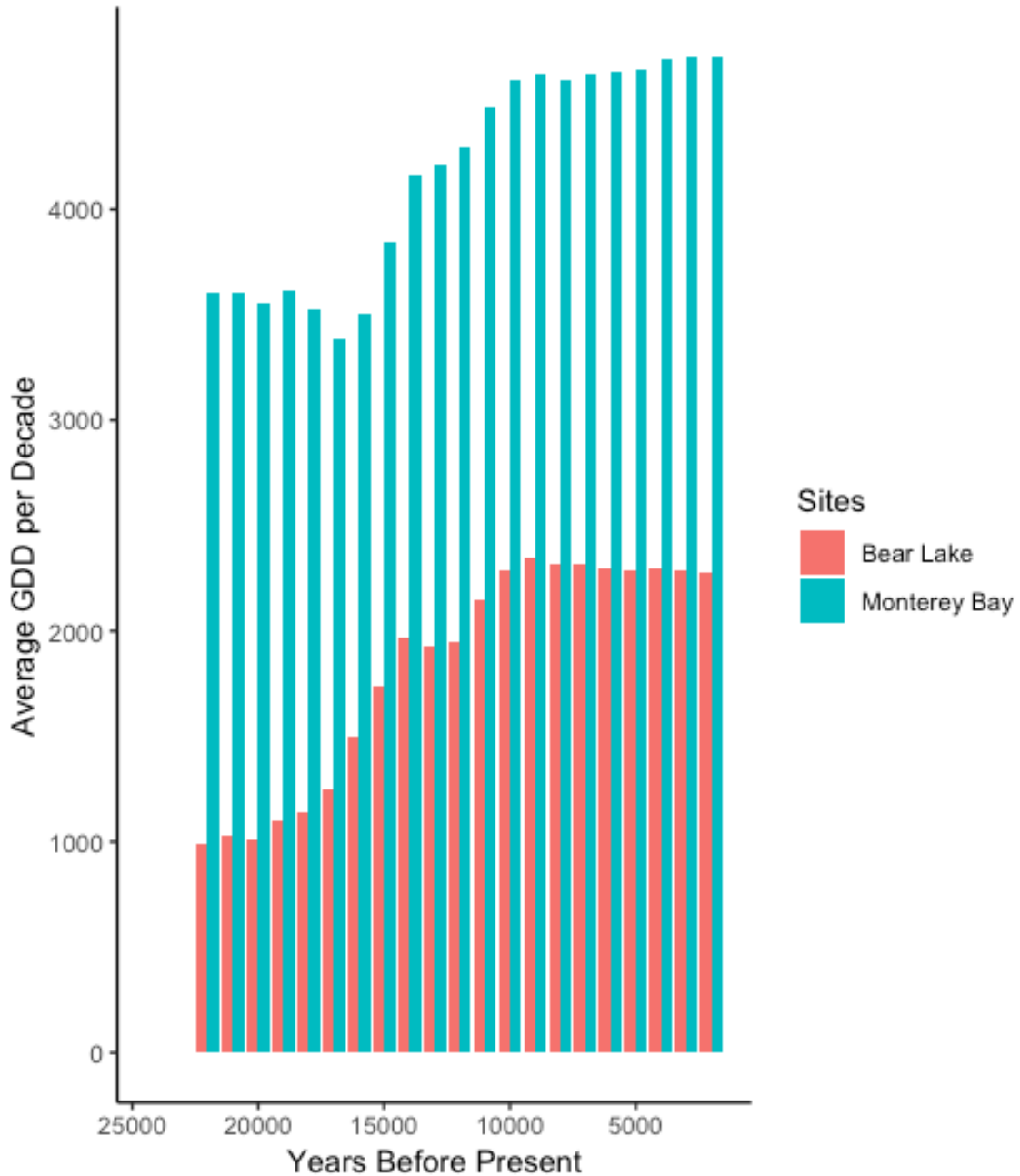


Figure 4: Modeled Growing Degree Days (GDD) over time in Monterey Bay, California (right bars, blue) and Bear Lake, Idaho (left bars, red). Both sites exhibit the same general postglacial warming trend that starts ~17 ka with a relatively rapid accumulation of GDD between 17–13 ka. While the same relative trends are evident in GDD models for both sites, absolute values are higher for Monterey Bay than for Bear Lake.

The climate model produced by Lorenz et al. (2016) predicts that Monterey Bay and Bear Lake were both subject to the same relative trends over the past 22000 years, reflecting the interconnections among ocean-atmosphere climate systems (Jiménez-Moreno et al. 2007). Both sites began an accumulation of GDD ~17 ka, saw an abrupt reversal of the trend ~13 ka, and another abrupt reversal ~12 ka. By contrast with Bear Lake, Monterey Bay had absolutely higher GDD values and seems to have been more sensitive to changes in climate trends. This sensitivity was likely a consequence of the latter site's location on the Pacific coast, subject to influence by El Niño-Southern Oscillation (ENSO) variability and the Pacific Decadal Oscillation (PDO; Moy et al., 2002; Lyle et al., 2010); sites further in the continental interior, such as Bear Lake, are buffered from the effects of ENSO and PDO (Cronin, 2010). Latitudinal differences were also a likely factor.

GDD data at both sites are significantly correlated with megafaunal disappearances. These correlations are consistent with global patterns at the end of the Pleistocene and remain one of the confounding factors in distinguishing specific agents of megafaunal turnover (Pielou, 1991; Koch & Barnosky, 2006; Barnosky et al., 2015; Emery-Wetherell et al., 2017).

More specific regional insights follow from differences in relative pollen abundance at the two analyzed sites. Both locations exhibit roughly similar trends in relative oak abundance until ~13 ka. After that time there was sharp increasing trend, with greater absolute millennial-scale variation, in Monterey Bay that is not matched in Bear Lake (see Figure 5).

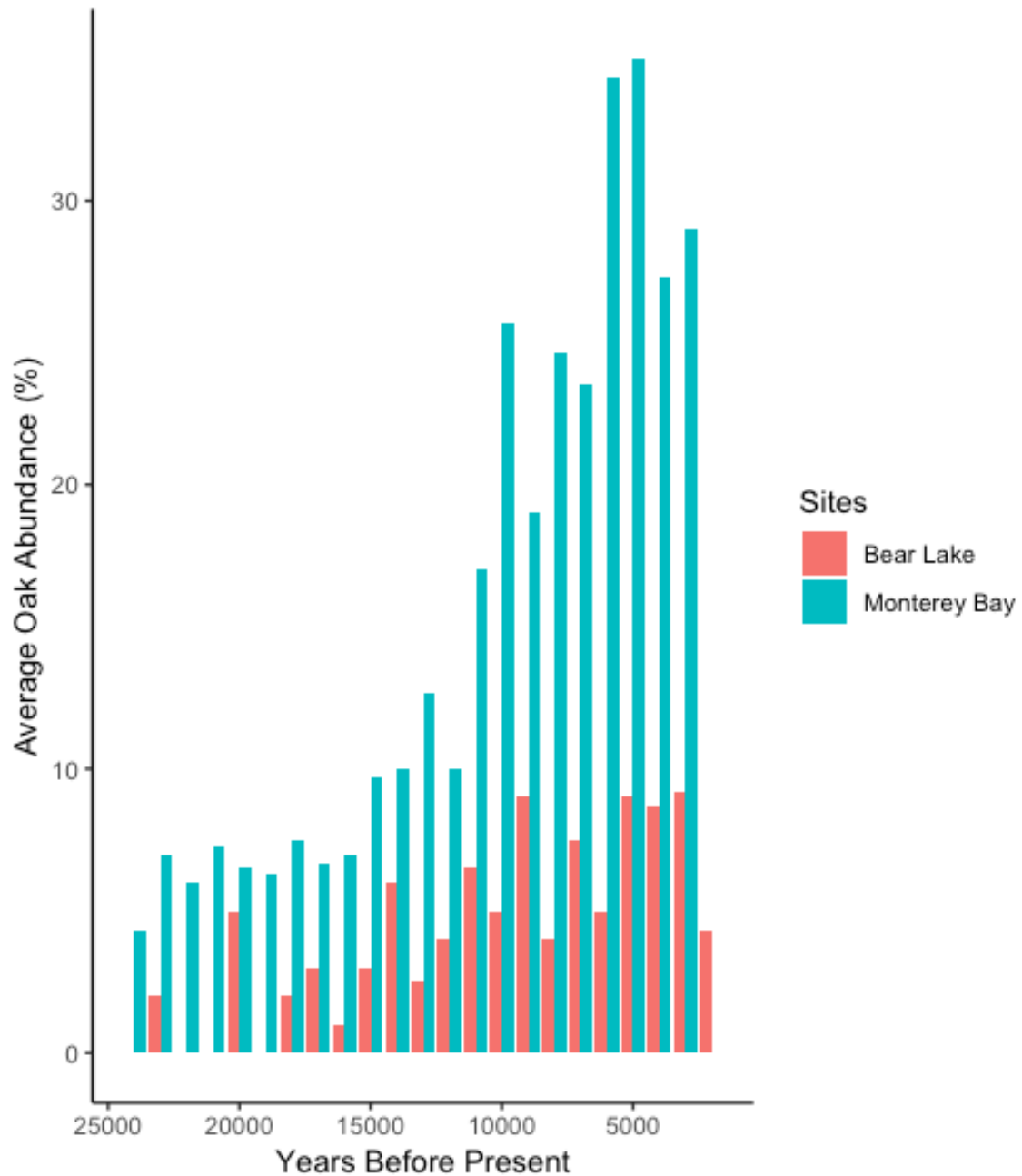


Figure 5: *Relative abundance of oak (Quercus) over time in Monterey Bay, California (right bars, blue) and Bear Lake, Idaho (left bars, blue). Both sites have similar trends in relative oak abundance in the period from 25–13 ka, although Monterey Bay shows greater millennial-scale variation. Starting ~13 ka, Monterey Bay sees a sharp increasing trend of relative oak abundance with greater absolute variation than Bear Lake, indicating overall greater warmth, aridity, and climatic variability in the last 13000 years.*

Two inferences follow. First, the Pacific coast witnessed an increase in oak forest cover starting ~13 ka that was not matched in the continental interior, where oak forest cover remained relatively less abundant than cold-weather forest (Doner, 2009). Second, because an increase in oak abundance is an indicator of increased warmth and decreased precipitation, one may infer that Monterey Bay was both generally warmer and more climatically variable than Bear Lake in the timeframe that includes the greatest number of megafaunal extinctions and human-associated specimens in this analysis (Jiménez-Moreno et al., 2007; Lyle et al., 2010). This difference implies some decoupling of more specific climate trends between the Pacific coast and the western American interior (*cf.* Jiménez-Moreno et al., 2007, Doner, 2009).

Decoupling of trends between sites would explain differences between sites in the relative contribution of vegetation change to megafaunal extinctions. Vegetation change at Bear Lake is indistinguishable from other factors in correlating with megafaunal disappearances, but the Monterey Bay data show significant correlation between megafaunal extinctions and vegetation change ($p < 0.10$).

This result is also consistent with an ecological state shift and particularly one triggered by the disappearance of *Mammuthus*. Mammoth grazing was elsewhere responsible for the maintenance of grassland ecosystems (Zazula et al., 2003); the disappearance of *Mammuthus* from the coastal ecosystem would be consistent with and conducive to the apparent spread of oak forest cover in that region (Barnosky et al., 2015). Marshall et al. (2015) argue that significant correlation between data in millennial time bins are sufficient to account for the

time-lagged effects of forest cover on megafaunal composition given that those effects are likely to take place in fewer than 1000 years (p. 10). Such a change is also consistent with time-lagged effects on other megafauna: those taxa may not have suffered any immediate consequence of an increase in relative oak abundance, but a change in biome would undoubtedly have longer-term effects that include the disappearance of taxa adapted to the earlier ecosystem (Eklöf & Ebenman, 2006; Doughty et al., 2008; *cf.* Marshall et al., 2015). In this sense, the initial increase of relative oak abundance on the coast might have portended greater changes to come.

This explanation has the added advantage of explaining the significant ($p < 0.05$) negative synergistic effects of human activity and vegetation changes on the coast. When faced with similar results, Marshall et al. (2015) suggest that changes in vegetation might inhibit human hunting activities. That is perhaps the case here, where it seems that the apparent decrease in human activity after 9 ka is counterbalanced by a sharp increase in relative oak abundance; however, it must be noted that the decrease is just as likely a result of sampling bias or transition between paleoanthropological cultures (*cf.* Pielou, 1991), if not more so.

Assessment of relative causal contributions to megafaunal extinctions

The results discussed here imply that global-scale climate changes, human activities, and negative synergistic effects between the two along the American west coast each made significantly different contributions to megafaunal extinctions in the American west. The results are all consistent with an account wherein initial human overkill or competitive exclusion leads to an ecological state shift; however, the results are also consistent with the hypothesis that each of the contributing factors

was causally independent of the others. I develop the state shift hypothesis here because it offers a testable, unified explanatory framework, and would therefore require less *post hoc* justification or appeal to coincidence than the alternative (Kitcher, 1989; Sober, 2015, pp. 153-199). The framework developed here is nevertheless open to several objections that I will consider below.

No matter the source of climate data, megafaunal disappearances in the western USA were significantly correlated with large-scale climatic trends. Given the above discussion, I offer the following scenario to explain the given results:

- Humans migrated into America down the Pacific coast. This migration resulted in the local extinction of megafaunal predators, whether through hunting or niche exclusion. This disappearance of megafaunal predators was concurrent with the human-assisted regional extinction of *Mammuthus*, which in turn spurred an increase in oak forest cover (*cf.* Ripple & Beschta, 2012). The disappearances of these taxa spurred large-scale ecological state shifts. These state shifts reduced and eventually eliminated other regional megafauna as a consequence of initial extinctions and accompanying vegetation changes.
- Shortly after migrating down the coast, humans moved into the continental interior. There they encountered relatively fewer megafaunal predators and so were less likely to be responsible for inciting large-scale ecological state shifts. Human activity nevertheless wrought local ecological shifts that had a deleterious effect on megafaunal populations.

The former scenario is admittedly better supported by the data than the latter, although the latter scenario is a consequence of salient differences in biodiversity, climate, and timing of human arrival between the Pacific coast and the continental interior. It is also borne out by contemporaneous data on small mammal communities. Barnosky et al. (2011) estimate an end-Pleistocene decrease in small mammal biodiversity of 50% above background extinction loss for communities along the coast and between 15 and 33% above background extinction loss for communities in the continental interior. While this loss of biodiversity was not a result of extinctions, as in the case of megafauna, small mammal communities seem likelier to respond to ecological state shifts through geographic range shifts (Terry et al., 2011; Barnosky et al., 2015).

The details of these scenarios depend principally upon the significant difference in precise extinction dates for relevant taxa. The significance of those results is a function of the power of this analysis; consequently, any reason to doubt the sufficiency of statistical power of the analysis would render these scenarios less likely.

Challenges to this analysis

One reason to doubt that this analysis is sufficiently powerful follows from the result showing negative synergy between human activity and vegetation changes in Monterey Bay. In their analysis of similar data, Marshall et al. (2015) argue that the low statistical power may account for such an unexpected result. Additional data are necessary to render a final verdict.

Additional data from more geographic sites would also be useful for making this analysis more spatially explicit. Monterey Bay and Bear Lake may be representative of distinct biogeographic provinces as defined by Faith & Surovell (2009), but delineation of boundaries between biogeographic provinces remains controversial and inconsistent between different authors (Emery-Wetherell et al., 2017). For example, Carrasco et al. (2009) distinguish three provinces in the continental interior region analyzed here as a single province; additionally, Barnosky (1985) notes that America's Pacific Northwest had a lower relative abundance of oak during the late Pleistocene than analyzed here in Monterey Bay, suggesting that the Pacific coast may include multiple biogeographic provinces (*cf.* Grigg & Whitlock, 1998; Gavin et al., 2007). Analyses in additional locations, particularly those representing the Columbia Plateau and South Great Basin provinces of Carrasco et al. (2009), would be useful in affirming or denying this analysis' success in conducting a spatially explicit analysis.

Unfortunately, current data are insufficient to that task. The current datasets, comprehensive as they may be, nevertheless do not include sufficiently many data points to conduct more thorough regional analyses. Regions with a sufficient number of megafauna-sampled radiocarbon dates lack a sufficient number of dated human-associated specimens for meaningful analysis; regions with sufficiently many dated human specimens lack a sufficient number of megafauna-sampled dates. Many more radiocarbon dates, for both megafaunal and human-associated specimens, are necessary before we will be capable of a comprehensive regional assessment of relative causal contributions to megafaunal extinctions.

The differential responses of megafaunal populations and small mammal populations to the proposed mechanism may also cast doubt on this account. The extinction rate for small-bodied mammals at the end of the Pleistocene did not rise above background extinction levels in North America (Barnosky et al., 2011). A large-scale ecological state shift ought to be a relatively indiscriminate cause of extinction; if such a shift caused an unusual number of megafaunal extinctions then one may reason that it should cause an unusual number of extinctions among smaller-bodied taxa. As noted above, however, local species diversity, richness, and evenness among small-bodied mammal taxa all fell dramatically at the end of the Pleistocene (Ibid). It is possible that differences in life history strategies between large- and small-bodied mammals may account for such a differential response to ecological state shifts, but that conclusion requires further research. More generally, application of the Marshall et al. (2015) model to data including small-bodied mammals would be useful for affirming or denying the account sketched above.

CHAPTER V

CONCLUSION

To summarize my principal findings:

1. GRIWM analysis predicts that eight megafaunal taxa went extinct in the American west during a temporal window spanning 17.1–5.3 ka, with six of the eight taxa disappearing in a narrow window between 13.7 and 8.1 ka. The first taxa to go extinct were carnivores and ecosystem engineers; this is consistent with end-Pleistocene extinction patterns elsewhere.
2. Least-squares regression analysis using the Marshall et al. (2015) model applied to these data shows that global climate trends significantly correlate with megafaunal extinction trends in the American west.
3. On the Marshall et al. (2015) model, coastal data also show significantly distinct correlations between megafaunal extinctions and human activity ($p < 0.05$). The same data show less significant correlations between megafaunal extinctions and counterbalancing effects of human activity and vegetation change ($p < 0.10$).
4. These results are consistent with the hypothesis that end-Pleistocene megafaunal extinctions in the American west were due to ecological state shifts.

These findings suggest an affirmative answer to the initial research question: the relative contributions to megafaunal extinctions of climate change and human

agency can be distinguished; choice between competing hypotheses that explain the end-Pleistocene extinctions is not underdetermined in principle.

In practice, the findings of this study admit of more ambiguous interpretations. Results given above may be a function of low statistical power rather than a true historical signal. Deciding between this interpretation and one that accepts my results at face value requires more data.

The call for more data, familiar in scientific research, may be practicable in these circumstances. As radiocarbon dating becomes more commonplace and less destructive of sampled material, our collective ability to read historical signals improves (Wood, 2015; Harvey et al., 2016). My research shows that further improvements have the capacity to resolve debate over the causes of end-Pleistocene megafaunal extinctions in relatively short order.

APPENDIX A

R CODE

```
rm(list=ls())
options(stringsAsFactors = FALSE)

##Load data
setwd("~/Dropbox/Research/FinkelMasters/Data")
dates<-read.csv("ContDivide.csv")
Human_data <- read.csv("HumanSites.csv")
pollen <- read.csv("BearLakePollen1.csv")
gdd <- read.csv("BearLakeGDD.csv")

##Load packages
install.packages(c("neotoma"))
install.packages(c("dplyr"))
library("neotoma")
library("ggplot2")
library("reshape2")
library("MASS")
library("dplyr")

##GRIWM extinction analysis
Taxa <- unique(dates$Genus)
LADS <- sapply(Taxa, function(x) min(dates[dates$Genus == x, "CalAge"]))
EXT_COUNT <- data.frame(bin = seq(2000, max(round(LADS, digits = -3)), by = 1000))
EXT_COUNT$NO_EXT <- sapply(EXT_COUNT$bin, function(x) sum(between(LADS, x,
x+999)))
EXT_OFF <- data.frame(bin = EXT_COUNT$bin + 500)
EXT_OFF$NO_EXT <- sapply(EXT_OFF$bin, function(x) sum(between(LADS, x, x+999)))
LADS_GRIWM <- data.frame(Taxa = Taxa, lwr95 = rep(0, length(Taxa)), med =
rep(0,length(Taxa)), upr95 = rep(0,length(Taxa)))

#looping the GRIWM----

for(taxon in Taxa){
  dat <- dates[dates$Genus == taxon,c("CalAge","CalSD")]
  if(nrow(dat)<5) next
  iter <- 10000
  alpha <- 0.05
  dat <- dat[order(dat[,1],decreasing=F),1:2]
  itdiv <- iter/(iter/100)
  date4 <- dat[,1]
  sd.vec <- dat[,2]
  k <- length(date4)
  T.up.vec <- T.mci.vec <- w.T.mci.vec <- rep(0,iter)
  T.up.vec <- T.mci.vec <- w.T.mci.vec <- rep(0,iter)
```

```

for (c in 1:iter) {
  date.samp <- rep(0,k)
  for (b in 1:k) {
    date.samp[b] <- round(rnorm(1,date4[b],sd.vec[b]))
  }
  date.samp <- (sort(date.samp))
  last.diff <- 1/(date.samp-date.samp[1])[-1]
  weight <- last.diff/last.diff[1]
  if (last.diff[1] == Inf) {
    weight <- last.diff/last.diff[2]
    weight <- weight[-1]}
  ldate <- length(date.samp)
  T.mci.lst.vec <- rep(0,ldate-1)
  for (m in 1:(ldate-1)) {
    date.it <- date.samp[1:(1+m)]
    date.age.it <- date.samp[1:(1+m)]
    date.mci.it <- rev(max(date.it) + 1 - date.it)
    k <- length(date.it)
    t.n <- date.mci.it[k]
    n <- k
    T.rng <- t.n - date.mci.it[1]
    i <- t.n
    p.iter <- 1
    while(p.iter > alpha)
    {
      i <- i + 1
      p.iter <- (1 - (n/t.n))^(i - t.n)
    }
    T.mci.lst.vec[m] <- max(date.it) + 1 - i
  }
  if (last.diff[1] == Inf) {
    w.T.mci.vec[c] <- round((sum(weight*T.mci.lst.vec[-1])/sum(weight),0)}

  if (last.diff[1] != Inf) {
    w.T.mci.vec[c] <- round((sum(weight*T.mci.lst.vec)/sum(weight),0)}
  if(c%%itdiv==0) print(paste(taxon,c))
}

prb <- 0.05
T.wmci.vec.lo <- quantile(na.omit(w.T.mci.vec),probs=(1-prb/2))
T.wmci.vec.med <- median(na.omit(w.T.mci.vec))
T.wmci.vec.up <- quantile(na.omit(w.T.mci.vec),probs=(prb/2))
w.mci.yng <- round(T.wmci.vec.up, 0)
w.mci.med <- round(T.wmci.vec.med, 0)
w.mci.old <- round(T.wmci.vec.lo, 0)
#
LADS_GRIWM[LADS_GRIWM$Taxa == taxon, c(2:4)] <- c(w.mci.old, w.mci.med, w.mci.yng)
round(w.mci.yng, 0); #upper boundary of the confidence interval (CI)
round(T.wmci.vec.med, 0); #median value = timing of extinction estimated
round(w.mci.old, 0) #lower boundary of CI
}

```

```

write.csv(LADS_GRIWM,paste0("LADS_GRIWM",format(Sys.time(), "%b %d %Y %H %M
%S"),".csv"))
GRIWM_files <- dir(pattern = "LADS_GRIWM+")
LADS_GRIWM <- read.csv(GRIWM_files)
LADS_GRIWM1 <- LADS_GRIWM[LADS_GRIWM$lwr95 > 0,]
EXT_COUNT$GRIWM_EXT <- sapply(EXT_COUNT$bin, function(x)
  sum(between(LADS_GRIWM1$med, x, x+999)))
EXT_OFF$GRIWM_EXT <- sapply(EXT_OFF$bin, function(x)
  sum(between(LADS_GRIWM1$med, x, x+999)))

##Extracting the climate data-----

gdd_bin <- data.frame(bin = EXT_COUNT$bin, total = rep(0,nrow(EXT_COUNT)))
gdd_bin$total <- sapply(gdd_bin$bin, function(x) mean(gdd[between(gdd$Age, x, x+999),
  "Total"]))
Climate <- gdd_bin$total[-nrow(gdd_bin)] - gdd_bin$total[-1]

##Extracting the pollen data-----

pollen_bin <- data.frame(bin = EXT_COUNT$bin, AVG = rep(0,nrow(EXT_COUNT)))
pollen_bin$AVG <- sapply(pollen_bin$bin, function(x) mean(pollen[between(pollen$Age, x,
  x+999), "PctOak"]))
Ecology <- pollen_bin$AVG[-nrow(pollen_bin)] - pollen_bin$AVG[-1]

##Extracting the human data-----

Humans_bin <- data.frame(bin = EXT_COUNT$bin, hum_count = rep(0,nrow(EXT_COUNT)))
Humans_bin$hum_count <- sapply(Humans_bin$bin, function(x)
  sum(between(Human_data$CalAge, x, x+999)))

##Calculate the change in humans...

Humans <- Humans_bin$hum_count[-nrow(Humans_bin)] - Humans_bin$hum_count[-1]

#Code from Marshall et al 2015-----

#Need to loop for each comparison class, i.e., humans, pollen, climate
#then loop for RAW vs. GRIWM
#finally, for offset time bins

#better yet, make a function and call it in a series of commands.

ext_reg <- function(E,C,H){
  #E,C,H are the extinction, climate, and human data binned up

  d <- data.frame(E,C,H)

  #Non-linear least squares fit
  fit <- nls(E~a*C+b*H+c*C*H, start = list(a=0.5, b=0.5, c=0.5), data = d)

```

```

fit_summary <- summary(fit)
return(fit_summary$parameters)

} #end of the ext_reg function
#H is the delta-H, or human impact.
# It is the only one of these that stays the same through all permutations...

H <- Humans

#create a df for the values to land in

Continental_summary <- data.frame(offset = character(),
                                climate = character(),
                                GRIWM = character(),
                                aparam = numeric(),
                                bparam = numeric(),
                                cparam = numeric(),
                                aerr = numeric(),
                                berr = numeric(),
                                cerr = numeric(),
                                aprob = numeric(),
                                bprob = numeric(),
                                cprob = numeric() )

#E is the megafaunal extinction count for each time bin
for(LAD_type in c("raw","GRIWM")){
  for(bin_type in c("regular","offset")){
    if(bin_type == "regular"){THIS_COUNT <- EXT_COUNT} else {THIS_COUNT <- EXT_OFF}
    #make the E variable for the regression
    if(LAD_type == "raw"){E <- THIS_COUNT$NO_EXT[-nrow(THIS_COUNT)]}
    else{E <- THIS_COUNT$GRIWM_EXT[-nrow(THIS_COUNT)]}

#make the climate_bin holder
climate_bin <- data.frame(bin = EXT_COUNT$bin, delta = rep(0,nrow(EXT_COUNT)))
for(climate_type in c("gdd","pollen")){
  if(climate_type == "gdd"){climate_bin$value <- sapply(climate_bin$bin, function(x)
  mean(gdd[between(gdd$Age, x, x+999), "Total"])}
  }else{ if(climate_type == "pollen") {climate_bin$value <- sapply(climate_bin$bin,
  function(x) mean(pollen[between(pollen$Age, x, x+999), "PctOak"])} }
  C <- climate_bin$value[-nrow(climate_bin)] - climate_bin$value[-1]
ext_params <- ext_reg(E,C,H)
Continental_summary[nrow(Continental_summary)+1,] <- c(bin_type climate_type,
LAD_type,
ext_params["a","Estimate"],
ext_params["c","Estimate"],
ext_params["b","Std. Error"],
ext_params["a","Pr(>|t|)"],
ext_params["c","Pr(>|t|)"],
ext_params["b","Estimate"],
ext_params["a","Std. Error"],
ext_params["c","Std. Error"],
ext_params["b","Pr(>|t|)"],

```


APPENDIX B

MEGAFUNA DATASET

Genus	Species	Site name	State/ Territory	Age (RC years BP)	Standard deviation (RC years BP)	Age (Calibrated years BP)	Standard deviation (Calibrated years BP)
<i>Arctodus</i>	<i>simus</i>	Rancho La Brea	CA	28350	470	32365	581
<i>Arctodus</i>	<i>simus</i>	Rancho La Brea	CA	28130	330	32081	449
<i>Arctodus</i>	<i>simus</i>	Lake Bonneville	UT	12650	70	15031	151
<i>Arctodus</i>	<i>simus</i>	Monroc Kearns Gravel Pit	UT	12650	70	15013	131
<i>Arctodus</i>	<i>simus</i>	Rancho La Brea	CA	27330	140	31218	104
<i>Arctodus</i>	<i>simus</i>	Huntington Reservoir Sinkhole	UT	10870	75	12775	68
<i>Arctodus</i>	<i>simus</i>	Huntington Dam	UT	10976	40	12831	66
<i>Bison</i>	<i>bison</i>	Rancho La Brea	CA	54400	535	54454	542
<i>Bison</i>	<i>latifrons</i>	Chuchi Lake	BC	34800	420	39370	466
<i>Bison</i>	<i>bison</i>	Clayhurst Gravel Pit	BC	10230	140	11939	285
<i>Bison</i>	<i>bison</i>	Clayhurst Gravel Pit	BC	10580	210	12394	280
<i>Bison</i>	<i>bison</i>	Clayhurst Gravel Pit	BC	10340	150	12135	271
<i>Bison</i>	<i>latifrons</i>	Rancho La Brea	CA	13500	170	16283	257
<i>Bison</i>	<i>latifrons</i>	Chuchi Lake	BC	30740	220	34669	221
<i>Bison</i>	<i>bison</i>	Clayhurst Gravel Pit	BC	10750	180	12640	211
<i>Bison</i>	<i>bison</i>	Clayhurst Gravel Pit	BC	10600	160	12458	205
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	43000	720	46403	765
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	41800	800	45298	764
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	41940	790	45426	760
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	9850	550	11413	754
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	41010	580	44538	537
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28580	380	32576	531
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28510	380	32498	528
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	25240	400	29410	488

Genus	Species	Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	39090	580	43032	465
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	35800	400	40446	449
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	10710	320	12499	411
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28620	200	32651	368
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28330	200	32230	348
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28310	170	32196	318
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28360	160	32258	313
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	24000	340	28128	308
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28430	140	32355	298
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	23600	330	27796	289
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28400	130	32311	288
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28270	130	32133	281
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	28070	130	31851	257
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	19580	190	23580	248
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	27860	140	31591	190
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	27890	130	31614	188
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	19380	100	23330	161
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	19640	100	23664	151
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	23110	160	27405	140
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	27680	140	31427	137
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	23080	150	27384	136
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	27660	120	31404	119
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	14040	50	17060	115
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	27560	130	31343	112
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	27460	130	31285	105
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	23060	90	27375	103
<i>Canis</i>	<i>dirus</i>	Rancho La Brea	CA	26840	120	30973	99

Genus	Species	Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
<i>Mammuthus</i>	<i>sp.</i>	Mammoth Alcove	UT	19300	600	23360	710
<i>Mammuthus</i>	<i>sp.</i>	Tse'An Kaetan Cave-Grand Canyon	AZ	26140	670	30234	647
<i>Mammuthus</i>	<i>columbi</i>	Southern Utah University Mammoth Jaw	UT	28670	260	32712	429
<i>Mammuthus</i>	<i>sp.</i>	Bechan Cave	UT	12400	250	14567	419
<i>Mammuthus</i>	<i>sp.</i>	Bechan Cave	UT	12620	220	14872	406
<i>Mammuthus</i>	<i>sp.</i>	Portage Pass	BC	25800	320	30017	393
<i>Mammuthus</i>	<i>sp.</i>	Bechan Cave	UT	11670	300	13590	369
<i>Mammuthus</i>	<i>sp.</i>	Owl Cave (Wasden Site)	ID	12250	200	14337	362
<i>Mammuthus</i>	<i>sp.</i>	Mammoth Alcove	UT	16630	280	20082	346
<i>Mammuthus</i>	<i>sp.</i>	Vedder Crossing	BC	22700	320	26958	337
<i>Mammuthus</i>	<i>sp.</i>	Saanich Peninsula	BC	17000	240	20525	309
<i>Mammuthus</i>	<i>sp.</i>	Likely Mammoth	BC	20190	190	24298	259
<i>Mammuthus</i>	<i>sp.</i>	Bechan Cave	UT	12900	160	15424	257
<i>Mammuthus</i>	<i>sp.</i>	Owl Cave (Wasden Site)	ID	12850	150	15348	256
<i>Mammuthus</i>	<i>sp.</i>	Withers Wallow	UT	12010	160	13900	226
<i>Mammuthus</i>	<i>sp.</i>	Bechan Cave	UT	11850	160	13707	185
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	12050	400	14193	585
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	13140	320	15743	501
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	12440	300	14638	486
<i>Nothrotheriops</i>	<i>shastense</i>	Rancho La Brea	CA	28590	240	32594	413
<i>Nothrotheriops</i>	<i>shastense</i>	Rancho La Brea	CA	28530	240	32504	410
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10035	250	11670	404
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10400	275	12124	394

Genus	Species	Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
<i>Nothrotheriops</i>	<i>shastense</i>	Rancho La Brea	CA	28350	240	32268	389
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	12470	170	14641	320
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	11370	300	13252	303
<i>Nothrotheriops</i>	<i>shastense</i>	Gypsum Cave	AZ	11690	250	13576	289
<i>Nothrotheriops</i>	<i>shastense</i>	Muav Caves	AZ	10650	220	12477	284
<i>Nothrotheriops</i>	<i>shastense</i>	Gypsum Cave	AZ	11360	260	13227	255
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10780	200	12671	232
<i>Nothrotheriops</i>	<i>shastense</i>	Muav Caves	AZ	11060	240	12958	216
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	11480	200	13332	197
<i>Nothrotheriops</i>	<i>shastense</i>	Muav Caves	AZ	11290	170	13145	170
<i>Nothrotheriops</i>	<i>shastense</i>	Muav Caves	AZ	11140	160	12998	152
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	11000	140	12895	118
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10940	120	12854	105
<i>Nothrotheriops</i>	<i>shastense</i>	Muav Caves	AZ	11810	70	13635	77
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10940	60	12816	72
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10930	60	12807	69
<i>Nothrotheriops</i>	<i>shastense</i>	Muav Caves	AZ	11610	60	13438	65
<i>Nothrotheriops</i>	<i>shastense</i>	Rampart Cave	AZ	10900	60	12782	60
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	28700	700	32729	756
<i>Oreamnos</i>	<i>harringtoni</i>	Tse'an Bida Cave	AZ	16150	600	19621	718
<i>Oreamnos</i>	<i>harringtoni</i>	Tse'an Bida Cave	AZ	16150	600	19621	718
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	15500	600	18861	712
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	10140	510	11763	677
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	12860	340	15272	569
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	16270	400	19678	478

Genus	Species	Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	19320	380	23305	443
<i>Oreamnos</i>	<i>harringtoni</i>	Tse'An Kaetan Cave-Grand Canyon	AZ	14220	320	17266	432
<i>Oreamnos</i>	<i>harringtoni</i>	Tse'An Kaetan Cave-Grand Canyon	AZ	17500	300	21176	392
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	20560	310	24780	386
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	20960	320	25201	381
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	19970	290	24054	370
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	13290	240	15973	359
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	18430	300	22280	349
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	22430	320	26723	349
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	22280	290	26587	333
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	12300	160	14396	314
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	23030	300	27280	285
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	12370	130	14493	273
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	19980	210	24042	260
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	13120	130	15724	210
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	16690	160	20144	208
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	10870	200	12786	203
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	13760	120	16639	200
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	13430	130	16170	195
<i>Oreamnos</i>	<i>harringtoni</i>	Tse'an Bida Cave	AZ	12930	110	15468	175
<i>Oreamnos</i>	<i>harringtoni</i>	Stanton's Cave	AZ	11490	180	13338	174
<i>Oreamnos</i>	<i>harringtoni</i>	Rampart Cave	AZ	20460	80	24625	173
<i>Panthera</i>	<i>leo</i>	Astor Pass	NV	16800	600	20385	749
<i>Panthera</i>	<i>leo</i>	Astor Pass	NV	17500	600	21214	732
<i>Panthera</i>	<i>leo</i>	Rancho La Brea	CA	14110	420	17120	558

Genus	Species	Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
<i>Panthera</i>	<i>leo</i>	Rancho La Brea	CA	13890	280	16839	398
<i>Panthera</i>	<i>leo</i>	Rancho La Brea	CA	14500	210	17650	266
<i>Panthera</i>	<i>leo</i>	Rancho La Brea	CA	15390	230	18644	255
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	33100	600	37362	753
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	21400	560	25690	635
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	30800	600	34862	578
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	23700	600	27958	577
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	15360	480	18663	558
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	14950	430	18172	500
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	28150	360	32121	477
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	19300	395	23287	459
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	13035	275	15585	436
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	13745	275	16647	396
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	11980	260	13972	395
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	18475	320	22337	376
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	19800	300	23842	371
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	12200	200	14256	360
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	26120	280	30329	336
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	26150	280	30350	332
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	12650	160	14929	327
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	28240	160	32105	306
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	28170	160	32016	301
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	12760	150	15171	294
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	28320	140	32202	292
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	24930	240	29003	268
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	11130	275	13022	255

Genus	Species	Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	25710	140	29910	246
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	14500	190	17653	240
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	15300	200	18544	218
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	25740	100	29935	214
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	27820	150	31558	189
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	12000	125	13865	160
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	11640	135	13478	140
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	27620	150	31388	134
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	27220	140	31161	103
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	27350	120	31226	97
<i>Smilodon</i>	<i>fatalis</i>	Rancho La Brea	CA	14360	35	17500	81

APPENDIX C

HUMAN ACTIVITY DATASET

Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
Double Adobe	AZ	8270	250	9206	319
Double Adobe	AZ	8760	210	9853	253
Double Adobe	AZ	8840	310	9966	394
Double Adobe	AZ	9120	270	10304	387
Lehner	AZ	9860	80	11323	126
Lehner	AZ	9900	80	11382	136
Lehner	AZ	10710	90	12637	73
Lehner	AZ	10940	100	12847	94
Lehner	AZ	10950	110	12857	99
Lehner	AZ	10950	90	12849	90
Lehner	AZ	11170	140	13019	143
Murray Springs	AZ	10760	100	12676	85
Murray Springs	AZ	10840	70	12745	55
Murray Springs	AZ	11150	450	13055	540
N/A	AZ	8140	220	9053	276
N/A	AZ	8390	190	9354	243
N/A	AZ	8650	180	9739	234
N/A	AZ	9340	180	10613	261
Gore Creek	BC	8250	115	9225	146
Arlington Springs	CA	10000	200	11609	334
Arlington Springs	CA	10960	80	12850	86
Charlie Range Basalt Ridge	CA	8390	130	9350	147
Mostin	CA	7700	90	8503	90
Mostin	CA	10260	340	11939	475
N/A	CA	8020	80	8874	128
Skyrocket	CA	7000	70	7830	73
Skyrocket	CA	8550	150	9588	210
Skyrocket	CA	9050	90	10192	143
Skyrocket	CA	9410	250	10715	349
Witt	CA	11380	70	13222	71
Beta Rockshelter	ID	8175	230	9092	287
Buhl	ID	10675	95	12607	90
Cooper's Ferry	ID	8410	70	9411	79
Cooper's Ferry	ID	8430	70	9431	73
Cooper's Ferry	ID	11370	70	13214	70
Cooper's Ferry	ID	11410	130	13261	120
Cooper's Ferry	ID	12020	170	13924	251
Hatwai	ID	8560	520	9682	686
Hatwai	ID	9160	230	10355	340
Hatwai	ID	9280	110	10479	151
Hatwai	ID	9880	110	11387	188
Hatwai	ID	10820	140	12748	140
Hetrick	ID	9730	60	11120	113
Hetrick	ID	10320	90	12149	183
Jackknife Cave	ID	8130	105	9070	172
Jaguar Cave	ID	10370	350	12061	474
Jaguar Cave	ID	11580	250	13451	268
McCulley Creek	ID	8760	70	9792	146

Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
Owl Cave/Wadsen	ID	7750	210	8633	255
Owl Cave/Wadsen	ID	8160	260	9078	319
Owl Cave/Wadsen	ID	9735	115	11082	190
Owl Cave/Wadsen	ID	10145	170	11798	310
Owl Cave/Wadsen	ID	10470	100	12355	165
Owl Cave/Wadsen	ID	10640	85	12588	90
Owl Cave/Wadsen	ID	10910	150	12837	131
Owl Cave/Wadsen	ID	12330	200	14457	359
Owl Cave/Wadsen	ID	12850	150	15348	256
Redfish Lake Overhang	ID	8060	190	8963	249
Redfish Lake Overhang	ID	9860	180	11371	318
Redfish Lake Overhang	ID	10500	180	12324	256
Saw Mill Canyon	ID	7650	400	8584	451
Wewukiyepuh	ID	10270	50	12034	124
Wewukiyepuh	ID	10390	40	12258	99
Wilson Butte Cave	ID	10230	90	11951	201
Wilson Butte Cave	ID	10700	100	12623	90
Bonneville Estates Rockshelter	NV	10040	70	11567	160
Bonneville Estates Rockshelter	NV	10080	50	11637	145
Bonneville Estates Rockshelter	NV	10100	60	11685	162
Fishbone Cave	NV	11200	250	13077	230
Spirit Cave	NV	9350	70	10560	109
Spirit Cave	NV	9360	60	10578	89
Spirit Cave	NV	9410	60	10651	102
Spirit Cave	NV	9430	60	10685	119
Spirit Cave	NV	9430	70	10699	141
Spirit Cave	NV	9440	60	10705	128
Spirit Cave	NV	9460	60	10749	142
Sunshine	NV	7420	60	8249	69
Sunshine	NV	8560	100	9573	120
Sunshine	NV	9040	190	10156	277
Sunshine	NV	9820	60	11242	62
Sunshine	NV	9880	50	11297	71
Sunshine	NV	9910	50	11337	91

Site name	State/ Territory	Age (RC years BP)	St. deviation (RC years BP)	Age (Calibrated years BP)	St. deviation (Calibrated years BP)
Sunshine	NV	9920	60	11373	114
Sunshine	NV	9940	50	11384	108
Sunshine	NV	10060	50	11592	138
Sunshine	NV	10240	80	11975	179
Sunshine	NV	10250	60	11992	137
Sunshine	NV	10320	50	12160	127
Sunshine	NV	10340	60	12195	131
Indian Sands	OR	10430	150	12268	236
Kennewick	WA	6940	30	7765	43
Kennewick	WA	8130	40	9078	59
Kennewick	WA	8410	40	9437	49
Kennewick	WA	8410	60	9420	69
Lind Coulee	WA	8600	65	9589	68
Lind Coulee	WA	8720	299	9822	377
Lind Coulee	WA	9810	40	11225	23
Lind Coulee	WA	10060	45	11590	130
Lind Coulee	WA	10250	40	11985	95
Marmes	WA	9820	300	11345	486
Marmes	WA	9840	300	11377	486
Marmes	WA	10130	300	11794	450

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