Synchronous extinction of North America's Pleistocene mammals

J. Tyler Faith[a,1] and Todd A. Surovell[b]

[a]Hominid Paleobiology Doctoral Program, Center for the Advanced Study of Human Paleobiology, Department of Anthropology, The George Washington University, 2110 G Street NW, Washington, DC 20052; and [b]Department of Anthropology, University of Wyoming, P.O. Box 3431, 1000 East University Avenue, Laramie, WY 82071

Edited by Steven M. Stanley, University of Hawaii, Honolulu, HI, and approved October 12, 2009 (received for review July 27, 2009)

The late Pleistocene witnessed the extinction of 35 genera of North American mammals. The last appearance dates of 16 of these genera securely fall between 12,000 and 10,000 radiocarbon years ago (≈13,800–11,400 calendar years B.P.), although whether the absence of fossil occurrences for the remaining 19 genera from this time interval is the result of sampling error or temporally staggered extinctions is unclear. Analysis of the chronology of extinctions suggests that sampling error can explain the absence of terminal Pleistocene last appearance dates for the remaining 19 genera. The extinction chronology of North American Pleistocene mammals therefore can be characterized as a synchronous event that took place 12,000–10,000 radiocarbon years B.P. Results favor an extinction mechanism that is capable of wiping out up to 35 genera across a continent in a geologic instant.

climate change | extraterrestrial impact | overkill | Quaternary extinctions | radiocarbon dates

During the late Pleistocene, North America lost 35 genera of large mammals. The majority (29 genera), including mastodons, saber-toothed cats, and giant ground sloths, became globally extinct at that time, whereas a handful (6 genera) vanished from North America while continuing to persist elsewhere (Table S1). For decades archaeologists and paleontologists have debated the causes of their extinction (1–5), with explanations including overkill (6–11), environmental change (12, 13), hyperdisease (14), and an extraterrestrial impact (15–17). Crucial to the development of explanatory models is the chronology of the extinctions, which some envision as a long-term process occurring throughout the late Pleistocene (18–21) and others characterize as a synchronous event that wiped out all taxa between 12,000 and 10,000 radiocarbon years B.P. (6–8, 13, 22, 23) (≈13,800–11,400 calendar years B.P.). The 12,000–10,000 radiocarbon years B.P. time period, referred to here as the terminal Pleistocene, is particularly relevant to the extinction debate in that it encompasses the appearance of Clovis hunter–gatherers in North America (24, 25), the onset of the Younger Dryas cold interval (26) (≈12.9 calendar years B.P.), and a possible extraterrestrial impact (15, 16). However, reaching a consensus as to the cause(s) of the extinctions will first require a consensus regarding the chronology.

Disagreement over the chronology of North American late Pleistocene extinctions stems largely from an incomplete fossil record. Of the 35 genera to disappear from North America, only 16 can be shown to have survived to between 12,000 and 10,000 radiocarbon years B.P. Those 16 genera known from the terminal Pleistocene have been observed to be better represented in the fossil record than those that are not (8, 18, 22). This raises the possibility that the remaining 19 genera have not been dated to the terminal Pleistocene because of their rarity in the fossil record (27). Terminal Pleistocene dates also possibly are lacking for some genera because they did not survive to that time. If so, then this would imply a more complex causality than that supposed by extinction hypotheses requiring a high degree of simultaneity (e.g., overkill or extraterrestrial impact).

Testing for Simultaneity. Here, we present an analysis of the chronology of North American late Pleistocene extinctions to evaluate the extent to which the extinctions can be characterized as a synchronous event. Our goal is to provide a statistical test of the hypothesis that the extinction occurred synchronously between 12,000 and 10,000 radiocarbon years B.P., with the absence of last appearance dates (LADs) for some taxa in that time interval attributed to sampling error.

To examine the possible effects of sampling error on the extinction chronology, our analysis requires a sample that illustrates the relative abundance of extinct Pleistocene mammals in the fossil record. These data are derived primarily from the number of stratigraphic occurrences reported by the FAUNMAP working group (28). This includes abundances of 31 genera from the contiguous United States during the last 40,000 years or so (Table 1). Four genera (*Pampatherium*, *Cuon*, *Neochoerus*, and *Saiga*) are not reported in the FAUNMAP database and are excluded from the analysis. Our analysis further requires a sample of terminal Pleistocene radiocarbon dates for a given taxon, referred to here as a taxon date. These dates were compiled from several key references (18, 22, 24, 29), following Meltzer and Mead's (29) criteria for evaluating the reliability of a radiocarbon date (Table S2). Radiocarbon dates were evaluated further according to the more rigorous system developed by Pettitt et al. (30). All dates used here (Table S2) score as either reliable or intermediate according to their criteria.

Last appearance dates were documented for the 31 genera reported in the FAUNMAP database (Table S3). Since suitable radiocarbon dates have been published for only 18 genera (Table S3), the remaining 13 genera are assigned a LAD corresponding to the youngest associated preterminal Pleistocene radiocarbon date recorded in FAUNMAP.

For North America's extinct Pleistocene mammals, there is a significant tendency for the LAD to decrease as the number of stratigraphic occurrences of a taxon increases (Fig. 1). This is true for the sample of reliably dated Pleistocene genera (Spearman's rho, $r_s = -0.564$, $P = 0.015$) and for the entire set of taxa ($r_s = -0.781$, $P < 0.001$). This relationship illustrates the important role of sampling effects on the extinction chronology. It also suggests that the absence of terminal Pleistocene LADs for some, if not all, of the extinct genera may be attributed to sampling error; the rarer a taxon is in the Pleistocene fossil record, the more difficult demonstrating a terminal Pleistocene LAD will be. The extent to which this is the case is explored in further detail below.

There are 1,955 stratigraphic occurrences of 31 genera of extinct North American mammals, with 66 terminal Pleistocene

Author contributions: J.T.F. and T.A.S. designed research; J.T.F. and T.A.S. performed research; J.T.F. and T.A.S. analyzed data; and J.T.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. E-mail: tfaith@gwmail.gwu.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0908153106/DCSupplemental.

ANTHROPOLOGY GEOLOGY

Table 1. Stratigraphic abundances and terminal Pleistocene taxon dates of extinct North American mammals (see also Table S2)

Genus	No. of stratigraphic. occurrences	No. of terminal Pleistocene dates
Aztlanolagus	1	0
Eremotherium	2	0
Glyptotherium	4	0
Brachyprotoma	5	0
Miracinonyx	5	0
Tetrameryx	5	0
Hydrochoerus	7	0
Homotherium	9	0
Navahoceros	9	0
Stockoceros	10	0
Palaeolama	15	1
Euceratherium	16	2
Tremarctos	18	0
Holmesina	22	0
Capromeryx	28	0
Castoroides	37	2
Smilodon	37	1
Arctodus	38	2
Cervalces	38	2
Nothrotheriops	44	8
Paramylodon	50	0
Mylohyus	53	1
Megalonyx	57	2
Hemiauchenia	58	0
Tapirus	65	2
Platygonus	97	2
Bootherium	112	1
Camelops	147	7
Mammut	222	9
Mammuthus	356	15
Equus	388	9
Total	1,955	66

taxon dates distributed among 16 of those genera. (Table 1 and Table S2). Twenty-four of those taxon dates, distributed among 11 genera, are considered highly reliable (30) (Table S2).

We developed two Monte Carlo simulations to determine whether this empirically observed pattern is consistent with a synchronous terminal Pleistocene extinction. In our first simulation, referred to as the continental simulation, each of the 1,955 stratigraphic occurrences are assigned randomly a pre- or post-12,000 radiocarbon years B.P. date based on the observed relative frequency of terminal Pleistocene taxon dates in the fossil record (3.4% for the complete set of radiocarbon dates and 1.3% when excluding radiocarbon dates of intermediate reliability). For each of 10,000 iterations, the number of genera receiving a terminal Pleistocene taxon date is calculated. All of the 31 genera included in the analysis are assumed to survive to the terminal Pleistocene, and all occurrences are assumed to be equally likely to receive a terminal Pleistocene taxon date. The continental simulation essentially estimates how many genera that we can expect to recover from the terminal Pleistocene if all of them had survived to that time, given the empirically derived probability of observing a terminal Pleistocene fossil occurrence. We ran two separate trials of the continental simulation, both including and excluding radiocarbon dates that received intermediate evaluation scores (30).

Our second simulation, referred to as the biogeographic simulation, recognizes that the extinct Pleistocene genera were not distributed uniformly across the continental United States and that some regions are more likely to provide a terminal Pleistocene taxon date than others. For example, the distribution of *Hydrochoerus* and *Holmesina* within the U.S. is limited to the southeast (28), an area that yields relatively few terminal Pleistocene taxon dates (Table S4). Because of their biogeographic ranges, these taxa are less likely to have been recovered from terminal Pleistocene deposits if they had survived to that time. This issue is addressed in our biogeographic simulation, which recognizes seven physiographic zones within the continental United States (31) (Fig. 2). In this simulation, the stratigraphic occurrences of a given genus are assigned randomly to a physiographic zone based on its relative abundance in that region (Table S4). In turn, the probability that a simulated occurrence will be assigned a terminal Pleistocene taxon date is based on the relative frequency of terminal Pleistocene fossil occurrences known from that zone (Table S4). For each of 10,000 iterations, the number of taxa receiving a terminal Pleistocene date is calculated. The biogeographic simulation also explores the possibility of preterminal Pleistocene extinctions. To do so, we prohibited between 0 and 15 randomly selected genera from receiving a terminal Pleistocene taxon date over 16 separate trials of 10,000 iterations. The biogeographic simulation estimates how many taxa that we can expect to recover from the terminal Pleistocene if anywhere from 16 to 31 genera had survived to that time. As with the continental simulation, we ran two trials of the biogeographic simulation, once using all of the terminal Pleistocene taxon dates and once excluding radiocarbon dates of intermediate reliability (30).

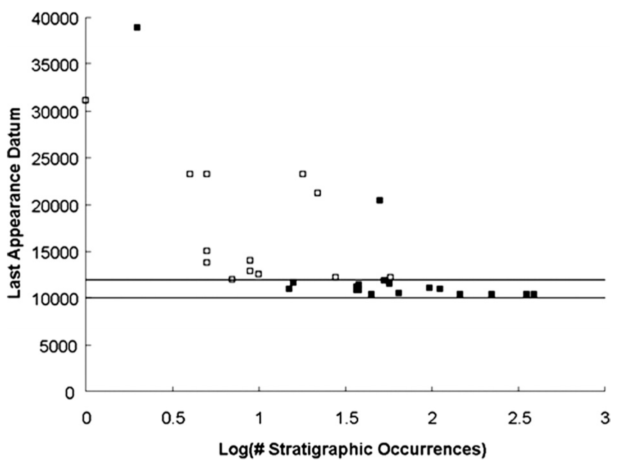

Fig. 1. Relationship between the log (base 10) of the number of stratigraphic occurrences of a taxon and its last appearance date in radiocarbon years. Reliably dated taxa, following Meltzer and Mead (29), are represented by solid squares. Horizontal lines are at 10,000 and 12,000 years.

Results

When the entire set of radiocarbon dates is included in the analysis, both simulations indicate that the observed extinction chronology is fully consistent with the simultaneous extinction of all 31 genera between 12,000 and 10,000 radiocarbon years B.P. (Fig. 2). For the continental simulation, 22.4% of the iterations documented 16 or fewer terminal Pleistocene genera (one-tailed $P = 0.224$). Thus, the empirical observation of 16 terminal Pleistocene genera falls comfortably within the range of taxa that we can expect to recover from that time in the event of a simultaneous extinction. When biogeographic ranges are taken into account, the results are increasingly compelling. In the trial allowing all of the taxa to survive to the terminal Pleistocene, the biogeographic simulation provides a mode value of 17 genera known from 12,000 to 10,000 radiocarbon years B.P. and suggests a 42.2% chance of observing 16 or fewer terminal Pleistocene

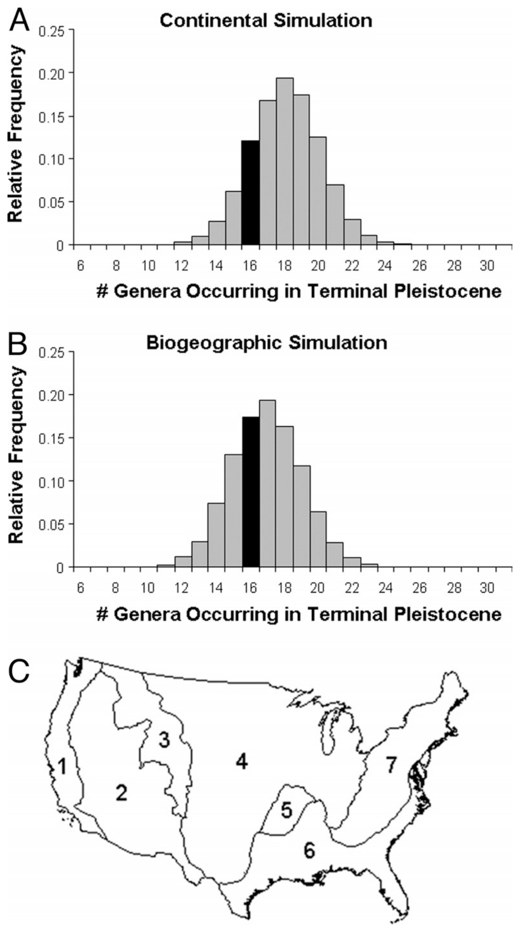

Fig. 2. Relative frequency histograms illustrating the number of terminal Pleistocene genera in the (*A*) continental simulation and (*B*) biogeographic simulation. The black bar represents the empirical observation of 16 terminal Pleistocene genera. The biogeographic simulation recognizes seven physiographic zones (*C*): 1, Pacific Mountain System; 2, Intermontane Plateau; 3, Rocky Mountain System; 4, Interior Plains; 5, Interior Highlands; 6, Atlantic Plains; 7, Appalachian Highlands.

genera (one-tailed $P = 0.422$). Once again, the observed pattern fits well within our expectations for a synchronous extinction chronology.

Our simulations of a synchronous terminal Pleistocene extinction provide an even better match for the fossil record when radiocarbon dates of intermediate reliability are excluded from the analysis (Fig. 3). We note that only 11 genera are associated with highly reliable terminal Pleistocene taxon dates (Table S2). Consistent with this observation, the continental simulation returns a mode value of 11 terminal Pleistocene genera and suggests a 53.0% chance of recovering 11 or fewer genera from the terminal Pleistocene (one-tailed $P = 0.530$). Similarly, in the trial allowing all of the taxa to survive to the terminal Pleistocene, the biogeographic simulation provides a mode of 11 terminal Pleistocene genera and suggests a 73.4% chance of recovering 11 or fewer terminal Pleistocene genera (one-tailed $P = 0.734$). Once again, our simulations indicate that the empirically observed chronology is fully consistent with a synchronous terminal Pleistocene extinction event.

Although the simulations indicate that the chronology is consistent with simultaneous extinctions, the biogeographic simulation indicates that the empirically observed chronology is statistically compatible with the preterminal Pleistocene extinctions of anywhere from 0 to 8 genera (Table 2). When all of the

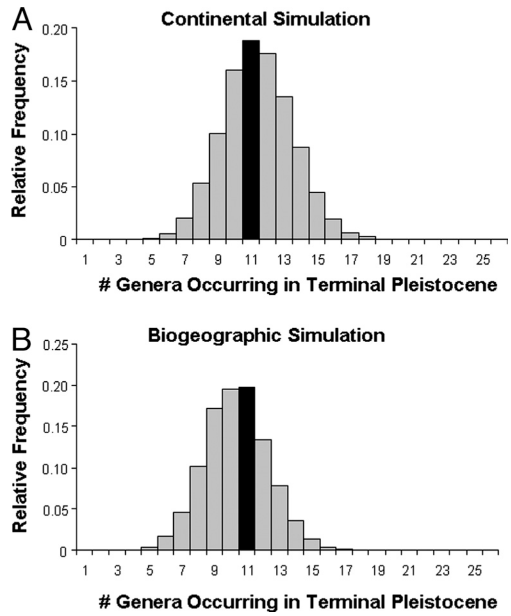

Fig. 3. Relative frequency histograms illustrating the number of terminal Pleistocene genera in the (*A*) continental simulation and (*B*) biogeographic simulation, when radiocarbon dates of intermediate reliability are excluded. The black bar represents the empirical observation of 11 terminal Pleistocene genera associated with highly reliable radiocarbon dates.

radiocarbon dates are considered, the recovery of 16 terminal Pleistocene genera is the most likely outcome with the disappearance of 2 genera before 12,000 radiocarbon years B.P. When radiocarbon dates of intermediate reliability are excluded, the recovery of 11 terminal Pleistocene genera is most likely with no preterminal Pleistocene extinctions, although it is consistent with a range of scenarios.

Discussion

Our analyses demonstrate that the structure of the chronology of North American late Pleistocene extinctions is consistent with the synchronous extinction of all taxa between 12,000 and 10,000 radiocarbon years. B.P. The significant negative relationship between the fossil abundance of a taxon and its last appearance in the fossil record (Fig. 1) indicates that the temporally staggered appearance of the extinction chronology is driven largely by sampling effects. As discussed by Signor and Lipps (27), in the event of an abrupt multiple-species extinction event, uncommon taxa will effectively disappear from the fossil record long before their true time of extinction. This appears to be the case for the North American Pleistocene extinctions. Our simulations provide further support for this argument. Both the continental and the biogeographic simulations indicate that the recovery of 16 terminal Pleistocene genera (or 11 in the case of our analysis that excludes intermediate radiocarbon dates) is to be expected in the case of a synchronous extinction (Figs. 2 and 3). The combination of these lines of evidence suggests that North American late Pleistocene extinctions are best characterized as a synchronous event.

The available evidence indicates that further sampling will almost certainly increase the number of genera known from the terminal Pleistocene (Figs. 1 and 2). This is supported by the historic trend, which has been for the number of terminal Pleistocene genera to increase in recent decades (22). We also observe that of those taxa lacking terminal Pleistocene radiocarbon dates, the four most abundant genera (Table 1; *Hemiauchenia*, *Paramylodon*, *Capromeryx*, and *Holmesina*) have been recovered in stratigraphic association with Paleo-Indian archae-

Table 2. Results of biogeographic simulation modeling the preterminal Pleistocene extinction of 0–15 genera

No. of genera extinct >12,000 radiocarbon yr B.P.	No. of terminal Pleistocene genera (all radiocarbon dates) Mode	≥16	<16	*P*	No. of terminal Pleistocene genera (excluding intermediate radiocarbon dates) Mode	≥11	<11	*P*
0	17	7,519	2,481	0.752	11	4,634	5,366	0.463
1	17	6,596	3,404	0.660	10	3,915	6,085	0.392
2	16	5,697	4,303	0.570	10	3,264	6,766	0.326
3	15	4,561	5,439	0.456	9	2,678	7,322	0.268
4	15	3,460	6,540	0.346	9	2,231	7,769	0.223
5	14	2,660	7,340	0.266	9	1,762	8,238	0.176
6	14	1,763	8,237	0.176	9	1,234	8,766	0.123
7	13	1,142	8,858	0.114	8	909	9,091	0.091
8	13	644	9,356	0.064	8	638	9,362	0.064
9	12	316	9,684	0.032	7	429	9,571	0.043
10	12	150	9,850	0.015	7	252	9,748	0.025
11	10	57	9,943	0.006	6	175	9,825	0.018
12	10	27	9,973	0.003	6	109	9,891	0.011
13	10	10	9,990	0.001	6	62	9,938	0.006
14	9	0	10,000	0	6	32	9,668	0.003
15	9	0	10,000	0	5	10	9,990	0.001

ology (32). In the absence of direct radiocarbon dates, whether these associations definitively demonstrate terminal Pleistocene survival is unclear. However, that the species most likely to be dated to the terminal Pleistocene already have been reported from latest Pleistocene deposits is perhaps no coincidence.

Our simulations do not rule out the possibility that some extinctions may have occurred before 12,000 radiocarbon years B.P. The biogeographic simulation suggests that anywhere from 0 to 8 genera could have disappeared before the terminal Pleistocene (Table 2). Even so, 23–31 genera abruptly disappeared at approximately the same time. Our results leave open the possibility for a small level of background extinctions (0–8 genera) followed by a surge in extinction rates that wiped out the remaining taxa (23–31 genera) between 12,000 and 10,000 radiocarbon years B.P. Whether or not background extinctions took place, that a catastrophic event or process occurred at the end of the Pleistocene is abundantly clear (23).

The evidence for a catastrophic terminal Pleistocene extinction requires that we attribute to the extinction cause a number of properties, most notably speed and breadth (19). Thus, explanations for the extinctions must be able to account for the disappearance of up to 35 genera, characterized by varied feeding habits and habitat preferences, in a geologic instant. A long-term piecemeal extinction process, similar to the driven late Pleistocene extinctions of Eurasia (18), is incompatible with the present chronology. We note that Pleistocene overkill and the extraterrestrial impact hypothesis require extinctions to occur in a geologic instant. Any version of the climate or environmental change hypothesis must now be formulated in a manner that accounts for simultaneous extinctions as well.

The surge in extinction rates between 12,000 and 10,000 radiocarbon years B.P. is particularly significant in that this time period encompasses the earliest secure evidence of human foragers in North America (24, 25), the Younger Dryas cold interval (26), and a possible extraterrestrial impact (15, 16). Thus, the chronology is consistent with anthropogenic, environmental, and extraterrestrial extinction mechanisms. The chronological synchroneity of these events means that we cannot readily identify a single mechanism responsible for the sudden surge in extinction rates. That the massive terminal Pleistocene losses are the direct result of the fortuitous intersection of these events also remains possible (33).

Although we are unable to point to any one causal mechanism, we note that a major criticism of Martin's (6, 8–10) overkill hypothesis is that humans could not possibly have contributed to the extinction of any animal that disappeared before human arrival on the continent (18–21). By extension, the same critique could be leveled at the extraterrestrial impact hypothesis. On the basis of our analysis, however, this argument no longer applies. That Clovis hunter–gatherers, an extraterrestrial impact, or both contributed to the disappearance of the entire suite of extinct North American mammals is certainly possible, although by no means certain.

Conclusion

Paleontologists and archaeologists have long provided conflicting interpretations of the chronology of North American late Pleistocene extinctions, with some arguing for a temporally staggered extinction (18, 20, 21) and others envisioning the extinction as an abrupt and catastrophic event (6–8, 10, 22, 23). This discrepancy has fueled the debate surrounding the mechanisms responsible for the extinction. Although the fossil record presents challenges for precise calibration of the extinction chronology, we now have quantitative evidence providing clear support for the latter interpretation. Further research on the biogeographic histories of individual species in relation to detailed paleoclimatic, paleoecological, and archaeological data could help to finally pin down the cause of North American end-Pleistocene extinctions (3, 4, 18).

Materials and Methods

Radiocarbon Dates. Terminal Pleistocene taxon dates were compiled from the literature and included in this study (Table S2) if they passed Meltzer and Mead's (29) criteria for evaluating the reliability of a radiocarbon date. Their system assesses dates based on the material dated and the strength of the association between that material and the taxon in question. In general, these criteria and their list of dates are widely accepted (3, 4, 18, 20, 22, 34).

Since the publication of Meltzer and Mead's radiocarbon ranking system, the widespread use of accelerator mass spectrometry (AMS) and advances in chemical treatment of bone have improved the precision and accuracy of radiocarbon dating (35–37). Ideal dates for extinct North American taxa are AMS radiocarbon dates on the purified bone collagen of the taxon in question. However, with a few exceptions (e.g., *Mammuthus*, *Cervalces*, *Castoroides*, and *Megalonyx*), such dates are few and far between. The AMS dates on unpurified bone collagen, however, are more common (38, 39) and generally considered reliable for building the extinction chronology. This study includes AMS dates on the bone collagen of extinct North American mammals. Holocene dates are disregarded as erroneous given that extinct taxa have never been recovered in situ from Holocene stratigraphic contexts in North America, except when redeposited.

Radiocarbon dates were evaluated further according to the criteria developed by Pettitt et al. (30). This system takes into account both chronometry (e.g., pretreatment) and interpretation (e.g., stratigraphy and associations). Radiocarbon dates on bone or dung were given perfect scores for their ''Sample Materials and Stratigraphic Issues'' category because the radiocarbon date applies directly to the taxon in question, irrespective of the potential stratigraphic mobility of dated sample. All dates used here score as either reliable or intermediate according to the ranking system. Following the recommendations of Pettitt et al. (30), we ran simulations that both include and exclude radiocarbon dates of intermediate rank.

Taxonomic Abundances. Taxonomic abundances reported in Table 1 are based primarily on the number of distinct stratigraphic occurrences documented by the FAUNMAP working group (28). For the genus *Equus*, specimens identified as *E. caballus* or from historic Holocene deposits are excluded. The abundance of *Bootherium* includes records for both *Bootherium* and *Symbos*. When a reliable terminal Pleistocene date for a locality not listed in the FAUNMAP database was encountered, the appropriate number of stratigraphic occurrences was added to the abundance list reported in Table 1.

Simulations. Further details on the simulations are presented in the *SI Methods*.

ACKNOWLEDGMENTS. We thank Kay Behrensmeyer, Stuart Fiedel, and two anonymous reviewers for constructive comments on previous versions of this article and Donald Grayson and David Meltzer for providing help along the way.

1. Martin PS, Klein RG (1984) *Quaternary Extinctions: A Prehistoric Revolution* (Univ of Arizona Press, Tucson, AZ).
2. MacPhee RDE (1999) *Extinctions in Near Time: Causes, Contexts, and Consequences* (Kluwer/Plenum, New York).
3. Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306:70–75.
4. Koch PL, Barnosky AD (2006) Late Quaternary extinctions: State of the debate. *Annu Rev Ecol Evol Syst* 37:215–250.
5. Haynes G (2009) *American Megafaunal Extinctions at the End of the Pleistocene* (Springer, Dordecht, The Netherlands).
6. Martin PS (2005) *Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of North America* (Univ of California Press, Berkeley, CA).
7. Alroy J (2001) A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292:1893–1896.
8. Martin PS (1984) in *Quaternary Extinctions: A Prehistoric Revolution*, eds Martin PS, Klein RG (Univ of Arizona Press, Tucson, AZ), pp 354–403.
9. Martin PS (1967) in *Pleistocene Extinctions: The Search for a Cause*, eds Martin PS, Wright HEJ (Yale Univ Press, New Haven, CT), pp 75–120.
10. Martin PS, Steadman DW (1999) in *Extinctions in Near Time: Causes, Contexts, and Consequences*, ed MacPhee RDE (Klewer/Plenum, New York), pp 17–52.
11. Steadman DW, et al. (2005) Asynchronous extinction of late Quaternary sloths on continents and islands. *Proc Natl Acad Sci USA* 102:11763–11768.
12. Guthrie RD (1984) in *Quaternary Extinctions: A Prehistoric Revolution*, eds Martin PS, Klein RG (Univ of Arizona Press, Tucson, AZ), pp 259–298.
13. Graham RW, Lundelius EL, Jr (1984) in *Quaternary Extinctions: A Prehistoric Revolution*, eds Martin PS, Klein RG (Univ of Arizona Press, Tucson, AZ), pp 223–249.
14. MacPhee RDE, Marx PA (1997) in *Natural Change and Human Impact in Madagascar*, eds Goodman SM, Patterson BD (Smithsonian Institution Press, Washington, DC), pp 169–217.
15. Kennett DJ, et al. (2009) Nanodiamonds in the Younger Dryas boundary sediment layer. *Science* 323:94.
16. Firestone RB, et al. (2007) Evidence for an extraterrestrial impact 12,900 years ago that contributed to the megafaunal extinctions and the Younger Dryas cooling. *Proc Natl Acad Sci USA* 104:16016–16021.
17. Kennett DJ, et al. (2008) Wildfire and abrupt ecosystem disruption on California's Northern Channel Islands at the Ållerød–Younger Dryas boundary (13.0–12.9 ka). *Quat Sci Rev* 27:2530–2545.
18. Grayson DK (2007) Deciphering North American Pleistocene extinctions. *J Anthropol Res* 63:185–213.
19. Grayson DK (1991) Late Pleistocene mammalian extinctions in North America. *J World Prehistory* 5:193–231.
20. Grayson DK, Meltzer DJ (2003) A requiem for North American overkill. *J Archaeol Sci* 30:585–593.
21. Grayson DK, Meltzer DJ (2002) Clovis hunting and large mammal extinction: A critical review of the evidence. *J World Prehistory* 16:313–359.
22. Fiedel S (2009) in *American Megafaunal Extinctions at the End of the Pleistocene*, ed Haynes GA (Springer, Dordrecht, The Netherlands), pp 21–37.
23. Haynes CV, Jr (2008) Younger Dryas ''black mats'' and the Rancholabrean termination in North America. *Proc Natl Acad Sci USA* 105:6520–6525.
24. Waters MR, Stafford TW (2007) Redefining the age of Clovis: Implications for the peopling of the New World. *Science* 315:1122–1126.
25. Meltzer DJ (2004) in *The Quaternary Period in the United States*, eds Gillespie AR, Porter SC, Atwater BF (Elsevier, Amsterdam), pp 539–563.
26. Alley RB (2000) The Younger Dryas cold interval as viewed from central Greenland. *Quat Sci Rev* 19:213–226.
27. Signor PW, Lipps JH (1982) Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. *Geological Society of America Special Publication* 190:291–296.
28. FAUNMAP (1994) A database documenting late Quaternary distributions of mammal species in the United States, Illinois State Museum Scientific Papers 25 (Illinois State Museum, Springfield, IL).
29. Meltzer DJ, Mead JI (1985) in *Environments and Extinctions: Man in Late Glacial North America*, eds Mead JI, Meltzer DJ (Center for the Study of Early Man, Orono, ME), pp 145–173.
30. Pettitt PB, Davies W, Gamble CS, Richards MB (2003) Paleolithic radiocarbon chronology: Quantifying our confidence beyond two half-lives. *J Archaeol Sci* 30:1685–1693.
31. Fenneman NM (1946) *Physical divisions of the United States* (U.S. Geological Survey, Washington, DC).
32. Surovell TA, Waguespack NM (2009) in *American Megafaunal Extinctions at the End of the Pleistocene*, ed Haynes GA (Springer, Dordecht, The Netherlands), pp 77–105.
33. Haynes CV, Jr (1991) Geoarcheological and paleohydrological evidence for a Clovis age drought in North America and its bearing on extinction. *Quat Res* 35:438–450.
34. Beck MW (1996) On discerning the cause of late Pleistocene megafaunal extinctions. *Paleobiology* 22:91–103.
35. Stafford TW, Hare PE, Currie L, Jull AJT, Donahue DJ (1991) Accelerator radiocarbon dating at the molecular level. *J Archaeol Sci* 18:35–72.
36. Steadman DW, Stafford TW, Funk RE (1997) Nonassociation of paleoindians with AMS-dated late Pleistocene mammals from the Dutchess Quarry Caves, New York. *Quat Res* 47:106–116.
37. Schubert BW, Graham RW, McDonald HG, Grimm EC, Stafford TW (2004) Latest Pleistocene paleoecology of Jefferson's ground sloth (*Megalonyx jeffersonii*) and elk-moose (*Cervalces scotti*) in northern Illinois. *Quaternary Res* 61:231–240.
38. Kooyman B, et al. (2001) Identification of horse exploitation by Clovis hunters based on protein analysis. *Am Antiq* 66:686–691.
39. Kelley RL, et al. (2006) Multiple approaches to formation processes: The Pine Spring site, southwest Wyoming. *Geoarchaeology* 21:615–638.