RESEARCH ARTICLE SUMMARY

PALEONTOLOGY

Pre–Younger Dryas megafaunal extirpation at Rancho La Brea linked to fire-driven state shift

F. Robin O'Keefe*, Regan E. Dunn, Elic M. Weitzel, Michael R. Waters, Lisa N. Martinez, Wendy J. Binder, John R. Southon, Joshua E. Cohen, Julie A. Meachen, Larisa R. G. DeSantis, Matthew E. Kirby, Elena Ghezzo, Joan B. Coltrain, Benjamin T. Fuller, Aisling B. Farrell, Gary T. Takeuchi, Glen MacDonald, Edward B. Davis, Emily L. Lindsey

INTRODUCTION: At the end of the Pleistocene, most of Earth's large mammals (megafauna) became extinct. These extinctions occurred at different times globally, resulting in a drastic reorganization of terrestrial ecosystems. Despite decades of research on extinction causality, the relative importance of late-Quaternary climate changes and spreading human impacts have been difficult to disentangle because poor chronological resolution in the fossil record has precluded alignment of these rapidly occurring, tightly linked phenomena.

RATIONALE: The Rancho La Brea (RLB) locality in Southern California provides a unique opportunity to investigate decadal-scale changes in megafaunal populations and community composition across the latest Pleistocene. At this site, naturally occurring asphalt seeps entrapped and preserved the bones of hundreds, and in some cases thousands, of individuals from numerous megafaunal species across the last 50,000 years of the Pleistocene. Nearly all of these osteological specimens preserve original collagen, which permits precise radiocarbon dating analysis.

RESULTS: We obtained radiocarbon dates on 172 specimens from seven extinct and one extant species: *Smilodon fatalis*, *Aenocyon dirus*, *Panthera atrox*, *Bison antiquus*, *Equus occidentalis*, *Paramylodon harlani*, *Camelops hesternus*, and *Canis latrans*, spanning 15.6 to 10.0 thousand calendar years before present (ka). We used the resulting high-resolution chronology of entrapment at RLB to analyze population dynamics across this time interval and the timing of local disappearance for different taxa. To investigate the potential roles of late-Quaternary environmental change and human activities in driving the observed patterns, we compared our analyses of population structure and megafaunal extirpation against well-resolved regional and continental paleoclimatic proxies, vegetation records, and modeled human demographic growth. We used time-series modeling to investigate the dynamics of ecosystem change and evaluate causal relationships among these different phenomena.

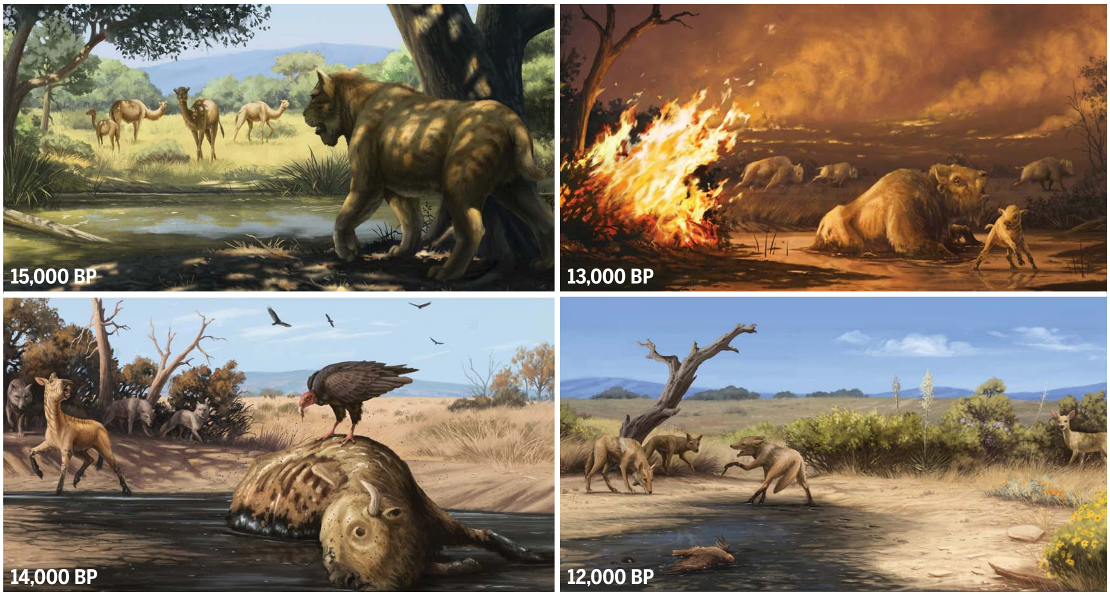
Modeling of extinction timing using several methods established that all taxa except coyotes were extirpated from RLB by 12.9 ka, before the onset of the Younger Dryas and well be the continental extinction of North Amer megafauna. The disappearance of all taxa was synchronous except for camels and sloths, which disappeared a few hundred years earlier in concert with aridification and tree loss during the Bølling–Allerød. The simultaneous disappearance of *Smilodon*, *Aenocyon*, *Panthera*, *Equus*, and *Bison antiquus* coincided with a regional ecological state shift characterized by floral community reorganization and unprecedented fire activity. Time-series modeling strongly implicates humans as the primary cause of the state shift and resulting extinctions.

CONCLUSION: Our data document a transition from a postglacial megafaunal woodland to a human-mediated chaparral ecosystem in Southern California before the onset of the Younger Dryas. This transition began with gradual opening and drying of the landscape over two millennia, and terminated in an abrupt (300-year) regime shift characterized by the complete extirpation of megafauna and unprecedented fire activity. This state shift appears to have been triggered by human-ignited fires in an ecosystem stressed by rapid warming, a megadrought, and a millennial-scale trend toward the loss of large herbivores from the landscape. This event parallels processes occurring in Mediterranean ecosystems today. ■

The list of author affiliations is available in the full article online.
*Corresponding author. Email: okeefef@marshall.edu

Cite this article as F. R. O'Keefe *et al.*, *Science* **381**, eabo3594 (2023). DOI: 10.1126/science.abo3594

S **READ THE FULL ARTICLE AT**
https://doi.org/10.1126/science.abo3594



Sequence of ecological events as recorded at Rancho La Brea, California. Top left: conditions around the tar pits were moist and cool, with abundant trees and megafaunal mammals. Bottom left: the onset of postglacial warming and drying begins as human pressure on herbivores increases. Top right: the synergy between climatic and human impacts enables a sudden ecological state transition characterized by unprecedented fire activity. Bottom right: a chapparal ecosystem is established; megafauna are extinct, and only coyote entrapment continues at the tar pits.

ILLUSTRATIONS BY C. TOWNSEND. COURTESY OF THE NATURAL HISTORY MUSEUMS OF LOS ANGELES COUNTY

RESEARCH ARTICLE

PALEONTOLOGY

Pre–Younger Dryas megafaunal extirpation at Rancho La Brea linked to fire-driven state shift

F. Robin O'Keefe[1,2]*, Regan E. Dunn[2,3], Elic M. Weitzel[4], Michael R. Waters[5], Lisa N. Martinez[6], Wendy J. Binder[2,7], John R. Southon[8], Joshua E. Cohen[2,7,9], Julie A. Meachen[2,10] Larisa R. G. DeSantis[2,11,12], Matthew E. Kirby[13], Elena Ghezzo[14,15], Joan B. Coltrain[16], Benjamin T. Fuller[17], Aisling B. Farrell[2], Gary T. Takeuchi[2], Glen MacDonald[6], Edward B. Davis[14,15], Emily L. Lindsey[2,3,18]

The cause, or causes, of the Pleistocene megafaunal extinctions have been difficult to establish, in part because poor spatiotemporal resolution in the fossil record hinders alignment of species disappearances with archeological and environmental data. We obtained 172 new radiocarbon dates on megafauna from Rancho La Brea in California spanning 15.6 to 10.0 thousand calendar years before present (ka). Seven species of extinct megafauna disappeared by 12.9 ka, before the onset of the Younger Dryas. Comparison with high-resolution regional datasets revealed that these disappearances coincided with an ecological state shift that followed aridification and vegetation changes during the Bølling-Allerød (14.69 to 12.89 ka). Time-series modeling implicates large-scale fires as the primary cause of the extirpations, and the catalyst of this state shift may have been mounting human impacts in a drying, warming, and increasingly fire-prone ecosystem.

The disappearance of two-thirds of Earth's large mammals outside of Africa at the end of the last Ice Age had profound impacts on global ecosystems (*1*, *2*), was the largest extinction event of the Cenozoic (*3*), and represents the initial pulse in the ongoing global extinction crisis that will likely result in Earth's sixth mass extinction (*4*). Across different continents, disappearances of megafauna (animals weighing >45 kg) coincided with both late-Quaternary climate changes and human colonization and growth (*5*–*7*). However, the causes, dynamics, and consequences of the end-Pleistocene extinctions remain poorly understood despite their obvious relevance for modern global change research. These lines of inquiry have been hobbled by the lack of reliably dated megafaunal fossils and the resulting lack of chronological precision of extinction timing relative to environmental and human demographic changes (*8*, *9*).

We radiocarbon dated fossils from the Rancho La Brea lagerstätte in Southern California to investigate the timing and dynamics of Pleistocene megafaunal disappearance in this region. The asphaltic deposits at La Brea preserve a nearly continuous record of megafaunal occupation of the Los Angeles Basin from >55 thousand calendar years before present (ka) through the Holocene (*10*), but a lack of stratigraphic control has limited inferences about megafaunal population structure, their history, and their ultimate demise. We developed a high-resolution radiocarbon chronology for the eight most common mammal species at La Brea [sabertoothed cat (*Smilodon fatalis*), dire wolf (*Aenocyon dirus*), coyote (*Canis latrans*), American lion (*Panthera atrox*), ancient bison (*Bison antiquus*), western horse (*Equus occidentalis*), Harlan's ground sloth (*Paramylodon harlani*), and yesterday's camel (*Camelops hesternus*)] from 15.6 to 10.0 ka (*11*) (Table 1). We estimated the timing of species disappearances based on last appearance dates and statistical modeling of extinction timing (*11*, *12*). We also inferred changes in entrapment rates over time using summed probability distributions (SPDs). Sampling effort in our analysis was approximately equal among species (rather than proportional to species occurrence); therefore, SPDs reflect changes in intraspecific entrapment rates and relative population sizes over time, but not absolute population sizes (*11*).

To investigate how large mammals were affected by late-Quaternary environmental and anthropogenic changes, we aligned the La Brea record of faunal change with well-resolved

Table 1. Last occurrences and modeled extirpation times for five extinct taxa at RLB. Dates are last occurrence in radiocarbon years (RC), calibrated last occurrence in years before 1950, and statistical GRIWM estimates of extirpation time [see section 1 of the supplementary materials (*11*)]. Most densely sampled taxa share a statistically identical extirpation time except for *Camelops*, which predeceases the others (**$P < 0.0001$, Welch's T). *Panthera* and *Paramylodon* have insufficient sample sizes to permit meaningful numerical comparison, but *Paramylodon* may disappear relatively early.

Taxon	No. dated	Last occurrence, RC, ±30	Last occurrence, ka 1-sigma	GRIMW extirpation estimate, ka 1-sigma
Aenocyon dirus	29	11,135	13,082; 12,965–13,117	12,908; 12,763–12,996
Bison antiquus	27	11,260	13,144; 13,097–13,183	12,932; 12,836–13,004
Camelops hesternus	17	11,820	13,683; 13,595–13,770	13,512**; 13,335–13,609
Equus occidentalis	27	11,100	13,029; 12,926–13,097	12,856; 12,737–12,929
Smilodon fatalis	30	11,090	13,021; 12,923–13,094	12,910; 12,821–12,998
Panthera atrox	8	11,160	13,097; 13,116–13,078	12,890; 12,744–13,008
Paramylodon harlani	8	11,940	13,806; 13,995–13,763	13,707; 13,580–13,804
All extinct				**12,957; 12,894–13,066**

---

[1]Department of Biological Sciences, Marshall University, Huntington, WV, USA. [2]La Brea Tar Pits and Museum, Natural History Museums of Los Angeles County, Los Angeles, CA, USA. [3]Department of Earth Sciences, University of Southern California, Los Angeles, CA, USA. [4]Department of Anthropology, University of Connecticut, Storrs, CT, USA. [5]Center for the Study of the First Americans, Department of Anthropology, Texas A&M University, College Station, TX, USA. [6]Department of Geography, University of California, Los Angeles, Los Angeles, CA, USA. [7]Department of Biology, Loyola Marymount University, Los Angeles, CA, USA. [8]Department of Earth System Science, University California, Irvine, Irvine, CA, USA. [9]Department of Biology, Pace University, New York, NY, USA. [10]Department of Anatomy, Des Moines University, Des Moines, IA, USA. [11]Department of Biological Sciences, Vanderbilt University, Nashville, TN, USA. [12]Department of Earth and Environmental Science, Vanderbilt University, Nashville, TN, USA. [13]Department of Geological Sciences, California State University, Fullerton, Fullerton, CA, USA. [14]Department of Environmental Sciences, Informatics, and Statistics, Università Ca' Foscari Venezia, Venice, Italy. [15]Department of Earth Sciences, University Oregon, Eugene, OR, USA. [16]Department of Anthropology, University of Utah, Salt Lake City, UT, USA. [17]Géosciences Environnement Toulouse, UMR 5563, CNRS, Observatoire Midi-Pyrénées, Toulouse, France. [18]Institute of the Environment and Sustainability, University of California, Los Angeles, Los Angeles, CA, USA.
***Corresponding author. Email: okeefef@marshall.edu**

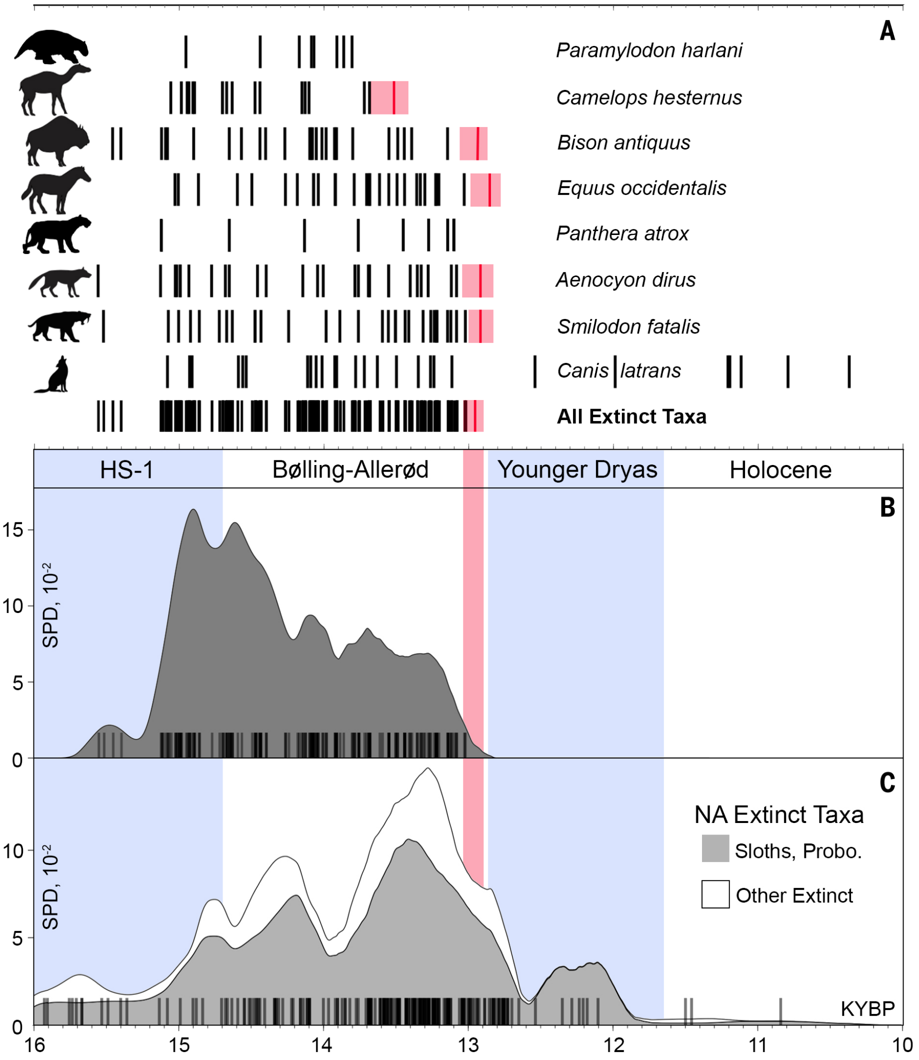


Fig. 1. Record of relative megafaunal occurrence and extirpation at La Brea compared with the North American Record. (**A**) Median calibrated dates for *Camelops* (*n* = 17), *Bison* (*n* = 27), *Equus* (*n* = 27), *Paramylodon* (*n* = 8), *Panthera* (*n* = 8), *Aenocyon* (*n* = 29), *Smilodon* (*n* = 30), *Canis latrans* (*n* = 27), and all extinct taxa pooled (*n* = 144) at La Brea. Hash marks are single, calibrated median carbon dates. The period HS-1 refers to Heinrich Stadial 1. Red lines and confidence intervals are extinction date estimates generated using the GRIWM method [see the supplementary materials section 2 (*11*)]. Last occurences and modeled extirpation times are reported in Table 1. (**B**) SPDs for all extinct taxa at La Brea. The overall trend is long-term decline followed by a precipitous fall to 0 starting at ~13.3 ka (**C**) Stacked SPDs for all extinct North American megafauna south of the Laurentide Ice Sheet, excluding La Brea. Dates drawn from (*9*) and (*14*) and a literature review were subjected to strict quality control and divided into proboscideans and sloths (light gray) and all other extinct species (dark gray). The regional extirpation precedes the continental extinction but coincides with continental decline.

regional paleoclimate, charcoal, and vegetation records and with continental-scale analyses of megafaunal extinction and human demographic growth in North America. Taken together, these data allow the first robust statistical modeling of extinction causality in Southern California.

Extinction timing and dynamics

We obtained accelerator mass spectrometry radiocarbon dates on 172 megafaunal individuals from La Brea (Fig. 1, A and B, and data S1) using a customized protocol for dating bone collagen from asphaltic contexts (*11*, *13*). These dates were then compared with a vetted compilation of published radiocarbon dates on North American megafauna south of Beringia [data S2; (*11*)]. The new dates presented here nearly double the number of reliable megafaunal dates for non-Beringian North America, and establish a precise chronology of Pleistocene megafaunal extirpation in Southern California. All extinct mammals dated in this study have last occurrence dates older than 13.00 ka, with a modeled extirpation time estimate across all taxa of 13.07 to 12.89 ka [using the Gaussian-Resampled Inverse-Weighted McInerney (GRIMW) extinction estimator; Table 1], placing the all-taxon extirpation almost certainly before the onset of the Younger Dryas (12.87 ± 0.03 ka) (*14*). Camels and ground sloths disappeared earlier, with last occurrences of 13.68 and 13.81 ka, respectively, whereas the disappearances of horses (13.03 ka), bison (13.14 ka), saber-toothed cats (13.02 ka), American lions (13.10 ka), and dire wolves (13.08 ka) are statistically contemporaneous (Table 1).

The disappearance of megafaunal species at La Brea precedes the North American megafaunal extinction by at least 1000 years (Fig. 1) but coincides with a precipitous decline in summed probability for North American megafauna at ~13.3 ka (Fig. 1C). Only 25 reliable, direct dates on North American megafauna fall within the Younger Dryas; more than half of these are on proboscideans, which were not dated in this study. Just six dates fall in the Holocene (after 11.7 ka), and all of these were obtained decades ago and should be redated (*11*). Of the seven extinct taxa examined in this study, only one (*Camelops*) has younger dates from elsewhere in North America. For *Smilodon*, *Panthera*, *Aenocyon*, *Equus*, and *Paramylodon*, the new dates reported here are the youngest reliably dated occurrences for North America. Although our database does not include any chronologically younger specimens diagnosed as *B. antiquus*, some authors have argued that this species survived into the mid-Holocene. *Bison bison*, the presumed chronospecies of *B. antiquus*, survives in inland areas of the continent today (*15*).

Occurrence rates of extinct taxa at La Brea decline gradually across the Bølling-Allerød, before beginning a precipitous drop ~13.25 ka. Herbivore and carnivore histories differ across this interval; herbivore summed probability declines steadily from 14.1 ka to the extinction (Fig. 2), whereas carnivore summed probability fluctuates across the interval. These differences in entrapment distributions are statistically significant, as determined by a mark permutation test [see Fig. 2 and section 2 of the supplementary materials (*11*)]. The numbers of extinct carnivores and herbivores dated are approximately equal, and the relative sizes of SPDs normalized, so the null expectation is that the entrapment rates should be equivalent. The observed bias toward carnivore entrapment just before the extinction may reflect increased predator reliance on asphalt-entrapped prey as large herbivores become scarce on the landscape. Coyotes do not mirror this late increase in entrapment frequency, possibly reflecting their ability to switch to smaller prey as large prey disappear and the competition with larger carnivores increases (*16*). Further scrutiny of the herbivore summed probabilities

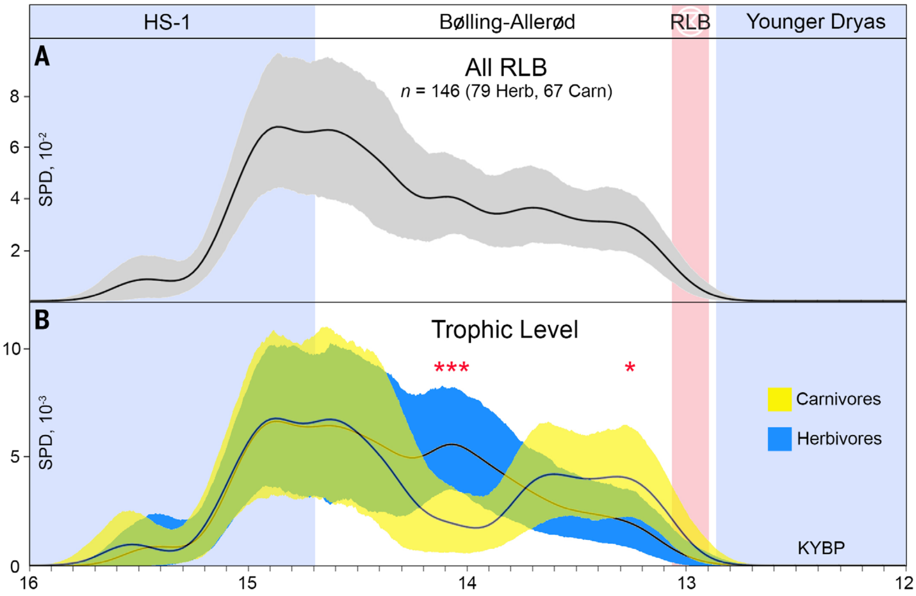


Fig. 2. Resampled summed probability distributions for the La Brea radiocarbon record. Lines are the SPDs for all taxa or indicated groups; envelopes are 95% confidence intervals based on 1000 bootstrap replicates. (**A**) All La Brea dates during the extinction interval; note that the terminal decline begins at ~13.2 ka. (**B**) Taxa split out by trophic level, with distributions for all extinct carnivores (*N* = 67, yellow) and all extinct herbivores (*N* = 79, blue). Red stars indicate areas where the curves differ significantly, as determined by a mark permutation test (*11*).

indicates a transition from a browser-dominated to a grazer-dominated herbivore community (*11*) (Fig. 3). Although the relative proportion of bison remains stable throughout the Bølling-Allerød, camels become less common and horses more common over time (Fig. 3). This changing assemblage likely reflects changing vegetation that favored grazers over browsers (*17*, *18*).

Coyotes (*Canis latrans*) are one of the few large mammal species to survive the extinction, so they serve as a "taphonomic control taxon" (*19*). Coyote occurrence rates drop coincident with those of La Brea megafauna, but occurrences resume at 12.54 ka (Fig. 1) and this continues into the Holocene. The continued deposition of postextinction coyotes is prima facie evidence that the potential for large mammal entrapment remained at La Brea. The absence of megafaunal deposition reflects their extirpation from the region rather than a taphonomic artifact. Neither taphonomic effects nor other sampling biases can explain the differences in herbivore and carnivore demographics noted above. However, these demographic shifts and subsequent extirpations coincided with profound ecological transitions in Southern California.

Climate and vegetation history

Climate warming from Heinrich Stadial 1 through the Bølling-Allerød in the Northern Hemisphere is well documented (*20*), but late-Pleistocene climate dynamics vary regionally. In Southern California, temperature and precipitation proxies indicate that the megafaunal disappearance at La Brea follows a period of significant regional warming and drying, particularly winter drying (*11*, *21*, *22*) (Fig. 3). Marine cores from the Santa Barbara Basin show warming of surface waters of 7 to 8°C from 17 to 15 ka (*23*). Mean annual air temperature proxy records from inland Lake Elsinore, ~100 km southeast of La Brea, show a later warming of 5.6°C between 14.0 and 13.0 ka and an additional 4.4°C warming from 13.0 to 11.8 ka (*24*) (Fig. 3C). Deglacial changes in hydroclimate toward drying at the onset of the Bølling-Allerød (14.7 ka) are evidenced at Lake Elsinore by decreased sand input from runoff, a proxy for precipitation (Fig. 3D), and leaf wax hydrogen isotopic records (*21*, *24*, *25*). Additionally, a steep rise in salinity caused by increased evaporation relative to freshwater input into Lake Elsinore is indicated between 13.7 and 13.2 ka (Fig. 3D) (*24*).

Pollen records from Lake Elsinore track the floral response to this warming and drying trend. Juniper (*Juniperus* spp.), a coniferous shrub or tree, declines with postglacial warming and drying starting ~16 ka (Fig. 4) after being dominant throughout the Last Glacial Maximum. This decline has been documented in most California pollen records (*22*, *26*–*28*). Oak (*Quercus* spp.) increases sharply at the beginning of the Bølling-Allerød, peaking in abundance at 13.6 ka. Then, between 13.2 and 12.9 ka, both oak and juniper decline, with almost complete extirpation of juniper by 12.87 ka. These taxa are then replaced by species with high fire resistance, including fire-tolerant pines (*29*) and grass and chaparral taxa (*30*). Although juniper is generally drought tolerant, it is vulnerable to soil water depletion from dry winters followed by hot, dry summers (*31*) and has low fire resistance (*32*). Today, severe juniper mortality is occurring at low-elevation sites in the Southwestern United States due to warming and drought (*31*).

To quantify floristic change during the extinction interval, we performed a nonmetric multidimensional scaling (NMDS) (Fig. 3E) (*11*) analysis on published Lake Elsinore pollen counts (*29*). NMDS axis 1 (NMDS1) scores reflect proportional changes of woodland tree (*Juniperus*, *Pinus*, and *Quercus*) versus chaparral taxa (Asteraceae, Rhamnaceae/Rosaceae, Amaranthaceae, *Eriogonum*, Cyperaceae, and Poaceae). Lower NMDS1 values indicate more short-statured, open, and xeric vegetation. The primary trend in pollen NMDS1 scores is a decline from 16.0 to 12.0 ka, indicating a drying and opening of habitats that correlates with the pattern of declining herbivore abundance (Fig. 3). The proportional replacement of camels and sloths by horses in the herbivore community (Fig. 3B) is consistent with this transition to a more open and herbaceous vegetational regime. Breakpoint analysis of the NMDS1 time series detects two periods of directional change in vegetation occurring at 13.88 and 13.21 ka (Fig. 3E). These breakpoints separate three stable trends in the vegetation: (i) the gradual opening and drying of habitats from 16.0 to 13.88 ka; (ii) a brief stabilization of this trend between 13.88 and 13.21 ka; and (iii) a rapid and punctuated decline in tree cover 13.21 to 12.90 ka, which is followed by continued opening of landscapes. Given the severity and rapidity of this last interval, we interpret this NMDS shift as a period of drought, probably driven primarily by evaporative water loss in response to rapidly rising temperatures (Fig. 3C). The modest decline in the sand-based proxy for runoff indicates that decreased precipitation may be contributing to increased aridity. A sharp increase in salinity concurrent with the substantial drop in NMDS values supports the inference of aridity during this time (Fig. 3D). Impacts to vegetation during this event include: (i) a tripling in the amount of grass pollen from 5 to 15%; (ii) a substantial decline in juniper and oak; (iii) an increase in herbaceous Asteraceae and Cyperaceae; and (iv) a slight increase in fire-adapted pine and chaparral shrubs (Rhamnaceae and Rosaceae). All of this coincides with the terminal decline and extirpation of the La Brea megafauna.

Fire activity

We analyzed charcoal accumulation rates from the Lake Elsinore sediment core (LEDC10-1),

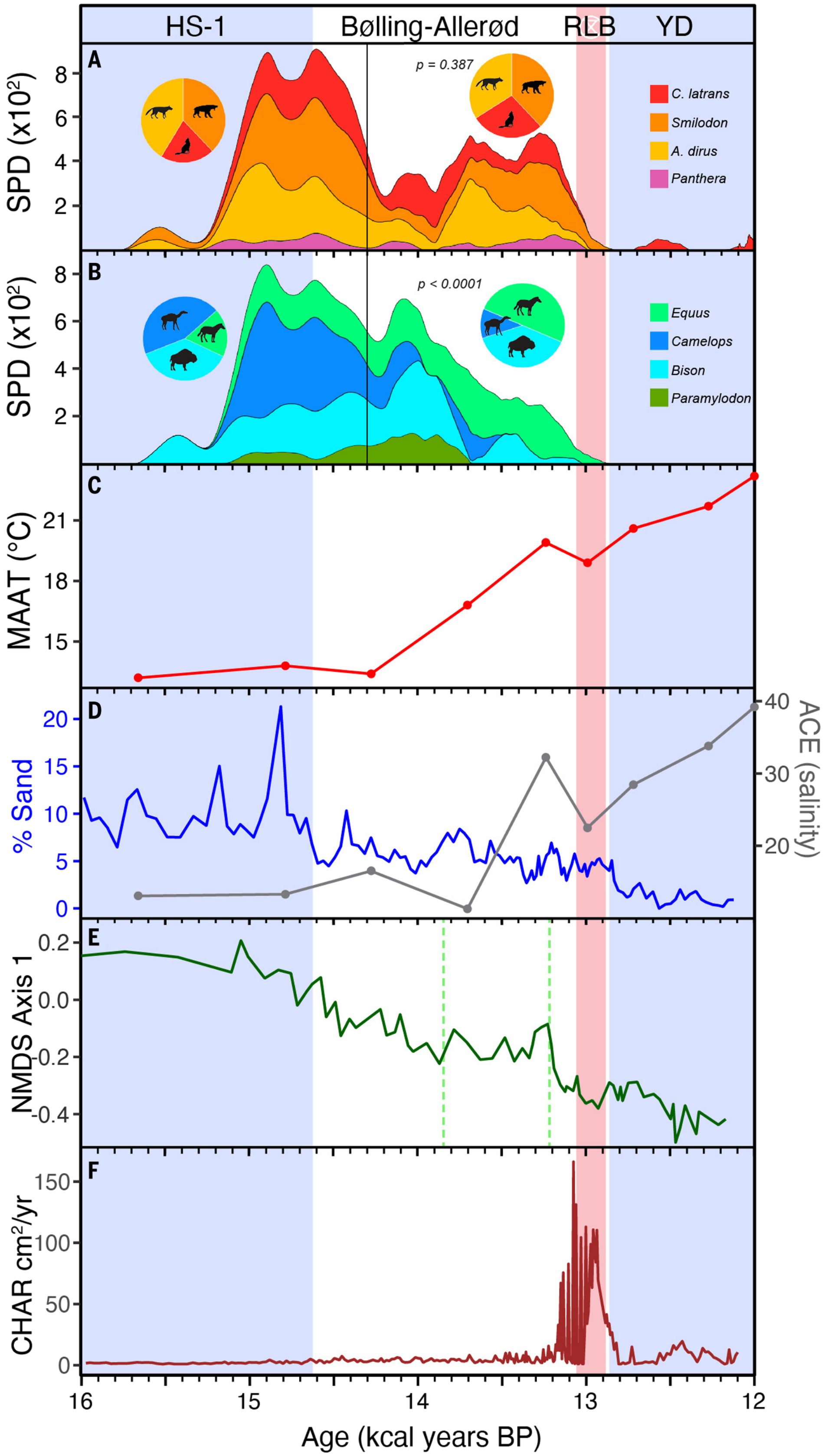


Fig. 3. Summed probability distributions for subsets of the La Brea radiocarbon record and end-Pleistocene records of biotic and abiotic change in Southern California. (**A** and **B**) SPDs for La Brea carnivores (N = 67) (A) and herbivores (N = 79) (B). The line at 14.3 ka marks the bins for the pie chart and chi-square tests (*11*). Proxy climate data from the Lake Elsinore core (LEDC10-1) including: mean annual air temperature (MAAT; red) derived from (*24*) (C) and sand fraction (blue), a proxy for precipitation (*25*) and salinity (gray) (*24*) (D). The marked rise in salinity reflects increasingly arid conditions driven more by rising temperatures rather than precipitation decrease. (**E**) NMDS1 scores depicting change in pollen composition from Lake Elsinore [see the materials and methods (*11*); data are from (*29*)]. Green vertical lines indicate shifts between regression regimes recovered from a subsidiary breakpoints analysis on pollen NMDS [see section 4 of the supplementary materials and methods (*11*)]. A steady decline in NMDS is followed by a brief stable period, then an abrupt floral transition toward a more open chaparral habitat containing more drought-tolerant and fire-adapted species starting at ~13.3 ka. (**F**) Charcoal particles per square centimeter per year from the Lake Elsinore core. The age model for the Lake Elsinore core, and associated error, can be found in fig. S1 and table S2.

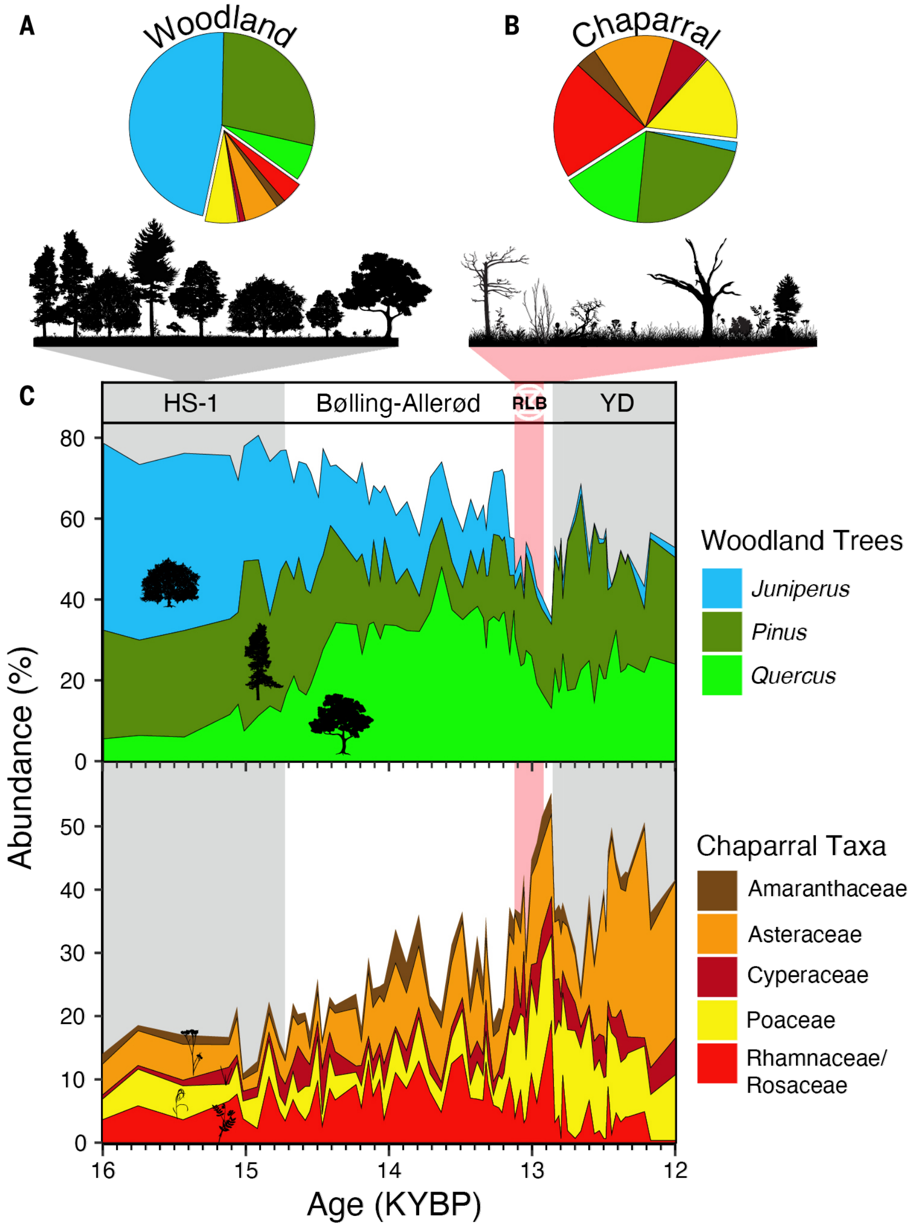


Fig. 4. Record of floral change from 16 to 12 ka based on pollen counts from Lake Elsinore. (**A** and **B**) Pie graphs showing vegetation abundance at 15.4 ka (A) and 13.0 ka (B) from Lake Elsinore (*27*). (**C**) Light gray bars denote the HS-1 and Younger Dryas cooler periods; red bar shows the GRIWM estimate for the La Brea megafaunal extirpation (Fig. 1). A shift from woodland tree dominance to xeric and fire-adapted, grassy and chaparral taxa occurs concurrently with the La Brea regional extinction. Percentages are of taxa representative of chaparral or woodland plant communities only; not all taxa present are shown.

measured as particles per square centimeter per year, from sediment spanning 16.0 to 12.0 ka (*11*) (Fig. 3F). Charcoal accumulation rates are low before the appearance of humans in the archeological record [including during times of previous drought (*29*, *33*)] and increase modestly as humans arrive and the climate warms and dries beginning ~13.5 ka. However, ~13.2 ka, charcoal accumulation rates suddenly increase 30-fold. This interval of significantly heightened charcoal input lasts for ~300 years and is attested in other regional charcoal records (*34*), the Santa Barbara Basin at 13.0 ka (*35*), and continent wide between 13.2 and 13.0 ka (*36*). This interval appears to be a tipping point for fire regimes in Southern California and across North America; after the initial spike, charcoal accumulation rates remain elevated relative to earlier Pleistocene levels during the Younger Dryas and then increase again in the Holocene (*36*). Although the increase in charcoal input observed in the Southern California record is consistent with observed changes in climate and vegetation, as well as with the disappearance of megaherbivores (*37*), its magnitude is unprecedented in the 33,000-year record (*33*). Its ignition source is open to question, but increased human impact on the ecosystem should be considered as a potential causal factor in the intense burning event ~13.2 ka.

Human record

Genetic and archeological data support a human presence south of the North American ice sheets by 16 ka (*38*, *39*) and possibly earlier. The megafauna-specialized Clovis technology is often invoked as the likely driver of North American megafaunal extinctions (*40*). However, the emergence and geographic expansion of the Clovis complex (~13.05 to 12.75 ka) (*41*) postdates the crash in megafaunal occurrences at La Brea at 13.25 ka, as well as the last occurrences of all dated taxa except *Smilodon* and *Equus*. Clovis also emerges after the North American megafauna begin to decline, but coincides with the final megafaunal decline across the continent (Figs. 1 and 5) (*41*). The modeled extirpation time for La Brea megafauna (13.07 to 12.89 ka) suggests an overlap with early Clovis, but Clovis continues for at least 140 years after the extirpation is complete.

The oldest unequivocal evidence of human presence in California is a partial skeleton from Arlington Springs on Santa Rosa Island ~12.89 ka (*42*) (Fig. 5A). No other archeological evidence of late-Pleistocene human presence or association between humans and megafauna has been documented in California. However, such sites would be rare and difficult to find because most deposits of this age are deeply buried or underwater (*43*). To better understand the potential impacts of humans on megafauna in Southern California, we constructed an SPD for human occupation sites in North America (between southern Canada and northern Mexico) to serve as a proxy for human population in the region (*11*). Data from the Canadian Archeological Radiocarbon Database (CARD) were subjected to strict data hygiene (*11*), and the probability distribution was binned to control for variation in sampling intensity (Fig. 5A). Our model indicates that North American human population density is low until ~13.2 ka, when it begins a sharp increase that continues into the Younger Dryas.

State shift

Together, these records of climate and vegetation change, megafaunal extirpation, human demographic growth, and biomass burning document a profound shift in ecosystem structure in Southern California near the end of the Bølling-Allerød. We analyzed the correlations among these time series using principal components analysis and applied a Bayesian structural

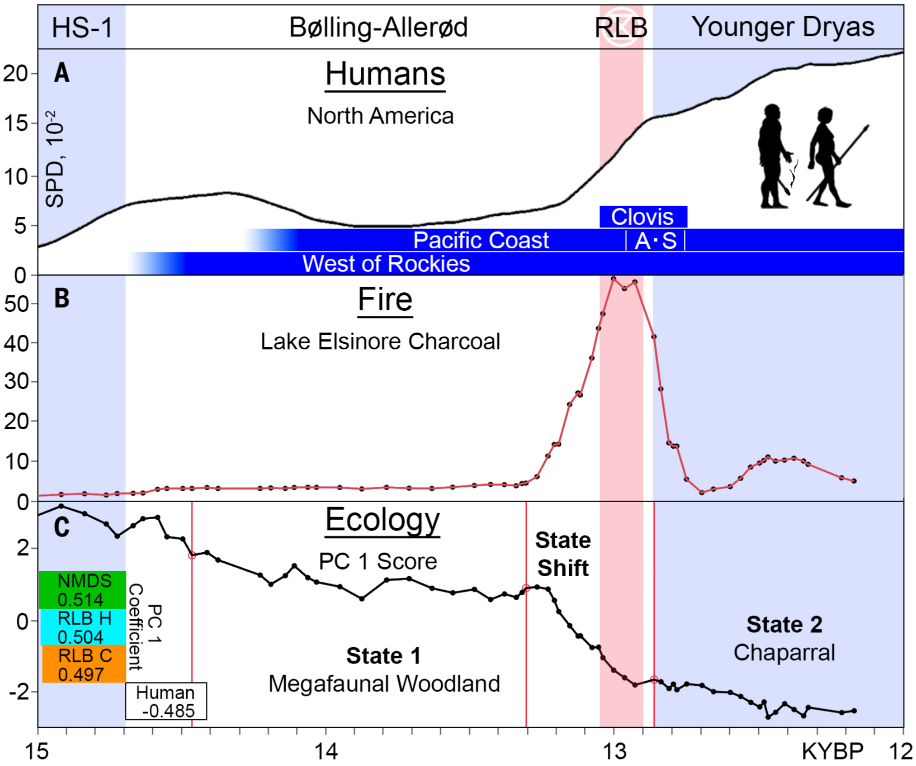


Fig. 5. Correlation among Southern California ecosystem variables. (**A**) Summed probability distribution of human occupation in North America derived from the CARD database (black line). Blue bars present archaeological data including age range for Clovis, earliest evidence of human occupation along the Pacific Coast, "AS" is the date of Arlington Springs Man, and earliest evidence of human occupation west of the Rocky Mountains [see materials and methods (*11*)]. (**B**) The fire record at Lake Elsinore as recorded by particles of charcoal per square centimeter per year; series is a 200-year running mean. (**C**) PC1 scores for ecosystem variables through time. Red regression lines are four regimes identified by breakpoint analysis [see section 4 of the supplementary materials (*11*)]: the drying transition out of the HS-1 and initial human arrival; relative stability for much of the Bølling-Allerød while humans were scarce ("Megafaunal Woodland"); an abrupt state shift from 13.3 to 13.0 ka ("State Shift"); and the establishment of a new regime ("Chaparral").

change analysis to identify significant shifts in principal component 1 (PC1) scores (*11*) (Fig. 5). These analyses identify four distinct periods of stable regression across the Bølling-Allerød, most notably an ecosystem state shift from 13.3 to 12.9 ka (Fig. 5). This state shift coincides with a 30-fold regional increase in charcoal accumulation rates and a shift in the floral community toward fire-adapted species. During this interval, tree abundance plummets and megafaunal occurrence rates fall to zero. At the end of the state shift, Southern California enters a new ecological regime characterized by chaparral vegetation, intensified fire activity, and complete absence of Pleistocene megafauna. Many large mammals that are associated with fire-adapted ecosystems today (e.g., elk, moose, and grizzly bear) likely do not arrive in non-Beringian North America until the early Holocene (*44*–*46*). Others, such as deer and pumas, are present but rare at La Brea.

Across this time interval, the coefficient for human population size is strongly negatively correlated with those for megafaunal populations and glacial floral communities (Fig. 5C). The trend over the Bølling-Allerød is toward an increasingly fire-prone ecosystem. The unprecedented biomass burning observed during the state shift could have resulted from the confluence of extreme warming and drying, fuel accumulation resulting from reduction of grazing herbivores (*37*), and new, anthropogenic ignition sources. Climate change thus may have facilitated the extinction by pushing the ecosystem toward a state where anthropogenic activities could trigger widespread fires. In Southern California, the Pleistocene megafauna are already gone, and the transition toward a Holocene chaparral is well advanced, before the Younger Dryas begins.

Causality

Numerous studies have found correlations between the timing of megafaunal disappearances and changes in climate (*9*), vegetation (*2*), human populations (*5*), and fire activity (*37*). We leveraged our highly resolved datasets to quantify causality using variable autoregression modeling with exogenous variables (VARX) (*11*) (Fig. 6). Vector autoregressive models use time-series data to identify whether, and to what degree, past values of one variable predict present values of others (*47*, *11*). Our time series included two exogenous variables: local precipitation inferred from percent sand from Lake Elsinore and NMDS1 scores from Lake Elsinore pollen. The NMDS1 scores are highly correlated with the MAAT estimates from Lake Elsinore ($R^2 = 0.67$; $P = 1.18 \times 10^{-12}$) (*11*), making pollen our most densely sampled proxy for terrestrial air temperature. Endogenous variables included charcoal accumulation rates from Lake Elsinore, the megafaunal probability distributions from La Brea, and the North American human probability distribution. The average time step was 43 years, and there were 57 steps across a 2382-year span. We limited interpretation of the model to the first two time lags (~85 years), or two parameters per time series. We ran the VARX model both including and excluding our human SPDs for North America. The VARX model fit is much better with the human distribution included [Akaike information criterion (AIC) of −19.71 versus −9.76 with and without humans, respectively; $P < 0.001$]. Given that an AIC difference of 2 is generally considered meaningful, this decrease of 10 is robust evidence that humans are a strong forcing factor in the model.

The VARX model (Fig. 6) identified several significant time-lagged causal relationships. These include: (i) climate warming and aridification predict an increase in charcoal input; (ii) declines in pollen NMDS1 also forecast an increase in charcoal input; and (iii) human population growth predicts a decrease in herbivore populations and, most strongly, an increase in charcoal input. Decrease in herbivore numbers at one lag predicts an increase in carnivore entrapment bias at La Brea. Some effects, such as the impact of vegetation change and fire activity on herbivore populations, likely occurred too rapidly to be captured by the 43-year time lag. The model supports inference of a potential positive feedback loop in which rising human populations cause enhanced fire activity both indirectly by depressing herbivore numbers (resulting in increased fuel loads) and by increasing ignition.

Small populations of humans can have disproportionate impacts on landscapes through the use of fire (*48*); significant increases in regional fire activity after the arrival of humans have also been noted in Australia (*49*), New Zealand (*50*), Panama (*51*), and many other regions worldwide (*52*). Today, changing fire regimes resulting from climate change and human activities are again driving some ecosystems toward tipping points (*53*). Not only can fire cause direct mortality of wildlife, but it can also alter the structure and function of

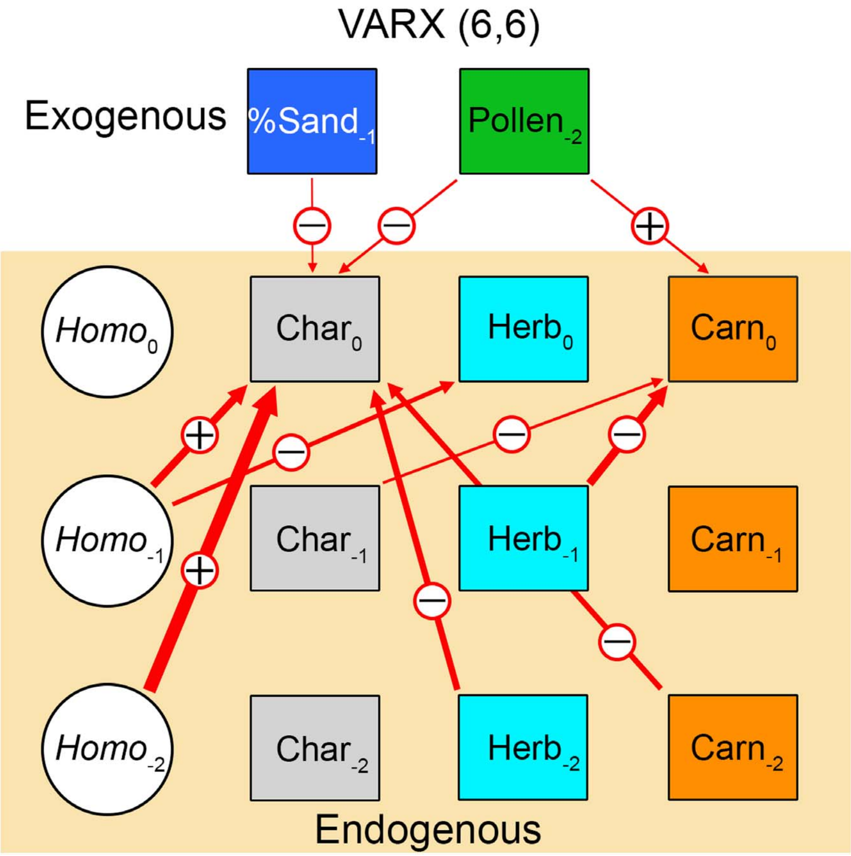


Fig. 6. Summary time-series VARX model of ecosystem variables expressed as a structural equation model. VARX 6,6 model incorporating probability distributions from La Brea herbivores ("Herb") and carnivores ("Carn"), charcoal from Lake Elsinore ("Char"), and our SPD for the North American human population ("*Homo*"). Exogenous variables include Lake Elsinore %Sand, a proxy for precipitation, and NMDS of Lake Elsinore pollen ("Pollen"), a proxy for onshore air temperature. Predictive relationships with effect size >0.4 are shown by red arrows with width scaled to coefficient magnitude. For exogenous variables, all effects are shown. See section 5 of the supplementary materials for values (*11*). Self-prediction is highly significant in most cases but is omitted because the probability distributions are smoothed to 200 years and the average step length is 43 years. For a further discussion of methods, see the supplementary materials (*11*).

vegetation, which affects the availability of key floral resources for animals, alters migration patterns, increases energetic costs of movement, and can put animals at higher risk of predation (*53*). Humans arriving in Southern California in the latest Pleistocene encountered a warming and increasingly arid climate coupled with ample flammable fuels. Anthropogenic hunting and burning could have precipitated a state shift toward today's chaparral ecosystem (Fig. 5).

The debate over the cause of the Pleistocene megafaunal extinctions has raged for decades (*5*). This study demonstrates the necessity of moving beyond dichotomous statements about single extinction drivers and instead moving toward a more nuanced view of past extinctions, one that considers the interplay among biotic and abiotic causal factors. Our results also highlight the importance of considering extinction dynamics on ecologically relevant spatial, temporal, and taxonomic scales. Studies from the northeastern United States (*2*), the Pacific Northwest (*52*), and Alaska (*54*) have also found pre–Younger Dryas disappearances of megafauna coinciding with climate-driven environmental changes, and radiocarbon dates from the Southwestern United States indicate that megafauna may have persisted there well into the Younger Dryas (Fig. 1 and data S2). The results of our study also suggest that individual taxa at La Brea responded differently to climate-driven vegetation shifts (Fig. 3)

A climate-human synergy such as the one we implicate in California's megafaunal extinctions may portend future ecological state shifts (*55*). Data from the National Oceanic and Atmospheric Administration (NOAA) show that Southern California has warmed >2°C over the past century, an order of magnitude faster than warming during the Bølling-Allerød. Anthropogenic climate warming is increasing the risk of prolonged droughts and wildfire activity in highly biodiverse Mediterranean regions worldwide (*56*). These events are predicted to worsen in coming decades, affecting wildlife already experiencing population declines caused by other factors (*57*). As critical thresholds are reached in Mediterranean ecosystems, state shifts are likely to occur, as they did at the end of the Pleistocene. Some such transitions have already begun: in the western United States, wildfire-burned area has increased fourfold in two decades (*58*). Moreover, postfire ecosystems are not recovering to preburned states, suggesting that critical thresholds for re-establishment have already been crossed (*59*). The conditions that led to the end-Pleistocene state shift in Southern California are recurring today across the western United States and in numerous other ecosystems worldwide. Understanding the interplay of climatic and anthropogenic forcings in driving the La Brea extinction event may be helpful in mitigating future biodiversity loss in the face of similar pressures.

REFERENCES AND NOTES

1. A. B. Tóth *et al.*, Reorganization of surviving mammal communities after the end-Pleistocene megafaunal extinction. *Science* **365**, 1305–1308 (2019). doi: 10.1126/science.aaw1605; pmid: 31604240
2. J. L. Gill, J. W. Williams, S. T. Jackson, K. B. Lininger, G. S. Robinson, Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**, 1100–1103 (2009). doi: 10.1126/science.1179504; pmid: 19965426
3. F. A. Smith, R. E. Elliott Smith, S. K. Lyons, J. L. Payne, Body size downgrading of mammals over the late Quaternary. *Science* **360**, 310–313 (2018). doi: 10.1126/science.aao5987; pmid: 29674591
4. A. D. Barnosky *et al.*, Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011). doi: 10.1038/nature09678; pmid: 21368823
5. P. L. Koch, A. D. Barnosky, Late Quaternary extinctions: State of the debate. *Annu. Rev. Ecol. Evol. Syst.* **37**, 215–250 (2006). doi: 10.1146/annurev.ecolsys.34.011802.132415
6. A. D. Barnosky, E. L. Lindsey, Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quat. Int.* **217**, 10–29 (2010). doi: 10.1016/j.quaint.2009.11.017
7. J. M. Broughton, E. M. Weitzel, Population reconstructions for humans and megafauna suggest mixed causes for North American Pleistocene extinctions. *Nat. Commun.* **9**, 5441 (2018). doi: 10.1038/s41467-018-07897-1; pmid: 30575758
8. D. J. Meltzer, Overkill, glacial history, and the extinction of North America's Ice Age megafauna. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 28555–28563 (2020). doi: 10.1073/pnas.2015032117; pmid: 33168739
9. M. Stewart, W. C. Carleton, H. S. Groucutt, Climate change, not human population growth, correlates with Late Quaternary megafauna declines in North America. *Nat. Commun.* **12**, 965 (2021). doi: 10.1038/s41467-021-21201-8; pmid: 33594059

10. C. Stock, J. M. Harris, Rancho La Brea: A record of Pleistocene life in California. *LACM Sci. Ser.* **37** (1992).
11. Materials and methods are available as supplementary materials.
12. C. J. A. Bradshaw, A. Cooper, C. S. M. Turney, B. W. Brook, Robust estimates of extinction time in the geological record. *Quat. Sci. Rev.* **33**, 14–19 (2012). doi: 10.1016/j.quascirev.2011.11.021
13. B. T. Fuller *et al*., Ultrafiltration for asphalt removal from bone collagen for radiocarbon dating and isotopic analysis of Pleistocene fauna at the tar pits of Rancho La Brea, Los Angeles, California. *Quat. Geochronol.* **22**, 85–98 (2014). doi: 10.1016/j.quageo.2014.03.002
14. H. Cheng *et al*., Timing and structure of the Younger Dryas event and its underlying climate dynamics. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 23408–23417 (2020). doi: 10.1073/pnas.2007869117; pmid: 32900942
15. J. M. Martin, J. I. Mead, P. S. Barboza, Bison body size and climate change. *Ecol. Evol.* **8**, 4564–4574 (2018). doi: 10.1002/ece3.4019; pmid: 29760897
16. J. A. Meachen, A. C. Janowicz, J. E. Avery, R. W. Sadleir, Ecological changes in Coyotes (*Canis latrans*) in response to the ice age megafaunal extinctions. *PLOS ONE* **9**, e116041 (2014). doi: 10.1371/journal.pone.0116041; pmid: 25551387
17. D. B. Jones, L. R. DeSantis, Dietary ecology of ungulates from the La Brea tar pits in southern California: A multi-proxy approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **466**, 110–127 (2017). doi: 10.1016/j.palaeo.2016.11.019
18. J. E. Cohen *et al*., Dietary stability inferred from dental mesowear analysis in large ungulates from Rancho La Brea and opportunistic feeding during the late Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **570**, 110360 (2021). doi: 10.1016/j.palaeo.2021.110360
19. S. M. Kidwell, S. M. Holland, The quality of the fossil record: Implications for evolutionary analyses. *Annu. Rev. Ecol. Syst.* **33**, 561–588 (2002). doi: 10.1146/annurev.ecolsys.33.030602.152151
20. K. K. Andersen *et al*., High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* **431**, 147–151 (2004). doi: 10.1038/nature02805; pmid: 15356621
21. M. E. Kirby, S. J. Feakins, N. Bonuso, J. M. Fantozzi, C. A. Hiner, Latest Pleistocene to Holocene hydroclimates from Lake Elsinore, California. *Quat. Sci. Rev.* **76**, 1–15 (2013). doi: 10.1016/j.quascirev.2013.05.023
22. K. C. Glover *et al*., Evidence for orbital and North Atlantic climate forcing in alpine Southern California between 125 and 10 ka from multi-proxy analyses of Baldwin Lake. *Quat. Sci. Rev.* **167**, 47–62 (2017). doi: 10.1016/j.quascirev.2017.04.028
23. I. L. Hendy, The paleoclimatic response of the Southern Californian Margin to the rapid climate change of the last 60 ka: A regional overview. *Quat. Int.* **215**, 62–73 (2010). doi: 10.1016/j.quaint.2009.06.009
24. S. J. Feakins, M. S. Wu, C. Ponton, J. E. Tierney, Biomarkers reveal abrupt switches in hydroclimate during the last glacial in southern California. *Earth Planet. Sci. Lett.* **515**, 164–172 (2019). doi: 10.1016/j.epsl.2019.03.024
25. M. E. Kirby *et al*., A late Wisconsin (32-10k cal a BP) history of pluvials, droughts and vegetation in the Pacific south-west United States (Lake Elsinore, CA). *J. Quaternary Sci.* **33**, 238–254 (2018). doi: 10.1002/jqs.3018
26. L. Heusser, Direct correlation of millennial-scale changes in western North American vegetation and climate with changes in the California Current system over the past ~60 kyr. *Paleoceanography* **13**, 252–262 (1998). doi: 10.1029/98PA00670
27. O. K. Davis, Pollen analysis of a late-glacial and Holocene sediment core from Mono Lake, Mono County, California. *Quat. Res.* **52**, 243–249 (1999). doi: 10.1006/qres.1999.2063
28. S. A. Mensing, Late-glacial and early Holocene vegetation and climate change near Owens Lake, eastern California. *Quat. Res.* **55**, 57–65 (2001). doi: 10.1006/qres.2000.2196
29. L. E. Heusser, M. E. Kirby, J. E. Nichols, Pollen-based evidence of extreme drought during the last glacial (32.6–9.0 ka) in coastal southern California. *Quat. Sci. Rev.* **126**, 242–253 (2015). doi: 10.1016/j.quascirev.2015.08.029
30. J. E. Keeley, Native American impacts on fire regimes of the California coastal ranges. *J. Biogeogr.* **29**, 303–320 (2002). doi: 10.1046/j.1365-2699.2002.00676.x
31. S. A. Kannenberg, A. W. Driscoll, D. Malesky, W. R. Anderegg, Rapid and surprising dieback of Utah juniper in the southwestern USA due to acute drought stress. *For. Ecol. Manage.* **480**, 118639 (2021). doi: 10.1016/j.foreco.2020.118639
32. J. T. Stevens, M. M. Kling, D. W. Schwilk, J. M. Varner, J. M. Kane, Biogeography of fire regimes in western US conifer forests: A trait-based approach. *Glob. Ecol. Biogeogr.* **29**, 944–955 (2020). doi: 10.1111/geb.13079
33. L. N. Martinez, "Climate, fire, and environmental dynamics at Lake Elsinore, California, from Late Marine Isotope Stage 3 through the Holocene," thesis, University of California, Los Angeles (2020).
34. M. Hardiman *et al*., Fire history on the California Channel Islands spanning human arrival in the Americas. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **371**, 20150167 (2016). doi: 10.1098/rstb.2015.0167; pmid: 27216524
35. L. E. Heusser, F. Sirocko, Millennial pulsing of environmental change in southern California from the past 24 ky: A record of Indo-Pacific ENSO events? *Geology* **25**, 243–246 (1997). doi: 10.1130/0091-7613(1997)025<0243:MPOECI>2.3.CO;2
36. J. R. Marlon *et al*., Wildfire responses to abrupt climate change in North America. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 2519–2524 (2009). doi: 10.1073/pnas.0808212106; pmid: 19190185
37. A. T. Karp, J. T. Faith, J. R. Marlon, A. C. Staver, Global response of fire activity to late Quaternary grazer extinctions. *Science* **374**, 1145–1148 (2021). doi: 10.1126/science.abj1580; pmid: 34822271
38. E. Willerslev, D. J. Meltzer, Peopling of the Americas as inferred from ancient genomics. *Nature* **594**, 356–364 (2021). doi: 10.1038/s41586-021-03499-y; pmid: 34135521
39. M. R. Waters, Late Pleistocene exploration and settlement of the Americas by modern humans. *Science* **365**, eaat5447 (2019). doi: 10.1126/science.aat5447; pmid: 31296740
40. J. E. Mosimann, P. S. Martin, Simulating overkill by Paleoindians: Did man hunt the giant mammals of the New World to extinction? Mathematical models show that the hypothesis is feasible. *Am. Sci.* **63**, 304–313 (1975).
41. M. R. Waters, T. W. StaffordJr., D. L. Carlson, The age of Clovis-13,050 to 12,750 cal yr B.P. *Sci. Adv.* **6**, eaaz0455 (2020). doi: 10.1126/sciadv.aaz0455; pmid: 33087355
42. J. R. Johnson, T. W. Stafford Jr, H. O. Ajie, D. P. Morris, "Arlington Springs revisited," in *Proceedings of the Fifth California Islands Symposium* (Santa Barbara Museum of Natural History, 2002), vol. 5, pp. 541–545.
43. M. R. Waters, B. F. Byrd, S. N. Reddy, Geoarchaeological investigations of San Mateo and Las Flores creeks, California: Implications for coastal settlement models. *Geoarchaeology* **14**, 289–306 (1999). doi: 10.1002/(SICI)1520-6548(199903)14:3<289::AID-GEA4>3.0.CO;2-R
44. P. S. Alagona, A. M. Mychajliw, Southern California's three-bear shuffle: Survival, extinction and recovery in an urban biodiversity hotspot. *Environ. Hist.* **27**, 308–313 (2022). doi: 10.1086/719611
45. M. Meiri *et al*., Subspecies dynamics in space and time: A study of the red deer complex using ancient and modern DNA and morphology. *J. Biogeogr.* **45**, 367–380 (2018). doi: 10.1111/jbi.13124
46. M. Meiri, A. Lister, P. Kosintsev, G. Zazula, I. Barnes, Population dynamics and range shifts of moose (*Alces alces*) during the Late Quaternary. *J. Biogeogr.* **47**, 2223–2234 (2020). doi: 10.1111/jbi.13935
47. J. Gan, Causality among wildfire, ENSO, timber harvest, and urban sprawl: The vector autoregression approach. *Ecol. Modell.* **191**, 304–314 (2006). doi: 10.1016/j.ecolmodel.2005.05.013
48. N. Pinter, S. Fiedel, J. E. Keeley, Fire and vegetation shifts in the Americas at the vanguard of Paleoindian migration. *Quat. Sci. Rev.* **30**, 269–272 (2011). doi: 10.1016/j.quascirev.2010.12.010
49. S. Rule *et al*., The aftermath of megafaunal extinction: Ecosystem transformation in Pleistocene Australia. *Science* **335**, 1483–1486 (2012). doi: 10.1126/science.1214261; pmid: 22442481
50. D. B. McWethy *et al*., Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 21343–21348 (2010). doi: 10.1073/pnas.1011801107; pmid: 21149690
51. D. R. Piperno, J. G. Jones, Paleoecological and archaeological implications of a Late Pleistocene/Early Holocene record of vegetation and climate from the Pacific coastal plain of Panama. *Quat. Res.* **59**, 79–87 (2003). doi: 10.1016/S0033-5894(02)00021-2
52. D. M. Gilmour *et al*., Chronology and ecology of late Pleistocene megafauna in the northern Willamette Valley, Oregon. *Quat. Res.* **83**, 127–136 (2015). doi: 10.1016/j.yqres.2014.09.003
53. L. T. Kelly *et al*., Fire and biodiversity in the Anthropocene. *Science* **370**, eabb0355 (2020). doi: 10.1126/science.abb0355; pmid: 33214246
54. R. D. Guthrie, New carbon dates link climatic change with human colonization and Pleistocene extinctions. *Nature* **441**, 207–209 (2006). doi: 10.1038/nature04604; pmid: 16688174
55. A. D. Barnosky *et al*., Approaching a state shift in Earth's biosphere. *Nature* **486**, 52–58 (2012). doi: 10.1038/nature11018; pmid: 22678279
56. N. S. Diffenbaugh, D. L. Swain, D. Touma, Anthropogenic warming has increased drought risk in California. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 3931–3936 (2015). doi: 10.1073/pnas.1422385112; pmid: 25733875
57. M. Goss *et al*., Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. *Environ. Res. Lett.* **15**, 094016 (2020). doi: 10.1088/1748-9326/ab83a7
58. V. Iglesias, J. K. Balch, W. R. Travis, U.S. fires became larger, more frequent, and more widespread in the 2000s. *Sci. Adv.* **8**, eabc0020 (2022). doi: 10.1126/sciadv.abc0020; pmid: 35294238
59. A. D. Syphard, T. J. Brennan, J. E. Keeley, Extent and drivers of vegetation type conversion in Southern California chaparral. *Ecosphere* **10**, e02796 (2019). doi: 10.1002/ecs2.2796

ACKNOWLEDGMENTS

Special thanks are due to B. Van Valkenburgh, M. Foote, S. Kidwell, P. Wagner, F. Saltré, C. Howard, K. Palmquist, and A. Axel for help at different stages of this research. Human and some mammal silhouettes used in this paper are from PhyloPic (https://www.phylopic.org/). La Brea mammal silhouettes are by J. Olsson. We thank S. Abramowicz for photography, and C. Townsend for life reconstructions. We also thank S. Vignieri and a host of anonymous reviewers; the review process was unusually beneficial and contributed greatly to the finished work. **Funding:** This work was supported by the National Science Foundation Division of Earth Sciences, Collaborative Research: RUI: Chronology and Ecology of Late Pleistocene Megafauna at Rancho La Brea (NSF EAR grants 1758117, 1757545, 1758116, 1758108, 1757236, and 1758110 to W.B., L.R.G.D., E.L.L., J.A.M., F.R.O., and J.R.S., respectively); NSF Department of Behavioral and Cognitive Sciences (BCS (FAIN): 1759756 to G.M. and L.M.); a UCLA John Muir Endowment to G.M. and L.M.; REFIND grant H2020-MSCA-GF-785821 to E.G.; a Drinko Distinguished Research Fellowship from John Deever Drinko Academy, Marshall University to F.R.O.; and the North Star Archaeological Research Program, Center for the Study of the First Americans, Texas A&M University (M.R.W.). **Author contributions:** Conceptualization: F.R.O., E.L.L., R.E.D., E.M.W., J.R.S., J.E.C., J.A.M., W.J.B., L.R.G.D.; Funding acquisition: W.J.B., F.R.O., J.A.M., E.L.L., L.R.G.D., J.R.S.; Methodology: F.R.O., E.M.W., E.L.L., R.E.D., B.T.F., J.R.S., J.A.M., J.E.C., W.J.B., L.R.G.D.; Investigation: all authors; Visualization: F.R.O., R.E.D., E.M.W., E.L.L., M.R.W.; Project administration: E.L.L., F.R.O., W.J.B., J.E.C., G.T.T., A.B.F.; Supervision: W.J.B.; Writing – original draft: F.R.O., E.L.L., R.E.D., M.R.W.; Writing – review and editing: all authors **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data are available in the main text or the supplementary materials. Data series taken from the literature are available in cited references. All dated megafaunal specimens are curated in the La Brea Tar Pits Museum collections. **Provenance:** All but two mammal fossils carbon dated for this paper reside in the historically collected Hancock Collection at the Tar Pit Museum, Los Angeles, CA. Specimen numbers and reference numbers for each carbon date may be found in data S1. Fossils were bulk collected from each pit deposit and soaked in gasoline to remove asphalt, then labeled in white paint with pit of origin, a coarse grid reference, and a specimen number. The Hancock Collection is under one accession number, A.239. The two Pit 91 specimens are under accession number A.11177.89-1.

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abo3594
Materials and Methods
Fig. S1
Tables S1 to S4
R Code Documents 1 to 5
References (*60*–*89*)
Materials Design Analysis Reporting Checklist
Data S1 to S3

Submitted 28 January 2022; resubmitted 30 January 2023
Accepted 12 July 2023
10.1126/science.abo3594

Pre–Younger Dryas megafaunal extirpation at Rancho La Brea linked to fire-driven state shift

F. Robin OKeefe, Regan E. Dunn, Elic M. Weitzel, Michael R. Waters, Lisa N. Martinez, Wendy J. Binder, John R. Southon, Joshua E. Cohen, Julie A. Meachen, Larisa R. G. DeSantis, Matthew E. Kirby, Elena Ghezzo, Joan B. Coltrain, Benjamin T. Fuller, Aisling B. Farrell, Gary T. Takeuchi, Glen MacDonald, Edward B. Davis, and Emily L. Lindsey

Science, **381** (6659), eabo3594.
DOI: 10.1126/science.abo3594

Editor's summary

It is well known that many large vertebrate species went extinct during the late Pleistocene in most regions of the world. What caused these extinctions remains debated, although both climate change and human impacts have been implicated. O'Keefe *et al*. used the extensive fossil record created by the entrapment of animals in the La Brea tar pits in conjunction with nearby core samples and found a clear relationship between an increase in fire—and fire-related ecosystems—and large mammal extinction. The authors argue that this increase in fire may have resulted from climate change–induced warming and drying in conjunction with increasing impacts of humans in the system. —Sacha Vignieri

---

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.