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Current Biology

Causes and Consequences of Pleistocene Megafaunal Extinctions as Revealed from Rancho La Brea Mammals

Highlights

- Sabertooth cats and dire wolves were not in competition for similar prey
- Sabertooth cats scavenged more intensively during cooler intervals
- Coyote diets were substantially affected by the extinction of megafauna
- Rancho La Brea fossils reveal that diets of carnivorans are not always conserved

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In Brief

The Rancho La Brea fossils of southern California provide rare insight into the ecological effects of the terminal Pleistocene extinction event. Here, DeSantis et al. determine that canids and felids are not in competition for similar prey leading up to the extinction, and coyote diets were substantially affected by the removal of top predators.

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Causes and Consequences of Pleistocene Megafaunal Extinctions as Revealed from Rancho La Brea Mammals

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SUMMARY

The fossils preserved in the Rancho La Brea "tar" seeps in southern California span the past ~50,000 years and provide a rare opportunity to assess the ecology of predators (e.g., the American lion, sabertooth cats, cougars, dire wolves, gray wolves, and coyotes), including clarifying the causes and consequences of the terminal Pleistocene extinction event. Here, a multi-proxy approach elucidates dietary responses of carnivorans to changing climates and megafaunal extinctions. Using sample sizes that are unavailable anywhere else in the world, including hundreds of carnivoran and herbivore specimens, we clarify the paleobiology of the extinct sabertooth cats and dire wolves—overturning the idea that they heavily competed for similar prey. Canids (especially the dire wolf) consumed prey from more open environments than felids, demonstrating minimal competition for prey throughout the latest Pleistocene and largely irrespective of changing climates, including just prior to their extinction. Coyotes experienced a dramatic shift in dietary behavior toward increased carcass utilization and the consumption of forest resources (prey and/or plant resources) after the terminal Pleistocene megafaunal extinction. Extant predators' ability to effectively hunt smaller prey and/or utilize carcasses may have been a key to their survival, especially after a significant reduction in megafaunal prey resources. Collectively, these data suggest that dietary niches of carnivorans are not always static and can instead be substantially affected by the removal of top predators and abundant prey resources.

INTRODUCTION

Rancho La Brea is a late Pleistocene lagerstätte in southern California that has been excavated for over 100 years, yielding more than 3.5 million specimens representing >600 species [1]. Colloquially termed the La Brea Tar Pits, Rancho La Brea "tar"—or rather asphaltum—trapped herbivorous species whose carcasses subsequently lured and trapped carnivores and scavengers [1]. More than 90% of excavated mammal bones belong to the order Carnivora, and these specimens provide a rare opportunity to clarify the paleobiology of carnivorans over the past ~50,000 years [1, 2], an interval that included profound climate change [3], the arrival of humans [4], and megafaunal extinctions [5].

Earlier studies of Rancho La Brea's carnivorans suggested that they experienced "tough times" prior to their extinction, as indicated by a greater incidence of broken teeth in extinct taxa as compared to extant carnivorans [6]. However, more recent studies that employed dental microwear texture analysis (DMTA) suggest that broken teeth were the consequence of hunting larger prey and/or increased defensive interactions—and not indicative of increased carcass utilization [7, 8]. Specifically, the cougar (*Puma concolor*), which survived the extinction event, consumed both flesh and bones with clear evidence of scavenging [9], in stark contrast to the extinct American lion (*Panthera atrox*) that had ~30% broken canines and primarily ate tough flesh [7]; the cougar's opportunistic diet may have been key to its survival [9].

The dire wolf (*Canis dirus*), the most abundant carnivoran at La Brea [1], ranged from Canada to South America during the Pleistocene [10] before becoming extinct. However, the coyote (*Canis latrans*), a smaller canid, survived the late Pleistocene extinction event, as did gray wolves, cougars, bobcats, and other smaller carnivorans [1]. As coyotes are highly opportunistic today, eating smaller prey (e.g., rodents and lagomorphs) and also scavenging larger prey, such as deer [11, 12], their "key to success" may have been similar to the La Brea cougars. Alternatively, coyotes—in contrast to cougars—may have opportunistically altered their diet following the extinction of numerous large

Table 1. Descriptive Statistics of Stable Carbon Isotope Values from All Taxa Examined from Rancho La Brea in Southern California

Diet	Order	Taxon	N	Min. (‰)	Max. (‰)	Range (‰)	Mean (‰)	SD (‰)
Carnivorous	Carnivora	*Canis dirus*	41	−10.8	−3.9	6.9	−8.7	1.5
		Canis latrans	50	−12.9	−5.2	7.7	−10.7	1.4
		Panthera atrox	8	−13.2	−9.8	3.4	−11.7	1.0
		Puma concolor	2	−11.6	−11.3	0.3	−11.5	0.2
		Smilodon fatalis	30	−13.9	−10.2	3.7	−11.9	0.9
Herbivorous	Artiodactyla	*Bison antiquus*[a]	31	−10.3	−4.9	5.4	−6.7	1.1
		Camelops hesternus[a]	16	−10.6	−5.2	5.4	−8.4	1.8
		Capromeryx minor	1	−7.1	−7.1	–	−7.1	–
	Proboscidea	*Mammuthus columbi*	4	−8.3	−5.2	3.1	−6.8	1.7
	Perissodactyla	*Equus occidentalis*[a]	26	−10.7	−2.0	8.7	−7.5	2.0
	Pilosa	*Nothrotheriops shastensis*	2	1.4	1.9	0.5	1.7	0.4
		Paramylodon harlani	6	1.9	7.5	5.6	5.4	2.1

See also Figure S1 and Tables S1–S3. Max., maximum; Min., minimum; N, number of specimens sampled; SD, SD (n − 1). Note that all $\delta^{13}C$ values of carnivorous taxa are raw $\delta^{13}C$ values (1.3‰ was not added to these values to reflect the $\delta^{13}C$ of prey consumed per [16]; however, an enrichment of 1.3‰ between predators-prey was included via MixSIAR).
[a]Includes published $\delta^{13}C$ data from [24].

predators and prey species, only recently becoming true opportunists.

Here, we clarify mesopredator (i.e., middle-sized predators that are also preyed upon) responses to changing climates and the terminal Pleistocene extinction event—of direct relevance to assessing long-term biotic responses to the loss of apex predators and subsequent trophic cascades, today. As predators are extraordinarily rare in the fossil record (absent of asphalt-seep localities, which are also rare) [1], this multi-proxy study represents the most comprehensive dietary analysis of both carnivorous and herbivorous mammals from any fossil locality, with the aim of understanding the consequence of megafaunal extinctions on surviving predators.

Dietary Proxies

Analysis of stable carbon isotopes preserved in tooth enamel bioapatite and bone collagen reflect the $\delta^{13}C$ values of diet sources (prey and vegetation for primary and secondary consumers, respectively) minus tissue- and taxon-specific isotope trophic discrimination factors [13–16] (STAR Methods). It is therefore possible to estimate the relative contributions of different food sources to the diets of consumers. Primary consumer $\delta^{13}C_{enamel}$ values $\leq -9‰$ are reflective of the consumption of a predominantly C_3 diet (with lower values indicative of consuming C_3 vegetation in denser forests) [13, 17, 18]. In contrast, values $\geq -3‰$ indicate the consumption of a predominantly C_4 diet (with C_4 grasses and/or shrubs occurring in more open habitats) [13, 17, 18]. Secondary consumer $\delta^{13}C_{enamel}$ values are reflective of the vegetation consumed by prey, as noted above, but are deplete by 1.3‰ as compared to primary consumers [16].

DMTA can further clarify the paleobiology and dietary niches of carnivorans through three-dimensional study of microwear textures, a method that also minimizes observer biases [19, 20]. Inferring dietary behavior of carnivores, including carcass utilization, is possible using DMTA [7–9, 19–22]. In extant felids [7–9, 21, 22] and canids [8], tough flesh consumers are inferred from high anisotropy (*epLsar*) values while high-complexity (*Asfc*) values are instead indicative of the consumption of hard-food items—such as bone. Further, high textural fill volume (*Tfv*) values indicate large features and are highest in taxa known to engage in increased bone processing [7–9, 19–22].

RESULTS AND DISCUSSION

Previous isotopic analysis of bone collagen demonstrated that the sabertooth cat *Smilodon fatalis* and *C. dirus* had overlapping $\delta^{13}C$ and $\delta^{15}N$ values, which suggested that they competed for similar prey [23]. In stark contrast to this interpretation, stable carbon isotope data from tooth enamel (from the first lower molar in both felids and canids) here reveals that *C. dirus* has significantly higher mean $\delta^{13}C_{enamel}$ values than *S. fatalis* ($p < 0.0001$) and all other co-occurring predators (i.e., all felids and *C. latrans*; Tables 1 and S1) with minimal overlap throughout the latest Pleistocene (~31–11 ka; Figure 1; Tables 1 and 2). *Canis dirus* had a distinct preference for prey occupying more open environments, even more so than *C. latrans* throughout the Late Pleistocene (Table S2). Although stable isotope-mixing models using MixSIAR [25] indicate the potential for competition for some similar prey (Figure S1; Table S3), these models also clearly demonstrate that Rancho La Brea felids relied on more closed-habitat prey than did most canids (Figure 1; Table S1)—consistent with habitat interpretations based on limb morphology [26]. Further, all felids have nearly identical means and ranges of $\delta^{13}C_{enamel}$ values and *S. fatalis* consistently consumed prey occupying more closed environments (i.e., all comparisons between pits 61/67, 13, and 77 yield $p > 0.26$). Note that *S. fatalis* is indistinguishable from *Pa. atrox* (Table S1); *Pu. concolor* values are within the ranges of both *S. fatalis* and *Pa. atrox* (Figure 1; Table 1), although the small sample size of cougars prohibits statistical comparisons. Extant coyotes from Santa Barbara (CA, USA) demonstrate a notable decline in $\delta^{13}C_{enamel}$ values as compared to *C. latrans* from Rancho La Brea (collectively, and as compared to each sampled pit, including the Holocene aged pit 10; Figure 1; Table S2),

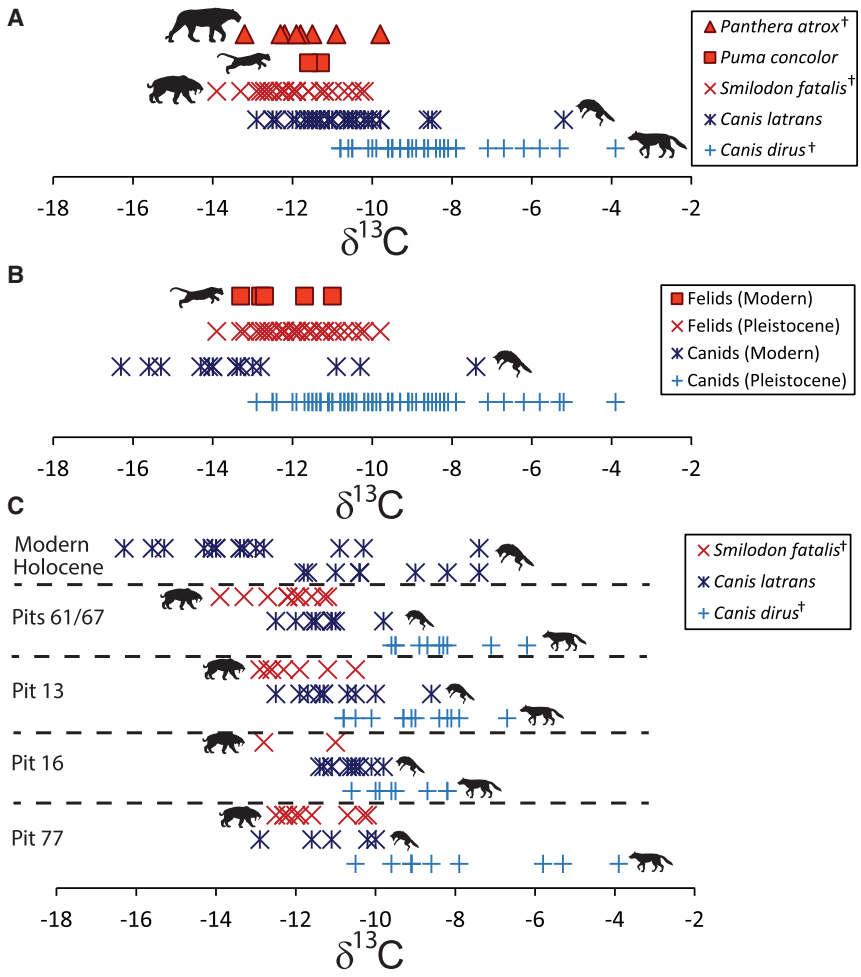

Figure 1. Stable Carbon Isotope Data of All Carnivorans Sampled from Fossil Specimens at Rancho La Brea and Modern *Canis latrans* and *Puma concolor* Specimens from Southern California

Stable carbon isotopes of all carnivorans examined at Rancho La Brea from Pleistocene deposits (A), extant canids and felids compared to Pleistocene aged canids and felids at Rancho La Brea (B), and stable carbon isotopes of the most abundant carnivorans (*Canis dirus*, *Canis latrans*, and *Smilodon fatalis*) through time in southern California (C). Predator $\delta^{13}C$ comparisons are summarized in Tables S1 and S2, with all values noted in Data S1. Note that these are all raw values and have not been corrected by +1.3‰ (per [16]) to equate to prey values; however, +1.5‰ was added to modern felid and canid values in (B) and (C) (per [13]). † denotes extinct taxa.
See also Figure S1, Tables S1–S3, and Data S1.

indicative of a shift in diet to prey from more forested C_3 environments (e.g., deer) and/or a more omnivorous diet, including C_3 plant components (e.g., fruits and seeds). Further, extant canids (represented by only *C. latrans*) demonstrate more negative $\delta^{13}C_{enamel}$ than all Pleistocene canids combined ($p < 0.0001$) and extant felids (represented by only *Pu. concolor*) are similarly indistinguishable from all Pleistocene felids combined. Today, felids are indistinguishable from canids in southern California ($p = 0.930$), and canids have more positive $\delta^{13}C_{enamel}$ values during the Pleistocene at Rancho La Brea ($p < 0.0001$). These isotopic data demonstrate a clear preference for forest resources, including forest-dwelling prey today (e.g., deer) by both *Pu. concolor* and *C. latrans* (in southern California), potentially due to the lack of other large megafauna and consistent with observational data [11, 12]. The reason for the difference between enamel and collagen $\delta^{13}C$ values for *C. dirus* and *S. fatalis* is unclear. It is possible that differences in $\delta^{13}C$ enamel and collagen values are due to ontogenetic differences in diet, with *C. dirus* consuming prey from more open environments at the time of enamel mineralization of the lower first molar and eating prey from forests during the last year of their life; however, such a dramatic shift in feeding ecology from open environments to denser vegetation is unlikely. Ongoing analyses instead demonstrate that canids have higher offsets between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$, but it is not yet clear whether these differences are due to physiological differences between canids and felids or differences in the prey consumed. Although further work is

Table 2. Summary Statistics of *Canis dirus* and *Smilodon fatalis* Stable Carbon Isotope Values from Each Pit Examined

Pit	Taxon	N	Min. (‰)	Max. (‰)	Range (‰)	Mean (‰)	SD (‰)	p Value	Overlap (‰)
61/67	*Canis dirus*	10	−9.6	−6.2	3.4	−8.4	1.1	<0.0001[a]	0
	Smilodon fatalis	11	−13.9	−11.2	2.7	−12.2	0.8		
13	*Canis dirus*	13	−10.8	−6.7	4.1	−9.1	1.2	<0.0001[a]	0.3
	Smilodon fatalis	7	−12.9	−10.5	2.4	−12	0.9		
77	*Canis dirus*	10	−10.5	−3.9	6.6	−7.9	2.2	<0.001[a]	0.3
	Smilodon fatalis	10	−12.5	−10.2	2.3	−11.6	0.9		

See also Figure S1 and Data S1. Overlap, the total isotopic overlap between the two taxa; p value, resulting p values from Student's t tests (for pit 13 and 61/67 taxonomic comparisons) and Mann-Whitney test for the pit 77 taxonomic comparison as *S. fatalis* from pit 77 had $\delta^{13}C$ values that were not normally distributed (Shapiro-Wilk); Pit, pit excavation number; Range, total range; Taxon, extinct species examined.
[a]p values are considered significant with alpha < 0.05.

Table 3. Descriptive Statistics of DMTA Attribute Values from All Carnivoran Taxa Examined from Pleistocene-Dated Pits at Rancho La Brea in Southern California

Family	Taxon	N		Min.	Max.	Range	Median	Mean	SD
Canidae	*Canis dirus*[a]	113	*Asfc*	0.831	12.213	11.382	3.565	4.097	2.363
			epLsar	0.0011	0.0059	0.0048	0.0025	0.0027	0.0010
			Tfv	4,919	18,568	13,649	12,149	12,161	2,498
	Canis latrans[a]	65	*Asfc*	0.558	3.182	2.624	1.830	1.798	0.611
			epLsar	0.0010	0.0053	0.0042	0.0026	0.0027	0.0010
			Tfv	7,111	15,271	8,160	11,574	11,607	1,875
	Canis lupus[a]	13	*Asfc*	0.865	6.563	5.698	3.033	3.142	1.860
			epLsar	0.0009	0.0052	0.0043	0.0023	0.0027	0.0012
			Tfv	8,939	14,800	5,861	12,461	12,589	1,752
Felidae	*Panthera atrox*[b]	15	*Asfc*	0.822	2.438	1.616	2.049	1.812	0.563
			epLsar	0.0017	0.0060	0.0043	0.0029	0.0033	0.0012
			Tfv	341	12,683	12,342	7,063	6,051	4,636
	Puma concolor[c]	12	*Asfc*	0.804	16.371	15.567	3.222	4.592	4.530
			epLsar	0.0009	0.0080	0.0071	0.0027	0.0035	0.0021
			Tfv	3,145	16,597	13,452	14,008	12,860	3,609
	Smilodon fatalis[b]	135	*Asfc*	0.950	8.443	7.493	3.368	3.822	1.928
			epLsar	0.0007	0.0080	0.0073	0.0026	0.0028	0.0015
			Tfv	38	18,725	18,688	10,310	9,654	4,790

See also Tables S4 and S5 and Data S1. *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume.
[a]Includes published DMTA data from [8].
[b]Includes published DMTA data from [7].
[c]Published DMTA data from [9].

needed to resolve the discrepancy between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ values, the pattern of canids (i.e., *C. dirus*) having more positive $\delta^{13}C_{enamel}$ values than felids (i.e., *S. fatalis*) persists through time at La Brea (Figure 1C; Table S2) and at sites in Florida during the Pleistocene (albeit different taxa, *Canis edwardii* and *Smilodon gracilis*) [27].

Dental microwear data of feliforms and caniforms (Tables 3 and S4–S6) [7, 8] suggest that *Pu. concolor*, *S. fatalis*, and *C. dirus* have DMTA attribute values indicative of moderate durophagy (Figure 2). The textural properties of *S. fatalis* dental microwear is highly variable over time (Figure 2D; Table S6). As ice sheets grew to their maximum extent between 33 and 26.5 ka

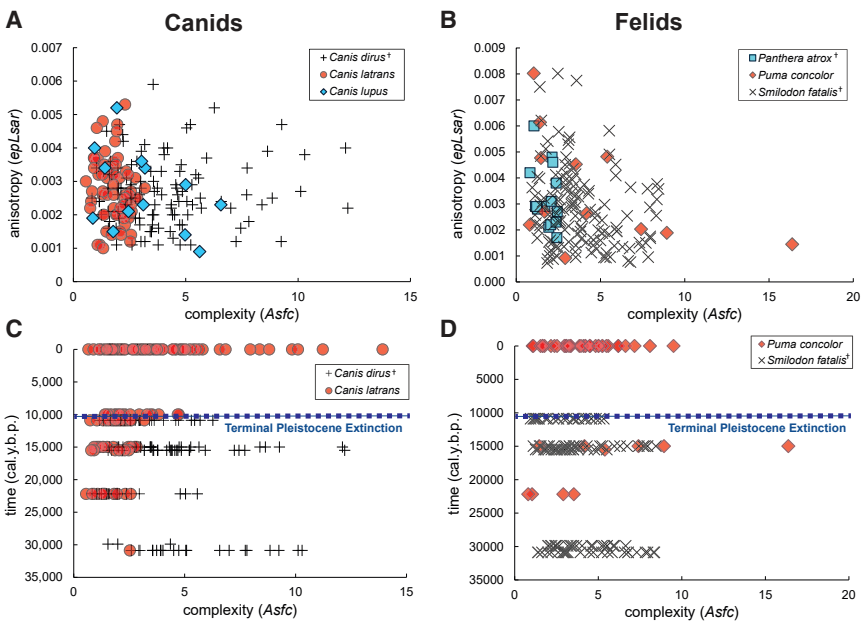

Figure 2. DMTA Attribute Values of Carnivorans at Rancho La Brea and Modern Ecosystems

(A and B) Complexity and anisotropy values of Rancho La Brea canids (A) and felids (B).

(C and D) Complexity values through time of *Canis dirus* (+) and *Canis latrans* (red circles, including modern samples from southern California and throughout the United States; C) and complexity values through time of *Smilodon fatalis* (X) and *Puma concolor* (red diamonds, including modern samples from southern California and Florida; D). † denotes extinct taxa. See also Tables S4–S10.

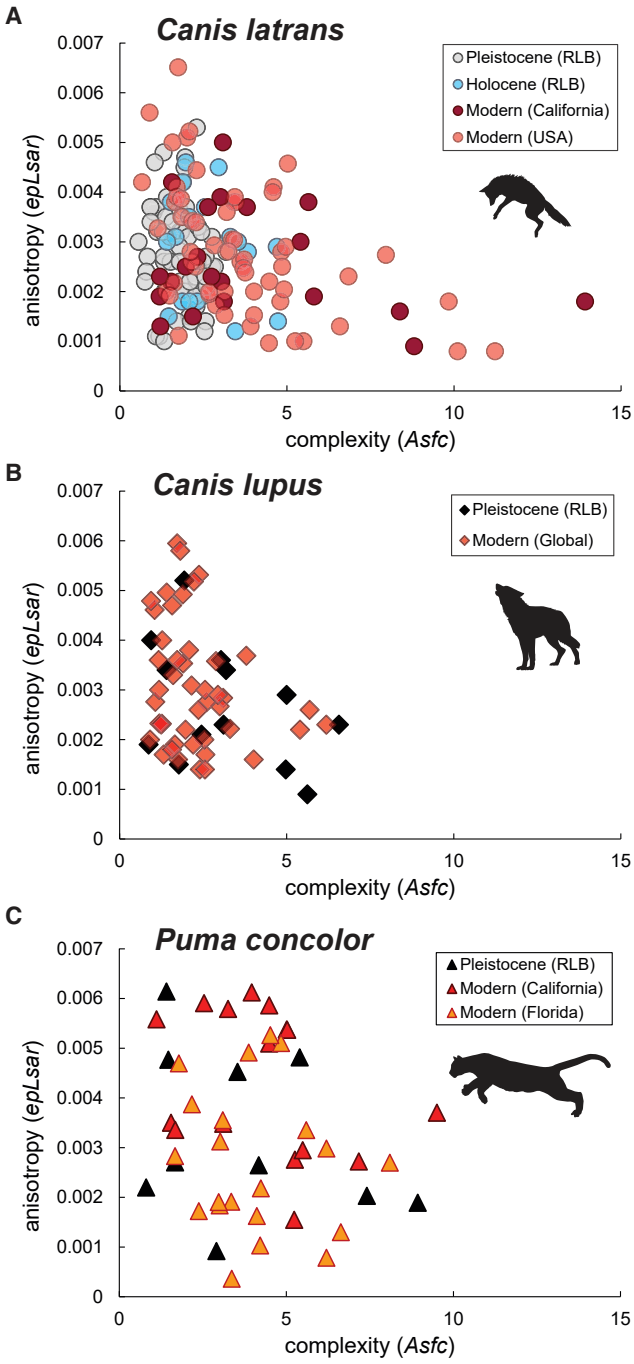

Figure 3. DMTA Attribute Values from Modern and Fossil Specimens of the Carnivorans that Survived the Terminal Pleistocene Extinction Event

Complexity and anisotropy values of *Canis latrans* (A), *Canis lupus* (B), and *Puma concolor* (C). Pleistocene Rancho La Brea (RLB) in black, Holocene Rancho La Brea in blue, and extant specimens in red and orange are shown. See also Tables S5 and S9–S11 and Data S1.

(pits 77 and 91), maintained their positions from 26.5 to 19 or 20 ka (pits 3, 13, and 16 all overlapping with this date range), and later shrank with the onset of Northern Hemisphere deglaciations (3; pits 61/67) during interglacial warming (Figure 2D), *S. fatalis* engaged in increased carcass utilization during cooler glacial periods as inferred from higher *Asfc* and *Tfv* values ($p = 0.031$ and $p = 0.013$, respectively). *C. dirus* has complexity values indistinguishable from extant African wild dogs and extant coyotes (Table S5) that are known to both take down prey and scavenge carcasses [28]. DMTA attributes of *C. dirus* fluctuate between pits yet are independent of body size fluctuation [29] and changing climates (Figure 2C; Table S7).

The extinction of top predators impacts the abundance of mesopredators (and their prey)—a phenomenon termed mesopredator release [30]. For example, the extirpation of *Canis lupus* (the gray wolf) in much of the contiguous United States has resulted in increased coyote populations, reduction of their prey, and/or the suppression of smaller bodied mesopredator populations (e.g., foxes) [30, 31]. Here, we document substantial shifts in the diet of coyotes after the extinction of numerous predators and prey at the end of the Pleistocene. Specifically, *C. latrans* exhibits lower complexity values than *C. dirus* throughout the latest Pleistocene (Figure 2C; Table S8), indicating that coyotes consistently consumed softer food items than dire wolves during the Pleistocene. Further, Pleistocene *C. latrans* specimens have significantly lower complexity values than Holocene specimens from La Brea and modern specimens (see data from *C. latrans* in southern California and *C. latrans* from throughout the USA; Figures 2 and 3; Tables S5, S9, and S10). Thus, the shift to harder foods occurs coincident with the shift to forest resources, indicative of new dietary preferences in southern California that include the scavenging of deer carcasses (as is observed today, and potentially also C_3 plant resources, 11–12). These data suggest a profound shift in coyote diets after the extinction of dire wolves (and numerous other top predators and large prey species) and following the historic extirpation of wolves from southern California. In contrast, the diets of two extant apex predators that were *Pleistocene mesopredators* (e.g., gray wolves and cougars) did not change over time (Figure 3; Table S11) [9].

It is challenging to disentangle the influence of the extinction of *C. dirus* and the extirpation of *C. lupus* on coyote diets in the past, but we gained insight by examining the dietary behavior of *C. lupus* and *C. latrans* where they co-exist in Alaska today. Whereas today *C. lupus* consumes tougher and softer foods than *C. latrans* in southern Alaska, coyotes from Alaska exhibit DMTA attribute values similar to those of coyotes in places where wolves are absent (Figures 3 and 4; Tables S11 and S12). Thus, the presence or absence of *C. lupus* likely has less of an impact on coyote diets than did the extinction of the dire wolves, numerous other large predators, and herbivorous megafauna. Although it is recognized that wolves are known to antagonize coyotes, which subsequently can result in coyotes avoiding wolves where they co-occur today [32–34], the presence of wolves can also benefit coyotes [35, 36] and facilitate year-round consumption of carrion, including increased carcass feeding in areas of high wolf use [37]. Although coyotes are fully capable of scavenging and are known to currently compete with wolves for access to carcasses [32, 35, 36], as one of the smallest members of the diverse guild of Pleistocene carnivorans [1] (despite being larger during the Pleistocene than modern coyotes) [38], *C. latrans* may not have been able to acquire and/or defend

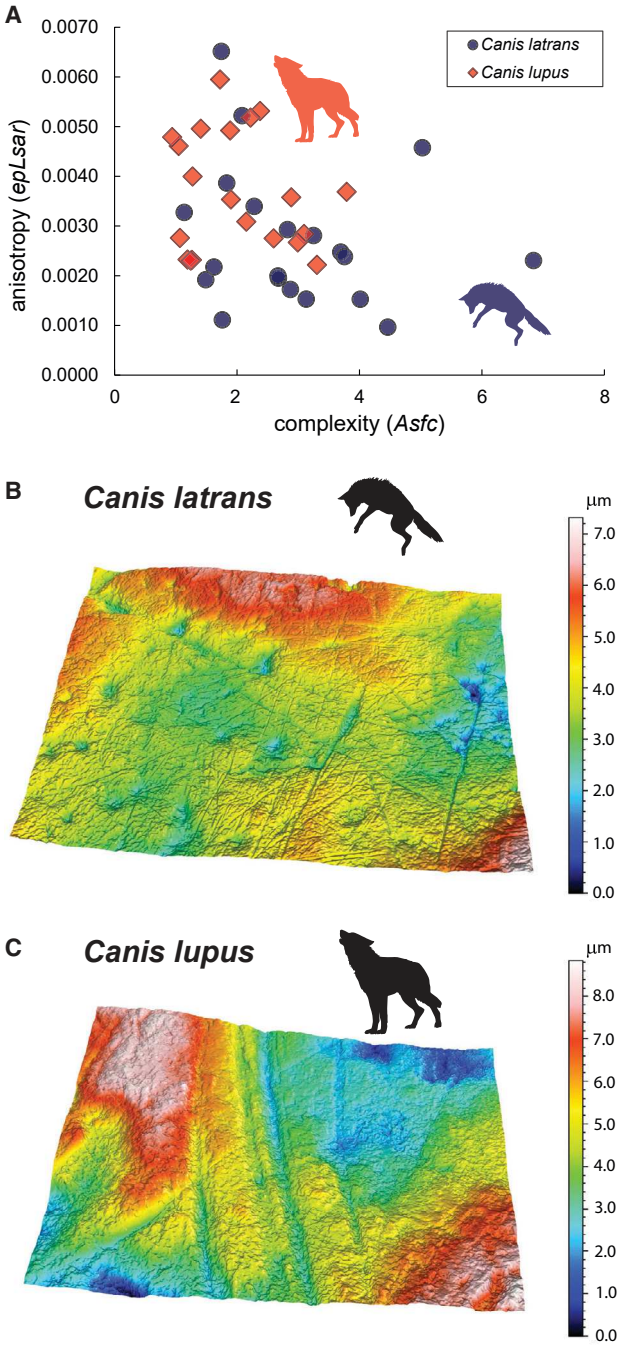

Figure 4. DMTA Attribute Values and 3D Models of Dental Microwear Features of Modern Specimens of *Canis latrans* and *Canis lupus* from Alaska

Complexity and anisotropy values of Alaskan canids from overlapping geographic ranges and collected between 1951 and 1971 (A); 3D models of dental microwear of *Canis latrans* (B; PSM 24875) and *Canis lupus* (C; PSM 24953).

See also Tables S11 and S12 and Data S1.

carcasses during the Pleistocene because of the presence of numerous competing predators. Alternatively, *C. latrans* may have had less catholic diets in the past as compared to today—consuming primarily flesh during the Late Pleistocene. The extinction of numerous large prey may have subsequently contributed to *C. latrans* engaging in increased durophagy today (even if only as a "pulsed" resource) [35]—consistent with a reduced shearing arcade and expanded grinding areas in their lower jaws and coincident with reduced body size that may be a result of reduced resource availability [38, 39].

Assessing the ubiquity of these results is challenging due to the rarity of carnivoran fossils outside of tar seeps; however, these data provide unique insights into the ecology of extant and extinct predators that would otherwise not be possible. Collectively, this multi-proxy analysis demonstrates that the Rancho La Brea felids and canids exhibited minimal competition for prey up to the time of their extinction. Most notably, coyotes exhibited profound dietary shifts following the terminal Pleistocene extinction event—indicating that the extinction of top predators and herbivorous megafauna had downstream impacts on mesopredators.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- LEAD CONTACT AND MATERIALS AVAILABILITY
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Stable isotope analyses
  - Dental microwear texture analyses
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND CODE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.06.059.

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AUTHOR CONTRIBUTIONS

L.R.G.D. designed the study; L.R.G.D. collected specimen data with help from T.E.C., A.B.F., K.F.-D., J.M.H., and G.T.T.; L.R.G.D. and R.S.F. analyzed stable isotope data; L.R.G.D. and J.M.C. analyzed DMTA data; and L.R.G.D. wrote the paper with editorial input from co-authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Stable isotope data from tooth enamel	This paper	Data S1
Dental microwear texture data	This paper	Data S1
Software and Algorithms		
ToothFrax	Surfract Corp.	http://www.surfract.com
Sfrax	Surfract Corp.	http://www.surfract.com
Markov Chain Monte Carlo simulation	MixSIAR [25]	https://githubcom/brianstock/MixSIAR; https://doi.org/10.5281/zenodo.56159

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Larisa DeSantis (larisa.desantis@vanderbilt.edu).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Faunal specimens of both fossil and modern specimens were accessed in publically accessible collections housed in the Denver Museum of Natural History (Denver, Colorado, USA), Natural History Museum of Los Angeles La Brea Tar Pits and Museum (Los Angeles, California, USA), Santa Barbara Museum of Natural History (Santa Barbara, California, USA), Slater Museum at the University of Puget Sound (Tacoma, Washington, USA), and University of Wyoming Geological Museum (Laramie, Wyoming, USA).

METHOD DETAILS

Stable isotope analyses

Geochemical bulk samples of tooth enamel were extracted from excavated faunal material from Rancho La Brea (La Brea Tar Pits and Museum, n = 238, including data from ref. 24; see Data S1 for dates associated with each pit examined) and extant *C. latrans* and *Pu. concolor* specimens from southern California (Santa Barbara Museum of Natural History, n = 20). All teeth sampled (see Data S1) were drilled with a low speed dental-style drill and carbide dental burrs. Bulk samples were taken parallel to the growth axis of the tooth. All enamel powder was pretreated with 30% hydrogen peroxide for 24 hours and 0.1 N acetic acid for 12 hours to remove organics and secondary carbonates, respectively [27, 40]. Approximately 1 mg of these samples were then run on a VG Prism stable isotope ratio mass spectrometer with an in-line ISOCARB automatic sampler in the Department of Geological Sciences at the University of Florida or the Department of Geology and Geophysics at the University of Utah. The analytical precision is ± 0.1‰, based on replicate analyses of samples and standards (NBS-19). Stable isotope data were normalized to NBS-19 and are reported in conventional delta (δ) notation for carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$), where $\delta^{13}C$ (parts per mil, ‰) = $((R_{sample}/R_{standard})-1)*1000$, and $R = {}^{13}C/{}^{12}C$; and, $\delta^{18}O$ (parts per mil, ‰) = $((R_{sample}/R_{standard})-1)*1000$, and $R = {}^{18}O/{}^{16}O$; and the standard is VPDB (Pee Dee Belemnite, Vienna Convention [41]. All stable isotopes (carbon and oxygen) are from the carbonate portion of tooth enamel hydroxylapatite.

Dental microwear texture analyses

Dental microwear replicas of all extant and fossil taxa (n = 648; see Data S1), including previously published data from refs [7–9, 22].) were prepared by molding and casting using polyvinylsiloxane dental impression material and Epotek 301 epoxy resin and hardener, respectively. Dental microwear texture analysis (DMTA) using white-light confocal profilometry and scale-sensitive fractal analysis (SSFA), was performed on all replicas of lower first molars (in felids) and lower second molars (in canids) that preserved ante-mortem microwear similar to prior studies [7–9, 22]. While some dental microwear studies have only examined the homologous lower m1 facet on all carnivorans (including felids and canids) [42], these facets do not record durophagous behavior in canids [43]—as lower m1 sheering facets and lower m2 crushing facets have different forms and functions [20].

All specimens were scanned in three dimensions in 9 areas (in a 3x3 grid), subsequently stitched together, leveled, and then subdivided into four adjacent areas of equal size (102 × 138 μm^2) for a total sampled area of 204 × 276 μm^2, identical sized areas as previously published DMTA data [7–9, 21]. The measured neighbor algorithm was applied to all areas on the scan where no data were collected, this is typically due to steep surfaces and approximately < 2% of a given surface, and resulting surface files (.sur) were created. The majority of specimens were scanned on a Sensofar *PLu neox* optical profiler at Vanderbilt University (n = 510).

Although some previously published data were analyzed on a white-light confocal microscope at the University of Arkansas (n = 138) [7–9, 21], these confocal microscopes yield DMTA data statistically indistinguishable from one another [44]. All scans were analyzed using SSFA software (ToothFrax and SFrax, Surfract Corp., http://www.surfract.com) to characterize tooth surfaces according to the variables of anisotropy (*epLsar*), complexity (*Asfc*), and textural fill volume (*Tfv*) [20, 45–47]. Complexity is the change in surface roughness with scale and used to distinguish taxa that consume hard, brittle foods (such as bone in carnivorous animals) from those that eat softer ones [7, 8, 20, 22, 45–47]. Anisotropy is the degree to which surfaces show a preferred orientation, such as the dominance of parallel striations having more anisotropic surfaces (as can occur in those eating primarily tough foods—including flesh) [7, 8, 20, 22, 45–47]. Textural fill volume measures the volume filled by large (10 μm diameter) and small (2 μm diameter) square cuboids, with high *Tfv* values indicating potentially deeper and/or larger features [7–9, 22, 47].

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses follow the same methods of *a priori* geochemical and DMTA analysis [7, 22, 27]. Specifically, all carbon isotope values were analyzed using ANOVA and post hoc Tukey HSD multiple comparisons, Student's t tests (for comparisons between two normally distributed samples), and other non-parametric alternatives when appropriate (Mann-Whitney tests and Kruskal-Wallis tests and Dunn's procedure for multiple comparisons) [48]. When comparing modern and fossil specimens of *C. latrans*, 1.5‰ was first added to all $\delta^{13}C$ values of modern specimens (per ref. 13). Pit ages are uncalibrated radiocarbon years before present (standard deviations noted in parentheses in Data S1), all ages are uncalibrated dates taken from ref. 2, with the exception of Pit 9 dates which are uncalibrated and taken from ref [49]. All statistical comparisons are noted in relevant supplemental tables.

Proportions of prey in predator diets were calculated using MixSIAR, a Bayesian isotopic mixing model [25]. An assumption for this model is that the $\delta^{13}C$ values from the prey groupings represent the sources from which the predators sampled. To identify sources, prey taxa from Rancho La Brea were compared using ANOVA and post hoc Tukey HSD tests, with significance set at $p < 0.05$. Taxa that were not statistically different from one another were combined into a single source. Three source groups were identified in this manner including (from highest to lowest mean $\delta^{13}C$ value): *Paramylodon harlani* and *Nothrotheriops shastensis*; *Bison antiquus*, *Capromeryx* sp., *Equus occidentalis* and *Camelops hesternus*; and, *Odocoileus* sp. and *Tapirus* sp. MixSIAR uses a Markov Chain Monte Carlo simulation to model the proportions of sources in a consumer's diet on the basis of the isotopic values of the prey sources and predators [25]. MixSIAR also incorporates the uncertainty in the isotopic trophic enrichment factor (i.e., discrimination factor) between the prey sources and the predators in the model. The trophic enrichment factor used ($-1.3‰ \pm 0.2‰$) was based on the discrimination factor between predator and prey bioapatite from previous studies [16]. Because of some uncertainty regarding the reliability of sloth isotope values (as their teeth are composed of dentin and lack enamel and thus more prone to diagenetic alteration) [50], besides the three source model, we ran an additional iteration of the model, a two source model where sloth taxa were not included. We confirmed model convergence using the MixSIAR diagnostics (e.g., Gelman-Rubin and Geweke tests) for each of the three model iterations. The mean and median proportions as well as the 95% credible interval are used to compare the contributions of the different sources for the predator species. Although the source proportions for a specific taxon change among the models, the overall pattern among predators among the two models is similar. Overall, the Bayesian model provided by MixSIAR provides a better understanding of the proportion of prey sources included in the diet of each predator (Figure S1; Table S3).

We were unable to isotopically sample tapirs from Rancho La Brea due to the limited fossils available (i.e., three individual elements, in the Hancock Collection, one jaw with teeth, and 2 phalanges from the University of California Museum of Paleontology pit 2051) and the small number of deer (likely mule deer, *cf. Odocoileus hemionus*) specimens available. Tapirs have limited carbon isotopic variability of only $-14.3‰$ to $-10.1‰$, spanning ~10 million years [51], with average values from two Pleistocene localities in Florida of $-12.7‰$ and $-12.8‰$ (from Leisey Shell Pit 1A and Inglis 1A, respectively) [52]. While the $\delta^{13}C$ values of deer can vary depending on their presence during glacial or interglacial periods, as seen in Florida [52], the values of white-tailed deer (*Odocoileus virginianus*) in Florida average $-12.8‰$ and one sample from the Pleistocene Fairmead locality in California is $-12.5‰$ [53]. Thus, we used $-12.7‰$ as the average isotopic value of C_3 browsers (with a range of $-15.3‰$ to $-10‰$, the total range of deer and tapir values spanning a glacial and interglacial site in Florida) [52]. Comparable isotopic data for tapirs and deer, beyond Fairmead (one deer sample), are not available from Pleistocene fossil sites in California.

Dental microwear texture analysis variables are not normally distributed (Shapiro-Wilk tests, $p > 0.05$ for DMTA variables for certain taxa); therefore, we used non-parametric statistical tests (Kruskal-Wallis) to compare differences among all taxa. Further, we used Dunn's procedure [48] to conduct multiple comparisons (between extant and/or extinct taxa) absent of the Bonferroni correction. As the Bonferroni correction is meant to reduce the likelihood of false positives (Type I errors) by taking into consideration the number of comparisons being made, it also increases the probability of false negatives (Type II errors) [54, 55]. Furthermore, we do not want the number of extant and/or extinct comparisons to affect statistical differences between taxa; thus, the Bonferroni correction is not appropriate for our comparisons.

DATA AND CODE AVAILABILITY

All data are available in Data S1 and Tables S1–S12.