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Dietary fidelity of Miocene ungulates in the context of environmental change in the Mojave Region, western North America

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ABSTRACT

The fossil record of mammals preserves evidence for dietary adaptations that allowed lineages to persist in dynamic ecosystems for tens of millions of years. We investigated ecological attributes of fossil mammals during the middle to late Miocene (17.5–8.5 Ma) in the western Mojave region of North America to evaluate the response of herbivorous ungulates to paleoenvironmental changes. Herbivores may utilize the same food resources across generations, relying on relationships with vegetation and habitats established over multiple generations. We employed stable isotopes of carbon and oxygen from ancient soils and herbivore tooth enamel to evaluate changes in vegetation and herbivore diets. We compiled isotopic data from published studies of three sequences from the warm Miocene Climatic Optimum and added new data from the Dove Spring Formation, which formed during the cooler Middle Miocene Climatic Transition. Herbivorous ungulates exhibited dietary fidelity for nearly nine million years, selectively consuming C_3 plants even as C_4 vegetation became more prevalent on the landscape. High oxygen stable isotope ratios in comparison to equids suggest that ancestral antilocaprids and camelids were likely facultative drinkers. These findings reveal enduring dietary preferences that enabled these herbivores to persist amid the profound environmental transitions of the Miocene.

1. Introduction

The survival strategies of ancient herbivorous mammals enabled them to endure environmental changes across long intervals of geologic time (Shotwell, 1961; Janis, 1993; Figueirido et al., 2012). Herbivorous mammals often exhibit dietary fidelity, meaning they maintain consistent feeding habits aligned with the availability of specific plant resources, even when the resources undergo major changes (Walker et al., 2023). Dependence on familiarity with vegetation and water resources is well documented in modern ungulates (hoofed mammals, including the even-toed artiodactyls and odd-toed perissodactyls) that occupy or return to the same locations to bear young and find predictable resources (Gunn and Miller, 1986; Switzer, 1993; Garfelt-Paulsen et al., 2021; Stoner et al., 2021). These patterns of interaction between herbivores and their environments extend beyond the lifetimes of individuals to populations, and may have deeper roots in the fossil record of ancient mammalian species (Miller, 2011; Miller et al., 2016). We used stable isotope analysis to investigate the relationship between fossil ungulates, vegetation change, and dietary fidelity in the Mojave region of North America. These insights from the fossil record allow a deeper understanding of the ecological needs of modern species in response to the rapidly shifting environments of today and the future (Maguire et al., 2015; Pringle et al., 2023; Walker et al., 2023).

Floral and faunal fossil assemblages throughout North America document the middle to late Miocene (ca. 15.97–5.33 Ma) expansion of open-canopy habitats and C_4 grasslands, providing insight into regime shifts of regional ecosystems over geologic time scales (Axelrod, 1985; Walker, 1992; Retallack, 2001; Janis et al., 2002). Although the Mojave region of southern California is now a desert with sparse vegetation, diverse plant and animal assemblages were supported by a wetter moisture regime during the Miocene (Smiley et al., 2018; Loughney et al., 2019; Steinthorsdottir et al., 2021). Ungulates in the fossil

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sequences of the Mojave had higher species richness than modern communities and exhibit physiological adaptations (such as hypsodont dentition or increased cursoriality) to the emergent grassland habitats (Cerling and Harris, 1999; Clementz and Koch, 2001; Perez-Barberia and Gordon, 2001; Schoeninger et al., 2002; Kohn, 2010; Kaiser et al., 2013). The dynamic tectonic history of the Mojave region (Fig. 1) generated mountain ranges and extensional basins that facilitated changes in the region's climate and vegetation. The resulting complex topography generated temperature, moisture, and vegetation gradients that led to a heterogeneous distribution of habitats available to terrestrial mammals (Finarelli and Badgley, 2010; Badgley et al., 2014).

Higher than modern temperatures occurred during the Miocene Climatic Optimum (16.9–14.7 Ma), followed by a period of global cooling known as the Middle Miocene Climatic Transition (beginning ca. 14.7 ma) (Steinthorsdottir et al., 2021; Heusser et al., 2022). Evidence from phytoliths, carbon isotopes of soil organic matter, and paleosol geochemistry suggest that the Mojave's climate became more arid during these intervals compared to preceding conditions, contributing to the emergence of C_4 grasses and the spread of open-canopy habitats in the region (Smiley et al., 2018; Loughney et al., 2019). A widespread increase in the proportion of grasslands is thought to have been a limiting factor for Miocene ungulates that exhibited a strong reliance on C_3 plants, but many North American lineages persisted for millions of years despite significant changes in climate and vegetation (Janis et al., 2000; Maguire, 2015). Herbivores often exhibit dietary specializations with a focus on consuming grasses (grazers) or the leaves of woody plants (browsers), but flexibility in feeding strategy and physiology would have allowed some taxa to feed on a variety of grasses and leaves in response to the replacement of forest habitat by woodlands and grasslands (Janis et al., 2000; Janis, 2003). However, modern ungulates exhibit preferences for either C_3 or C_4 plants when both vegetation types are available in a particular habitat (Tieszen et al., 1979; Ambrose and DeNiro, 1986; Ehleringer and Monson, 1993).

We evaluated changes in vegetation and the dietary ecology of large mammalian herbivores (>5 kg) during periods of significant change in climate and topography in the western Mojave region from 17.1 Ma to 8.5 Ma using a compilation of new and published stable carbon and oxygen isotope data from fossil tooth enamel (n = 296) and paleosol sources (n = 178). Published data come from the Barstow (19.3–13.3 Ma), Cajon Valley (18.0–12.7 Ma), Crowder (17.5–7.1 Ma), and Dove Spring formations (12.5–8.5 Ma) (Feranec and Pagnac, 2013; Bowman et al., 2017; Smiley et al., 2018; Loughney et al., 2019). These formations are recognized for their rich mammalian fossil assemblages, robust age control via radiometric and paleomagnetic dating methods, and well-resolved stratigraphy that constrains fossil horizons to distinct lithological units. We report new stable isotopic results from mammalian tooth enamel (n = 156) and paleosol carbonates (n = 56; Fig. 1; Tables S1 and S2) of the Dove Spring Formation as well as temporal context for published samples (Tables S3-S6).

Stable isotopes of carbon and oxygen preserved in mammalian enamel represent snapshots of the vegetation consumed by individuals during their first year of life, while isotopes from ancient soils represent vegetation on the landscape over periods of hundreds to thousands of years (Cerling and Quade, 1993; Cerling et al., 1993; Behrensmeyer et al., 2007). Fossil assemblages of herbivores that adhere to a specific diet should exhibit persistent mean and variation in enamel isotopic values that are independent of changes in paleosol values. Such a pattern would indicate that herbivores consistently select plants for consumption despite potential changes in local vegetation composition or structure (Latorre et al., 1997; Pagani et al., 1999; Behrensmeyer et al.,

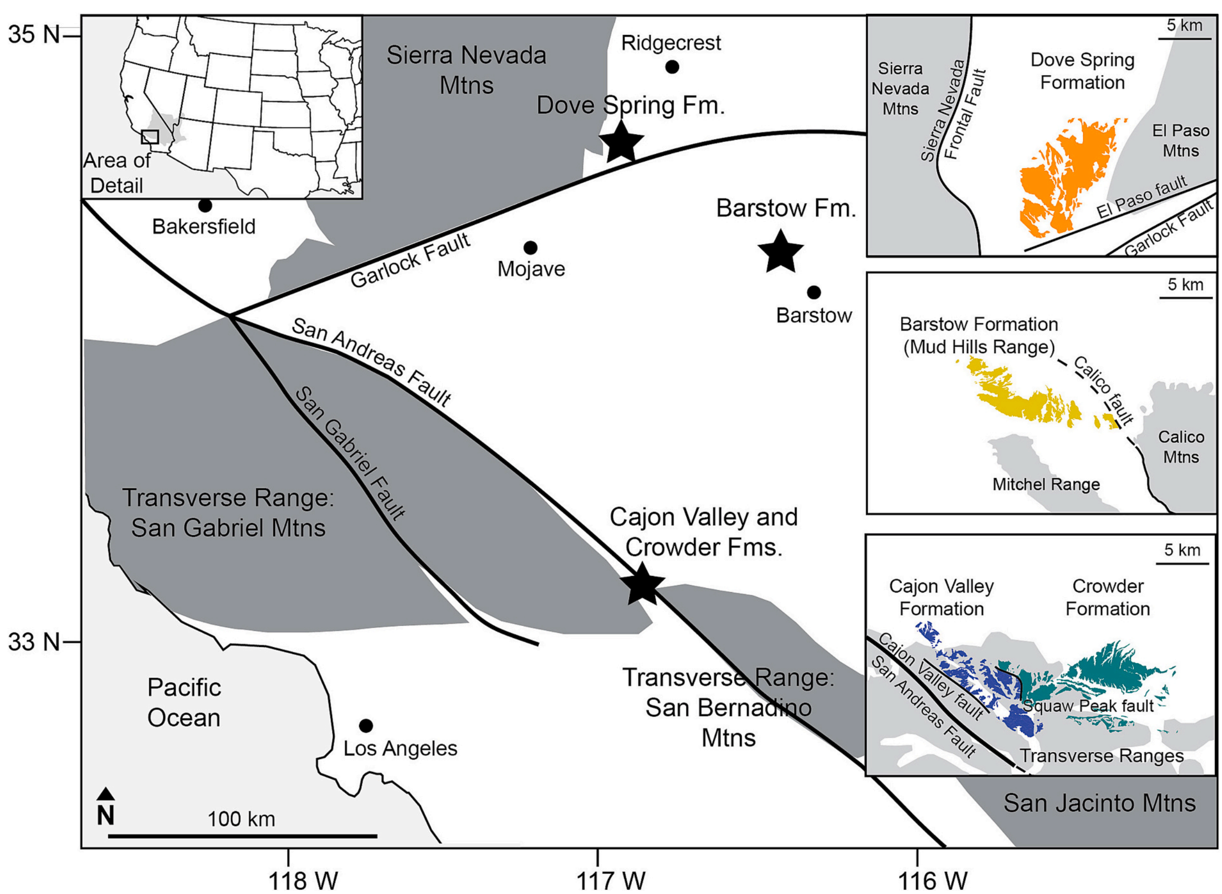

Fig. 1. Area map of the western Mojave region, illustrating the locations of four middle to late Miocene basins. Major faults and mountain ranges are provided for geographic and structural context.

2007). (1) We used carbon stable isotope data from ancient soil carbonates to determine the proportions of C_3 and C_4 plants on the landscape and whether changes in dominant vegetation type occurred. (2) We analyzed carbon stable isotope data from herbivore enamel to infer the diets of species from three ungulate families (Antilocapridae, Camelidae, and Equidae) that are well represented in each basin sequence. (3) We evaluated whether herbivore diets followed the regional trend of $\delta^{13}C$ values in vegetation, as evident from paleosol data. (4) We utilized oxygen stable isotopes to assess whether some artiodactyls maintained hydration by obtaining moisture from the plants in their diet (facultative drinking), or drank from meteoric water sources (obligate drinking) in response to changes in the local moisture regime. We hypothesized that if C_4 grasses were readily available in landscapes of the western Mojave during the middle to late Miocene, then herbivores that consumed diets with a substantial component of grass would incorporate this novel food resource. A high proportion of C_4 grasses in herbivore diets would result in higher $\delta^{13}C$ values for those lineages. Our paired analyses of paleosol and herbivore records of vegetation provide insight into the dietary fidelity of ungulates during a period of environmental changes spanning nine million years.

1.1. Mojave landscape and faunal history

The Mojave region contains numerous fossiliferous basins that span much of the Miocene (ca. 23–5 Ma), including the four basins featured here. Regional tectonic extension was the primary driver of basin expansion as the Mojave increased in area, and the basins have all been shifted westward from their original positions (Dokka, 1986; Loomis and Burbank, 1988; Bahadori et al., 2018; Loughney and Smiley, 2019a). High elevations in the Sierra Nevada Mountains have been present since at least 16.0 Ma, projecting a rain shadow that has been documented in fossil localities throughout the Basin and Range (Poage and Chamberlain, 2002; Crowley et al., 2008). Local variations in tectonic setting and drainage among the four basins also led to notable differences in ancient environments, which are reconstructed using paleoenvironmental indicators preserved in their sediments (Loomis and Burbank, 1988; Loughney and Badgley, 2017; Smiley et al., 2018). The three older basin sequences (Barstow, Cajon Valley, and Crowder formations) contain soil organic matter, biomarkers, and plant microfossils known as phytoliths (Smiley et al., 2018; Loughney et al., 2019). These datasets provide insight into the dominant vegetation composition during soil formation and the distribution of open and closed canopy habitats (Koch, 1998; Strömberg et al., 2018). The younger Dove Spring Formation contains paleosols that preserve information about the photosynthetic pathways of ancient vegetation (Whistler and Burbank, 1992).

In the Barstow Formation, rapid extension at 17 Ma contributed to a shift from a playa lake with colluvial basin margins to a fluvial landscape that supported riparian habitats by 16 Ma (Loughney et al., 2019). The cooling temperatures of the Middle Miocene Climatic Transition coincided with the appearance of wooded-grassland habitats between 14.0 and 13.8 Ma, based on phytolith and soil organic matter (Loughney et al., 2019). By 13.6 Ma, increasingly arid conditions promoted the development of spatially heterogeneous open-canopy vegetation with C_4 grasses based on phytolith data and carbon isotopes of soil organic matter (Loughney et al., 2019). An increase in fire activity was also indicated by a substantial increase in the concentration of charcoal particles through the sequence (Loughney et al., 2023). The earliest evidence of herbivore C_4 consumption in the Mojave region comes from an equid tooth dating to ca. 15.7 Ma, while paleosol records in soil organic matter, biomarkers, and phytolith assemblages indicate the presence of C_4 vegetation by approximately 15.4 Ma (Feranec and Pagnac, 2013; Loughney et al., 2019).

Barstow depositional environments were a strong control on preservation and fossil productivity, which increased as the basin grew over time (Loughney and Badgley, 2017). The rich fossil assemblages of the Barstow Formation contain numerous taxa that are used for biostratigraphic correlation throughout North America (Woodburne et al., 1990; Pagnac, 2009). The formation contains at least 63 species of large mammals, including ungulates in the families Antilocapridae (pronghorn), Camelidae (camels), Equidae (horse), Paleomerycidae (giraffe-like ruminants), Rhinocerotidae (rhinoceros), and Tayassuidae (peccaries) (Woodburne et al., 1990; Pagnac, 2009; Loughney and Smiley, 2019a). Carnivores include Canidae (wolves and dogs), Felidae (cats) and Ursidae (bears), with the first appearance of the ursid *Plithocyon* ca. 16.0 Ma defining the base of the Barstovian North American Land Mammal Age (Woodburne et al., 1990; Pagnac, 2009). Proboscideans (mastodons and gomphotheres) were present after 14.8 Ma, nearly two million years after their first appearance in the Great Basin ca. 16.5 Ma (Prothero and Hopkins, 2008; Pagnac, 2009). Coinciding with the establishment of riparian habitats as the basin expanded ca. 16 Ma, the number of equid and antilocaprid species increased until a peak at about 15 Ma (Woodburne et al., 1990; Loughney and Badgley, 2020). Total species richness in the Barstow Formation began to decrease significantly by 14.0 Ma, as wooded grasslands became the dominant form of vegetation (Loughney and Badgley, 2017; Loughney, 2018).

The contemporaneous Crowder and Cajon Valley formations were deposited in broad (20–35 km wide), low relief basins with landscapes dominated by braided channels and floodplains (Loughney and Smiley, 2019). These formations were geographically isolated during most of their depositional history but were juxtaposed by movement along the Squaw Peak thrust fault at approximately 9 Ma (Meisling and Weldon, 1989). Middle Miocene conditions in these basins supported forested ecosystems, based on the phytolith assemblages, $\delta^{13}C$ of soil organic matter ($\delta^{13}C_{SOM}$), and the presence of lignite deposits (Smiley et al., 2018; Loughney and Smiley, 2019). Both basins shifted from systems dominated by large channels to floodplains by 16 Ma and vegetation changed to woodland and shrubland in both basins, paralleling global cooling trends and regional aridification (Smiley et al., 2018; Loughney and Smiley, 2019, a). The Cajon Valley Formation contains soil organic matter with the isotopic signature of C_4 vegetation at 15.8 Ma (Smiley et al., 2018). Phytolith assemblages from the Crowder Formation exhibited 65–86 % proportion of grass morphotypes, indicating a greater proportion of open-canopy habitats than the Cajon Valley Formation by 16 Ma (Smiley et al., 2018). Together with phytolith records, fossil plant impressions indicate that the floral assemblages of the Barstow, Cajon Valley, and Crowder formations contained palms, woody dicots, and C_3 and C_4 grasses (Smiley et al., 2018).

The Crowder and Cajon Valley Formations exhibit lower species richness than that of the Barstow Formation, with 11 and 14 species of large mammals, respectively (Smiley et al., 2018). Due to the steepness of outcrops and small exposure area, the majority of specimens were recovered through screenwashing massive amounts of sediments during road excavations (Reynolds et al., 2008; Smiley et al., 2018). As a result, large mammals are under-sampled in these formations and cannot be realistically compared to the faunal assemblages of the Barstow and Dove Spring Formations.

Deposition in the Dove Spring Formation began at 12.5 Ma, shortly after the rate of regional extension diminished (Loomis and Burbank, 1988; Loughney et al., 2021). The nearby El Paso Mountains to the east were the source of water and sediments to the basin until ca. 10.5 Ma, when the basin underwent rotation and translation along the Garlock fault (Fig. 1) (Loomis and Burbank, 1988). This shearing episode interrupted drainage channels and increased sediment accumulation rates within the basin as floodplain habitats expanded (Loomis and Burbank, 1988; Gawthorpe and Leeder, 2000; Hardy and Badgley, 2023). Extension resumed around 9.5 Ma, as new drainages transported water and sediments from the Sierra Nevada Mountains on the western side of the El Paso Basin (Loomis and Burbank, 1988). The Dove Spring Formation has been interpreted as having pure C_3 vegetation based on prior isotopic analysis of mammalian herbivore tooth enamel and a sparse plant record that includes silicified grass stems and tree stumps (Whistler et al., 2009; Bowman et al., 2017; Liddy et al., 2018).

The Dove Spring Formation contains at least 44 species of large mammals, including most of the families found in the Barstow Formation, except for Paleomerycidae and Ursidae (Whistler et al., 2009). Total species richness in the Dove Spring Formation fluctuated between 15 and 40 species during 200 kyr intervals, peaking in the middle of the sequence and exhibiting significant change in species-level faunal composition at 10.5 Ma (Hardy and Badgley, 2023). Although changes in species richness appear to have been driven in part by landscape changes related to tectonic episodes, several peaks in preservation rate do not correspond to an increase in the number of localities, specimens, or sediment accumulation rate, suggesting that some faunal changes were caused by preservational biases (Hardy and Badgley, 2023). The first local appearances of several species of antilocaprids, camelids, and carnivores coincided with the shearing tectonic episode that changed the direction and source of drainages at 10.5 Ma (Hardy and Badgley, 2023). These findings were among the motivations for this study, so that we could investigate whether changes in faunal composition coincided with variation in dietary ecology.

Significant faunal turnover occurred in both the Barstow and Dove Spring Formations, but an average of 13 ungulate species were present during any half-million-year interval. This level of ungulate diversity was common during the Miocene, whereas most modern North American ecosystems host only four to six species (Janis et al., 2000). Such high species richness is now observed only in the savanna habitats of Africa, where more than 20 species of ungulates coexist (Janis et al., 2000). Continuity in faunas that included so many large-bodied ungulates throughout the Mojave indicates the presence of habitats and resources that supported similarly diverse communities over geologic time (Table S7). Modern ecosystems with high mammal species richness and redundancy of organismal traits are more resilient to disturbances to climate and nutrient availability, both of which are characteristic of the middle to late Miocene (Holling, 1973; Johnson et al., 1996; Gunderson, 2000; Steinthorsdottir et al., 2021).

1.2. Stable isotopes

Ungulate teeth are common fossils and are useful for studies of paleoecology due to mineral composition that incorporates the carbon isotopic signal of ingested diet (Cerling and Harris, 1999; Passey, 2017). The teeth of Antilocapridae (pronghorns), Camelidae (camels), and Equidae (horses) are readily identifiable to the family, genus, or species level and provide a long isotopic record for ungulates of the western Mojave. Ungulate tooth enamel exhibits a consistent enrichment in $\delta^{13}C$ values of approximately +14.0 ‰ relative to diet due to biological fractionation, with some variability among individuals from the same population (Cerling and Harris, 1999; Passey et al., 2002). Factoring in changes in the atmospheric composition of the middle to late Miocene and the fractionation relative to diet of carbon isotopes in tooth enamel, herbivores that lived during this interval and consumed a diet consisting exclusively of C_3 plants would have had a $\delta^{13}C$ value of −8.0 ‰ or less, while individuals consuming an entirely C_4 diet would have $\delta^{13}C$ values of +2.0 ‰ or higher (Cerling and Harris, 1999; Passey et al., 2002; Feranec and Pagnac, 2013). Individuals with values between −8.0 ‰ and + 2.0 ‰ would have consumed a mixed diet of C_3 and C_4 plants. Oxygen isotopes are influenced by the hydrologic cycle and are used as indicators of past temperature and moisture conditions (Duplessy et al., 1970; Hays and Grossman, 1991; Bryant et al., 1994; Blumenthal et al., 2017). Enamel $\delta^{18}O$ values are fractionated relative to ocean water by a series of well-documented physical factors including temperature and annual precipitation (Dansgaard, 1964; Rozanski et al., 1992; Schoeninger et al., 2002; Minnich et al., 2007; Tian et al., 2018). The isotopic signal of a rain shadow east of the Sierra Nevada Mountains results in $\delta^{18}O$ values lower by approximately 6.0 ‰ relative to those found west of the range (Crowley et al., 2008). A summer-dry/winter-wet Mediterranean climate in southern coastal California is inferred from the benthic foraminifera isotopic record of the nearby marine Monterey Formation and supported by fossil pollen analyses (Flower and Kennett, 1993; Heusser et al., 2022).

Animals can be classified either as obligate or facultative drinkers, based on their patterns of water intake (Kihwele et al., 2020). Obligate drinkers ingest water directly from sources within their habitats, such as streams or ponds, while facultative drinkers obtain water from the food they consume, such as leaves and fruit (Kohn, 1996; Levin et al., 2006; Reid et al., 2019). Most ungulates are obligate drinkers that whose enamel $\delta^{18}O$ values closely track the $\delta^{18}O$ values of drinking water and provide a record of climatic conditions that affected the isotopic composition of meteoric water (Dansgaard, 1964; Rozanski et al., 1992). Obligate drinkers, such as equids, have $\delta^{18}O$ values that follow local or regional trends, but some artiodactyls are facultative drinkers when in arid habitats (Kohn, 1996; Tutken et al., 2013). The sensitivity of leaf water ^{18}O composition to evaporation yields higher values within the plant tissue relative to atmospheric and soil water (Levin et al., 2006; Barbour, 2007). Facultative drinkers in turn exhibit higher $\delta^{18}O$ values relative to atmospheric values due to their consumption of ^{18}O-enriched plant tissues in environments where evaporation is high (Kohn, 1996; Levin et al., 2006; Tutken et al., 2013). This phenomenon is observed in modern antilocaprids and camelids (Gauthier-Pilters, 1971; Rivals and Semprebon, 2006; Semprebon and Rivals, 2010; Yann et al., 2013; Fraser et al., 2021). If some Miocene artiodactyls were also facultative drinkers, then their enamel should exhibit greater $\delta^{18}O$ values relative to those of equids during time intervals when evaporation was high.

While herbivore teeth provide information about the plants they consumed, the animals are mobile and consume resources throughout their home range. In-situ isotopic records such as ancient soil data provide context for interpretations of basin-scale climate and vegetation. Soil organic matter preserves the $\delta^{13}C$ signal of vegetation and allows for interpretations of the relative abundance of C_3 and C_4 plants in point locations on the landscape (Koch, 1998). Nodular carbonates from paleosols also have demonstrated utility in studies of paleovegetation (Quade and Cerling, 1995; Behrensmeyer et al., 2007; Levin et al., 2011; Du et al., 2019). Soil carbonates precipitate in isotopic equilibrium with the surrounding soil, capturing the isotopic composition of local vegetation over time (Cerling, 1992; Koch et al., 1992; Levin et al., 2011). Fractionation due to the diffusion of CO_2 and the precipitation of calcite yields an enrichment factor of +14–15 ‰ relative to plant-derived CO_2, allowing for near-direct comparison with herbivore tooth enamel (Cerling et al., 1997; Koch et al., 1997; Quade et al., 2013).

2. Methods

We were granted access by the Natural History Museum of Los Angeles County (NHM) to collect samples of enamel powder from 153 teeth belonging to the Antilocapridae, Camelidae, and Equidae from the fossil assemblages of the Dove Spring Formation. The buccal and lingual surfaces of selected teeth exhibited minimal macroscopic wear. These relatively unworn surfaces preserve primary enamel, reducing the likelihood of diagenetic alteration. By targeting bulk enamel rather than serial microsampling, we reduce the likelihood of seasonal bias. This approach ensures that the isotopic signal reflects long-term dietary trends rather than being skewed toward a specific season of mineralization. We resampled 16 teeth that were previously reported by Bowman et al. (2017) and found that our results were consistent with their reported values. We drilled each tooth for at least 5 mg of enamel powder, with some larger specimens yielding more material. At the University of Michigan, we treated each powder sample according to the methods described in Koch et al. (1997). We crushed samples with a mortar and pestle to homogenize grain size, then treated with 30 % H_2O_2 at 0.08 volume to weight for 24 h, followed by 0.05 volume to weight of 0.1 M Ca-buffered acetic acid for 24 h. We froze and subsequently lyophilized each sample prior to analysis at the University of Michigan Stable Isotope Laboratory on a ThermoFisher MAT253 and Kiel IV carbonate device. We report all $\delta^{13}C$ and $\delta^{18}O$ values relative to the Vienna Pee Dee Belemnite (V-PDB) standard. Analytical precision was better than ±0.1 ‰ based on international standards for carbonate (NBS 18, NBS 19) and an internal standard (Carrara) that is cross-calibrated to NBS 18 and 19.

We collected 34 sediment samples containing nodular soil carbonates from paleosols in the Dove Spring Formation. Collection sites were selected based on the presence of pedogenic features (root casts, clay content, blocky fracture, and slickensides) in close proximity to

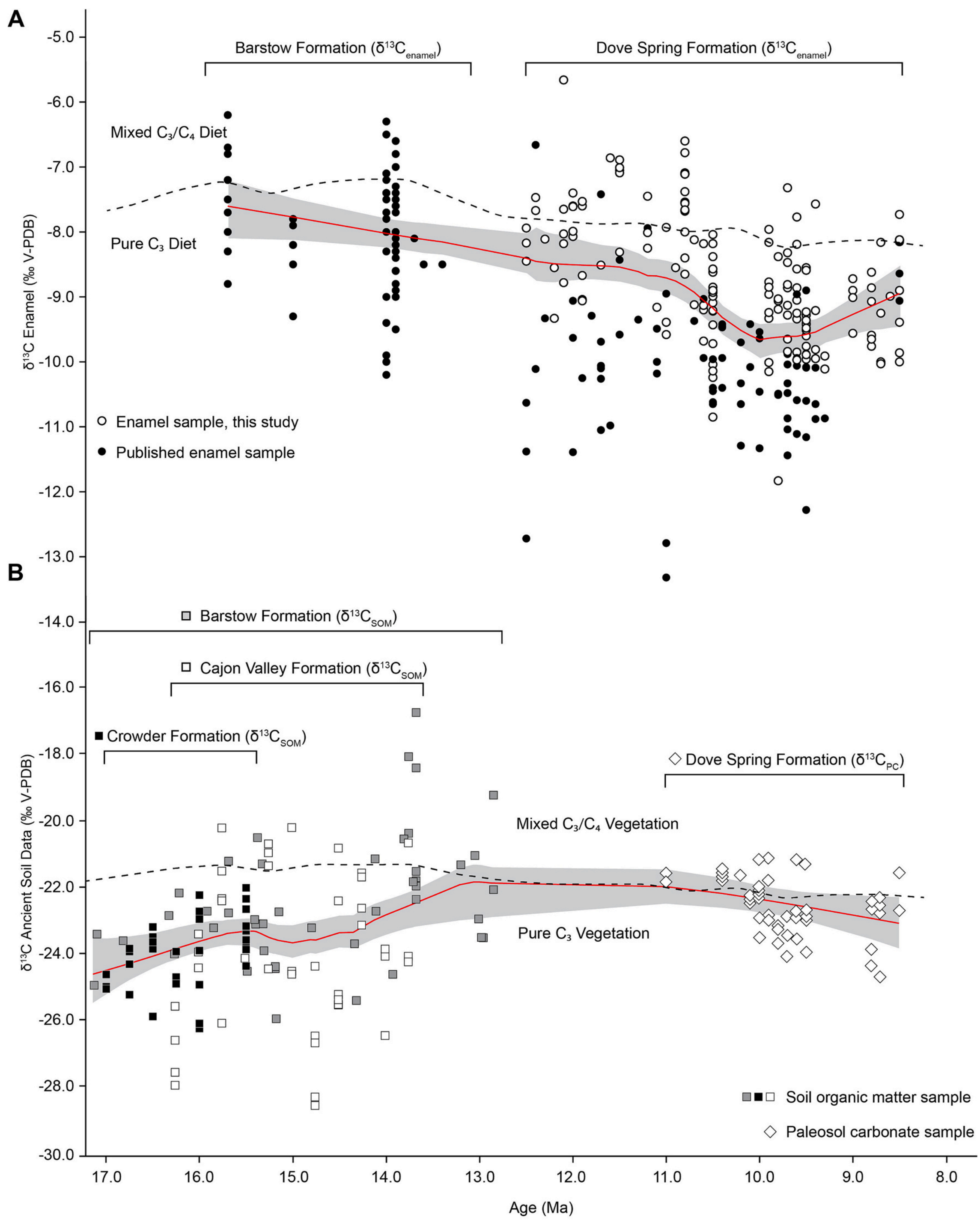

Fig. 2. A) Carbon isotopic composition of herbivore tooth enamel from the Barstow and Dove Spring Formations. Barstow δ^{13}C values include data from seven genera collected by Feranec and Pagnac (2013, 2017) with the temporal component based on the stratigraphic position of fossil localities. Dove Spring results include values from 21 genera and data from Bowman et al. (2017). B) In-situ carbon isotopic composition of soil organic matter ($\delta^{13}C_{SOM}$; squares) and paleosol carbonates ($\delta^{13}C_{PC}$; diamonds) from the western Mojave region. Cajon Valley and Crowder results from Smiley et al. (2018); Barstow results from Loughney et al. (2019). Dashed lines indicate the upper threshold of pure C_3 vegetation in diets or soils based on atmospheric CO_2 values calculated at half-million-year intervals by Passey et al. (2009). The lower threshold for pure C_4 vegetation in $\delta^{13}C_{soil}$ is 12 ‰ higher than the average value for C_3 vegetation and not shown in this plot. Red lines represent 40 % locally weighted regression (LOESS) with 95 % confidence bands based on 999 bootstrap replicates to illustrate change over time in herbivore dietary carbon (A) and paleosol indicators (B) of vegetation composition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fossiliferous localities. Together with the consistent directionality of carbonate rinds on the underside of large clasts at sample sites, these features allowed us to recognize paleosol horizons that were not reworked from older deposits. Soil carbonate nodules were crushed using a mortar and pestle and analyzed at the University of Michigan Stable Isotope Laboratory using identical methods as enamel carbonate samples. We used Miocene atmospheric CO_2 values calculated by Passey et al. (2009) to determine $\delta^{13}C$ thresholds for the presence of C_4 vegetation at half-million year time intervals (Fig. 2) (Passey et al., 2009). We subtracted 15.0 ‰ from measured isotopic ratios of soil carbonates for comparison with $\delta^{13}C$ values of soil organic matter based on the established enrichment between plant biomass and pedogenic carbonate (Passey, 2017).

Published stable isotopic data for the Barstow, Cajon Valley, and Crowder formations were compiled as part of the comparative framework for this study (Feranec and Pagnac, 2013; Feranec and Pagnac, 2017; Smiley et al., 2018; Loughney et al., 2019). Data from herbivore tooth enamel and soil organic matter samples from the three formations were placed into temporal context based on their stratigraphic positions to a resolution of 200–300 kyr.

We applied locally-estimated scatterplot smoothing (LOESS) to all isotopic data from the western Mojave using PAST software v4.15 to examine variation in sample values over time (Hammer et al., 2001). This non-parametric method of regression analysis fits a curve of smoothed estimates to the isotopic data and illustrates temporal trends better than a linear regression due to the changing variability of data and small sample size in some intervals. We selected a 0.4 smoothing span, which means that 40 % of the data points closest to the point of interest are used to fit the local regression model at that point. This smoothing level was a compromise to capture trends in the data and avoid sensitivity to error and outliers.

3. Results

Herbivore tooth enamel and paleosol $\delta^{13}C$ values document regional signals of vegetation in four basin sequences from 17.0 to 8.0 Ma. We present the record of $\delta^{13}C_{enamel}$ in Fig. 2A, with data for individual teeth in Tables S1 and S2. Seven ungulate genera from four families in the Barstow Formation and 15 genera from seven families in the Dove Spring Formation were analyzed. We present the record of $\delta^{13}C_{soil}$ in Fig. 2B, with data for individual sediment samples in Tables S1 and S2. Soil isotope data were sampled from maximum lateral extents of about 5 km in the Barstow Formation and about 10.5 km in the Dove Spring Formation. Each isotopic dataset is displayed with an associated LOESS curve to illustrate overall trends. With the exception of the Crowder Formation, all formations exhibit $\delta^{13}C$ values that indicate the presence of C_3 and C_4 vegetation (Fig. 2). Two long-term trends are apparent. Mean $\delta^{13}C_{enamel}$ values decreased by 1.6 ‰ over a span of seven million years, with a standard deviation of ± 0.8 ‰ for each 200-kyr interval, except between 12.5 Ma and 11.0 Ma when the standard deviation increased to ± 1.3 ‰ (Fig. 2A). Mean $\delta^{13}C_{soil}$ values increased by about 2.0 ‰ over the same time span, with samples from the Dove Spring Formation exhibiting narrower variation (standard deviation ± 0.6 ‰) than during the earlier parts of the record (± 1.5 ‰; Fig. 2B).

The ungulate enamel record for the Barstow and Dove Spring formations exhibits a gradual decrease from a mean of -7.4 ‰ at 15.5 Ma to -9.0 ‰ at 8.5 Ma (Fig. 2A). A sharper decrease in mean $\delta^{13}C_{enamel}$ values occurred between 11.0 and 9.5 Ma, with most values falling below the threshold for pure C_3 diets. Enamel values rebounded to their prior mean values by 8.5 Ma. Whereas the isotopic range for individual genera varied, the standard deviation of $\delta^{13}C_{enamel}$ values for each genus did not exceed ± 1.1 ‰. Ancient soil carbon values in the Cajon Valley, Crowder, and Barstow formations increased from a mean of -24.3 ‰ at 17.1 Ma to -20.8 ‰ at 12.9 Ma ($+3.5$ ‰). In the Dove Spring Formation, soil organic matter values decreased from a mean of -21.7 ‰ at 11.0 Ma to -22.2 ‰ at 8.5 Ma (-0.5 ‰).

The oxygen isotopic record of herbivores shows less change over time than the carbon record, with a mean $\delta^{18}O_{enamel}$ value of -6.1 ± 1.5 ‰ and no notable trends over time (Fig. 3). The standard deviation in $\delta^{18}O_{enamel}$ was low before 13.9 Ma (about ± 0.8 ‰), after which it increased to about ± 1.8 ‰ through the end of the fossil record. Published $\delta^{18}O_{enamel}$ data from the Barstow Formation are limited to equids, while the dataset from the Dove Spring Formation includes members of the Antilocapridae, Camelidae, Equidae, Merycoidodontidae, Gomphotheriidae, and Rhinocerotidae. Equids from the Barstow Formation exhibit a narrow range of $\delta^{18}O_{enamel}$ values (± 1.0 ‰) until about 14.0 Ma, when their isotopic range more than triples (± 3.7 ‰). Ungulates from the Dove Spring Formation exhibit $\delta^{18}O_{enamel}$ values that ranged between -10.8 ‰ and $-$ 3.3 ‰, with one very low outlier from a camelid. Antilocaprids and camelids exhibited $\delta^{18}O_{enamel}$ values 2.0 ‰ higher than those of equids at 10.5 Ma and 9.5 Ma (Fig. 4). In-situ $\delta^{18}O_{soil}$ values are limited to paleosol carbonates from the Dove Spring Formation. Paleosol $\delta^{18}O_{soil}$ values ranged from -13.1 ‰ to -7.7 ‰, with a mean of -10.4 ‰ and standard deviation of ± 7.5 ‰. Mean $\delta^{18}O$ values of soil carbonates exhibited an increase of approximately 3.0 ‰ between 10.5 Ma and 8.5 Ma, which is more variation than measured in tooth enamel.

4. Discussion

We explore three key topics to investigate how environmental changes influenced vegetation and dietary ecology in fossil ungulates from four basins in the Mojave region over a span of nine million years. First, we discuss the region's vegetation composition based on carbon isotope data and other environmental indicators such as phytoliths. Next, we discuss the dietary ecology of the Antilocapridae, Camelidae, and Equidae in comparison to changes in the major plant types. We also discuss the regional moisture regime using oxygen stable isotopes to infer the effects of seasonality on precipitation. Finally, we discuss evidence that some artiodactyls were facultative drinkers during periods of increased aridity. Together, these topics provide new insight into the impacts of environmental and vegetation changes on the dietary ecology of ungulates that occupied the region for millions of years.

4.1. Miocene vegetation in the western Mojave

The appearance of C_4 vegetation signals in both the enamel and paleosol carbon isotopic records indicates that some ungulates began consuming C_4 plants as soon as they became available (Fig. 2). However, isotopic records from paleosols from the three older basins indicate that C_3 vegetation remained dominant in the western Mojave during the MCO. While a slight trend of increasing aridity is reflected in the increasing $\delta^{18}O_{soil}$ values of paleosol carbonates, mean $\delta^{13}C_{soil}$ values only increased from -24.2 ‰ at the base of the Barstow and Crowder formations to -22.3 ‰ at the top of the Dove Spring Formation for a total increase of about 1.9 ‰ (Fig. 2B). As the rate of tectonic extension throughout the region increased after 17.0 Ma, spatially heterogeneous habitats developed in the Barstow and Cajon Valley formations and supported C_4 grasses, although the majority of vegetation utilized the C_3 photosynthetic pathway (Smiley et al., 2018; Loughney et al., 2019). Wooded grasslands and fire activity were increasingly prominent in the Barstow Formation by 13.5 Ma (Loughney et al., 2019). The range of moderately enriched $\delta^{13}C_{soil}$ ratios indicates a mixture of water-stressed C_3 vegetation and C_4 plants that persisted from the end of the Miocene Climatic Optimum through the top of the Barstow sequence (Loughney et al., 2019; Loughney et al., 2023).

The Crowder Formation also contains phytolith evidence for C_4 grasses, but the corresponding isotopic signal is absent from its sediments, suggesting that the biomass of C_4 plants was low (Smiley et al., 2018). The Dove Spring Formation exhibits a narrow range of $\delta^{13}C_{soil}$ values, suggesting less habitat heterogeneity in terms of the proportions of C_3 and C_4 plants than that of the older basins. The isotopic signature of

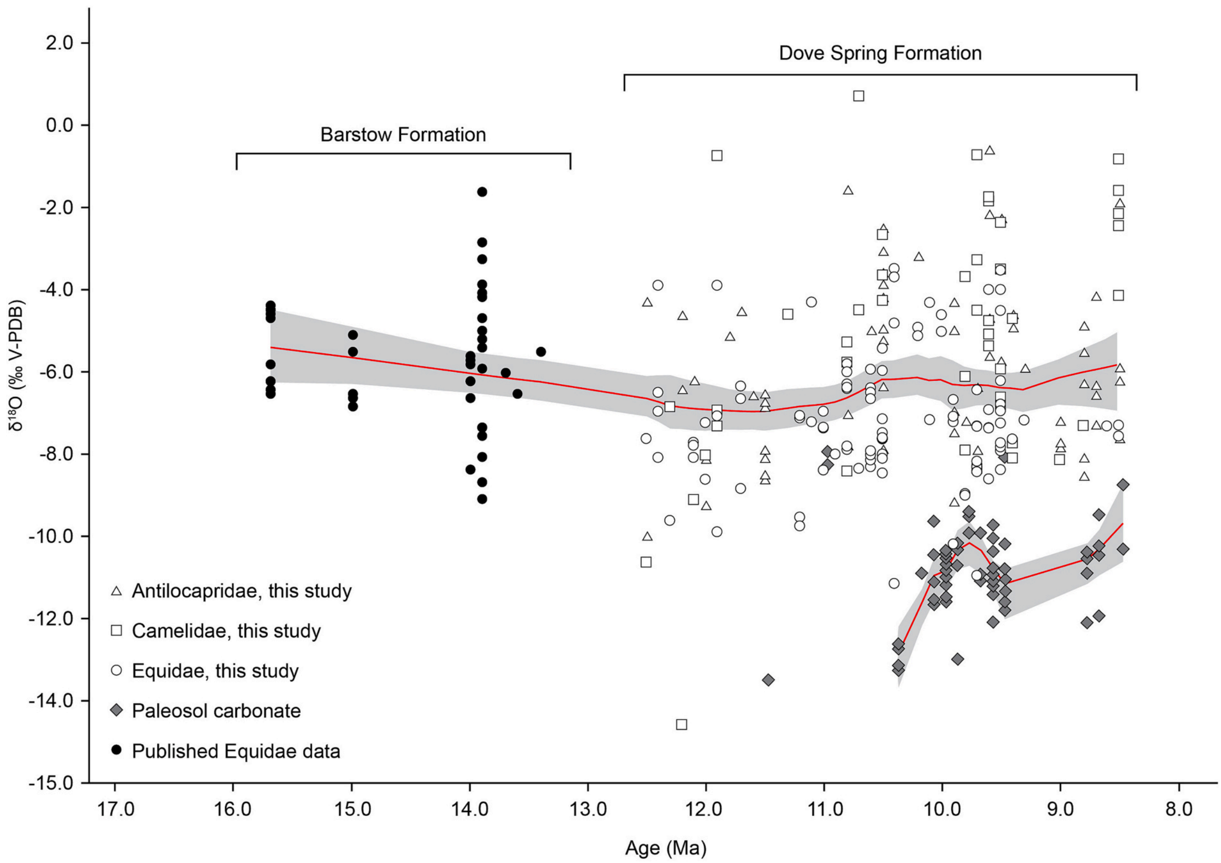

Fig. 3. Oxygen isotopic composition of herbivore tooth enamel and paleosol carbonates from the Barstow and Dove Spring Formations. Barstow $\delta^{18}O$ values represent data collected by Feranec and Pagnac (2013, 2017) with the temporal component based on the stratigraphic position of fossil localities. The red lines represent 40 % locally weighted regression (LOESS) with a 95 % confidence band based on 999 bootstrap replicates to illustrate change over time in herbivore dietary oxygen and paleosol carbonate values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

C_4 plants is present throughout the Dove Spring Formation, with the oldest recovered soil carbonates exhibiting a signal of mixed C_3 and C_4 vegetation. However, a slight negative trend in $\delta^{13}C_{soil}$ from 11.0 Ma to 8.5 Ma suggests the expansion of C_3-dominated habitats. The narrow isotopic range and clustering of $\delta^{13}C_{soil}$ values near the threshold for pure C_3 plants indicates that the Dove Spring Formation likely preserves an ecosystem dominated by water-stressed C_3 vegetation with minor components of C_4 vegetation. Collectively, the carbon isotopic records from Mojave basins indicate that the presence of C_4 vegetation was variable, with local conditions strongly influencing the distribution of mixed C_3/C_4 habitats.

4.2. Dietary fidelity of Miocene ungulates

Dietary $\delta^{13}C$ ($\delta^{13}C_{enamel}$) values decreased during the Miocene Climatic Optimum, with an expanded range that included more negative values over time. This signal suggests that many herbivores selectively consumed C_3 plant resources, despite the establishment of novel C_4 vegetation. Enamel carbon isotope results from the three older basins support earlier interpretations based on biomarker and phytolith analyses that closed-canopy, riparian habitats with palms and woody dicots were present in the region as temperatures cooled leading into the Middle Miocene Climatic Transition (Feranec and Pagnac, 2013; Smiley et al., 2018; Loughney et al., 2019).

Herbivores from the younger Dove Spring Formation exhibit a wider range of carbon isotopic ratios than those from older assemblages, with the majority of $\delta^{13}C_{enamel}$ values below the threshold of C_4 consumption. A gradual negative trend continued until the local onset of basin rotation and translation in the Dove Spring Formation around 10.5 Ma, when $\delta^{13}C_{enamel}$ values decreased. During this tectonic interval, herbivores appear to have exclusively consumed C_3 vegetation despite the continued presence of C_4 plants as indicated by $\delta^{13}C_{soil}$ values (Fig. 2). The signal of C_4 consumption was absent for approximately 0.5 million years before mean values returned to their previous levels at 9.9 Ma. This isotopic shift with lower maximum $\delta^{13}C_{enamel}$ values coincides with the first appearance of several species of antilocaprids and camelids, while equids maintained their species richness. The rebound suggests dietary fidelity across these families, as they consumed familiar resources in a region where C_3 plants were more prominent than C_4 vegetation. At 8.8 Ma, isotopic variation narrowed and minimum $\delta^{13}C_{enamel}$ values increased. This narrowing coincides with $\delta^{13}C_{soil}$ values that indicate water stress and a more restricted range of plant types as the habitat became more open through the top of the formation (Fig. 2).

Patterns of C_4 vegetation availability and herbivore utilization varied across Miocene ecosystems. In the grasslands and woodland of the Great Plains, $\delta^{13}C_{soil}$ values indicate that C_4 plants formed a small proportion of the total vegetation until ca. 9 Ma (Passey et al., 2002; Fox and Koch, 2003; Tipple and Pagani, 2007; Fox et al., 2011; Passey, 2017). Ungulate diets in the Great Plains also reflect the uncommon nature of C_4 plants during the middle Miocene, with few, if any, individuals exhibiting $\delta^{13}C_{enamel}$ values that correspond to the unambiguous consumption of C_4 vegetation before ~9 Ma (Passey et al., 2002; Kita et al., 2014; Nguy and Secord, 2022). In the woodlands of the Columbia Plateau (~16.0–13.5 Ma), the dietary niche stability of C_3-browsing equids has been interpreted as a lack of C_4 grasses throughout the region, which agrees with paleoenvironmental reconstructions of a consistently moist environment with no seasonal drying (Maguire, 2015). In contrast, the

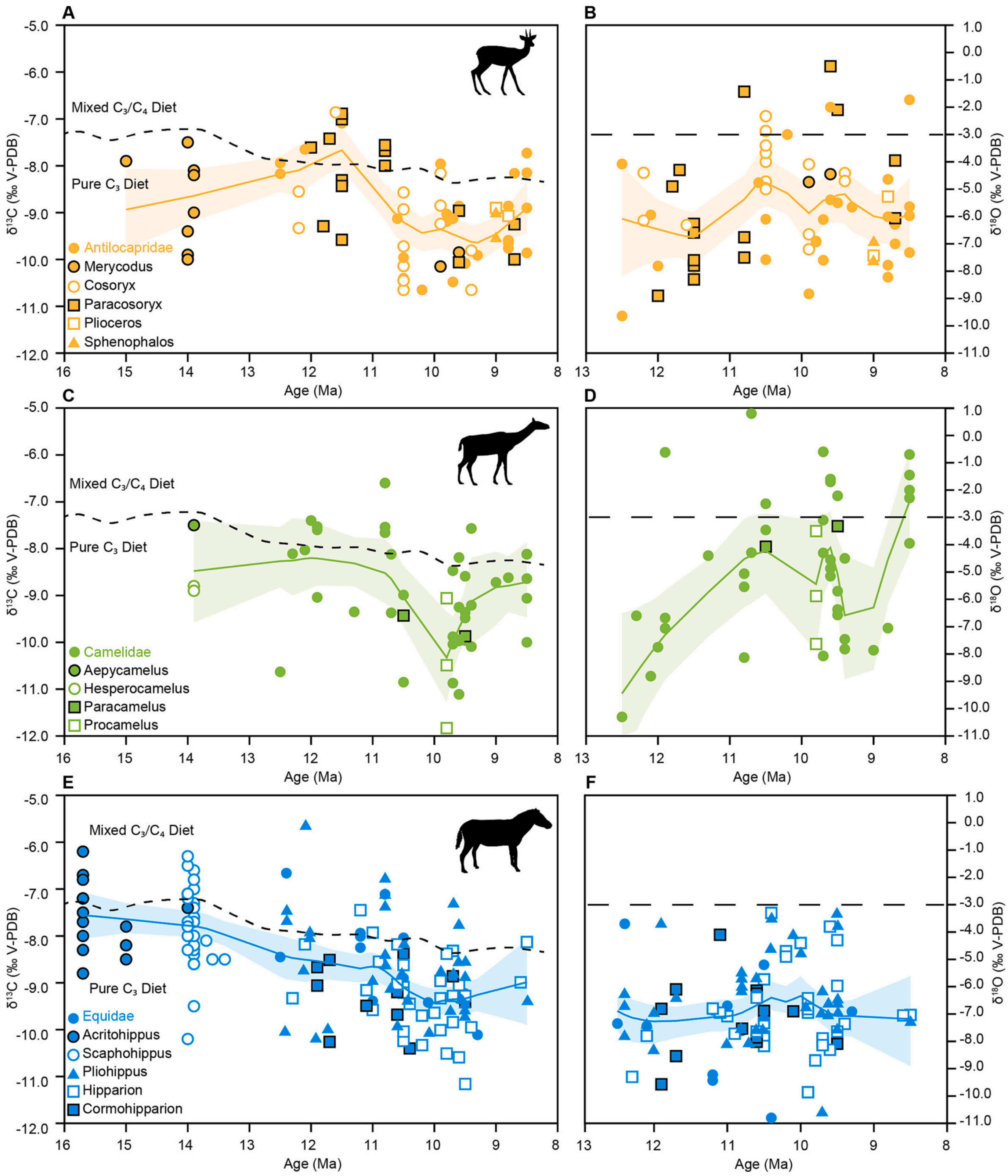

Fig. 4. Carbon and oxygen isotopic composition of ungulate families with 40 % locally weighted regression (LOESS) curves and 95 % confidence bands based on 999 bootstrap replicates of each dataset. Dashed line in $\delta^{13}C$ plots indicates the upper threshold of pure C3 vegetation consumption. Dashed line in $\delta^{18}O$ plots indicates the upper limit (−3.0 ‰) of enamel oxygen composition in equids (obligate drinkers). A) Antilocapridae δ13C. B) Antilocapridae δ18O. C) Camelidae $\delta^{13}C$. D) Camelidae δ18O. E) Equidae δ13C. F) Equidae δ18O. Silhouettes courtesy of PhyloPic.

Mojave region appears to have supported patchy but locally abundant C_4 vegetation that was largely avoided as a resource by ungulates, highlighting distinct plant-herbivore dynamics between these environments.

Faunal turnover in the western Mojave corresponds more closely with tectonically driven shifts in dominant depositional environment than with changes in vegetation resources (Smiley, 2016; Loughney et al., 2021; Hardy and Badgley, 2023). Based on comparisons of $\delta^{13}C_{soil}$ and $\delta^{13}C_{enamel}$, low proportions of C_4 vegetation were present prior to significant changes in faunal composition. However, the dietary trends of younger taxa were consistently similar to those of their predecessors. For example, the equid genera *Cormohipparion* and *Pliohippus* occurred contemporaneously ca. 15.0 Ma and exhibited some degree of dietary partitioning based on the higher $\delta^{13}C_{enamel}$ values of *Pliohippus* and the C_3 signal of *Cormohipparion* (Fig. 4E). The genus *Hipparion* diverged from *Cormohipparion* ca. 13.5 Ma and exhibited average $\delta^{13}C_{enamel}$ values $\leq$1 ‰ greater than its ancestor, suggesting that it incorporated a small proportion of C_4 vegetation. The presence of shared ungulate genera throughout the Mojave indicates that while local environments determined resource availability and habitat type, dietary fidelity contributed to the persistence of diverse ungulate assemblages during the Miocene.

4.3. Facultative drinkers in the Miocene

Herbivore carbonate $\delta^{18}O$ ($\delta^{18}O_{enamel}$) mean values changed little in the Barstow and Dove Spring Formations between 16.0 Ma and 8.5 Ma. The early equids (15.7–15.0 Ma) of the Barstow Formation exhibit a narrow range of $\delta^{18}O_{enamel}$ values, indicating a relatively stable local moisture regime during the MCO. The subsequent widening of $\delta^{18}O_{enamel}$ ranges in the Dove Spring Formation suggests an increase in the seasonality of precipitation during the MMCT as temperatures cooled. In general, the slight increases in Dove Spring Formation $\delta^{18}O_{enamel}$ values over time follow the regional trend of increasing aridity established by phytoliths and biomarker data from the older basins (Smiley et al., 2018; Loughney et al., 2019; Loughney et al., 2023).

Our most notable findings concerning $\delta^{18}O_{enamel}$ are the changes in isotopic range observed within the Antilocapridae and Camelidae in the Dove Spring Formation. These two families exhibit significant widening of their $\delta^{18}O_{enamel}$ ranges (from $\pm$2.0 ‰ to $\pm$4.0 ‰) at 10.5 Ma and 9.5 Ma, as well as enriched oxygen isotopic signatures relative to equids and other ungulates sampled (Fig. 4B, D, F). Equids exhibit a mean $\delta^{18}O_{enamel}$ value of -6.9 ± 1.5 ‰, fluctuating very little throughout the sequence. Conversely, high and variable $\delta^{18}O_{enamel}$ values above -5.0 ‰ are common in antilocaprids and camelids. The timing of the highest $\delta^{18}O_{enamel}$ values coincides with an interval of increased aridity between 10.5 Ma and 9.0 Ma (Fig. 4). If we consider the possibility that Miocene antilocaprids and camelids possessed the ability to obtain most of their water through consumed vegetation, then these results are intriguing.

Along with a contemporaneous increase in $\delta^{18}O_{soil}$ values, the enrichment in $\delta^{18}O_{enamel}$ across all taxa between 10.5 and 9.5 Ma suggests that the evaporative potential of the environment increased during a shear tectonic episode (Fig. 4). During this episode, existing channel networks in the Dove Spring Formation were disrupted, potentially altering the availability of water resources for herbivores. In response to similar conditions, desert camels and some modern pronghorn decrease their drinking water consumption and increase their water intake from food (Gauthier-Pilters, 1971; Yagil and Etzion, 1988; Fox, 1997; Tluczek, 2012). Equid $\delta^{18}O$ values more consistently followed regional temperatures and precipitation, and did not track changes in evaporative potential. These findings indicate that equids and other obligate drinkers are more reliable indicators of meteoric precipitation, tracking atmospheric conditions more closely than facultative drinkers such as antilocaprids or camelids.

5. Conclusion

While significant changes in landscape and climate occurred throughout the western Mojave region of North America, an 8.5-million-year pattern of stable herbivore diets was present among at least 19 genera from three ungulate families. Antilocaprids, camelids, and equids exhibited dietary fidelity by selectively consuming C_3 plants despite the appearance and expansion of C_4 vegetation during the Miocene Climatic Optimum and beyond. The region became more arid and supported a less diverse vegetation assemblage over time, but these factors were insufficient for ungulates to alter their dietary ecology. While changes in faunal composition and species richness did occur within individual basins, the widespread distribution of shared ungulate taxa and dietary fidelity throughout the western Mojave indicates that the region supported high species richness of large, herbivorous ungulates over geologic time. The wide range of $\delta^{13}C_{enamel}$ values from the younger Dove Spring Formation in conjunction with the narrow range of $\delta^{13}C_{soil}$ values suggests that while open canopy habitats were more common than in older basins, herbivores continued to select C_3 vegetation. Additional basin records with high-resolution fossil and sedimentary records will add to our understanding of the prevalence and limits of dietary fidelity.

CRediT authorship contribution statement

Fabian Cerón Hardy: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Xiaoming Wang:** Resources, Data curation. **Chelsie N. Bowman:** Investigation, Data curation. **Yang Wang:** Resources. **Catherine Badgley:** Writing – review & editing, Supervision, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2025.113013.

Data availability

Data will be made available on request.

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