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Ungulate diets reveal patterns of grassland evolution in North America

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ABSTRACT

Equids from the late Miocene (Hemphillian North American Land Mammal Age) of Texas evolved C_4 dominated diets earlier than their Nebraska counterparts, leading researchers to hypothesize a northward expansion of C_4 grasses between 8 and 6 Ma. However, competing hypotheses from multiple paleoecological proxies support one of three hypotheses: that northward C_4 expansion occurred at the expense of C_3 woodlands, C_3 grasslands, or was not occurring during the Hemphillian. We test these alternative hypotheses by comparing the ecosystems of Hemphillian Texas and Nebraska (6.3–7.5 Ma) using hoofed mammal dietary reconstruction (hypsodonty and digestive strategy) and by incorporating published tooth enamel isotopes, paleosol isotopes, and phytolith assemblage data. We also use hypsodonty, mesowear, and microwear in a detailed comparison of two localities that are roughly contemporary (Cambridge, Nebraska at 7 Ma and Coffee Ranch, Texas at 6.6 Ma) to rule out time averaging as an explanatory variable. Through analogy with modern African communities, we reconstruct Texas and Nebraska ecosystems as bushland and woodland, respectively. Using the proportions of hypsodont taxa we estimate mean annual precipitation values of 1217 mm/year for Nebraska and 1368 mm/year for Texas. Using rarefaction we also do not find differences in the richness of brachydont, hypsodont, and hindgut fermenting taxa. We therefore conclude that both ecosystems were largely similar in hoofed mammal faunal structure during the late Miocene. When compared to published paleosol and phytolith data, which show no differences in C_3/C_4 biomass among latitudes, our results allow us to reject hypotheses of northward C_4 expansion during the late Miocene. We therefore suggest that the equid enamel isotopes may have been biased by two potential factors: the primary reliance on a single locality of appropriate age and possible behavioural lag in C_4 feeding among Nebraska equids. These results suggest that the formation of a modern C_3/C_4 latitudinal gradient occurred later than is previously suggested by equid enamel carbon isotopes.

1. Introduction

The Great Plains of North America is an iconic ecosystem that spans from the northern coniferous forests to the Gulf of Mexico and from the Rocky Mountains to the eastern deciduous forests (Jacobs et al., 1999). Ecosystems in the Great Plains may have been relatively open and grassy by at least the early Miocene as a consequence of the Cenozoic cooling and drying trend (Zachos et al., 2001; Edwards et al., 2010). However, C_4 plants did not become a large component of ecosystems in the Great Plains until the latest Miocene or early Pliocene (Fox et al., 2012a,b). The late Miocene was characterized by declining temperatures and increasing aridity that may have spurred C_4 expansion (Cerling et al., 1993, 1997; Pearson and Palmer, 2000; Retallack, 2001; Edwards et al., 2010; McInerney et al., 2011; Strömberg and McInerney, 2011). A decline in atmospheric CO_2 below the threshold for C_3 dominance may also have resulted in the expansion of C_4 plants from low latitudes to higher latitudes (Edwards et al., 2010; Foster et al., 2012). However, determining the patterns by which C_4 plants expanded in the Great Plains of North American is complicated by conflicting evidence from multiple paleoecological proxies. For example, studies of ungulate and proboscidean ecomorphology have suggested that the expansion C_4 grasslands occurred during the late Miocene (~7 Ma) at the expense of C_3 woodlands (Hypothesis 1) (Cerling et al., 1993; Wang et al., 1994; Janis et al., 2000, 2004). Phytolith and equid tooth enamel carbon isotopes suggest that C_4 grass expansion occurred at the expense of C_3 grasslands (Hypothesis 2) (Passey et al., 2002; McInerney et al., 2011). In complete contrast, paleosol carbon isotopes and phytolith assemblages show limited northward expansion of C_4 plants, suggesting little effect of late Miocene cooling (Hypothesis 3) (Fox and Koch, 2004; Strömberg and McInerney, 2011; Fox et al., 2012a,b). We test these three alternative hypotheses by comparing late Miocene (Hemphillian North American Land Mammal Age or NALMA ~6.3–7.1 Ma) ecosystems of Texas and Nebraska using a variety of hoofed mammal dietary proxies (hypsodonty, mesowear, microwear, and digestive strategy) and combining our reconstructions with published tooth enamel isotopes, paleosols isotopes, and phytoliths (Passey et al., 2002; Fox and Koch, 2004; McInerney et al., 2011; Strömberg and McInerney, 2011.

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The majority of modern plants use the C_3 (trees and some grasses) and C_4 (grasses) photosynthetic pathways. Modern C_4 plants dominate in the southern Great Plains while C_3 plants dominate the north, a fact that is attributed to metabolic differences (Teeri and Stowe, 1976; Edwards et al., 2010). Prior to the Miocene (~7 Ma), the plant biomass of the Great Plains was C_3 dominated, including only a small C_4 component (Cerling et al., 1997; Fox and Koch, 2004). Until relatively recently, the majority of evidence for Miocene C_4 expansion came from equid tooth enamel carbon isotopes, which showed that southern (Texas) late Miocene equids had more C_4 dominated diets than their northern counterparts (Nebraska). In other words, the equids demonstrated the presence of a C_3/C_4 latitudinal gradient that appeared to suggest northward expansion of C_4 plants between 8–6 Ma (Cerling et al., 1993; Wang et al., 1994; Cerling et al., 1997; Passey et al., 2002). Increasing continental aridity and a drop in atmospheric CO_2 may have resulted in an episode of northward C_4 expansion in North America, the cessation of which was the formation of the modern C_3/C_4 latitudinal gradient (Teeri and Stowe, 1976; Cerling et al., 1997; Ehleringer et al., 1997; Cerling et al., 1998; Passey et al., 2002; Foster et al., 2012). However, paleosol (fossilized soil) carbon isotopes do not show a significant northward expansion of C_4 biomass during the late Miocene and therefore suggest that formation of the modern C_3/C_4 latitudinal gradient occurred more recently (Fox and Koch, 2004; Fox et al., 2012a,b). In fact, pedogenic carbonates suggest that C_4 expansion occurred in three episodes from the early late Miocene (Clarendonian NALMA, 12–9 Ma) and late Pleistocene (early Irvingtonian NALMA, 2.5-1.0 Ma) (Fox et al., 2012a,b).

McInerney et al. (2011) simultaneously tested for C_4 expansion and vegetation change using phytolith assemblages and phytolith carbon isotopes during the Miocene. In apparent support of C_4 expansion at the expense of C_3 grasses (Hypothesis 2), they identified an increase in late Miocene open habitat C_4 grasses and an associated shift toward C_4 carbon isotopic values of siliceous phytoliths. They did not, however, explicitly test for northward C_4 expansion by comparing contemporary localities among latitudes. We therefore attempt to differentiate among northward C_4 expansion at the expense of C_3 woodlands (Hypothesis 1), at the expense of C_3 grasslands (Hypothesis 2), and no northward expansion (Hypothesis 3) by incorporating data on hoofed mammal ecomorphology and using a total evidence approach.

We compare paleoenvironments between Hemphillian (late Miocene, with median ages from 7.1 to 6.3 Ma) localities in Nebraska and Texas using ungulate and proboscidean community composition as a proxy (Fig. 1). Ecomorphological and enamel isotopic studies have often focused on the Equidae (horses) because they radiated into the grazing niche during the Miocene (Cerling et al., 1997). However, a single family of herbivores cannot reveal ecosystem structure (proportions of trees and grasses) and therefore cannot test the hypotheses outlined above (Janis et al., 2004). For this reason, we reconstruct the diets of entire ungulate and proboscidean communities. We use ungulates and proboscideans because they are large and well preserved at many fossil localities, their ecology and behaviour is among the best understood of all mammalian herbivores, and their community composition (proportions of browsers, grazers, and mixed feeders) is an indirect proxy of the local plant community, allowing us to reconstruct ancient ecosystems by analogy (Reed, 1998; Janis et al., 2000, 2004).

We use the proportions of hypsodont (high crowned teeth) and non-hypsodont (intermediate or low crowned teeth) as well as the proportions of hindgut (HGFs) and foregut fermenters (FGFs) to reconstruct the plant communities of Nebraska and Texas (Janis et al., 1994, 2000, 2004; Damuth and Janis, 2011). We also use hypsodonty, mesowear, and microwear for a comparison of hoofed mammal diets between two nearly contemporary late Miocene fossil localities (Coffee Ranch, Texas (~6.7 Ma) and Cambridge, Nebraska (~7 Ma)). Our comparison of Coffee Ranch and Cambridge represents a small time interval relative to our analysis of all Texas and Nebraska localities between the ages of 6.3 and 7.1 Ma (median ages). Comparison of Coffee Ranch and Cambridge therefore enables us to rule out time averaging as a confounding factor. Finally, we combine our paleoecological reconstructions with published equid tooth enamel (Passey et al., 2002), paleosol (Fox and Koch, 2004), and phytolith isotopes (McInerney et al., 2011) as well as phytolith assemblage data (McInerney et al., 2011; Strömberg and McInerney, 2011).

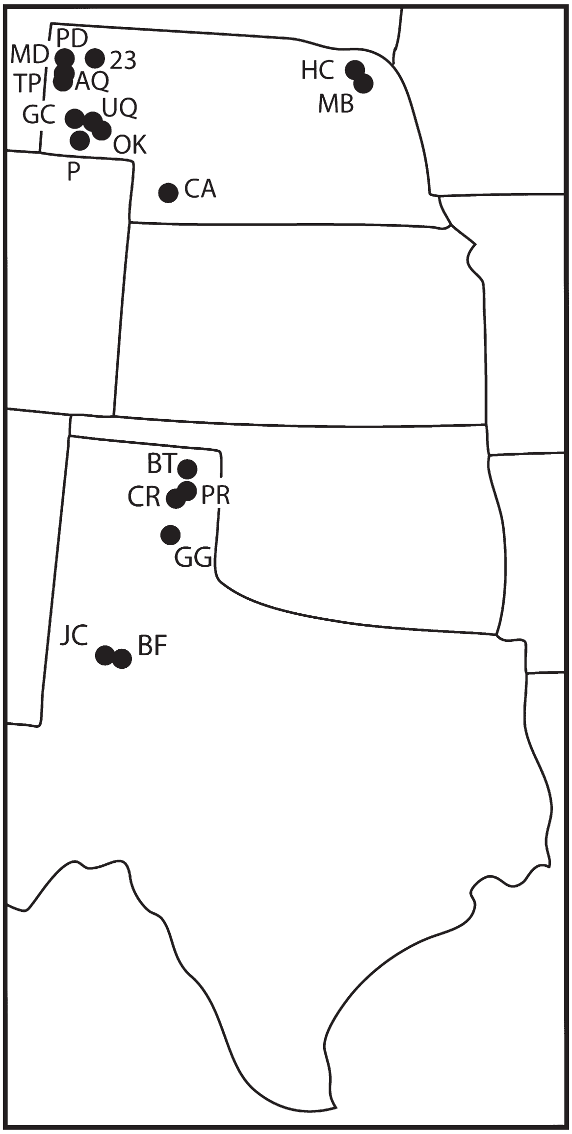

Fig. 1. Sampled late Miocene localities from Texas and Nebraska. Locality acronyms are as follows: 23 mi. S of Agate (23), Aphelops Quarries (AQ), Box T (BT), Bridwell Formation (BF), Cambridge (*Amebelodon Fricki* Quarry; CA), Coffee Ranch Quarry (CR), General Goodnight Fauna (GG), Greenwood Canyon Quarry (GC), Honey Creek (HC), J.C. Strange Gravel Quarry (JC), Mailbox (MB), Merychippus Draw (MD), Oshkosh (OK), Parcell Ranch (PR), Pliohippus draw (PD), Potter (P), The Pits (TP), and Uptegrove Quarry (UQ).

Hypothesis one (loss of C_3 woodlands) is supported if hoofed mammal proxies show wooded ecosystems in the northern Great Plains, grassier ecosystems in the south, and if carbon isotopes and phytolith assemblages show a stronger C_4 signal in the south. Hypothesis two (loss of C_3 grasslands) is supported if we do not find differences between ungulate communities in the northern and southern Great Plains but carbon isotopes and phytolith assemblages show a C_3 grass signal in the north and C_4 grass signal in the south. Finally, Hypothesis three (no C_4 expansion) is supported if there are no ungulate community, isotopic, or phytolith differences between the northern and southern Great Plains.