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Dietary paleoecology of bison and horses on the mammoth steppe of eastern Beringia based on dental microwear and mesowear analyses

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ABSTRACT

In contrast to the modern Arctic, high-latitude ecosystems of the Late Pleistocene supported a diverse range of large mammalian herbivores, including abundant bison (*Bison priscus*) and horses (*Equus* sp.). This 'mammoth steppe' biome has no extant analog and modern tundra vegetation is likely incapable of supporting such a high density of large mammals. Compared to modern Arctic ecosystems, higher diversity and biomass of Late Pleistocene large mammal populations may have been sustained by more nutritious forage and/or dietary niche partitioning. We used dental microwear texture analysis and dental mesowear analysis of bison and horses (*Bison priscus, Equus* sp.) to characterize diet and assess the degree to which dietary differences supported co-existence of these dominant and likely competing herbivores on the mammoth steppe. Additionally, we compared microwear and mesowear of Late Pleistocene specimens to modern Alaska bison (reintroduced *Bison bison athabascae* and introduced *Bison bison bison*) and published microwear and mesowear data for extant bovids and equids. Our results demonstrate that Late Pleistocene bison and horses had less abrasive diets than modern obligate grazers, suggesting that these "grazers" of the mammoth steppe likely incorporated more forbs in their diets than modern grazers. Furthermore, Late Pleistocene bison and horses ate foods with similar textures, indicating that dietary niche partitioning alone cannot explain their co-occurrence. However, taphonomic differences between bison and horse specimens indicate potential spatial or temporal niche partitioning during the Late Pleistocene.

1. Introduction

High-latitude environments of the far north have undergone dramatic ecological restructuring during the last 50,000 years (Bigelow et al., 2003; Guthrie, 2001; Lanoë et al., 2017; Mann et al., 2019, 2015; Schwartz-Narbonne et al., 2019). Today, the diversity of megaherbivores in northern Alaska (herbivores larger than 44 kg; Martin and Klein, 1989; Koch and Barnosky, 2006) is dominated by seasonally abundant migratory caribou with rare moose and musk oxen, the latter having been reintroduced in the 1970s after extirpation in the 1800s (Klein, 1996; Tape et al., 2016). However, modern megaherbivore diversity in Alaska, particularly across the North Slope (Fig. 1; the region bounded to the south by the Brooks Range mountains and to the north by the Arctic Ocean), has not always been so low. Late Pleistocene mammal assemblages of the North Slope, which included equids (*Equus* sp.), bison (*Bison priscus*), mammoth (*Mammuthus primigenius*), caribou (*Rangifer tarandus*), saiga (*Saiga tatarica*), and musk oxen (*Ovibos moschatus*), were richer and had more even species abundance distributions than modern ecosystems (Mann et al., 2013). In addition to higher diversity, Late Pleistocene megaherbivores also appear to have been more abundant, with estimated population densities roughly six times higher on the North Slope (Mann et al., 2013) compared to modern populations and
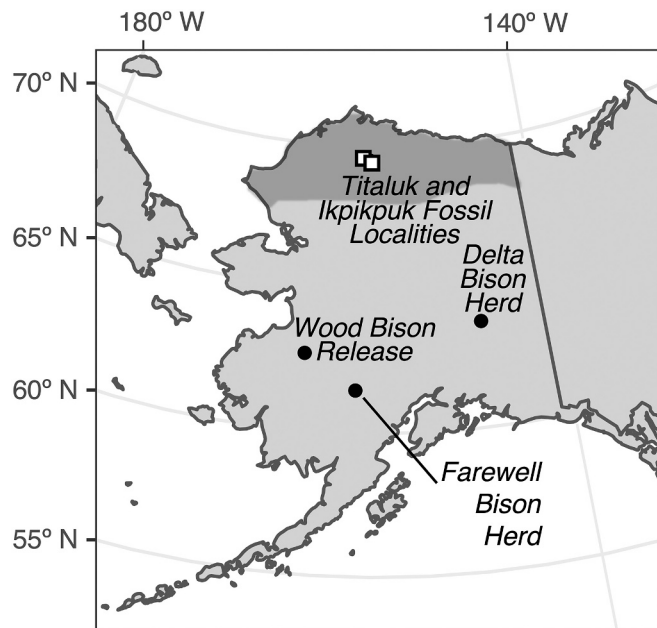
Fig. 1. Map of Alaska showing locations of fossil and modern specimens. Open squares indicate approximate regions of Pleistocene fossil surveys along Ikpikpuk and Titaluk rivers (Mann et al., 2013). Filled circles show locations of the Delta and Farewell *B. b. bison* herds and the reintroduction site of Wood Bison, *B. b. athabascae*. Shading identifies the North Slope, which is bounded by the Brooks Range mountains to the south and the Arctic Ocean to the north.

ten times higher in parts of Siberia (Zimov et al., 2012).

The mechanisms by which Arctic ecosystems of the Pleistocene supported such diverse and apparently abundant megafaunal populations remains an actively debated question. Though anthropogenic impacts are thought to be broadly responsible for Late-Pleistocene megafaunal declines globally, extinctions and extirpations in Beringia are more closely associated with climate and environmental shifts (Koch and Barnosky, 2006; Zazula et al., 2017, 2014). Vegetation during the Late Pleistocene may have provided more nutritious forage, thus supporting a more abundant and diverse megafauna assemblage (Guthrie, 1990; Zimov et al., 2012). Fossil macroflora (Kienast et al., 2005; Zazula et al., 2003), ancient DNA (Willerslev et al., 2014) and megaherbivore gut-content analysis (Guthrie, 1990) all indicate that high latitude vegetation of the Late Pleistocene was more protein-rich and forb-dominated, more analogous to modern steppe environments (Guthrie, 2001; Willerslev et al., 2003; Zazula et al., 2003; Zimov et al., 2012). Pollen data also indicate more productive, steppe-like environments in the Late Pleistocene high latitudes (Blinnikov et al., 2011; Eisner and Colinvaux, 1990). Resource partitioning may also have contributed to high megafauna diversity (Mann et al., 2015; Schwartz-Narbonne et al., 2019). Because segregation of dietary resources may facilitate the co-occurrence of multiple competing megaherbivore species in a shared geographic range, such niche partitioning is often considered an important driver of high local and regional diversities in communities of Late Pleistocene megafauna (Bocherens, 2003; Fox-Dobbs et al., 2008; Guthrie, 1984; Rivals et al., 2007; Schwartz-Narbonne et al., 2015; Smith and DeSantis, 2020).

However, assessing the degree to which more nutritious forage opportunities and niche partitioning contributed to high diversity on the North Slope first requires a detailed understanding of Late Pleistocene megafauna diets. Megaherbivore dietary niches are typically described along a grazer – browser continuum (Fortelius and Solounias, 2000; McNaughton and Georgiadis, 1986). In this framework, herbivores classified as "obligate grazers" eat monocot graminoids (grasses and sedges), "obligate browsers" feed on forbs, shrubs and trees (generally dicot), and "mixed feeders" eat a combination of both. Though the term "grazer" is sometimes used to broadly describe diets including both graminoids and herbaceous forbs, here we use the term strictly to refer to primarily graminoid diets. Obligate frugivory may also be included as a third end-member in temperate and tropical environments (Bodmer, 1990), but this dietary niche was likely not significant on the mammoth steppe.

Here, we focus on two of the most abundant megaherbivores of the Pleistocene North Slope, *B. priscus* and *Equus* sp.. Species level designations for North Slope equid specimens are currently unavailable, but metacarpal measurements indicate they likely belong to the *Equus ferus* species complex (Mann et al., 2013) and we refer to all North Slope equid specimens as *Equus* sp.. Although *B. priscus* and *Equus* sp. are typically grouped with mammoths as the "Big Three" grazers of the mammoth steppe (Guthrie, 1990), temporal and geographic offsets in peak abundances of Beringian *B. priscus* and *Equus* sp. are consistent with differences in ecological niches between the two taxa. On the North Slope, *Equus* sp. were more abundant during the Last Glacial Maximum (LGM), while *B. priscus* were more abundant during the slightly warmer interval from ca. 45–35 ka (Fig. 2; Mann et al., 2019, 2015, 2013). Extant bison often incorporate woody browse in their diets and have broad dietary niches at seasonal-, population-, and species-scales (Campbell and Hinkes, 1983; Jones and DeSantis, 2017; Larter and Gates, 1991; Rivals et al., 2007). Since migrating to North America ca. 195 ka (Froese et al., 2017), bison have occupied both grazing and mixed-feeding dietary niches (Jones and DeSantis, 2017; McDonald, 1981; Rivals et al., 2007). In contrast, horses evolved to be grazing specialists, though modern wild horses are also known to at least seasonally incorporate non-grass forage in their diets (Crane et al., 1997; Salter and Hudson, 1979), and some populations from Pleistocene Europe are thought to have been primarily mixed feeders (Rivals, 2012; Rivals et al., 2015, 2009). Guthrie and others have suggested that horses were more tolerant of harsher conditions because large equid hindguts may more efficiently extract nutrients from poorer quality forage than ruminants like bison (Duncan et al., 1990; Guthrie, 2006, 2003; Kuntz et al., 2006). Thus, identifying the degree to which both taxa subsisted on available graminoid vs. herbaceous or shrubby plants on the North Slope and how much their dietary niches overlapped is integral to understanding the mammoth steppe ecosystem on the North Slope.

Stable isotope studies have provided some dietary insight and suggest potential dietary niche differences (Fox-Dobbs et al., 2008; Mann et al., 2013; Schwartz-Narbonne et al., 2015), yet two factors of the Late Pleistocene far north complicate the resolution with which we interpret ecological niche from isotopic data. First, the carbon isotopic variation in plant material is relatively low due to the lack of C_4 plants at high latitudes (Wooller et al., 2007). Second, nitrogen isotopes in ecosystems can be influenced by moisture availability and there were large changes in aridity throughout the Late Pleistocene (Rabanus-Wallace et al., 2017). Additionally, physiological differences between species may lead to predictable offsets in stable isotope values. For example, ruminant artiodactyls (e.g., bison) may lose more isotopically light carbon during digestion than hindgut-fermenting perissodactyls (e.g., equids; Cerling and Harris, 1999; Codron et al., 2018, 2012; Hedges, 2003; Passey et al., 2005). Due to these environmental and physiological complexities, it is difficult to link isotopic signals preserved in enamel and collagen directly to dietary content. Additional independent proxies of dietary niche are necessary to characterize diet and assess niche partitioning at high latitudes.

Here, we use dental (tooth) wear techniques to characterize the diets of *B. priscus* and *Equus* sp. along the grazer-browser continuum. Patterns of dental wear have generated multiple widely used proxies for evaluating diet of extant and extinct vertebrates (Fortelius and Solounias, 2000; Teaford and Walker, 1984; Ungar et al., 2003). Dental wear can be subdivided into mesowear, the macroscopic profile of a molar tooth that arises from chewing food (Fortelius, 1985; Fortelius and Solounias, 2000), and microwear, microscopic features such as pits and scratches that develop on enamel chewing surfaces during mastication (DeSantis,
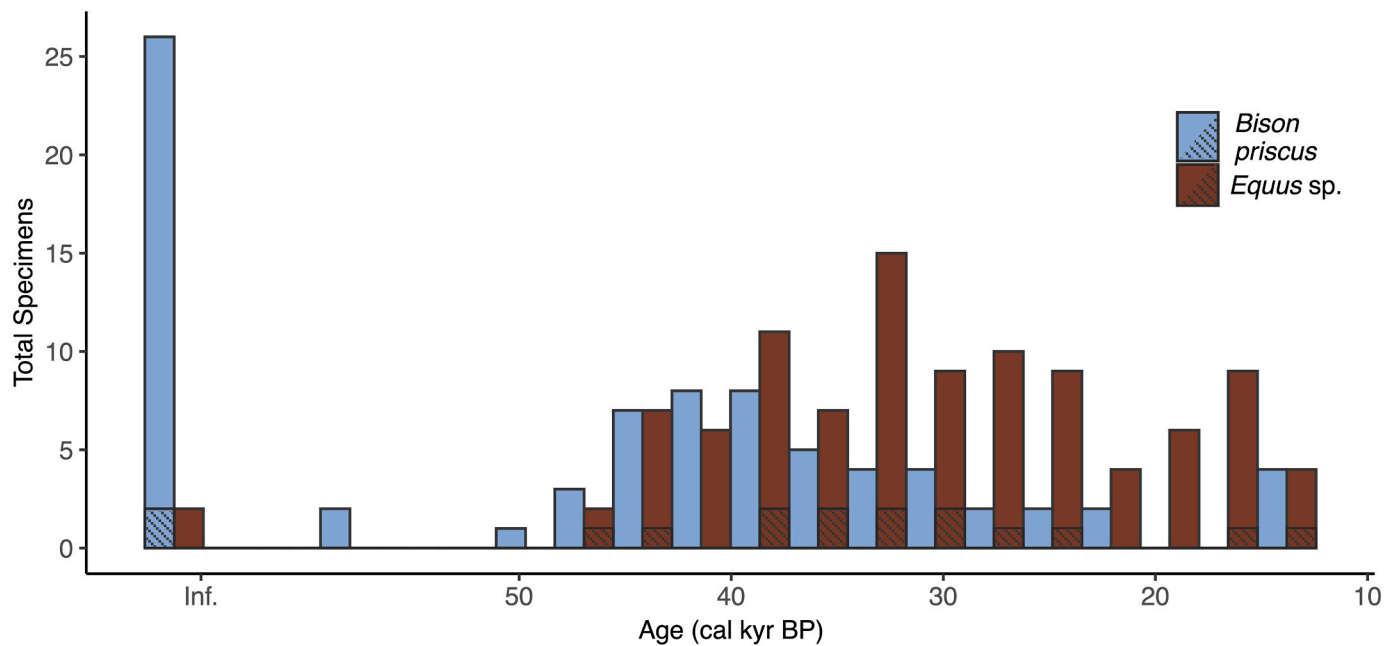
Fig. 2. Age frequency distribution of calibrated radiocarbon dates (IntCal 09) for *Bison* and *Equus* bones collected from the North Slope. Specimens with insufficient ^{14}C for accurate dating are designated as "Inf" ("Infinite dates"). Data depicted here represent all *Bison* and *Equus* bones published by Mann et al. (2013). Most dates are from bones other than mandibles and maxillae. Mandibles and maxillae assessed for micro- and/or mesowear (this study) and also dated by Mann et al. (2013) are shown as shaded portions of bars ($n_{Bison} = 2$, $n_{Equus} = 14$).

2016; Teaford and Walker, 1984). Grazing diets are especially abrasive due to high phytolith (biogenic plant silica) content in graminoids and possibly greater overall prevalence of grit and dust (Ackermans et al., 2020b; Merceron et al., 2016a, 2016b). This abrasiveness contributes to blunter mesowear profiles and more scratched microwear textures (Bezeau et al., 1966; Fortelius, 1985; Merceron et al., 2016a, 2016b). When diet is less abrasive, tooth-on-tooth attrition may be a more significant source of wear; browsing diets are correlated with sharper mesowear profiles and enamel surfaces with more pits and fewer scratches (Fortelius, 1985; Fortelius and Solounias, 2000; Scott, 2012a).

Both microwear and mesowear signals are dependent on the textures of food (and other particles) consumed and the animal doing the chewing, and thus there is the potential for phylogenetic differences to impact results (Fraser et al., 2018; but see DeSantis et al., 2018). However, bovids and equids have both evolved to chew via a primarily single-phase transverse shearing motion and have similar, flat occlusal planes on their molars, suggesting wear signals may be comparable if not perfectly analogous (Fortelius and Solounias, 2000; Mihlbachler et al., 2016). As is true for many proxies (e.g., stable isotopes), within-taxon comparisons may provide more readily interpretable results than comparisons between taxa. Thus, while we directly compare Beringian *B. priscus* to *Equus* sp., we also perform within-genus comparisons using a range of published microwear and mesowear data for bovids and equids.

Mesowear, similar to stable isotopes from bone collagen, provides a more time-averaged dietary proxy for diet than microwear because it is an accumulative signal of food-on-tooth and tooth-on-tooth wear (Ackermans et al., 2020a; Fortelius and Solounias, 2000). Modern bison from Wood Buffalo National Park (Canada) have molar wear rates of about 1.7 mm per year, suggesting that mesowear signals may show annual resolution (Haynes, 1984). Microwear, on the other hand, records information across shorter timescales because "damage" can be worn away and overprinted over time (Hoffman et al., 2015; Rivals et al., 2007; Teaford and Walker, 1984). Thus, microwear is generally considered a record of diet over the last few days to months of life (Hoffman et al., 2015; Merceron et al., 2016a, 2016b; Teaford and Oyen, 1989; Winkler et al., 2020). While this can increase the inherent

variability of microwear data because of potential short-term stochastic variation in diet, it provides opportunities to evaluate diet and dietary partitioning at finer temporal scales.

Dental microwear, including the semi-automated and standardized dental microwear texture analysis (DMTA), has proven useful for discriminating grazing, browsing, and a range of intermediate diets in modern and fossil bovids and other ungulates (Non-DMTA: Rivals et al., 2007; Rivals and Semprebon, 2011; Semprebon et al., 2016; DMTA: Bignon-lau et al., 2017; Jones and DeSantis, 2017; Merceron et al., 2014, 2016a; Scott, 2012a; Ungar et al., 2003, 2007). Previously, dental microwear and mesowear have been utilized to study the megaherbivore assemblage of the Late Pleistocene near Fairbanks, Alaska (Rivals et al., 2010). Results indicated unusual wear patterns in interior Alaska during this time: microwear textures were characterized by especially fine scratches that are atypical for extant mixed feeders and grazers. Further, mesowear data suggested that bison diets were less abrasive than horse diets (Rivals et al., 2010). The growing "library" of standardized DMTA data for modern and ancient ungulate populations provides a useful reference for studying diet, but DMTA has only rarely been applied to studying past and present megaherbivores from the far north (but see Bignon-lau et al., 2017).

Here, we use DMTA and mesowear analyses to infer the diets of Late Pleistocene bison and horses of Alaska's North Slope between >50 ka and circa 12.5 ka to assess differences in diet and the potential for niche partitioning. We also use these proxies to quantify the diets of two populations of modern Alaska bison using specimens from a free roaming herd of reintroduced wood bison (*Bison bison athabascae*) and a herd of introduced plains bison (*Bison bison bison*). These populations provide a valuable modern analog to the Pleistocene specimens and also add to the growing atlas of DMTA data for modern species and populations with observable diets. Additionally, we compare microwear and mesowear of our modern and fossil specimens with previously published data from fossil and extant bovids and equids across a spectrum of grazing to browsing diets (Jones and DeSantis, 2017; Merceron et al., 2014; Rivals et al., 2010; Scott, 2012a, 2012b). Finally, we evaluate the taphonomy of North Slope specimens. Taphonomic analysis can provide data on the ecological or biological processes impacting preservation of

biological hard parts (Behrensmeyer and Kidwell, 1985), and thus taphonomic differences between taxa may be indicative of differing modes of mortality or landscape use.

2. Materials and methods

2.1. Specimens

Quaternary megafauna have been a focus of collection efforts on Alaska's North Slope for decades. One of the most geographically extensive efforts focused on fossil-rich sections of the Ikpikpuk and Titaluk rivers (Fig. 1), the collections of which are curated in the Earth Sciences Collection at the University of Alaska Museum (UAMES). Across several decades, over 4000 specimens have been collected directly from permafrost bluffs in the upper reaches of these rivers or, more commonly, downstream along riverbanks and bars (Mann et al., 2013). Accelerator Mass Spectrometry radiocarbon dating by Mann et al. (2013) of a subset of these remains reveals bison and horse specimens range from >50 cal. kyr B.P. ("infinite" radiocarbon dates) to ca. 12.5 cal. kyr B.P. (Fig. 2). In this study, we focused on specimens likely to provide representative data on diet of the broader population. To this end, we selected all available mandibles and maxillary fragments from the collection with adult or near-adult dentition (third molar erupting or in wear), in addition to well-preserved isolated molars. We excluded specimens with malocluded teeth (where the worn profile of the teeth indicated misalignment) or teeth worn to the gumline in order to avoid teeth with potential for non-representative wear. A total of 37 *B. priscus* and 45 *Equus* sp. specimens were initially selected for study.

To provide a modern comparison to Pleistocene *B. priscus*, we sampled teeth of 18 wood bison (*B. b. athabascae*) from the herd reintroduced to Alaska in 2015 by the Alaska Department of Fish and Game (ADF&G). Specimens represent individuals culled from the herd prior to release and specimens that died after release. Additionally, we sampled eight plains bison (*B. b. bison*) from the Delta (*n* = 7) and Farewell (*n* = 1) herds. These plains bison were first introduced to the Delta Junction region of central Alaska in 1928. Individuals from the Delta herd were used to establish a separate Farewell herd in 1968 (Campbell and Hinkes, 1983). Delta and Farewell herd specimens represent hunted individuals and those that died from unknown causes. Modern *Bison* specimens are curated in the Mammalogy Collection at the University of Alaska Museum (UAM; Delta herd and some *B. b. athabascae* specimens) and the offices of the ADF&G (*B. b. athabascae* specimens, one Delta *B. b. bison* and one Farewell *B. b. bison*). Dates of death recorded for four individuals curated at University of Alaska Museum indicate bison primarily died in the fall and winter.

2.2. Taphonomic analysis

The weathering stage of each fossil mandible and maxilla was scored using the standard six weathering stages (WS), such that WS 0 is unweathered bone and WS 5 is heavily weathered bone (Behrensmeyer, 1978). Weathering stages were identified by visual inspection of each specimen. Due to available sample sizes, we combined weathering stages 0 and 1 into a "minimally weathered" category. We used Chi-square (χ^2) tests to evaluate differences in weathering stage distributions between taxa. None of the modern specimens were visibly taphonomically altered (some tool marks due to specimen preparation and preservation were observed) and were not assessed for weathering stage.

2.3. Dental Microwear Texture Analysis (DMTA)

Dental Microwear Texture Analysis (DMTA) is a highly standardized method of microwear analysis that also reduces some observational biases that can be more pronounced when counting pits and scratches in two-dimensional images (DeSantis et al., 2013; Scott et al., 2006; Ungar et al., 2003). DMTA uses scale-sensitive fractal analysis to assess the textures of high-resolution 3-dimensional maps of tooth wear surfaces produced by confocal microscopy (Fig. 3). First and second molars were preferentially targeted for analyses (per Kaiser and Fortelius, 2003). For specimens with weathered or otherwise degraded first or second molars, we focused on the third or fourth premolar. Only one tooth from each individual was evaluated for DMTA to avoid pseudo-replication. Teeth that appeared to have glue or sealants on the occlusal surfaces were excluded. Following these criteria, *B. priscus* (*n* = 16), *B. b. athabascae* (*n* = 9), *B. b. bison* (*n* = 8), and *Equus* sp. (*n* = 35) were chosen for dental microwear texture analysis.

For each fossil and modern specimen with the appropriate quality of preservation, microwear was evaluated using DMTA. Due to space constraints of the microscope, microwear textures of large mammal teeth were observed from high fidelity epoxy casts (Epotek 301), optimized for imaging. Specimen preparation of the casting procedures entailed cleaning, molding, and casting steps: the occlusal surface of one molar was cleaned with a cotton swab dipped in acetone, molded using polyvinylsiloxane dental impression material (President's Jet, Coltene-Whaledent Corp), and subsequently cast using epoxy (Epotek 301, Epoxy Technology) that set for at least 72 h.

Prior to microwear scanning, the occlusal surface of the enamel cast was visually inspected for taphonomic alteration. Acid etching and abrasion are known to degrade wear surfaces; acid etching may increase the roughness of the texture and abrasion may remove all surface features in characteristic ways (King et al., 1999). Macroscopic taphonomic alteration was identified by visual inspection of specimens prior to molding. Additionally, prior to scanning, the cast of each enamel surface was visually inspected at 20× using a stereomicroscope. Specimens were excluded if their enamel textures were exceptionally rough and appeared similar to acid-etched specimens (King et al., 1999). The buccal protoconid facet (lower molars) and lingual paracone facet (upper molars) were targeted for DMTA (Mihlbachler et al., 2016).

High resolution 3-dimensional maps of the specimens' enamel textures were made using a Sensofar PLu neox optical profiler (Solarius Development) at Vanderbilt University. For consistency with previous studies (e.g., Jones and DeSantis, 2017; Ungar et al., 2003), each tooth was scanned nine times, with a resulting scan of 204 × 276 μm area; this surface was subsequently divided into four quadrants. The microwear textures of each quadrant were quantified using standard DMTA metrics (see below) via ToothFrax and SFrax software (Ungar et al., 2003).

Following Scott (2012a), the DMTA metrics assessed for each specimen were textural complexity, heterogeneity, anisotropy, and textural fill volume. These metrics are summarized here; for a more detailed discussion, see Scott et al. (2006) and DeSantis (2016). Complexity (*Asfc*) measures the maximum change in surface roughness as the scale of observation increases. Textures with lots of pits of varying sizes or pits (especially deep pits) and scratches overlying each other have higher complexity values. Heterogeneity (*HAfc*) measures the variation of complexity across the surface. The surface is split into subregions (here, equally spaced grids of 3 × 3 and 9 × 9) and the heterogeneity is quantified as the absolute deviation in complexity divided by the median complexity. Anisotropy (*epLsar*) measures the "directionality" of the texture, such that lots of parallel scratches yield higher anisotropy values. Textural fill volume (*Tfv*) measures the volume required to fill the "damaged" enamel surface. This estimate is calculated by summing the number of cubes required to fill the surface. To accommodate the overall geometries of tooth surfaces (e.g., the slight curve of the enamel ridge) the final textural fill volume estimate measures the general shape of the scan with large cubes (10 μm³) and subtracts this value from the detailed volume estimate produced by measuring with small cubes (2 μm³).

For most subsequent analyses, we summarized microwear metrics for each individual as the median of the four quadrants of the scan. We used Mann-Whitney *U* tests to evaluate differences in dental microwear textures between taxa (Mann and Whitney, 1947), similar to Jones and DeSantis, 2017); Levene's Test was used to evaluate differences in
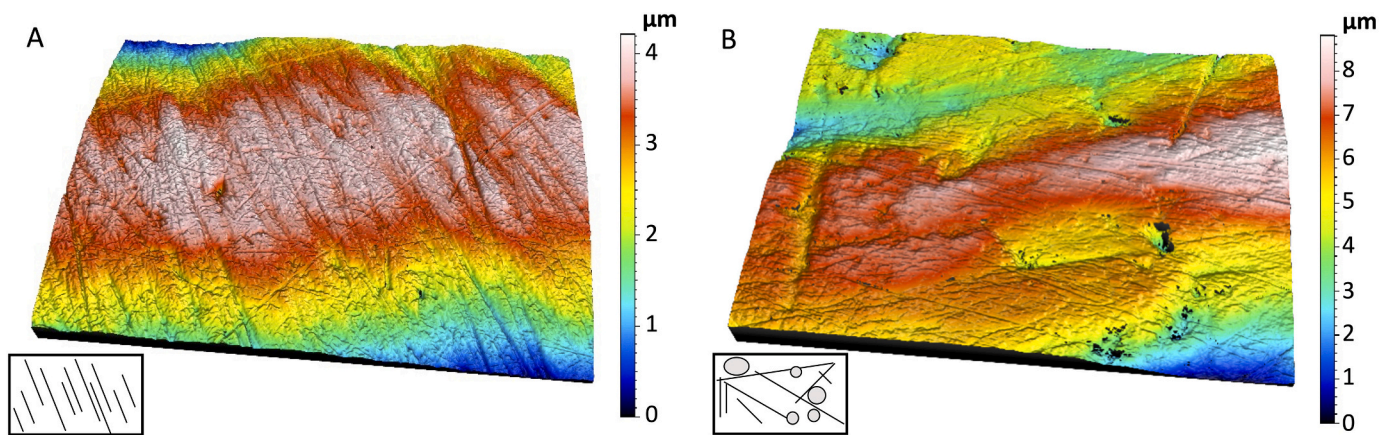
Fig. 3. Example of 3D surface models of dental microwear textures of *Bison* and *Equus* sp. specimens. Scanned area is 204 × 276 μm. Color scale indicates height of tooth wear surface – note the different scales in (A) and (B). A) Consistent parallel scratches (largely oriented upper left to lower right quadrants) yields relatively high anisotropy: *epLsar* = 4.676×10^3 in this specimen (UAMES 36096; *Equus* sp.). B) Scratches and pits of varying sizes yield relatively high complexity values: *Asfc* = 2.291 in this specimen (UAMES 23488; *Bison priscus*). Lower left insets show simplified cartoons of (A) high anisotropy and (B) high complexity surfaces.

variance of DMTA attribute values between taxa (Levene, 1960). Non-parametric tests were preferable because they can better accommodate non-normal distributions that often characterize DMTA data and are preferable when dealing with small sample sizes (Gotelli, 2008), as is the case for available specimens from extant Alaska bison populations. Because comparisons among species and populations are partially nested, rather than strictly pairwise, we do not employ Bonferroni corrections and instead report raw *p*-values (Cabin and Mitchell, 2000). To supplement these summary analyses, we incorporated the four scans generated per specimen to compare taxa using mixed models. In this context, each specimen is treated as a random effect: a "grouping" variable that allows for non-random replicate data to be appropriately incorporated into the model (Bates et al., 2015).

We also compared DMTA results collected for this study with published DMTA results for other fossil and modern bison and equid species, specifically Late Pleistocene *Bison antiquus* and *Equus occidentalis* specimens collected from the La Brea tar pits and modern plains *B. b. bison* and modern zebra (*Equus burchelli* and *Equus zebra*) published by Jones and DeSantis (2017) and modern European wood bison (*Bison bonasus*) published by Merceron et al. (2014). For these analyses, we only performed Mann-Whitney *U* tests and Levene's test of variance because only median DMTA data for each specimen were reported. We restricted analyses to anisotropy and complexity because these DMTA measures are the most useful for segregating herbivores along the grazer-browser continuum (Scott, 2012a).

Finally, we compared our DMTA data to Scott's 2012 dataset of extant African bovids (Scott, 2012b) using discriminant function analysis (Davis, 2002) to test how well DMTA measures (*epLsar, Asfc, Tfv, HAsfc$_{3x3}$, HAsfc$_{9x9}$*) group specimens and species into dietary categories. For this analysis, Scott's 2012 dataset of African bovids is especially useful because it includes multiple species for multiple dietary categories. We used a simplified version of Scott's dietary categories: excluding frugivores and grouping generalists and browser-grazer intermediates together. The predictive accuracy of the discriminant function was evaluated using the leave-one-out (jacknife) method, and then applied to our data. We also tested the discriminant function on modern zebra DMTA values (Jones and DeSantis, 2017) to assess its predictive ability when applied to North Slope *Equus* sp.. We ran two discriminant analyses. The first grouped individual specimens into their dietary categories; we selected a quadratic discriminant function for this analysis because of large available sample sizes and better model performance (*i.e.*, the model correctly categorized more specimens during the leave-one-out evaluation). Our interest in this analysis was to quantify variability within populations rather than the dietary category

of particular specimens. To this end, we summarized results as the proportion of specimens in each dietary class. For the second analysis, we focused on species means of DMTA metrics and their associated dietary categories; sample sizes of individuals per species ranged from 20 to 25. At the species level, we used a linear discriminant function because sample sizes for this second analysis were too low to use a quadratic discriminant function.

2.4. Dental mesowear

Mesowear analysis was conducted on lower molars because available fossil material was dominated by lower teeth. Upper and lower molars wear differently, so it is not appropriate to combine them in a single analysis without correction (Kaiser and Fortelius, 2003). Mesowear observations were performed on photographs of specimens. While specimens selected for mesowear analysis generally overlapped those described above for microwear analysis, there were a few exceptions. For example, some specimens were coated with epoxy or glue and therefore were unsuitable for microwear analysis but viable for mesowear analysis. Some specimens chosen for microwear analysis had broken cusps making them unsuitable for mesowear analysis. Ultimately, *B. b. athabascae* specimens (*n* = 15), *B. b. bison* (*n* = 4), and *B. priscus* (*n* = 15) specimens were selected for mesowear analysis, in addition to *Equus* sp. (*n* = 20) specimens. For each specimen, M_1 and M_2 were assessed, though some specimens did not retain both teeth.

Following established protocols (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003), tooth cusp shape was scored as "sharp," "round," or "blunt", with either "high relief" or "low relief". Equid molars were also given an overall mesowear value using the mesowear ruler developed by Mihlbachler et al. (Loffredo and DeSantis, 2014; Mihlbachler et al., 2011). For clarity, we refer to this overall value as the "Mesowear Numerical Score" (MNS) per Loffredo and DeSantis (2014). An MNS score of 0 is a maximally sharp equid cusp and 6 is a completely blunted or flattened cusp. "High relief" molars have an MNS score between 0 and 3, and "low relief" molars have an MNS score $\geq$ 4. To address inter-observer variability in mesowear scoring, each molar was scored independently by six graduate student observers (Loffredo and DeSantis, 2014). *Bison* and *Equus* sp. teeth were scored during separate sessions, and observers were trained for 5–10 min using example photographs of the relevant taxa before scoring mesowear. Observers had no prior experience scoring mesowear, which is reasonable as it is a teachable method where the power of the analysis comes from multiple individuals scoring the same specimens (Loffredo and DeSantis, 2014).

For statistical analysis, shape and relief scores were translated into numerical values. For mesowear shape: "blunt" = 1, "round" = 2, and "sharp" = 3. For mesowear relief: "blunt" = 1 and round = "2". Following Jones and DeSantis (2017), based on assignments from all six evaluators, each tooth was assigned a median score for all three metrics (shape, relief, and MNS). North Slope Pleistocene *B. priscus* mesowear shape and relief scores were compared to modern Alaska bison (both *B. athabascae* and *B. b. bison* binned together) using Mann Whitney tests. For each test, the same tooth was compared between groups (e.g., *B. priscus* M_1 to extant *Bison* M_1).

Finally, because visual assessment suggested that there might be differences in bison tooth relief between modern and Pleistocene specimens, we also assessed differences in mesowear relief for statistical significance by comparing observed results to a modeled null expectation using randomization (Kowalewski and Novack-Gottshall, 2010). For our test statistic, we focused on the difference between the proportion of modern and Pleistocene bison that were scored as having "high" relief. To calculate this for each observer, we first calculated the proportion of teeth they scored as "high" for modern bison (h_{modern}) and Pleistocene bison (h_{Pleist}). We then calculated the differences in these proportions (h_{diff}) between modern and Pleistocene bison. To calculate our final test statistic, we summarized data from all observers by calculating the mean observed difference in "high" teeth between modern and Pleistocene bison ($\overline{h}_{diff}$). We compared our observed data to a modeled null expectation to test the significance of observed differences between Pleistocene and modern bison, given our sampling. Our null model was generated by maintaining the total "high" and "low" scores for each observer but randomizing how the scores were assigned to each specimen. We calculated the modeled test statistic 10,000 times, which established a null distribution centered around the null expectation of 0.0 (no difference between groups), with positive values indicating Pleistocene bison teeth are sharper than modern teeth, and negative values indicating modern bison teeth are sharper. We assessed statistical significance by calculating the proportion of $\overline{h}_{diff\_modeled}$ values equal to or more extreme than our observed $\overline{h}_{diff}$ (both positive and negative); this is equivalent to a two-sided *p*-value (Kowalewski and Novack-Gottshall, 2010; Miller et al., 2014).

All statistical analyses were carried out in R (version 3.5.1, R Core Team, 2018). Mixed models and discriminant analyses were built using the lme4 (Bates et al., 2015) and MASS (Venables and Ripley, 2002) libraries, respectively. Figures were built using the cowplot wrapper for the ggplot2 library (Wilke, 2019; Wickham, 2016). DMTA data for each dietary category were visually summarized using ggplot2's 'stat_ellipse' function, which plots a 95% confidence ellipse around the species means (Wickham, 2016). Spline curves were built using the 'geom_smooth' function in the ggplot2 library (Wickham, 2016).

3. Results

3.1. Taphonomy

Out of the 36 Pleistocene *B. priscus* specimens initially selected for this study, only 16 (44%) had no visible evidence of taphonomic alteration, thus meeting the criteria for inclusion. Of the 45 *Equus* sp. specimens, 38 (84%) met the criteria for inclusion. *Bison priscus* specimens were significantly more likely to have weathered or degraded microwear textures than *Equus* sp. specimens ($\chi^2 = 8.15$, df = 1, p-value = 0.004). There was no significant difference in bone weathering stage distributions between *B. priscus* and *Equus* sp. ($\chi^2 = 4.62$, df = 4, p-value = 0.33). For both *B. priscus* and *Equus* sp., teeth from mandibles or maxillae with higher weathering stages were more likely to have wear facets that were degraded by post-mortem weathering; the trend was especially pronounced for bison specimens in weathering stage 3 or higher (Fig. 4). Isolated molars for both bison and horses were more likely to have degraded microwear; again, this trend was more pronounced for bison
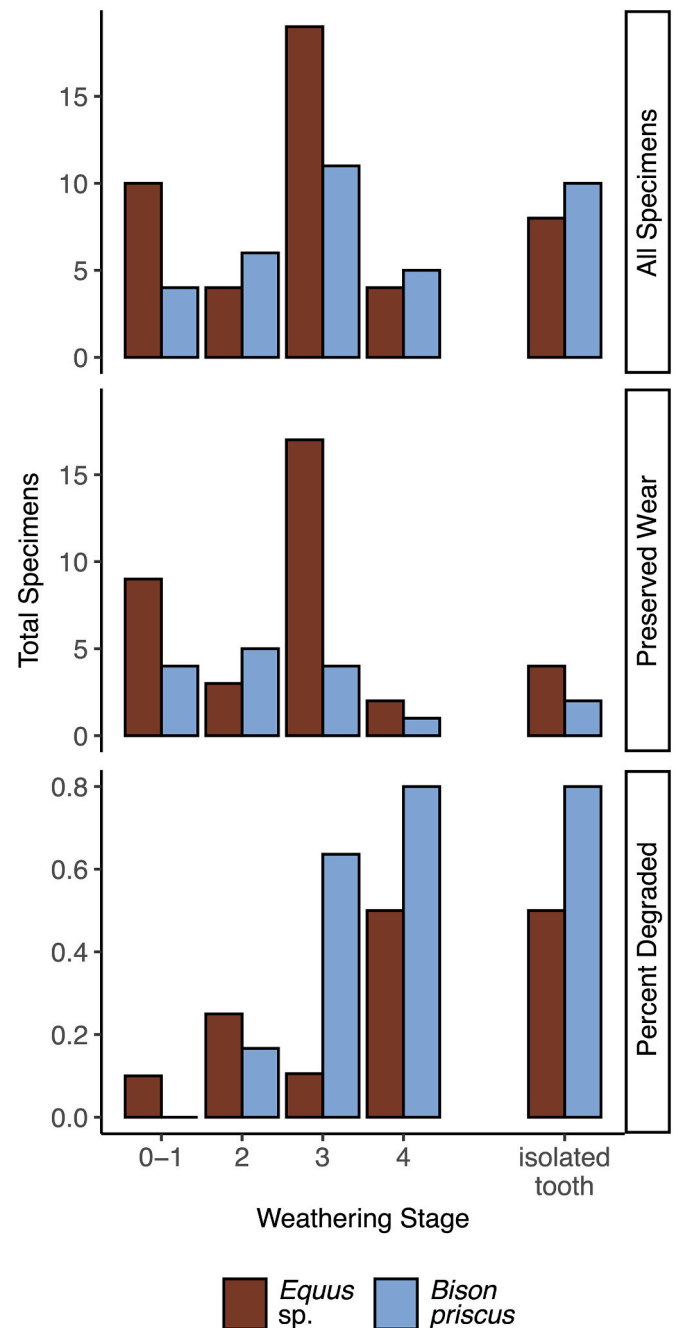

Fig. 4. Weathering stage distributions and counts of isolated teeth. Data illustrated for all specimens initially selected for this study (top), specimens showing preserved tooth wear facets (middle), and the proportion of specimens with taphonomically degraded microwear facets (bottom). Only specimens with well-preserved microwear facets (middle plot) were used for dental microwear analyses. No Pleistocene specimens examined here were in weathering stage 5.

specimens (Fig. 4). For all DMTA analyses (below), only data from specimens with preserved antemortem microwear are presented.

3.2. Microwear

The dental microwear textures of Pleistocene bison and horses from the North Slope were indistinguishable from one another for the DMTA measures of anisotropy, complexity, and textural fill volume (Fig. 5 A–C), though bison had higher heterogeneity values at both the 3×3 and 9×9 scales (Fig. 5 D–E, Table 1). Additionally, variances between
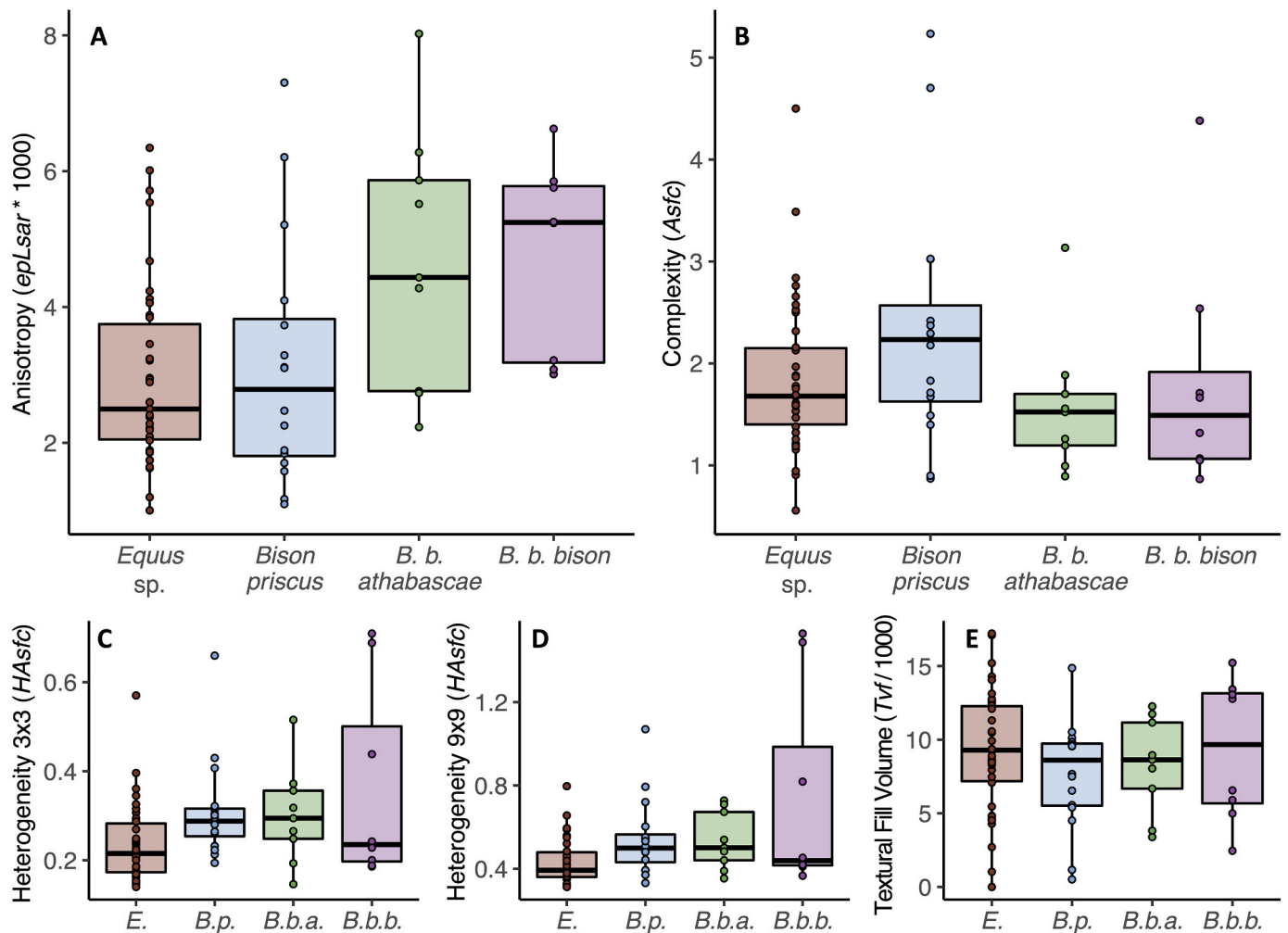
Fig. 5. Boxplots comparing distributions of DMTA metrics between Pleistocene *Equus* sp. and *B. priscus* from the North Slope and modern *B. b. athabascae* and Delta *B. b. bison*. Median values for each specimen overlay boxplots summarizing results for each taxon: A) anisotropy, B) complexity, C) heterogeneity at the 3×3 scale, D) heterogeneity at the 9×9 scale, and E) textural fill volume. Boxplots show median value for each taxon (midline) bounded by the 1st and 3rd quartiles (colored box); whiskers extend to farthest point within 1.5 times the interquartile range.

bison and horses were not significantly different for any DMTA attribute (Levene's test, $p > 0.10$, Table 1).

Modern *B. athabascae* were indistinguishable from modern *B. b. bison* for all DMTA measures (Fig. 5, *B. b. athabascae* and *B. b. bison*), though *B. b. bison* had slightly higher anisotropy values on average, as supported by both Mann Whitney tests and mixed model results (Table 1, Table 2). Two *B. b. bison* specimens from the Delta herd had especially high heterogeneity values at both the 3×3 and 9×9 scales, but median values were similar between the two modern bison subspecies. The *B. b. bison* specimens had significantly higher variance in textural fill volume than *B. b. athabascae* specimens (Table 2). No other DMTA attribute had significantly different variances between modern Alaska bison.

Late Pleistocene *B. priscus* had significantly lower anisotropy values than modern Alaska bison (Fig. 5, Table 2, $p = 0.014$), though not when accounting for within-specimen variation (the mixed model). *B. priscus* also had marginally lower anisotropy values than modern Montana plains bison (Fig. 6A, Table 3; Mann-Whitney test, $p = 0.055$). Compared to modern European wood bison (*B. bonasus*), *B. priscus* had significantly lower complexity values (Mann-Whitney test, $p < 0.001$) and similar anisotropy values (Fig. 6A, Table 3).

North Slope *Equus* sp. had significantly lower complexity ($p < 0.001$) than *Equus occidentalis* from the La Brea tar pits dating to the Late Pleistocene, but statistically indistinguishable anisotropy (Fig. 6B, Table 3). Compared to modern zebra, North Slope *Equus* sp. fossils had

significantly lower anisotropy ($p < 0.001$) but similar complexity values (Fig. 6B, Table 3). All microwear data newly reported here are available in Supplemental Table 1.

The quadratic discriminant function for African bovid DMTA successfully classified the dietary guild of 86% of extant African specimens using leave-one-out cross validation. This same model classified most specimens of modern Alaskan bison and Pleistocene bison and horses as either generalists or variable grazers, though modern zebra were classified as mixed feeders (Table 4). When performed using species medians rather than individual specimen DMTA values, leave-one-out linear discriminant analysis was 100% successful at assigning extant African species to their known dietary categories. This discriminant function classified the reintroduced *B. b. athabascae* and *B. b. bison* as variable grazers and North Slope Pleistocene bison and horses as generalists.

3.3. Mesowear

The majority of *B. priscus* M_1 teeth were scored as "round" with "low" relief, and majority bison M_2 teeth were scored as "round" with "high" relief (Figs. 7, 8). For both M_1 and M_2, there were no significant differences between modern Alaska bison and North Slope Pleistocene bison for mesowear scores of shape and relief (Mann Whitney tests, $p > 0.1$). Though molars of Pleistocene *B. priscus* were qualitatively more

Table 1
Summary statistics for DMTA metrics for taxa assessed in this study and modern species with known diets for comparison.

Taxon	Diet	N	epLsar*10^3 (med., sd)	Asfc (med., sd)	HAfsc 3 × 3 (med., sd)	HAfsc 9 × 9 (med., sd)	Tfv (med., sd)
B. b. athabascae	–	9	4.44, 1.92	1.52, 0.67	0.29, 0.11	0.50, 0.14	8634, 3224
B. b. bison	–	8	5.25, 1.43	1.49, 1.16	0.24, 0.22	0.44, 0.50	9667, 4821
B. priscus	–	16	2.79, 1.81	2.23, 1.21	0.29, 0.11	0.50, 0.19	8610, 3654
Equus sp.	–	38	2.50, 1.34	1.68, 0.75	0.22, 0.09	0.39, 0.11	9292, 4073
Bison antiquus[1]	–	44	3.20, 1.29	2.36, 1.70	0.50, 0.25	0.80, 0.40	13,303, 1548
Equus occidentalis[1]	–	33	3.00, 1.56	3.36, 1.83	0.47, 0.19	0.83, 0.29	13,883, 1847
Bison bison[1]	–	27	4.00, 1.78	1.85, 0.55	0.30, 0.19	0.57, 0.25	12,790, 1830
Equus burchelli[1]	–	21	4.50, 1.65	2.22, 0.84	0.30, 0.11	0.59, 0.16	13,940, 1730
Equus zebra[1]	ob. grazer	21	4.80, 1.59	1.97, 0.52	0.40, 0.15	0.66, 0.25	13,212, 1273
Aepyceros melampus[2]	generalist	20	3.75, 1.84	1.81, 0.48	0.46, 0.14	0.75, 0.24	5720, 1062
Antidorcas marsupialis[2]	generalist	21	3.63, 1.22	2.06, 1.14	0.48, 0.14	0.80, 0.14	5734, 1269
Damiliscus lunatus[2]	ob. grazer	22	6.60, 0.78	0.91, 0.25	0.44, 0.07	0.67, 0.07	1912, 945
Damiliscus pygargus[2]	var. grazer	22	5.15, 1.40	1.26, 0.39	0.39, 0.09	0.61, 0.08	4917, 1664
Gazella granti[2]	var. grazer	25	4.30, 0.84	1.82, 0.45	0.36, 0.07	0.69, 0.12	3070, 1243
Hippotragus niger[2]	var. grazer	23	6.34, 1.29	1.53, 0.48	0.54, 0.09	0.74, 0.10	4929, 1048
Kobus ellipsyprymnus[2]	var. grazer	22	6.07, 0.85	1.36, 0.45	0.54, 0.27	0.80, 0.77	3474, 1077
Kobus leche[2]	ob. grazer	24	5.75, 0.77	0.95, 0.27	0.38, 0.06	0.75, 0.12	2975, 981
Litocranius walleri[2]	browser	25	2.40, 0.59	3.26, 1.10	0.70, 0.18	0.99, 0.20	10,685, 1875
Neotragus batesi[2]	browser	23	2.10, 0.52	4.12, 1.10	0.60, 0.11	0.93, 0.13	9875, 1604
Oreotragus oreotragus[2]	generalist	24	3.66, 0.74	2.22, 0.57	0.45, 0.08	0.74, 0.18	8587, 1851
Raphicerus campestris[2]	generalist	21	2.55, 0.91	2.35, 0.54	0.49, 0.09	0.87, 0.16	8421, 1617
Raphicerus sharpei[2]	generalist	25	4.10, 1.20	2.52, 0.43	0.58, 0.10	0.93, 0.15	4863, 1355
Redunca arundinum[2]	ob. grazer	25	6.20, 0.88	0.87, 0.22	0.37, 0.04	0.79, 0.09	3497, 1001
Redunca fulvorfula[2]	ob. grazer	23	7.55, 1.91	1.19, 0.25	0.42, 0.10	0.62, 0.09	1677, 517
Sylvicapra grimmia[2]	browser	25	2.76, 0.74	3.20, 0.77	0.61, 0.29	0.88, 0.16	11,599, 3233
Syncerus caffer[2]	var. grazer	22	5.03, 1.21	1.48, 0.45	0.44, 0.08	0.73, 0.14	2873, 1185
Taurotragus oryx[2]	generalist	21	3.80, 1.19	2.13, 0.45	0.50, 0.16	0.84, 0.22	6830, 1290
Tragelaphus angasi[2]	generalist	22	3.78, 1.28	1.88, 0.73	0.44, 0.09	0.79, 0.15	9882, 1506
Tragelaphus euryceros[2]	browser	22	1.92, 0.46	3.80, 0.82	0.62, 0.11	0.97, 0.18	12,741, 2306
Tragelaphus imberbis[2]	generalist	23	3.92, 1.35	1.96, 0.61	0.46, 0.09	0.87, 0.23	7128, 2063
Tragelaphus spekii[2]	var. grazer	22	4.33, 1.42	1.88, 0.45	0.40, 0.06	0.88, 0.13	2546, 1020
Tragelaphus strepsiceros[2]	generalist	25	4.56, 0.91	2.39, 0.65	0.47, 0.07	0.87, 0.18	9027, 1914

[1]Data from Jones and DeSantis (2017). [2]Data from Scott (2012b). Diets of living species are based on feeding observations as classified by Gagnon and Chew (2000) and reported by Scott (2012a, 2012b). N = total individuals, *epLsar*$*10^3$ = anisotropy, *Asfc* = complexity, *Hafsc* 3 × 3 = Heterogeneity at 3 × 3 scale, *Hafsc* 9 × 9 = Heterogeneity at 9 × 9 scale, *Tfv* = textural fill volume, med. = median, sd = standard deviation.

likely to be scored as "high" relief than modern bison molars, we found that this tendency was also non-significant using our modeled null expectation ($p = 0.19$; Fig. 7).

The majority of all assessed *Equus* sp. teeth (PM$_1$, M$_1$, M$_2$, and M$_3$) were scored as "round" or "blunt" with "low" relief (Fig. 7). The MNS scores were 5.8, 5.5, 4, and 5 for PM$_1$, M$_1$, M$_2$, and M$_3$ respectively. Mesowear data are available in Supplemental Table 2.

3.4. Dietary signal through time

Fourteen of the *Equus* sp. specimens selected for this study were previously radiocarbon dated by Mann et al. (2013). Evaluating DMTA complexity values through time, we find a decrease between 50 and 30 ka before increasing again (Fig. 9), though with such limited data these trends cannot be rigorously tested. Anisotropy values are generally higher around 30 ka. Though two of the bison selected for this study were radiocarbon dated by Mann et al. (2013; Fig. 2), both yielded infinite dates and therefore were not useful for evaluating change in microwear through time.

4. Discussion

4.1. Taphonomic signal

We found that occlusal surfaces of *B. priscus* were significantly more likely to have taphonomically altered microwear surfaces than *Equus* sp., despite overall similarity in bone weathering. While a detailed taphonomic analysis of this weathering paradox is beyond the scope of this work, substantial differences in enamel damage between North Slope *B. priscus* and *Equus* sp. teeth warrant preliminary discussion. All specimens were collected from similar sedimentary facies and extensive

radiocarbon dating of the fossil collection (including specimens other than mandibles and maxillae) suggests *B. priscus* and *Equus* sp. have broadly overlapping age ranges (Fig. 2). Thus, it is most likely that the observed taphonomic disparity in enamel preservation arises from either (1) physical and/or chemical differences in the enamel, or (2) different pathways to preservation.

While the chemical makeup of dental enamel is highly conserved across mammals (Koenigswald and Clemens, 1992), there are known phylogenetic differences in enamel microstructure, likely related to diet (Pfretzschner, 1993; Sathe, 2000; Vislobokova and Dmitrieva, 2000). It is possible that differences in enamel microstructure could contribute to the observed difference in enamel weathering between horse and bison specimens. However, while hypsodont dentition developed separately in these two lineages, convergent evolution appears to have resulted in the development of similar enamel microstructures. In horses, the evolution of hypsodont cheek teeth was associated with modification of enamel microstructures, likely a response to the increased abrasion of grazing diets (Pfretzschner, 1993); similar modified radial enamel evolved in artiodactyl hypsodonts including bison (Sathe, 2000). Without experimental data comparing enamel weathering between these groups, we cannot definitively rule out a phylogenetic signal reflected in taphonomy. However, it should be noted that enamel preservation is often similar between horses and bison in North American fossil deposits (e.g. Rancho La Brea in California, Leisey 1A in Florida), suggesting that differences observed here are taphonomic in origin.

Observed differences in enamel taphonomy likely reflect different preservation pathways. The similar weathering stage distribution between horse and bison specimens would initially suggest similar post-mortem histories, yet it is possible that enamel breakdown responds to different weathering processes and/or occurs at a different rate than bone. Differences in enamel vs. bone preservation are not uncommon

Table 2

Significance estimates (*p*-values) for tests comparing DMTA metrics between taxa.

	DMTA metric	Mann Whitney	Mixed Model	Levene's
North Slope *B. priscus* (*n* = 16) vs. *Equus* sp. (*n* = 38)	*Asfc*	0.127	0.055	0.115
	epLsar	0.887	0.830	0.212
	Tfv	0.348	0.229	0.707
	Hasfc 3 × 3	0.004* *B. priscus*	0.002* *B. priscus*	0.734
	Hasfc 9 × 9	0.015* *B. priscus*	0.001* *B. priscus*	0.196
Alaska *B. b. bison* (*n* = 8) vs. *B. b. athabascae* (*n* = 9)	*Asfc*	0.888	0.609	0.386
	epLsar	0.815	0.897	0.430
	Tfv	0.606	0.529	0.041* *B. b.bison*
	Hasfc 3 × 3	0.888	0.569	0.268
	Hasfc 9 × 9	0.963	0.291	0.179
North Slope *B. priscus* (*n* = 16) vs. modern AK bison (grouped; *n* = 17)	*Asfc*	0.053	0.074	0.370
	epLsar	0.014* Modern bison	0.008* Modern bison	0.999
	Tfv	0.488	0.367	0.494
	Hasfc 3 × 3	0.763	0.873	0.199
	Hasfc 9 × 9	0.986	0.490	0.266

Tests shown are Mann-Whitney U tests (performed on median values for each specimen), Linear Mixed Models, and Levene's test of variance (performed on median values for each specimen) comparing Pleistocene *B. priscus* with *Equus* sp.; modern Alaskan *B. b. athabascae* (Wood bison) with the Delta herd of *B. b. bison* (Plains bison); and Pleistocene *B. priscus* with all modern Alaskan bison pooled together. Asterisks highlight statistical significance at the *p* < 0.05 level; in cases of significant differences, the species with the higher value is listed (median and standard deviation are reported in Table 1). DMTA abbreviations as in Table 1.

(Behrensmeyer, 1978). Importantly, the scale of evaluation between bones (visual study) and teeth (microscopic study) was very different and may highlight different taphonomic processes such as UV breakdown and/or wet-dry cycling (bones) versus microscopic abrasion and/or acid etching (teeth). Thus, differences in enamel preservation between horse and bison specimens may reveal differences in how they were incorporated into the fossil record that are not captured by bone weathering stage data.

One possible explanation for taphonomic distinction between *B. priscus* and *Equus* sp. is different pre-burial histories, possibly generated by different patterns of landscape use. The progression of taphonomic alteration is related to the length of subaerial exposure prior to burial and to a lesser degree, the transport distance prior to final burial (Aslan and Behrensmeyer, 1996; Miller, 2012; Miller et al., 2013; Miller et al., 2021; Rogers et al., 2007; Behrensmeyer, 1990). Carcass disarticulation and consumption by carnivores, exposure durations of skeletal remains to sunlight, freeze-thaw cycles, wet-dry cycles, exposure to organic acids above the permafrost, and the frequency of final burial events are all taphonomic processes that could vary across microhabitats (Behrensmeyer, 1978; Haynes, 1982; Hill, 1979; Mech and Peterson, 2003; Oliver and Graham, 1994; Pokines et al., 2016). If *B. priscus* and *Equus* sp. populations used the landscape differently and were more likely to die in different microhabitats (e.g., lowland tundra versus upland stream valleys; wet vs. dry; shaded vs. exposed), then the differing pre-burial weathering rates and frequency of final burial events could contribute to the taphonomic distinction we observed between *B. priscus* and *Equus* sp.. Finally, radiocarbon dates suggest slightly different relative abundances through time: *B. priscus* specimens are on average more likely to be older than *Equus* sp. specimens, though the distributions are highly overlapping (Fig. 2). Since climate could impact both pre-burial conditions and the frequency of final burial events,

differences in the temporal distribution of *B. priscus* and *Equus* sp. could contribute to the observed taphonomic differences.

4.2. Diet

4.2.1. Late Pleistocene diet

We found that Pleistocene *B. priscus* had values of dental microwear anisotropy and complexity between modern bison with obligate/variable grazing diets (Alaska *B. b. athabascae* and *B. b. bison,* and mid-continent *B. b. bison*) and the more browse-enriched diets of European bison, *B. bonasus* (Campbell and Hinkes, 1983; Coppedge et al., 1998; Kerley et al., 2012; Larter and Gates, 1991; Peden et al., 1974; Waggoner and Hinkes, 1986). Further, we found that *B. priscus* mesowear profiles had marginally higher relief than modern Alaska bison, also suggesting a less graminoid-rich diet for Pleistocene *B. priscus* compared to modern Alaska bison. Previous microwear studies (low-magnification) have also demonstrated that Pleistocene bison populations occupied a wider spectrum of dietary niches than modern Plains bison, and generally consumed less abrasive diets, though diets varied significantly between geographic and temporal populations (Rivals et al., 2007). Rivals et al. (2010) found that in central Alaska, Late Pleistocene *B. priscus* had similar numbers of microwear pits and scratches to modern grazers, but inexplicably narrow scratches unlike any documented modern herbivores.

We found that *Equus* sp. specimens from the North Slope exhibited significantly lower anisotropy values compared to modern equid grazers (zebras), indicating a less graminoid-dominated diet. North Slope *Equus* sp. specimens had significantly lower complexity values than Pleistocene *E. occidentalis* from Rancho La Brea, indicating that they may have consumed less woody material than contemporary horses at Rancho La Brea, though horse at Rancho La Brea varied the amount of woody material consumed through time (Jones and DeSantis, 2017). Thus, as we found for *B. priscus,* our results show that North Slope Pleistocene *Equus* sp. have dental microwear textures indicative of the consumption of both grass and browse. For mesowear, we found that the majority of *Equus* sp. lower molars were blunt with low relief and had MNS values between 4 and 6. In upper molars, these values would be indicative of grazing or variable grazing diets (Mihlbachler et al., 2011). Lower molars are known to be blunter than upper molars (Kaiser and Solounias, 2003), but our mesowear results are consistent with North Slope *Equus* sp. specimens foraging on more than just graminoids.

While the above within-genus comparisons offer the most conservative dietary inferences, Scott's (2012a, 2012b) DMTA study of African bovids across the grazing-browsing spectrum provides an additional useful reference. Compared to African bovids, Pleistocene *B. priscus* DMTA values are most similar to African bovids that occupy a more generalist dietary niche (Scott, 2012a, 2012b; Fig. 6). The same discriminant function classified Alaskan *B. b. athabascae* and *B. b. bison* as variable grazers. This finding aligns well with independent assessments of herd diets, which suggest they seasonally incorporate >50% non-monocot shrubs, forbs and lichens (Larter and Gates, 1991; Waggoner and Hinkes, 1986). Thus, despite potential differences between African and far northern vegetation textures, it appears that the African bovid-trained discriminant function may be an informative tool for interpreting bison diet from DMTA. While North Slope *Equus* sp. specimens are also most similar to African bovid mixed-feeders and generalists in the discriminant function, African bovids are likely a less-appropriate comparative framework for interpreting equid diets. Notably, this discriminant function classified modern zebras as mixed feeders when they are known to have a more grass-dominated diet (McNaughton and Georgiadis, 1986; Owaga, 1975). Thus, our direct comparisons to other *Equus* species (North Slope *Equus* sp. versus *E. occidentalis, E. burchelli* and *E. zebra*) likely provide more robust dietary information.

Our results show that *B. priscus* and *Equus* sp., the dominant morphologically inferred "grazers" of the North Slope, were more
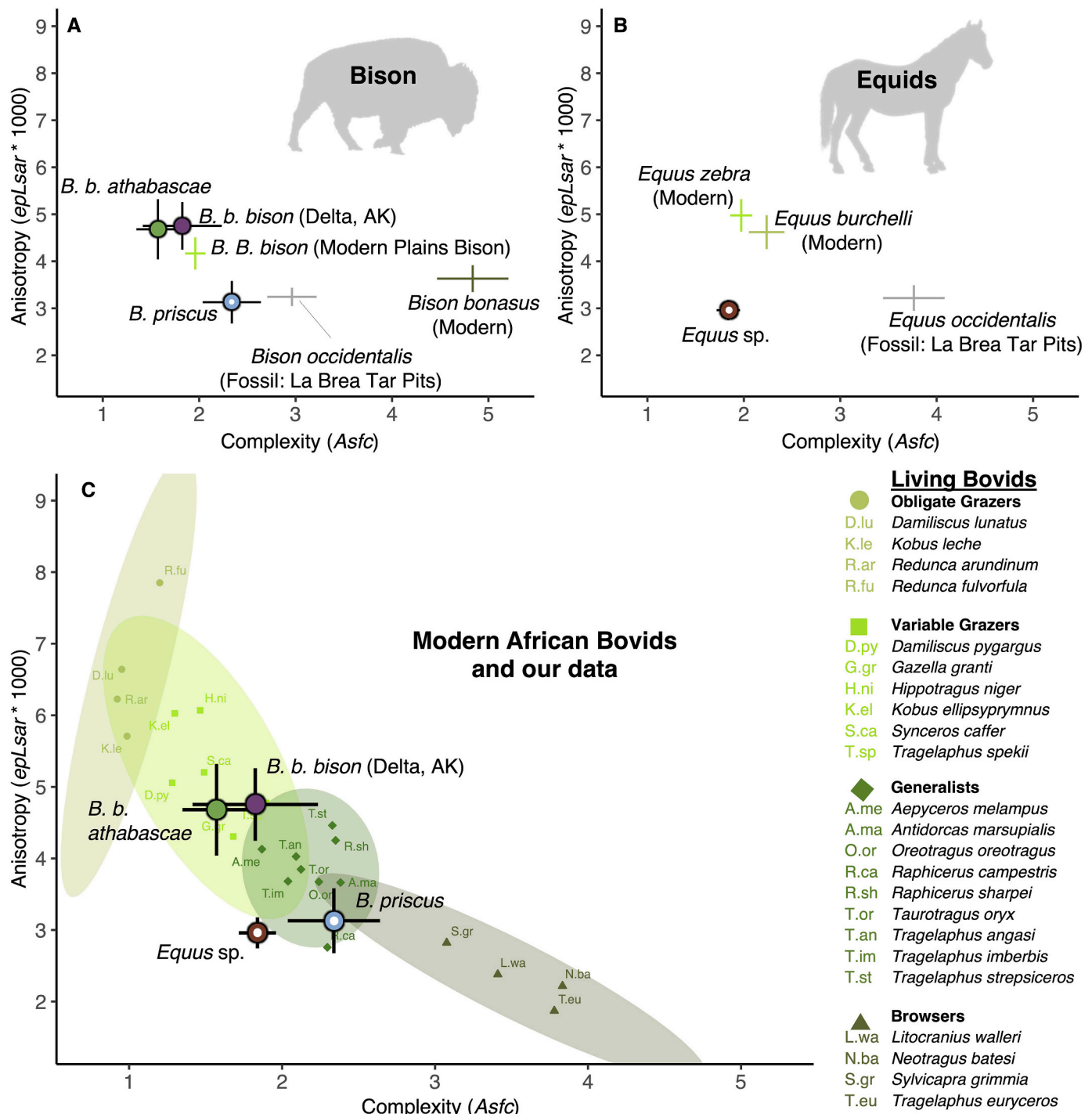
Fig. 6. Comparison of DMTA results with previously published DMTA data. Data and comparisons summarized for (A) *Bison,* (B) *Equus* sp.. Alaska bison and horse (our results) also compared to DMTA values from (C) modern African bovids (Scott, 2012b) corresponding to a continuum of dietary niches from obligate grazing to obligate browsing. Ellipses show 95% confidence around the dietary category means for complexity and anisotropy. All horizontal and vertical error bars show one standard error on either side of the population mean. Data on Modern Plains Bison, *Bison occidentalis,* and *Equus occidentalis* from Jones and DeSantis et al. (2019), *Bison bonasus* from Merceron et al. (2014), and modern African bovids from Scott (2012b).

dietarily similar to modern mixed feeders than modern grazers. Rather than subsisting on a graminoid-dominated diet, Late Pleistocene bison and horses of the North Slope likely incorporated a wider variety of protein-rich forbs and/or shrubs in their diets than modern grazers. DMTA-based dietary estimates also agree with other lines of evidence, including gut content analysis, ancient DNA, and plant macrofossils that suggest forb-rich diets for Late Pleistocene bison and horses (Guthrie, 1990; Kienast et al., 2005; Willerslev et al., 2014, 2003; Zazula et al.,

2003; Zimov et al., 2012). These results support differences in available Late Pleistocene forage on the North Slope of Alaska compared to today; a likely contributor to higher diversity and population densities of megafauna in the Late Pleistocene than supported by modern tundra floras.

4.2.2. Niche partitioning

B. priscus and *Equus* sp. specimens from the Pleistocene North Slope

Table 3
Significance estimates (p-values) for tests comparing taxa assessed in this paper with previously published data.

	DMTA Metric	Mann Whitney	Levene's
North Slope *B. priscus* (*n* = 16) vs. La Brea *B. antiquus* (*n* = 44)[1]	*Asfc*	0.292	0.157
	epLsar	0.408	0.130
North Slope *B. priscus* (*n* = 16) vs. modern plains *B. b. bison* (*n* = 27)[1]	*Asfc*	0.390	0.038* *B. b. bison*
	epLsar	0.055	0.818
North Slope *B. priscus* (*n* = 16) vs. modern European *B. bonasus* (*n* = 45)[2]	*Asfc*	< 0.001* *B. bonasus*	0.019* *B. bonasus*
	epLsar	0.254	0.765
North Slope *Equus* sp. (*n* = 38) vs. La Brea *E. occidentalis* (*n* = 33)[1]	*Asfc*	< 0.001* *E. occidentalis*	< 0.001* *E. occidentalis*
	epLsar	0.489	0.401
North Slope *Equus* sp. (*n* = 38) vs. modern zebras (*n* = 42)[1]	*Asfc*	0.058	0.960
	epLsar	< 0.001* Zebras	0.315

[1]Data from Jones and DeSantis (2017). [2]Data from Scott (2012b). Asterisks highlight statistical significance at the *p* < 0.05 level; in cases of significant differences, the species with the higher value is listed (median and standard deviation are reported in Table 1). DMTA abbreviations as in Table 1.

have very similar dental microwear textures, indicating that they consumed vegetation with similar textural properties and likely had significant overlap in their diets. Additionally, both taxa had similar variability in microwear textures, suggesting similar dietary niche breadth. Our DMTA results do not support the hypothesis that the coexistence of bison and horses was driven by dietary niche partitioning.

At face value, our mesowear results do support niche differences between *B. priscus* and *Equus* sp.. *Equus* sp. teeth were blunter with lower relief compared to *B. priscus* teeth, indicating that *Equus* sp. may have had an overall more abrasive diet than *B. priscus*. However, direct comparisons of *Bison* and *Equus* mesowear scores may be problematic due to gross differences in dental morphology. While both taxa have hypsodont molars, *Bison* molars have a selenodont morphology while *Equus* molars have a plagiolophodont morphology (Janis, 2008). Thus, we view the differences in mesowear scores between *B. priscus* and *Equus* sp. with caution. In other studies (Jones and DeSantis, 2017; Rivals et al., 2010) comparing *Bison* and *Equus* species, mesowear results have contrasted with DMTA and stable isotope results. In a comparison of *E. occidentalis* and *B. antiquus* from the La Brea tar pits, Jones and DeSantis (2017) found that, while both taxa had DMTA values most similar to mixed feeders or browsers, *E. occidentalis* had blunter mesowear indicating a more abrasive diet than bison. Further, both taxa had stable isotope values indicative of C$_3$ and C$_4$ dominant vegetation (DeSantis et al., 2019; DeSantis et al., 2020). Additional experimental work exploring how identical diets are reflected in mesowear across artiodactyl and perissodactyl groups is necessary for more confident interpretation of these results.

It is also possible that the different temporal scales recorded by mesowear and microwear may explain the contrasting results. Mesowear represents an integrated signal of several years of wear (Fortelius and Solounias, 2000), while depending on the abrasiveness of their diet, dental microwear textures can reflect diet over the past few days to

months (Merceron et al., 2016a, 2016b; Teaford and Oyen, 1989). Therefore, the dietary record as inferred via dental microwear can be biased towards recording diet just prior to death (e.g., season of death). If diets vary seasonally and the fossil assemblage is also seasonally biased, the resulting microwear record may not be representative of annual diets. High seasonal dietary variability is common among ungulates in the far north (Forchhammer and Boomsma, 1995; Larter and Nagy, 2004; Thompson and McCourt, 1981). Extant bison in Alaska and Canada are known to eat more sedges in winter and consume more shrubs, forbs and lichens in late summer (Campbell and Hinkes, 1983; Larter and Gates, 1991).

While it is not known if North Slope permafrost records are seasonal biased, mortality rates of adult ungulates in living temperate and Arctic populations are often highest in the winter (Wolfe, 1977; Houston, 1978; Lubinski and O'brien, 2001). Thus, it is possible that dental microwear primarily reflects winter diets as suggested by Rivals et al. (2010). While the different timescales recorded in microwear and mesowear provide valuable and nuanced records of how dietary niches may vary at seasonal scales, an improved understanding of the seasonal biases of permafrost records is necessary to more fully interpret the record.

In addition to potential seasonal variation in diet, seasonal differences in landscape use and the microhabitats occupied prior to death could also contribute to differences between microwear and mesowear. Observed differences in enamel taphonomy (*Equus* sp. enamel facets were more likely to show preserved antemortem microwear than *B. priscus* facets) may also support differences in landscape use between taxa. Both the *B. b. bison* herds and the newly introduced *B. b. athabascae* herd vary their landscape use seasonally (AK Department of Fish and Game, 2018; Campbell and Hinkes, 1983; Funck et al., 2020a; Waggoner and Hinkes, 1986), and it is likely that Late Pleistocene Alaskan ungulates did as well (Funck et al., 2020b, 2020c).

Previous efforts to characterize the niche partitioning and paleoecology of the North Slope megafauna have focused on stable isotopes. For example, Mann and colleagues showed that bison $\delta^{13}C_{collagen}$ values are on average 1‰ higher than horse values, and bison $\delta^{15}N_{collagen}$ values are on average 1.5‰ lower than horse values (Mann et al., 2013). While this may suggest differences in diet, linking isotopic values to actual diets poses several challenges. First, there is essentially no C$_4$ vegetation in Alaska (Blinnikov et al., 2011; Wooller et al., 2007); consequently, unlike in lower latitude environments where C$_4$ graze contributes a unique isotopic signal, the difference between graminoid and non-graminoid herb $\delta^{13}C$ values are minimal. In general, modern steppe and tundra plants have $\delta^{13}C$ pattern of shrub < herb (graminoid and forb) < lichen, though herbs and shrubs overlap and sometimes do not differ significantly (Drucker et al., 2010; Kohn, 2010; Kristensen et al., 2011; Munizzi, 2017; Schwartz-Narbonne et al., 2019; Song et al., 2008; Tahmasebi et al., 2017). For individuals of the same plant species, microhabitat differences in water and nutrient availabilty can also shift carbon and nitrogen isotopes by magnitudes similar to isotopic differences observed between different plant taxa (Chen et al., 2005; Toft et al., 1989; Wooller et al., 2007). Because of these complex factors, in a review of isotopic analyses of mammoth steppe paleoecology, Schwartz-Narbonne et al. (2019) cautioned "against direct use of the plant isotopic compositions to calculate herbivore diets."

Table 4
Dietary predictions of Alaska *Bison* and *Equus* sp. and modern zebra as evaluated by the quadratic discriminant analysis.

	Modern *B. b. athabascae*	Modern *B. b. bison*	Pleist.*B. priscus*	Pleist.*Equus* sp.	Modern *E. burchelli*	Modern *E. zebra*
% browser	0	0	6.2	0	0	0
% generalist	0	50.0	18.8	22.0	0	0
% variable grazer	77.8	37.5	56.2	75.6	81.0	90.5
% obligate grazer	0	12.5	18.8	2.4	19.0	9.5

Results shown are percentages of individuals from each taxon classified to each dietary category. The quadratic discriminant algorithm was trained using all published DMTA metrics (*Asfc*, *epLsar*, *HAsfc* 3 × 3, *HAsfc* 9 × 9 and *Tfv*) for African bovids and their known dietary categories (Scott, 2012b). "Pleist." = Pleistocene.
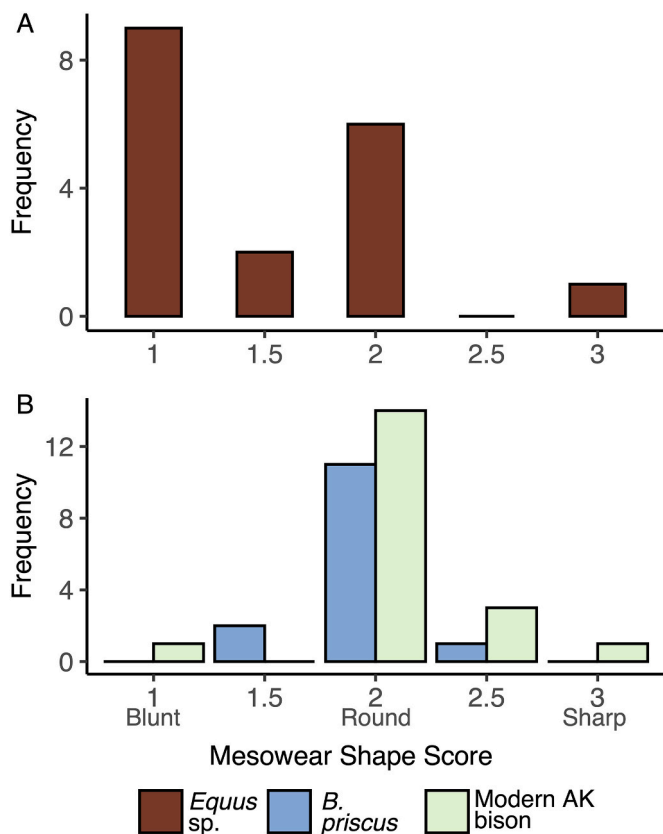
Fig. 7. Frequency of mesowear shape scores for teeth of (A) Pleistocene *Equus* sp., and (B) Pleistocene *B. priscus* and modern Alaska bison (combined *B. b. athabascae* and *B. b. bison*). For each molar (all M₂), the mesowear value is the median score for all six observers.

Differences in $\delta^{13}C_{collagen}$ values between North Slope bison and horses is also within the predicted range of fractionation differences between hindgut versus ruminant digestion (Cerling and Harris, 1999; Codron et al., 2012; Hedges, 2003). Differences in body size can also contribute to $\delta^{13}C$ offsets between bison and horses (Tejada-Lara et al.,

2018), as bison may have been more than twice the body mass of horses leading to marginally higher fractionation coefficients (female *B. b. athabascae* ≈ 540 kg, male *B. b. athabascae* > 910 kg, Beringian *Equus* sp. ≈ 290 kg; Guthrie, 1968; AK Department of Fish and Game, 2018). Differences in $\delta^{15}N_{collagen}$ are also challenging to interpret. Precipitation and aridity can affect vegetation and megafaunal diet $\delta^{15}N$ values, so it is possible that differences between *B. priscus* and *Equus* sp. $\delta^{15}N_{collagen}$ values represent different habitat choices: lower bison $\delta^{15}N_{collagen}$ values support a preference for vegetation growing in wetter conditions (Ambrose, 1991; Drucker et al., 2003; Heaton et al., 1986; Rabanus-Wallace et al., 2017). However, animal $\delta^{15}N$ values can also increase during times of nutritional or physical stress (Hobson et al., 1993; Kempster et al., 2007; Mosbacher et al., 2016; Polischuk et al., 2011), such as seasonal migration or starvation as demonstrated in Alaskan *B. b. athabascae* (Funck et al., 2020c). While $\delta^{15}N_{collagen}$ values likely represent an integrated lifetime signal, it is unclear how much periods of nutritional stress influences $\delta^{15}N_{collagen}$ values. Alternative approaches to successfully achieve finer temporal resolution include analyses of incremental layers of bison horn sheaths or hair samples (Funck et al., b, c). Ultimately, no dietary proxy is perfect, and all methods depend to varying degrees on the physiology and behavior of the organism of interest and the specific characteristics of their habitat and even preservation histories. While some differences in mesowear and isotope geochemistry may suggest some dietary partitioning between these dominant herbivores, the data are not overwhelming. Despite the complexities of available proxy data, the composite picture emerges that Late Pleistocene bison and horses on the North Slope consumed broadly similar diets that included forbs as well as grasses.

4.2.3. Niche shifts through time

Changes in horse DMTA complexity values through time (Fig. 9) may indicate dietary change, though these results should be treated as preliminary due to the low sample size of dated specimens. At the onset of increasingly glacial conditions circa 29 ka, complexity values are generally low while anisotropy values are generally high, indicating more abrasive, graminoid-dominated diets. Interestingly, this also occurs at a time of higher *Equus* sp. abundance (Fig. 2), hinting that higher *Equus* sp. population density coincided with, and may have been driven by, a period of graze-rich forage. During this time, bison were relatively less abundant, perhaps suggesting that though the diets of these two
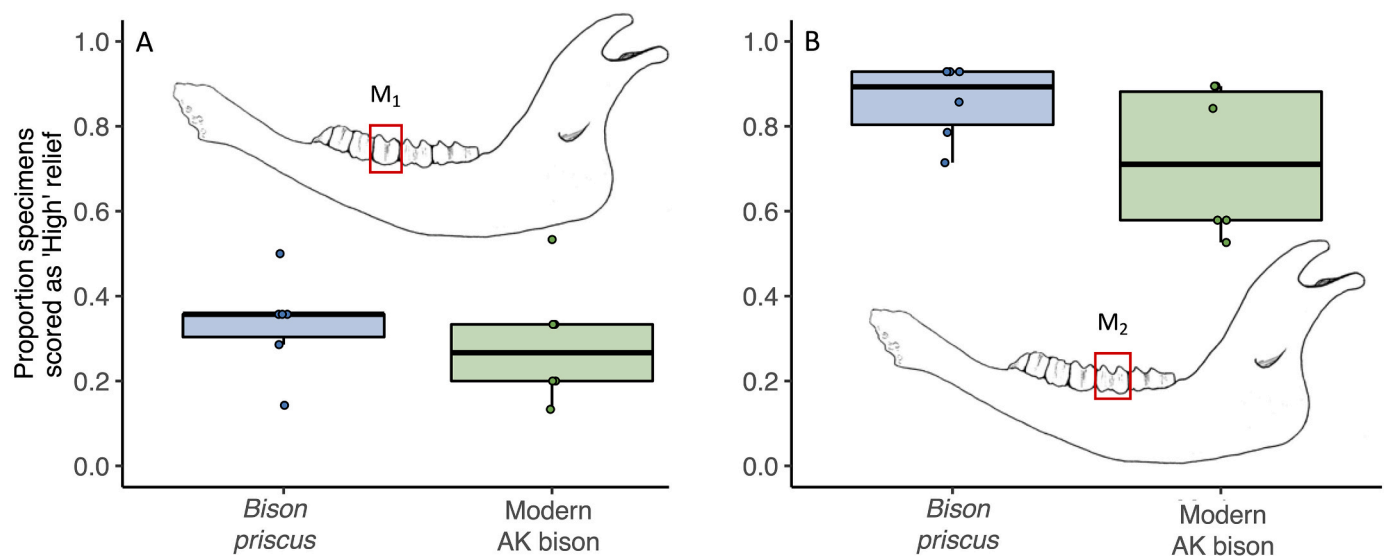

Fig. 8. Mesowear relief results for modern Alaskan bison (*B. b. athabascae* and *B. b. bison*) and Pleistocene *B. priscus* for (A) lower first molar and (B) lower second molar. Points show the proportion of specimens scored as having "high" relief (as opposed to "low" relief) for each of six observers. Values are slightly offset along the x-axis to make overlapping points visible. Boxplots show median value for each taxon (midline) bounded by the 1st and 3rd quartiles (colored box); whiskers extend to farthest point within 1.5 times the interquartile range.
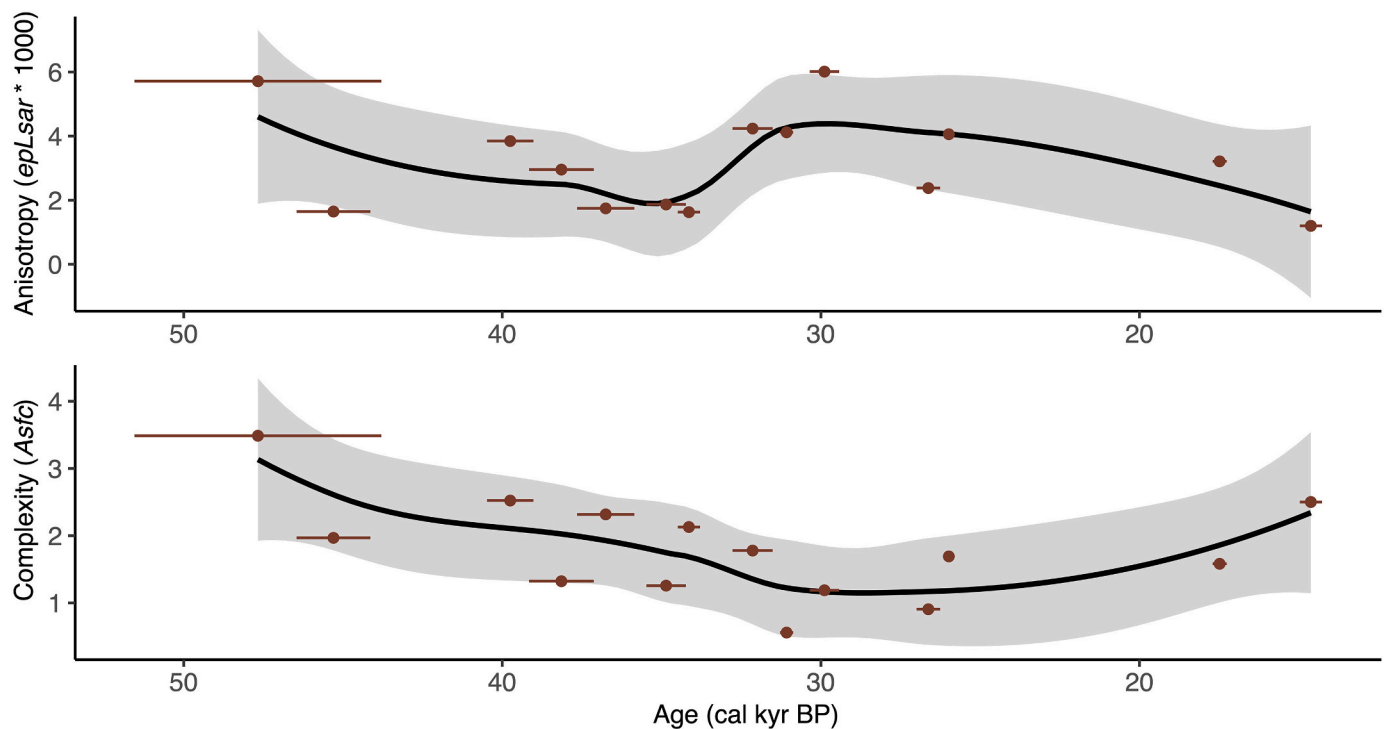
Fig. 9. Anisotropy (top) and complexity (bottom) values through time for dated *Equus* sp. specimens. Radiocarbon dates from Mann et al. (2013). Line is a loess spline with shaded 95% confidence interval. Horizontal lines around points show 2-sigma error for calibrated radiocarbon dates.

herbivores were similar overall, changing vegetation regimes altered the competitive advantage of *B. priscus* and *Equus* sp. through time. Future work increasing the dated sample size of large mammals of the North Slope is necessary to fully explore dietary trends over time. These efforts should focus on mandibles and maxillae because these elements contain information on diet, body size, maturity, mobility and other facets of the organism's paleoecology.

5. Conclusions

Dental wear of Late Pleistocene bison and horses on the North Slope of Alaska suggests that both taxa incorporated forbs and grasses into their diets. The dental microwear textures of both *B. priscus* and *Equus* sp. are most similar to the microwear textures of mixed-feeder ungulates. Our mesowear and DMTA results support previous microwear and isotope work and are consistent with the body of work indicating that the North Slope of Alaska had a broader mix of vegetation (i.e., more forbs and shrubs) during the Late Pleistocene than exists today. Dental microwear does not indicate disparate diets between bison and horses, nor does it indicate that either taxa occupied a broader dietary niche than the other. However, as DMTA records dietary information just prior to death, these results may reflect increased competition between bison and horses during the season of highest mortality. Dental mesowear suggests some dietary differences may have manifested between bison and horse, though these results are complicated by dental morphology differences between *Bison* and *Equus* sp. teeth. While we do not find strong evidence of dietary partitioning between species, taphonomic differences between bison and horse tooth enamel preservation may indicate spatial or temporal niche partitioning, either due to different patterns of seasonal landscape use and migration or through differing habitat preferences.

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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.

References

Ackermans, N.L., Martin, L.F., Codron, D., Hummel, J., Kircher, P.R., Richter, H., Kaiser, T.M., Clauss, M., Hatt, J.-M., 2020a. Mesowear represents a lifetime signal in sheep (Ovis aries) within a long-term feeding experiment. Palaeogeogr. Palaeoclimatol. Palaeoecol. 553, 109793. https://doi.org/10.1016/j.palaeo.2020.109793.

Ackermans, N.L., Winkler, D.E., Martin, L.F., Kaiser, T.M., Clauss, M., Hatt, J.-M., 2020b. Dust and grit matter: abrasives of different size lead to opposing dental microwear textures in experimentally fed sheep (Ovis aries). J. Exp. Biol. 223 https://doi.org/10.1242/jeb.220442.

AK Department of Fish and Game, 2018. Wood Bison Species Profile. Alaska Department of Fish and Game [WWW Document]. URL. http://www.adfg.alaska.gov/index.cfm?adfg=woodbison.main (accessed 5.13.18).

Ambrose, S.H., 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. J. Archaeol. Sci. 18, 293–317. https://doi.org/10.1016/0305-4403(91)90067-Y.

Aslan, A., Behrensmeyer, A.K., 1996. Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming. Palaios 11, 411–421. https://doi.org/10.2307/3515209.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162. https://doi.org/10.1017/S0094837300005820.

Behrensmeyer, A.K., 1990. Terrestrial vertebrate accumulations. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the Data Locked in the Fossil Record, Topics in Geobiology. Plenum Press, New York.

Behrensmeyer, A.K., Kidwell, S.M., 1985. Taphonomy's contributions to paleobiology. Paleobiology 11, 105–119.

Bezeau, L.M., Johnston, A., Smoliak, S., 1966. Silica and protein content of mixed prairie and fescue grassland vegetation and its relationship to the incidence of silica urolithiasis. Can. J. Plant Sci. 46, 625–631. https://doi.org/10.4141/cjps66-105.

Bigelow, N.H., Brubaker, L.B., Edwards, M.E., Harrison, S.P., Prentice, I.C., Anderson, P. M., Andreev, A.A., Bartlein, P.J., Christensen, T.R., Cramer, W., Kaplan, J.O., Lozhkin, A.V., Matveyeva, N.V., Murray, D.F., McGuire, A.D., Razzhivin, V.Y., Ritchie, J.C., Smith, B., Walker, D.A., Gajewski, K., Wolf, V., Holmqvist, B.H., Igarashi, Y., Kremenetskii, K., Paus, A., Pisaric, M.F.J., Volkova, V.S., 2003. Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present. J. Geophys. Res. 108, 8170. https://doi.org/10.1029/2002JD002558.

Bignon-lau, O., Catz, N., Berlioz, E., Veiberg, V., Strand, O., Merceron, G., 2017. Dental microwear textural analyses to track feeding ecology of reindeer: a comparison of two contrasting populations in Norway. Mam. Res. 62, 111–120. https://doi.org/10.1007/s13364-016-0304-y.

Blinnikov, M.S., Gaglioti, B.V., Walker, D.A., Wooller, M.J., Zazula, G.D., 2011. Pleistocene graminoid-dominated ecosystems in the Arctic. Quat. Sci. Rev. 30, 2906–2929.

Bocherens, H., 2003. Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna. Deinsea 9, e76.

Bodmer, R.E., 1990. Ungulate frugivores and the browser-grazer continuum. Oikos 57, 319–325. https://doi.org/10.2307/3565960.

Cabin, R.J., Mitchell, R.J., 2000. To bonferroni or not to bonferroni: when and how are the questions. Bull. Ecol. Soc. Am. 81, 246–248.

Campbell, B.H., Hinkes, M., 1983. Winter diets and habitat use of alaska bison after wildfire. Wildl. Soc. Bull. 11 (1973–2006), 16–21.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363. https://doi.org/10.1007/s004420050868.

Chen, S., Bai, Y., Lin, G., Han, X., 2005. Variations in life-form composition and foliar carbon isotope discrimination among eight plant communities under different soil moisture conditions in the Xilin River Basin, Inner Mongolia, China. Ecol. Res. 20, 167–176.

Codron, D., Sponheimer, M., Codron, J., Hammer, S., Tschuor, A., Braun, U., Bernasconi, S.M., Clauss, M., 2012. Tracking the fate of digesta 13C and 15N compositions along the ruminant gastrointestinal tract: Does digestion influence the relationship between diet and faeces? Eur. J. Wildl. Res. 58, 303–313. https://doi.org/10.1007/s10344-011-0581-3.

Codron, D., Clauss, M., Codron, J., Tütken, T., 2018. Within trophic level shifts in collagen–carbonate stable carbon isotope spacing are propagated by diet and digestive physiology in large mammal herbivores. Ecol. Evol. 8, 3983–3995. https://doi.org/10.1002/ece3.3786.

Coppedge, B.R., Leslie, D.M., Shaw, J.H., 1998. Botanical composition of bison diets on tallgrass prairie in Oklahoma. Rangeland Ecol. Manag/J. Range Manag. Arch. 51, 379–382.

Crane, K.K., Smith, M.A., Reynolds, D., 1997. Habitat selection patterns of feral horses in Southcentral Wyoming. J. Range Manag. 50, 374–380. https://doi.org/10.2307/4003303.

Davis, J.C., 2002. Statistics and Data Analysis in Geology. Wiley.

DeSantis, L.R.G., 2016. Dental microwear textures: reconstructing diets of fossil mammals. Surf. Topogr.: Metrol. Prop. 4, 023002. https://doi.org/10.1088/2051-672X/4/2/023002.

DeSantis, L., Fortelius, M., Grine, F., Janis, C., Kaiser, T., Merceros, G., Purnell, M., Schulz-Kornas, E., Saarinen, J., Teaford, M., Ungar, P., Zliobaite, I., 2018. The phylogenetic signal in tooth wear: What does it mean? Ecology and Evolution 8, 11359–11362. https://doi.org/10.1002/ece3.4541.

DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B.M., Stolk, C.A.V., Winburn, A.A., Greshko, M.A., O'Hara, M.C., 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. PLoS One 8, e71428. https://doi.org/10.1371/journal.pone.0071428.

DeSantis, L.R.G., Crites, J.M., Feranec, R.S., Fox-Dobbs, K., Farrell, A.B., Harris, J.M., Takeuchi, G.T., Cerling, T.E., 2019. Causes and consequences of pleistocene megafaunal extinctions as revealed from Rancho La Brea mammals. Curr. Biol. 29 https://doi.org/10.1016/j.cub.2019.06.059, 2488-2495.e2.

DeSantis, L.R.G., Feranec, R.S., Fox-Dobbs, K., Harris, J.M., Cerling, T.E., Crites, J.M., Farrell, A.B., Takeuchi, G.T., 2020. Reply to Van Valkenburgh et al. Curr. Biol. 30, R151–R152. https://doi.org/10.1016/j.cub.2020.01.011.

Drucker, D., Bocherens, H., Bridault, A., Billiou, D., 2003. Carbon and nitrogen isotopic composition of red deer (Cervus elaphus) collagen as a tool for tracking palaeoenvironmental change during the Late-Glacial and Early Holocene in the

northern Jura (France). Palaeogeogr. Palaeoclimatol. Palaeoecol. 195, 375–388. https://doi.org/10.1016/S0031-0182(03)00366-3.

Drucker, D.G., Hobson, K.A., Ouellet, J.-P., Courtois, R., 2010. Influence of forage preferences and habitat use on 13C and 15N abundance in wild caribou (Rangifer tarandus caribou) and moose (Alces alces) from Canada. Isot. Environ. Health Stud. 46, 107–121.

Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G., Lloyd, M., 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia 84, 411–418.

Eisner, W.R., Colinvaux, P.A., 1990. A long pollen record from Ahaliorak Lake, Arctic Alaska. Rev. Palaeobot. Palynol. 63, 35–52. https://doi.org/10.1016/0034-6667(90)90005-4.

Forchhammer, M.C., Boomsma, J.J., 1995. Foraging strategies and seasonal diet optimization of muskoxen in West Greenland. Oecologia 104, 169–180. https://doi.org/10.1007/BF00328582.

Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. In: Acta zoologica Fennica. Finnish Zoological Publ, Board, Helsinki.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. Am. Mus. Novit. 3301, 1–36. https://doi.org/10.1206/0003-0082(2000)301<0001:FCOUMU>2.0.CO;2.

Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia: Paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. Palaeogeogr. Palaeoclimatol. Palaeoecol. 261, 30–46. https://doi.org/10.1016/j.palaeo.2007.12.011.

Fraser, D., Haupt, R.J., Barr, W.A., 2018. Phylogenetic signal in tooth wear dietary niche proxies. Ecology and Evolution 8, 5355–5368. https://doi.org/10.1002/ece3.4052.

Froese, D., Stiller, M., Heintzman, P.D., Reyes, A.V., Zazula, G.D., Soares, A.E.R., Meyer, M., Hall, E., Jensen, B.J.L., Arnold, L.J., MacPhee, R.D.E., Shapiro, B., 2017. Fossil and genomic evidence constrains the timing of bison arrival in North America. PNAS 114, 3457–3462. https://doi.org/10.1073/pnas.1620754114.

Funck, J., Kellam, C., Seaton, C.T., Wooller, M.J., 2020a. Stable isotopic signatures in modern wood bison (Bison bison athabascae) hairs as telltale biomarkers of nutritional stress. Can. J. Zool. https://doi.org/10.1139/cjz-2019-0185.

Funck, J., Bataille, C., Rasic, J., Wooller, M., 2020b. A bio-available strontium isoscape for eastern Beringia: a tool for tracking landscape use of Pleistocene megafauna. J. Quat. Sci. https://doi.org/10.1002/jqs.3262.

Funck, J., Heintzman, P.D., Murray, G.G.R., Shapiro, B., McKinney, H., Huchet, J.-B., Bigelow, N., Druckenmiller, P., Wooller, M.J., 2020c. A detailed life history of a pleistocene steppe bison (Bison priscus) skeleton unearthed in Arctic Alaska. Quat. Sci. Rev. 249, 106578. https://doi.org/10.1016/j.quascirev.2020.106578.

Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African bovidae. J. Mammal. 81, 22.

Gotelli, N.J., 2008. A Primer of Ecology. Sinauer.

Guthrie, R.D., 1968. Paleoecology of the large-mammal community in interior alaska during the late pleistocene. Am. Midl. Nat. 79, 346–363. https://doi.org/10.2307/2423182.

Guthrie, R.D., 1984. Mosaics, allelochemics and nutrients: an ecological theory of late Pleistocene megafaunal extinctions. In: Quaternary Extinctions: A Prehistoric Revolution, p. 1984.

Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe. University of Chicago Press.

Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quat. Sci. Rev. 20, 549–574.

Guthrie, R.D., 2003. Rapid body size decline in Alaskan Pleistocene horses before extinction. Nature 426, 169.

Guthrie, R.D., 2006. New carbon dates link climatic change with human colonization and Pleistocene extinctions. Nature 441, 207.

Haynes, G., 1982. Utilization and skeletal disturbances of North American prey carcasses. Arctic 35. https://doi.org/10.14430/arctic2325.

Haynes, G., 1984. Tooth Wear Rate in Northern Bison. J. Mammal. 65, 487–491. https://doi.org/10.2307/1381099.

Heaton, T.H.E., Vogel, J.C., von la Chevallerie, G., Collett, G., 1986. Climatic influence on the isotopic composition of bone nitrogen. Nature 322, 822–823. https://doi.org/10.1038/322822a0.

Hedges, R.E.M., 2003. On bone collagen—apatite-carbonate isotopic relationships. Int. J. Osteoarchaeol. 13, 66–79. https://doi.org/10.1002/oa.660.

Hill, A., 1979. Disarticulation and scattering of mammal skeletons. Paleobiology 5, 261–274. https://doi.org/10.1017/S0094837300006552.

Hobson, K.A., Alisauskas, R.T., Clark, R.G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95, 388. https://doi.org/10.2307/1369361.

Hoffman, J.M., Fraser, D., Clementz, M.T., 2015. Controlled feeding trials with ungulates: a new application of in vivo dental molding to assess the abrasive factors of microwear. J. Exp. Biol. 218, 1538–1547. https://doi.org/10.1242/jeb.118406.

Houston, D.B., 1978. Elk as winter-spring food for carnivores in northern Yellowstone National Park. J. Appl. Ecol. 653–661.

Janis, C., 2008. An evolutionary history of browsing and grazing ungulates. In: The Ecology of Browsing and Grazing. Springer, pp. 21–45.

Jones, D.B., DeSantis, L.R.G., 2017. Dietary ecology of ungulates from the La Brea tar pits in southern California: A multi-proxy approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 466, 110–127. https://doi.org/10.1016/j.palaeo.2016.11.019.

Kaiser, T.M., Fortelius, M., 2003. Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypsodont horses. J. Morphol. 258, 67–83.

Kaiser, T.M., Solounias, N., 2003. Extending the Tooth Mesowear Method to Extinct and Extant Equids, p. 25.

Kempster, B., Zanette, L., Longstaffe, F.J., MacDougall-Shackleton, S.A., Wingfield, J.C., Clinchy, M., 2007. Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. Oecologia 151, 365–371. https://doi.org/10.1007/s00442-006-0597-7.

Kerley, G.I.H., Kowalczyk, R., Cromsigt, J.P.G.M., 2012. Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35, 519–529. https://doi.org/10.1111/j.1600-0587.2011.07146.x.

Kienast, F., Schirrmeister, L., Siegert, C., Tarasov, P., 2005. Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. Quat. Res. 63, 283–300. https://doi.org/10.1016/j.yqres.2005.01.003.

King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. Am. J. Phys. Anthropol. 108, 359–373. https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-AJPA10>3.0.CO;2-9.

Klein, D.R., 1996. Arctic ungulates at the northern edge of terrestrial life. Rangifer 16, 51. https://doi.org/10.7557/2.16.2.1197.

Koch, P.L., Barnosky, A.D., 2006. Late quaternary extinctions: state of the debate. Annu. Rev. Ecol. Evol. Syst. 37, 215–250. https://doi.org/10.1146/annurev.ecolsys.34.011802.132415.

Koenigswald, W.V., Clemens, W.A., 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. Scanning Microsc. 6, 195–217.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proc. Natl. Acad. Sci. 107, 19691–19695. https://doi.org/10.1073/pnas.1004933107.

Kowalewski, Novack-Gottshall, P., 2010. Resampling methods in paleontology. Paleontol. Soc. Special Papers 16, 19–54.

Kristensen, D.K., Kristensen, E., Forchhammer, M.C., Michelsen, A., Schmidt, N.M., 2011. Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C3 plants, faeces, and wool. Can. J. Zool. https://doi.org/10.1139/z11-073.

Kuntz, R., Kubalek, C., Ruf, T., Tataruch, F., Arnold, W., 2006. Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (Equus ferus przewalskii) I. Energy intake. J. Exp. Biol. 209, 4557–4565. https://doi.org/10.1242/jeb.02535.

Lanoë, F.B., Reuther, J.D., Holmes, C.E., Hodgins, G.W.L., 2017. Human paleoecological integration in subarctic eastern Beringia. Quat. Sci. Rev. 175, 85–96. https://doi.org/10.1016/j.quascirev.2017.10.003.

Larter, N.C., Gates, C.C., 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Can. J. Zool. 69, 2677–2685. https://doi.org/10.1139/z91-376.

Larter, N.C., Nagy, J.A., 2004. Seasonal changes in the composition of the diets of Peary caribou and muskoxen on Banks Island. Polar Res. 23, 131–140. https://doi.org/10.1111/j.1751-8369.2004.tb00003.x.

Levene, H., 1960. Robust tests for equality of variances. Ingram Olkin, Harold Hotelling, et alia. In: Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling. Stanford University, pp. 278–292.

Loffredo, L.F., DeSantis, L.R., 2014. Cautionary lessons from assessing dental mesowear observer variability and integrating paleoecological proxies of an extreme generalist Cormohipparion emsliei. Palaeogeogr. Palaeoclimatol. Palaeoecol. 395, 42–52.

Lubinski, P.M., O'brien, C.J., 2001. Observations on seasonality and mortality from a recent catastrophic death assemblage. J. Archaeol. Sci. 28, 833–842. https://doi.org/10.1006/jasc.2000.0603.

Mann, H.B., Whitney, D.R., 1947. On a test of whether one of two random variables is stochastically larger than the other. Ann. Math. Stat. 18, 50–60. https://doi.org/10.1214/aoms/1177730491.

Mann, D.H., Groves, P., Kunz, M.L., Reanier, R.E., Gaglioti, B.V., 2013. Ice-age megafauna in Arctic Alaska: extinction, invasion, survival. Quat. Sci. Rev. 70, 91–108. https://doi.org/10.1016/j.quascirev.2013.03.015.

Mann, D.H., Groves, P., Reanier, R.E., Gaglioti, B.V., Kunz, M.L., Shapiro, B., 2015. Life and extinction of megafauna in the ice-age Arctic. PNAS 112, 14301–14306. https://doi.org/10.1073/pnas.1516573112.

Mann, D.H., Groves, P., Gaglioti, B.V., Shapiro, B.A., 2019. Climate-driven ecological stability as a globally shared cause of Late Quaternary megafaunal extinctions: the Plaids and Stripes Hypothesis. Biol. Rev. 94, 328–352. https://doi.org/10.1111/brv.12456.

Martin, P.S., Klein, R.G., 1989. Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press.

McDonald, J.N., 1981. North American bison: their classification and evolution. Univ of California Press.

McNaughton, S.J., Georgiadis, N.J., 1986. Ecology of African grazing and browsing mammals. Annu. Rev. Ecol. Syst. 17, 39–66. https://doi.org/10.1146/annurev.es.17.110186.000351.

Mech, L., Peterson, R., 2003. Wolf-Prey Relations. USGS Northern Prairie Wildlife Research Center.

Merceron, G., Hofman-Kamińska, E., Kowalczyk, R., 2014. 3D dental microwear texture analysis of feeding habits of sympatric ruminants in the Białowieża Primeval Forest, Poland. For. Ecol. Manag. 328, 262–269. https://doi.org/10.1016/j.foreco.2014.05.041.

Merceron, G., Novello, A., Scott, R.S., 2016a. Paleoenvironments inferred from phytoliths and Dental Microwear Texture Analyses of meso-herbivores. In: Koufos, G.D., Kostopoulos, D.S. (Eds.), Geobios, Palaeontology of the Upper Miocene Vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece), Vol. 49, pp. 135–146. https://doi.org/10.1016/j.geobios.2016.01.004.

Merceron, G., Ramdarshan, A., Blondel, C., Boisserie, J.-R., Brunetiere, N., Francisco, A., Gautier, D., Milhet, X., Novello, A., Pret, D., 2016b. Untangling the environmental from the dietary: dust does not matter. Proc. R. Soc. B 283, 20161032. https://doi.org/10.1098/rspb.2016.1032.

Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G.M., 2011. Dietary Change and Evolution of Horses in North America. Science 331, 1178–1181. https://doi.org/10.1126/science.1196166.

Mihlbachler, M.C., Campbell, D., Ayoub, M., Chen, C., Ghani, I., 2016. Comparative dental microwear of ruminant and perissodactyl molars: Implications for paleodietary analysis of rare and extinct ungulate clades. Paleobiology 42, 98–116. https://doi.org/10.1017/pab.2015.33.

Miller, J.H., 2012. Spatial fidelity of skeletal remains: elk wintering and calving grounds revealed by bones on the Yellowstone landscape. Ecology 93, 2474–2482. https://doi.org/10.1890/12-0272.1.

Miller, J.H., Druckenmiller, P., Bahn, V., 2013. Antlers on the Arctic Refuge: capturing multi-generational patterns of calving ground use from bones on the landscape. Proc. R. Soc. Lond. B Biol. Sci. 280, 20130275.

Miller, J.H., Behrensmeyer, A.K., Du, A., Lyons, S.K., Patterson, D., Tóth, A., Villaseñor, A., Kanga, E., Reed, D., 2014. Ecological fidelity of functional traits based on species presence-absence in a modern mammalian bone assemblage (Amboseli, Kenya). Paleobiology 40, 560–583.

Miller, J.H., Crowley, B.E., Bataille, C.P., Wald, E.J., Kelly, A., Gaetano, M., Bahn, V., Druckenmiller, P., 2021. Historical landscape use of migratory caribou: new insights from old antlers. Front. Ecol. Evol. 8, 512.

Mosbacher, J.B., Michelsen, A., Stelvig, M., Hendrichsen, D.K., Schmidt, N.M., 2016. Show me your rump hair and i will tell you what you ate – The dietary history of muskoxen (Ovibos moschatus) revealed by sequential stable isotope analysis of guard hairs. PLoS One 11, e0152874. https://doi.org/10.1371/journal.pone.0152874.

Munizzi, J.S., 2017. Rethinking Holocene Ecological Relationships Among Caribou, Muskoxen, and Human Hunters on Banks Island, NWT, Canada: A Stable Isotope Approach (Ph.D. Thesis). The University of Western Ontario.

Oliver, J.S., Graham, R.W., 1994. A catastrophic kill of ice-trapped coots: time-averaged versus scavenger-specific disarticulation patterns. Paleobiology 20, 229–244. https://doi.org/10.1017/S0094837300012707.

Owaga, M.L., 1975. The feeding ecology of wildebeest and zebra in Athi-Kaputei plains. Afr. J. Ecol. 13, 375–383. https://doi.org/10.1111/j.1365-2028.1975.tb00145.x.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO2, and bioapatite in different mammals. J. Archaeol. Sci. 32, 1459–1470. https://doi.org/10.1016/j.jas.2005.03.015.

Peden, D.G., Van Dyne, G.M., Rice, R.W., Hansen, R.M., 1974. The trophic ecology of bison bison L. on shortgrass plains. J. Appl. Ecol. 11, 489–497. https://doi.org/10.2307/2402203.

Pfretzschner, H.U., 1993. Enamel microstructure in the phylogeny of the Equidae. J. Vertebr. Paleontol. 13, 342–349. https://doi.org/10.1080/02724634.1993.10011514.

Pokines, J.T., King, R.E., Graham, D.D., Costello, A.K., Adams, D.M., Pendray, J.M., Rao, K., Siwek, D., 2016. The effects of experimental freeze-thaw cycles to bone as a component of subaerial weathering. J. Archaeol. Sci. Rep. 6, 594–602. https://doi.org/10.1016/j.jasrep.2016.03.023.

Polischuk, S.C., Hobson, K.A., Ramsay, M.A., 2011. Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Can. J. Zool. https://doi.org/10.1139/z01-007.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabanus-Wallace, M.T., Wooller, M.J., Zazula, G.D., Shute, E., Jahren, A.H., Kosintsev, P., Burns, J.A., Breen, J., Llamas, B., Cooper, A., 2017. Megafaunal isotopes reveal role of increased moisture on rangeland during late Pleistocene extinctions. Nat. Ecol. Evol. 1, 0125.

Rivals, F., 2012. Ungulate feeding ecology and middle Pleistocene paleoenvironments at Hundsheim and Deutsch-Altenburg 1 (eastern Austria). Palaeogeogr. Palaeoclimatol. Palaeoecol. 317–318, 27–31. https://doi.org/10.1016/j.palaeo.2011.12.006.

Rivals, F., Semprebon, G.M., 2011. Dietary plasticity in ungulates: Insight from tooth microwear analysis. Quat. Int. Late Quat. Mam. Ecol. 245, 279–284. https://doi.org/10.1016/j.quaint.2010.08.001.

Rivals, F., Solounias, N., Mihlbachler, M.C., 2007. Evidence for geographic variation in the diets of late Pleistocene and early Holocene Bison in North America, and differences from the diets of recent Bison. Quat. Res. 68, 338–346. https://doi.org/10.1016/j.yqres.2007.07.012.

Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulates dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space. Quat. Sci. Rev. 28, 3388–3400. https://doi.org/10.1016/j.quascirev.2009.09.004.

Rivals, F., Mihlbachler, M.C., Solounias, N., Mol, D., Semprebon, G.M., de Vos, J., Kalthoff, D.C., 2010. Palaeoecology of the Mammoth Steppe fauna from the late Pleistocene of the North Sea and Alaska: Separating species preferences from geographic influence in paleoecological dental wear analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 286, 42–54. https://doi.org/10.1016/j.palaeo.2009.12.002.

Rivals, F., Julien, M.-A., Kuitems, M., Van Kolfschoten, T., Serangeli, J., Drucker, D.G., Bocherens, H., Conard, N.J., 2015. Investigation of equid paleodiet from Schöningen 13 II-4 through dental wear and isotopic analyses: archaeological implications.

J. Human Evol. Special Issue. 89, 129–137. https://doi.org/10.1016/j.jhevol.2014.04.002.

Rogers, R.R., Eberth, D.A., Fiorillo, A.R., 2007. Bonebeds: Genesis, Analysis, and Paleobiological Significance. University of Chicago Press. https://doi.org/10.7208/chicago/9780226723730.001.0001.

Salter, R.E., Hudson, R.J., 1979. Feeding Ecology of Feral Horses in Western Alberta. J. Range Manag. 32, 221–225. https://doi.org/10.2307/3897127.

Sathe, V., 2000. Enamel ultrastructure of cattle from the quaternary period in India. Environ. Archaeol. 5, 107–115. https://doi.org/10.1179/env.2000.5.1.107.

Schwartz-Narbonne, R., Longstaffe, F.J., Metcalfe, J.Z., Zazula, G., 2015. Solving the woolly mammoth conundrum: amino acid 15N enrichment suggests a distinct forage or habitat. Sci. Rep. 5, 9791. https://doi.org/10.1038/srep09791.

Schwartz-Narbonne, R., Longstaffe, F.J., Kardynal, K.J., Druckenmiller, P., Hobson, K.A., Jass, C.N., Metcalfe, J.Z., Zazula, G., 2019. Reframing the mammoth steppe: insights from analysis of isotopic niches. Quat. Sci. Rev. 215, 1–21. https://doi.org/10.1016/j.quascirev.2019.04.025.

Scott, Jessica R., 2012a. Dental microwear texture analysis of extant African Bovidae. Mammalia 76, 157–174.

Scott, Jessica R., 2012b. Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution (Ph.D.). University of Arkansas, United States – Arkansas.

Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. J. Hum. Evol. 51, 339–349. https://doi.org/10.1016/j.jhevol.2006.04.006.

Semprebon, G.M., Rivals, F., Solounias, N., Hulbert, R.C., 2016. Paleodietary reconstruction of fossil horses from the Eocene through Pleistocene of North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 442, 110–127. https://doi.org/10.1016/j.palaeo.2015.11.004.

Smith, G.J., DeSantis, L.R.G., 2020. Extinction of North American Cuvieronius (Mammalia: Proboscidea: Gomphotheriidae) driven by dietary resource competition with sympatric mammoths and mastodons. Paleobiology 46, 41–57. https://doi.org/10.1017/pab.2020.7.

Song, M., Duan, D., Chen, H., Hu, Q., Zhang, F., Xu, X., Tian, Y., Ouyang, H., Peng, C., 2008. Leaf δ13C reflects ecosystem patterns and responses of alpine plants to the environments on the Tibetan Plateau. Ecography 31, 499–508. https://doi.org/10.1111/j.0906-7590.2008.05331.x.

Tahmasebi, F., Longstaffe, F.J., Zazula, G., Bennett, B., 2017. Nitrogen and carbon isotopic dynamics of subarctic soils and plants in southern Yukon Territory and its implications for paleoecological and paleodietary studies. PLoS One 12, e0183016.

Tape, K.D., Gustine, D.D., Ruess, R.W., Adams, L.G., Clark, J.A., 2016. Range expansion of moose in Arctic Alaska linked to warming and increased shrub habitat. PLoS One 11, e0152636. https://doi.org/10.1371/journal.pone.0152636.

Teaford, M.F., Oyen, O.J., 1989. In vivo and in vitro turnover in dental microwear. Am. J. Phys. Anthropol. 80, 447–460. https://doi.org/10.1002/ajpa.1330800405.

Teaford, M.F., Walker, A., 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of Sivapithecus. Am. J. Phys. Anthropol. 64, 191–200.

Tejada-Lara, J.V., MacFadden, B.J., Bermudez, L., Rojas, G., Salas-Gismondi, R., Flynn, J.J., 2018. Body mass predicts isotope enrichment in herbivorous mammals. Proc. R. Soc. B Biol. Sci. 285, 20181020. https://doi.org/10.1098/rspb.2018.1020.

Thompson, D.C., McCourt, K.H., 1981. Seasonal diets of the porcupine caribou herd. Am. Midl. Nat. 105, 70–76. https://doi.org/10.2307/2425011.

Toft, N.L., Anderson, J.E., Nowak, R.S., 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. Oecologia 80, 11–18. https://doi.org/10.1007/BF00789925.

Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, A., 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning 25, 185–193.

Ungar, P.S., Merceron, G., Scott, R.S., 2007. Dental microwear texture analysis of Varswater bovids and early Pliocene paleoenvironments of Langebaanweg, Western Cape Province, South Africa. J. Mamm. Evol. 14, 163–181.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Fourth edition. Springer, New York. ISBN 0-387-95457-0.

Vislobokova, I.A., Dmitrieva, E.L., 2000. Changes in Enamel Ultrastructure at the Early Stages of Ruminant Evolution, 34, p. 9.

Waggoner, V., Hinkes, M., 1986. Summer and Fall Browse Utilization by an Alaskan Bison Herd. J. Wildl. Manag. 50, 322–324. https://doi.org/10.2307/3801921.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilke, C.O., 2019. cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 1.0.0. https://CRAN.R-project.org/package=cowplot.

Willerslev, E., Hansen, A.J., Binladen, J., Brand, T.B., Gilbert, M.T.P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D.A., Cooper, A., 2003. Diverse plant and animal genetic records from Holocene and Pleistocene sediments. Science 300, 791–795.

Willerslev, E., Davison, J., Moora, M., Zobel, M., Coissac, E., Edwards, M.E., Lorenzen, E.D., Vestergaard, M., Gussarova, G., Haile, J., et al., 2014. Fifty thousand years of Arctic vegetation and megafaunal diet. Nature 506, 47.

Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., Codron, D., Leichliter, J., Hummel, J., Martin, L.F., Clauss, M., Tütken, T., 2020. The turnover of dental microwear texture: Testing the "last supper" effect in small mammals in a controlled feeding experiment. Palaeogeogr. Palaeoclimatol. Palaeoecol. 557, 109930. https://doi.org/10.1016/j.palaeo.2020.109930.

Wolfe, M.L., 1977. Mortality patterns in the isle royale moose population. Am. Midl. Nat. 97, 267–279. https://doi.org/10.2307/2425093.

Wooller, M.D., Zazula, G., Edwards, M., Froese, D., Boone, R., Parker, C., Bennett, B., 2007. Stable carbon isotope compositions of Eastern Beringian Grasses and sedges: investigating their potential as paleoenvironmental indicators. Arct. Antarct. Alp. Res. 39, 318–331. https://doi.org/10.1657/1523-0430(2007)39[318:SCICOE]2.0.CO;2.

Zazula, G.D., Froese, D.G., Schweger, C.E., Mathewes, R.W., Beaudoin, A.B., Telka, A.M., Harington, C.R., Westgate, J.A., 2003. Palaeobotany: ice-age steppe vegetation in east Beringia. Nature 423. https://doi.org/10.1038/423603a.

Zazula, G.D., MacPhee, R.D.E., Metcalfe, J.Z., Reyes, A.V., Brock, F., Druckenmiller, P.S., Groves, P., Harington, C.R., Hodgins, G.W.L., Kunz, M.L.J., Longstaffe, F., Mann, D.H., McDonald, H.G., Nalawade-Chavan, S., Southon, J.R., 2014. American mastodon extirpation in the Arctic and Subarctic predates human colonization and terminal Pleistocene climate change. Proc. Natl. Acad. Sci. U. S. A. 111, 18460–18465. https://doi.org/10.1073/pnas.1416072111.

Zazula, G.D., MacPhee, R.D.E., Southon, J., Nalawade-Chavan, S., Reyes, A.V., Hewitson, S., Hall, E., 2017. A case of early Wisconsinan "over-chill": New radiocarbon evidence for early extirpation of western camel (Camelops hesternus) in eastern Beringia. Quat. Sci. Rev. 171, 48–57. https://doi.org/10.1016/j.quascirev.2017.06.031.

Zimov, S.A., Zimov, N.S., Tikhonov, A.N., Chapin, F.S., 2012. Mammoth steppe: a high-productivity phenomenon. Quat. Sci. Rev. 57, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005.