

Enamel hypoplasia and dental wear of North American late Pleistocene horses and bison: an assessment of nutritionally based extinction models

Christina I. Barrón-Ortiz, Christopher N. Jass, Raúl Barrón-Corvera, Jennifer Austen, and Jessica M. Theodor

Abstract.—Approximately 50,000–11,000 years ago many species around the world became extinct or were extirpated at a continental scale. The causes of the late Pleistocene extinctions have been extensively debated and continue to be poorly understood. Several extinction models have been proposed, including two nutritionally based extinction models: the coevolutionary disequilibrium and mosaic-nutrient models. These models draw upon the individualistic response of plant species to climate change to present a plausible scenario in which nutritional stress is considered one of the primary causes for the late Pleistocene extinctions.

In this study, we tested predictions of the coevolutionary disequilibrium and mosaic-nutrient extinction models through the study of dental wear and enamel hypoplasia of *Equus* and *Bison* from various North American localities. The analysis of the dental wear (microwear and mesowear) of the samples yielded results that are consistent with predictions established for the coevolutionary disequilibrium model, but not for the mosaic-nutrient model. These ungulate species show statistically different dental wear patterns (suggesting dietary resource partitioning) during preglacial and full-glacial time intervals, but not during the postglacial in accordance with predictions of the coevolutionary disequilibrium model. In addition to changes in diet, these ungulates, specifically the equid species, show increased levels of enamel hypoplasia during the postglacial, indicating higher levels of systemic stress, a result that is consistent with the models tested and with other climate-based extinction models. The extent to which the increase in systemic stress was detrimental to equid populations remains to be further investigated, but suggests that environmental changes during the late Pleistocene significantly impacted North American equids.

*Christina I. Barrón-Ortiz** and *Jessica M. Theodor*. Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4, Canada. E-mail: christina.barron-ortiz@gov.ab.ca. *Present address: Quaternary Palaeontology Program, Royal Alberta Museum, Edmonton, Alberta T5J 0G2, Canada.

Christopher N. Jass. Quaternary Palaeontology Program, Royal Alberta Museum, Edmonton, Alberta T5J 0G2, Canada.

Raúl Barrón-Corvera. Programa de Ingeniería Civil, Universidad Autónoma de Zacatecas, Zacatecas 98000, Mexico.

Jennifer Austen. Department of Archaeology, University of Reading, Reading RG6 6AH, United Kingdom.

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Introduction

The late Pleistocene extinction is one of the largest extinction events in North America in the past 55 Myr (Alroy 1999), and it is particularly notable because of the role it had in shaping current biodiversity patterns (Koch and Barnosky 2006; Hofreiter and Stewart 2009; Smith et al. 2016). Mammals were among the most adversely affected groups, and it is estimated that more than 30 genera disappeared from the continent (Grayson 1991, 2007; Koch and Barnosky 2006; Faith and Surovell 2009; Meltzer 2015; Stuart 2015). The causes of the

extinction have been extensively debated, and several extinction models have been proposed. Some models identify climate change as the primary causal factor (e.g., Graham and Lundelius 1984; Guthrie 1984; Kiltie 1984; King and Saunders 1984; Barnosky 1986; Ficarelli et al. 2003; Forster 2004; Scott 2010; Cooper et al. 2015), others point to overhunting and alteration of ecosystems by early human populations (Martin 1967, 1984; Mosimann and Martin 1975; Diamond 1989; Fisher 2009; Ripple and Van Valkenburgh 2010), and yet others point to a combination of climate change and human

impacts (e.g., Koch and Barnosky 2006; Emery-Wetherell et al. 2017). Another set of extinction models invoke catastrophic events, such as a bolide impact (Firestone et al. 2007) or a hyper-disease (MacPhee and Marx 1997).

Currently there is little support for the catastrophic extinction models (e.g., Lyons et al. 2004; Koch and Barnosky 2006; Surovell et al. 2009; Holliday et al. 2014; Meltzer et al. 2014), and much of the debate regarding the late Pleistocene extinctions is focused on the relative importance of climate change versus human impacts, particularly hunting. Some of the climate change extinction models point to nutritional stress as the primary factor responsible for the extinctions (e.g., Graham and Lundelius 1984; Guthrie 1984). The recent development of different methodologies for the reconstruction of mammalian paleodiets (e.g., dental wear and stable isotopes) may shed new light on this matter by allowing the formulation and testing of novel hypotheses about patterns of feeding ecology expected under different extinction models.

Here, we employ methodologies based on dental wear (i.e., mesowear and low-magnification dental microwear) to study dietary patterns of horses and bison from three geographic areas of North America. We use those data to evaluate two nutritionally based extinction models relating to climate-induced vegetation changes during the terminal Pleistocene: the coevolutionary disequilibrium (Graham and Lundelius 1984) and mosaic-nutrient extinction models (Guthrie 1984). We also examine the prevalence of enamel hypoplasia in the samples of horse and bison as a proxy for the incidence of early systemic stress in these ungulates during the late Pleistocene. In the context of the late Pleistocene extinctions, the study of enamel hypoplasia provides the opportunity to test whether herbivorous mammals were potentially experiencing increased levels of systemic stress during the terminal Pleistocene, as predicted by the coevolutionary disequilibrium and mosaic-nutrient models as well as other climate-based extinction models. We emphasize that a comprehensive test of both models would require comparing changes in dental wear and enamel hypoplasia during earlier

glacial–interglacial transitions as well as during the terminal Pleistocene. However, the temporal resolution needed to undertake such a study is presently lacking for previous glacial–interglacial transitions. Therefore, the objective of the present study is to evaluate the consistency of the data on dental wear and enamel hypoplasia collected for North American late Pleistocene horses and bison with respect to predictions established for the coevolutionary disequilibrium and mosaic-nutrient models.

We chose horses and bison for this study because they were relatively abundant in North American, late Pleistocene landscapes and are well represented in the fossil record of that continent (Faunmap Working Group 1994; Grayson 2016). In addition, some studies suggest that these ungulate mammals may have interacted ecologically as competitors for food resources (e.g., Feranec et al. 2009).

The Coevolutionary Disequilibrium Extinction Model

The coevolutionary disequilibrium extinction model assumes that late Pleistocene communities were highly coevolved systems, similar to those currently found on the African savannas (Graham and Lundelius 1984). The present-day African grazing succession is an example of a coevolved system in which grazing by one mammalian herbivore species stimulates the growth of plant species or plant parts that in turn form the food resource of another herbivore species. In this ecosystem, coevolved foraging sequences partition the environment through well-defined niche differentiation, allowing the coexistence of many large herbivores (e.g., Gwynne and Bell 1968; Bell 1971; Murray and Brown 1993).

Paleontological evidence suggests that organisms responded individually to the climatic changes at the end of the Pleistocene (e.g., Graham et al. 1996; Stewart 2009). The coevolutionary disequilibrium model proposes that the individualistic response of plant species during this time interval resulted in large-scale restructuring of vegetation, causing a disruption of coevolutionary interactions between plants and animals (Graham and Lundelius 1984). These changes are postulated to

have reduced niche differentiation among large herbivorous mammals, leading to competition for dietary resources and causing nutritional stress in some species. Competition may have driven species with reduced fitness to extinction, whereas species better adapted to the new community patterns would have thrived and established a new interaction sphere (Graham and Lundelius 1984).

Testable assumptions/predictions of the coevolutionary disequilibrium model include chronological congruence of plant community changes and animal extinctions, the occurrence of relictual populations of animals and plants in association with one another, and divergence and habitat partitioning of surviving large herbivores as a consequence of competition (Graham and Lundelius 1984). Using newer analytical techniques, we can now expand the testing of assumptions of the coevolutionary disequilibrium model. Specifically, evaluation of mesowear and low-magnification microwear permits testing of well-defined niche differentiation and potential resource competition in large ungulates both before and after the onset of major environmental changes at the terminal Pleistocene as follows:

H1₀: Before rapid climatic changes at the end of the Pleistocene, sympatric species of horse and bison inhabiting North America did not differ significantly in their diets, suggesting that they did not partition the available food resources.

H1_A: Before rapid climatic changes at the end of the Pleistocene, sympatric species of horse and bison differed significantly in their diets, indicating that they partitioned the available food resources.

H1 prediction: If sympatric species of horse and bison partitioned food resources before the rapid climatic changes of the postglacial (i.e., during the preglacial and full-glacial time intervals), then the signals of the dietary proxies (mesowear and low-magnification microwear, in this study) should be statistically different for horse and bison.

H2₀: During the postglacial, sympatric species of horse and bison did not differ significantly in their diets, suggesting that they were not

partitioning the available food resources and were potentially competing for them.

H2_A: During the postglacial, sympatric species of horse and bison from this time interval differed significantly in their diets, indicating that they were partitioning the available food resources.

H2 prediction: If sympatric species of horse and bison were not partitioning available food resources during the postglacial, as would be consistent with the assumptions of coevolutionary disequilibrium, then the signal of each dietary proxy (i.e., dental microwear and mesowear) should not be significantly different for horse and bison.

The Mosaic-Nutrient Extinction Model

Like the coevolutionary disequilibrium model, the mosaic-nutrient model for extinction focuses on an altered vegetational landscape as a primary driver of terminal Pleistocene extinctions. This model assumes that before the terminal Pleistocene, a mosaic vegetation pattern was present and allowed ungulates, especially large caecalid ungulates (e.g., horse and mammoth), to obtain a proper mix of nutrients needed for survival (Guthrie 1984). Unlike caecalid ungulates, ruminants (e.g., bison and deer) are able to synthesize some essential nutrients in the rumen through the help of microbial activity (Guthrie 1984). In addition, ungulates are adapted to overcome some plant defenses but not others. For example, large caecalid grazers like horse and mammoth have dental and digestive physiological adaptations to deal with grass phytoliths and a high concentration of fiber (Janis 1976, 1988), but are not as efficient at detoxifying allelochemicals, which are commonly found in forbs and other browse, as is the case for ruminants (Janis 1976; Guthrie 1984). Therefore, as long as a diversity of plant species were available, large caecalids may have acquired a proper mix of nutrients by diluting a variety of different toxins, which could be detoxified in reduced quantities (Guthrie 1984).

The mosaic-nutrient model proposes that at the end of the Pleistocene, changes in seasonal climatic regimes (i.e., increased seasonality and less intra-annual variability) led to decreased local plant diversity and increased zonation of plant communities and resulted in

a shift in net anti-herbivore defenses (Guthrie 1984). Collectively, those changes may have differentially impacted the ability of some herbivores (e.g., caecalid ungulates) to effectively obtain nutrients because of limitations in digestive physiology (Guthrie 1984).

As with the coevolutionary disequilibrium model, newer analytical techniques permit direct testing for dietary change that may support or refute the mosaic-nutrient model. Specifically, evaluation of mesowear and low-magnification microwear permits testing of changes in the variety of food resources consumed by megafauna both before and at the terminal Pleistocene as follows:

H3₀: Bison and horse species did not suffer a decrease in the variety of plant species consumed during the postglacial relative to preglacial and full-glacial periods.

H3_A: Bison and horse species underwent a significant decrease in the variety of plants consumed during the postglacial, potentially due to a reduction in local plant diversity.

H3 prediction: If species of horse and bison experienced a significant decrease in the variety of plants in their diets during the postglacial, then the statistical dispersion (measured by the variance) of the variables of each dietary proxy (i.e., low-magnification microwear variables and mesowear score) should be significantly smaller for this time interval than for the preglacial and full-glacial periods.

A Test for Both Models: Systemic Stress and Enamel Hypoplasia

Both the coevolutionary disequilibrium and mosaic-nutrient extinction models point to systemic stress, particularly nutritional stress, on herbivorous mammals as one of the primary factors responsible for the late Pleistocene extinctions (Graham and Lundelius 1984; Guthrie 1984). This would trigger a “bottom-up” ecosystem collapse starting with the herbivores and filtering upward to the apex carnivores. For either extinction model to be considered feasible, not only do the formulated predictions have to be met, but also the occurrence of broad systemic stress in herbivores

during the terminal Pleistocene must be demonstrated. Recent advances regarding the inference of physiological stress from dental remains permit testing of this hypothesis.

Periods of disruption in tooth development correlated with systemic stress during enamel matrix formation are recorded in the teeth in the form of tooth defects known as enamel hypoplasia (Goodman and Rose 1990; Moggi-Cecchi and Crovella 1991; Hillson 1996, 2005; Kierdorf and Kierdorf 1997; Guatelli-Steinberg 2000, 2003; Witzel et al. 2008). These tooth defects have been extensively used in anthropological and archaeological studies to infer the health of past and present primate populations, including humans (e.g., Goodman and Rose 1990; Moggi-Cecchi and Crovella 1991; Skinner and Goodman 1992; Hillson 1996, 2005; Guatelli-Steinberg 1998, 2000, 2003; Lukacs 2001, 2009; Skinner and Hopwood 2004; King et al. 2005; Schwartz et al. 2006; Witzel et al. 2008; Guatelli-Steinberg et al. 2012; Smith and Boesch 2015). In contrast, fewer studies have been conducted on archaeological and paleontological non-primate mammals, including Neogene rhinoceroses (Mead 1999; Roohi et al. 2015), domestic pigs and wild boar (Dobney and Ervynck 2000; Dobney et al. 2004; Witzel et al. 2006), late Pleistocene and Holocene bison (Niven 2002; Niven et al. 2004; Byerly 2007), Pliocene giraffids (Franz-Odenaal et al. 2004), cattle (Kierdorf et al. 2006), Pleistocene equids (Timperley and Lundelius 2008), domestic sheep and goats (Kierdorf et al. 2012; Upex et al. 2014), and the Pleistocene notungulate *Toxodon* (Braunn et al. 2014).

The Federation Dentaire Internationale (FDI) established an international index for the study of enamel hypoplasia that recognizes different categories of this defect: single pits, areas missing enamel, nonlinear grooves, nonlinear multiple pits, horizontal linear grooves, and horizontal linear pits (FDI 1982). Nonlinear pits and areas missing enamel are thought to result from localized physical trauma, usually associated with a thinning of the bone covering the developing tooth commonly caused by poor maternal diet (deficiencies in calcium, vitamin A, or vitamin D) and premature births (Skinner and Hung 1986). Small horizontal linear pits and horizontal linear grooves are

known as linear enamel hypoplasia. Linear defects have been associated with different systemic stressors (e.g., weaning, parturition, nutritional stress, and illness) at the time of tooth formation (Franz-Odendaal 2004; Franz-Odendaal et al. 2004). Some researchers consider that the width and depth of linear enamel hypoplasia correspond, respectively, to the duration of the stress episode and its severity (Goodman et al. 1980; Suckling 1989).

In this study, we examined the prevalence of enamel hypoplasia in the cheek teeth of North American late Pleistocene equids and bison as a proxy for the incidence of early systemic stress. The hypotheses tested are:

H4₀: Horse and bison do not show a significant difference in the frequency of enamel hypoplasia and number of hypoplastic events per affected tooth during the terminal Pleistocene (postglacial) relative to previous time intervals.

H4_A: Horses, in contrast to bison, show a significant increase in the frequency of enamel hypoplasia and number of hypoplastic events per affected tooth during the terminal Pleistocene (postglacial), potentially caused by an increase in systemic stress (specifically nutritional stress) due to new vegetational associations.

H4 prediction: The coevolutionary disequilibrium and mosaic-nutrient extinction models both predict an increase in systemic stress (specifically nutritional stress), particularly for the species that became extinct. Systemic stress encountered by an individual while the dentition was being formed can be inferred by examining for enamel hypoplasia. If horses experienced an important increase in systemic stress during the postglacial, the frequency of enamel hypoplasia and the number of hypoplastic events per affected tooth for this time interval should be significantly greater than those for earlier time periods (full-glacial and preglacial).

Materials and Methods

The samples for study consisted of late Pleistocene equid and bison cheek teeth (both isolated as well as from skulls and mandibles)

from Bluefish Caves, Yukon Territory; the Edmonton area gravel pits and Wally's Beach site, Alberta; and several sites in the American Southwest, including Dark Canyon Cave, Dry Cave, and Blackwater Draw, New Mexico, as well as Sharbauer Ranch and Lubbock Lake sites, Texas (Fig. 1). These sites were selected for study because they are primarily arranged in a north-south transect along the Western Interior of North America, allowing us to evaluate responses in diet and systemic stress of horses and bison at different latitudes. All of the specimens we studied are deposited in the following institutions, with corresponding institutional acronyms and geographic location indicated in parentheses: Archaeology Collection (Bluefish Caves; MgVo-1, 2, and 3) of the Canadian Museum of History (CMH; Gatineau, Quebec, Canada); Quaternary Paleontology (P) and Archaeology collections (Wally's Beach site; DhPg-8) of the Royal Alberta Museum (RAM; Edmonton, Alberta, Canada); Vertebrate Paleobiology Collection, Laboratory for Environmental Biology, University of Texas at El Paso (UTEP; El Paso, Texas, USA); and the Vertebrate Paleontology collection of the Vertebrate Paleontology Laboratory, Jackson School Museum of Earth History, University of Texas at Austin (TMM; Austin, Texas, USA).

The horse and bison teeth were identified using different published sources. Species identification was based on the studies by Lundelius (1972), Jass et al. (2011), and Harris (2015) for the bison teeth and Barrón-Ortiz et al. (2017) for the equid teeth. *Bison antiquus* was identified for the American Southwest sample and *Bison* sp. for the sample from Alberta. We identified two equid species, caballine and non-caballine, for the American Southwest, but only the caballine species was identified in the samples from Alberta and the Yukon Territory. Given the state of flux in equid taxonomy, we refer to the caballine species as *Equus "ferus"* and to the non-caballine species as "*Equus conversidens*," to acknowledge that the nomenclature may change with additional taxonomic studies. Following a proposal by Gentry et al. (1996), the International Commission on Zoological Nomenclature has ruled that the names for some wild forms have precedence over those for domestic forms, if these

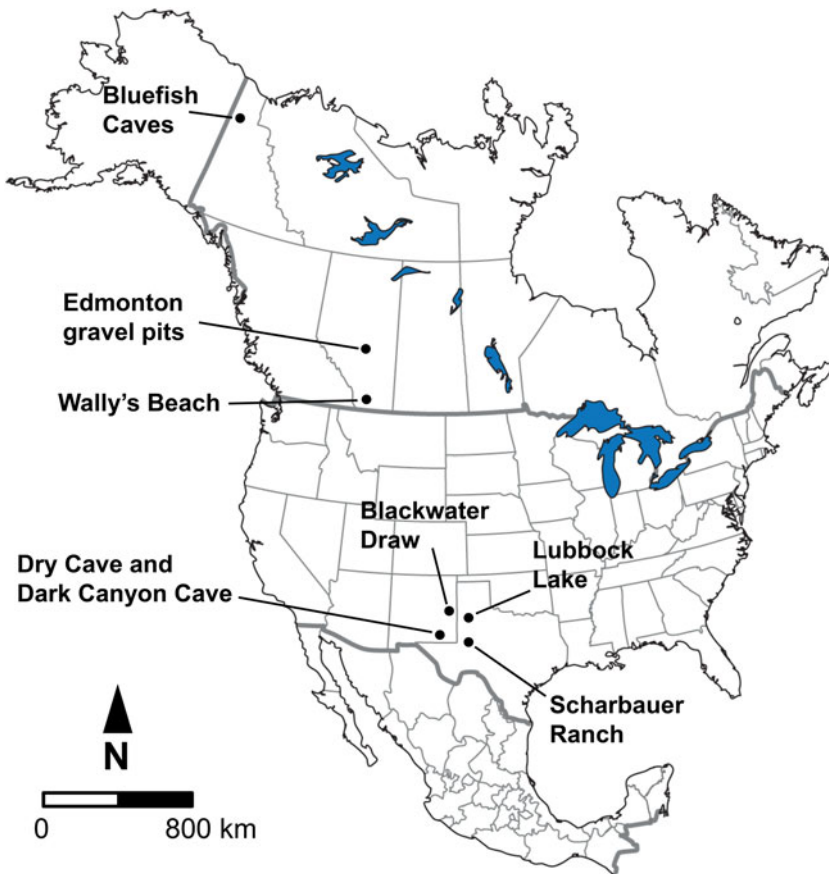


FIGURE 1. Geographic location of the fossil sites considered in this study.

are considered conspecific (ICZN 2003; Gentry et al. 2004). Therefore, *Equus ferus* Boddaert, 1785 has precedence over *Equus caballus* Linnaeus, 1758; however, this has not been consistently followed in the literature (Wilson and Reeder 2005). *Equus conversidens* is considered a valid taxon in some studies (e.g., Scott 1996; Azzaroli 1998; Bravo-Cuevas et al. 2011; Priego-Vargas et al. 2017) and a nomen dubium in other studies (e.g., Winans 1985, 1989; Heintzman et al. 2017). The generic name *Haringtonhippus* was recently proposed for the non-caballine horse (Heintzman et al. 2017). However, a recent phylogenetic analysis identified *Haringtonhippus* within the group that includes species traditionally assigned to *Equus* (Barrón-Ortiz et al. 2018). Regardless of how the caballine and non-caballine species are named, several studies consistently identify them as distinct lineages (e.g., Weinstock et al.

2005; Barrón-Ortiz et al. 2017; Heintzman et al. 2017); therefore, their recognition as separate taxonomic units in the present study is well supported.

The data we collected were arranged into preglacial, full-glacial, and postglacial time intervals. The material from Bluefish Caves, which consisted of only one equid species (*E. "ferus"*), could only be divided into two time intervals: preglacial/full-glacial (~31–14 kyr RCBP [radiocarbon years before the present]) and postglacial (~14–10 kyr RCBP) (Table 1). Specimens were assigned to one of these two time intervals based on published work (Cinq-Mars 1979; Morlan 1989), documents on file at the CMH (CMH Archives A2002-9 [Jacques Cinq-Mars's documents]: box 11, f.7), and the spatial and stratigraphic provenance of equid specimens (retrieved from specimen catalogs and maps in the CMH Archives; A2002-9:

TABLE 1. Temporal distribution of the late Pleistocene equid and bison samples studied. Post-LGM = postglacial; LGM = full-glacial; Pre-LGM = preglacial. An asterisk (*) indicates the sample spans Pre-LGM and LGM time intervals.

Time interval	Bluefish Caves <i>Equus "ferus"</i>	Alberta		American Southwest		
		<i>Equus "ferus"</i>	<i>Bison</i> sp.	<i>Equus "ferus"</i>	<i>"Equus conversidens"</i>	<i>Bison antiquus</i>
Post-LGM	X	X	X	X	X	X
LGM	X*			X	X	
Pre-LGM		X	X		X	

box 2, f.1, f.2, f.4; box 3, f.1, f.3 – f.9, f.13; box 8, f.4, f.5) relative to directly radiocarbon-dated bones (Canadian Archaeological Radiocarbon Database [CARD 2.0]). These divisions correspond to a change in the vegetation of the region from tundra during the preglacial/full-glacial to dwarf birch during the postglacial (Cinq-Mars 1979; Ritchie et al. 1982). Different publications mention the occurrence of bison remains at Bluefish Caves (Cinq-Mars 1979, 1990), but we were unable to locate any bison cheek teeth in the collection of the CMH. Thus, we only studied equid specimens from this site.

The samples from Alberta were divided into preglacial (>60–21 kyr RCBP) and postglacial time intervals (~13–0 kyr RCBP) (Table 1) based on published radiocarbon dates (Waters et al. 2015) and the association of specimens with localities that have only yielded dates of preglacial or postglacial age (Burns 1996; Jass et al. 2011). Fossil material from the full-glacial is not represented in Alberta, because most of the province was covered by the Laurentide and Cordilleran ice sheets at that time (Young et al. 1994, 1999; Burns 1996; Jass et al. 2011). The specimens from Alberta consisted of only one equid species (*E. "ferus"*; although a second less common species, "*E. conversidens*," is recognized from the Edmonton area gravel pits [Barrón-Ortiz et al. 2017]) and material referable to *Bison* sp.

The fossil material from the American Southwest (specifically eastern New Mexico and western Texas) was divided into preglacial (~25–20 kyr RCBP), full-glacial (~20–15 kyr RCBP), and postglacial (~15–10 kyr RCBP) ages (Harris 1987, 1989, 2015; Tebedge 1988; Haynes 1995; Holliday and Meltzer 1996) (Table 1). We were able to obtain data for only one equid species ("*E. conversidens*") during the preglacial, whereas for the full-glacial we

were able to collect data for two equid species (*E. "ferus"* and "*E. conversidens*"). We also collected data for postglacial specimens of *E. "ferus"* and "*E. conversidens*." For *B. antiquus*, only specimens from postglacial localities showed a state of preservation that allowed us to study dental wear and enamel hypoplasia; therefore, the analyses for this species were limited to this time interval. The sampling limitations for these and all other localities studied were imposed by the preservation of the specimens and their availability at the repository institutions.

Analysis of Dental Wear

We used the extended mesowear (Franz-Odenaal and Kaiser 2003; Kaiser and Solounias 2003) and low-magnification microwear methods (Solounias and Semprebon 2002; following the modifications by Fraser et al. [2009]), to test the outlined hypotheses for the coevolutionary disequilibrium and mosaic-nutrient extinction models. A total of 122 specimens for the dental microwear analysis and 102 specimens for the mesowear analysis were studied, consisting mostly of isolated teeth (Supplementary Tables 1 and 2).

Low-Magnification Microwear.—Low-magnification microwear and microwear texture analysis are currently the most widely applied methodologies for the study of dental microwear (e.g., Solounias and Semprebon 2002; Ungar et al. 2003, 2010; Scott et al. 2005, 2006; Semprebon et al. 2004; Merceron et al. 2004, 2005, 2010; Nelson et al. 2005; Gomes Rodrigues et al. 2009). In this study, we examined dental microwear at a low magnification (35×) using high-resolution clear-epoxy casts. We counted microwear features on high dynamic range images (HDR; Fig. 2) prepared following the methodology in Fraser et al. (2009), using an Olympus E-M10 digital camera and a Nikon SMZ1500

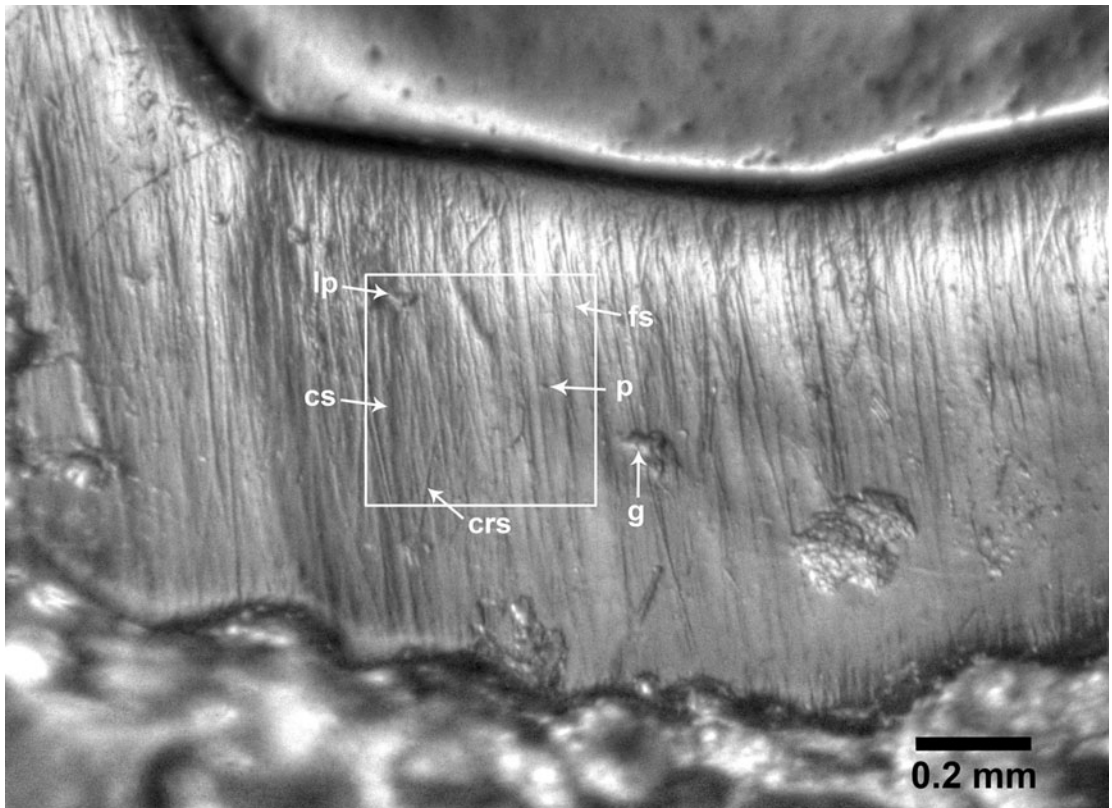


FIGURE 2. High dynamic range image of the paracone lingual enamel band of an equid tooth (upper right M1; UTEP 22-1609) showing one of the 0.4×0.4 mm counting areas and the microwear features evaluated in this study. Abbreviations: crs = cross scratch; cs = coarse scratch; fs = fine scratch; g = gouge; lp = large pit; p = small pit.

stereomicroscope; the digital resolution of the images obtained is $0.6 \text{ pixels}/\mu\text{m}$. Cleaning, molding, and casting of the teeth studied were done according to Solounias and Semprebon (2002). Only teeth in middle stages of wear were used. To minimize systematic biases during data collection, we randomized the order of the specimens during photography and the order of the HDR images was also randomized before data collection to ensure observer blindness (Mihlbachler et al. 2012). All counts were done by the same researcher (C.I.B.-O.).

The majority of the specimens we studied consisted of isolated upper (M1–M3) and lower (m1–m3) molars. Previous studies of low-magnification dental microwear have identified that homologous upper and lower teeth show comparable dental microwear features (Merceron et al. 2004; Semprebon et al. 2004); therefore, upper and lower molars

were not studied separately. In the case of teeth belonging to the same individual, we studied the second molar, and if this tooth was damaged or absent we selected at random one of the other associated molars that were well-preserved. We preferentially studied microwear features on the lingual enamel band of the paracone and/or metacone for the upper molars and the lingual enamel band of the protoconid and/or hypoconid for the lower molars. For specimens in which these enamel bands were damaged, we collected microwear data from the lingual enamel band of the fossettes for the upper molars and the buccal enamel band of the protoconid and/or hypoconid for the lower molars.

The microwear variables scored per tooth specimen are partially based on those presented by Solounias and Semprebon (2002) and include the average number of scratches

and pits per two counting areas on the enamel band, each 0.4×0.4 mm. Pits are microwear features that are circular to subcircular in outline with a length to width ratio of less than 4:1, whereas scratches are elongated features, typically with a length to width ratio of at least 4:1. We also recorded scratch texture for each counting area by noting whether the scratches present consisted of fine scratches (scratches that appear the narrowest), coarse scratches (scratches that appear wider), or mixed scratches (a combination of both fine and coarse scratches). We subsequently assigned a score of 0 if a counting area consisted of fine scratches, 1 if it consisted of fine and coarse scratches, and 2 if it consisted of coarse scratches (e.g., Rivals et al. 2007; Rivals and Athanassiou 2008). The average scratch texture score of the two counting areas was then calculated for each specimen. We also documented the average number of cross scratches (scratches oriented at an oblique angle with respect to the majority of scratches), average number of large pits (which are at least twice the diameter of small pits), and the average number of exceptionally wide scratches (at least twice the width of coarse scratches) for the two counting areas. Finally, we recorded the presence of gouges (large, irregular microwear scars) on the visible enamel band of the photograph, providing a score of 1 if the feature was present or 0 if it was absent. Raw data are listed in Supplementary Table 1.

We conducted nonparametric multivariate analyses of variance tests (NP-MANOVA), as the assumptions of parametric MANOVA tests (i.e., normality, equality of variances and covariances) were violated by the data. NP-MANOVA tests were used to evaluate whether horse and bison samples possessed different microwear patterns during the preglacial/full-glacial time intervals, but not during the postglacial, as predicted by the coevolutionary disequilibrium model. In these tests, significance was estimated by permutation, using 10,000 replicates and the Mahalanobis distance measure. Bonferroni-corrected pairwise comparisons were used to identify which samples were significantly different from one another. These analyses were performed using PAST 2.17 (Hammer et al. 2001) on the data in Supplementary Table 1.

To evaluate whether the variance of the microwear variables was smaller for the postglacial samples than for previous time intervals (as predicted by the mosaic-nutrient model), we calculated the quotient resulting from the division of the variance of a specific microwear variable at time interval 1 by the variance of that variable at time interval 2. Significance of the variance quotient was assessed by a two-sample *F*-test for equal variances (right-tailed) using the bootstrap resampling method (10,000 replicates) in MATLAB R2018a (MathWorks 2018; code available in Supplementary File 1). For this analysis we examined the counted microwear variables found in Supplementary Table 1: average number of scratches, average number of pits, average number of cross scratches, average number of large pits, and average number of wide scratches.

Extended Mesowear Method.—In this study, we used the extended mesowear methods proposed for equids (Kaiser and Solounias 2003) and ruminants (Franz-Odenaal and Kaiser 2003). We collected mesowear data for teeth in middle stages of wear (i.e., heavily worn as well as very little worn teeth were not included in the analysis). Most of the specimens studied consisted of isolated teeth. In the case of horses, we recorded mesowear data from P4 to M3. For bison, we obtained mesowear data from M2 and M3; however, to increase sample size, in some cases we obtained mesowear data from M1 teeth. In some instances we encountered teeth belonging to the same individual. In those cases, we preferentially recorded mesowear data from the M2. If the M2 was damaged or absent, we randomly selected one of the other tooth positions that were well preserved. Sometimes we encountered specimens in which the right and left M2 were present in a good state of preservation. In those cases we selected one of the two teeth at random. We recorded mesowear data by direct observation of the specimens, and the frequency of the different variables was obtained for each sample. Subsequently, we calculated the mesowear score (Kaiser 2011), which combines cusp relief and shape into a single value: 0 (high and sharp cusps), 1 (high and round cusps), 2 (low and sharp cusps), 3 (low and round cusps), and 4 (low and blunt cusps) (Fig. 3). All of the teeth

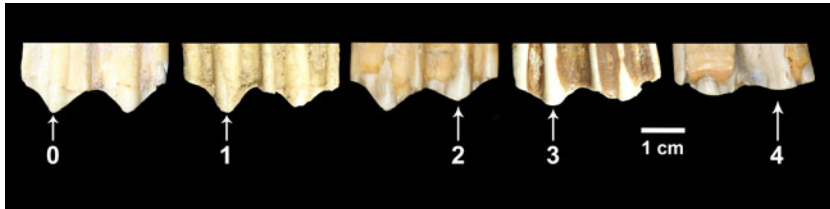


FIGURE 3. Buccal view of the molar cusps of five bison upper cheek teeth showing the mesowear score values considered in this study. 0 = high and sharp cusp; 1 = high and round cusp; 2 = low and sharp cusp; 3 = low and round cusp; 4 = low and blunt cusp.

were examined and scored by the same researcher (C.I.B.-O.). Raw data are listed in Supplementary Table 2.

We conducted Kruskal-Wallis tests (Hammer and Harper 2006) using the software PAST 2.17 (Hammer et al. 2001) to assess whether the mesowear score significantly differed among sympatric bison and horse species. Significant differences would indicate dietary resource partitioning. The coevolutionary disequilibrium model predicts resource partitioning during preglacial/full-glacial time intervals, but not during the postglacial.

We also evaluated the variance of the mesowear score for each equid and bison sample and then calculated the quotient resulting from the division of the variance of the mesowear score at time interval 1 by the variance at time interval 2. Significance of the variance quotient was assessed by a two-sample *F*-test for equal variances (right-tailed) using the bootstrap resampling method (10,000 replicates) in MATLAB R2018a (MathWorks 2018; code available in Supplementary File 1). As predicted by the mosaic-nutrient extinction model, a reduction in variance of postglacial samples would reflect a reduction in the diversity of available vegetation for consumption by megaherbivores.

Analysis of Enamel Hypoplasia

Using both direct observations ($n = 429$) and observations on CT scans of specimens ($n = 3$), we analyzed a total of 432 specimens consisting mostly of isolated teeth (Supplementary Table 3) for both the presence/absence of enamel hypoplasia and the number of hypoplastic events present per affected tooth. We treated isolated teeth as separate individuals,

unless there was evidence that isolated teeth were associated as part of the same tooth row, in which case the associated teeth were treated as a single individual. The sample included worn and unworn teeth to increase sample size. Any form of enamel hypoplasia was included in the analysis, because separation of the tooth defects into the categories established by the FDI for the study of enamel hypoplasia (FDI 1982) resulted in very small sample sizes. We calculated the percentage of specimens (i.e., individuals) presenting enamel hypoplasia in the different study samples to determine the prevalence of this tooth defect. We also calculated the mean number of hypoplastic events per affected tooth per sample, to shed light on the recurrence of episodes of systemic stress leading to hypoplasia during tooth development. To accomplish this task, we assumed that hypoplastic defects occurring at comparable heights on the same tooth crown resulted from the same stress event and could therefore be counted as a single hypoplastic event.

Initial assessments focused on a single tooth position; however, this resulted in very small sample sizes. We therefore included in the analysis as many complete teeth as we could reliably identify from various tooth positions. In the case of isolated teeth, we studied premolars (P2–P4; p2–p4) and molars (M1–M3; m1–m3) for equids, and molars for bison (M1–M3; m1–m3). We did not study premolars for bison, because the premolars are not molarized as they are in horses and as a result are morphologically different and much smaller than the molars. This difference in size could potentially bias the preservation of premolars in the fossil record relative to molars, and it could also affect

their representation in research collections as a result of collecting biases. Moreover, the difference in size between premolars and molars of bison might indicate that these two tooth groups have a different dental developmental geometry, a factor that is known to affect the identification of enamel hypoplasia when using macroscopic methods (Hillson and Bond 1997; Hillson 2014).

When dealing with associated teeth (i.e., teeth belonging to the same individual), we examined either the P4 or M3 for enamel hypoplasia in addition to the M1 (p4 or m3, and m1 for lower teeth) in equids, and the M1, M2, and M3 (m1, m2, and m3 for lower teeth) in bison. This is because the timing of tooth crown formation in equids for the P4/p4 and M3/m3 minimally overlaps with the timing of crown formation for the M1/m1 (Hoppe et al. 2004). Thus, hypoplastic defects not occurring on the apical portion of the tooth crown (immediately below the area of the cusps) of the P4/p4 or M3/m3 can be identified as separate stress events from those present in the M1/m1. In bison the timing of tooth crown formation for each molar minimally overlaps (Gadbury et al. 2000; Niven et al. 2004). Therefore, hypoplastic defects not occurring on the apical portion of the tooth crown (immediately below the area of the cusps), especially of M2/m2 and M3/m3, can be considered as distinct stress episodes. For a given individual, we noted the presence or absence of enamel hypoplasia on any of the teeth (*Equus*: P4 or M3, and M1 [p4 or m3, and m1 for lower teeth]; *Bison*: M1, M2, and M3 [m1, m2, and m3 for lower teeth]) and counted this as a single observation. This observation was added to the corresponding data set used to calculate the percentage of specimens presenting enamel hypoplasia for a specific study sample. We also added the number of hypoplastic events in each tooth considered (P4 or M3, and M1 in equids [p4 or m3, and m1 for lower teeth], and M1, M2, and M3 in bison [m1, m2, and m3 for lower teeth]) and divided this value by the number of teeth scored to determine the mean number of hypoplastic events per tooth. This result was included in the corresponding data set used to calculate the mean number of hypoplastic events per affected tooth for a specific study sample.

All of the specimens, except three equid dentaries from the Wally's Beach site, Alberta, were examined via direct observation (Fig. 4). We used oblique lighting to facilitate the identification of enamel hypoplasia. The vast majority of the equid cheek teeth from Wally's Beach are encased in dentaries or maxillaries, preventing the direct assessment of these specimens for enamel hypoplasia. Therefore, three dentaries from this site were CT-scanned to allow examination of the cheek teeth. The specimens were CT-scanned at the Department of Anthropology, University of Western Ontario, using a Nikon XT H 225 ST MicroCT Scanner with the following settings: 190 kVp, 85 microamps, 500 ms exposure time, averaged 2 frames/projection, and voxel size of 70 μm . The software Inspect-X v. 4.3 was used for scan capture, CT-Pro 3D v. 4.3 was used for volume reconstruction, and VG Studio Max v.2.2 was used for visualization and export to dicom. The CT-scan raw data we used are available in the Supplementary Material. We created 3D surface models of the CT-scanned specimens using the computer software AMIRA 5.3.3 for Mac OS X (Visage, Chelmsford, MA, <http://www.visage.com>). We adjusted the threshold to digitally remove the dentary and the cementum

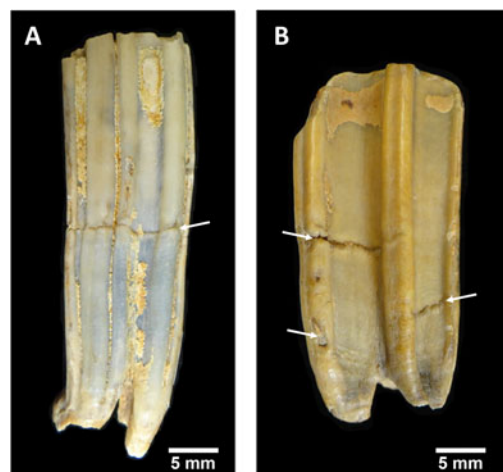


FIGURE 4. Examples of equid cheek teeth illuminated with oblique lighting to highlight enamel hypoplasia (indicated by the white arrows). A, Lingual view of a lower left m1 (RAM P90.6.37). B, Buccal view of an upper right P4 (RAM P89.13.610).

from the cheek teeth in order to be able to detect the presence of enamel hypoplasia on the surface of the tooth crown (Fig. 5A). We then prepared digital histological sections using the ObliqueSlice module in AMIRA 5.3.3 to verify that the tooth defects identified on the external surface of the tooth crown corresponded to enamel hypoplasia (Fig. 5B). All of the tooth defects identified in the 3D surface models showed thinning of the imbricational enamel (Fig. 5B), which is characteristic of enamel hypoplasia (Goodman and Rose 1990). These observations support the contention that similar tooth defects identified in the specimens that we assessed via direct observation corresponded to enamel hypoplasia. Only clearly defined, deep grooves were classified as enamel hypoplasia, following previous studies (e.g., Goodman and Rose 1990; Franz-Odenaal et al. 2004).

One potential complication of the study of enamel hypoplasia of equids and bison is the presence of cementum covering the tooth crown, which helps to anchor the tooth into the maxilla or dentary while the roots develop and the tooth erupts into the mouth (Kierdorf et al. 2006; Upex et al. 2014). Cementum did not pose a serious problem to the examination and study of enamel hypoplasia in our study,

because weathering and degradation of cementum exposed the enamel underneath. When examining the specimens, we qualitatively scored the extent to which cementum covers the tooth crown using a scoring system that ranges from 0 to 5: 0 indicating that the tooth crown is not covered by cementum, 1 denoting that 1–25% of the tooth crown is covered by cementum, 2 indicating that 26–50% of the tooth crown is covered by cementum, 3 denoting that 51–75% of the tooth crown is covered by cementum, 4 indicating that 76–95% of the tooth crown is covered by cementum, but that the cementum present consists of a thin layer, and 5 denoting that the entire tooth crown is covered by a thick layer of cementum. We did not use specimens with a score of 5 in the analysis, because the cementum covering the tooth made it difficult to consistently evaluate whether enamel hypoplasia was present in the tooth. Some equid teeth from Bluefish Caves had one side of the tooth crown (the buccal side in lower teeth and the lingual side in upper teeth) completely covered by cementum, but not the remaining sides. We decided to score the exposed sides for enamel hypoplasia and include these specimens in the analysis, because otherwise the sample size for this locality would have been too low for statistical analysis.

For each geographic region and species, we conducted *z*-tests of proportions (left-tailed) to determine whether the percentage of specimens with enamel hypoplasia (i.e., prevalence of enamel hypoplasia) increased during the postglacial relative to the previous time interval(s). Similarly, we conducted *t*-tests (left-tailed) using the bootstrap resampling method (10,000 replicates) to determine whether the number of hypoplastic events per affected tooth increased during the postglacial, potentially indicating that stress events became more recurrent during this time interval as compared with full-glacial and preglacial intervals. We performed these tests for bison and equid samples separately, because it is not known whether both ungulate groups are equally sensitive to the development of enamel hypoplasia. Furthermore, the tooth crown of bison teeth develops faster than that of equids. For example, crown formation of the m3 takes on average 16 months in Plains bison (Niven

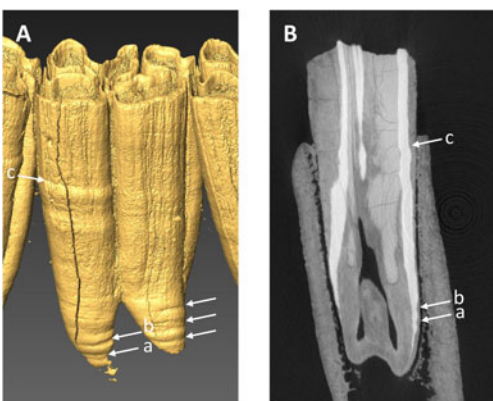


FIGURE 5. Example of CT-scan data used to determine the presence of enamel hypoplasia in three equid mandibles from Wally's Beach, Alberta. A, Three-dimensional digital surface model of lower m1 (RAM DhPg-8 864) showing four hypoplastic events (horizontal linear grooves) indicated by the arrows. B, Radial digital section through the anterior portion of the same tooth showing the three hypoplastic events found on the protoconid column (a, b, c).

et al. 2004), whereas it takes 34 months in domestic horse (Hoppe et al. 2004). Thus, equid teeth can potentially record more stress events than bison teeth, especially if these occurred periodically with a periodicity of up to 2.5 years in the longer-developing teeth such as the P4/p4, M2/m2, and M3/m3. All statistical tests were conducted using the software package MATLAB R2018a (MathWorks 2018) (code available in Supplementary Files 2 and 3). The significance level for all tests was set to a *p*-value of 0.05.

Assumptions and Limitations

Dental Wear.—One of the primary assumptions made in this study is that consumption of different plant species and plant parts is recorded in the dental wear of herbivore teeth and that those differences can be observed at different scales (e.g., browser vs. grazer, or more importantly, differences within those broad categorizations). A large number of studies of dental wear at different scales and using different techniques (e.g., low-magnification microwear, texture microwear analysis, conventional mesowear, mesowear using the mesowear ruler) have consistently shown that dental wear varies significantly across broad dietary groups such as grazers, browsers, mixed feeders, frugivores, and generalists (e.g., Solounias et al. 1988; Fortelius and Solounias 2000; Solounias and Semperebon 2002; Merceron et al. 2005; Ungar et al. 2007). However, finer dietary differences within these broad trophic groups have to be detected to test the extinction models considered here.

For example, the coevolutionary disequilibrium extinction model uses the present-day grazing succession of the African savannas as an example of a highly coevolved system (Graham and Lundelius 1984). This particular system consists of several grazers, such as the plains zebra (*Equus quagga*), wildebeest (*Connochaetes taurinus*), hartebeest (*Alcelaphus buselaphus*), and topi (*Damaliscus lunatus*). Field studies have shown that in some areas, these grazers partition dietary resources by feeding on different plant parts and grasses at different growth stages (e.g., Gwynne and Bell 1968; Bell 1971; Murray and Brown 1993). It is reasonable to propose that each of these grazers occupies a unique

niche within the “grazer” spectrum and that there may be observable differences in tooth microwear and mesowear as a result. The results of a mesowear analysis of these ungulate mammals generally support this assumption (Fortelius and Solounias 2000).

The results of other dental wear studies (e.g., Scott 2012; Barrón-Ortiz et al. 2014) also indicate that it is possible to detect finer differences within the broad dietary groups that have traditionally been recognized. However, what those differences actually indicate about the feeding ecology of the ungulates investigated is less clear. Despite extensive research, there is still no consensus about the primary agent responsible for the formation of dental wear features. Phytoliths, lignin, and cellulose, as well as exogenous grit, have each been proposed as the primary factor producing dental wear (e.g., Walker et al. 1978; Ungar et al. 1995; Merceron et al. 2007; Sanson et al. 2007; Lucas et al. 2013; Schulz et al. 2013; Tütken et al. 2013). If phytoliths are the primary agent causing dental wear, then plants or plant parts differing in their concentration and type of phytoliths would produce different dental wear patterns. Alternatively, if exogenous grit is responsible for producing dental wear, then differences in dental wear may reflect feeding in different microhabitats (i.e., dusty vs. less dusty), or it may also reflect feeding on plant species or plant parts that differentially accumulate dust on their surface. More complexly, it is also possible that both exogenous grit and the physical properties of the vegetation contribute, or might even interact, to produce dental wear. While resolution of this issue is beyond the scope of this study, the assumption that differences that we observe are ecologically meaningful is essential and seems reasonable based on emerging data.

An additional assumption that we make in this study relates to the different digestive physiologies of equids and bison. Specifically, we assume that differences in digestive physiology of the investigated equid and bison species do not significantly bias dental wear patterns. Equids are hindgut fermenters with high chewing efficiency and rapid passage times. They consume large amounts of plant material, and that material passes rapidly through the digestive

system and is then fermented by microbial activity in the caecum (Janis 1976; Clauss et al. 2009). Equids also have molarized premolars that greatly assist in the mechanical breakdown of plant material (Janis 1988), possess highly hypsodont teeth (Janis 1988), and have a greater enamel complexity than bison (Famoso et al. 2013).

Bison are ruminant foregut fermenters and have a four-chambered stomach in which microbial fermentation of plant material occurs in the rumen, the first chamber of the stomach (Janis 1976). To complement the fermentation process, ruminants periodically regurgitate the food located in the rumen and rechew it (Janis 1976). The second (reticulum) and third (omasum) chambers act as filters, and the fourth chamber (abomasum) is the true stomach (Janis 1976). The digestive system of ruminants achieves a high degree of particle size reduction, greater than that observed for hindgut fermenters and nonruminant foregut fermenters (Fritz et al. 2009).

Few studies have investigated whether differences in digestive physiology systematically bias the dental wear patterns produced. A recent study that examined microwear on occlusal enamel bands located in the lingual, center, and buccal sides of upper molars of eight species of ruminants and perissodactyls found that microwear features were distributed homogeneously across ruminant molars, but not in the perissodactyl molars (Mihlbachler et al. 2016). In the latter group, microwear features from the labial side of the molars were more strongly predictive of diet (Mihlbachler et al. 2016); however, further studies examining more specimens and additional taxa are needed to corroborate these patterns.

Enamel Hypoplasia.—Testing of the coevolutionary disequilibrium (Graham and Lundelius 1984) and mosaic-nutrient (Guthrie 1984) extinction models requires assessment of nutritional stress in Pleistocene herbivore mammals. Several studies indicate that enamel hypoplasia can be associated with nutritional stress (e.g., Goodman and Rose 1990; Hillson 1996; Larsen 1997; Zhou and Corruccini 1998; Dobney and Ervynck 2000; Hillson 2005; Guatelli-Steinberg and Benderlioglu 2006), and we make the assumption that our observations of hypoplasia are reflective of that stress. That said, we

acknowledge that this tooth defect has a multifactorial etiology, and a variety of other stressors, in addition to malnutrition, have been associated with its development. Systemic and infectious diseases, severe fevers, premature births, parturition, weaning, parasite infestation, and intoxication with fluoride are some of the stressors linked to the development of enamel hypoplasia in mammals (Shearer et al. 1978; Shupe and Olson 1983; Skinner and Hung 1986; Suckling et al. 1986, 1988; Miles and Grigson 1990; Kierdorf et al. 1993, 2000, 2004; Hillson 1996, 2005; Larsen 1997; Dobney and Ervynck 2000). Inferring which stressor potentially caused enamel hypoplasia in a given individual cannot be accomplished without additional lines of evidence, such as knowledge of the diet and life history of the species under study (e.g., Dobney and Ervynck 2000; Franz-Odenaal et al. 2004; Niven et al. 2004). Therefore, the presence of enamel hypoplasia is more commonly treated as an indicator of overall health during tooth development. In that sense, any indication of hypoplasia would be consistent with nutritional stress, but not necessarily indicative of nutritional stress.

Results

Microwear

The summary statistics of the microwear variables of the late Pleistocene equid and bison samples studied are shown in Table 2. The analysis of the low-magnification microwear data (Supplementary Table 1) indicates statistically significant differences in some of the samples studied for evaluating the hypotheses of the coevolutionary disequilibrium extinction model. The NP-MANOVA test (Table 3) reveals that the microwear pattern of *E. conversidens* from the American Southwest is marginally statistically different from the microwear pattern of *E. ferus* for the full-glacial time interval ($F = 1.713$, $p = 0.0496$). In contrast, the microwear pattern of these two equid species, as well as that of *B. antiquus*, is not significantly different for the postglacial (NP-MANOVA test, $F = 0.8747$, $p = 0.6263$). In the case of the specimens from Alberta, the comparison of the horse and bison samples for the glacial time interval is marginally

TABLE 2. Summary statistics of microwear variables of late Pleistocene equid and bison samples studied. n = number of specimens; s = average number of scratches; p = average number of pits; cs = average number of cross scratches; lp = average number of large pits; g = average gouge score, ranging from 0 (none present) to 1 (all enamel bands observed had at least 1 gouge present); ws = average number of wide scratches; ts = average texture score.

Locality and species	Time interval	n	s	p	cs	lp	g	ws	ts
Bluefish Caves <i>Equus</i> "ferus"	Preglacial/Full-glacial	13	22.46	16.77	2.54	1.12	0.12	0.73	0.65
	Postglacial	12	25.63	16.21	4.00	1.17	0.46	0.50	0.67
Alberta <i>E.</i> "ferus"	Preglacial	7	25.07	16.07	2.36	1.79	0.79	1.00	0.86
	Postglacial	7	23.64	25.29	3.00	1.07	0.64	1.29	0.86
Alberta <i>Bison</i> sp.	Preglacial	9	23.39	18.67	3.28	1.22	0.61	1.67	1.00
	Postglacial	9	24.78	18.89	3.11	0.78	0.61	1.06	0.83
American Southwest " <i>Equus conversidens</i> "	Preglacial	15	28.67	16.00	3.20	0.77	0.50	0.70	0.93
	Full-glacial	6	27.50	17.42	3.33	0.83	0.33	1.42	1.00
	Postglacial	13	23.58	21.12	1.69	2.15	0.85	2.00	1.08
American Southwest <i>E.</i> "ferus"	Full-glacial	12	25.46	16.75	2.63	1.33	0.63	0.71	0.88
	Postglacial	10	23.10	22.65	2.50	1.75	0.90	1.25	1.00
American Southwest <i>Bison antiquus</i>	Postglacial	9	25.11	22.50	3.17	1.78	1.00	1.50	0.94

not significant (NP-MANOVA test, $F = 1.556$, $p = 0.0790$), likely due to the small sample sizes for these species. The microwear patterns of postglacial horse and bison samples from Alberta are not statistically different (NP-MANOVA test, $F = 0.9605$, $p = 0.5284$).

The variance of the five counted microwear variables of each species sample did not significantly decrease during the postglacial relative to full-glacial and preglacial time intervals (Table 4). Only two pairwise comparisons are statistically significant, and four other comparisons show the opposite trend, in which the variance significantly increased during the postglacial (Table 4).

Mesowear

Overall, the mean mesowear score of each sample analyzed (Table 5) plots on the abrasion end of the mesowear spectrum (Fig. 6). The mesowear score of "*E. conversidens*" from the American Southwest is not statistically

different from the mesowear score of *E. "ferus"* for the full-glacial time interval (Kruskal-Wallis test, $H = 1.00$, $p = 0.2834$), although it should be pointed out that the sample size of "*E. conversidens*" consists of only two specimens (Table 6). The mesowear scores for these two equid species, along with the specimens of *B. antiquus*, for the postglacial of the American Southwest are also not significantly different (Kruskal-Wallis test, $H = 1.309$, $p = 0.4851$). The Kruskal-Wallis test reveals that the mesowear score for the preglacial samples of horse and bison from Alberta are significantly different ($H = 5.442$, $p = 0.0134$), but this is not the case for the postglacial samples of these ungulates ($H = 1.771$, $p = 0.1582$).

The variance of the mesowear score of each species sample did not significantly decrease during the postglacial relative to full-glacial and preglacial time intervals (Table 7). None of the pairwise comparisons are statistically significant, and in one comparison (preglacial vs.

TABLE 3. Results of NP-MANOVA tests (10,000 replications and using the Mahalanobis distance measure) used to evaluate the hypotheses of the coevolutionary disequilibrium extinction model using the variables in Supplementary Table 1. n = sample size; F = F -statistic; p = p -value. Statistically significant p -values are shown in bold.

Locality	Species	Time interval	n	F	p
Alberta	<i>Equus</i> "ferus"	Preglacial	7	1.556	0.0790
	<i>Bison</i> sp.		9		
	<i>E.</i> "ferus"	Postglacial	7	0.9605	0.5284
American Southwest	<i>Bison</i> sp.	Full-glacial	9	1.713	0.0496
	" <i>Equus conversidens</i> "		6		
	<i>E.</i> "ferus"	Postglacial	12	0.8747	0.6263
	" <i>E. conversidens</i> "		13		
	<i>E.</i> "ferus"		10		
	<i>Bison antiquus</i>		9		

TABLE 4. Results of two-sample *F*-tests for equal variances (right-tailed) using the bootstrap resampling method (10,000 replicates) conducted to test the hypotheses of the mosaic-nutrient extinction model using four counted microwear variables: *s* = average number of scratches; *p* = average number of pits; *cs* = average number of cross scratches; *lp* = average number of large pits; *ws* = average number of wide scratches; VarQ = variance quotient (variance at time interval 1 divided by variance at time interval 2); *p* = *p*-value. Statistically significant *p*-values are indicated in bold. An asterisk (*) identifies comparisons in which the variance at time interval 2 is greater than at time interval 1.

Locality and species	Time interval comparisons	<i>s</i>		<i>p</i>		<i>cs</i>		<i>lp</i>		<i>ws</i>	
		VarQ	<i>p</i>	VarQ	<i>p</i>	VarQ	<i>p</i>	VarQ	<i>P</i>	VarQ	<i>p</i>
Bluefish Caves <i>Equus</i> “ <i>ferus</i> ”	Preglacial/Full-glacial	1.24	0.37	1.03	0.48	0.97	0.52	1.85	0.28	0.52	0.81
Alberta <i>E.</i> “ <i>ferus</i> ”	Preglacial	0.54	0.80	0.65	0.70	2.94	0.13	3.54	0.04	1.35	0.27
	Postglacial										
Alberta <i>Bison</i> sp.	Preglacial	0.22	0.98*	0.71	0.72	0.64	0.78	0.32	0.77	1.09	0.44
	Postglacial										
American Southwest “ <i>Equus conversidens</i> ”	Preglacial	1.44	0.32	1.32	0.40	1.77	0.25	0.82	0.63	0.18	0.99*
	Full-glacial										
	Postglacial	0.61	0.69	0.54	0.82	0.76	0.55	0.61	0.70	0.79	0.67
American Southwest <i>E.</i> “ <i>ferus</i> ”	Preglacial	0.88	0.61	0.71	0.77	1.35	0.30	0.51	0.82	0.14	1.00*
	Postglacial										
	Full-glacial	3.30	0.04	0.31	0.97*	1.43	0.28	0.42	0.96*	0.49	0.89
Postglacial											

postglacial samples of “*E. conversidens*” from the American Southwest), the opposite trend was observed (Table 7).

Enamel Hypoplasia

Enamel hypoplasia was observed in all equid and bison samples studied. The prevalence of this tooth defect showed a larger range in equids than in bison. The prevalence of enamel hypoplasia in the equid samples ranged from 31.25% in the preglacial sample of “*E. conversidens*” from the American Southwest to 64.29% in the postglacial sample of *E. “ferus”* from Alberta (Fig. 7; Table 8). In contrast, the prevalence of enamel hypoplasia in the bison samples ranged from

25.71% in the preglacial sample of *Bison* sp. from Alberta to 29.41% in the postglacial samples of *Bison* sp. from Alberta and *B. antiquus* from the American Southwest (Fig. 7; Table 8).

The prevalence of enamel hypoplasia in equids increased during the postglacial in two out of four samples in which this comparison was made (Table 9). The sample of “*E. conversidens*” from the American Southwest shows a prevalence of enamel hypoplasia of 31.25% for the preglacial and 51.61% for the postglacial, and this difference is statistically significant (*z*-test of proportions, *z* = -1.8099, *p* = 0.0352). Similarly, the frequency of enamel hypoplasia of *E. “ferus”* from Alberta increased from

TABLE 5. Summary statistics of the mesowear variables of late Pleistocene equid and bison samples studied. *n* = number of specimens; MS = mesowear score; *h* = percentage of specimens with high occlusal relief; *l* = percentage of specimens with low occlusal relief; *s* = percentage of specimens with sharp cusps; *r* = percentage of specimens with round cusps; *b* = percentage of specimens with blunt cusps.

Locality and species	Time interval	<i>n</i>	MS	<i>h</i>	<i>l</i>	<i>s</i>	<i>r</i>	<i>b</i>
Bluefish Caves <i>Equus</i> “ <i>ferus</i> ”	Preglacial/Full-glacial	8	2.63	12.50	87.50	25.00	62.50	12.50
	Postglacial	5	3.00	0.00	100	20.00	60.00	20.00
Alberta <i>E.</i> “ <i>ferus</i> ”	Preglacial	21	3.05	14.29	85.71	4.76	57.14	38.10
	Postglacial	7	2.86	0.00	100	28.57	57.14	14.29
Alberta <i>Bison</i> sp.	Preglacial	6	1.67	66.67	33.33	0.00	100.00	0.00
	Postglacial	7	1.86	57.14	42.86	14.29	71.43	14.29
American Southwest “ <i>Equus conversidens</i> ”	Preglacial	8	3.38	0.00	100	0.00	62.50	37.50
	Full-glacial	2	3.50	0.00	100	0.00	50.00	50.00
	Postglacial	14	2.71	14.29	85.71	21.43	57.14	21.43
American Southwest <i>E.</i> “ <i>ferus</i> ”	Full-glacial	6	2.33	33.33	66.67	16.67	66.67	16.67
	Postglacial	10	2.50	20.00	80.00	30.00	50.00	20.00
American Southwest <i>Bison antiquus</i>	Postglacial	8	1.88	50.00	50.00	25.00	62.50	12.50

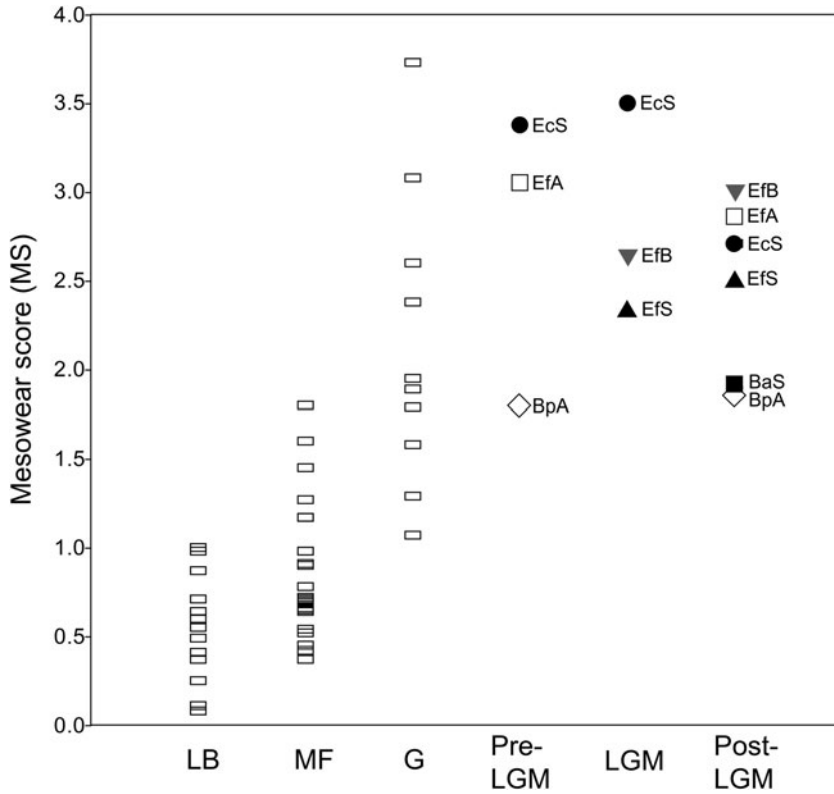


FIGURE 6. Average mesowear score for the late Pleistocene bison and equid samples studied and extant ungulate species reported in Kaiser et al. (2013). Each data point is the average for a species sample. Abbreviations: LB = leaf browsers; MF = mixed feeders; G = grazers; Pre-LGM = preglacial; LGM = full-glacial; Post-LGM = postglacial; BaS = *Bison antiquus* (American Southwest); BpA = *Bison* sp. (Alberta); EcS = “*Equus conversidens*” (American Southwest); EFA = *Equus “ferus”* (Alberta); EfB = *E. “ferus”* (Bluefish Caves, Yukon); EFS = *E. “ferus”* (American Southwest).

43.05% in the preglacial to 64.29% during the postglacial. This is the largest increase in enamel hypoplasia of the samples we studied, although this difference only approaches statistical significance (z -test of proportions, $z = -1.5286$, $p = 0.0632$) because of the reduced sample size of the postglacial sample. We predict that this

trend will be further supported with the discovery and analysis of more specimens of appropriate geologic age. The prevalence of enamel hypoplasia for the postglacial sample of *E. “ferus”* from Bluefish Caves is not significantly greater than the prevalence calculated for the preglacial/full-glacial interval (53.85% vs.

TABLE 6. Results of Kruskal-Wallis tests used to evaluate the hypotheses of the coevolutionary disequilibrium extinction model using the mesowear score (MS). n = sample size; H = H -statistic; p = p -value. Statistically significant p -values are shown in bold.

Locality	Species	Time interval	n	H	p
Alberta	<i>Equus “ferus”</i>	Preglacial	21	5.442	0.0134
	<i>Bison</i> sp.		6		
	<i>E. “ferus”</i>	Postglacial	8	1.771	0.1582
American Southwest	<i>Bison</i> sp.		7		
	“ <i>Equus conversidens</i> ”	Full-glacial	2	1.000	0.2834
	<i>E. “ferus”</i>		6		
	“ <i>E. conversidens</i> ”	Postglacial	14	1.309	0.4851
	<i>E. “ferus”</i>		10		
	<i>Bison antiquus</i>		8		

TABLE 7. Results of two-sample *F*-tests for equal variances (right-tailed) using the bootstrap resampling method (10,000 replicates) conducted to test the hypotheses of the mosaic-nutrient extinction model using the mesowear score (MS). Var = variance of each sample; VarQ = variance quotient (variance at time interval 1 divided by variance at time interval 2); *p* = *p*-value. Statistically significant *p*-values are indicated in bold. An asterisk (*) identifies comparisons in which the variance at time interval 2 is greater than at time interval 1.

Locality and species	Time interval comparisons	MS		
		Var	VarQ	<i>p</i>
Bluefish Caves <i>Equus</i> “ferus”	Preglacial/Full-glacial	1.4107	2.8214	0.3106
	Postglacial	0.5000		
Alberta <i>E.</i> “ferus”	Preglacial	1.0476	2.5507	0.1719
	Postglacial	0.4107		
Alberta <i>Bison</i> sp.	Preglacial	1.0667	0.4978	0.8653
	Postglacial	2.1429		
American Southwest “ <i>Equus conversidens</i> ”	Preglacial	0.2679	0.5357	0.6971
	Full-glacial	0.5000		
	Full-glacial	0.5000	0.5056	0.5388
	Postglacial	0.9890		
	Preglacial	0.2679	0.2708	0.9546*
American Southwest <i>E.</i> “ferus”	Postglacial	0.9890		
	Full-glacial	2.2667	1.1027	0.4488
	Postglacial	2.0556		

52.94%; $z = -0.0492$, $p = 0.4804$). Also not significant is the comparison of the full-glacial (41.67%) and postglacial (54.55%) samples of *E.* “ferus” from the American Southwest (*z*-test of proportions, $z = -0.8092$, $p = 0.2092$), as well as preglacial (25.71%) and postglacial (29.41%) *Bison* sp. samples from Alberta (*z*-test of proportions, $z = -0.3437$, $p = 0.3655$).

The average number of hypoplastic events per affected tooth increased during the postglacial in

all of the equid pairwise comparisons except one (Fig. 8; Table 10). The largest increase was observed in *E.* “ferus” from Bluefish Caves, in which the average number of hypoplastic events per affected tooth increased from 1.33 in the preglacial/full-glacial interval to 3.43 in the postglacial (*t*-test, $t = -4.062$, $p = 0.0000$). The average number of hypoplastic events also increased in the equid samples from the American Southwest, where it went from 1.23 in the preglacial

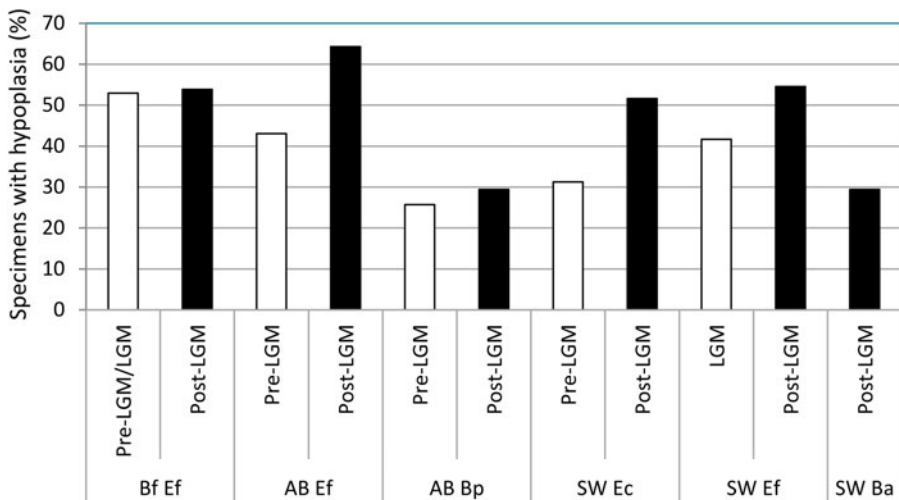


FIGURE 7. Prevalence of enamel hypoplasia in the equid and bison samples studied. Bf Ef = *Equus* “ferus,” Bluefish Caves; AB Ef = *E.* “ferus,” Alberta; AB Bp = *Bison* sp., Alberta; SW Ec = “*Equus conversidens*,” American Southwest; SW Ef = *E.* “ferus,” American Southwest; SW Ba = *Bison antiquus*, American Southwest. Time interval abbreviations: Pre-LGM = preglacial; LGM = full-glacial; Post-LGM = postglacial.

TABLE 8. Summary statistics of enamel hypoplasia data for the equid and bison samples studied. n = total number of specimens examined; H = number of specimens with enamel hypoplasia; PH = percentage of specimens with enamel hypoplasia; ME = mean number of hypoplastic events per affected specimen.

Locality and species	Time interval	n	H	PH (%)	ME
Bluefish Caves <i>Equus</i> “ferus”	Preglacial/Full-glacial	17	9	52.94	1.33
	Postglacial	13	7	53.85	3.43
Alberta <i>E.</i> “ferus”	Preglacial	151	65	43.05	2.16
	Postglacial	14	9	64.29	1.37
Alberta <i>Bison</i> sp.	Preglacial	35	9	25.71	1.31
	Postglacial	34	10	29.41	1.30
American Southwest “ <i>Equus conversidens</i> ”	Preglacial	48	15	31.25	1.23
	Full-glacial	5	3	60.00	1.33
	Postglacial	31	16	51.61	1.78
American Southwest <i>E.</i> “ferus”	Full-glacial	12	5	41.67	1.60
	Postglacial	55	30	54.55	2.30
American Southwest <i>Bison antiquus</i>	Postglacial	17	5	29.41	0.80

to 1.78 in the postglacial for “*E. conversidens*” (t -test, $t = -1.963$, $p = 0.0297$) and 1.60 in the full-glacial to 2.30 in the postglacial for *E.* “ferus” (t -test, $t = -2.246$, $p = 0.0437$). Contrary to these trends, the average number of hypoplastic events per affected tooth significantly decreased during the postglacial in *E.* “ferus” from Alberta (2.16 events in the preglacial versus 1.37 in the postglacial; t -test [right-tailed], $t = 2.338$, $p = 0.0128$), whereas in *Bison* sp. from the same geographic region, the average number of events appears to remain constant in the preglacial (1.31) as in the postglacial (1.30) (t -test, $t = 0.029$, $p = 0.5287$).

Discussion

Dental Wear Patterns and Nutritional Extinction Models

The coevolutionary disequilibrium (Graham and Lundelius 1984) and mosaic-nutrient

(Guthrie 1984) extinction models are two climate-based models that were proposed to explain the late Pleistocene megafaunal extinction. The coevolutionary disequilibrium model emphasizes competition for food resources among species as a result of changing vegetational assemblages (Graham and Lundelius 1984), whereas the mosaic-nutrient model proposes that a change from a mosaic vegetation pattern to a more zonal, low-diversity pattern decreased the dietary supplements available to herbivores (Guthrie 1984). Although these models present different scenarios that lead to nutritional stress and extinction of some herbivore species, they are not mutually exclusive. In theory both could have operated, resulting in a scenario in which herbivores were faced with a decreased diversity of plants in their diets and a disruption of coevolved foraging sequences, increasing competition among species. However, the results of our analyses are overall

TABLE 9. Results of z -tests of proportions (left-tailed) used to determine whether the incidence of enamel hypoplasia significantly increased during the postglacial relative to the previous time interval(s). n = total number of specimens examined; PH = percentage of specimens with enamel hypoplasia; z = z -statistic; p = p -value. Statistically significant p -values are shown in bold. “*Equus conversidens*” from the American Southwest for the full-glacial interval was excluded from the analysis because of its small sample size.

Locality and species	Time interval comparisons	n	PH (%)	z	p
Bluefish Caves <i>Equus</i> “ferus”	Preglacial/Full-glacial	17	52.94	-0.0492	0.4804
	Postglacial	13	53.85		
Alberta <i>E.</i> “ferus”	Preglacial	151	43.05	-1.5286	0.0632
	Postglacial	14	64.29		
Alberta <i>Bison</i> sp.	Preglacial	35	25.71	-0.3437	0.3655
	Postglacial	34	29.41		
American Southwest “ <i>Equus conversidens</i> ”	Preglacial	48	31.25	-1.8099	0.0352
	Postglacial	31	51.61		
American Southwest <i>E.</i> “ferus”	Full-glacial	12	41.67	-0.8092	0.2092
	Postglacial	55	54.55		

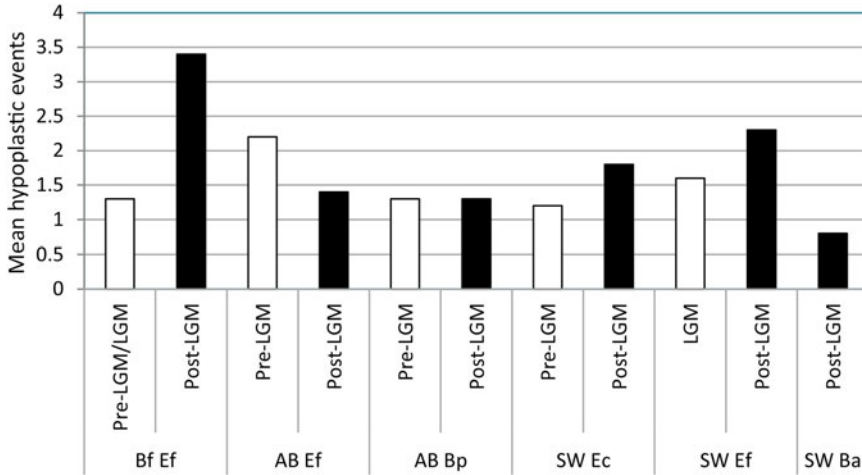


FIGURE 8. Mean number of hypoplastic events per affected specimen in the equid and bison samples studied. Bf Ef = *Equus "ferus,"* Bluefish Caves; AB Ef = *E. "ferus,"* Alberta; AB Bp = *Bison* sp., Alberta; SW Ec = "*Equus conversidens*," American Southwest; SW Ef = *E. "ferus,"* American Southwest; SW Ba = *Bison antiquus*, American Southwest. Time interval abbreviations: Pre-LGM = preglacial; LGM = full-glacial; Post-LGM = postglacial.

consistent with the predictions established for the coevolutionary disequilibrium model, but not with the prediction established for the mosaic-nutrient model.

The results of the analysis of dental wear are overall consistent with the two predictions established for the coevolutionary disequilibrium extinction model. The first prediction states that before the severe climatic changes that occurred during the terminal Pleistocene, sympatric species of ungulate herbivores partitioned available food resources (Graham and Lundelius 1984). In this case dietary niche partitioning would be reflected by a statistically

significant difference in dental microwear and mesowear score. This prediction is generally supported for the ungulates studied from the American Southwest and Alberta (Tables 3 and 6). The dental microwear of "*E. conversidens*" and *E. "ferus"* from the American Southwest during the full-glacial is significantly different (Table 3), and statistically significant differences were also detected for the mesowear score of *E. "ferus"* and *Bison* sp. from preglacial deposits of Alberta (Table 6).

Although the results of the microwear and mesowear analyses support the hypothesis of dietary resource partitioning in sympatric

TABLE 10. Results of *t*-tests (left-tailed) using the bootstrap resampling method (10,000 replicates) to determine whether the number of stress events per affected specimen increased during the postglacial relative to the previous time interval(s). *nH* = total number of specimens with enamel hypoplasia; ME = mean number of hypoplastic events per affected specimen; *t* = *t*-statistic; *p* = *p*-value. Statistically significant *p*-values are shown in bold. An asterisk (*) identifies comparisons in which the mean number of hypoplastic events per affected specimen significantly decreased during the postglacial (i.e., showing a trend opposite to the one being tested). "*Equus conversidens*" from the American Southwest for the full-glacial interval was excluded from the analysis because of its small sample size.

Locality and species	Time interval comparisons	<i>nH</i>	ME	<i>t</i>	<i>p</i>
Bluefish Caves <i>Equus "ferus"</i>	Preglacial/Full-glacial	9	1.33	2.338	0.9894*
	Postglacial	7	3.43		
Alberta <i>E. "ferus"</i>	Preglacial	65	2.16	2.338	0.9894*
	Postglacial	9	1.37		
Alberta <i>Bison</i> sp.	Preglacial	9	1.31	0.029	0.5287
	Postglacial	10	1.30		
American Southwest " <i>Equus conversidens</i> "	Preglacial	15	1.23	-1.963	0.0297
	Postglacial	16	1.78		
American Southwest <i>E. "ferus"</i>	Full-glacial	5	1.60	-2.246	0.0437
	Postglacial	30	2.30		

bison and equid species from the American Southwest and Alberta before the postglacial, the analysis of dental wear provides little insight into the mechanism by which this division of resources might have taken place. Extant ungulates partition dietary resources in a variety of ways: feeding on different plant species, feeding on different plant parts and growth stages of the same species, feeding at different heights, and feeding in distinct microhabitats (e.g., Bell 1971; Jarman and Sinclair 1979; McNaughton and Georgiadis 1986; du Toit 1990; Spencer 1995; Stewart et al. 2002). Dental wear data alone cannot determine which of these alternatives for partitioning food resources was employed by the bison and equid species studied. Additional lines of evidence, such as stable isotope analysis and ecomorphological studies, in conjunction with the results of dental wear are needed to establish hypotheses as to how these ungulates might have partitioned dietary resources.

The second prediction outlined for the coevolutionary disequilibrium extinction model states that sympatric species of horse and bison were competing for available food resources during the terminal Pleistocene as a result of change in the composition of vegetational communities. Under this scenario dental microwear and mesowear should not be significantly different for bison and horse at the end of the Pleistocene. This is the pattern that is observed for the postglacial ungulate species from the American Southwest (i.e., "*E. conversidens*," *E. "ferus*," and *B. antiquus*; Tables 3 and 6). The same was found for the horse and bison samples of *E. "ferus"* and *Bison* sp. from postglacial deposits of Alberta (Tables 3 and 6). The results of the microwear and mesowear analyses of the postglacial ungulate species from the American Southwest and Alberta are, therefore, consistent with the second prediction of the coevolutionary disequilibrium extinction model.

The results of a number of dental wear (Rivals et al. 2008, 2010) and stable isotope (Koch et al. 1998; Hoppe and Koch 2006; Sánchez et al. 2006; Fox-Dobbs et al. 2008) studies also support the assumption of dietary resource partitioning postulated for the coevolutionary disequilibrium extinction model. In other

cases, however, dietary niche overlap is the emerging pattern (e.g., Feranec 2004; Prado et al. 2005; Hoppe and Koch 2006; Fox-Dobbs et al. 2008; Pérez-Crespo et al. 2012). Nevertheless, it is important to point out that all of the studies cited, and also the study presented here, examined only one or two dietary proxies, which shed light on only a small portion of the feeding ecology of the Pleistocene megafauna.

Dietary niche partitioning may occur along any of countless multidimensional axes (Hutchinson 1957). Therefore, identification of statistically significant differences among species using one dietary proxy would provide support for dietary niche partitioning, but the opposite is not true. Inability to detect significant differences among species using one dietary proxy does not necessarily indicate they were competing for food resources, because the species could be segregating along another dimensional axis not considered in the study. This is an important point that is often missed in paleoecological studies. A multiproxy approach to reconstructing feeding ecology is required to better elucidate community feeding structure during the Pleistocene at different temporal and spatial scales. In that sense, the results of our study may be reevaluated as additional paleoecological proxies (e.g., stable isotope analysis) become available. With that consideration, we conclude that the analyses of mesowear and dental microwear do not reject the hypothesis of competition for food resources during the postglacial in the bison and equid samples investigated.

We note that a pattern consistent with competition for resources was recovered for bison and horse in both Alberta and the American Southwest, even though these two regions experienced different ecosystem dynamics during the terminal Pleistocene. Preglacial ecosystems in Alberta were completely eliminated during the full-glacial by the advance and coalescence of the Laurentide and Cordilleran ice sheets (Young et al. 1994, 1999; Burns 1996). Radiocarbon dating of mammalian specimens indicates that most of Alberta remained covered by the ice sheets for approximately 9000 radiocarbon years (Burns 1996). As the ice sheets receded, new ecosystems with new community associations were established. In

contrast to Alberta, the American Southwest was not covered by ice sheets; nevertheless, important environmental changes occurred in this region during the postglacial. Paleontological and palynological evidence indicates that the American Southwest experienced significant changes in temperature, precipitation, and humidity (Connin et al. 1998; Polyak et al. 2012). Both regions experienced different, but nonetheless major, ecological disturbances during the terminal Pleistocene.

In contrast to the support for the coevolutionary disequilibrium model, our analyses of microwear and mesowear were less consistent with the mosaic-nutrient extinction model. Working under the assumption that feeding on different vegetation is reflected in the dental wear pattern, a population of herbivores feeding on a restricted number of plant species during the terminal Pleistocene would produce a dental wear sample in which the statistical dispersion of the microwear and mesowear variables is small relative to populations feeding on a greater diversity of plant species during preglacial and full-glacial times. Analyses of the dental wear data do not support this prediction (Tables 4 and 7). The variance of the microwear variables and the mesowear score are, for the most part, not significantly smaller during the postglacial. Only two pairwise comparisons involving the postglacial were statistically significant, and five other comparisons showed the opposite trend, with a significantly greater variance during the postglacial (Tables 4 and 7). There are a number of potential explanations that can be advanced to account for the lack of a statistically significant decrease in dental wear variance during the postglacial: 1) local plant diversity did not actually decrease during the postglacial; 2) local plant diversity decreased, but ungulates were able to extend their home ranges or migrate to obtain the right mix of nutrients; or 3) local plant diversity decreased, but the resulting change in diet is not recorded in the dental wear. The consistency of our results with these potential explanations are beyond the scope of this study, but we do stress that the evaluation of our results in the context of regional paleoenvironmental studies may be possible with comparisons to pollen records (e.g., Ritchie et al. 1982; Anderson et al. 2003;

Hall 2005; Strong and Hills 2005; Zazula et al. 2006), plant macrofossil records (e.g., Lamb and Edwards 1988; Hall 2005; Zazula et al. 2006), and studies on ancient DNA from soils (e.g., Willerslev et al. 2014).

Implications for a New Ecological Extinction Model

One emerging pattern common to Alberta, the American Southwest, and other regions of North America is the increased abundance of bison relative to other large herbivorous mammals, including equids and mammoth, during the latest Pleistocene. Although both bison and equids returned to Alberta as the Laurentide and Cordilleran ice sheets receded, bison became the most abundant ungulate species, in contrast to preglacial ecosystems in which equids had higher abundances relative to bison (Jass et al. 2011). A similar increase in the relative abundance of bison was reported for the midcontinent of North America (McDonald 1981), Alaska and the Yukon Territory (Guthrie 2006), the southern Great Plains (Wyckoff and Dalquest 1997), and the Pacific Coast (Scott 2010). The great abundance and geographic distribution of bison during the latest Pleistocene, especially in western North America, led to a recently proposed ecological extinction model for the late Pleistocene megafaunal extinctions in which bison played a pivotal role (Scott 2010).

One major difference of the Pleistocene–Holocene transition with respect to previous glacial–interglacial transitions was the proliferation of bison, especially *B. antiquus*, a large, herd-dwelling ruminant (Scott 2010). The ecological extinction model recently advanced proposes that bison and other late Pleistocene megafauna, including mammoths and equids, were competing for available resources (Scott 2010). Shifts in resource abundance and distribution due to changing climatic factors associated with the end of the Wisconsinan glaciation would have increased competition for those resources, and typical responses of large herbivorous mammals to earlier climatic shifts (e.g., selection of different forage, reduction of body size, or migration to a different area) would have been altered by the widespread abundance and population density of

bison. Even communities where bison were rare or absent could also be impacted, as large mammals displaced by bison in other regions moved in, increasing the competition among herbivores (Scott 2010).

Isotope data for herbivorous mammals from Rancho La Brea, California, and Florida have been cited to support the argument that bison competed for resources with other late Pleistocene megafauna. Bison and equids from Rancho La Brea seemed to have relied heavily on C₃ plants (Coltrain et al. 2004; Feranec et al. 2009), with bison periodically incorporating C₄ plants in their diet, suggesting that these ungulates were seasonally competing for food resources (Feranec et al. 2009). Similar results have been reported for Florida, where mammoths, bison, and equids apparently had similar diets, although these diets varied geographically across the state (Feranec 2004). However, the fact that these herbivorous mammals fed on plants with similar isotope compositions does not necessarily imply that they were competing for food resources. For instance, African grazing ungulates feed mostly on C₄ grasses, and their mean $\delta^{13}\text{C}$ values largely overlap (e.g., Cerling et al. 2003), yet many of these grazing herbivores partition available grass resources by feeding on different structural components and/or grasses at different growth stages (e.g., Gwynne and Bell 1968; Bell 1971; Murray and Brown 1993). As emphasized by McNaughton and Georgiadis (1986), grass is not a homogeneous resource, and nutritional quality varies among its major structural components (leaf, sheath, and stem) as well as seasonally.

Based on the results obtained from the present study, the pattern of competition among bison and other late Pleistocene ungulates postulated by Scott (2010) is supported for the equid and bison samples from the postglacial of Alberta and the American Southwest, but not for the preglacial of Alberta. Overall, the pattern in our data is more consistent with the coevolutionary disequilibrium extinction model (Graham and Lundelius 1984) than with the model proposed by Scott (2010). However, additional studies are needed to further validate the patterns presented in our study and evaluate these two extinction models.

Systemic Stress in Late Pleistocene Equids and Bison

Both the coevolutionary disequilibrium (Graham and Lundelius 1984) and mosaic-nutrient (Guthrie 1984) extinction models propose that populations of large mammals, especially the species that became extinct, were exposed to increased levels of systemic physiological stress, particularly nutritional stress, resulting from climatic and environmental changes. The results of the analysis of enamel hypoplasia of late Pleistocene equids and bison from the Western Interior of North America indicate that disruptions in tooth development, particularly in the equid taxa studied, increased during the postglacial relative to earlier time intervals. Working under the assumption that enamel hypoplasia primarily reflects episodes of systemic stress (Goodman and Rose 1990), these results support the hypothesis that equids experienced increased levels of systemic physiological stress during the postglacial. In all of the equid samples studied, the prevalence of enamel hypoplasia and/or recurrence of hypoplastic events increased during this time interval (Tables 9 and 10). However, we note that these changes were not spatially or temporally uniform.

The specimens of *E. "ferus"* from Bluefish Caves show that although the prevalence of enamel hypoplasia did not significantly change from the preglacial/full-glacial to the postglacial (both time intervals show a prevalence of hypoplasia of ~53%), the number of hypoplastic events per affected tooth significantly increased during the postglacial from 1.33 to 3.43. These results indicate that *E. "ferus"* in eastern Beringia, which apparently was already exposed to relatively high levels of systemic stress during the preglacial/full-glacial, with more than 50% of the specimens showing enamel hypoplasia, experienced more recurrent severe stress events during the postglacial. Assuming that the average cheek tooth of extinct populations of *E. "ferus"* took approximately 26 months to form, as is the case for extant domestic horses (Hoppe et al. 2004), some of the postglacial specimens of *E. "ferus"* were experiencing more than one severe stress event in a single year.

In Alberta, postglacial specimens of *E. "ferus"* show a greater prevalence of enamel

hypoplasia, with 64.29% of specimens displaying a hypoplastic defect as compared with the preglacial sample, in which the prevalence is 43.05%. Contrary to the increase in the prevalence of hypoplasia, the number of hypoplastic events per affected tooth is significantly smaller in the postglacial (1.37) than in the preglacial (2.16). These results might indicate that stress events encountered by *E. "ferus"* from Alberta were less recurrent during the postglacial, but when they did occur, they were more severe, affecting a greater proportion of individuals. In contrast to these results, the postglacial sample of *Bison* sp. from Alberta does not show a significantly greater prevalence of enamel hypoplasia or a greater number of hypoplastic events per affected tooth than preglacial specimens. This suggests that, in contrast to *E. "ferus,"* *Bison* sp. did not endure significantly greater levels of systemic stress during the postglacial relative to what members of this ungulate group encountered during preglacial times.

The two equid species studied from the American Southwest, "*E. conversidens*" and *E. "ferus,"* show an increase in the average number of hypoplastic events per affected tooth during the postglacial. In the case of "*E. conversidens*" the number of hypoplastic events significantly increased from 1.23 in the preglacial to 1.78 in the postglacial, whereas in *E. "ferus"* it increased from 1.60 in the full-glacial to 2.30 in the postglacial. The prevalence of enamel hypoplasia also increased during the postglacial in both equid species, but it was only statistically significant in "*E. conversidens*," which shows an increase from 31.25% in the preglacial to 51.61% in the postglacial. These results suggest that episodes causing systemic stress might have increased in severity and also probably became more recurrent. The postglacial sample of *B. antiquus* shows comparable levels of hypoplasia as the preglacial and postglacial *Bison* sp. samples from Alberta, with a hypoplasia prevalence of 29.41%.

The implication of the results of our evaluation of hypoplasia for the late Pleistocene extinction debate requires a determination of whether the prevalence and number of hypoplastic defects, especially for postglacial equid samples, are sufficiently high to suggest a dramatic increase in the morbidity of these

ungulates. Unfortunately, data on enamel hypoplasia and its relationship to population dynamics in extant wild equids are lacking, but for bison there are some data on the prevalence of enamel hypoplasia in extant wild populations.

Bison examined as part of a macroscopic study of dental pathologies in terminal Pleistocene and Holocene archaeological assemblages included a collection of modern bison specimens from Montana (collected in 1886) and Yellowstone (donated to the Smithsonian Institution between 1909 and 1919; Byerly 2009). The prevalence of enamel hypoplasia in the individuals with the cemento-enamel junction visible is 22.2% for the sample from Montana and 25.0% for Yellowstone, although the sample size for the latter is very small, with only 4 individuals versus 27 for the sample from Montana (Byerly 2009). These values are relatively lower than those obtained for the postglacial bison samples from Alberta and the American Southwest.

The prevalence of enamel hypoplasia in the archaeological assemblages studied by Byerly (2009), for samples greater than 10, ranges from 7.7% in the Horner I assemblage, Wyoming (~9500 yr RCBP [radiocarbon years before the present]), to 36.8% in the Frasca site, Colorado (~8900 yr RCBP). Comparable values were reported for Buffalo Creek, Wyoming (~2500 yr RCBP), and Kaplan-Hoover, Colorado (~2700 yr RCBP), in which 32.3% and 14.1%, respectively, of the molars examined show enamel hypoplasia (Niven et al. 2004). In this context, the prevalence of hypoplasia in postglacial bison samples from Alberta and the American Southwest is within the upper range reported for Holocene samples. At the least, this shows a heightened state of systemic stress in bison relative to Holocene populations. Whether this suggests that postglacial bison were experiencing detrimental levels of stress is equivocal, in part due to a lack of clear understanding of levels of hypoplasia found in healthy, stable populations relative to systemically stressed populations. This is a topic that merits further investigation.

To our knowledge, only one previous study has examined enamel hypoplasia in North

American late Pleistocene equids. A preliminary survey macroscopically analyzed enamel hypoplasia in the upper and lower cheek tooth dentition of equid specimens from three terminal Pleistocene localities (Blackwater Draw, Cueva Quebrada, and Gault) and three older Rancholabrean sites (Curry Gravel Pit, Norman Valley Pit, and Trinity River Terraces) in Texas and New Mexico (Timperley and Lundelius 2008). Except for Cueva Quebrada, where two species (*Equus scotti* and *Equus francisci*) were previously identified (Lundelius 1984), this study was conducted at the generic level (Timperley and Lundelius 2008). In contrast to our results, the equid specimens from the terminal Pleistocene localities did not show a greater prevalence of enamel hypoplasia than the older Rancholabrean sites: Blackwater Draw 40%; *E. scotti* and *E. francisci* from Cueva Quebrada, 16% and 13%, respectively; Gault, 19%; Curry Gravel Pit, 56%; Norman Valley Pit, 26%; and Trinity River Terraces, 25% (Timperley and Lundelius 2008). Moreover, the prevalence of hypoplasia for the terminal Pleistocene samples of Cueva Quebrada and Gault are significantly lower than the ones obtained for the terminal Pleistocene (postglacial) samples from Bluefish Caves, Alberta, and the American Southwest. The discrepancy of these results could reflect actual differences in the prevalence of enamel hypoplasia among the sites studied or they could potentially be due to differences in data-collection protocol.

We suspect that geographically widespread taxa, such as *Equus*, would potentially encounter certain regions with relatively more optimal conditions for growth and reproduction than others. The area in the vicinity of the Cueva Quebrada and Gault sites, in Texas could potentially have harbored such favorable habitats. Alternatively, the low prevalence of enamel hypoplasia reported for these two sites could be due to different methods of data collection. Methods of data collection for specimens with cementum preserved on the tooth crown were unclear in previous studies (i.e., Timperley and Lundelius 2008). Cementum develops after the enamel is secreted and mineralized in response to continuous tooth eruption and can obscure evidence of enamel

hypoplasia (Kierdorf et al. 2006; Upex et al. 2014).

A further complication of comparing the results of other studies (e.g., Timperley and Lundelius 2008) with ours is the potential inter-observer difference in the scoring of enamel hypoplasia. Macroscopic recording of hypoplasia using the naked eye or a low-magnification hand lens introduces difficulties in the comparison between studies (Hillson 2005). Under this approach, it is up to the individual observer to determine the lower limit for recording the smallest hypoplastic defects, so the comparability between studies can be affected (Hillson and Bond 1997; Hillson 2005). Regardless, the differences in results are notable, and indicate the need for further comparative work under consistent data-collection protocols.

The concurrent identification of an increase in enamel hypoplasia in the equid samples and dental wear patterns consistent with the coevolutionary disequilibrium extinction model may indicate a potential link. However, we are cautious in interpreting these patterns as being directly linked and specify only that they are consistent with the coevolutionary disequilibrium extinction model. We are cautious for two primary reasons, including the complexity of environmental changes at the end of the Pleistocene and potential impacts to other aspects of the biology of organisms (e.g., birth seasonality) and the array of potential causes of enamel hypoplasia (e.g., Shearer et al. 1978; Shupe and Olson 1983; Skinner and Hung 1986; Suckling et al. 1986, 1988; Miles and Grigson 1990; Kierdorf et al. 1993, 2000, 2004; Hillson 1996, 2005; Larsen 1997; Dobney and Ervynck 2000).

Conclusions

The study of dental microwear and mesowear of bison and equid species from three geographic regions of North America (the American Southwest [eastern New Mexico and western Texas], Alberta [Wally's Beach Site and the Edmonton area gravel pits], and eastern Beringia [Bluefish Caves, Yukon Territory]) yielded results that are generally consistent with the predictions formulated for the coevolutionary disequilibrium model, but not for the mosaic-nutrient model. Sympatric

species of *Bison* and *Equus* show statistically different dental wear patterns during the pre-glacial and full-glacial, indicating that these ungulates were partitioning available dietary resources during these time intervals. In contrast, the dental wear of postglacial sympatric species of these ungulates is not significantly different, suggesting that they were not partitioning available food resources and were potentially competing for them as predicted under the coevolutionary disequilibrium model (Graham and Lundelius 1984).

Conversely, the decrease in dietary supplements during the terminal Pleistocene required by certain ungulate species, such as equids and mammoths, as proposed in the mosaic-nutrient model (Guthrie 1984), is not supported by the analyses of dental wear. The statistical dispersion of the microwear and mesowear variables did not significantly decrease during the post-glacial in either equid or bison samples, as would be expected under a more homogeneous diet. Nevertheless, the validity of these conclusions rests on the assumption that dental wear is able to record subtle differences in diet. Although some studies hint at the possibility that this might indeed be the case (e.g., Fortelius and Solounias 2000; Scott 2012; Barrón-Ortiz et al. 2014), further investigations into the dietary resolution of dental wear are needed, not only for testing of nutritional extinction models, but also to allow for finer reconstructions of ungulate feeding ecology.

Recognition that equid and bison species were potentially competing for food resources during the terminal Pleistocene does not in itself indicate that this resulted in increased nutritional stress for these ungulates. Although the multifactorial etiology of enamel hypoplasia makes it virtually impossible to determine whether a specific hypoplastic defect is due to nutritional stress without additional independent data, the significant increase in enamel hypoplasia observed in postglacial samples, particularly in equids, is consistent with both extinction models investigated as well as other climate-based extinction models that have been proposed to explain the late Pleistocene megafaunal extinctions (e.g., Kiltie 1984; King and Saunders 1984; Barnosky 1986; Scott 2010).

The prevalence of enamel hypoplasia and/or the number of hypoplastic events per affected tooth increased in the equid samples during the postglacial, suggesting that environmental changes negatively affected populations of these ungulates before their extinction. The impact of early human populations on the extinction of North American Pleistocene equids cannot be discounted (e.g., Kooyman et al. 2001, 2006), of course, but our results may indicate that humans migrating into the continent encountered equid populations that were already in a less than optimal state. However, we reiterate that further studies examining changes in enamel hypoplasia in equid populations from earlier glacial–interglacial transitions are needed to fully evaluate whether late Pleistocene equids were experiencing unusually high levels of systemic stress that could have contributed to their extinction in a significant way.

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