Regional variation in the browsing diet of Pleistocene *Mammut americanum* (Mammalia, Proboscidea) as recorded by dental microwear textures

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ABSTRACT

Analyses into the feeding ecology of *Mammut americanum* have reconstructed this extinct proboscidean as a forest-dwelling browser that thrived across North America during the Pleistocene. However, the level of variability in mastodon diet that may have existed across its spatio-temporal range remains unresolved. We address this deficiency through comparison of dental microwear textures in a large sample ($N = 65$) of *M. americanum* teeth from six geographic and chronologically distinct locations from the Late Pleistocene of North America. Mastodon microwear textures correspond to a woody browsing diet, congruent with results from other dietary proxies. However, microwear textures reveal that southern populations from Florida (associated with a cypress swamp habitat) had a slightly softer, tougher browsing diet compared to northern populations (associated with boreal forest and open-pine parkland habitats) in the Late Pleistocene. In addition, there was no significant difference in microwear variables associated with food hardness or toughness in mastodons from two temporally distinct populations from Missouri, despite a significant environmental shift from open-pine parkland to boreal forest through time. Our findings elucidate *M. americanum* as a species with some plasticity in its browsing strategy across its range, with regional populations capable of having different diets yet able to maintain their ecological niche in the face of local environmental shifts in the Late Pleistocene. This has implications for the future testing of environmentally-induced extinction hypotheses during the latest Pleistocene and also illustrates the importance of measuring population-level dietary variation to better understand total feeding ecology in an extinct species.

1. Introduction

The American mastodon (*Mammut americanum*) is one of the most common faunal members of Pleistocene terrestrial communities across North America. As far back as the mid-1800s (Warren, 1855), this proboscidean has been recognized as a browser (defined as predominantly consuming woody material, leaves, and fruit). This paleodietary hypothesis remains supported today by numerous independent lines of evidence from stable carbon isotopes in tooth enamel (Bauman and Crowley, 2014; DeSantis et al., 2009; Hoppe and Koch, 2006; Koch, 1998; Koch et al., 1998; MacFadden and Cerling, 1996; Metcalfe et al., 2013; Metcalfe and Longstaffe, 2014), associated gut contents (Lepper et al., 1991; Warren, 1855), fecal contents (Laub et al., 1994; Newsom and Mihlbachler, 2006;), tooth morphology (Saunders, 1996), floral associations (Dreimanis, 1968; McAndrews and Jackson, 1988; Teale and Miller, 2012) and low-magnification stereoscopic dental microwear (Green et al., 2005; Rivals and Semprebon, 2012; Rivals et al., 2012).

Analyses that detail the feeding ecology of the mastodon during the Pleistocene often focus on reconstructing diet on a local or regional basis, such as only targeting individuals from the Rancholabrean of Florida (Koch et al., 1998) or the Great Lakes region (Metcalfe and Longstaffe, 2014). These localized analyses provide excellent snapshots of *M. americanum* ecology but do not always elucidate potential variation that may exist across a species' range. For example, mastodons from Florida, New York, Ontario, and Texas all have enamel $\delta^{13}C$ values ranging from $-9.5‰$ to $-13.1‰$ (DeSantis et al., 2009; Hoppe and Koch, 2006; Koch, 1998; Koch et al., 1998; Metcalfe et al., 2013), suggesting a primarily C_3 vegetative diet (likely browse, at least in Florida and Texas where C_3 grasses are rare; Stowe and Teeri, 1978; Teeri and Stowe, 1976; Teeri et al., 1978), with little isotopic variation among these regions. However, the flora associated with these populations varies significantly across these regions. For example, Florida populations are usually recovered in cypress-swamp habitats (Newsom and Mihlbachler, 2006), whereas contemporary populations from the Great Lakes region inhabited spruce-dominated boreal forest habitats (Saunders, 1996). What specific C_3 plants were mastodons exploiting

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within their home range? This follow-up question is mainly answered through examination of gut and/or fecal contents (Newsom and Mihlbachler, 2006), which can provide an incredibly detailed record of an individual's diet at a very restricted moment in time, but can be clouded by opportunistic feeding (i.e., the contents from an individual's stomach or a dung pile are not always representative of population-level diet). Isotopic analyses reveal broad scale resolution in ecology (covering a time scale of months to years of feeding), while gut/fecal contents present very fine temporal resolution (covering usually the last meal). Additionally, isotopic changes may remain fairly constant despite differences in the textural properties of food (e.g., Jones and DeSantis, 2017), while the latter are usually rare in the fossil record. What remains unanswered is whether different regional populations of mastodons exploited different browse sources through time (i.e., were mastodons homogenous in their browsing niche across their geographic and temporal range?). This deficiency in our knowledge of intra-specific variation in mastodon feeding ecology can be clarified via the analysis of dental microwear textures.

Dental microwear refers to microscopic wear deposited on the occlusal surface of a tooth during chewing and is a well-established proxy for diet (e.g., Teaford and Walker, 1984; Walker et al., 1978). Although the timeframe recorded by foods of varying textural properties is likely positively correlated with abrasiveness, dental microwear typically represents food consumed of the past few days to weeks of an animal's life and can provide a short-term indication of diet when gut/fecal contents are unavailable (Grine, 1986). Dental microwear texture analysis (DMTA) is an automated technique that can provide an accurate estimate of differences in feeding habits (DeSantis, 2016; Scott et al., 2005, 2006; Ungar et al., 2003), even at the intra-specific level (Merceron et al., 2010). Thus, DMTA is an appropriate tool to clarify variation in diet and feeding behavior among different mastodon populations. Here, we compare DMTA variables in six distinct populations of Pleistocene *M. americanum* to address the question of whether the textural properties of foods consumed by mastodons vary across the spatio-temporal distribution of the species. Specifically, we test two hypotheses: 1) *M. americanum* microwear varies significantly among geographically and/or temporally different populations; 2) *M. americanum* microwear varies significantly among populations that occupied different habitats.

2. Background

2.1. American mastodon behavioral ecology and migratory potential

Comparing among disparate populations of *Mammut americanum* requires an underlying assumption that individual mastodons stayed within local to regional settings and did not migrate pan-continental distances. Comparison to modern analogues (including Asian and African elephants) provides insight into how mastodons may have migrated, and how population home range sizes may have varied. In general, modern elephant migration patterns tend to be impacted by human population centers and farmland distribution, with the bulk of migration pathways typically falling into riparian zones or areas of water and food availability during the dry season (Kumar et al., 2010). However, modern correlates can still provide useful criteria with which to evaluate the movement of extinct faunas.

For example, home range sizes exceeding 600 km^2 have been recorded for female Asian elephants in southern India (Baskaran et al., 1995), while home range sizes in northern India have been recorded at 184–326 km^2 for females and 188–407 km^2 for males (Williams, 2003). Substantially smaller home range sizes (30–160 km^2 for females and 53–345 km^2 for males) have been recorded in Sri Lanka (Fernando et al., 2005). By contrast, African savanna elephants (*Loxodonta africana*) inhabiting the Namib Desert have considerably larger home range sizes; ranges for female family units of 2851–18,681 km^2 (Lindeque and Lindeque, 1991) and for males of 210–14,310 km^2 (Leggett, 2010) have been recorded. Further, these Namib Desert-dwelling African elephants

are known to engage in seasonal migrations in search of water at distances of 251–625 km over a period of up to five months (Leggett, 2006), maintaining genetic interrelatedness with elephants in Etosha National Park (Ishida et al., 2016). The factors that likely play the largest role in determining modern elephant migrations are food and water availability – the lush and productive forests of the Indian subcontinent permit Asian elephant family units to stay in comparatively smaller home ranges than the nomadic African savannah elephants of the nutrient-depauperate Namib Desert. Assuming similar physiological requirements and capabilities as modern elephants (Haynes, 1991), American mastodons occupying late Pleistocene North America were unlikely to have been as nutrient-starved as these desert-dwelling African savannah elephants and thus probably occupied home range sizes closer to that of modern Asian elephants in Sri Lanka and India – approximately 30–400 km^2 (Baskaran et al., 1995; Williams, 2003; Fernando et al., 2005).

One tool that can provide indirect insight into the migration patterns and behavior of extinct organisms is the use of strontium isotopes. Strontium does not typically undergo measurable biological fractionation due to the small relative mass difference between isotopes (e.g., ^{87}Sr and ^{88}Sr) (Price et al., 1985); thus, strontium isotopes preserved in mammalian tissues (including bone or enamel) more typically reflect the distribution of strontium in the local bedrock, which gets taken up via plant roots and is later incorporated into herbivorous mammals (Ben-David and Flaherty, 2012). In areas where there is a disparity in bedrock strontium levels (a function of time since crystallization), the disparity in strontium levels between enamel and bone can be informative of migration patterns. For example, by comparing the strontium levels in mastodon and mammoth tissues to bedrock and local floral/faunal strontium levels from Florida, Hoppe et al. (1999) showed that mastodons migrated into the southern Appalachians within the lifetime of the individual – a distance of 120–300 km away. By contrast, mammoths stayed within coastal Florida, suggesting that seasonal fluctuations in moisture or food availability did not drastically impact their migratory behavior. Although mastodons may therefore have engaged in longer distance seasonal migrations than did mammoths, this distance is still much less than the distance between the sites included in this study (e.g., Florida, New York, Indiana). Further, if the home range sizes of mastodons were equitable to the home range sizes of modern elephants, the spectrum of vegetation encountered by *M. americanum* individuals recovered from a single site is likely to have been broadly similar.

2.2. Fossil populations

We selected 65 *M. americanum* teeth from six Late Pleistocene populations, each representing individuals from a unique locality/region and/or a specific time range. Associated paleoenvironmental plus geochronologic data for each population are listed in Table 1 and the spatial distribution of localities is mapped in Fig. 1, with additional evidence of mastodon behavior and diet within each population outlined below.

2.2.1. Aucilla River

The Aucilla River includes a large watershed with a network of Late Pleistocene sinkhole deposits that have yielded significant paleontological and archaeological finds in northern Florida (Webb and Simons, 2006). Aucilla material sampled here include specimens from stratigraphically constrained localities with associated radiocarbon dates (Page-Ladson, Latvis-Simpson), as well as some collected as surface material with limited geochronologic resolution (Ohmes Collection; see Supplemental Table 1). All teeth recovered from the Aucilla fall within the range of 11,000–40,000 uncalibrated radiocarbon years before present (RCYBP) (Table 1; Hoppe and Koch, 2006). Aucilla mastodons had a C$_3$ browsing diet (Green et al., 2005; Hoppe and Koch, 2006), with little seasonality (Hoppe and Koch, 2006; but see also Fisher and

Table 1

Summary of fossil localities sampled here, including geochronology and habitat data with authorities. Locality ages represent the estimated interval when *M. americanum* occupied the associated location.

Locality	Habitat	Locality age (RCYBP)	N
Aucilla River, Florida	Cypress swamp[a]	11,000–40,000[b]	17
Boney Spring, Missouri	Spruce-dominated boreal forest[c]	13,600–16,200[d]	12
Hiscock Site, New York	Spruce-dominated boreal forest[e]	10,515–11,033[f]	7
Indiana	Spruce-dominated boreal forest[g]	11,440–15,540[g]	13
Jones Spring, Missouri	Open-pine parkland[c]	38,000–51,000[h]	11
Trolinger Spring, Missouri	Open-pine parkland[c]	29,000–34,000[d]	5

Abbreviations: RCYBP = uncalibrated radiocarbon years before present; N = number of specimens sampled.

  [a] Hansen (2006).
  [b] Hoppe and Koch (2006), Webb and Dunbar (2006).
  [c] King (1973).
  [d] Saunders (1977).
  [e] McAndrews (2003).
  [f] Laub (2003).
  [g] R. Richards (pers. comm.), Richards et al. (1987), Smith (2010), Swinehart et al. (2005), Whitehead et al. (1982).
  [h] Haynes (1985).

Fox, 2006). Dung deposits from the Latvis-Simpson (32,000 RCYBP) and Page-Ladson (12,350 RCYBP) sites are very similar and reveal a bulk-foraging strategy that targeted mainly *Taxodium* (bald cypress) twigs, supplemented with different species of nut and fruit (Mihlbachler, 1998; Newsom and Mihlbachler, 2006). Together, these lines of evidence suggest that, in general, mastodons frequented the Aucilla during wetland (cypress swamp) conditions in the Late Pleistocene and maintained a similar diet across this time frame. Aucilla mastodons were nomadic migrants in late to post-glacial times, traveling upwards of 150–200 km during the year (Hoppe and Koch, 2007) and seemed to frequent the Aucilla sinkhole during autumn (Fisher and Fox, 2006; Newsom and Mihlbachler, 2006). Although their migratory behavior would have taken them outside of Florida, they would not have interacted with any other population sampled (all other populations are > 1000 km from the Aucilla). Additionally, the high turnover rate of microwear (days to weeks; Teaford and Oyen, 1989) suggests that any patterns on Aucilla mastodon teeth should reflect their diet during occupation. Thus, the Aucilla group represents an independent conglomeration of individuals (both environmentally and geographically) that can be pooled for comparison with all others sampled here.

2.2.2. Boney Spring

Boney Spring in Missouri represents one of the largest aggregations of *M. americanum* individuals from a single locality (MNI = 31; Saunders, 1977). Fossil accumulation probably occurred during the latter part of the chronologic range of the unit (Table 1; Saunders, 1977). Palynological records reveal that mastodons here inhabited a spruce-dominated forest with deciduous elements during the late Wisconsin full-glacial (King, 1973). Mastodons during this time period had cheek teeth with smooth enamel and uninterrupted valleys (referred to as the "smooth variety"), as opposed to the "rugged" morphotype found in earlier deposits from Missouri (Saunders, 1977). The smooth morphotype has been suggested as an adaptation for browsing on spruce foliage (Saunders, 1977; King and Saunders, 1984).

2.2.3. Hiscock Site

The well-studied Hiscock Site, New York, includes an attritional sample of mastodon fossils (MNI = 10; Laub, 2003) from the latest Pleistocene (Table 1; Fisher and Fox, 2003; Laub, 2003). Associated

pollen records support a spruce-dominated woodland (McAndrews, 2003), in which mastodons consumed C_3 vegetation (Metcalfe et al., 2013) inferred as browse via dental microwear (Rivals and Semprebon, 2012) with little seasonal variation in diet as inferred from serial samples of tusk dentin (Fisher and Fox, 2003). Similar to Aucilla, there are also mastodon dung deposits that reflect heavy consumption of the distal ends of evergreens (*Picea* in this case, as opposed to *Taxodium* at Aucilla; Laub et al., 1994; Teale and Miller, 2012). Mastodons at this site likely also consumed soil rich in minerals to supplement their nutritive requirements and also to possibly detoxify food (Haynes, 2003; Laub, 2003; McAndrews, 2003)

2.2.4. Indiana

The Indiana population represents a conglomeration of 13 individuals from different sites across the state (Supplemental Table 1), including four from the Bothwell assemblage (MNI = 7; Smith, 2010). 10 of the 13 specimens have associated radiocarbon dates falling in the 11,440–15,540 RCYBP range (Table 1; Supplemental Table 1) and it is likely that the other three individuals for whom radiocarbon dates are not known fall into this chronologic timeframe (R. Richards, pers. comm.). Previous work has suggested that mastodons in this part of the Great Lakes were regional residents rather than nomadic migrants (Bauman and Crowley, 2014); however, this conclusion was based on low variability in $^{87}Sr/^{86}Sr$ preserved in mastodon tissues, and this and recent work (Widga et al., 2017b) has shown that bedrock $^{87}Sr/^{86}Sr$ does not vary substantially. Thus, it is difficult to classify the extent to which mastodons migrated in this region using strontium isotopes. Although we are therefore unable to classify the assemblage of individuals we sampled as a distinct "population", we pooled them into one group and consider them distinct from other populations based on temporal segregation from Jones Spring and Trolinger Spring (both LGM sites) and spatial segregation from all other sites (e.g., Boney Springs, MO is ~800 km from the Bothwell Site). Pollen profiles from Indiana during the late Wisconsin to early postglacial period (including data associated with several individuals sampled here; Supplemental Table 1) record spruce-dominated boreal forest with some deciduous elements (Richards et al., 1987; Swinehart et al., 2005; Whitehead et al., 1982). The Bothwell population preserves a typical C_3 dietary signal in tusk dentin, with some seasonal variation (Smith, 2010).

2.2.5. Jones Spring

Jones Spring lies in the vicinity of Boney Spring in Missouri, yet is deposited during the Mid-Wisconsin period when the environment was dominated by open-pine parkland and spruce vegetation was rare (Table 1; King, 1973), with *M. americanum* fossils extremely abundant (MNI = 25; King and Saunders, 1984). Faunal deposition likely occurred over the chronologic range of the unit (38,000–51,000 RCYBP; King and Saunders, 1984). Molars of *M. americanum* from Jones fit the "rugged variety," having rugose enamel and interrupted valleys and greater rates of tooth wear relative to their eruption state (Saunders, 1977). This increased wear is hypothesized to reflect a more abrasive diet of pine relative to spruce vegetation (King and Saunders, 1984).

2.2.6. Trolinger Spring

Trolinger Spring (29,000–34,000 RCYBP) lies in the immediate vicinity of and stratigraphically above Jones Spring (King and Saunders, 1984). Mastodon remains are abundant here (MNI = 15; King and Saunders, 1984) and fossil accumulation occurred over time and not at once (King and Saunders, 1984). There is one report of purported mastodon stomach contents containing straw and twig fragments (Haynes, 1985), supporting their ecological role as browsers in this environment. The habitat and dental morphology of *M. americanum* at Trolinger Spring is the same as Jones Spring (Table 1; King, 1973; King and Saunders, 1984; Saunders, 1977).
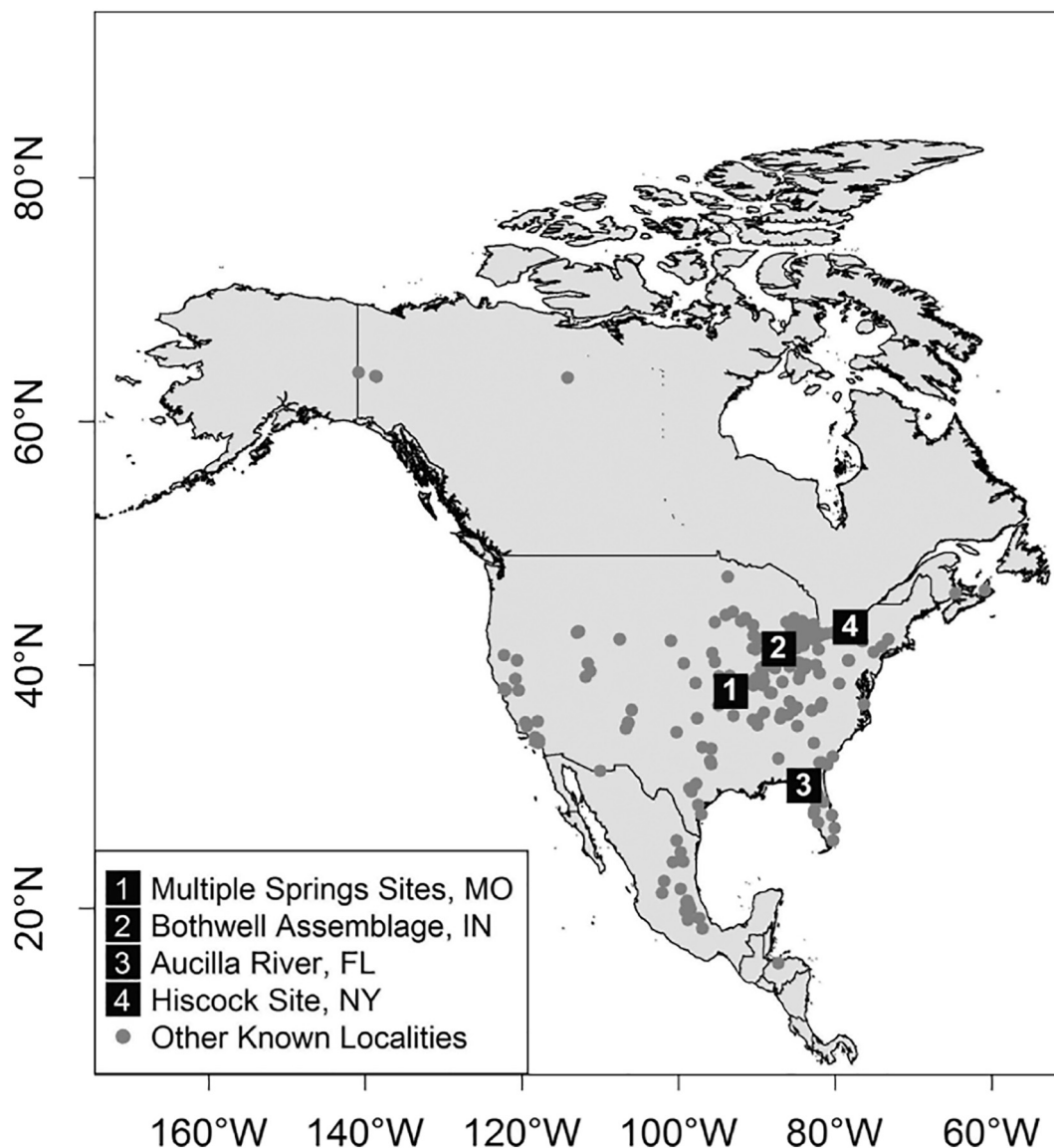
Fig. 1. Map of known range of *Mammut americanum* in the Late Pleistocene (Rancholabrean North American Land Mammal Age) of North America. Grey dots show *M. americanum* remains reported from Canada and the United States using FAUNMAP (www.ucmp.berkeley.edu/faunmap/) and from Mexico using Polaco et al. (2001). Black squares represent localities examined in this study; site 1 includes Boney Spring, Trolinger Spring, and Jones Spring, which were all found relatively close to one another in Missouri.

2.3. Dental microwear

Dental microwear patterns in *M. americanum* were first described and qualitatively analyzed by Laub (1996) to infer jaw movement during chewing. As a dietary proxy, they have thus far been quantified solely using low-magnification stereomicroscopy (Green et al., 2005; Rivals and Semprebon, 2012; Rivals et al., 2012). Green et al. (2005) studied a large sample of mastodons from different localities across Florida, concluding that mastodon microwear was comparable to that of extant ungulate browsers, being most similar to *Alces alces* (moose) and *Diceros bicornis* (black rhino). Semprebon et al. (2012) found a similar browsing signature in individuals from Texas and South Carolina, while Rivals and Semprebon (2012) identified significantly higher scratch counts in Hiscock mastodons as compared to those from Texas. This initial work is significant in that it supports the utility of microwear as a proxy for paleodiet in megaherbivores, whose teeth are dramatically larger than the size of the wear facets that are examined. Specifically, although the length of a third molar of *M. americanum* might exceed 150 mm in length (Green, 2006), the wear facet (i.e., the region which wears from attrition and abrasion) is significantly smaller

(for this study, the center of the mesial enamel band on the metaloph/-id, roughly a few cm long). This area captures the textural properties of foods processed on the facet and the level of magnification employed helps identify taphonomic damage and artifacts (Teaford, 1988).

In addition, the aforementioned initial microwear studies suggest that mastodon feeding behavior may have been variable between geographic localities. Although low-magnification light microscopy can elucidate both broad and fine-scale ecological differences (e.g., Solounias and Semprebon, 2002; Rivals and Solounias, 2007), researchers must still deal with potential issues of subjectivity in user identification of wear features (e.g., DeSantis et al., 2013; Mihlbachler et al., 2012) and no way to consistently quantify the depth of features, reducing the ability to discern subtle dietary differences (DeSantis et al., 2013).

In contrast, DMTA is an automated, three-dimensional analytical technique that reduces potential problems with user-identification of microwear features and yields a detailed microtopographic profile of the tooth surface (DeSantis et al., 2013; Scott et al., 2005, 2006). DMTA does not quantify counts of discrete events (e.g., scratches, pits) as in traditional SEM or light microscopy techniques, but rather quantifies

the complex surface of a wear facet using variables that describe the total complexity of the entire surface. The variables calculated by DMTA include anisotropy (*epLsar*), complexity (*Asfc*), textural fill volume (*Tfv*), and heterogeneity of complexity compared among a total of 9 sub-surfaces in a 3×3 grid ($HAsfc_{3 \times 3}$) and 81 sub-surfaces in a 9×9 grid ($HAsfc_{9 \times 9}$) grids (DeSantis, 2016; Scott, 2012; Scott et al., 2005, 2006; Ungar et al., 2003). Anisotropy (exact-proportion length-scale anisotropy of relief – *epLsar*) is the orientation of wear features; high anisotropy values generally result from the processing of tougher foods, such as grass or leaves, which tend to leave elongate scratches aligned with the direction of food processing (DeSantis, 2016; Scott et al., 2005, 2006; Ungar et al., 2003). Complexity (area-scale fractal complexity – *Asfc*) is a measure of surface roughness at varying scales; higher complexity values are typically indicative of hard or brittle foods, including woody browse, fruits, and/or nuts and seeds (DeSantis, 2016; Scott, 2012; Scott et al., 2005, 2006; Ungar et al., 2003). The relationship between *epLsar* and *Asfc* values can be used to shed insight into the varying proportion of woody browse or leafy foliage incorporated in the diet of disparate populations of browsing taxa such as mastodons. Textural fill volume, which quantifies the total depth of microwear features using square cuboids to fill features (Scott et al., 2006), can be used to make estimates into the degree of hardness of foods consumed. Because DMTA is capable of distinguishing between subtler dietary niches than two-dimensional microwear analysis (DeSantis et al., 2013), we conduct DMTA on *M. americanum* from a diversity of regions and habitats to assess intraspecific variability in the textural properties of food consumed.

3. Materials and methods

3.1. Specimens

A total of 65 M2/m2s and M3/m3s in wear stage 2, 2 +, or 3 (representing young adult to adult stage; sensu Green, 2006 and Green and Hulbert, 2005) were sampled. In these defined wear stages, a pronounced facet (appropriate for molding) had developed on the enamel surface and chewing motion was more unidirectional in a buccal-lingual plane (Laub, 1996). In earlier stages of wear, the orientation of visible scratches change from the enamel crest (where scratches appear more random) to the sloping crescentoid (where scratches appear more parallel) on the same tooth because these surfaces come into contact with opposing teeth at different phases of the chewing cycle (Laub, 1996). To minimize potential intra-tooth variation in microwear, we maintained consistency in the location on the facet sampled across all individuals (see Section 3.2). Only molars with an undamaged enamel band on the metaloph/−id were selected to reduce the possibility of taphonomic alteration of original microwear. Only one tooth per isolated maxillae/mandibles and complete skulls was chosen. M2/m2s were preferentially selected to ensure consistency of microwear sampling within the tooth row, although M3/m3s were sometimes targeted if the second molar in a complete mandible/maxilla was missing or damaged, or, in the case of the Aucilla and Indiana groups, sampling of molars extended across multiple sub-sites, thereby limiting the possibility of sampling the same individual twice. Isolated molars from a single locality were only sampled if they could not be qualitatively matched in relative size and degree of wear to a previously sampled tooth. For example, if an isolated left and right M2 were the same size with the same degree of occlusal wear (i.e., they possibly originate from the same individual), only one was molded. This standardized procedure helps ensure that every molded tooth represents a different individual in our study.

3.2. Dental microwear texture analysis

The central region (i.e., junction of the pretrite and postrite cusps) of the metaloph/−id was the standardized sampling location for each tooth. This surface was first cleaned with acetone and cotton-swabs to remove exogenous preservative, and then washed with ethanol and allowed to dry completely. Multiple applications of acetone were required for specimens with thick coatings of preservative, and these were repeated until the enamel surface was no longer tacky. Only tooth surfaces where preservative could be removed from the central region were molded. Each surface to be molded was then washed with ethanol as a second cleaning step and allowed to dry completely. Two molds of the cleaned surface were made with a two-part polyvinylsiloxane impression material (President Jet Plus MicroSystem, regular body). The first mold was discarded as a final cleaning step. The second mold was cast in clear epoxy resin (Buehler EpoKwick) and allowed to polymerize for at least 48 h. The replica casts were scanned under a Sensofar *PLu neox* optical profiler (Solarius Development, Inc., Sunnyvale, CA) at Vanderbilt University (Department of Earth and Environmental Sciences) using a $100 \times$ objective lens.

A total area of $204 \times 276\ \mu m^2$ was scanned, split into a 2×2 grid (a total of four scans). All tooth surfaces underwent scale-sensitive fractal analysis (SSFA) via analysis of tooth surfaces using both tooth-frax and Sfrax (Surfract Corp., http://www.surfract.com/) software. The median value of the four scans was used to represent a given specimen.

The scans were analyzed for complexity (*Asfc*), anisotropy (*epLsar*), textural fill volume (*Tfv*), and heterogeneity (*HAsfc*). Variability in the roughness of a surface at different scales of observation is quantified as complexity, with high complexity occurring in animals that eat harder and/or more brittle objects including woody browse (DeSantis, 2016; DeSantis et al., 2017; Jones and DeSantis, 2017; Prideaux et al., 2009; Scott, 2012; Scott et al., 2005, 2006; Ungar et al., 2003). The relative orientation of surface features is recorded as anisotropy, with high anisotropy corresponding to a surface with more consistently oriented features and correlated with tough food consumption (DeSantis, 2016; DeSantis et al., 2017; Jones and DeSantis, 2017; Prideaux et al., 2009; Scott, 2012; Scott et al., 2005, 2006; Ungar et al., 2003). Textural fill volume measures the amount of material that has been removed from a surface, with high values describing a surface with deep features (DeSantis, 2016; Scott et al., 2006). Heterogeneity examines how complexity changes across a surface. To do so, it compares the complexity of the entire surface to subdivided surfaces (i.e., a given surface is divided into 2×2 to 12×12 sub-surfaces, a total of 4 to 144 sub-surfaces, respectively; e.g., DeSantis, 2016; Scott et al., 2006). Low heterogeneity is present on surfaces with a more uniform texture (Scott, 2012). Although $HAsfc_{3 \times 3}$ (9 sub-surfaces) was the only heterogeneity variable initially reported (Scott et al., 2006), subsequent studies also reported $HAsfc_{9 \times 9}$ (81 sub-surfaces) (e.g., DeSantis et al., 2013; Jones and DeSantis, 2017; Ramdarshan et al., 2016). Thus, we report $HAsfc_{3 \times 3}$ and $HAsfc_{9 \times 9}$ to maintain consistency with and facilitate easier comparison with these and future studies.

As DMTA values are typically not normally distributed (Shapiro-Wilk tests were also run to confirm this), non-parametric tests were used to compare all fossil specimens of *M. americanum* to one another, between different sites and habitats using Kruskal-Wallis tests and Dunn's procedure. *P*-values < 0.05 were considered significant.

4. Results

Dental microwear data for specimens of *M. americanum* analyzed here are summarized in Table 2 (with all primary data presented in Supplemental Table 1, with examples of 3D wear surfaces noted in Fig. 2) and graphically represented in Fig. 3.

Summary data of *M. americanum* specimens grouped by locality is in Table 3, with pairwise comparisons among different localities (with samples sizes > 10) are presented in Table 4 and graphically depicted in Fig. 3a. Most notably, *M. americanum* from Jones Spring and Boney Spring have significantly greater *Asfc* values than Aucilla individuals (Tables 3–4). *M. americanum* individuals from Jones Spring also have

Table 2

Descriptive statistics of DMTA attribute values for all *Mammut americanum* specimens here examined (*n* = 65).

Statistic	*Asfc*	*epLsar*	*Tfv*	*HAsfc$_{3 \times 3}$*	*HAsfc$_{9 \times 9}$*
Mean	1.950	0.0035	10,305	0.365	0.704
Median	1.675	0.0036	11,234	0.349	2.634
Standard deviation (n − 1)	1.315	0.0017	3600	0.149	0.357
Minimum	0.032	0.0005	168	0.143	0.277
Maximum	5.937	0.0084	15,271	0.933	2.396
Total range	5.905	0.0079	15,103	0.790	2.119
Skewness (Fisher)	1.120	0.438	− 1.299	1.482	2.529

Abbreviations: *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc$_{3 \times 3}$*, *HAsfc$_{9 \times 9}$*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid, respectively.

significantly lower *epLsar* values than Aucilla individuals (with comparisons between Boney Spring and Aucilla yielding a *p*-value of exactly 0.050, not < 0.05). Further, Boney Spring individuals have more homogenous surfaces as compared to Aucilla (in both *HAsfc$_{3 \times 3}$* and *HAsfc$_{9 \times 9}$*), Jones Spring (*HAsfc$_{9 \times 9}$* only), and Indiana (*HAsfc$_{3 \times 3}$* only) (Tables 3–4).

Summary data of *M. americanum* specimens grouped by habitat (as described in Section 2.1.) is presented in Table 5, with pairwise comparisons among different habitats in Table 6 and graphically depicted in Fig. 3b. Individuals from cypress swamps (those located at Aucilla) have significantly lower *Asfc* than individuals from Boreal habitats (Boney Spring, Hiscock, Indiana) and from open-pine parklands (Jones and Trolinger Springs; Tables 5–6). Further, individuals from cypress swamps also have significantly higher *epLsar* values than individuals from open-pine parklands and less homogenous surfaces (*HAsfc$_{9 \times 9}$* only) than boreal forest mastodons (Tables 5–6).

5. Discussion

In general, our results support a woody browsing diet in all *M. americanum* populations analyzed here, consistent with previous microwear studies, gut/fecal contents, and isotopic analyses (reviewed in Section 1). When compared to each other, mastodons from similar northern latitudes (the individual Boney Spring, Jones Spring, and Indiana populations, as well as spruce-dominated boreal forest and open-pine parkland habitat pooled groups) show a similar low anisotropy-high complexity textural pattern that does not significantly differ (Tables 4, 6), supporting a generally homogenous browsing diet for these populations, despite existing in different regions and at different times (Table 1; Fig. 1). However, heterogeneity, which is linked to specialized vs. generalized feeding in suids (Souron et al., 2015) and also distinguishes grass and clover feeders in sheep (Merceron et al., 2016), does differ significantly (Table 4). If the same relationship in suids holds true for proboscideans, significantly lower heterogeneity suggests that the Boney Spring population may have been more specialized in their browsing habits compared to other regions. Significant differences in complexity, anisotropy, and heterogeneity arise when northern localities are compared to the southern Aucilla group and when boreal and open-pine parkland habitats are directly compared to cypress swamps (Table 6). Specifically, this suggests that at least some populations of *M. americanum* had regionally specific feeding ecologies. However, we see no significant difference in anisotropy or complexity through time among the two chronologically-distinct Missouri localities (Boney Spring versus Jones Spring; Table 4), suggesting no chronologic change in the dietary texture in the same region. Below we explore the possible sources and causes of the variation at the regional-level and discuss the implications of a temporally stable dietary niche.
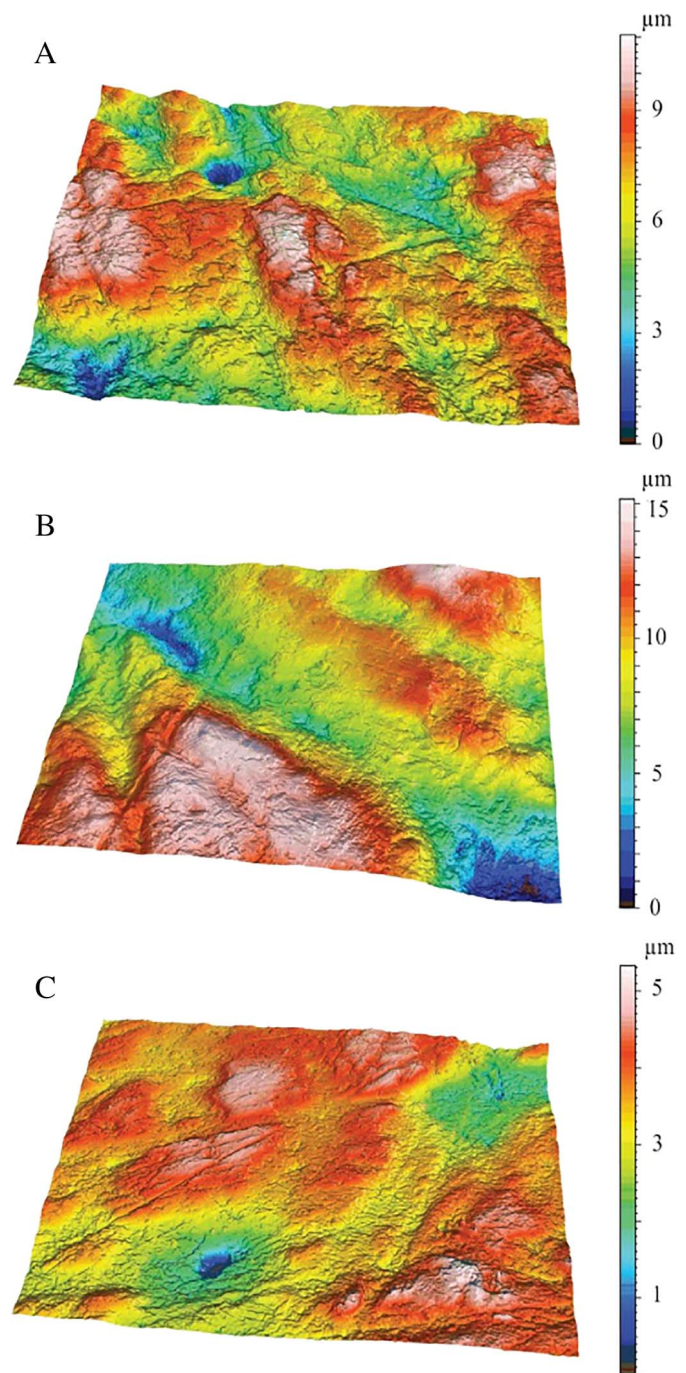

Fig. 2. 3D surface models displaying microwear features of *Mammut americanum* from three habitat categories: (A) spruce boreal forest (BUFFH5NE-282); (B) open-pine parkland (ISM 52JS73); (C) cypress swamp (UF 180505). Abbreviations: BUFF = Buffalo Museum of Science; ISM = Illinois State Museum of Natural History; UF = Florida Museum of Natural History.

5.1. Regional differences in microwear texture

Complexity, which is indicative of hard food consumption such as woody browse in herbivores (DeSantis, 2016; DeSantis et al., 2017; Jones and DeSantis, 2017; Prideaux et al., 2009; Scott, 2012; Scott et al., 2005, 2006; Ungar et al., 2003), is significantly less in cypress swamp mastodons compared to the other habitats. However, pairwise comparisons found differences only between the two Missouri populations compared to Aucilla, which suggests these two loci may be the primary source of this difference. As such, differences in complexity
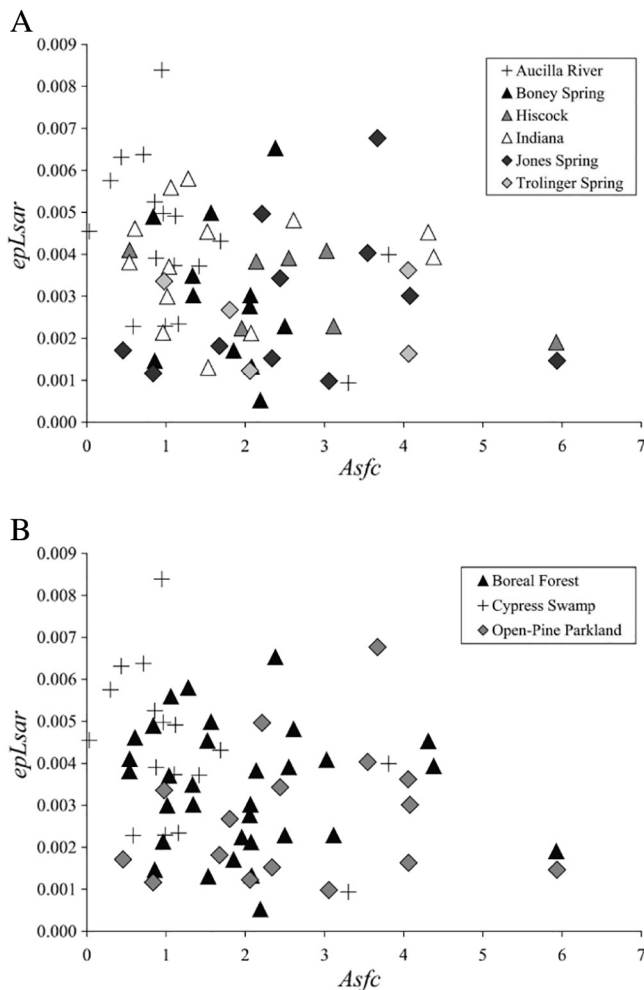
A

B

may not only stem from differences in habitat but also differences in geographic regions. What specific differences in food texture could explain this variation? Dung deposits reconstruct Aucilla mastodons as predominantly feeding on the distal ends of *Taxodium* sp. (bald cypress) branches during their autumn occupation (Newsom and Mihlbachler, 2006). Purported mastodon stomach and dung remains from northern boreal environments suggest *M. americanum* in these regions also targeted distal coniferous twigs as abundant low-quality forage, but the taxa consumed are different and more diverse than those consumed at Aucilla, as remains of *Picea* sp. (spruce), *Tsuga* sp. (hemlock), *Juniperus* sp. (juniper), *Abies* sp. (fir), *Thuja* sp. (cedar) and *Larix* sp. (larch) have all been reported (Bishop, 1921; Dreimanis, 1968; Drumm, 1963; Hay, 1923; Warren, 1855; but see also Lepper et al., 1991, who found a ground-level non-coniferous diet for the Burning Tree mastodon from Ohio).

Differences in the hardness of wood species consumed between these regions could theoretically explain the complexity differences we report. Since many of the plant species mentioned above are still living today, their mechanical properties have been quantitatively determined. Specifically, side hardness (recorded in N) refers to the measure of resistance of wood to indentation on a surface perpendicular to the grain using a modified Janka hardness test, with higher values reflecting more force required for deformation (Weimann and Green, 2007). Thus, a wood with greater side hardness may result in higher complexity on a wear surface during mastication. Wood of *Taxodium distichum* (bald cypress) in the green state has a side hardness of

1730 N, whereas the average side hardness of extant northern conifer greenwood varies [e.g., *Abies* sp. = 1466.25 N (n = 8 species); *Juniperus virginianus* = 2880 N; *Larix* sp. = 2135 N (n = 4 species); *Picea* sp. = 1463.33 N (n = 6 species); *Tsuga* sp. = 1890 N (n = 3 species); side hardness data from Weimann and Green, 2007]. Therefore, mastodons in Boney Spring regularly consuming twigs of conifers harder than *Taxodium* could account for the higher complexity relative to Aucilla. More homogenous textural surfaces in the Boney Spring population, as compared to Aucilla River mastodons, suggests that foods consumed resulted in fairly uniform wear surfaces in regards to complexity.

At Jones Spring, the main conifer present during the mastodon occupation was likely *Pinus banksiana* (jack pine) (King, 1973), which has only a slightly higher side hardness than bald cypress (1770 N; Weimann and Green, 2007). If mastodons were predominately consuming *P. banksiana* at this site, we would not expect a significant difference in complexity. Alternatively, deciduous hardwoods (e.g., *Quercus* sp., which has a side hardness exceeding 4000 N; Weimann and Green, 2007) were also present at both Boney Spring and Jones Spring, albeit in lower abundance relative to *Picea* sp. in the former site and *Pinus* sp. in the latter (King, 1973). Regular consumption of deciduous hardwood twigs, along with hard-objects such as seeds and nuts, in the Jones and Boney Spring mastodons may also account for the observed disparity in complexity. Ultimately, we have no direct evidence from gut contents from either Boney or Jones Spring mastodons and so the hypothesis that mastodons were preferentially consuming harder woody browse in these regions compared to those from the southeastern coastal plain is supported by DMTA, but difficult to test further.

It should also be noted that although side hardness provides a commonly available measure of relative hardness among wood species, the correlation between how much change is required in this variable to elicit a deformative response on an enamel surface has not yet been tested and is beyond the scope of our study here. It is possible that all of the species above are similar enough to each other to create a negligible response in complexity. Further complicating this situation, in vitro experiments suggest that increasing food stiffness (assumed to be proportional to hardness) does not always correlate with increasing complexity for some mammals (Daegling et al., 2016), although proboscidean dentitions were not specifically tested in that study. Thus, we must acknowledge it is possible that the mechanical properties of consumed wood may not be the main influence in the variation we report here. Exogenous grit on plant surfaces may have been prominent in the more arid environment of Jones Spring compared to the Aucilla wetland. While recent experimental evidence suggests that abrasive dust does not strongly influence microwear textures (Merceron et al., 2016), it can play an ancillary role (Hedberg and DeSantis, 2017; Merceron et al., 2016). Ultimately, more work is required to better resolve how the mechanical properties of food and those of exogenous grit may be influencing microwear in *M. americanum* and other proboscideans.

Aucilla mastodons also exhibit significantly higher anisotropy than open-pine parkland populations (i.e., Jones Spring). In primates, an increase in dietary toughness is correlated with longer feeding time and more repeated chewing cycles (Coiner-Collier et al., 2016). This increased mastication causes microwear features to be formed in a parallel fashion on the tooth surface (Scott et al., 2006). Anisotropy is higher in more folivorous browsers compared to woody browsers (DeSantis, 2016; DeSantis et al., 2017; Prideaux et al., 2009; Scott, 2012; Ungar et al., 2003), so the most parsimonious explanation here would be that the Aucilla group consumed large amounts of foliage. However, dung from this locality preserves cypress twigs with little to no evidence of needle/foliage consumption (Newsom and Mihlbachler, 2006). If mastodons were truly consuming higher amounts of foliage, this should be reflected in the composite dung samples preserved. Alternatively, softer twigs could result in similar results if water content of wood alters the textural properties. The green sapwood of *Taxodium* sp. has a higher average moisture content compared to that of upland

Table 3
Descriptive statistics of DMTA attribute values for all *Mammut americanum* specimens here examined (*n* = 65) as subdivided based on locality.

Variable	Site	N	Median	Mean	SD	Min.	Max	Range
Asfc	Aucilla River	17	0.964	1.194	0.978	0.032	3.812	3.780
	Boney Spring	12	1.955	1.756	0.561	0.839	2.499	1.660
	Hiscock	7	2.550	2.751	1.644	0.541	5.926	5.386
	Indiana	13	1.280	1.764	1.276	0.537	4.379	3.842
	Jones Spring	11	2.440	2.749	1.553	0.456	5.937	5.480
	Trolinger Spring	5	2.059	2.591	1.399	0.976	4.062	3.086
epLsar	Aucilla River	17	0.0043	0.0044	0.0018	0.0009	0.0084	0.0075
	Boney Spring	12	0.0029	0.0030	0.0018	0.0005	0.0065	0.0060
	Hiscock	7	0.0038	0.0032	0.0010	0.0019	0.0041	0.0022
	Indiana	13	0.0039	0.0038	0.0014	0.0013	0.0058	0.0045
	Jones Spring	11	0.0018	0.0028	0.0018	0.0010	0.0068	0.0058
	Trolinger Spring	5	0.0027	0.0025	0.0010	0.0012	0.0036	0.0024
Tfv	Aucilla River	17	11,375	9039	4701	168	14,142	13,974
	Boney Spring	12	10,628	10,217	2848	4016	14,237	10,222
	Hiscock	7	10,887	10,287	3161	5345	14,072	8727
	Indiana	13	12,111	11,840	2124	8181	15,271	7090
	Jones Spring	11	10,434	9537	4210	739	13,965	13,226
	Trolinger Spring	5	13,012	12,544	1222	11,233	13,644	2411
HAsfc$_{3 \times 3}$	Aucilla River	17	0.379	0.409	0.174	0.205	0.933	0.728
	Boney Spring	12	0.249	0.276	0.089	0.143	0.440	0.297
	Hiscock	7	0.399	0.375	0.161	0.181	0.659	0.479
	Indiana	13	0.368	0.374	0.111	0.157	0.545	0.388
	Jones Spring	11	0.387	0.384	0.195	0.168	0.867	0.699
	Trolinger Spring	5	0.349	0.347	0.090	0.255	0.472	0.217
HAsfc$_{9 \times 9}$	Aucilla River	17	0.649	0.916	0.541	0.403	2.396	1.993
	Boney Spring	12	0.481	0.509	0.164	0.277	0.916	0.639
	Hiscock	7	0.682	0.641	0.187	0.353	0.908	0.554
	Indiana	13	0.664	0.627	0.160	0.388	0.835	0.448
	Jones Spring	11	0.775	0.757	0.347	0.436	1.402	0.966
	Trolinger Spring	5	0.675	0.622	0.127	0.461	0.769	0.309

Abbreviations: *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc$_{3 \times 3}$*, *HAsfc$_{9 \times 9}$*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid, respectively. N, number of samples per habitat group, SD, standard deviation (n − 1), Min., minimum values, Max., maximum value, Range, total range of all values per attribute.

Table 4
Pairwise comparisons of DMTA attributes values of *Mammut americanum* specimens between sites with > 10 specimens per site (*n* = 53).

Variable	Site	Boney Spring	Indiana	Jones Spring
Asfc	Aucilla River	**0.041**	0.139	**0.002**
	Boney Spring		0.573	0.289
	Indiana U			0.103
epLsar	Aucilla River	0.050	0.462	**0.024**
	Boney Spring		0.242	0.746
	Indiana U			0.141
Tfv	Aucilla River	0.890	0.123	0.913
	Boney Spring		0.197	0.981
	Indiana U			0.199
HAsfc$_{3 \times 3}$	Aucilla River	**0.013**	0.881	0.537
	Boney Spring		**0.028**	0.097
	Indiana U			0.654
HAsfc$_{9 \times 9}$	Aucilla River	**0.004**	0.206	0.544
	Boney Spring		0.115	**0.039**
	Indiana			0.572

Bold denotes significance (*p* < 0.05). Abbreviations: *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc$_{3 \times 3}$*, *HAsfc$_{9 \times 9}$*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid, respectively.

pines (Glass and Zelinka, 2010), yet fracture toughness (resistance to cracking) decreases as moisture content in woody tissues increases (King et al., 1999). Our data therefore do not match what we would predict if moisture availability was responsible for differences in anisotropy between cypress swamp and open-pine parkland mastodon populations. After all, wood is a composite biological tissue and there are likely other structural variables not considered here (e.g., lignin content, collenchyma vs. sclerenchyma tissue abundance, cell wall thickness) beyond moisture content that may be influencing its ability to resist fracture (e.g., Lucas, 2004). For example, the modulus of elasticity (measure of the resistance of an object to elastic deformation)

and the modulus of rupture (maximum stress that an object can flex before failing) for *Taxodium* sp. are 8100 MPa and 46,000 kPa, respectively, versus only 7400 MPa and 41,000 kPa for *P. banksiana*, respectively (Kretschmann, 2010). These values suggest that bald cypress twigs would be generally tougher than jack pine, but whether this difference is appreciable enough to elicit a significantly higher anisotropy signal is currently unknown. As stated earlier, microwear formation is a complex process that can be influenced by other variables besides the structural properties of food (e.g., Daegling et al., 2016). The specific cause of the higher anisotropy signal in Aucilla mastodons requires further investigation.

As alluded to above, there are limits to dietary interpretations made based on dental microwear texture data from fossil populations, as we are attempting to draw broad-scale ecological interactions based on indirect associations (e.g., the Aucilla dung deposits and microwear data are from the same locality but do not necessarily come from the same individuals). We can generally conclude that microwear texture supports *M. americanum* as a woody browser, yet Aucilla individuals consumed a softer, tougher diet compared to some northern boreal and open-pine parkland inhabitants. Latitudinal variation in DMTA is congruent with the significant difference in scratch counts observed by Rivals and Semprebon (2012). Although the specific foods responsible for this textural difference remain uncertain at this time, our data confirm that regional populations of *M. americanum* were capable of adapting their diet to available vegetation across their range, supporting plasticity in their browsing niche.

It is possible that geographic differences in the dietary preferences of regional *M. americanum* groups were influenced by presence of sympatric browsing or mixed feeding megafauna. Browsing *Odocoileus* sp. (usually *O. virginianus*) co-occured with mastodons at all regions sampled here (Laub et al., 1988; Richards, 1983; Saunders, 1977, 1988; Webb and Simons, 2006). In northern localities only, other common cervids included the browsing *Cervus elephas*, *Rangifer tarandus*, and

Table 5
Descriptive statistics of DMTA attribute values for all *Mammut americanum* specimens here examined (*n* = 65) as subdivided based on habitat.

Variable	Habitat	N	Median	Mean	SD	Min.	Max	Range
Asfc	Boreal	32	1.904	1.977	1.200	0.537	5.926	5.389
	Cypress Swamp	17	0.964	1.194	0.978	0.032	3.812	3.780
	Pine Parkland	16	2.389	2.700	1.461	0.456	5.937	5.480
epLsar	Boreal	32	0.0036	0.0034	0.0015	0.0005	0.0065	0.0060
	Cypress Swamp	17	0.0043	0.0044	0.0018	0.0009	0.0084	0.0075
	Pine	16	0.0022	0.0027	0.0016	0.0010	0.0068	0.0058
Tfv	Boreal	32	11,221	10,892	2682	4016	15,271	11,255
	Cypress Swamp	17	11,375	9039	4701	168	14,142	13,974
	Pine	16	11,234	10,476	3779	739	13,965	13,226
HAsfc$_{3 \times 3}$	Boreal	32	0.327	0.337	0.122	0.143	0.659	0.517
	Cypress Swamp	17	0.379	0.409	0.174	0.205	0.933	0.728
	Pine	16	0.368	0.373	0.167	0.168	0.867	0.699
HAsfc$_{9 \times 9}$	Boreal	32	0.573	0.586	0.173	0.277	0.916	0.639
	Cypress Swamp	17	0.649	0.916	0.541	0.403	2.396	1.993
	Pine	16	0.680	0.715	0.298	0.436	1.402	0.966

Abbreviations: *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc$_{3 \times 3}$*, *HAsfc$_{9 \times 9}$*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid, respectively. N, number of samples per habitat group, SD, standard deviation (n − 1), Min., minimum values, Max., maximum value, Range, total range of all values per attribute.

Table 6
Pairwise comparisons of DMTA attributes values of *Mammut americanum* specimens between habitats (*n* = 65).

Variable	Habitat	Cypress Swamp	Pine Parkland
Asfc	Boreal Forest	**0.013**	0.145
	Cypress Swamp		**< 0.001**
epLsar	Boreal Forest	0.078	0.111
	Cypress Swamp		**0.004**
Tfv	Boreal Forest	0.355	0.931
	Cypress Swamp		0.383
HAsfc$_{3 \times 3}$	Boreal Forest	0.184	0.601
	Cypress Swamp		0.493
HAsfc$_{9 \times 9}$	Boreal Forest	**0.023**	0.165
	Cypress Swamp		0.462

Bold denotes significance (*p* < 0.05). Abbreviations: *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc$_{3 \times 3}$*, *HAsfc$_{9 \times 9}$*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid, respectively.

Cervalces scotti, as well as the giant beaver *Castoroides ohioensis* (Laub, 2003; Richards, 1983; Saunders, 1977, 1988; Whitehead et al., 1982). *Tapirus* sp. (most commonly *T. veroensis*) is reported from Aucilla, Jones Spring, and Boney Spring (Saunders, 1977, 1988; Webb and Simons, 2006). For camelids, *Palaeolama mirifica* (browser) and *Hemiauchenia macrocephala* (mixed feeder) were associated with Aucilla (Webb and Simons, 2006), whereas *Camelops* sp. (mixed feeder) was present in Jones Spring (Saunders, 1988). The browsing *Bootherium* sp. was sympatric with mastodon in Trolinger and Jones Spring faunas (Saunders, 1977, 1988). Finally, the ground sloth *Megalonyx jeffersoni*, a likely browser, was present at Aucilla and Indiana (Richards, 1983; Webb and Simons, 2006). Dietary assignment in all the above taxa is supported by carbon isotope data (France et al., 2007; Hoppe and Koch, 2006; Yann et al., 2016) or dental microwear (Resar et al., 2013; Rivals and Semprebon, 2012). Of note, Aucilla is the locality where the associated competition includes a diverse mixture of camelid, xenarthran, tapir, and cervid taxa. Perhaps the diet of Aucilla mastodons was influenced by competition - resulting in a diet of vegetation with disparate textural properties as compared to other regions. Finding significantly lower anisotropy in other browsers from this locality would support this hypothesis, although other biotic and abiotic factors beyond competition could likely be in play as well. Future comparison of DMTA variables between *M. americanum* specimens and sympatric browsing/mixed-feeding taxa in localities we sampled would help further elucidate niche partitioning with respect to food texture in Pleistocene browsing megafauna.

5.2. Temporal stability in microwear textures

The Boney Spring (13,600–16,200 RCYBP) and Jones Spring (38,000–51,000 RCYBP) populations existed within the immediate vicinity of one another in Missouri, yet occupied different habitats (Table 1). This provides an excellent opportunity to test hypotheses of chronologic dietary shifts in these populations. Mastodons from Jones and Trolinger Springs exhibit a "rugged" molar morphology, while Boney Spring mastodons had "smooth" cheek teeth (Saunders, 1977). These two dental morphologies have been proposed as adaptations for more abrasive diets consisting of pine and a softer diet consisting of spruce, respectively (King and Saunders, 1984). This hypothesis is plausible given the drastic environmental differences between these loci, yet has not been tested except through circumstantial evidence. As dental microwear is caused by fine-scale damage during mastication, DMTA variables should detect a significant shift in dietary abrasiveness between these temporally-distinct populations if one exists. Complexity and anisotropy (the variables most closely associated with the physical properties of food) do not differ between Jones Spring and Boney Spring (Table 4). Although it is logical that mastodons at Jones Spring consumed available pine, while Boney Spring preferentially fed on available spruce, the actual difference in abrasiveness between these two conifers may be too subtle to cause a significant shift in dental wear. In other words, the diet may have changed, but did not actually become more abrasive. Thus, the hypothesis that the shift in dental morphology and size was in response to accelerated wear through time (King and Saunders, 1984) can be rejected. However, other chronologic differences between the two populations may be present. More homogenous wear surfaces (at least at the 9 × 9 level; Tables 3–4) might suggest that the individuals associated with the boreal forest were more specialized feeders compared to the open-pine parkland population. This interpretation is based on data from suids (Souron et al., 2015), however, and the actual significance of this variable to proboscidean feeding ecology remains to be tested. In all, our data supports the conservation of the dietary hardness and toughness of *M. americanum* in this region through time, meaning that chronologically-disparate populations consumed foods of the same relative texture even during the significant environmental and climatic shifts of the Wisconsin glacial period. Although we were not able to include Trolinger Spring in our statistical comparisons due to small sample size, this population clusters with Jones Spring in its complexity and anisotropy values (Fig. 3a), further supporting niche stability in Missouri populations through time.

Aucilla mastodons exhibit a similar pattern as Missouri, with dung deposits from the Latvis/Simpson site (32,000 RCYBP) and Page-Ladson (12,350 RCYBP) bearing remarkably homogenous compositions

(Mihlbachler, 1998; Newsom and Mihlbachler, 2006). Our Aucilla sample includes teeth from both sites with dung along with multiple teeth from undated sites within the same region, thus representing a time-averaged depiction of mastodon diet. The low sample size of individuals from specific sites within the Aucilla River precludes statistical comparison. However, the relatively tight clustering of this sample in terms of complexity (with the exception of 2 individuals; Fig. 3a) suggests this low hardness diet was conserved through time. Thus, high homogeneity in DMTA variables within the Aucilla and Missouri groups, coupled with some significant differences between the two regions, begin to paint a picture of *M. americanum* as a species with some plasticity in its dietary regime across its range. Regional populations were able to conserve their respective dietary niche despite changes in their environment through time, suggesting that this species may have been more adaptable (in terms of diet) to local environmental shifts than hypothesized by others (e.g., Dreimanis, 1967, 1968; King and Saunders, 1984; Yansa and Adams, 2012). Additionally, temporal shifts in molar and limb bone size in resident populations from Florida and Missouri (King and Saunders, 1984; Green, 2006) and apparent geographical differences in body size between eastern and western populations (Springer et al., 2009) suggest high adaptability in *M. americanum*. It is possible that these observed skeletal shifts may be an ecophenotypic response to differences in diet for the affected groups. Along these lines, ongoing research is comparing microwear variability in Pleistocene mastodons from other eastern (e.g., Ohio) and southern regions (e.g., Texas; Smith and DeSantis, in review), as well as comparisons with more western (e.g., California) and northern (e.g., Alaska) regions across North America.

In terms of extinction scenarios, having an adaptable diet in and of itself does not preclude susceptibility to significant changes in the surrounding environment, as mastodons still relied heavily on forested ecosystems much like tapirs (DeSantis and MacFadden, 2007), so significant reductions in this general habitat type could still impact their survival. An extinction event that is driven by vegetation loss should manifest itself in slowed growth, resulting in depressed reproductive timelines in the affected animal, yet sampled individuals from the Great Lakes region do not show reduced growth rates or delayed maturation (see Fisher, 2009 for a more detailed discussion). Whether this observed pattern holds true as more individuals from the Great Lakes and other regions across North America are analyzed remains to be seen, and the debate about the cause of the end-Pleistocene event continues. Indeed, mastodon extinction may not have been induced by a single cause (e.g., environmental or human impact), but rather may have resulted from a combination of events that may have varied regionally across the range of the species (Haynes, 1991; Widga et al., 2017a). A more structured comparison of microwear texture between pre-extinction and latest Pleistocene populations is needed to further test whether changes in food texture and diet could have played a role in mastodon die-offs. Combining microwear data not only with isotopic data, but also growth and life history records from associated tusks (e.g., Smith and Fisher, 2011, 2013) on a continental-wide scale has the potential to reveal detailed information about the paleobiology of mastodons and may inform about the extirpation of this species.

6. Conclusions

Here, we present the largest, most comprehensive analysis to date of within-species variation in microwear for *Mammut americanum*. A subtle, yet significant difference in microwear texture exists among geographically-distinct populations in the Late Pleistocene. This difference is tied to regional-scale variation (rather than temporal shifts) in browse preference between southern and northern populations, where the former maintained a slightly softer, tougher diet compared to the latter. In Missouri, there was no significant change in dietary hardness or toughness during the Late Pleistocene habitat shift from open-pine parkland to boreal forest.

Our findings are significant in that they reconstruct *M. americanum* as a species with adaptability in its browsing strategy across its range, with regional populations able to maintain their diet in the face of local environmental shifts in the Late Pleistocene. This has implications for the future testing of environmentally-induced mastodon extinction hypotheses during the latest Pleistocene. A more detailed understanding of how available plant materials correlates with microwear textures in lophodont dentitions will further expound upon the range of dietary adaptations employed by *M. americanum* and other proboscideans during their North American occupation (see Smith and DeSantis, in review). This work also highlights the importance of measuring within-species dietary variation to better understand microevolutionary changes in feeding ecology.

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