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Rapid response: dietary shifts by grey wolves in response to palaeoclimatic variations during the last glaciation☆

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ABSTRACT

Following the Last Interglacial (~125 ka), Britain experienced a series of pronounced climatic fluctuations that drove major shifts in environmental conditions and habitat structure during the last glaciation. Despite broader faunal turnover, grey wolves (*Canis lupus* L., 1758) persisted throughout these changing landscapes, reflecting considerable ecological resilience.

This study examines the dietary behaviour of last glaciation wolves in Britain, using dental microwear texture analysis (DMTA). Variation in microwear textures is used to evaluate differences in feeding behaviour across distinct climatic intervals, including the Marine Oxygen Isotope Stage (MIS) 5a interstadial, the climatic complexity of the middle part of the last glaciation (Devensian/Weichselian, MIS 3) and the Last Glacial Maximum (late Devensian, MIS 2). As diet is a fundamental component of ecological adaptation, dental microwear texture parameters offer direct insight into feeding strategies and carcass processing intensity in fossil carnivores.

Results indicate that dental microwear texture patterns vary systematically with climatic context. Wolves from the coldest phase of the last glaciation (MIS 2) exhibit surface textures distinct from those of the interstadial periods, consistent with reduced durophagous behaviour. In contrast, wolves from MIS 3 and MIS 5a display higher surface complexity, with MIS 3 showing the broadest range of texture values and thus the greatest variability among the intervals examined. These findings are interpreted in relation to potential driving factors, including palaeoclimatic conditions, prey availability, and the presence of competing carnivores. Integrating dental microwear and palaeoenvironmental evidence provides new insights into how this keystone species responded to climatic variability during the Late Pleistocene.

1. Introduction

The rapid and abrupt climatic fluctuations of the last glaciation, c.110–14.7 kya (Marine Oxygen Isotope [sub]Stages [MIS] 5d-2 inclusive) created an exceptionally challenging backdrop for mammalian life in the far north-west of Europe, none more so than for the British fauna, which occupied a climatically sensitive geographical position adjacent to the North Atlantic. Following the climatic optimum of the Last Interglacial (MIS 5e, c. 125,000 years ago) (Candy et al., 2016), the fauna in Britain was subjected to an unparalleled period of climatic instability, interrupted by 25 distinct warming and cooling events seen in the Greenland ice core record, termed Dansgaard-Oeschger events (Rasmussen et al., 2014).Greenland Ice-core Project (GRIP) Members (1993) These were initiated by a decrease in summer insolation at high northern latitudes, leading to a series of time-transgressive changes in both the terrestrial and marine realms, including extensive vegetation change on land (Fletcher et al., 2010). As the ice sheets in the Northern Hemisphere began to grow and expand, these changes became increasingly pronounced and affected every aspect of mammalian species existence, driving turnover at the community level (Lyons, 2005;

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Currant and Jacobi, 2011), species-level range shifts (Zimina and Gerasimov, 1973; Seersholm et al., 2020), regional or total extinctions (Brace et al., 2012; Stuart and Lister, 2014; Wang et al., 2021), allopatric speciation (Lister and Sher, 2001; Lister, 2004; Lan et al., 2022) and changes in herbivore and carnivore foraging behaviour (Drucker et al., 2003; Rivals et al., 2009; Flower et al., 2021).

The grey wolf (*Canis lupus*) has been a regular component of the western European fauna since the late Middle Pleistocene (Iurino et al., 2022) and, along with brown bear (*Ursus arctos*), it is the only species to be recorded in every biozone associated with the various climatic episodes of the Late Pleistocene in Britain (Currant and Jacobi, 2011; Fig. 1). British Late Pleistocene sequences are therefore ideal for testing hypotheses of the ecological resilience of this keystone predator, since they preserve a series of chronologically well constrained faunal assemblages that track the succession of rapid and abrupt climate changes. The success of the grey wolf, in terms of responding to long-term climatic change during the Pleistocene, has previously been highlighted by studies identifying both flexibility in prey choice and flesh versus non-flesh items (Flower and Schreve, 2014; Flower et al., 2021; Landry et al., 2021), together with evidence of morphological variation, including body mass change and the evolution of specialist ecomorphs (Leonard et al., 2007; Boudadi-Maligne, 2012; Flower, 2016). However, to date, no study has examined the ecological resilience of this species in the face of exceptionally rapid and abrupt climate change, as exemplified by the last glaciation in northern Europe.

Palaeodietary reconstruction offers new insights into the ecological resilience of large carnivores, as it reflects the combined influence of local environmental conditions, prey availability, and competition from other predators. The analytical approach adopted here is dental microwear texture analysis (DMTA), which quantifies the microscopic surface textures formed on teeth during food processing and reflects the properties of foods consumed during the last few days to weeks of an individual's life (Teaford and Oyen, 1989; Winkler et al., 2020). Experimental and controlled-feeding studies have demonstrated that foods with different material properties produce distinct dental microwear textures, providing a direct link between surface texture attributes and dietary behaviour (Walker et al., 1978; Teaford and Walker, 1984; Teaford and Oyen, 1989; Ungar et al., 2008; Purnell et al., 2012; Schulz et al., 2013; Ramdarshan et al., 2016).

These microwear textures consist of microscopic scratches, pits, and

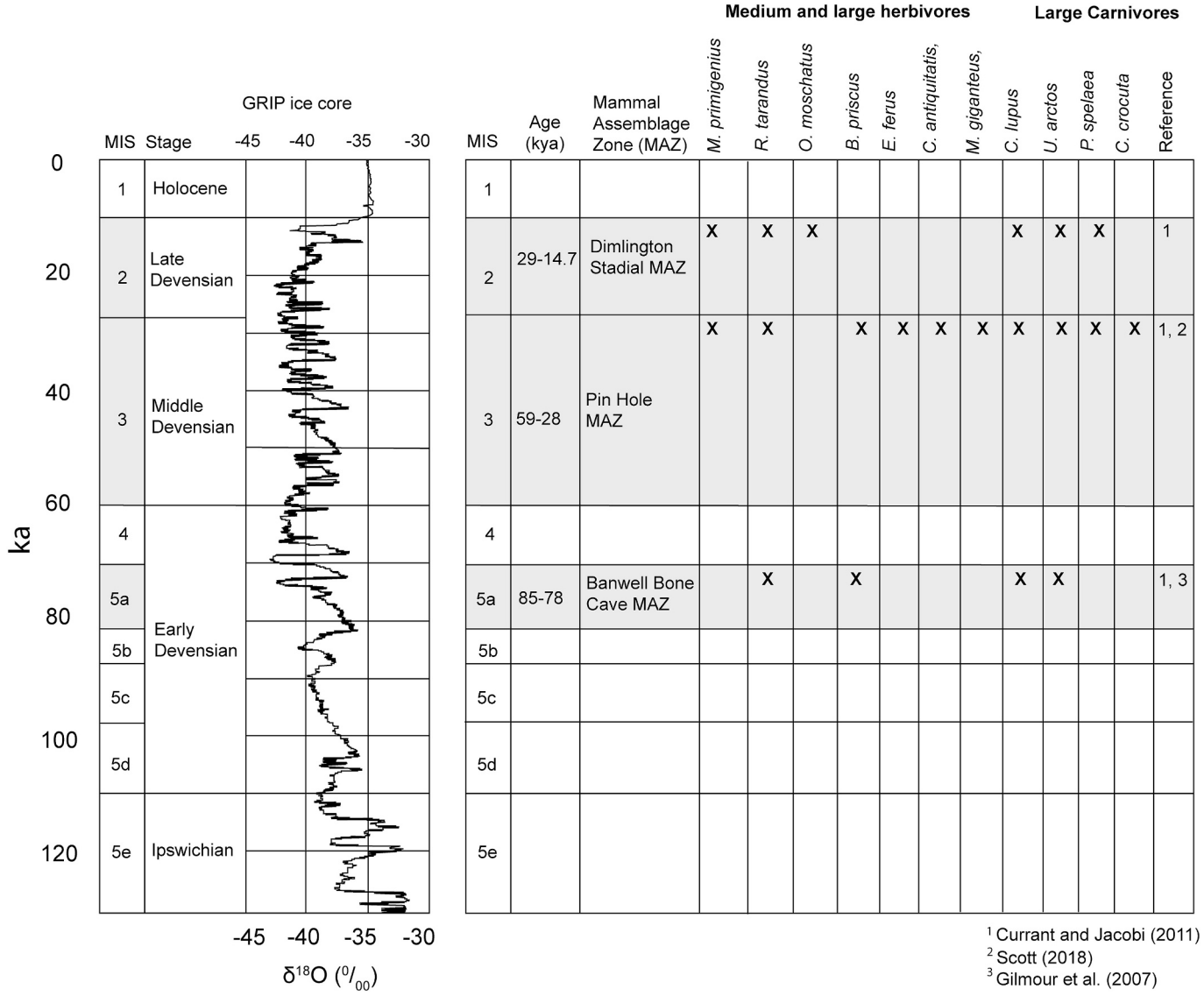

Fig. 1. Chronological framework showing Marine Isotope Stages (MIS), the GRIP-2 $\delta^{18}O$ record, Mammal Assemblage Zones (MAZs), and the occurrence of selected herbivore and carnivore taxa in Britain. The GRIP-2 $\delta^{18}O$ record is modified after Smith et al. (2019). Faunal occurrence data after Gilmour et al. (2007), Currant and Jacobi (2011), and Scott, 2018.

other wear features on the enamel surface of teeth and have been widely used to reconstruct the dietary behaviours of both extinct and extant mammals (e.g. Teaford and Walker, 1984; Hillson, 2005; Scott et al., 2006; Ungar et al., 2010; DeSantis et al., 2015). DMTA combines non-contact surface profilometry with scale-sensitive fractal analysis (SSFA) and analysis of areal surface texture parameters, most of which follow ISO 25178-2 standards, to provide robust three-dimensional quantification of dental microwear.

In carnivores, DMTA is particularly effective for assessing the degree of durophagy, the consumption of hard, brittle foods associated with intensive carcass processing and increased consumption of bone and cartilage. Analysis of grinding molar facets is particularly informative because these surfaces directly record the processing of hard food items during mastication. Numerous analyses of teeth in a range of vertebrates (not just mammals) have shown that increasing proportions of hard, brittle foods in diets results in tooth surfaces that are, in colloquial terms, rougher. This is reflected in DMTA by higher levels of parameters that capture complexity (Asfc, Sdr), and the volume and sharpness of voids/valleys and peaks in a surface (e.g. Ungar et al., 2010; DeSantis et al., 2015; Purnell and Darras, 2016; Schulz-Kornas et al., 2024). Fig. 2 shows rendered and greyscale photo simulations of tooth surfaces with different complexity values. In contrast, anisotropy is associated with the processing of tough, fibrous foods such as flesh and is expressed through the alignment of striations across the enamel surface. High anisotropy values indicate a strongly unidirectional orientation of these features (Schubert et al., 2010; Ungar et al., 2010; Donohue et al., 2013).

Beyond the consumption of bone and flesh of vertebrates, wolves also take a small proportion of non-meat foods in their diet, including a wide range of berries (Homkes et al., 2020), nuts and other fruits (Meriggi et al., 1996), insects (Gade-Jørgensen and Stagegaard, 2000; Barton et al., 2020), and even grasses (Jędrzejewski et al., 2000) (the last possibly acting as a scouring agent against internal parasites (Peterson, 1977).

Here we test the hypothesis that the diets of Late Pleistocene wolves differed across major climatic episodes. Wolves' hunting success is correlated today with winter severity, since deep snow makes it easier to bring down ungulate prey already disadvantaged by limited vegetation availability (Jędrzejewski et al., 1992; Mech and Peterson, 2003; Gable et al., 2018). During milder winters, wolves are therefore driven to scavenge more intensively and to exploit carcasses more fully (Gable et al., 2024). Increased durophagy has accordingly been highlighted as a marker of wolf trophic behaviour during periods of decreased winter severity, both in modern wolves from North America (Burtt and DeSantis, 2022) and Poland (Burtt et al., 2026) and from Last Interglacial (MIS 5e) wolves in Britain (Burtt et al., 2026). Based on previous studies of carnivores using DMTA, we hypothesise that dental surface textures will differ between wolves inhabiting colder glacial phases (e.g. MIS 2, including the Last Glacial Maximum) and those living during warmer intervals (e.g. MIS 5a and the interstadials of MIS 3). Specifically, we predict that wolves from warmer climatic phases will exhibit more complex and rougher tooth surface textures, reflected by higher values of parameters associated with surface complexity and roughness, than wolves from colder phases. We also predict that wolves from climatically unstable periods (e.g. MIS 3) will exhibit greater variability of microwear texture values, reflecting increased variation in resource availability and feeding behaviour associated with rapidly fluctuating palaeoenvironmental conditions.

The climatic oscillations of the last glaciation, therefore, offer a detailed backdrop against which dietary flexibility (and accordingly, ecological resilience) can be tested in grey wolves, taking into account changing prey and predator presence, as well as changes in the wider environment. The choice of DMTA here complements previous isotopic and morphological investigations of British Pleistocene wolves (Flower and Schreve, 2014; Flower et al., 2021) by providing direct evidence of feeding behaviour immediately prior to death.

2. Material and methods

Thirty-three wolf teeth with intact enamel and well-preserved microwear surfaces were sampled from established, chronologically secure sites in Britain (Fig. 3, Table S1 and S2). Specimens exhibiting substantial enamel loss attributable to injury or advanced wear were excluded. Dental microwear texture data were collected from grinding facets, focusing on the anterolingual surface of the hypoconid cusp on lower second molars (m2) and the talonid basin of the first mandibular molar (m1). Post-carnassial surfaces are considered ideal for assessing bone-consumption textures and serve as the established benchmark in dental microwear texture analyses of carnivorans. Data derived from these surfaces facilitate direct comparison with other studies using DMTA (Scott et al., 2005, 2006; Ungar et al., 2010; DeSantis et al., 2015; Tanis et al., 2018; DeSantis et al., 2019). In cases where both molars were available for a single individual, only data from the second molar (m2) were retained for subsequent analyses. Data from m1 and m2 are presented together because previous studies have demonstrated that these tooth positions yield indistinguishable values for the key DMTA parameters used to infer dietary behaviour (Tanis et al., 2018; Burtt et al., 2026). Functionally, both the talonid basin of the lower carnassial (m1) and the occlusal surface of the second molar (m2) form part of the post-carnassial grinding complex and are primarily involved in crushing and grinding food during mastication (Van Valkenburgh, 1989). Their analogous role in food processing likely accounts for the similar microwear textures observed between these tooth positions. Our sample consists of the following teeth from individuals by temporal group: MIS 2 (m1, $n = 4$; m2 = 6), MIS 3 (m1, $n = 8$; m2, $n = 6$) and MIS 5a (m1, n = 6; m2, $n = 3$).

Teeth were replicated by moulding the enamel surfaces and producing a cast. The dental specimen moulding method involves a non-abrasive cleaning of the occlusal tooth surface by swabbing with acetone/ethanol mixture. Subsequently, polyvinylsiloxane dental impression material (President The Original: Regular Body Coltene-Whaledent Corp., Altsatten, Switzerland) is applied. Post-curing, the moulding medium is easily removed from teeth. The cleaning and moulding process is limited to the occlusal surfaces of mandibular second molars and the talonid basin of the mandibular first molar. Tooth surface casts were produced using high-resolution epoxy (Epotek 301; Epoxy Technologies Corp., Billerica, MA, USA), which is optimal for confocal imaging purposes. Epoxy tooth replicas were scanned with a Sensofar S neox profiler in the School of Geography, Geology and the Environment at the University of Leicester with the following settings: confocal scanning, 100× ELWD lens (numerical aperture 0.8), green LED light source (530 nm), z-step size 0.07 μm, CCD 2448 × 2048 pixels, field of view 169 × 141 μm, spatial resolution (x,y) 0.07 μm. Four adjacent fields of view were scanned and cropped to an area of 242 × 181 μm.

MountainsMap (version V10, Digital Surf, Besançon, France) was utilised to process surface scans and generate both SSFA and areal texture parameters for DMTA (the latter mostly defined in ISO 25178). Our scan processing protocol in MountainsMap comprises: 1) levelling with least squares plane (LSPL) to correct surface inclination, 2) threshold application to eliminate the upper and lower 0.1% of data, 3) filling of non-measured point using the smooth shape calculated from neighbours function, 4) surface point retouching to manually edit dust and extraneous particles followed by filling of missing data points using the smooth shape calculated from neighbours function, 5) level again for generating SSFA parameters, 6) form removal with polynomial of degree 2 (7) spatial filtering (robust Gaussian, order 0 (ISO 16610-71) with a cut-off value of 0.025 μm) for generating ISO parameters.

Prior to statistical analysis, Shapiro–Wilk tests were used to assess normality within temporal groups. A substantial proportion of raw DMTA parameters were found to deviate from normality, particularly among ISO texture parameters. Log10-transformation markedly reduced non-normality across all parameter sets. Similar improvements were

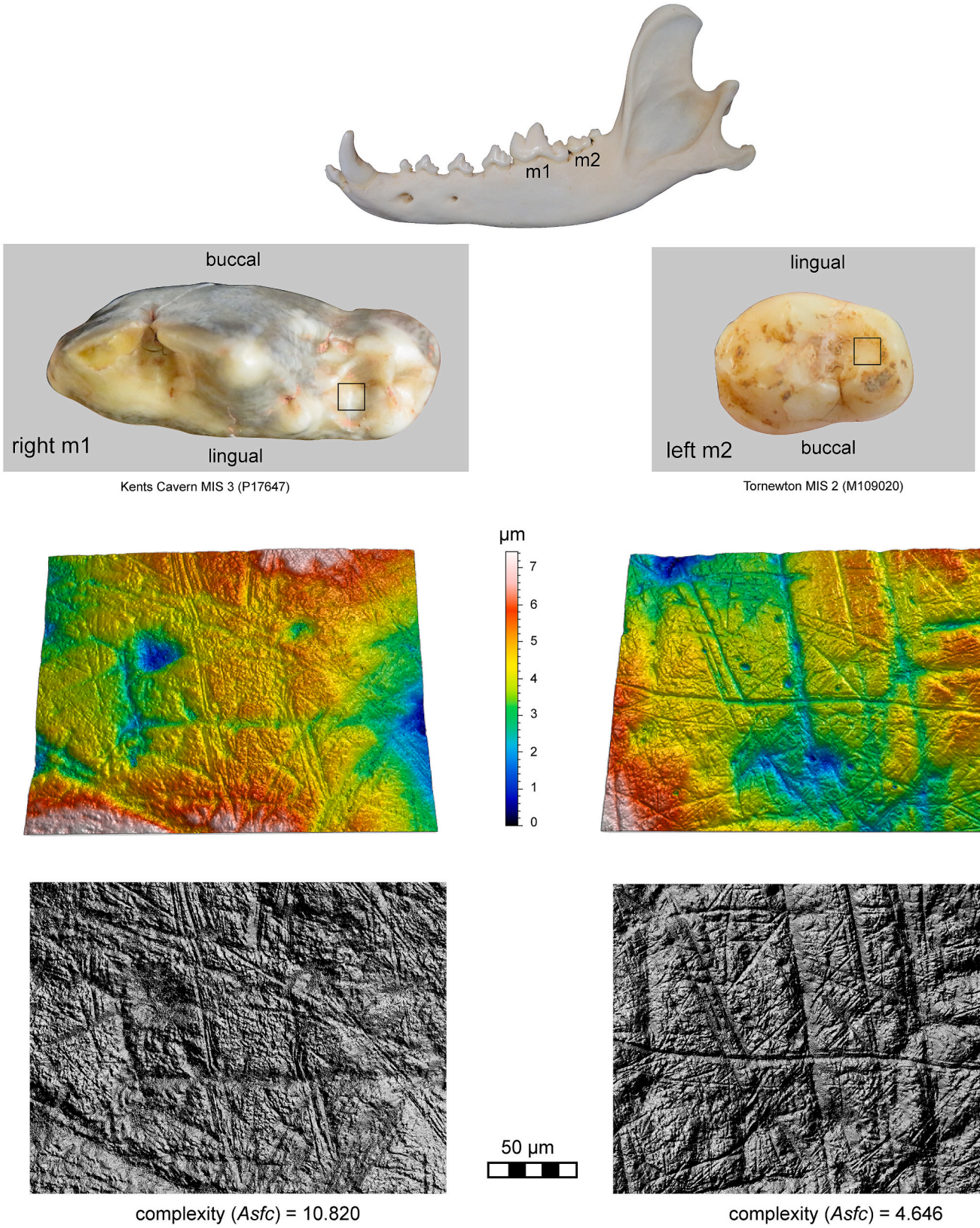

Fig. 2. DMTA sampling locations and illustrative examples of generally rougher and smoother tooth surfaces (e.g. complexity (Asfc and Sdr). Left wolf jaw, first and second molar labelled, areas of the tooth sampled on the m1 (talonid basin) and m2 (hypoconid cusp). Rendered scans of wolf tooth surfaces with topographic contouring, illustrating a range of values for complexity (Asfc), greyscale photo simulation of the same surface.

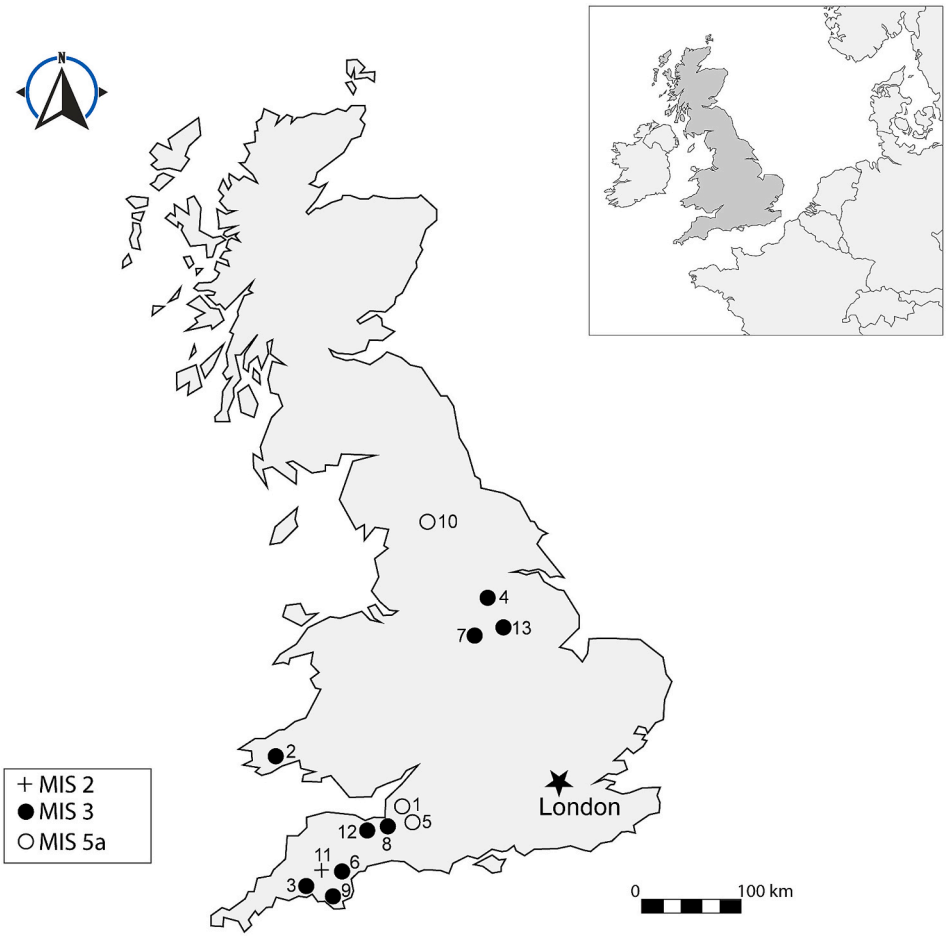

Fig. 3. Sampling sites for last glaciation fossil wolves in Britain: (1) Banwell Bone Cave, (2) Black Rock Quarry, (3) Cattedown Cave, (4) Church Hole, Creswell Crags, (5) Gully Cave, (6) Kents Cavern, (7) Pin Hole, Creswell Crags (8) Sandford Hill, (9) Sherford, (10) Stump Cross Cave, (11) Tornewton Cave, (12) Uphill, (13) Yew Tree Shelter. Further details given in Supporting Information Table S2.

observed for SSFA parameters, and log10-transformed data were used for subsequent parametric analyses. Anisotropy was quantified using NewEpLsar, which replaces epLsar following correction of a coding error in the original ToothFrax (Surfract Corp., Worcester, MA) software package (Calandra et al., 2021).

Exploratory analyses of variance (ANOVA) were conducted, with Tukey's HSD post hoc tests used to assess pairwise differences where results were significant. Parameters showing significant differences were then included in a principal components analysis (PCA) to explore multivariate structure. PCA has been demonstrated in previous studies to be an effective approach for analysing multivariate dental microwear texture data across a wide range of fossil and extant taxa and dietary regimes (e.g. Purnell et al., 2012, 2013; Gill et al., 2014; Winkler et al., 2019; Bestwick et al., 2020; Louail et al., 2026). PCA was used here to test the null hypothesis that temporal wolf groups do not differ in their dental microwear textures.

3. Results

Of the 85 ISO areal texture parameters examined, eight were found to differ significantly between temporal groups (ANOVA of log10-transformed parameters, $P < 0.05$; Table 1). These included Sal, Sdr, Svc, Svq, Shrn, Shff, Shar, and Sded, which describe aspects of surface complexity, vertical relief, spatial organization, and peak morphology. Complete results for all ISO areal texture parameters are provided in Tables S3–S7.

Tukey's HSD post hoc analyses (log10-transformed data) revealed significant differences between MIS groups for multiple ISO areal

Table 1
Descriptive statistics and ANOVA results for ISO 25178 areal texture parameters exhibiting significant differences among temporal groups. Values are reported as mean ± standard deviation. Superscript letters indicate results of Tukey's HSD post hoc comparisons; groups sharing a letter are not significantly different ($p < 0.05$). One-way ANOVA tests were performed on log10-transformed variables.

Parameter	MIS 2 ($n = 10$)	MIS 3 ($n = 14$)	MIS 5a ($n = 9$)	F(2,30)	p
Sal	7.22 ± 1.09^{a}	10.37 ± 3.52^{b}	8.98 ± 2.09^{ab}	4.16	0.025
Sdr	2.55 ± 0.31^{a}	3.42 ± 1.02^{b}	3.42 ± 0.65^{b}	4.42	0.021
Svc	-11.16 ± 2.53^{a}	-18.23 ± 7.66^{b}	-14.53 ± 5.65^{ab}	3.46	0.045
Svq	0.61 ± 0.11^{a}	0.90 ± 0.35^{b}	0.96 ± 0.34^{b}	5.14	0.012
Shrn	0.501 ± 0.021^{a}	0.478 ± 0.020^{b}	0.486 ± 0.010^{ab}	4.56	0.019
Shff	0.480 ± 0.027^{a}	0.447 ± 0.026^{b}	0.459 ± 0.023^{ab}	4.77	0.016
Shar	2.499 ± 0.157^{a}	2.663 ± 0.145^{b}	2.590 ± 0.062^{ab}	4.69	0.017
Sded	11.37 ± 1.09^{a}	9.82 ± 1.63^{ab}	9.48 ± 1.78^{b}	4.16	0.025

texture parameters, with the strongest and most consistent contrasts separating MIS 2 from the interstadial groups MIS 3 and MIS 5a (Table 1). Parameters associated with increased surface complexity, vertical relief, and broader spatial organization, including Sal, Sdr, Svq, and Shar, are generally higher in samples from interstadial intervals (MIS 3 and MIS 5a). In contrast, parameters describing finer-scale peak morphology, including Svc, Shrn, Shff, and Sded, are elevated in MIS 2.

Ten SSFA parameters differ significantly between temporal groups (ANOVA of log10-transformed parameters, $P < 0.05$; Table 2). Complete results for all SSFA parameters are provided in Tables S8–S12. Tukey's HSD post hoc analyses (log10-transformed data) revealed that, consistent with patterns observed in the ISO areal texture parameters, the strongest contrasts separated MIS 2 from the interstadial groups MIS 3 and MIS 5a (Table 2). Measures of surface complexity, including Asfc and associated summary statistics, are significantly higher in samples from interstadial intervals, indicating greater overall complexity and heterogeneity of enamel surface textures. Parameters describing the spatial organization of complexity, including Das, Lsfc, and Dls, are similarly elevated in samples from the interstadial intervals. Overall, MIS 3 and MIS 5a surfaces are characterized by higher and more heterogeneous surface complexity across spatial scales relative to MIS 2, whereas no significant differences are detected between the two interstadial groups for the DMTA parameters that quantify surface complexity.

For ease of comparison with previous SSFA-based DMTA, bivariate plots of Asfc versus NewEpLsar are presented as raw values rather than as log10-transformed data (Fig. 4). No significant differences in NewEpLsar were detected among temporal groups.

Principal components analysis (PCA) was performed on log10-transformed ISO areal texture and SSFA parameters to explore multivariate structure within the dataset. The first two principal components accounted for 68.8% of the total variance (PC1 = 53.7%; PC2 = 15.1%). PCA loadings for all parameters are provided in Table S13.

Samples were structured primarily along PC1 (Fig. 5a), with MIS 2 plotting predominantly at negative PC1 values and interstadial samples (MIS 3 and MIS 5a) shifted toward positive PC1 values. Separation between MIS 3 and MIS 5a was comparatively limited in PC1–PC2 space, indicating broadly similar multivariate texture signatures for the two interstadial groups. Loadings indicate that PC1 was primarily associated with increased surface complexity, roughness, and spatial organization, whereas PC2 reflected variation in complexity heterogeneity (Table S13). Overall, the PCA indicates that MIS 3 and MIS 5a exhibit greater surface complexity and roughness than MIS 2, which is characterized by finer-scale surface features.

To test the hypothesis that dietary behaviour differed between MIS groups, PC1 scores were subjected to a one-way ANOVA with MIS as the grouping factor. PC1 differed significantly among MIS groups ($F_{2,30} = 13.73$, $p < 0.001$), whereas PC2 did not differ significantly ($p > 0.05$). Tukey's HSD post hoc comparisons of PC1 scores indicate that MIS 2 differs from the others: scores for MIS 3 and MIS 5 are significantly higher than those for MIS 2 (respectively: $\Delta = 4.74$, $p < 0.001$; $\Delta = 4.36$, $p < 0.001$). PC1 scores for MIS 3 and MIS 5a did not differ from one another ($\Delta = 0.39$, $p = 0.92$). The distribution of PC1 scores for each MIS group is shown in Fig. 6.

4. Discussion

This study demonstrates that dental microwear textures in British grey wolves vary systematically across major climatic divisions of the last glaciation, reflecting shifts in feeding behaviour in response to changing environmental conditions.

Wolves from the Last Glacial Maximum (Dimlington Stadial; MIS 2), the most extensive phase of the last Devensian glaciation exhibit consistently lower surface complexity and roughness. In contrast, individuals from interstadial intervals MIS 3 and MIS 5a show significantly more complex enamel textures and greater variability. Multivariate analyses make this clear, with MIS 2 specimens occupying distinct regions of texture space, and significantly different PC1 values, relative to interstadial populations (Figs. 5 and 6). Together, these results indicate that wolf feeding strategies were closely coupled with climatic context, supporting the hypothesis that dietary flexibility underpinned the long-term persistence of this keystone predator in Late Pleistocene Britain.

During the Last Glacial Maximum of the Devensian glaciation (taken either as approximately 27–23,000 cal years BP following Clark et al. (2012) or c. 23–19,000 cal years BP by Mix and Bard, 2001), the British-Irish Ice Sheet (BIIS) extended over the whole of Scotland and Ireland, most of Wales and across the northern counties of England, edging down to the coast of north Norfolk (Clark et al., 2004). Although lying south of the limits of the BIIS, the immediate environs of Tornewton Cave in Devon would have been subject to periglacial conditions with permafrost (Gilbertson and Hawkins, 1978) and extremely cold winters. Continuation of lowered global sea levels at this time and maintenance of the land bridge across the southern North Sea basin further acted to enhance cold stage continentality (Clark et al., 2004). Quantitative palaeotemperature estimates for this period, based on coleopteran records, are not possible because of the limited record and extremely species-impoverished insect assemblages. However, Coope et al. (1971) reported an insect fauna from the type-site of Dimlington in East Yorkshire that was exclusively composed of arctic-alpine species and those tolerant of very low summer temperatures. They concluded that only the most cold-hardy species were able to survive this harsh climate and proposed mean summer temperatures well below 10 °C, considerably lower than for earlier parts of the last cold stage.

Mammalian faunal remains from this period are equally sparse, with Currant and Jacobi (2011) reporting only arctic hare (*Lepus timidus*), red fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), woolly mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*), an undetermined large cervid and musk ox (*Ovibos moschatus*) from their Dimlington Stadial Mammal Assemblage-Zone, together with modern human (*Homo sapiens*). The Glutton Stratum at Tornewton Cave has further yielded remains of lion (*Panthera spelaea*), as well as wolverine (*Gulo gulo*), after which the level was named; the latter have been radiocarbon dated to

Table 2
Descriptive statistics and ANOVA results for SSFA parameters exhibiting significant differences among temporal groups. Values are reported as mean ± standard deviation for raw variables. Superscript letters indicate results of Tukey's HSD post hoc comparisons; groups sharing a letter are not significantly different ($p < 0.05$). One-way ANOVA tests were performed on log10-transformed variables.

Parameter	MIS 2 (n = 10)	MIS 3 (n = 14)	MIS 5a (n = 9)	F(2,30)	p
Fractal complexity (Asfc)	6.27 ± 1.01^{a}	8.86 ± 2.13^{b}	8.80 ± 1.28^{b}	8.997	<0.001
Mean Asfc	14.05 ± 2.22^{a}	20.65 ± 5.58^{b}	20.32 ± 3.42^{b}	8.600	0.001
Median Asfc	13.67 ± 2.65^{a}	19.13 ± 5.55^{b}	19.96 ± 3.99^{b}	6.552	0.004
Standard deviation of Asfc (StdDevAsfc)	2.82 ± 0.82^{a}	6.76 ± 3.58^{b}	5.48 ± 1.90^{b}	11.265	<0.001
Median absolute deviation of Asfc (MadAsfc)	1.57 ± 0.91^{a}	3.99 ± 2.00^{b}	3.12 ± 1.75^{b}	8.680	0.001
Heterogeneity of Asfc (HAsfc)	0.173 ± 0.066^{a}	0.294 ± 0.148^{b}	0.227 ± 0.084^{ab}	4.207	0.025
Fractal dimension (Das)	2.013 ± 0.002^{a}	2.018 ± 0.004^{b}	2.018 ± 0.003^{b}	8.485	0.001
Fractal complexity (Lsfc)	4.62 ± 0.24^{a}	6.35 ± 0.45^{b}	6.52 ± 0.35^{b}	8.499	0.001
Fractal dimension (Dls)	1.0046 ± 0.0002^{a}	1.0063 ± 0.0005^{b}	1.0065 ± 0.0003^{b}	6.623	0.004

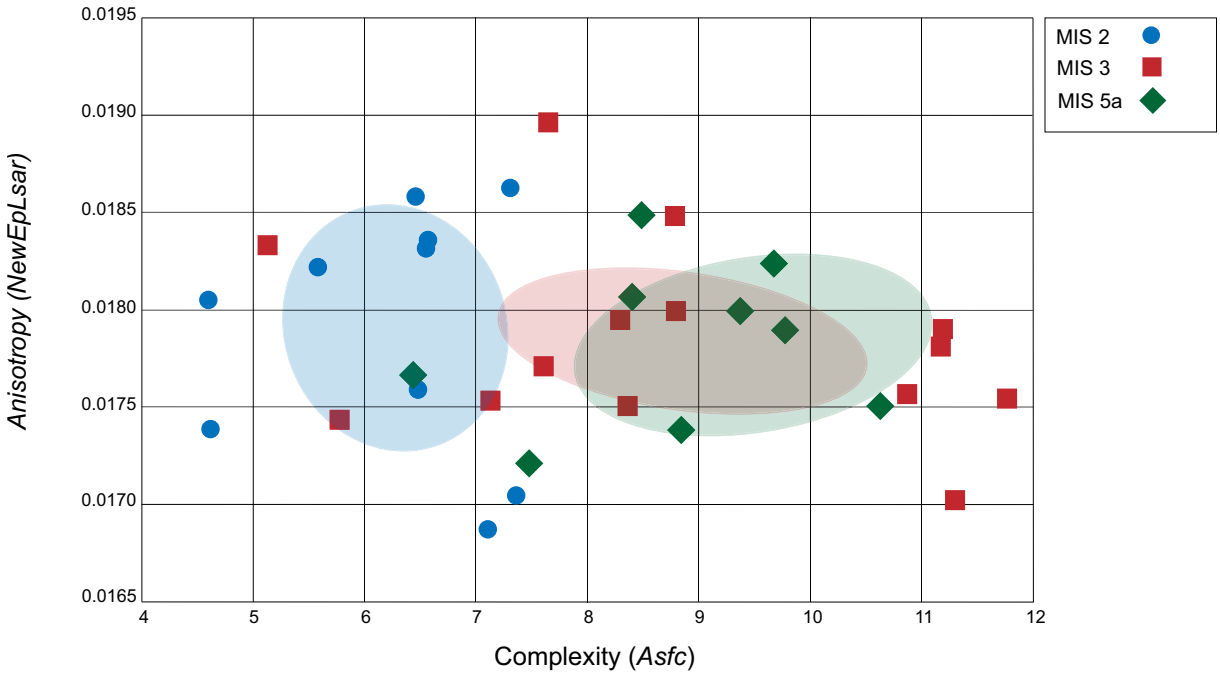

Fig. 4. Bivariate plot of raw Asfc versus NewEpLsar values. Raw variables are shown to maintain consistency with traditional DMTA visualizations; statistical analyses were conducted on log10-transformed data. Ellipses represent 95% confidence regions for group means. Significant differences between temporal groups were observed for complexity (Asfc), whereas anisotropy (NewEpLsar) did not differ significantly between groups.

22,160 ± 460 yr BP (OxA-4587) (Currant, 1996). The occurrence of obligate cold-adapted taxa with high latitude distributions today, such as reindeer, musk ox and wolverine, attest to the presence of extreme cold conditions and significant snow cover.

Although no pollen records exist for this period in Britain, the continuous peat bog sequence from La Grande Pile in north-eastern France serves as a useful reference point for north-west Europe at this time. The pollen spectra from the MIS 2 levels reveal the highest values for *Artemisia* and Poaceae in the Late Pleistocene, denoting cold, dry and open conditions (Woillard, 1978). At the same time, the coleopteran assemblage records the disappearance of the entire tree-dependent beetle fauna and the appearance of several high Arctic-alpine species that are restricted today to northern Europe, Fennoscandia and the circumpolar regions of Russia, mostly above the treeline (Ponel, 1995).

Wolves from MIS 2 display microwear textures consistent with limited durophagous activity. This pattern aligns with palaeoecological expectations for the Last Glacial Maximum, when deep and persistent snow cover increased prey vulnerability by restricting movement and access to forage. Under such conditions, wolves are more likely to secure fresh kills and to preferentially consume soft tissues, reducing the need for intensive carcass processing (Jędrzejewski et al., 2002; Mech and Peterson, 2003). A comparable relationship between prey vulnerability and dental microwear texture has also been documented in modern North American wolf populations (Burtt and DeSantis, 2022). The microwear signal from MIS 2 specimens therefore suggests that British wolves during the Last Glacial Maximum engaged in less intensive durophagous behaviour than wolves from other climatic intervals, likely reflecting favourable hunting conditions despite the severe cold and overall environmental harshness.

In contrast, wolves from the Middle Devensian (MIS 3) exhibit the broadest range of microwear texture values, indicating substantial heterogeneity in feeding behaviour at this time. The broad range of microwear textures observed in MIS 3 wolves may partially reflect the greater spatial and temporal breadth of the sampled material, as this interval encompasses a larger number of localities and a longer duration than either MIS 2 or MIS 5a. However, MIS 3 was also characterized by repeated climatic oscillations that produced substantial environmental heterogeneity across Britain. Consequently, the elevated dietary variability observed in MIS 3 wolves is consistent with a population responding to fluctuating ecological conditions, although the contribution of increased spatial and temporal sampling cannot be entirely excluded. Although radiocarbon dates are available on faunal material from many of the MIS 3 study sites (e.g. Jacobi et al., 2006), individual wolf remains cannot be definitively attributed to a particular stadial or interstadial, given the level of dating precision presently achievable at 95.4% confidence levels. Nevertheless, some key points can be made about palaeoclimates and palaeoenvironments at this point, which allow the variation in dental microwear results to be contextualised. MIS 3 was overall relatively warmer compared to both the Early and Late Devensian but the climate was subject to rapid and abrupt, often millennial-scale oscillations, resulting in a succession of warmer interstadials and cold stadials (Rasmussen et al., 2014). This climatic variability has led to the reconstruction of a range of mean July temperatures, between 8 °C and 17 °C, and of winter temperatures between −4 °C and − 22 ± 10 °C (Coope et al., 1971; Schreve et al., 2013).

The landscape in Britain at this time is regarded as part of the 'Mammoth Steppe' (Guthrie, 1990), a non-analogue steppe-tundra biome, extending from northern Eurasia into North America. The 'Mammoth Steppe' was significantly drier, with increased evaporation, higher seasonality and deeper summer thaws, compared to the tundra today (Guthrie, 1990). A combination of climatic controls on the growth of woody plants and the grazing and dunging activity of millions of large herbivores, including woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), horse (*Equus ferus*) and bison (*Bison priscus*) consequently led to the development of rich, open grasslands (Zimov et al., 2012). Although high in biodiversity, this was a notably dry environment with low snow cover. Estimates of annual precipitation for the 'Mammoth Steppe' range from 150 to 300 mm (Velichko and Zelikson, 2001; Zimov et al., 2012), rather less than experienced (for example) in the modern short-grass steppe of the Great Plains of North America (mean 310 mm, range 115-595 mm; Milchunas et al., 1989).

The range of surface relief and roughness values observed in British fossil wolves from this interval (MIS 3) likely reflects fluctuating reliance

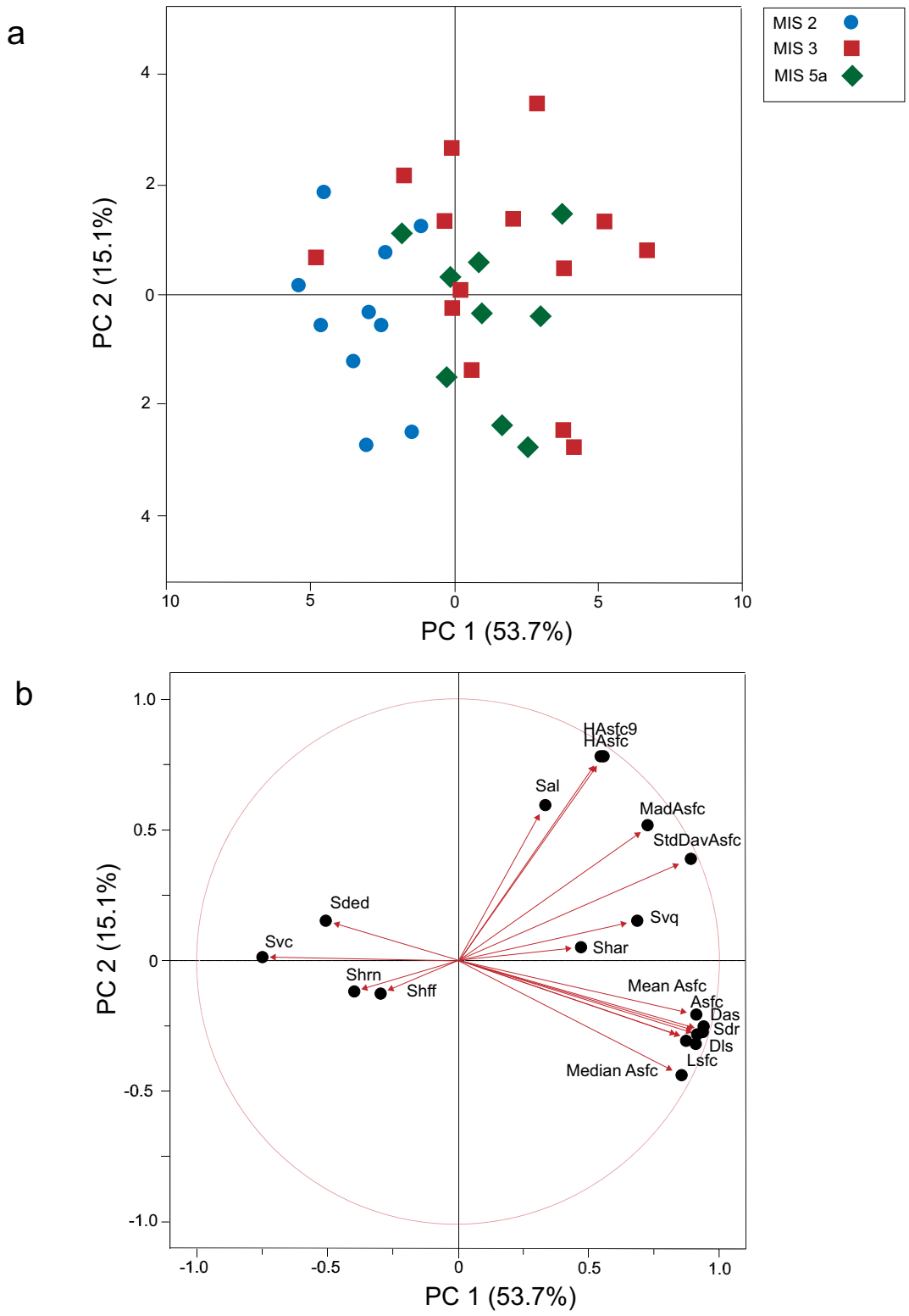

Fig. 5. Principal components analysis (PCA) of combined ISO and SSFA texture parameters. (A) Scores plot showing primary separation of MIS 2 from interstadial samples (MIS 3 and MIS 5a) along PC1 (53.7% of variance), with limited separation between MIS 3 and MIS 5a. (B) Loadings plot indicating that PC1 is driven by higher surface complexity and broader spatial organization, whereas PC2 captures secondary variation related to complexity heterogeneity.

on fresh kills versus carcass processing and scavenging, driven in large part by climatic oscillations and snow conditions. Such variability is consistent with a flexible foraging strategy, enabling wolves to respond rapidly to short-term environmental change (Mech and Frenzel, 1971; Sidorovich et al., 2017). During interstadial summers, a wide range of insect and plant foods would also have been available, with MIS 3 sites in Britain yielding abundant remains of invertebrates and berries, such as bilberry (*Vaccinium* spp.) and crowberry (*Empetrum nigrum*) (e.g. Boismier et al., 2003; Buckland et al., 2019), which are commonly consumed by grey wolves today (Gade-Jørgensen and Stagegaard,

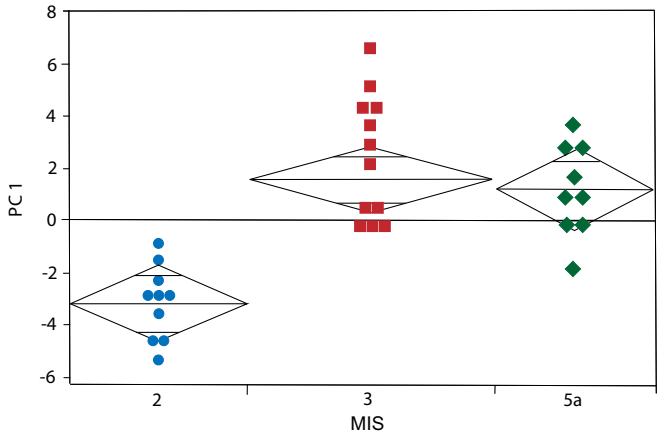

Fig. 6. Principal component 1 (PC1) scores by Marine Oxygen Isotope Stage (MIS). Points represent individual specimens, and diamonds show group means with 95% confidence intervals. MIS 2 exhibits significantly lower PC1 scores than MIS 3 and MIS 5a, whereas MIS 3 and MIS 5a do not differ significantly.

2000).

Other factors, such as enhanced interspecific competition, may also be influential at this time. For example dietary stable isotope analysis (^{13}C, ^{15}N) on MIS 3 wolves from Britain has revealed that they were consuming horse, woolly rhinoceros and steppe bison, and were in direct competition for resources with spotted hyaena (*Crocuta crocuta*) (Flower et al., 2021). Such competition was not the case later in MIS 2, since the spotted hyaena was already extinct in Britain (Stuart and Lister, 2014). While the climatic oscillations during MIS 3 would have influenced the abundance, body condition and spatial distribution of wolf prey at the local scale, the need to process carcasses more intensely may have been further exacerbated by prey species becoming rarer in the landscape. Abrupt climate change not only impacted habitats but also fragmented populations and ranges, leading ultimately to the widespread extirpation or indeed complete extinction of many prey taxa across western Europe (Lister and Stuart, 2008; Brace et al., 2012; Davoli et al., 2024). Rather than representing a single dietary mode, MIS 3 wolves appear to have occupied a dynamic space, shaped by episodic shifts in prey vulnerability and resource predictability.

Wolves from the MIS 5a interstadial show a pattern similar to that of MIS 3, but with a narrower range of values representing surface roughness. Compared to the MIS 2 age group, they show elevated surface complexity, reflecting more intensive or more frequent processing of hard food items. Again, similar environmental factors may be invoked to explain these patterns. MIS 5a was an interstadial in the early Devensian but is characterized by a low diversity mammalian fauna in Britain more reminiscent of cold-climate periods. Reindeer and steppe bison are the only two ungulate species, with wolf and brown bear the only two large carnivores present (e.g. Scott, 2018). This faunal grouping is thought to have entered Britain across the southern North Sea basin land bridge during a preceding cold stadial (MIS 5b) and to have become trapped by high sea level in the ensuing interstadial (Currant and Jacobi, 2011). Palaeoenvironmental records from MIS 5a age deposits in Britain indicate the presence of coniferous trees, including abundant *Pinus* (pine), with *Picea* (spruce) and *Abies* (silver fir) and smaller numbers of thermophiles such as *Quercus* (oak). Grasses and sedges are also well represented (Maddy et al., 1998). The overall picture of the vegetation is thus one of open woodland of boreal Fenno-scandian character. Mean temperatures were reconstructed as 17 °C -18 °C in summer and − 4 °C to +4 °C in winter (Maddy et al., 1998), similar to southern England today.

During warmer climate periods, reduced snow cover and improved prey condition are expected to lower hunting success, encouraging greater reliance on scavenging and more complete carcass utilization (Huggard, 1993; Post et al., 1999; Vucetich et al., 2012; Gable et al., 2024). Flower and Schreve (2014) observed a high proportion of broken and severely worn teeth in MIS 5a wolves from across Britain. Binder et al. (2002) concluded that increased tooth fracture and wear in groups of Late Pleistocene *Aenocyon dirus* (dire wolf) from Rancho La Brea (USA) reflected high levels of competition in a resource-limited environment and, particularly, an increase in the need to consume carcasses quickly and completely. Although elevated DMTA complexity values are often interpreted as evidence of increased carcass utilization and durophagy, this relationship is not necessarily accompanied by increased tooth fracture or wear. For example, wolves from the Last Interglacial (MIS 5e) of Britain exhibit similarly high complexity values but do not display the extensive tooth breakage observed in MIS 5a populations (Burtt et al., 2026). This suggests that elevated complexity alone cannot fully explain the pattern of dental damage in MIS 5a wolves. Additionally, because DMTA requires preserved wear facets, individuals with the most severely damaged teeth may be underrepresented.

The ecological context of MIS 5a (compared to 5e) in Britain differs substantially, with grey wolves facing relatively limited competition from other large carnivores. Instead, the unusually low diversity of available herbivore prey may have promoted more intensive carcass utilization, potentially increasing tooth wear and fracture independently of overall levels of complexity of tooth surface roughness. While recent evidence has challenged previous assumptions that steppe bison were migratory (Julien et al., 2012), migratory behaviour characterises many modern reindeer populations (Gunn, 2016) and has also been documented in Pleistocene reindeer (e.g. Britton et al., 2011). The seasonal absence of reindeer herds may therefore have limited resources for wolves in MIS 5a environments, leading to enhanced carcass utilization. Warmer interstadial conditions may also have increased the availability of alternative food resources, including plant matter and invertebrates, although the contribution of such resources to the observed microwear patterns remains uncertain.

Evidence from other Pleistocene carnivores suggests that dietary responses to climatic change were not uniform. Stable isotope analyses of extinct species of *Canis* and *Smilodon* by Feranec and DeSantis (2014) revealed shifts in prey preferences and trophic interactions between glacial and interglacial settings, indicating that environmental change altered resource use within carnivore communities. However, the magnitude of dietary change differed between taxa: populations of *Canis edwardii* exhibited broadly similar dietary patterns across temporal groups, whereas *Smilodon gracilis* showed greater variation in prey use and habitat associations. The results presented here further suggest that DMTA is capable of detecting fine-scale variation in wolf feeding behaviour associated with climatic change, providing insight into ecological responses that may not be evident from broader measures of resource use alone.

In summary, the observed microwear patterns highlight the capacity of grey wolves to adjust their feeding strategies rapidly in response to changing circumstances. This behavioural plasticity likely played a critical role in the persistence of wolves through the pronounced climatic volatility of the last glaciation in Britain. In particular, our results have highlighted the distinctiveness of Last Glacial Maximum wolves, which exhibit significantly lower dental microwear textural complexity than wolves from other climatic intervals. We interpret this as indicating reduced durophagous behaviour and less intensive processing of hard food items, facilitated by extremely cold conditions and extensive snow cover that rendered prey more vulnerable. In contrast, wolves from the Middle Devensian demonstrate the widest spectrum of palaeodietary behaviours, revealed by a broad range of complexity values in their dental microwear textures. The limitations of chronological control mean that it is unfortunately not possible to attribute individual wolf specimens to discrete climatic episodes within MIS 3 and thereby to make a precise comparison between the dental microwear signatures of wolves from stadials or interstadials. However, a combination of rapid

and abrupt climate change, as well as competition from a more diverse large carnivore guild, likely acted to enhance carcass consumption behaviour, especially during warm interstadials with reduced snow cover, compared to MIS 2. The complexity values of wolves from the MIS 5a interstadial nest within the spread of MIS 3 data but are clustered toward the higher end of the complexity spectrum. Again, the palaeoclimatic characteristics of this warm interstadial may have been a powerful driving force in determining wolf palaeodietary behaviour, with the limited herbivore spectrum and seasonal availability of resources contributing to high complexity values. Integrating DMTA with palaeoecological and palaeoclimatic evidence thus offers a powerful framework for assessing the tempo and mechanisms of ecological resilience in large carnivores and particularly, for identifying and indeed predicting periods of dietary stress. Incorporating fossil data from periods with different climatic and environmental parameters consequently provides a vital fresh perspective into how grey wolves may respond to current and future climate change.

CRediT authorship contribution statement

Amanda A. Burtt: Visualization, Methodology, Investigation, Formal analysis, Data curation, Writing – review & editing, Writing – original draft. **Mark A. Purnell:** Investigation, Formal analysis, Writing – review & editing, Writing – original draft. **Angela L. Lamb:** Visualization, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Writing – review & editing. **Danielle C. Schreve:** Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2026.114120.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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