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Title: Tracking late-Quaternary extinctions in interior Alaska using megaherbivore bone remains and dung fungal spores

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ABSTRACT

One major challenge in the study of late-Quaternary extinctions (LQEs) is providing better estimates of past megafauna abundance. To show how megaherbivore population size varied before and after the last extinctions in interior Alaska, we use both a database of radiocarbon-dated bone remains (spanning 25-0 ka) and spores of the obligate dung fungus, *Sporormiella,* recovered from radiocarbon-dated lake-sediment cores (spanning 17-0 ka). Bone fossils show that the last stage of LQEs in the region occurred at about 13 ka ago, but the number of megaherbivore bones remains high into the Holocene. *Sporormiella* abundance also remains high into the Holocene and does not decrease with major vegetation changes recorded by arboreal pollen percentages. At two sites, the interpretation of *Sporormiella* was enhanced by additional dung fungal spore types (e.g. *Sordaria*). In contrast to many sites where the last stage of LQEs is marked by a sharp decline in *Sporormiella* abundance, in interior Alaska our results indicate the continuance of megaherbivore abundance, albeit with a major taxonomic turnover (including *Mammuthus* and *Equus* extinction) from predominantly grazing to browsing dietary guilds. This new and robust evidence implies that regional LQEs were not systematically associated with crashes of overall megaherbivore abundance.

Key words (10): Beringia, paleoecology, megafauna, herbivore, *Sporormiella*, *Sordaria*, coprophilous fungal spores, fossil, late glacial maximum, transition

INTRODUCTION

Late-Quaternary megafaunal extinctions (LQEs) occurred during a period of global, time-transgressive extinctions that selectively affected megafauna (terrestrial vertebrates weighing >44kg) from 50 to 4 ka (Koch and Barnosky, 2006; Stuart, 2015). The causes and consequences of this are still extensively debated (Johnson, 2009; Gill, 2014; Sandom et al., 2014; Hempson et al., 2015; Malhi et al., 2016; Rabanus-Wallace et al., 2017; Galetti et al., 2018). In several regions of the world, such as Australia and North America, LQEs appear approximately synchronous with human colonisation events; however, direct causality remains uncertain (e.g. Johnson, 2009; Broughton and Weitzel, 2018). Current research is actively exploring the consequences of LQE for ecosystem functioning and biodiversity. For example, the loss of key megaherbivores has been linked to changes in fire regimes (Gill, 2014), differences in nutrient cycling (Doughty et al., 2013) and dispersal limitation in certain plant species (Peres et al., 2016). Understanding both the causes and consequences of past megafaunal extinctions is important because extant megafauna is under threat of extinction today and is a strong focus of global nature conservation efforts.

One critical challenge in the study of LQEs is a better understanding of past megafauna abundance (Bradshaw et al., 2003). Past distribution of megaherbivores is typically researched using radiocarbon-dated and identified bone remains recovered from, for example, archaeological sites, sedimentary deposits and caves. The main weaknesses of this evidence is that, to be compelling in terms of abundance, it needs to be based on extremely comprehensive collections as it focuses on presence of animal remains; absence of evidence cannot be taken as evidence of absence (Stuart, 2015). For example, low abundance may be undetected when using bone remains alone and can be mistaken for extinction events (Haile et al., 2009).

A useful methodology to address the presence/absence and abundance of megafauna uses the abundance of dung fungal spores along with fossil pollen recovered from sedimentary archives (Davis and Shafer, 2006; Gill et al., 2013; Baker et al., 2016). This method focuses on spores of ascomycete fungi whose life cycle is fully reliant on vertebrate herbivores and whose presence in sediments are consequently interpreted as compelling evidence for the presence of megaherbivores (van Geel et al., 2003; Davis and Shafer, 2006; Baker et al., 2013; Johnson et al., 2015). The spores produced during sexual reproduction are unintentionally ingested by megaherbivores while grazing. They subsequently germinate after digestion when deposited with dung. Depending on local conditions, such as moisture levels and temperature within the deposited dung, successful mycelium growth and fructification release explosively sticky spores onto surrounding vegetation, ready to be ingested. Some spores do not complete their biological cycle and are lost into the environment. A fraction of these lost spores will be integrated into sedimentary archives after transportation by turbulent air (Gill et al., 2013), water flow (Etienne et al., 2013) or slope run-offs (Baker et al., 2016). Despite the promise of this approach, there are some weaknesses, including the reliance on sampling sites such as lakes and bogs that may not be representative of the landscape. In addition, many studies using dung fungal spores rest on the identification of *Sporormiella* spores and do not include other types of dung fungal spores such as *Sordaria* and *Podospora* (Baker et al., 2013; Perrotti and van Asperen, 2019).

Radiocarbon-dated bone collections and dung fungal spores are complementary archives but are rarely applied together. However, there is the potential to develop such an approach where bone and spore results are directly compared, when the geographical relevance of both proxies is understood, for example, on islands (Graham et al., 2016) and in other isolated regions.

In North America, LQEs were particularly severe, with 69% of megafauna species greater than 45 kg going extinct before the onset of the Holocene (Stuart, 2015). Most species survived until the Pleistocene-Holocene transition (14-10 ka) and dramatic megaherbivore losses, in terms of abundance, have been identified using *Sporormiella* at sites across North American (excluding east Beringia) at about 14 ka (Robinson et al., 2005, Davis and Shafer, 2006, Gill et al., 2009, Perrotti et al., 2018).

In northern Alaska and north-eastern Siberia, bone collections have been used to estimate temporal changes in faunal communities. Using a large database of radiocarbon-dated megaherbivore remains from the Alaska North Slope, Mann et al. (2013) suggest that between 45 and 10 ka there were 6 times more individuals and 30 times greater biomass of megaherbivores than at present. Dominant taxa were chiefly *Mammuthus* (mammoth), *Equus* (horse) and *Bison* (bison or buffalo), now extinct in the region (apart from reintroduced bison). Similar values have been calculated by Zimov et al. (2012) for north-eastern Siberia, but it is not clear how far these estimates can be extrapolated to other northern regions, such as that of interior Alaska (i.e., the unglaciated region between the Brooks and Alaska Ranges, Fig. 1).

Conditions at high latitudes such as those of interior Alaska were unusual in the last glacial phase because the megafauna inhabited a biome that now has no modern analogue, often termed the ‘mammoth-steppe’ (Guthrie, 1968; Guthrie, 1982; Williams and Jackson, 2007) or ‘steppe-tundra (Anderson et al. 2004). Paleobotanical records indicate vegetation was dominated by herbs (e.g. *Cyperaceae*, *Poaceae*, *Artemisia* and other forbs), with only a minor component of trees and shrubs (*Larix*, *Betula, Salix;* Anderson et al. 2004; Zazula et al., 2007; Gaglioti et al., 2011; Willerslev et al., 2014). Moreover, the palaeo-geography of Alaska was unusual. During the late-glacial maximum, northern and interior Alaska were biologically isolated from the rest of America until the opening of an inland ice-free corridor between the Laurentide and the Cordilleran ice sheets along the eastern slopes of the Rocky Mountains (Kitchen et al., 2008). The estimated date at which the corridor opened and permitted megaherbivore exchange between interior Alaska and the rest of North America varies between 13.4 ka (Heintzman et al., 2016) and 12.6 ka (Pedersen et al., 2016).

In contrast with the southern part of the continent, in Alaska there appear to have been staggered extinctions similar to those observed in Eurasia (Stuart, 2015), Including an *Equus* species (‘hemione-like’ ass) prior to the last glacial maximum (Guthrie, 2003). The last stage of LQEs in Alaska happened during the Pleistocene-Holocene transition and saw the loss of other species of *Equus* (caballine horses), *Mammuthus*, and *Saiga* (Saiga antelope). Evidence from the North Slope and Fairbanks region has provided an estimate of temporal change in megafaunal abundance in the region around the last stages of the LQE but this is based exclusively on an extensive collection of radiocarbon dated bones (Mann et al., 2013).

The combination of *Sporormiella* records and bone data that we use here promises a more robust estimate of change in animal numbers. Our main aim is to study changes in population size and diversity of megaherbivores in interior Alaska across the final stage of LQEs (i.e. the last extinctions believed to have occurred by about 13 ka, Stuart, 2015). We hypothesise that the faunal loss during the final stage of the LQE in interior Alaska was associated with a sharp reduction in total population size across all megaherbivores, as indicated by *Sporormiella* and changes in vegetation cover. Our objectives are as follows:

1. Identify the timing of the last extinctions by compiling a database including all existing, spatially-explicit, radiocarbon-dated megaherbivore bone remains in the region.
2. Assess if three new *Sporormiella* spore records from interior Alaska have different *Sporormiella* spore accumulation rates before and after the last extinctions (as defined in 1).
3. Examine the temporal sequences of 1 and 2 in relation to increasing dominance of woody vegetation across the Pleistocene-Holocene transition (based on existing dated pollen records) to assess any systematic signs of correlation between megaherbiore abundance and tree cover.

The second aim is to compare records of *Sporormiella* and other obligate dung fungal spores to improve the interpretation of dung fungal spore records in this study and in future studies. *Sporormiella* records have been shown to be informative in their own right but they could be improved by extending identification to a wider range of spore types. Here, our objectives are to:

1. Use a wider range of dung fungal spores, such as *Sordaria* and *Podospora* to assess the added interpretative values of these spore types; and
2. Compare the spore record at two nearby sites to assess the local variation of dung fungal spore records.

MATERIALS AND METHODS

Faunal remains database

Geo-located and radiocarbon-dated megaherbivore bone remains from Alaska and the Yukon dated 25,000 calibrated ^{14}C years BP or younger were compiled from relevant published work (Guthrie, 2006; Campos et al., 2010; Lorenzen et al., 2011; Martindale et al., 2016; Meiri et al., 2013; Mann et al., 2013). This time range was chosen to cover a long period before and after the last stage of LQEs. This database approach provides the most comprehensive knowledge of the past distribution of megaherbivores in the region to date and includes the taxa: *Mammuthus*, *Equus*, *Saiga*, *Bison*, *Alces* (moose or elk in British English), *Ovibos* (muskox), *Rangifer* (caribou, or reindeer in British English) and *Cervus* (elk or red deer in British English). Records of exceptional Holocene survival of *Mammuthus* on St Paul Island (Graham et al., 2016) were excluded.

The dated megaherbivore bone remains are drawn from very large collections of bones made over more than a century, and both the original collecting and the selection of bones for dating were made largely without regard to stratigraphic context, as they were surface finds made opportunistically on river bars and point bluffs (Guthrie, 2006, Mann et al., 2013). In this respect, the dates are a near-random reflection of faunal remain presence or absence in space and time. Importantly, although species composition changes dramatically, the overall record of bone dates is almost continuous through the study period. In addition, the geographical distribution of bone remains is widespread across Alaska and the western Yukon (Fig. 1A). This supports the assumption that the rise and decline of remains for individual taxa in our database is likely to be a reflection of past population dynamics.

All dates were made on bone or tooth collagen and 95% (519 out of 546) were obtained by Accelerator Mass Spectrometry (AMS) (Supplementary Table 2). Further confidence in the dating is provided by their permafrost and/or anaerobic context, which maximises endogenous collagen preservation and limits diagenesis (Guthrie, 2006, Mann et al., 2013). Although ultrafiltration and hydroxyproline dating can increase accuracy (Kosintsev et al., 2019), even in permafrost-preserved bones (Zazula et al., 2017), this mostly affects specimens dated to >25 ka, beyond the range of the present study. Raw radiocarbon age determinations were calibrated using IntCal13 in OxCal (Reimer et al., 2013) and all ages are presented as thousands of calibrated ^{14}C years before present (ka).

Coring sites, pollen and fungal spores

Four lakes in interior Alaska, Jan Lake, Windmill Lake, Ruppert Lake and Woody Bottom Pond, were cored. Table 1 summarises site characteristics, coring years and original publications for core chronologies, while the location of each lake is mapped in Figure 1. Jan Lake's basin (Fig. 1B) is formed by an alluvium dam from the Tanana River and its watershed characterised by metamorphic bedrock hills, with no major inlets. The surrounding vegetation is spruce, birch and aspen forest. Windmill Lake (Fig. 1C) lies in a closed moraine-dammed basin with no major inlets. It is surrounded today by open sedge tussock vegetation with willow and nearby birch and spruce. Ruppert Lake (Figs. 1D, 1E) is a kettle lake on a terminal moraine. It has one inlet, one outlet and the surrounding forest is dominated by spruce, aspen, birch and willow. Woody Bottom Pond (Figs. 1E, 1F) is another kettle lake situated in close proximity (about 650m) to Ruppert Lake. It has no inlet and is located in a bowl-shaped depression, surrounded by a well-drained moraine ridge. The lake is fringed by sedges, peat mosses and spruce trees, while the surrounding slopes support shrub birch and aspen. All four lakes are located at similar elevations and have similar surface areas of open water (Fig. 1, Table 1).

To study changes in population size and diversity of megaherbivores (first aim), we counted *Sporormiella* spores and pollen from the same samples. Samples were prepared for pollen analysis from 1cm^3 of wet sediment using a standard method outlined in Moore et al. (1991). Pollen and spores were identified at 400x and 1000x magnification. In order to maximise reliability, we counted a minimum of 300 pollen grains (Willis and Bennett, 2001) and *Sporormiella* spores observed during pollen counting were identified and counted. In order to calculate pollen and spore concentrations and accumulation rates, an exotic marker, i.e. a known number of *Lycopodium annotinum* spores, was added to the samples during the laboratory procedure (Wood and Wilmshurst, 2013). *Lycopodium annotinum* spores tablets were provided by Lund University and the tablet batch number for each sample is included in Supplementary Table 1. Identification of dung fungal spores was based on resources listed in Baker et al. (2013). Figure 2 was created using the programme C2 v 1.3 (Juggins, 2007) and the R package Beeswarm (Eklund, 2016). At two sites, Ruppert Lake and Woody Bottom Pond, we also extended spore identification to other dung fungal spores (including *Sordaria* and *Podospora*) commonly reported in the literature (e.g. van Geel et al., 2003) (second aim).

RESULTS

Faunal remains database

Records of 546 georeferenced and radiocarbon-dated megaherbivore fossils from Alaska and the Yukon were collated (Fig. 1; Supplementary Table 2). The most numerous megaherbivore genera for the study period (25 ka to present) were *Equus* (n = 108), followed by *Rangifer* (n = 95), *Alces* (n = 93), *Mammuthus* (n = 85), *Cervus* (n = 69), *Bison* (n = 63), *Ovibos* (n = 26) and finally *Saiga* (n = 7). Taken at face value, temporal distribution of dated radiocarbon megaherbivore remains indicates that *Mammuthus* and *Equus* were dominant until about 16-15 ka, when *Bison* and *Cervus* numbers increased (Fig. 2). Following the extinction of *Mammuthus* and *Equus* at about 13 ka, and subsequently during the Holocene, *Alces* was dominant, with *Rangifer* increasing in number from the mid-Holocene. We consider the marked regional turnover of megaherbivore dominant taxa around 13 ka indicating the last stage of the LQE in interior Alaska.

The small proportion of bones dated by gas counting (i.e. pre-AMS) do not affect this result: they comprise pre-15 ka *Equus*, *Bison* and *Mammuthus*, Holocene *Rangifer*, *Alces* and *Ovibos*, and three *Bison* in the range 14-13 ka (Supplementary Table 2). All of these are corroborated by AMS dates on other specimens, and none determines a first or last appearance datum. When plotted chronologically (Fig. 2), the data show that the number of megaherbivore bones recovered in Alaska remained high and relatively constant throughout the period under consideration, despite an important turnover of dominant taxa.

Coring sites, pollen and fungal spore

The stratigraphies and chronologies for the four cores have been published previously (Table 1) and the age-depth models are reproduced in Supplementary Figure 1. The core sediments are described in Supplementary Table 3. The median age and sediment accumulation rates (for each sample analysed for pollen or spore) are presented in Supplementary Table 1.

Ages were calibrated and age-depth models were created using the IntCal13 calibration curve (Reimer et al., 2013) and the R package 'rbacon' version 2.3 (Blaauw and Christen, 2011). The models used 21, 9, 11 and 9 AMS radiocarbon dates based as far as possible on macro- and micro-fossils for Jan Lake, Windmill Lake, Ruppert Lake and Wood Bottom Pond, respectively. In addition, a tephra layer related to the Aniakchak Caldera Forming Event II, dated to 3.595 ± 0.004 ka in Greenland ice cores (Denton and Pearce 2008; Pearce et al., 2017), was identified and used to further constrain the models in Ruppert Lake and Woody Bottom Pond (Monteath et al., 2017). Finally, the start of a distinct rise in *Alnus* pollen in a high-resolution pollen record from Ruppert Lake (Higuera et al., 2009) was dated to 7.56 ± 0.050 ka. Because of the very close proximity of the two sites, this pollen-inferred date was transposed to the Woody Bottom Pond and included in the age model.

At the three sites straddling the last stage of LQEs (i.e. Jan Lake, Windmill Lake, Ruppert Lake), the overall abundance of *Sporormiella* does not diminish after the last extinctions at the transition between the late Glacial and the Holocene (Table 2; Fig. 2). Spore values are highly variable and spore accumulation is plotted together with spore abundance relative to the pollen sum in Supplementary Figures 2-5. At these three sites, *Sporormiella* spores occurred in fewer than half the counted samples at Ruppert Lake, but in all samples at Jan Lake and Windmill Lake (Table 2). A total of 208 individual S*porormiella* spores were identified at these sites (20, 131, and 57, respectively). Accumulation rates varied between 0 and 371.6 spores cm^{-2} yr^{-1} (Table 2). Ruppert Lake spore average accumulation values (Table 2) are similar before and after the last extinctions (4.1 vs 3.4 spores cm^{-2} yr^{-1}). At Windmill, after the last extinctions, values are lower than before (70.2 vs 105.5; Table 2); here, pre-LQEs higher values pre-dating the last extinctions are mostly driven by a peak of *Sporormiella* accumulation rate occurring near 13 ka (Fig. 2). Jan Lake has high average accumulation rates after the last extinctions (146.0), compared with an average of 70.9 before. At this site, the earliest record may have been derived from terrestrial or very shallow sediments, and thus reflecting differential recruitment of spores to the site (Carlson and Finney, 2004; ME and MvH personal observation). Our fourth site, Woody Bottom Pond, does not span the last stage of the LQE and 30 individual *Sporormiella* spores were counted with an average accumulation rate of 8.4 spores cm^{-2} yr^{-1} over the Holocene.

For the two sites with a more detailed spore analysis, Ruppert Lake and Woody Bottom Pond, the most common fungal spore was *Sordaria* (n = 36; n = 47, respectively), followed by *Sporormiella* (n = 20; n = 39, respectively) with only one occurrence of *Podospora*. At Ruppert Lake, there was a near-significant correlation (p=0.052) between *Sporormiella* and *Sordaria* using a Spearman's rank test, while at Woody Bottom Pond this correlation was highly significant (p<0.001).

At Ruppert Lake, *Sordaria* shows higher accumulation rates after the last extinctions (average 6.7 spores cm^{-2} yr^{-1}) compared with an average of 2.6 spores cm^{-2} yr^{-1} before. The Holocene record from Woody Bottom Pond has greater average *Sporormiella* accumulation rates than the entire Ruppert Lake record, with an average accumulation rate of 8.4 spores cm^{-2} yr^{-1} (range 0 – 84.3 spores cm^{-2} yr^{-1}). *Sordaria* has an average accumulation rate of 9.2 spores (Table 2). Few spores are recorded in the last ~3000 years of the record and, as at Ruppert Lake, values fluctuate from sample to sample.

At the three sites straddling the last stage of LQEs, pollen of woody taxa rises around 14 ka, signalling the shift from herbaceous vegetation to shrub tundra and then to woodland and boreal forest as a response to deglacial climate change (Anderson et al 2004). There is no correlation between *Sporormiella* abundance and arboreal pollen percentages (Fig. 2).

DISCUSSION

Our main aim was to study changes in the population size and diversity of megaherbivores in interior Alaska at the final stage of LQEs (i.e. the last extinctions believed to have occurred by about 13 ka). We hypothesise that faunal loss at the final stage of LQEs in interior Alaska is associated with a sharp reduction in megaherbivore population size and changes in vegetation cover. Our secondary aim was to investigate the significance of using a wider range of dung fungal spores at two close-by sites to improve the interpretation of dung fungal spore records in this study and in future studies.

At four sites covering different time intervals (Ruppert Lake 17-0 ka, Jan Lake 14.2-4.6 ka, Windmill Lake 14.8-9.8 ka and Woody Bottom Pond, 9.5-0 ka), significant numbers of *Sporormiella* spores occur from 17 ka to the present. Spore numbers and estimated accumulation rates show variability within each core and among sites. This is typical of *Sporormiella* records (e.g. Davis and Shafer, 2006), which are often described informally as a 'noisy' signal. However, the presence of *Sporormiella* in all samples at two of our sites (Windmill Lake and Jan Lake) suggests the continuous presence of megaherbivores into the Holocene. At Ruppert Lake, *Sporormiella* spores were not observed in all samples, which could be interpreted as low numbers (or absence) of megaherbivores visiting the lake. Here, overall *Sporormiella* counts are low when compared with the other sites (Table 2), and it is therefore difficult to assess if these zero-counts represent true absence or if the small quantity falls below the detection limit (e.g. Walanus and Nalepka, 2013). For future investigations, uncertainty regarding *Sporormiella* zero counts could be avoided by more strictly adhering to the guidelines set by Etienne and Jouffroy-Bapicot (2014) recommending high exotic marker counts, independently from pollen sum. We also found that, when

Sordaria, another reliable indicator of megaherbivores (Baker et al., 2013; Perrotti and van Asperen, 2019) is counted, the number of samples with indicative spores (i.e. *Sporormiella* and/or *Sordaria*) is doubled (12 vs 25 samples of 48 total). Therefore, including other dung fungal spores such as *Sordaria* appears to be an effective additional measure to minimise the uncertainty associated with *Sporormiella* zero counts.

Besides megaherbivore abundance, other factors affect spore abundance (van Asperen et al., 2019). These factors include (1) moisture availability for fungal growth and hydrology (Wood and Wilmshurst, 2011), (2) shoreline morphology, (3) seasonality of climate and wind impacting fungal growth and dispersal (van Asperen, 2017), (4) taphonomic effects including the sedimentary environment and spore preservation, and (5) laboratory procedures (van Asperen et al., 2016). Thus, with each site having unique environmental and sedimentary conditions, there is unlikely to be a direct relationship between the number of dung fungal spores and the abundance of megaherbivores that applies across sites. Despite these caveats, when megaherbivore abundance is driven by a region-wide process, synchronous and local changes in dung fungal spore abundances can be expected at each site.

Comparison of values of spores before and after the last extinctions (Fig. 2) shows that at Ruppert Lake the range of values remained similar, at Jan Lake there was an increase and at Windmill Lake the values remained similar but for a peak at 14-13 ka. From these data, we can conclude that there was no dramatic change in megaherbivore biomass associated with the LQE and the onset of the Holocene at any of the sites, and by extension at the regional level.

At Ruppert Lake, we extended the counting and identification to a wider range of dung fungi, including *Sporormiella*, *Sordaria* and *Podospora*. We also analysed an additional well-dated core from nearby Woody Bottom Pond that spanned most of the Holocene. We found substantial differences between these two sites, but these differences were reduced when accounting for a wider range of dung fungal spores (Fig. 2). Different species of dung fungi have preferences for certain types of dung (e.g. Richardson, 2001, 1972) and demonstrate species-specific responses to different environmental conditions (Dix and Webster, 1995; Krug et al., 2004). Consequently, some taxa may grow better in certain conditions, resulting in spore assemblages dominated by one species or a group of species with similar ecology. Dix and Webster (1995) also highlight the importance of competition between species as a driver for the composition of the dung fungal community. This suggests that dung fungal biomass, and thus ultimately spore production, is strongly limited by factors such as space, nutrient and moisture availability. Therefore, the sum of individual dung spores, and not the types taken individually, may provide the most appropriate proxy for megaherbivore biomass. In fact, we find that some of the apparent randomness in our record can be reduced when considering both *Sporormiella* and *Sordaria* together (Fig. 2).

Even when considering *Sporormiella* and *Sordaria* together, however, Ruppert Lake and Woody Bottom Pond did not show the same temporal pattern of abundance. Although appearing counter-intuitive because these two sites are located close together, this result reinforces earlier findings that the dung fungal spore signal can relate to extremely small spatial scales (e.g. Kamerling et al., 2017; Davies, 2019). This may be explained by the observation of Baker et al. (2016), who found that shore run-off (within <10 m distance from the water) was the most significant process transporting spores into a series of ponds in the Oostvaardersplassen nature reserve, the Netherlands. In the only quantitative dispersal study we are aware of, Gill et al. (2013) demonstrated the importance of short-distance wind dispersal (<100 m) to explain the significant relationship between local bison distribution and spore abundance in the Konza Prairie, Kansas, USA. While the latter was conducted in grasslands, away from wetland depositional environments, both studies indicate key dispersal distances considerably less than the 650 m separating these two lakes. The emerging pattern within these studies and others (e.g. Raper and Bush, 2009; Etienne et al., 2013; Davies, 2019) is that dung fungal spores produce a local, short-distance signal of megaherbivore activity. In a vast region such as interior Alaska there is a need for using as many sites as possible to gain a landscape-wide understanding of megaherbivore distribution and abundance.

Uniquely, we are able to compare spore counts with fossil bone data. During the period leading to the final stage of LQEs, there was a significant taxonomic turnover of dominant megaherbivores in the bone fossil record (Fig. 2). An initial assemblage dominated by *Mammuthus* and *Equus* (and in the late-glacial, *Cervus*) was followed, after a period of transition ending around 13 ka, by an assemblage dominated by *Bison*, *Alces* and, later in the Holocene, by *Rangifer*. The period of transition is characterised by the extinction in North America of three genera (*Mammuthus*, *Equus* and *Saiga*; Stuart, 2015), although *Mammuthus* survived on the Island of St Paul until 5600 years ago (Graham et al., 2016). It appears that most of the extinctions and the period of dominance turnover occurred before the opening of the ice-free corridor, estimated at 13.4 ka (Heintzman et al., 2016) or 12.6 ka (Pedersen et al., 2016). It is unclear how isolation from the rest of North America would have impacted megaherbivore abundance. The lack of North-South exchange in North

America may have limited long-distance dispersal, believed to be key to megaherbivore species survival in the region (Mann et al., 2015, 2019). The extinctions associated with the transition around 13 ka seen here represent the final wave of megafauna extinction in the area.

Several records from North America (not Alaska) indicate a causal relationship linking megaherbivore extinctions to subsequent change in forest composition and wildfire regimes (Robinson et al., 2005; Gill et al., 2009; Perrotti, 2018). In interior Alaska our three sites spanning the final stage of LQEs show that the period 15-12 ka features an increase in woody taxa (largely *Salix* and *Betula*; Bigelow and Edwards, 2001; Carlson and Finney, 2004; Higuera et al., 2009). In two out of three instances the increase in arboreal pollen precedes faunal turnover and in none of the three instances major synchronous decline in *Sporormiella* abundance is evident. Spore accumulation rates either increase or remain stationary following the last extinctions. The last extinctions in the bone dataset at about 13 ka actually represents a major taxonomic turnover, but there is no apparent change in total herbivore numerical abundance. Thus, the stability, or even increase, of spore accumulation rates into the Holocene, which might seem unexpected given results from other regions, is in fact consistent with the maintenance of herbivore population size, albeit via a new suite of taxa. The dominant grazers of the Pleistocene, *Mammuthus* and *Equus*, vanished from the record shortly after the vegetation shift and their places are taken primarily by *Alces*, which is a browser, and later by *Rangifer*.

In interior Alaska, a major ecosystem change developed through the Pleistocene-Holocene transition, and as available feeding niches changed, taxa better adapted to woodland conditions became dominant. The Holocene interior climate likely favoured higher plant biomass than that of the Pleistocene, providing the nutrition (largely but not entirely) for browsers (see Guthrie 2003). Our finding of a shift from a predominantly grazing to browsing herbivore guild, following an increase in woody taxa, suggests that megafaunal extinction may be at least partly related to climate-induced vegetation change, at least in this region. Another significant factor to account for when studying megaherbivore abundance in Alaska is the antiquity of human settlement, potentially dating back earlier than 15 ka and the impact these populations had on their environment with activities such as fire and hunting (Vachula et al., 2019). Moreover, megaherbivore abundance may have remained relatively constant due to a complex history of isolation from the rest of North America until about 13 ka, allowing already resident taxa to expand.

CONCLUSION

In North America, the LQEs were particularly severe, with 69% of megafauna species becoming extinct, mostly around the time of the Pleistocene-Holocene transition (14-10 ka) (Stuart, 2015). Dramatic megaherbivore abundance losses associated with the final stage of LQEs have been identified using spores of dung fungus *Sporormiella* at sites from North America, and across the globe. However, such studies are lacking from interior Alaska, a region biologically isolated by ice from the rest of North America until about 13 ka. To study changes in population size and diversity of megaherbivores in interior Alaska, we used a combination of radiocarbon-dated bone data and *Sporormiella* records spanning before and after the final stage of LQEs (i.e. the last extinctions believed to have occurred by about 13 ka).

Based on the bone data, we found that there was a major turnover of dominant megaherbivore species around 13 ka attributable to the final stage of LQEs but, taken at face value, the abundance of bone did not markedly change over time. At the three coring sites spanning the final stage of LQEs, the overall abundance of *Sporormiella* spores did not diminish after the last extinctions. Because there were no synchronous decreases in spore abundance across the three sites, there is no indication that megaherbivore abundance was driven by a region-wide process during this period of time.

There did not appear to be any direct correlation between *Sporormiella* abundance and major vegetation change in the region, which saw pollen of woody taxa pollen rise around 14 ka as a response to deglacial climate change. The rise in woody taxa is associated with an increase in bones of browser species such as *Alces* at two out of three of our sites, suggesting important changes in ecosystem function. By the same token, the loss of the grazing taxa *Mammuthus* and *Equus*, and great reduction in *Bison,* may suggest extinction causality, at least in part, due to climate-driven vegetation change. However, our work did not focus on assessing causes of LQE and other potential drivers of extinction such as ancient human population active in interior Alaska during this period would require consideration in future research.

Spore values show high variability which is dampened when including *Sordaria*, the only other dung fungal spore type found in significant abundance in our study. From a methodological point of view, our results indicate that high counts and the inclusion of *Sordaria* (and any additional spore type reliably indicating megaherbivore) can improve reliability of results when applying the dung fungal spore method. To confirm the turnover and spatial distribution in megaherbivores across the region, future work should also include more sites with spore studies and additional lines of evidence such as ancient sedimentary DNA or other biomarkers preserved in lake sediments.

The significant strength of our approach is the use of two complementary and independent indicators regarding the presence and abundance of megaherbivores in the past, namely radiocarbon-dated bone remains and accumulation rates of dung fungal spores recovered from radiocarbon-dated lake cores. These two congruent lines of evidence based on state-of-the-art methodology (including three *Sporormiella* records and one bone database) make us relatively confident that there was no long-lasting dramatic loss of megaherbivore abundance in interior Alaska around 13 ka associated with LQE. This new and robust evidence should act as a cautionary tale against the assumption that regional LQEsare systematically associated with megaherbivore biomass crashes, in addition to taxonomic turnovers. The implication is that studying the consequences of LQE requires thoroughly testing changes in megaherbivore abundance in time, a critical first step we achieved for interior Alaska. Studies of megaherbivore abundance during periods of substantial climate change such as the last stage of LQEs and the onset of the Holocene can provide valuable insight as we attempt to predict changes in biodiversity and ecosystem function that may occur under future climate scenarios.

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Figures and tables

Table 1: Characteristics of the lake study sites

	New Data (this paper)	Surface area (ha)	Water depth (m)	Altitude (m asl)	Latitude (N)	Longitude (W)	Year cored	Core Chronology
Jan Lake	*Sporormiella*	10.1	11.7	503	63.57	142.90	1994	Carlson and Finney, 2004
Windmill Lake	*Sporormiella*	2.0	4	630	63.65	148.80	1994	Bigelow and Edwards 2001; Carlson and Finney, 2004
Ruppert Lake	All fungal spores	4.9	5.8	230	67.07	154.24	2013	Monteath et al. 2017; McGowan et al. 2018
Woody Bottom Pond	All fungal spores	0.7	4.3	310	67.07	154.23	2013	Monteath et al. 2017; McGowan et al. 2018

Table 2: Summary of spore counts. Note that total dung fungal spore counts in Ruppert Lake includes one *Podospora* spore, in addition to *Sordaria* and *Sporormiella* spores.

	Jan Lake	Windmill Lake	Ruppert Lake	Woody Bottom Pond
Age range (ka)	14.2 - 4.6	14.8 - 9.5	17 - 0	9.5 - 0
Total *Sporormiella* spores counted	131	57	20	39
Frequency of *Sporomiella* occurrence relative to all samples	20 out of 20	11 out of 11	12 out of 48	17 out of 45
Pre-LQE *Sporomiella* average accumulation rates, range between parentheses (spores cm^{-2} yr^{-1}).	70.9 (57.3 - 90.4)	105.5 (31.5 - 212.9)	4.1 (0 - 39.0)	n/a
Post-LQE *Sporomiella* average accumulation rates, range between parentheses (spores cm^{-2} yr^{-1}).	146.0 (11.5 – 371.6)	70.2 (41.1 – 113.7)	3.4 (0 -25.7)	8.4 (0 - 84.3)
Total *Sordaria* spores counted			36	47
Frequency of *Sordaria* occurrence relative to all samples			17 out of 48	15 out of 45
Pre-LQE *Sordaria* average accumulation rates, range between parentheses (spores cm^{-2} yr^{-1}).			2.6 (0 – 35.5)	n/a
Post-LQE *Sordaria* average accumulation rates, range between parentheses (spores cm^{-2} yr^{-1}).			6.7 (0 -46.0)	9.2 (0 – 77.8)
Total dung spores counted			57	86
Frequency of dung spores occurrence relative to all samples			25 out of 48	22 out of 45
Pre-LQE dung spores average accumulation rates, range between parentheses (spores cm^{-2} yr^{-1}).			6.6 (0 - 39.0)	n/a
Post-LQE dung spores average accumulation rates, range between parentheses (spores cm^{-2} yr^{-1}).			13.1 (0 - 56.5)	8.4 (0 - 84.3)

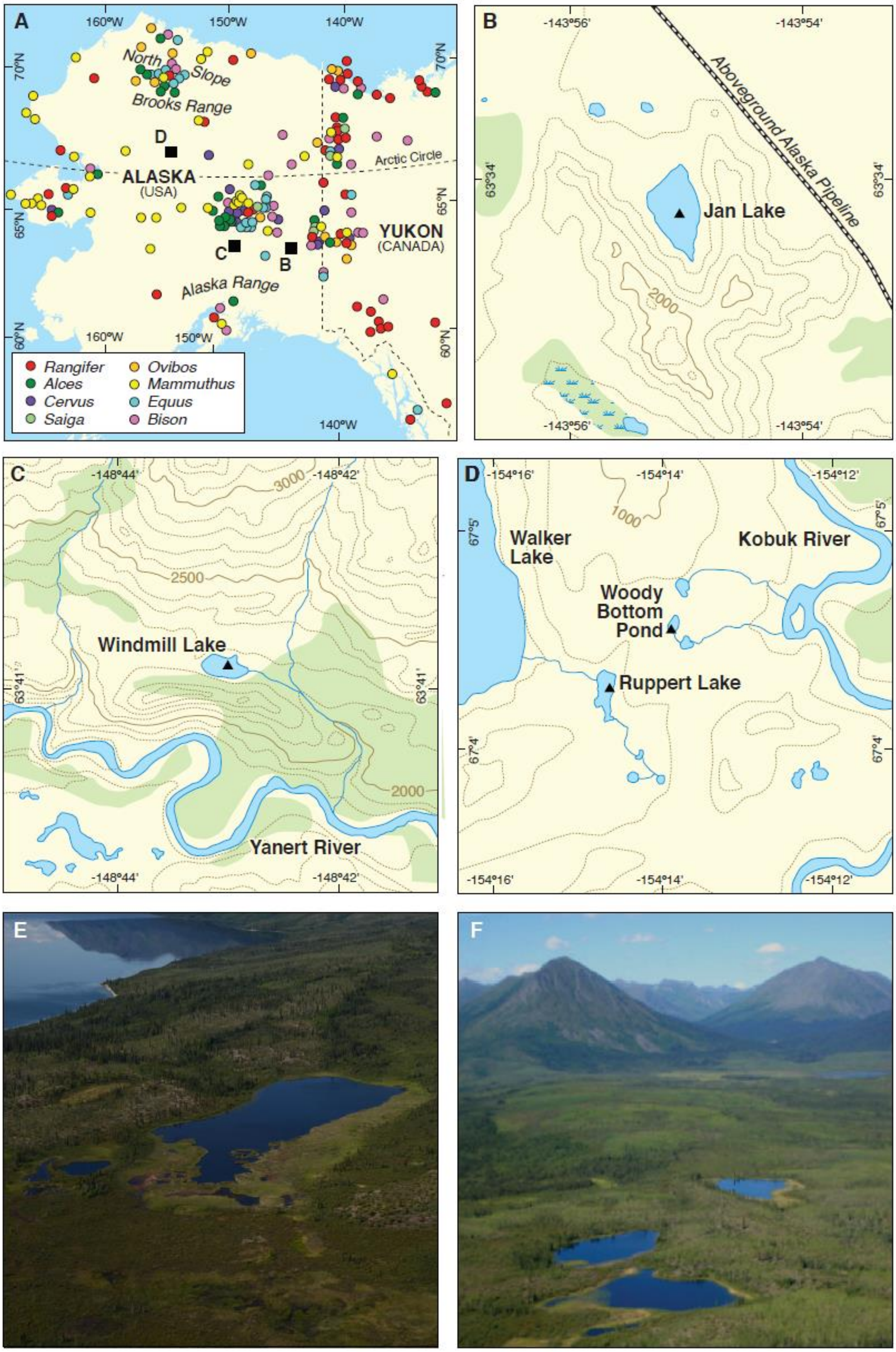
A
160°W
150°W
140°W
70°N
65°N
60°N
North Slope
Brooks Range
D
ALASKA
(USA)
Arctic Circle
C
B
YUKON
(CANADA)
Alaska Range
Rangifer
Alces
Cervus
Saiga
Ovibos
Mammuthus
Equus
Bison
B
-143°56'
-143°54'
63°34'
Aboveground Alaska Pipeline
Jan Lake
2000
C
-148°44'
-148°42'
3000
2500
2000
63°41'
Windmill Lake
Yanert River
D
-154°16'
-154°14'
-154°12'
1000
67°5'
67°4'
Walker Lake
Kobuk River
Woody Bottom Pond
Ruppert Lake
E
F

Figure 1. Location of bone remains and lake sites. A: Map of Alaska locating megaherbivore bone remains 25 ka or younger (circles, see source publication in methods and Supplementary Table 2) and lake sites (squares). B. Jan Lake, an alluvium-dammed basin with spore and pollen record spanning 14.2-4.6 ka. C. Windmill Lake, a moraine-dammed basin with spore and pollen record spanning 14.8-9.5 ka. D. Ruppert Lake and Woody Bottom Pond, two kettle lakes with spore and pollen records spanning 17-0 ka and 9.5-0 ka, respectively. E. Oblique aerial photograph of Ruppert Lake with the larger Walker Lake, top left (photo by Tom Roland). F. Oblique aerial photograph of Woody Bottom Pond (middle lake, photo by Maarten van Hardenbroek). Altitude is reported in feet.

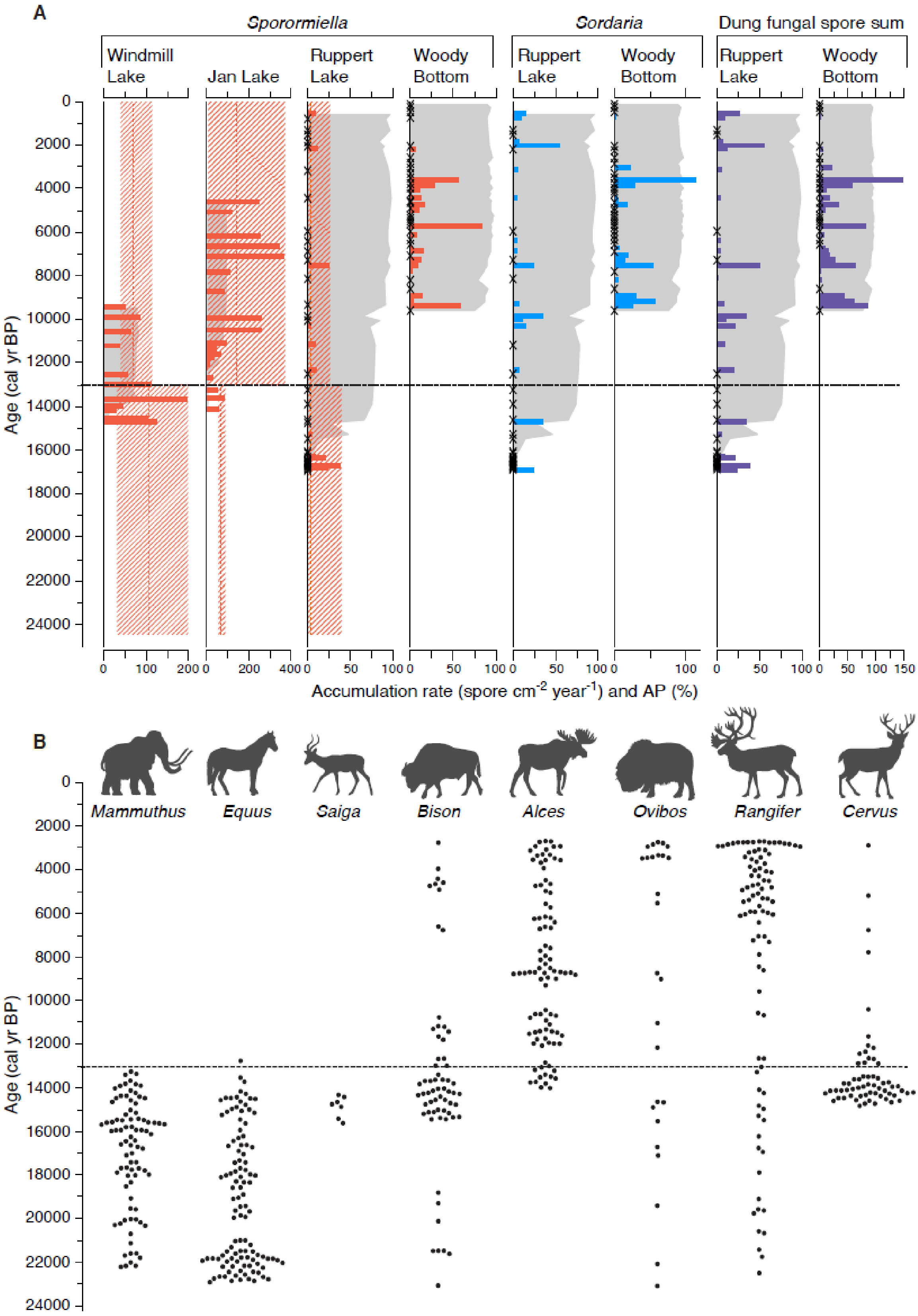
A
Sporormiella
Sordaria
Dung fungal spore sum
Windmill Lake
Jan Lake
Ruppert Lake
Woody Bottom
Ruppert Lake
Woody Bottom
Ruppert Lake
Woody Bottom
Age (cal yr BP)
0
2000
4000
6000
8000
10000
12000
14000
16000
18000
20000
22000
24000
0 100 200
0 200 400
0 50 100
0 50 100
0 50 100
0 100
0 50 100
0 50 100 150
Accumulation rate (spore cm^{-2} year^{-1}) and AP (%)
B
Mammuthus
Equus
Saiga
Bison
Alces
Ovibos
Rangifer
Cervus
Age (cal yr BP)
0
2000
4000
6000
8000
10000
12000
14000
16000
18000
20000
22000
24000

Figure 2. Spore and bone diagram. A. Dung fungal spore accumulation rates (spore per cm^2 per year) are shown as coloured bars and percent arboreal pollen (%AP) is shown as grey shading. The mean and range of spore accumulation rates before and after the last extinctions is indicated with a dotted line and hashed zones, respectively. A small cross indicates samples where no dung fungal spores were encountered. B. Megaherbivore bone remains 25 ka or younger from Alaska, plotted against time. Each bone is plotted as a dot using the median calibrated radiocarbon date.