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ORIGINAL ARTICLE

The southern coastal Beringian land bridge: cryptic refugium or pseudorefugium for woody plants during the Last Glacial Maximum?

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ABSTRACT

Aim The Bering Land Bridge (BLB) connected Asia and North America during glacial periods, supported a diverse ecosystem of now-vanished megafauna, and is a proposed glacial refugium. This study tests whether southern coastal Beringia was a refugium for woody taxa during the Last Glacial Maximum (LGM) and hypotheses about habitats available on the BLB before and after megafaunal extinction.

Location St. Paul Island, Alaska.

Methods We analysed sediment cores from the Lake Hill, with a new age model anchored by 18 radiocarbon dates and multiple palaeoecological indicators (sedimentary ancient DNA [sedaDNA], macrobotanical fossils, and pollen) for the presence/absence of four woody genera: *Picea, Betula, Alnus* and *Salix*. We reconstructed vegetation history and compare St. Paul tundra composition to mainland counterparts.

Results St. Paul has been continuously occupied by graminoid-forb tundra with prostrate shrubs (*Salix*, Ericaceae) since 18,000 years before present (yr BP). Fossil pollen of *Picea, Pinus, Betula* and *Alnus* is present in the Lake Hill sediments at low relative abundances and accumulation rates, consistent with long-distance transport. Macrobotanical fossils and sedaDNA analyses do not support *Picea, Betula* and *Alnus* presence. The St. Paul modern and fossil pollen assemblages are compositionally unlike mainland counterparts, but most closely resemble Arctic herbaceous tundra. Stratigraphically constrained cluster analysis indicates no major change in the vegetation after woolly mammoth extinction at 5600 yr BP, although Poaceae, Cyperaceae, *Equisetum* and forb abundances increase.

Main conclusions This study strongly indicates that St. Paul and, by implication, southern coastal Beringia were not refugia for woody taxa during the LGM. The persistence of prostrate shrub-graminoid tundra supports interpretations that herbaceous tundra prevailed on southern Beringia during the LGM, whilst not ruling out the possibility of mesic shrub tundra in the interior. This herbaceous tundra supported an island refugium for woolly mammoth for 8000 years, showing no major vegetation composition changes after extinction.

Keywords

alder, ancient DNA, Beringia, birch, cryptic refugia, macrobotanical fossils, pollen, pseudorefugia, spruce, woolly mammoth

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INTRODUCTION

The Bering Land Bridge (BLB) is a low-lying continental shelf that served as a biogeographical corridor and filter between north-eastern Asia and western Alaska during Pleistocene glacial periods, when sea level dropped > 100 m below the present levels (Elias & Crocker, 2008). Unlike most other high-latitude Northern Hemisphere landmasses, Beringia essentially remained unglaciated during the last glacial cycle, and hence served as a glacial refugium for Holarctic plant taxa (Anderson *et al.*, 2006), a migration route for humans into the Americas (Hoffecker *et al.*, 2014), and habitat for a diverse and now-vanished ecosystem of megafauna (Barnosky *et al.*, 2004). Yet, the ecosystems and environments of Beringia remain incompletely understood, in part because central Beringia is now under water. In this study, we present a new well-dated, multi-proxy, palaeovegetation record from the Lake Hill (St. Paul Island, Alaska), a classic site from the southern coastal Beringia (Colinvaux, 1967a,b, 1981), and use this record to address three questions of interest to biogeographers, archaeologists and palaeoecologists: First, what environments and habitats were available to megafauna and early humans as they occupied or traversed the BLB? Second, was the southern coastal BLB a refugium for woody taxa during the Last Glacial Maximum (LGM; 26,500–19,000 yr BP) and can we discriminate cryptic refugia (small historical populations undetected by fossil proxies) (Gavin *et al.*, 2014) from pseudorefugia (false inferences of past species presence, also called mystic refugia) (Tzedakis *et al.*, 2013)? Third, what were the trophic effects of the late-Quaternary megafaunal extinctions on vegetation structure and composition (Gill, 2014)?

Current debates about Beringian vegetation during the LGM centre primarily on the prevalence of mesic shrub tundra versus graminoid-herb tundra (Ager & Phillips, 2008; Elias & Crocker, 2008). One perspective, based on fossil pollen and insect data, holds that mesic shrub tundra was widespread during the LGM, particularly in low-lying and now-submerged portions of Beringia (Elias & Crocker, 2008; Hoffecker *et al.*, 2014), which possibly acted as a biogeographical barrier to steppe-adapted plants and animals (Guthrie, 2001). However, others have argued that graminoid-forb tundra prevailed across Beringia during the LGM, based on fossil pollen, macrofossils and stable isotope analyses in Alaska and on Bering Sea island remnants (Colinvaux, 1981; Ager, 2003; Bigelow *et al.*, 2003; Kaplan *et al.*, 2003; Ager & Phillips, 2008). In the latter interpretation, the graminoid-forb tundra was maintained by dry climates and, perhaps, grazers (Blinnikov *et al.*, 2011), and provided habitat for the diverse Pleistocene megafaunal guilds of Beringia (Willerslev *et al.*, 2014). Shrub taxa were in dwarf form or restricted to local habitats such as riparian or wetland settings.

A parallel conversation has focussed on whether current Arctic tree populations source from long-distance migrations from south of the LGM ice sheets or from small local refugia (Hultén, 1968). These small northerly refugia are sometimes referred as 'cryptic' because of the difficulty in detecting them in the fossil record (Stewart & Lister, 2001; Provan & Bennett, 2008; Gavin *et al.*, 2014). Prior studies support the existence of Beringian glacial refugia for woody taxa such as *Picea* (spruce), *Betula* (birch) and *Alnus* (alder) (Colinvaux, 1967a; Brubaker *et al.*, 2005; Elias & Crocker, 2008). For example, genetic surveys of contemporary populations of *Picea glauca* strongly suggest a Beringian refugium (Anderson *et al.*, 2006), and deciduous broadleaved shrublands and forests were well-established in the eastern Beringia by 13,500 years ago (Edwards *et al.*, 2005). However, no single line of evidence for refugia is definitive (Gavin *et al.*, 2014), and each creates the possibility of mystic or pseudorefugia, in which presence is falsely inferred (Tzedakis *et al.*, 2013). For example, the problem of long-distance pollen transport is acute in the Arctic where atmospheric circulation is pronounced and local pollen productivity often is low (Bourgeois *et al.*, 1985). Similarly, the reliability of sedaDNA can be challenged on the grounds of possible contamination, unknown provenance, and variable quality (Birks *et al.*, 2012; Parducci *et al.*, 2012a,b). Macrofossils usually are diagnostic of local presence when found, but their absence rarely proves the absence of the organism. Thus, multi-proxy site studies are needed to confirm the absence or presence, precise location and extent of proposed Beringian refugia.

Another conversation concerns the two-way relationship between megafaunal extinctions and vegetation composition. Causal hypotheses for the Pleistocene extinctions include food resource loss because of the mesic shrub tundra expansion (Guthrie, 2001; Elias & Crocker, 2008; Willerslev *et al.*, 2014) and human settlement (Yesner, 2001). Proposed ecosystem effects of megafaunal extinctions include increase of palatable woody species and biomass because of herbivory release, enhanced fire regime as a result of increased woody biomass, formation of no-analogue plant communities (Gill *et al.*, 2009; Gill, 2014), and albedo-related surface-atmosphere feedbacks (Doughty, 2013).

Our paper addresses these questions by presenting a new, well-dated, and multi-proxy record for the last 18,000 years from the Lake Hill on St. Paul Island, Alaska (Fig. 1), a remnant of the southern coastal BLB. Lake Hill, also called Cagaloq Lake, was previously cored by Paul Colinvaux (1967a,b, 1981), who rejected hypotheses that *Picea* was locally present on the southern coast of Beringia, because of low pollen accumulation rates. Our record adds 12 new radiocarbon dates to those reported by Graham *et al.* (2016) and extends the age model to the base of the Lake Hill core. We present new analyses of three independent palaeoecological proxies from this core: fossil pollen, macrobotanical fossils, and sedaDNA. This multi-proxy study enables stronger inferences about the regional environments on southern coastal Beringia for the last 18,000 years and whether this region was a glacial refugium for woody plants.

MATERIALS AND METHODS

St. Paul Island (57°11′ N, 170°16′ W) is a volcanic island of the Pribilof Islands in the Bering Sea, nearly 500 km

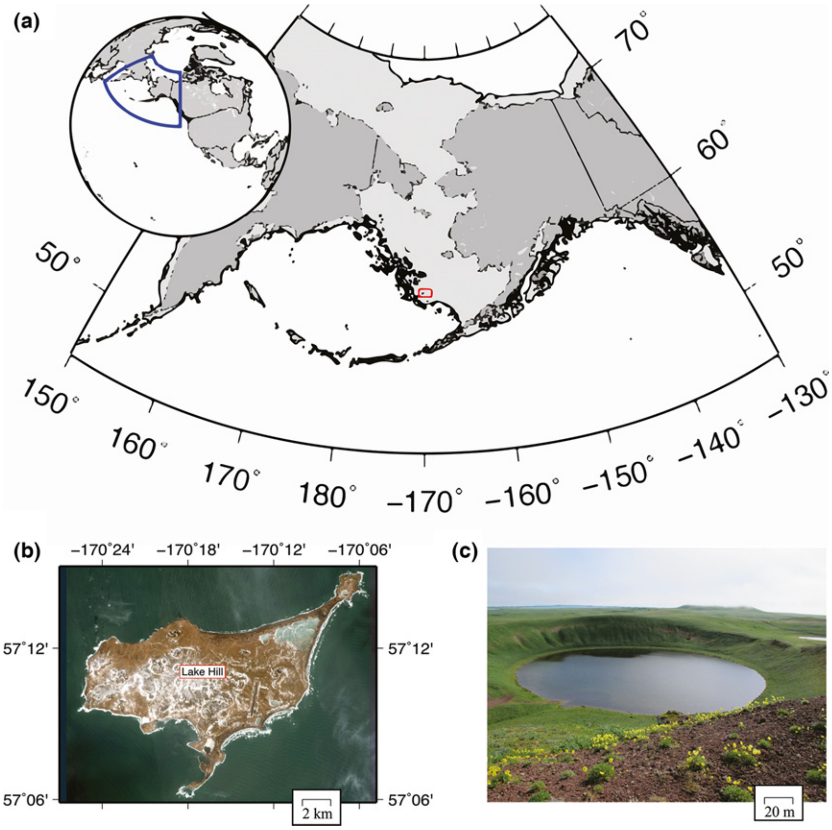

Figure 1 Map of Beringia and St. Paul Island, modified from Graham *et al.* (2016). Plot a) shows the current continents (dark grey) and the past location of the Bering Land Bridge (light grey) with red box indicating St. Paul Island. Plot b) shows the location of Lake Hill on St. Paul Island. Plot c) shows a photograph of the Lake Hill and its crater to indicate the topography and adjacent tundra community. The photograph was taken in July, 2013 by Yue Wang.

west-southwest from the mainland Alaska and about 400 km north-northeast from the Aleutian Islands (Fig. 1). Island area at present is 109 km^2. Climates are maritime; in 1981–2010, the average temperature ranged from −6.5 to 10.4 °C, whilst the average annual rainfall and snowfall were 605 mm and 1567 mm, respectively (http://w2.weather.gov/climate/xmacis.php?wfo=pafc). The island is snow-covered in the winter. Summer vegetation is mainly forb-graminoid tundra (Fig. 1c) with prostrate shrub willow (*Salix*) (< 20 cm) and Ericaceae, as well as Poaceae, Cyperaceae, Apiaceae and other forbs. The vertebrate fauna is depauperate: Arctic fox (*Vulpes lagopus*) and Pribilof Island shrew (*Sorex pribilofensis*) are present today, fur seals (*Callorihinus ursinus*) are abundant on the coasts, and reindeer (*Rangifer tarandus*) were introduced to the island in AD 1911 (Scheffer, 1951). Woolly mammoth (*Mammuthus primigenius*) was present until 5600 yr BP (Graham *et al.*, 2016), and polar bear fossils (*Ursus maritimus*) are dated to 4800 and 4400 yr BP (Veltre *et al.*, 2008). Humans apparently first arrived in AD 1787 (Veltre & Veltre, 1981).

Lake Hill is a closed circular volcanic lake, about 200 m wide and 1.3 m deep (Fig. 1). Three cores were taken from the lake centre in March 2013 under a *c.* 30 cm ice layer, and a master composite profile was built from the three cores (Graham *et al.*, 2016). All depths are reported here as master composite depth (MCD) and represent centimetres below the sediment-water interface. The age model is based on 18 radiocarbon dates from plant fossils and aquatic invertebrates chitin, and one tephra dates at 3595 ± 4 yr BP corresponding to the Aniakchak eruption (Kaufman *et al.*, 2012) (Table 1). The tephra and upper six radiocarbon dates were previously published by Graham *et al.* (2016); the lower twelve dates are new to this study (Table 1). *Bacon* 2.2 was used to create the age-depth model (Blaauw & Christen, 2011), and the parameters were set as values in Table S1.1 in Supporting Information. All ages are reported here as calendar years before AD 1950 (yr BP) unless otherwise noted.

We surveyed modern vegetation and took modern soil pollen samples in July 2013, focussing on eleven sites including graminoid-forb tundra in wetlands near the Lake Hill and sparsely vegetated tundra on the barren rock ground at the top of the hill (Table S1.2). For macrobotanical fossil analysis, 2-cm^3 sediment samples were selected approximately every 10 cm. A total of 84 samples were intensively analysed for macrobotanical remains. An additional 55 samples underwent cursory inspection and were not further analysed because of a paucity of botanical material. Plants were identified according to pictures and resources listed in the Appendix S1 (Fig. S1.1).

We counted fossil pollen and spores following a slightly modified version of methods described in Graham *et al.* (2016). For sediments between 671 and 893 cm, where pollen and spore concentration was low, heavy liquid separation using sodium polytungstate (SPT) was applied to enrich pollen and spore concentrations and facilitate counting, following a protocol developed at the University of Maine (Nurse,

Table 1 Radiocarbon dates and other age controls for *Bacon* age model for lake cores from the Lake Hill, St. Paul Island. Previously published sample dates (sample IDs 01-07) are from Graham *et al.* (2016).

Sample ID	AMS Lab ID	LacCore Section ID	Section depth (cm)*	MCD (cm)	Material dated	^{14}C Age (BP)	Calibrated age (BP)#
01	UCIAMS-128455	LAHI13-1B-1B-1	40.5	21.5	Bryophyta, cf. Polytrichopsida†	225 ± 15	305–0
02	UCIAMS-128456	LAHI13-1A-2L-1	62.0	181.0	Bryophyta,cf. *Brachythecium*†	2585 ± 15	2755–2720
03	UCIAMS-128457	LAHI13-1D-2B-1	77.5	274.5	Leaf skeleton fragment, cf. *Salix*†	3280 ± 20	3565–3455
04	*Aniakchak Tephra*			*294*	*N/A*	*N/A*	*3595 ± 4*
05	UCIAMS-128458	LAHI13-1B-6L-1	29.0	489.0	Leaf/stem fragment, cf. *Salix*†	4575 ± 20	5435–5080
06	UCIAMS-128459	LAHI13-1D-5B-1	45.0	535.0	Leaf fragments	5380 ± 20	6280–6030
07	UCIAMS-128460	LAHI13-1B-8L-1	87.5	738.5	Bryophyta, cf. Polytrichopsida†	9990 ± 30	11,615–11,280
08	UGAMS-24340	LAHI13-1B-9L-1	34.5	802.0	Dicot leaf	10,260 ± 40	11,1818–12,158
09	UGAMS-22547	LAHI13-1D-10L-1	35.5	1037.5	Spore cases	11,680 ± 50	13,411–13,592
10	UGAMS-24030	LAHI13-1A-11L-1	56.5	1081.5	Cladoceran chitin	12,010 ± 50	13,743–14,018
11	UGAMS-22548	LAHI13-1A-12L-1	47.5	1169.5	Chironomid pupae and head capsule chitin	12,570 ± 65	14,457–15,171
12	UGAMS-22549	LAHI13-1A-13L-1	22.5	1205.5	Chironomid pupae and head capsule chitin	13,160 ± 60	15,587–16,041
13	UGAMS-22550	LAHI13-1A-13L-1	38.5	1221.5	Chironomid pupae and head capsule chitin	13,330 ± 55	15,829–16,233
14	UGAMS-22551	LAHI13-1A-13L-1	38.5	1221.5	Plant fragments	14,000 ± 40	16,764–17,192
15	UGAMS-24032	LAHI13-1A-14L-1	8.5	1257.5	Plant fragments	14,140 ± 50	17,013–17,434
16	UGAMS-24031	LAHI13-1A-14L-1	8.5	1257.5	Cladoceran chitin	14,170 ± 50	17,064–17,464
17	UGAMS-22553	LAHI13-1A-13L-1	61.5	1309.5	Chironomid pupae and head capsule chitin	13,310 ± 70	15,778–16,231
18	UGAMS-22552	LAHI13-1A-13L-1	61.5	1309.5	Plant fragments	14,090 ± 45	16,943–17,379
19	UGAMS-24033	LAHI13-1A-14L-1	89.5	1337.5	Plant fragments	15,350 ± 50	18,494–18,757

*Depths expressed as cm below sediment surface.

#Range defined by 2σ.

†Dated materials modifications from Graham *et al.*, 2016.

MCD: mean composite depth; UCI: University of California, Irvine; UG: University of Georgia, Center for Applied Isotope Studies.

pers. comm.). We analysed 134 1-cm^3 samples for pollen and spores. Taxon abundances were calculated as percentages relative to a sum of total pollen and spores. Fossil pollen and spore assemblages were divided into zones using the stratigraphically constrained ordination technique (CONISS), implemented in the R package 'rioja' (Juggins, 2015) in R version 3.2.3 (R Core Team, 2015). The minimum dissimilarity between each fossil pollen sample and its closest modern pollen analogue was calculated as a squared chord distance (SCD), using 'analogue' in R (Williams *et al.*, 2001; Simpson, 2007). For the modern-analogue analyses, the modern pollen and spore dataset consisted of the 11 soil surface pollen assemblages from St. Paul and 64 modern pollen assemblages from mainland Alaska (Anderson & Brubaker, 1986; Whitmore *et al.*, 2005) assigned to tundra types based on the North American Seasonal Land Cover vegetation classification (Anderson, 1976). The threshold for non-analogue communities was set as 0.36, calculated based on minimum SCDs and receiver operating characteristic (ROC) analysis (Gavin *et al.*, 2003) and a comparison of St. Paul modern pollen assemblages to modern mainland Alaskan tundra pollen assemblages. The rationale here is that St. Paul modern pollen assemblages already differ compositionally from mainland counterparts and thus St. Paul assemblages would have to exceed this to be considered non-analogue. We used principal component analysis (PCA) to analyse the major trends in pollen and spore composition with 'ggbiplot' in R (Vu, 2011), and included only pollen and spores from plant taxa with a maximum abundance higher than 2% and at least five occurrences in the combined fossil and modern datasets.

Taking advantage of published genome sequences, we used a shotgun sequence approach to sedaDNA analyses to test hypotheses about the presence of *Picea*, *Betula* and *Salix*. *Alnus* was not examined, as there is currently no publicly available *Alnus* reference genome. This approach is more sensitive to presence of DNA in mixed samples than metabarcoding approaches, as DNA fragments from across the genome can be used to confirm a taxon's presence in a sedaDNA extract. The sedaDNA sequence dataset of Graham *et al.* (2016) was supplemented with sequence data from 21 additional samples and two additional negative extraction controls, following the methods described there (Table S2.4). A slightly modified version of the bioinformatic pipeline outlined in Graham *et al.* (2016) was followed. The filtered sequence data from each sample was independently mapped to five reference genomes (three *Picea*, one *Salix*, one *Betula*; Table S2.5). The mapped sequence reads were filtered by two methods to remove spurious alignments. First, for the *Salix* and *Betula* alignments, we removed reads that mapped to both genomes. Second, for all alignments, we compared the remaining mapped sequences to the NCBI nucleotide database (release date, 2015/11/01) and removed sequences that either uniquely hit or had a higher-score hit to a non-Pinales (*Picea*), non-Saliceae (*Salix*), or non-Betulaceae (*Betula*) sequence in the NCBI database. For these three taxa to be considered present in a Lake Hill sample, the proportion of sequences assigned to each woody plant taxon in a given sample had to be greater than the proportion observed in the negative extraction controls. This allowed us to assess the potential background contaminating DNA that may be present in reagents or the laboratory. Furthermore, after aligning reads to reference genomes, we assessed whether the characteristic ancient DNA damage patterns were present. Ancient DNA is often characterized by short fragment lengths (< 100 base pairs [bp]) and by changes to the DNA molecules manifesting either as incorrectly copied sequences because of cytosine deamination at the ends of DNA molecules, or as depurination-induced fragmentation (Dabney *et al.*, 2013). We also assessed the ancient DNA damage patterns in the control samples aligned to the *Picea* and *Betula* reference genomes (Birol *et al.*, 2013; Nystedt *et al.*, 2013). Novel sequencing data are available from the Short Read Archive (SRA), under BioProject PRJNA320875, with SRA accessions: SRR3992608-SRR3992630.

RESULTS

Age model and stratigraphy

The *Bacon* 2.2 age-depth model converged successfully (Fig. 2). The lowest radiocarbon date is at 1337.5 cm (core basal depth is 1341 cm) has a calibrated age of 18,494–18,757 yr BP, indicating that the Lake Hill core spans from the end of the LGM to present. The basal date is younger than reported in Colinvaux (1981), in which Colinvaux estimated that the basal sediments at 1460 cm corresponded to the mid-Wisconsin interstadial (*c.* 25,000 yr BP), based on pollen stratigraphy and a bulk-sediment radiocarbon date of 17,800 radiocarbon yr BP at 1007 cm. The age model reported here and Colinvaux (1981) also differ over the timing of the major sedimentary transition (at 550 cm in Colinvaux (1981) and 503 cm in the new cores), which consists of a shift from sandy sediments to algal gyttja, accompanied by a decrease in magnetic susceptibility and increase in organic carbon content. This transition was dated to 10,900 calendar yr BP (9500 radiocarbon yr BP) in Colinvaux (1981) based on bulk-sediment dates and to 5600 calendar yr BP in the new cores, based on AMS dates of terrestrial macrofossils Graham *et al.* (2016). The age model reported here should replace that of Colinvaux (1967a, 1981), because of the use here of more precise AMS dating methods, dating of substrates less subject to contamination by old carbon, and the greater number of radiocarbon dates.

The uppermost sediments (0–500 cm) are a dark olive massive gyttja with occasional fibrous materials and plant macrofossils. Between 500 and 717 cm, sediments shift to a silty gytta. Below 717 cm to base, sediments are predominantly mineral silts, with interbedded tephras and sand layers (Table S1.3, Fig. S1.2). Lacustrine conditions are indicated

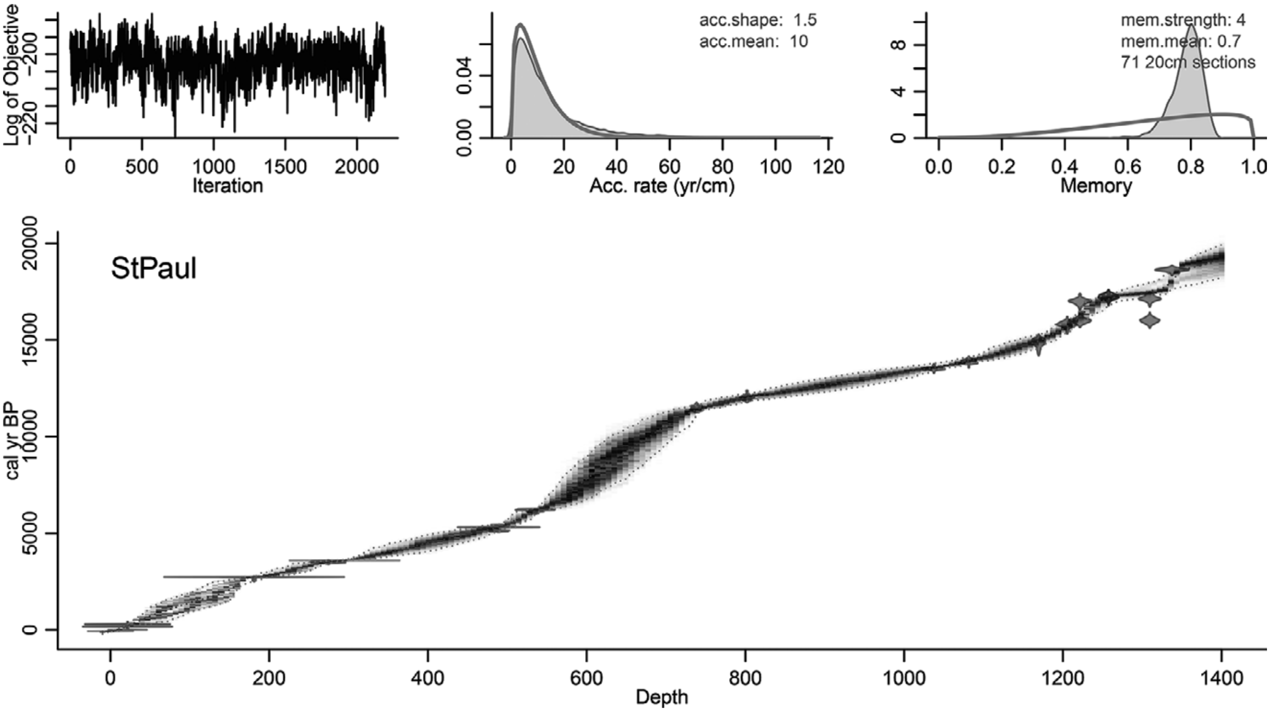

Figure 2 *Bacon* age–depth model for Lake Hill (Blaauw & Christen, 2011). Upper left: the MCMC iterations, showing a stationary distribution with little structure amongst iterations. Upper middle: prior (grey curve) and posterior (filled grey curve) distribution of accumulation rates. The prior for mean accumulation rate was set to 0.1 cm/yr. Upper right: the prior and posterior probability distributions for memory (i.e., autocorrelation strength). Lower plot: the age–depth model. Individual radiocarbon dates are shown in probability density functions of calibrated ages. The grey area indicates the uncertainty envelope of the age model with dashed lines indicating 95% confidence intervals.

throughout the core by the presence of freshwater diatoms and cladocerans, although they are in very low concentrations between *c.* 800 and 1000 cm (*c.* 12,000–13,300 yr BP) (Wooller *et al.*, unpublished data).

Vegetation History since the Last Glacial Maximum

The modern vegetation survey indicates forb-graminoid tundra with prostrate *Salix* and mosses. *Salix* and *Carex* are the most abundant shrub and graminoid taxa, respectively; *Achillea borealis* and *Angelica lucida* are the most abundant forb taxa; and whereas mosses are ubiquitous, *Sphagnum* is rare on the island (Fig. S1.3) (Macoun, 1899). No trees are present, and all shrubs are lower than 20 cm (Fig. 1c). *Alnus* and *Betula* pollen occur in modern soil samples (Fig. S1.3), despite their absence in our floristic survey and historical surveys of the Pribilofs (Macoun, 1899; Colinvaux, 1967a).

The fossil pollen record from St. Paul Island comprises 43 pollen and spore types (Fig. 3), encompassing seven woody taxa – *Salix*, Ericaceae, *Alnus*, *Betula*, *Picea*, *Pinus* and *Populus*, 32 herbaceous taxa, and four spore types – *Equisetum*, *Lycopodium*, *Polypodium* and *Sphagnum*. Poaceae is the most

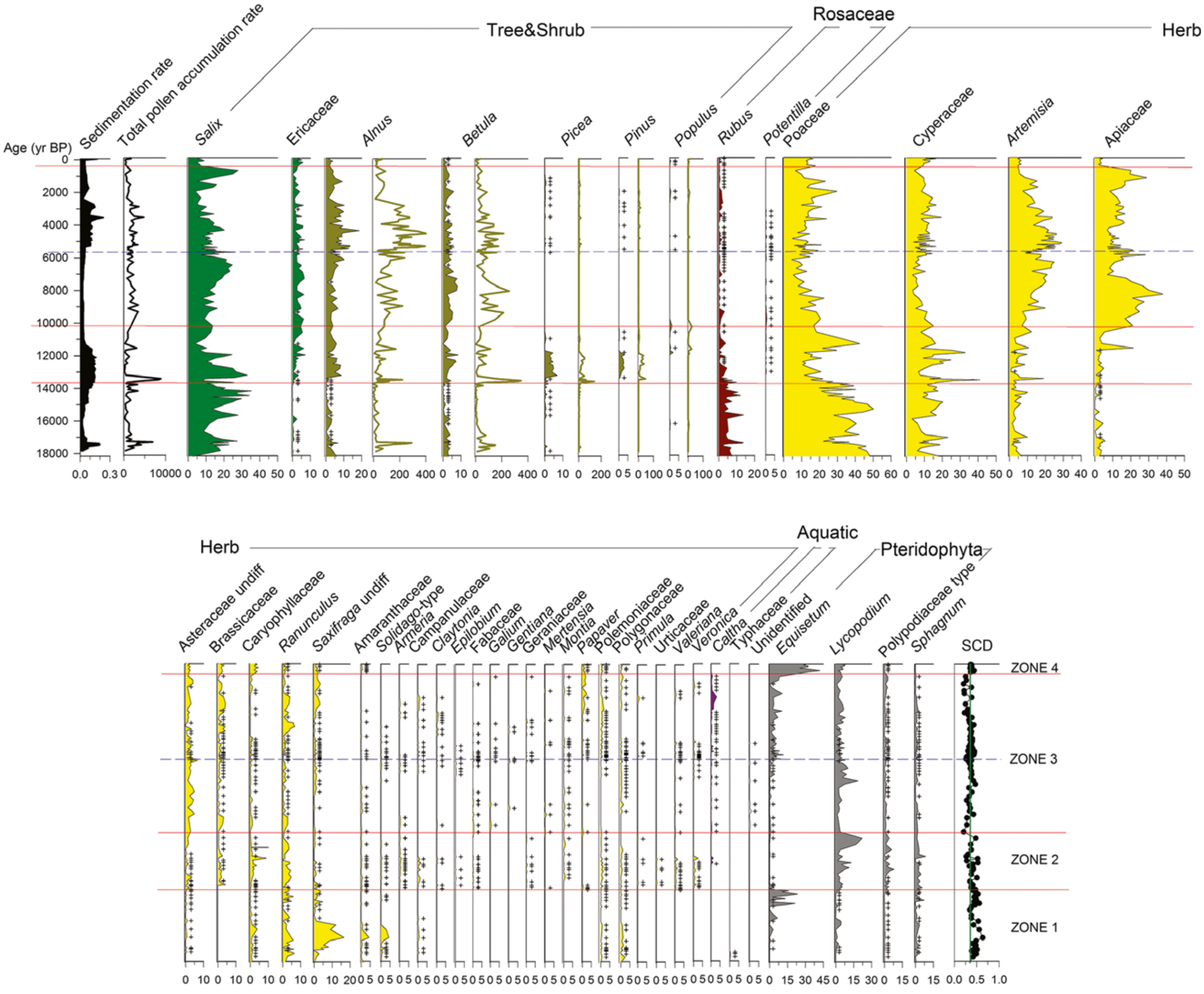

Figure 3 Vegetation history of St. Paul Island from 18,000 yr BP to the present, based on pollen diagram from the Lake Hill showing relative pollen abundances for all taxa (%), pollen accumulation rates for long-distance-transport taxa (grains/cm^2/yr), total pollen accumulation rates (grains/cm^2/yr), sedimentation rate (cm/yr), and minimum squared chord distances. Green shading indicates woody taxa interpreted to be locally present on St. Paul Island and the southern margin of the Beringian Land Bridge, whilst brown shadings indicate pollen types interpreted as false presences, i.e. because of long-distance transport. Dark red shadings indicate woody Rosaceae taxa, yellow shadings indicate herbaceous taxa, and grey colours indicate Pteridophyte taxa and *Sphagnum*. Pollen and spore taxa abundances are calculated as percent abundances of total pollen and spore types. Cross signs (+) indicate percentage < 1%. Red lines indicate the division of the pollen record into four zones by CONISS in R package 'rioja' (Grimm, 1987; Juggins, 2015). The blue dashed line represents the timing of woolly mammoth extinction estimated at 5600 yr BP (Graham *et al.*, 2016). Minimum SCDs show the dissimilarity between each fossil sample and its closest analogue in the modern pollen reference dataset.

abundant pollen type, averaging 20% throughout the core, and *Salix* is the most abundant shrub pollen type, averaging 14%. Of the herbaceous pollen taxa, 22 are minor, with a maximum pollen percentage < 3%. Minimum SCDs are consistently high (> 0.21), indicating vegetation communities that differ from the mainland of North America. Non-analogue communities are present before the Holocene (SCDs> 0.36, Fig. 3).

The fossil pollen record indicates stable forb-graminoid tundra with a minor shrub component on St. Paul Island during the last 18,000 years (Fig. 3). CONISS analyses divide the Lake Hill pollen and spore record into four zones (Fig. 3). Zone 1, from 18,200 to 13,800 yr BP, is characterized by high Poaceae and fluctuating *Salix* pollen abundances from the last glacial period until several centuries before the Younger Dryas (YD) onset at 12,900 yr BP. Arctic forbs such as *Saxifraga*, *Artemisia* and *Ranunculus* have elevated abundances, with Amaranthaceae and *Solidago*-type abundant until 16,700 yr BP. *Equisetum* is rare before 14,790 yr BP, but increases to 23% by the end of Zone 1, possibly indicating an increase in the moisture availability. Zone 2, from 13,800 to 10,600 yr BP, is characterized by the presence of moderate Poaceae, Cyperaceae and *Salix* pollen abundances during most of the YD. *Picea* and *Pinus* pollen are found in low abundances (< 5%) between 13,250 and 11,850 yr BP, interpreted as originating from long-distance transport. All *Pinus* grains are poorly preserved and present only as bladders or bodies with one bladder. The high abundances of *Picea*, *Alnus* and *Betula* occur only when total pollen accumulation rate is lower than 5000 grains/cm^2/yr (Fig. S3.4), further suggesting a non-local source. Zone 3, representing most of the Holocene (10,610 to 690 yr BP), is characterized by higher forb diversity and moderate Poaceae, Cyperaceae, *Salix, Artemisia* and Apiaceae pollen abundances. Woolly mammoth extinction at 5600 yr BP (Graham *et al.*, 2016) is in the middle of Zone 3, and shows generally small vegetation changes, consisting of gradual increases in Poaceae and Cyperaceae pollen abundances, a gradual decline in *Artemisia*, and a rapid drop then gradual recovery of Apiaceae. Abundances of minor forb taxa and *Equisetum* also increase after 5600 yr BP. The main feature of Zone 4, from 690 yr BP to the present, is abundant *Equisetum*, interpreted to indicate a wet environment with well-drained substrate. *Salix* declines, whilst Ericaceae, Caryophyllaceae and Brassicaceae increase, and other forbs are in low abundances or absent.

PCA analysis indicates two main components for the modern and fossil pollen assemblages (Fig. 4), with PC1 explaining 16.1% of the variance in pollen abundances and PC2 explaining 10.2%. There is low compositional overlap in the pollen assemblages between modern mainland tundra sites and St. Paul sites. The closest mainland counterparts are from herbaceous Arctic tundra (Fig. 4). The mainland tundra assemblages have higher abundances of pollen from woody taxa, including *Picea, Betula,* Ericaceae and *Alnus,* whilst the St. Paul assemblages have a higher diversity of forb taxa and higher *Salix* abundances. The St. Paul modern assemblages are the closest analogues for the St. Paul fossil assemblages. Together, the PCA and SCDs analyses indicate that the vegetation communities on St. Paul have been compositionally distinct from modern mainland tundra communities throughout the past 18,000 years.

Assessing local presence of woody taxa on St. Paul Island

The combination of pollen, macrobotanical fossils, and sedaDNA analyses allow strong inferences about local species presence. There is no evidence that *Picea* has been present on St. Paul, or in its near vicinity, for the last 18,000 years. No *Picea* macrofossils are found in the sediments (Fig. 5), and *Picea* is absent from St. Paul today based on our survey and a historical vegetation survey (Macoun, 1899) (Fig. S1.1). *Picea* pollen abundances are highest during the YD, at 7%, when *Picea* pollen accumulation rates are very low (averaging 31 grains/cm^2/yr) (Fig. 3), suggesting that this peak is caused by decreased local pollen productivity and intensified atmospheric circulation, resulting in a higher proportion of exotic pollen. This finding matches Colinvaux's (1981) report of *Picea* pollen between 706 and 1160 cm at high-relative abundances but low concentrations. Analyses from the Galapagos Islands also show that the relative mixture of local versus long-distance components in pollen assemblages is highly sensitive to changes in local pollen productivity (van der Knaap *et al.*, 2012). SedaDNA also does not support *Picea* presence. Either the same proportion or fewer DNA fragments are identified as *Picea* in the samples as in the negative controls (Fig. 5), suggesting that the few fragments that map to either *Picea* genome are indistinguishable from background noise. This inference is supported by the short length of these molecules (< 35 bp), which can lead to erroneous read mapping because of low information content (Fig. 6). Further, these DNA fragments do not exhibit typical aDNA damage patterns, such as elevated deamination rates at the ends of molecules (Fig. 6, S8.5), suggesting that these are not true *Picea* aDNAs (Dabney *et al.*, 2013).

Similarly, we find no evidence supporting the presence of *Betula* and *Alnus* on St. Paul during and after the LGM. *Betula* and *Alnus* pollen are consistently present but at low accumulation rates and relative abundances, varying around 65 and 125 grains/cm^2/yr, and 4% and 8%, lower than the typical thresholds for local presence of 30% and 20% (Anderson & Brubaker, 1986) (Fig. 3, 5). No *Betula* or *Alnus* are found in the modern and historical vegetation surveys, nor any *Betula* or *Alnus* macrofossils in the sediments (Fig. 5). SedaDNA data for *Betula* also indicate local absence, with inferred *Betula* DNA in the samples at concentrations ~1-2 orders of magnitude lower than those found in the negative extraction controls (Fig. 5). We find no evidence of DNA damage patterns in the inferred *Betula* DNA, suggesting, as for *Picea*, that these are not truly *Betula* aDNAs, but are rather false matches to the *Betula* reference genome (Fig. 6, S8.5). Hence, as with *Picea*, multiple lines of

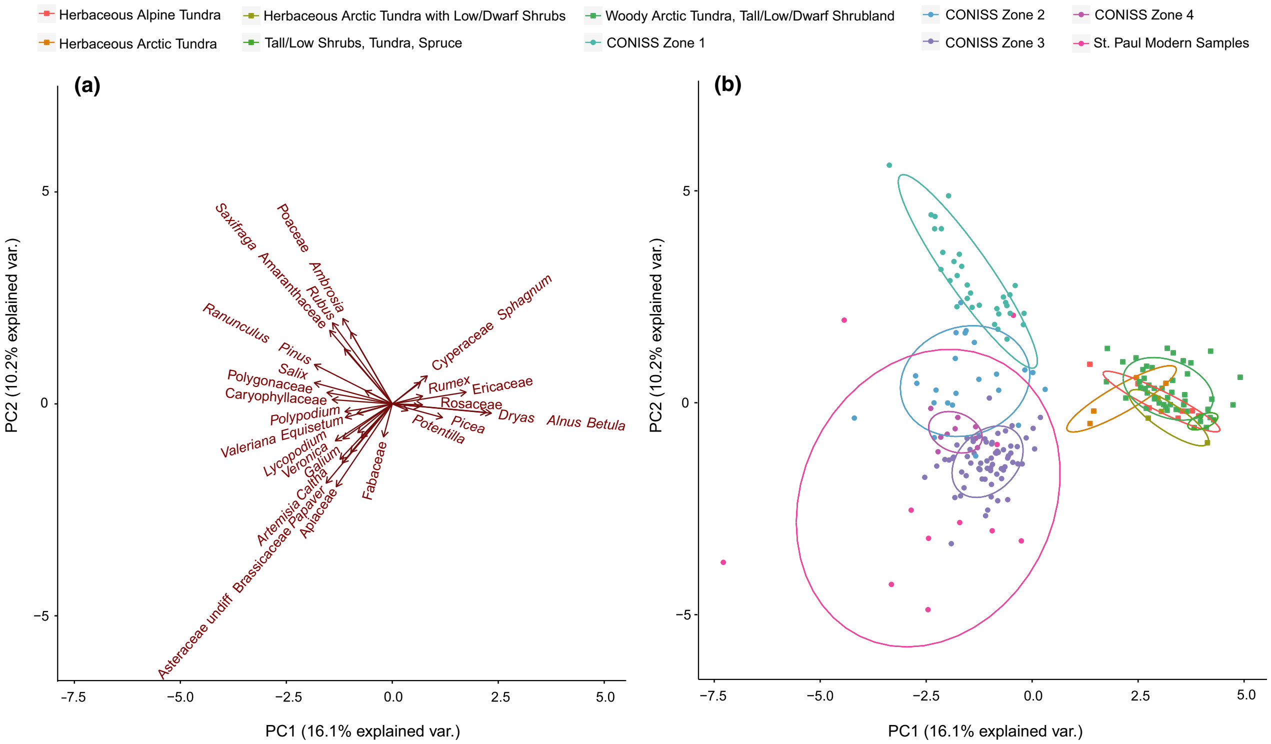

Figure 4 Principal component analysis (PCA) for fossil pollen samples from Lake Hill and modern North America tundra pollen assemblages. Plot a) shows the variance analysis for all taxa, and plot b) shows that all the pollen assemblages, including fossil St. Paul assemblages, modern St. Paul assemblages, and modern mainland assemblages. Principal component 1 (PC1) explains 16.1% of the variance in the pollen data, whilst PC2 explains 10.2% of the variance. Classification of pollen assemblages is based on different procedures for fossil and modern assemblages: fossil samples are classified by CONISS zones (zones 1–4); modern pollen samples from St. Paul are given their own group; mainland pollen types are classified into five groups based on North American Seasonal Land Cover vegetation classification for their location (Anderson, 1976): herbaceous Alpine tundra, herbaceous arctic tundra, herbaceous arctic tundra with low/dwarf shrubs, tall/low shrubs/tundra/spruce, and woody arctic tundra/tall/low/dwarf shrubland. The fossil sample at 11,320 BP in CONISS zone 2 is outside the bounds of plot b located at the point of (−5.8, 9.5). Ellipses are drawn for each group with 68% (1σ) variance.

evidence indicate that neither *Betula* nor *Alnus* were locally present on St. Paul Island and the southern Beringia for the last 18,000 years.

In contrast to *Picea*, *Betula* and *Alnus*, we find multiple lines of evidence supporting the continuous presence of *Salix* on St. Paul Island during the past 18,000 years. *Salix arctica* and *S. reticulata* are present today on the island as low-stature shrubs (1-20 cm tall) and are moderately common (Fig. S1.1). Fossil pollen abundances are higher than the other three woody taxa and similar to modern *Salix* pollen abundances on St. Paul (Fig. 5, S6.3). Macrobotanical fossils of *Salix*, including stem (wood) and fragmentary, generally skeletonized leaves, are common in the Holocene sediments (Fig. 5, S3.1). The dearth of Pleistocene macrobotanical fossils is probably becaue of the poorer preservation associated with the sandy late-glacial sediments, but may indicate sparser plant densities. Concentrations of inferred *Salix* DNA in the samples are always higher than in the negative extraction controls (Fig. 5), often by an order of magnitude. The presence of authentic *Salix* sedaDNA in the samples is further supported by DNA damage patterns, including typical deamination and depurination-induced fragmentation signatures (Fig. 6), which are not observed in the negative extraction controls (Fig. S3.5).

Besides the taxa discussed above, *Pinus* and *Populus* pollen grains are also found in the core (Fig. 3). However, their pollen abundances are even lower than 5%, which is the usual threshold for the local deposition of *Pinus* and *Populus* pollen, thus these pollen types also likely source from non-local plant populations. The period of elevated *Pinus* abundances (up to 3.4%) corresponds to the period of elevated *Picea* abundances during the YD, suggesting a common distant source.

DISCUSSION

Refugia, cryptorefugia and pseudorefugia

This multi-proxy study provides unusually strong evidence that *Picea*, *Betula* and *Alnus* were not present in the Lake Hill watershed and, presumably, on St. Paul Island for the last 18,000 years. Fossil pollen abundances of *Picea*, *Betula*

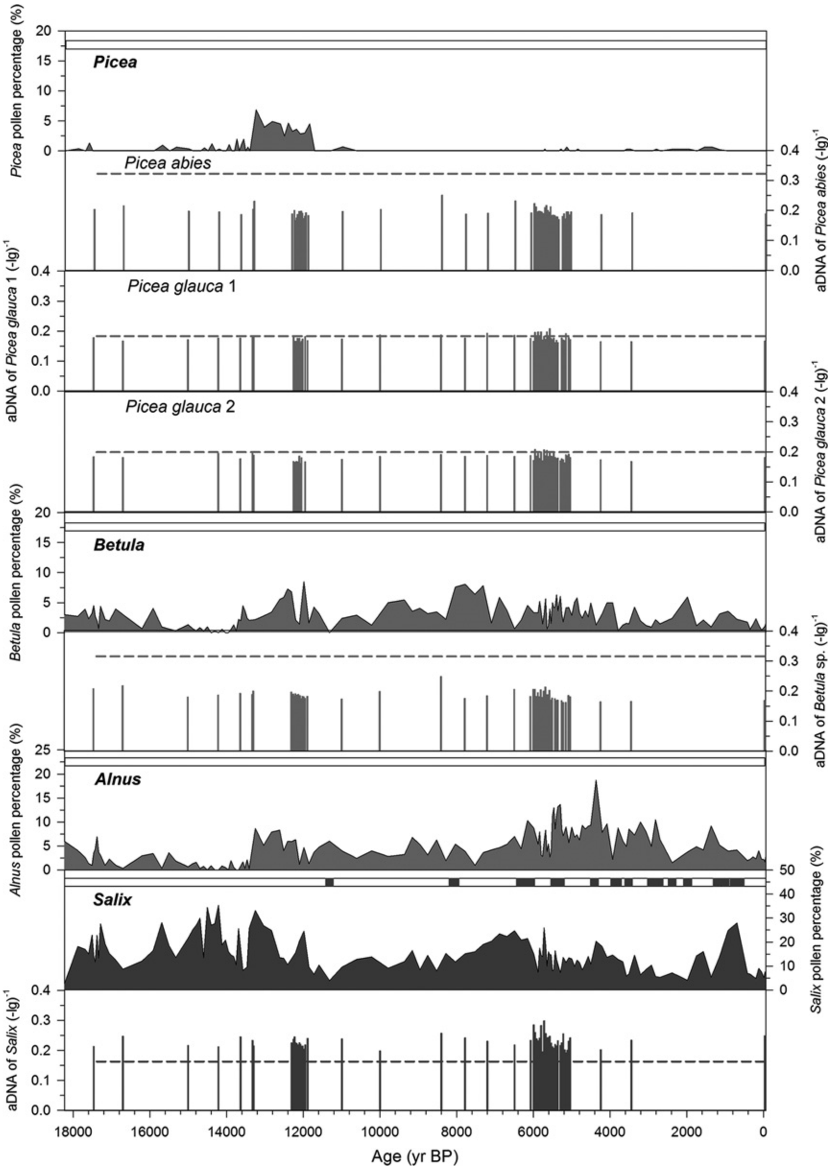

Figure 5 Pollen, macrobotanical fossils and sedaDNA of *Picea*, *Betula, Alnus* and *Salix* from the Lake Hill. For each genus, solid curves represent pollen percent abundances of total pollen and spore sum, vertical bars represent the concentration of sedaDNA fragments matched to that taxon, and the horizontal bar above each solid curve indicates the presence or absence of macrobotanical fossils. In the sedaDNA plots, the dashed line illustrates the average concentration of sedaDNA fragments found in the negative extraction controls. In the macrofossil bars, empty space indicates that no plant macrofossils were found at these depths. Of these taxa, macrofossils were only found for *Salix*, which is also present on the island today.

and *Alnus* are low and consistent with long-distance transport, and no presence was detected in sedaDNA, macrobotanical fossils, and contemporary vegetation. Establishing the absence of these genera is a negative result, but an important one. When constraining biogeographical models of the climatic and historical controls on past species range shifts, confidently establishing the absence of a species at a location is as important as establishing its presence. Multiple lines of evidence can indicate the presence of past refugia, including species distribution models, phylogeographic surveys, molecular, micro- and macrofossils (Hu *et al.*, 2009; Gugger *et al.*, 2010; Gavin *et al.*, 2014; Tollefsrud *et al.*, 2015). However, no single contemporary or fossil indicator is a definitive indicator of the past presence or absence, creating the possibility of cryptorefugia and pseudorefugia. Plant macrofossils are usually definitive evidence of the presence within a watershed, but little can be inferred from their absence (Gavin *et al.*, 2014). Fossil pollen data are better able to capture spatiotemporal distributions of plant abundances and less able to definitively establish range limits, despite long-standing efforts to identify signals of range limits or species establishment. Ancient DNA has revealed cryptic refugia, but can be subject to challenges of contamination (Birks *et al.*, 2012) or post-depositional mobilization within a stratigraphic profile (Haile *et al.*, 2009). Contemporary phylogenetic surveys that indicate high genetic diversity or unique genetic markers have been interpreted as signs of cryptic populations (McLachlan *et al.*, 2005), but not all genetic markers are equally informative (Tzedakis *et al.*, 2013), and phylogeographic inferences about post-glacial range dynamics of plant species can be confounded by introgression (Thomson *et al.*, 2015). Therefore, multi-proxy studies such as this one are needed confidently to establish the absence or presence of taxa.

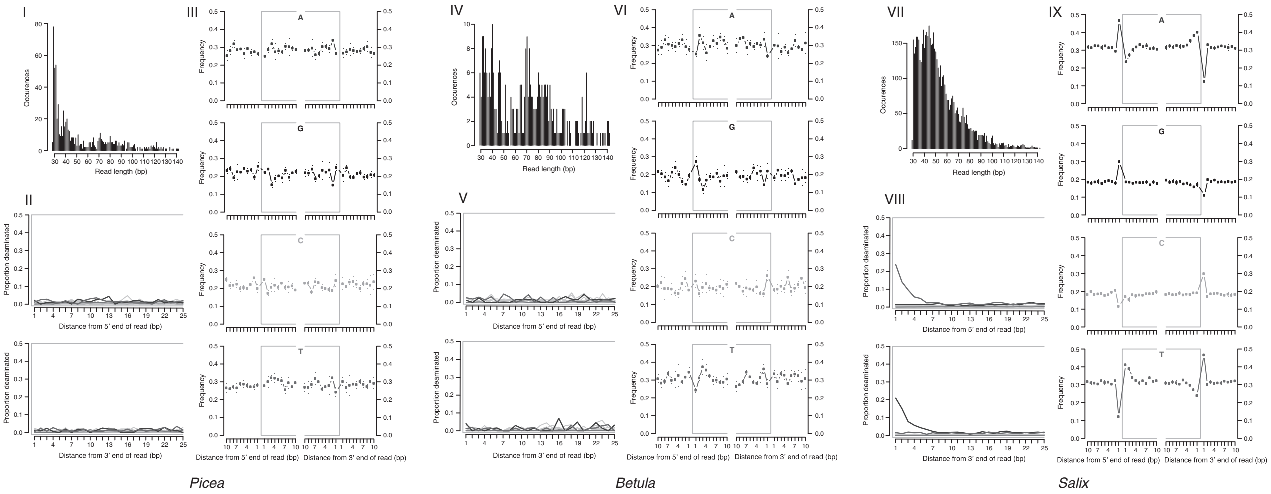

Figure 6 Ancient DNA damage profiles of fragments inferred to have originated from *Picea* (I-III), *Betula* (IV-VI) and *Salix* (VII-IX) from the Lake Hill core samples. Panels I–III are based on alignment to the *Picea abies* genome. Panels I, IV, and VII show distributions of DNA fragment lengths. Panels II, V, and VIII show the proportions of deaminated sites at the 5′ and 3′ ends of the molecules. Ancient DNA is characterized by elevated rates of cytosine to thymine misincorporations at the 5′ end and a corresponding elevation in the rate of guanine to adenine at the 3′ end. Panels III, VI, and IX show the frequency of the four bases (guanine (G), adenine (A), cytosine (C) and thymine (T)) around the 5′ and 3′ ends of the DNA molecules. Depurination-induced fragmentation, a characteristic of aDNA, is indicated by elevated frequencies of G and A immediately upstream of the 5′ end and corresponding increases of C and T immediately downstream of the 3′end of DNA molecules. These aDNA damage patterns are consistent with the presence of authentic *Salix* aDNA, but not the presence of authentic *Picea* or *Betula* aDNA.

Our results also suggest that *Picea*, *Alnus* and *Betula* were not present on the south-central BLB, although this conclusion relies on indirect inference. The Lake Hill is an unusually-sheltered site (Fig. 1) with a continuously present lake since the LGM (Graham *et al.*, 2016; Wooller *et al.*, unpub.), so local site conditions were favourable for shrub establishment. No dispersal barrier existed at the LGM to prevent these taxa from reaching the St. Paul region. Hence, the absence of *Alnus*, *Betula* and *Picea* suggests that regional climates on the southern coastal BLB prevented establishment by these taxa. Elias & Crocker (2008) note that island remnants of Beringia may be unrepresentative of vegetation at lower elevations. However, elevational gradients as a strong filter on species presence is unlikely given that the Lake Hill currently is only 37 m above the sea level. Given that the sea level at the LGM was 130 m lower than the present (a high-end estimate) and a normal lapse rate of 6.4 °C/1000 m, the maximum elevational and temperature difference between the Lake Hill and low-lying sites would have been 170 m and only 1.1 °C. This temperature difference is ecologically meaningful, but does not seem sufficient to preclude the local establishment of woody shrubs or trees such as *Betula*, *Picea*, or *Alnus* at the Lake Hill if they had been present in the regional species pool. Insofar as Lake Hill is representative of environments along the southern coastal BLB, then this region appears to have not been a glacial refugium for these taxa.

The proximity of *Picea*, *Alnus* and *Betula* populations to this site remains unclear. Low pollen productivity and stronger atmospheric circulation during the YD likely enabled enhanced long-distance components of pollen. Colinvaux (1981) proposed two long-distance sources of *Picea* pollen: south of continental ice sheets, with pollen transported by episodically strong spring winds, or from restricted relict populations on Beringia, such as the old delta of the Yukon-Kuskokwim system on the south Beringia coast. *Picea* forest is found around Lake Baikal in south-eastern Siberia during the Bølling-Allerød warming (Shichi *et al.*, 2009), pollen sites with abundant *Alnus* occur in eastern Siberia after the LGM (Brubaker *et al.*, 2005), and *Pinus pumila* is found in the Upper Kolyma region during the LGM (Anderson *et al.*, 2010), making eastern and north-eastern Siberia a potential source for woody taxa pollen on St. Paul Island. Eastern Beringia is also a likely refugium for *Picea glauca* (Brubaker *et al.*, 2005; Anderson *et al.*, 2006), and pollen evidence is consistent with at least scattered *Betula* presence in some habitats across Beringia (Brubaker *et al.*, 2005).

Vegetation history in southern coastal Beringia after the LGM

The Lake Hill record suggests prostrate shrub-graminoid tundra on St. Paul Island after the LGM, with varying proportions of graminoids and forbs and persistent presence of *Salix* and Ericaceae, presumably in the prostrate form. The plant community appears to have been mostly stable, except for *Equisetum* peaks that may indicate wetter conditions before the YD and after 690 yr BP. This prostrate shrub-graminoid tundra is similar to graminoid-forb tundra found at other glacial-aged sites in south-central Beringia (Colinvaux, 1967b; Ager, 2003; Ager & Phillips, 2008). The persistence of this dry tundra over the whole period of record may have been facilitated by soils that today are thin and well-drained, with little paludification and underlain by a volcanic and porous substrate.

This inference suggests that southern Beringia was covered by graminoid-forb tundra under cold and dry climates during the past 18,000 years. Mesic shrub tundra has been proposed as a glacial refugium for woody taxa and a source of wood fuel for ancient people in Beringia (Hoffecker *et al.*, 2014). Evidence includes mesic beetle fossils, relatively abundant *Betula* pollen, and *Sphagnum* spores (Elias *et al.*, 1996, 1997). Ager (2003) and Ager & Phillips (2008), however, have argued that graminoid-forb-*Salix* tundra vegetation associated with cold and dry climate extended into the lowlands of Beringia during the LGM. Our results support the latter hypothesis by showing that LGM Beringia was primarily covered by graminoid-forb tundra with shrub elements present in prostrate form or in restricted habitats, but does not rule out the possibility of localized areas of mesic shrub tundra in now-submerged portions of Beringia.

Trophic consequences of megafaunal extinction

One debate has centred on whether arctic herbaceous tundra, with its low productivity, can provide sufficient forage to support extensive Pleistocene megafauna populations (Elias & Crocker, 2008). It is known, however, that the St. Paul Island ecosystem sustained an isolated woolly mammoth population from ca. 14,500 yr BP, when the island became isolated from the mainland, until 5600 yr BP (Graham *et al.*, 2016). This persistence of woolly mammoth indicates that prostrate shrub and graminoid tundra, even on a small island (109 km^2), can provide sufficient food resources to sustain a grazing megaherbivore population for thousands of years.

The lack of major change in vegetation composition on St. Paul Island at the time of the woolly mammoth extinction around 5600 yr BP (Graham *et al.*, 2016) suggests that the vegetation on St. Paul Island was less affected by megafaunal grazing than has been shown in more temperate ecosystems (Gill *et al.*, 2009). One likely reason for this difference is that fire, which drives megaherbivore-biomass feedbacks that amplify vegetation turnover in temperate and subtropical ecosystems, is effectively absent from St. Paul Island (initial surveys of the Lake Hill core for sedimentary charcoal indicated effectively zero charcoal). Vegetation composition also appears to have been minimally affected by climatic changes during the last deglaciation and Holocene, likely because of the barriers to immigration for thermophilous taxa.

However, the trophic effects of the woolly mammoth extinction may manifest as small changes in the tundra composition and substantial changes in the rates of sediment erosion and mobilization. The observed increase in forb abundance (from 28% to 38% in the sum of forb taxa abundance after the extinction) could indicate a release from megaherbivore suppression, consistent with evidence that herbs were a major dietary resource for megafaunal grazers (Willerslev *et al.*, 2014). The megafaunal extinction event also closely coincides with a significant sedimentary transition at 5.03 m (a shift from organic-rich silts to gyttja), which may indicate that mammoths locally increased erosion rates in the Lake Hill crater (Graham *et al.*, 2016).

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REFERENCES

Ager, T.A. (2003) Late Quaternary vegetation and climate history of the central Bering land bridge from St. Michael Island, western Alaska. *Quaternary Research*, **60**, 19–32.

Ager, T.A. & Phillips, R.L. (2008) Pollen evidence for late Pleistocene Bering Land Bridge environments from Norton Sound, Northeastern Bering Sea, Alaska. *Arctic, Antarctic, and Alpine Research*, **40**, 451–461.

Anderson, J.R. (1976) *A land use and land cover classification system for use with remote sensor data (Vol. 964)*. US Government Printing Office, Washington.

Anderson, P.M. & Brubaker, L.B. (1986) Modern pollen assemblages from northern Alaska. *Review of Palaeobotany and Palynology*, **46**, 273–291.

Anderson, L.L., Hu, F.S., Nelson, D.M., Petit, R.J. & Paige, K.N. (2006) Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proceedings of the National Academy of Sciences USA*, **103**, 12447–12450.

Anderson, P.M., Lozhkin, A.V., Solomatkina, T.B. & Brown, T.A. (2010) Paleoclimatic implications of glacial and postglacial refugia for *Pinus pumila* in western Beringia. *Quaternary Research*, **73**, 269–276.

Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. & Shabel, A.B. (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science*, **306**, 70–75.

Bigelow, N.H., Brubaker, L.B., Edwards, M.E., Harrison, S.P., Prentice, I.C., Anderson, P.M., Andreev, A.A., Bartlein, P.J., Christensen, T.R. & Cramer, W. (2003) Climate change and Arctic ecosystems: 1 Vegetation changes north of

55 N between the last glacial maximum, mid-Holocene, and present. *Journal of Geophysical Research: Atmospheres*, **108**, 8170.

Birks, H.H., Giesecke, T., Hewitt, G.M., Tzedakis, P.C., Bakke, J. & Birks, H.J. (2012) Comment on "Glacial survival of boreal trees in northern Scandinavia". *Science*, **338**, 742; author reply 742.

Birol, I., Raymond, A., Jackman, S.D. *et al.* (2013) Assembling the 20 Gb white spruce (*Picea glauca*) genome from whole-genome shotgun sequencing data. *Bioinformatics*, **29**, 1492–1497.

Blaauw, M. & Christen, J.A. (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis*, **6**, 457–474.

Blinnikov, M.S., Gaglioti, B.V., Walker, D.A., Wooller, M.J. & Zazula, G.D. (2011) Pleistocene graminoid-dominated ecosystems in the Arctic. *Quaternary Science Reviews*, **30**, 2906–2929.

Bourgeois, J.C., Koerner, R.M. & Alt, B.T. (1985) Airborne pollen: a unique air mass tracer, its influx to the Canadian High Arctic. *Annals of Glaciology*, **7**, 16.

Brubaker, L.B., Anderson, P.M., Edwards, M.E. & Lozhkin, A.V. (2005) Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography*, **32**, 833–848.

Colinvaux, P.A. (1967a) Bering land bridge: evidence of spruce in late-wisconsin times. *Science*, **156**, 380–383.

Colinvaux, P.A. (1967b) A long pollen record from St. Lawrence island, Bering Sea (Alaska). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **3**, 29–48.

Colinvaux, P. (1981) Historical ecology in Beringia – the south land bridge coast at St. Paul Island. *Quaternary Research*, **16**, 18–36.

Dabney, J., Meyer, M. & Pääbo, S. (2013) Ancient DNA damage. *Cold Spring Harbor Perspectives in Biology*, **5**, a012567.

Doughty, C.E. (2013) Preindustrial human impacts on global and regional environment. *Annual Review of Environment and Resources*, **38**, 503–527.

Edwards, M.E., Brubaker, L.B., Lozhkin, A.V. & Anderson, P.M. (2005) Structurally novel biomes: a response to past warming in Beringia. *Ecology*, **86**, 1696–1703.

Elias, S.A. & Crocker, B. (2008) The Bering Land Bridge: a moisture barrier to the dispersal of steppe–tundra biota? *Quaternary Science Reviews*, **27**, 2473–2483.

Elias, S.A., Short, S.K., Nelson, C.H. & Birks, H.H. (1996) Life and times of the Bering land bridge. *Nature*, **382**, 60–63.

Elias, S.A., Short, S.K. & Birks, H.H. (1997) Late Wisconsin environments of the Bering Land Bridge. *Palaeogeography Palaeoclimatology Palaeoecology*, **136**, 293–308.

Gavin, D.G., Oswald, W.W., Wahl, E.R. & Williams, J.W. (2003) A statistical approach to evaluating distance metrics and analog assignments for pollen records. *Quaternary Research*, **60**, 356–367.

Gavin, D.G., Fitzpatrick, M.C., Gugger, P.F. *et al.* (2014) Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytologist*, **204**, 37–54.

Gill, J.L. (2014) Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytologist*, **201**, 1163–1169.

Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B. & Robinson, G.S. (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, **326**, 1100–1103.

Graham, R.W., Belmecheri, S., Choy, K., Culleton, B.J., Davies, L.J., Froese, D., Heintzman, P.D., Hritz, C., Kapp, J.D., Newsom, L.A., Rawcliffe, R., Saulnier-Talbot, E., Shapiro, B., Wang, Y., Williams, J.W. & Wooller, M.J. (2016) Timing and causes of mid-Holocene mammoth extinction on St. Paul Island, Alaska. *Proceedings of National Academy of Sciences USA*, **113**, 9310–9314.

Grimm, E.C. (1987) CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, **13**, 13–35.

Gugger, P.F., Sugita, S. & Cavender-Bares, J. (2010) Phylogeography of Douglas-fir based on mitochondrial and chloroplast DNA sequences: testing hypotheses from the fossil record. *Molecular Ecology*, **19**, 1877–1897.

Guthrie, R.D. (2001) Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews*, **20**, 549–574.

Haile, J., Froese, D.G., Macphee, R.D., Roberts, R.G., Arnold, L.J., Reyes, A.V., Rasmussen, M., Nielsen, R., Brook, B.W., Robinson, S., Demuro, M., Gilbert, M.T., Munch, K., Austin, J.J., Cooper, A., Barnes, I., Moller, P. & Willerslev, E. (2009) Ancient DNA reveals late survival of mammoth and horse in interior Alaska. *Proceedings of National Academy of Sciences USA*, **106**, 22352–22357.

Hoffecker, J.F., Elias, S.A. & O'Rourke, D.H. (2014) Anthropology. Out of Beringia? *Science*, **343**, 979–980.

Hu, F.S., Hampe, A. & Petit, R.J. (2009) Paleoecology meets genetics: deciphering past vegetational dynamics. *Frontiers in Ecology and the Environment*, **7**, 371–379.

Hultén, E. (1968) *Flora of Alaska and neighboring territories: a manual of the vascular plants*. Stanford University Press, Palo Alto.

Juggins, S. (2015) *rioja: Analysis of Quaternary Science Data*. R package version (0.9-9). Available at: http://cran.r-project.org/package=rioja.

Kaplan, J., Bigelow, N., Prentice, I.C., Harrison, S.P., Bartlein, P.J., Christensen, T., Cramer, W., Matveyeva, N., McGuire, A. & Murray, D. (2003) Climate change and Arctic ecosystems: 2. Modeling, paleodata model comparisons, and future projections. *Journal of Geophysical Research: Atmospheres*, **108**, 8171.

Kaufman, D.S., Jensen, B.J.L., Reyes, A.V., Schiff, C.J., Froese, D.G. & Pearce, N.J.G. (2012) Late Quaternary tephrostratigraphy, Ahklun Mountains, SW Alaska. *Journal of Quaternary Science*, **27**, 344–359.

Macoun, J.M. (1899) *A list of the plants of the Pribilof Islands, Bering Sea: with notes on their distribution*. US Government Printing Office, Washington.

McLachlan, J.S., Clark, J.S. & Manos, P.S. (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, **86**, 2088–2098.

Nystedt, B., Street, N.R., Wetterbom, A. *et al.* (2013) The Norway spruce genome sequence and conifer genome evolution. *Nature*, **497**, 579–584.

Parducci, L., Edwards, M.E., Bennett, K.D., Alm, T., Elverland, E., Tollefsrud, M.M., Jorgensen, T., Houmark-Nielsen, M., Larsen, N.K., Kjaer, K.H., Fontana, S.L., Alsos, I.G. & Willerslev, E. (2012a) Response to comment on "Glacial survival of boreal trees in northern Scandinavia". *Science*, **338**, 742–742.

Parducci, L., Jorgensen, T., Tollefsrud, M.M. *et al.* (2012b) Glacial survival of boreal trees in northern Scandinavia. *Science*, **335**, 1083–1086.

Provan, J. & Bennett, K.D. (2008) Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology and Evolution*, **23**, 564–571.

R Core Team (2015) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org/).

Scheffer, V.B. (1951) The rise and fall of a reindeer herd. *Scientific Monthly*, **73**, 356–362.

Shichi, K., Takahara, H., Krivonogov, S.K., Bezrukova, E.V., Kashiwaya, K., Takehara, A. & Nakamura, T. (2009) Late Pleistocene and Holocene vegetation and climate records from Lake Kotokel, central Baikal region. *Quaternary International*, **205**, 98–110.

Simpson, G.L. (2007) Analogue methods in palaeoecology: using the analogue package. *Journal of Statistical Software*, **22**, 1–29.

Stewart, J.R. & Lister, A.M. (2001) Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology and Evolution*, **16**, 608–613.

Thomson, A.M., Dick, C.W., Dayanandan, S. & Carine, M. (2015) A similar phylogeographical structure among sympatric North American birches (*Betula*) is better explained by introgression than by shared biogeographical history. *Journal of Biogeography*, **42**, 339–350.

Tollefsrud, M.M., Latałowa, M., van der Knaap, W.O., Brochmann, C. & Sperisen, C. (2015) Late Quaternary history of North Eurasian Norway spruce (*Picea abies*) and Siberian spruce (*Picea obovata*) inferred from macrofossils, pollen and cytoplasmic DNA variation. *Journal of Biogeography*, **42**, 1431–1442.

Tzedakis, P.C., Emerson, B.C. & Hewitt, G.M. (2013) Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends in Ecology and Evolution*, **28**, 696–704.

van der Knaap, W., van Leeuwen, J.F., Froyd, C.A. & Willis, K.J. (2012) Detecting the provenance of Galápagos non-native pollen: the role of humans and air currents as transport mechanisms. *The Holocene*, **22**, 1373–1383.

Veltre, D.W. & Veltre, M.J. (1981) A preliminary baseline study of subsistence resource utilization in the Pribilof Islands. *Contract*, **81**, 119.

Veltre, D.W., Yesner, D.R., Crossen, K.J., Graham, R.W. & Coltrain, J.B. (2008) Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear remains, Pribilof Islands, Alaska. *Quaternary Research*, **70**, 40–50.

Vu, V.Q. (2011) *ggbiplot: A ggplot2 based biplot*. R package version (0.55). Available at: https://github.com/vqv/ggbiplot.

Whitmore, J., Gajewski, K., Sawada, M., Williams, J.W., Shuman, B., Bartlein, P.J., Minckley, T., Viau, A.E., Webb, T., Shafer, S., Anderson, P. & Brubaker, L. (2005) Modern pollen data from North America and Greenland for multi-scale paleoenvironmental applications. *Quaternary Science Reviews*, **24**, 1828–1848.

Willerslev, E., Davison, J., Moora, M. *et al.* (2014) Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature*, **506**, 47–51.

Williams, J.W., Shuman, B.N. & Webb, T. (2001) Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology*, **82**, 3346–3362.

Yesner, D.R. (2001) Human dispersal into interior Alaska: antecedent conditions, mode of colonization, and adaptations. *Quaternary Science Reviews*, **20**, 315–327.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Core information, vegetation survey, fossils.
Appendix S2. sedaDNA reference genomes and metadata.
Appendix S3. Woody taxa pollen & ancient DNA.

BIOSKETCH

Yue Wang is a PhD student in the Department of Geography at the University of Wisconsin-Madison. Her research foci are palaeoecology and palaeoclimatology, with a particular emphasis on the vegetation and megafaunal dynamics in North America during the late Quaternary. Her research employs a combination of palaeoecological proxies, analyses of palaeoclimatic simulations from earth system models, and mechanistic ecological modelling.

Author contributions: Y.W. and J.W.W. conducted pollen and spore analysis, with interpretations aided by N.H.B. P.D.H. and B.S. conducted sedaDNA analysis. L.N. conducted macrobotanical fossils analysis. M.J.W. led the sampling for radiocarbon dating below 7 m. All authors contributed to the article writing, with writing led by Y.W. and J.W.W.

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