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Vegetation change and human impacts on Rebun Island (Northwest Pacific) over the last 6000 years

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ABSTRACT

This study presents a high-resolution, chronologically well-constrained pollen record from Lake Kushu (45°25′58″N, 141°02′05″E) and a record of archaeobotanical remains from the nearby Hamanaka 2 archaeological site. The pollen record suggests continuous long-term cooling, which parallels the decline in Northern Hemisphere summer insolation. This cooling trend is overlaid by several rather quick transitions towards cooler conditions (ca. 5540/5350, 1550, and 390 cal BP) and one distinct decadal-scale cold event around 4130 cal BP. These shifts, on one hand, correspond with major hemispherical or global-scale climate transitions/events, including the 'Holocene Climate Transition', the onset of the 'Dark Ages Cold Period' main phase, the 'Little Ice Age', and the '4.2 kiloyear event', respectively. On the other hand, the shifts partly coincide with transformations in the Hokkaido prehistoric cultural sequence including the onset of the Middle Jomon (ca. 5000 cal BP), the Middle/Late Jomon transition (ca. 4000 cal BP), the immigration of Okhotsk culture groups (from ca. 1500 cal BP), and the establishment of the Classic Ainu culture (ca. 350 cal BP). AMS radiocarbon dating of charred macrobotanical remains from Hamanaka 2 suggests three discontinuous occupational periods ca. 390–50 BCE, 420–970 CE, and from 1640 CE, which correspond to the northern Hokkaido Epi Jomon (ca. 300–100 BCE), Okhotsk (ca. 500–1000 CE), and Classic Ainu (ca. 1600–1868 CE) cultural phases, respectively. While impact on the island's natural environments (forest clearance) was marginal during the Epi Jomon phase, it became significant during the Okhotsk and the Classic Ainu culture phases.

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1. Introduction

In view of modelling future climate scenarios, knowledge about climatic and environmental variation during the last 6000 years is of particular interest (Wanner et al., 2008). Unlike the early Holocene, the last 6000 years were not influenced by the effects of glacial retreat, but characterised by environmental boundary conditions that are comparable to those of today. Therefore, climate fluctuations during this period represent better analogues for future climate dynamics. In order to illustrate global spatio-temporal patterns of past climate change, we need an array of robustly dated and high-resolution data from different regions. From the continental East Asian summer monsoon domain, several strong records have been published (e.g. Hu et al., 2008; Stebich et al., 2015). Several Holocene pollen records and pollen-based palaeoenvironmental reconstructions have been published in the last years for the NW Pacific region (e.g. Igarashi, 2013; Leipe et al., 2013; Leipe et al., 2015; Razjigaeva et al., 2013), which is significantly influenced by ocean currents and monsoonal atmospheric circulation (Qiu, 2001). Although, continuous high-resolution and well-dated records are still lacking in this region.

Knowledge about palaeoenvironmental changes is also essential

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to understand past human–environment interactions (Dearing et al., 2006), and many of the major Holocene climate fluctuations have been associated with cultural dynamics in different parts of the world (Büntgen et al., 2011). This also applies to the prehistory of Japan, where different cultural transitions have been related to climatic shifts (Imamura, 1996; Kawahata et al., 2009); although, the perception of such linkages is hampered by the lack of high-resolution, well-dated palaeoenvironmental records.

In 2011, Rebun Island, in NW Hokkaido (Fig. 1a and b), was identified by the international multidisciplinary Baikal-Hokkaido Archaeology Project (BHAP: http://bhap.artsrn.ualberta.ca) as a unique place to study the development of regional Holocene hunter–gatherers including potential causal links to environmental change (Tarasov et al., 2013; Weber et al., 2013). Pilot studies on Rebun Island have demonstrated the potential of pollen (Müller et al., 2016), diatom (Schmidt et al., 2016), and archaeobotanical (Leipe et al., 2017) analyses from Lake Kushu, and the Hamanaka 2 archaeological site (Fig. 1c) for reconstructing the island's environmental history and prehistoric subsistence economies.

This paper presents a key palynological record from Lake Kushu covering the last 6000 years – the first high-resolution and robustly dated fossil record from the entire region. Surface pollen samples from the island were analysed to facilitate interpretation of the fossil pollen assemblages, which are used for reconstructing vegetation changes and for better understanding the underlying driving factors (i.e. climatic or/and anthropogenic) of those changes. We discuss our findings in comparison to other regions and in view of known major (hemispheric- to global-scale) climate fluctuations. In addition, we analysed archaeobotanical samples extracted from Epi Jomon and Ainu cultural layers at Hamanaka 2. A sub-set of the recovered archaeobotanical remains have been AMS radiocarbon dated and used, together with pollen-based information on past forest cover, for reconstructing plant use, occupational phases, and human impact on the island environments. Furthermore, we correlate the paleoenvironmental results to the cultural chronology of northern Japan to test whether shifts in vegetation and climate coincide with those found in the archaeological record.

2. Study sites and environments

Rebun Island is located in the northern part of the Sea of Japan (Fig. 1a), ca. 45 km west of Hokkaido and ca. 10 km northwest of Rishiri Island Rebun occupies an area of about 82 km^2 (Schmidt et al., 2016), extending for about 20 km along the 141°E longitude. The island stretches ca. 6–7.5 km wide in the northern and central parts and is less than 2 km wide in the south. The landscape is hilly, with the highest point (490 m a.s.l.) situated on the western part of the island (Fig. 1b). Lake Kushu, located in the north (Fig. 1c), is the only fresh water lake on the island. It is separated by a ca. 230–400 m narrow sandy strip reaching up to 15 m a.s.l. from the Funadomari Bay of the Sea of Japan. The lake is kidney-bean shaped, with a maximum length of ca. 1100 m, a maximum water depth of ca. 6 m, and an average depth of about 3–5 m (Müller et al., 2016).

The archaeological site complex of Hamanaka 2 is located about 1500 m west of Lake Kushu and ca. 100 m south of Funadomari Bay (Fig. 1c). The site deposits constitute a well-stratified shell-midden on top of a sand-dune formation featuring different cultural layers including, the Late, Final, and Epi Jomon layers, as well as the Okhotsk and Ainu cultural layers, dating between the beginning of the 2nd millennium BCE and mid-19th century CE. Archaeological finds include human and dog burials, pig remains, ceramic and lithic artefacts, and abundant remains of sea mammals, fish, and shellfish (Lynch et al., 2016).

The climate conditions of Rebun Island are mainly controlled by the East Asian monsoon system. The East Asian summer monsoon (EASM) circulation transports warm and moist air in a northern to north-western direction, into the study area following the air pressure gradient between the Asiatic Low (Siberia) and the Hawaiian High (northern Pacific Ocean). The development of the Aleutian Low and the Siberian High during autumn and the associated reversal of the ocean–continent pressure gradient results in the East Asian winter monsoon (EAWM) circulation, distinguished by cold continental air flow in a southern to south-eastern direction. Another important climatic control in the study region is the Tsushima warm current (TWC) – a northern branch of the Kuroshio warm current (Fig. 1b). Especially during winter, the TWC promotes moisture uptake by the predominant winter monsoon winds,

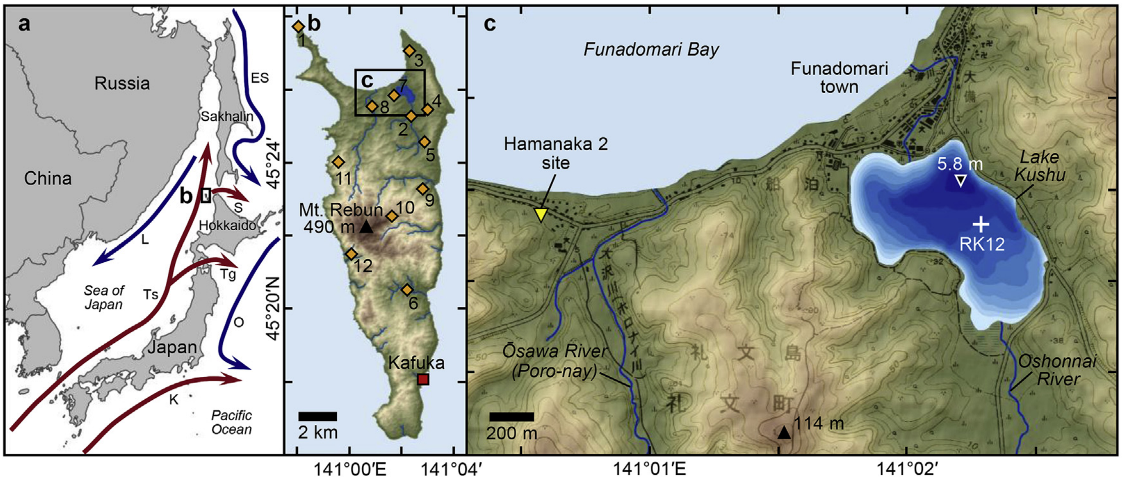


Fig. 1. Map compilation showing (a) the Northwest Pacific and major warm (red) and cold (blue) marine currents including the Kuroshio (K), Tsushima (Ts), Tsugaru (Tg), Soya (S), Oyashio (O), Liman (L), and East Sakhalin (ES) currents; (b) Rebun Island and the locations of the palynologically analysed (Fig. 2) surface samples REB-11-01–12 (yellow diamonds); and (c) Lake Kushu (white cross indicates location of the RK12 core) and Hamanaka 2 in the northern part of the island. Topographic maps are based on elevation Shuttle Radar Topography Mission (SRTM) V4.1 data (Jarvis et al., 2008) and a topographic map (Geospatial Information Authority of Japan, 2012). Bathymetry of Lake Kushu (0.5 m isolines) is based on survey data provided by T. Haraguchi (Osaka City University). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

which results in enhanced snowfall and prevents sea ice formation (Nikolaeva and Shcherbakova, 1990). Mean monthly precipitation values vary between 55 (March) and 130 mm (September), and the mean annual precipitation is about 1100 mm. The annual mean temperature is 6.1 °C. During the warmest month (August), the mean temperature reaches 19.4 °C. In winter (December–March), the mean temperature drops below 0 °C, with the mean temperature of the coldest month (January) as low as −6.4 °C (Hijmans et al., 2005).

Rebun Island is situated within the cool mixed forest (COMX) biome zone (Nakagawa et al., 2002). The natural vegetation is dominated by a combination of cool temperate and boreal woody plants (see Müller et al., 2016 for details and references). Typical representatives include boreal evergreen conifers, like *Abies sachalinensis* (Sakhalin fir), *Picea jezoensis* (Jezo spruce), *Pinus pumila* (Siberian dwarf pine), and boreal/temperate deciduous broadleaf trees including several species of *Betula* (birch), *Alnus* (alder), and *Salix* (willow), as well as *Quercus crispula* (Mongolian oak), *Sorbus commixta* (Japanese rowan), *Acer pictum* subsp. *mono* (painted maple), *Fraxinus mandschurica* (Manchurian ash), *Juglans ailantifolia* (Japanese walnut), *Morus australis* (Chinese mulberry), *Phellodendron amurense* (Amur cork tree), *Ulmus davidiana* var. *japonica* (Japanese elm), *U. laciniata* (Manchurian elm), *Tilia japonica* (Japanese linden), and woody vines, like *Hydrangea petiolaris* (hortensia) and *Toxicodendron orientale* (syn. *Rhus ambigua*, Asian poison ivy) (Haruki et al., 2004). The annually mild maritime climate and deep snow cover in winter might explain the presence of some warm-temperate taxa such as *Ilex* spp. (holly), *Aralia* spp. (spikenard), *Skimmia japonica* (Japanese skimmia), and *Kalopanax septemlobus* (prickly castor oil tree) on the island. Despite recent efforts to re-establish natural forests, large parts of Rebun Island are still covered by dense stands of dwarf bamboo, knotweed, and other herbaceous plants.

3. Study material

3.1. RK12 sediment section and surface samples

Palynological analysis of the current study is based on the upper part (i.e. 10.4 m below the estimated core top) of the RK12 sediment core (total length: 19.5 m), extracted from the centre of Lake Kushu (Fig. 1) in February 2012 by the commercial company Dokon Co. (Sapporo) using a hydro-pressure thin-walled piston sampler. Due to its unconsolidated state, the uppermost ca. 50 cm of lake sediment could not be recovered, so that the analysed core section stretches from 1040 to 50 cm sediment depth. Between 1040 and 850 cm, the sediment column consists of clayey material that is mostly finely laminated with sections of relatively low to high concentrations of organic matter. The upper 850 cm consists of homogeneous organic-rich clayey material (Müller et al., 2016). The well-constrained chronology of the entire RK12 core is based on a set of 57 AMS radiocarbon dates, whilst the uppermost 10 m section chronology relies on 30 AMS age determinations (see Müller et al., 2016 for details) and the tephra date of the Millennium (B-Tm) eruption of Changbaishan Volcano (Chen et al., 2016). The best-fit age-depth model suggests that the upper 10.4 m of RK12 were continuously deposited at high and principally steady accumulation rates (ca. 15 mm/a) during the past 6000 years. To satisfy requirements of both geoscientists and archaeologists, in this paper ages are given in 'cal BP' and 'CE/BCE', which refers to calendar ages before present (where 'present' equals 1950 Common Era) and ages of Common Era/before Common Era, respectively.

The RK12 core segments were cut into two halves and continuously sub-sampled in 1-cm increments using the double-L channel (LL-channel) technique (Nakagawa, 2007). The palynological results presented in this paper are based on a sub-set of 231 sediment samples (of which 14 samples were investigated in a pilot study by Müller et al., 2016) each comprising about 1 cm^3, picked every 3–4 cm, corresponding to an average temporal resolution of 18–24 years.

In August 2011, a set of 12 reference samples from moss pollsters and surface mud layers were collected for palynological analysis to better understand local pollen–vegetation relationships. We sampled locations across the northern and central parts of Rebun Island (Fig. 1b), which represent different vegetation settings, including forests, meadows, and alpine communities (see Supplemental Table S1 for details), over an altitudinal range of 5–300 m a.s.l.

3.2. Flotation samples from Hamanaka 2

During consecutive summer excavation campaigns between 2013 and 2016, a total of 143 sediment samples were collected from Hamanaka 2 for water flotation and further archaeobotanical analysis. The samples represent different cultural layers, including those of the Final and Epi Jomon, Okhotsk, and Ainu, which were defined by the BHAP archaeological team using pottery characteristics and lithological features of the excavated profile (Müller et al., 2016). While the samples associated with the Okhotsk occupation period (stratigraphic units IIIa–V) were investigated in a previous study focusing on barley finds (Leipe et al., 2017), the flotation samples ($n = 108$) extracted from Final Jomon (VIII), Epi Jomon (VI–VII), and Ainu (II–I) layers have not been presented or discussed elsewhere. The volume of processed sediments for each cultural layer was 50, 374.5, and 544.5 litres, respectively.

4. Methods

4.1. Pollen and non-pollen palynomorph analysis

Samples for palynological investigation were processed following standard procedures (Cwynar et al., 1979; Fægri et al., 1989), including 7-mm ultrasonic fine sieving, HF (hydrofluoric acid) treatment and subsequent acetolysis. Two tablets of *Lycopodium* marker spores (batch no. 177745), each containing 18,584 spores ($\sigma = \pm 1853$), were added to every sediment sample prior to chemical treatment for calculating palynomorph concentrations (Stockmarr, 1971). Water-free glycerol was used for sample storage and preparation of the microscopic slides. Pollen and spores were identified at magnifications of 400 × and 600 × with the aid of published pollen keys and atlases (Beug, 2004; Demske et al., 2013; Miyoshi et al., 2011; Nakamura, 1980a; b; Reille, 1992, 1995; 1998; Shimakura, 1973) and a modern pollen reference collection stored at Freie Universität Berlin. Preservation of extracted pollen and spores was generally good; although, bisaccate pollen grains of *Abies* were frequently broken. The terrestrial pollen content of the samples was sufficiently high to allow for counting a minimum of 400 grains per sample. In addition to pollen, spores of vascular cryptogams, green algae remains (*Pediastrum, Botryococcus*), and other preserved non-pollen palynomorphs (NPP) were identified (e.g. Jankovská and Komárek, 2000; Ralska-Jasiewiczowa and van Geel, 1992; Sorsa, 1964; van Geel, 2001) and counted. A photographic documentation of the most common pollen and spore taxa is provided as an appendix (Supplemental Fig. S2).

For all analysed fossil pollen samples, calculated pollen percentages refer to the sum of terrestrial pollen grains. Other counted taxa percentages, including pollen of aquatic plants, spores of ferns, fungi, and mosses, algae remains, and other NPPs were calculated using the total terrestrial pollen sum plus the sum of palynomorphs in the respective group. Tilia® version 1.7.16 (Grimm, 2011) was used for calculating pollen and NPP taxa percentages and drawing the diagrams.

4.2. Biome reconstruction method

Pollen-based reconstruction of natural vegetation can be objectively performed using the quantitative method of biomization (Prentice et al., 1996). This approach allows assignment of terrestrial pollen taxa to plant functional types (PFTs) and to major vegetation types (i.e. biomes) based on the modern ecology, bioclimatic tolerance, and geographical distribution of pollen-producing plants. The biomization requires constructing a taxa-PFT-biome matrix, which allows us to determine the numerical affinity of each pollen sample with every potential biome. The biome with the highest affinity score is assumed to be dominant and assigned to the respective pollen spectrum. In case scores of several biomes are equal, the one defined by a smaller number of PFTs gets priority. To minimise possible noise due to long-distance transport or re-deposited exotic pollen grains, we applied the universal threshold of 0.5% to the pollen percentage values, as recommended by Prentice et al. (1996). We performed the biome score calculation using PPPBase software (Guiot and Goeury, 1996).

For reconstructing natural vegetation in Japan, two different taxa-PFT-biome matrices are presented in the literature. In one of the biomization approaches (Takahara et al., 2000) all arboreal and non-arboreal pollen (AP and NAP) taxa are considered; in the other one (Gotanda et al., 2002) only 32 arboreal taxa are used to infer the natural forest biomes distribution across the Japanese islands. Using a representative set of modern pollen data, Leipe et al. (2013) tested the applicability of both schemes in the Hokkaido region. The results of their test show that the approach put forward by Gotanda et al. (2002) yields a higher agreement between pollen-reconstructed biomes and actual natural vegetation and, therefore, we use it in the current study.

4.3. Analysis and dating of archaeobotanical remains

Our analysis of archaeobotanical remains is based on the sedimentary light fraction, which we extracted from the collected samples using water flotation by means of a SMAP-style overflow machine (Watson, 1976). We identified seed and fruit parts using morphological traits, with the aid of a binocular microscope. Uncarbonised plant remains found in the context of prehistoric deposits may be intrusive and were, therefore, not considered in the current study. To avoid counting seeds more than once, fragments comprising less than 50% of their original size were not recorded. For photographic documentation and morphometric measurements, including maximum length, width, and thickness, of the recovered barley grains we used a VH-Z20 R (x20–x200) zoom lens mounted on a Keyence VHX-1000 microscope. Length and width dimensions were measured with the seed dorsal side facing up. Weight was determined with a Mettler Toledo WXTS205DU precision scale. Extracted carbonised barley seeds and other macrobotanical remains were directly AMS radiocarbon dated at the Poznan Radiocarbon Laboratory. To ensure reliable age determination, each dated specimen had a weight of more than 2 mg. AMS ^{14}C dates were calibrated to calendar ages using OxCal v4.2.3 software (Bronk Ramsey, 2013) and the calibration curve Intcal13 (Reimer et al., 2013).

5. Results and interpretations

5.1. Modern pollen assemblages from Rebun Island

We interpret the palynological results of the 12 surface samples from Rebun Island (Fig. 2, Supplemental Table S1) to clearly reflect the current patchy vegetation structure. Some samples (REB-11-01–03, 05, and 11) represent deforested areas dominated by herbaceous plants. The remaining samples mirror patches of more natural vegetation or areas of reforestation. This results in a large variation in arboreal pollen (AP) abundances, ranging from 5% (REB-11-02) to 94% (REB-11-09). Calculation of arithmetical means of pollen taxa percentages of all 12 samples suggests that herbaceous plants (ca. 26%), which are mostly represented by Poaceae, *Artemisia*, and other Asteraceae, play a significant role on the island today. The exceptionally high abundance of Poaceae pollen (>80%) in the sample from a meadow in the wetlands south of current Lake Kushu (REB-11-02) illustrates the reed vegetation belt around the lake composed of *Phragmites* and other grasses. Regarding arboreal taxa, the pollen spectra reflect the dominance of cold tolerant trees (i.e. *Abies* and *Betula*). By contrast, pollen of temperate deciduous trees, like *Quercus* and *Ulmus*, which are less resistant to low minimum temperatures (Prentice et al., 1996), appear less frequently reflecting the minor presence of these taxa on the island today. The relatively high frequencies of Poaceae pollen result from human-induced vegetation disturbance. The tree pollen frequencies mirror the location of Rebun Island close to the transitional zone of the COMX and taiga (TAIG) biomes (Leipe et al., 2015), beyond which temperate deciduous trees are not a constituent of the zonal vegetation and may only occasionally grow in favourable micro-habitats. Calculation of biome scores for the average pollen percentage reveals that COMX is the dominate biome on the island showing that the modern vegetation reflects the zonal climate and natural vegetation in the study area (Tarasov et al., 2011).

5.2. RK12 fossil pollen record

From the sediment column, representing the last 6000 years, we analysed 231 subsamples, in which we identified 103 terrestrial and 6 aquatic plant pollen taxa. Regarding NPPs, we distinguished different types of spores from ferns and mosses ($n = 18$), fungi ($n = 11$), algae remains ($n = 2$), and other NPPs ($n = 7$), including plant fragments and dinoflagellate cysts. Based on the pollen spectra composition and relative abundances, the RK12 pollen diagram is subdivided into six stratigraphic units, representing local pollen zones (LPZs) and subzones (LPSZs). The main characteristics of the LPZs are outlined graphically (Fig. 3) and described in the following paragraphs in a bottom-to-top order. The biomization results reveal that COMX was the dominant biome on Rebun Island throughout the covered period. The COMX scores vary slightly around a value of 25. For the TAIG biome, adjacent to the north and currently dominating large parts of Sakhalin and the continental Russian Far East, scores gradually increase (from ca. 13 to 18) from the bottom to the top of the record, reflecting the spread of boreal broadleaf and coniferous taxa, thus indicating a progressive cooling trend.

With around 82% for AP, LPZ RK12-3 (1041.5–822.5 cm; ca. 6000–5030 cal BP, 4050–3080 BCE) reflects the dominance of forest. The most abundant pollen taxon is *Betula*, a strong pollen producer and typical constituent of the COMX biome. Regarding the overall pollen record, this zone is characterised by moderate abundance of *Abies* (ca. 18%), a boreal/cool-temperate coniferous taxon, in comparison to relatively high abundance of arboreal temperate deciduous taxa. The arboreal taxa include *Fraxinus* (ca. 3%), *Quercus* (ca. 18%), *Ulmus* (ca. 7%), and *Juglans* (ca. 1%), of which the latter three reach their highest percentages in this zone. The relatively high proportions of deciduous trees, which have a less dense canopy than conifers, thus promoting understory growth, may explain the relative abundance of Poaceae, contributing 10% on average and up to 20% to the total pollen sum. Another feature is

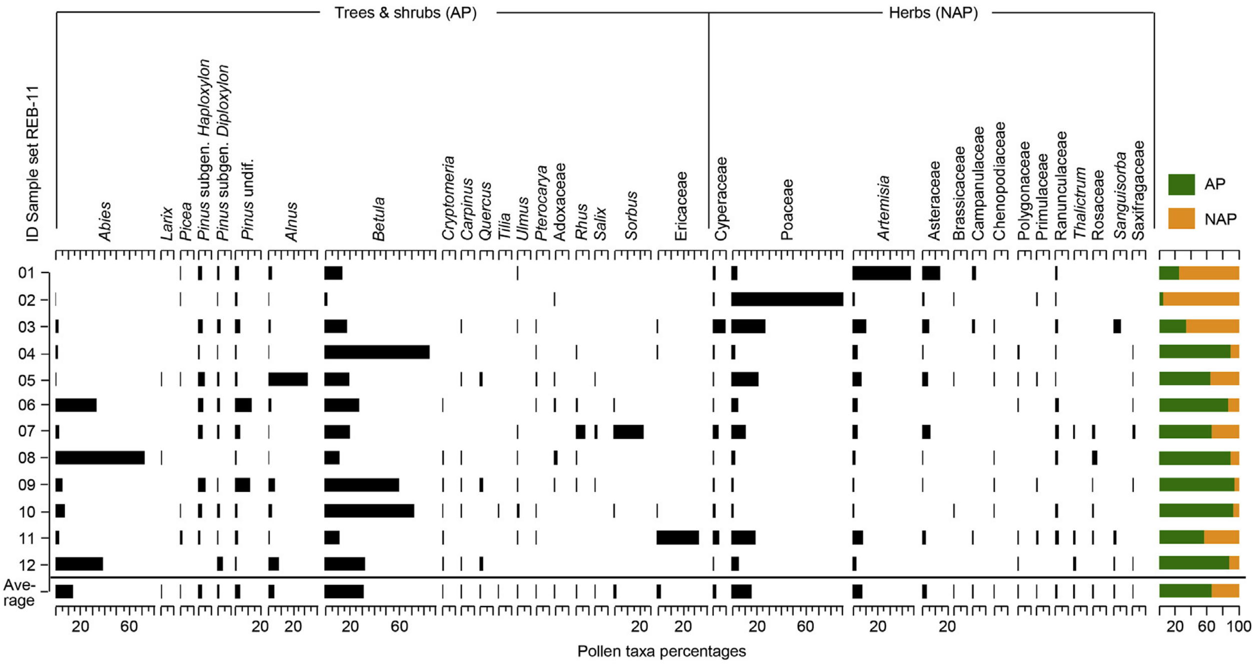


Fig. 2. Simplified percentage pollen diagram for the 12 surface samples collected across Rebun Island. Average represents the arithmetic means of all 12 surface samples. See Fig. 1b for sample locations.

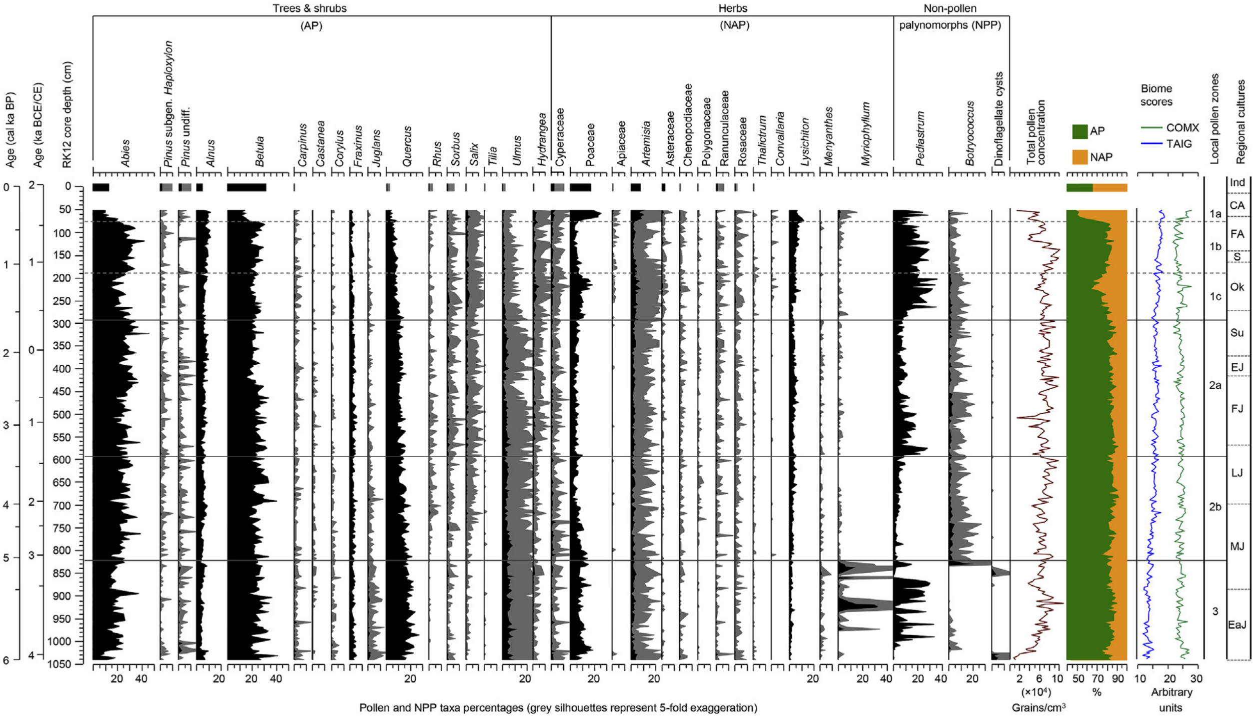


Fig. 3. Simplified percentage pollen diagram of the terrestrial arboreal (AP) and non-arboreal (NAP) pollen and non-pollen palynomorphs (NPP), counting results and defined local pollen zones (LPZ) and subzones (LPSZ) of the upper (10.4 m) RK12 sediment core from Lake Kushu plotted against depth and age axes. Biome scores are provided for cool mixed forest (COMX) and taiga (TAIG). The chronology of prehistoric and early historic cultures of northern Hokkaido including the Early (EaJ), Middle (MJ), Late (LJ), Final (FJ), and Epi (EJ) Jomon, as well as Susuya (Su), Okhotsk (Ok), Satsumon (S), Formative (FA) and Classic (CA) Ainu cultural periods, and Industrial Age (Ind) (see caption of Fig. 6 for details).

the appearance of marine dinoflagellate cysts at the bottom and top of this zone. Together with the strongly fluctuating abundances of *Myriophyllum*, an aquatic plant growing in shallow fresh to brackish water, this indicates short-term, though intensive sea water influx to early Lake Kushu. If this influx happened during the flowering period, the anthers of the *Myriophyllum* plants were probably submerged causing more pollen to enter the lake. This interpretation is supported by the results of a diatom analysis (Schmidt, 2018) performed on the same sediment core indicating a lagoon phase of predominantly fresh to brackish water conditions intercalated by marine conditions between ca. 6000 and 5000 cal BP (Fig. 5a). The near absence of *Botryococcus* and strongly fluctuating percentages of *Pediastrum* are further indicators of unstable lake conditions.

In LPSZ RK12-2b (822.5–588.5 cm; ca. 5030–3330 cal BP, 3080–1380 BCE) AP values are slightly increased (ca. 84%). *Abies* pollen percentages are higher compared to the previous zone and range around an average of 25%. By contrast, the parallel decreasing trends of temperate deciduous taxa (*Quercus*, *Ulmus*, and *Juglans*) and Poaceae percentages, which started in RK12-4, continue in this LPSZ. The decline in grass pollen is likely the result of the growing contribution of *Abies* to the forest cover, whereas falling percentages of temperate deciduous taxa is due to a steady cooling trend. This is also manifested in raising scores for the taiga biome, which is mainly driven by increasing *Abies* values. It seems that the low, but constant *Pediastrum* percentages and the appearance of *Botryococcus* indicate a change towards more stable conditions and the onset of a predominantly freshwater lake phase after ca. 5000 cal BP, which is supported by the near absence of marine dinoflagellate cysts and marine diatoms frequently recorded during the preceding lagoon phase (Schmidt, 2018, Fig. 5a).

While the AP/NAP ratio in LPSZ RK12-2a (588.5–289.5 cm; ca. 3330–1580 cal BP, 1380 BCE–370 CE) remains unchanged, the gap between *Abies* abundances (ca. 28%) and those of temperate deciduous trees, including *Quercus* (ca. 11%), *Ulmus* (ca. 4%), and *Juglans* (ca. 0.3%), continues to become wider compared to the previous LPSZ. Contemporaneously, Poaceae values are at their lowest – around 5%. *Botryococcus* algae percentages (ca. 2%) remain at stable levels. On the other hand, *Pediastrum* coenobia show an increase, especially in the lower part of this subzone. This may point to hydrological changes.

RK12-1c (289.5–181.5 cm; ca. 1580–1100 cal BP, 370–850 CE) is characterised by a significant decline in AP percentages and several distinctive changes in AP, NAP, and NPP taxa frequencies, including a strong decline of *Abies* values accompanied by a substantial rise in Poaceae, *Artemisia*, and *Pediastrum* abundances. We interpret this development as a result of human influence on Rebun Island, suggesting the exploitation (i.e. clearance) of *Abies*, which led to higher landscape openness. The latter promoted the spread of shrubs and herbaceous taxa on forest clearings or open ground, as indicated by increased *Hydrangea*, Poaceae, *Artemisia*, and Apiaceae pollen percentages. The rise in *Lysichiton* values (from ca. 2–5%) likely indicates the impact of forest reduction in the immediate vicinity of Lake Kushu. The trend towards increased openness of the landscape appears to reverse towards the top of this subzone (ca. 1235–1100 cal. ka BP), when Poaceae values decrease and *Abies* values increase, suggesting local fir population recovery. Further evidence for substantial environmental change during RK12-1c is given by a dramatic increase in *Pediastrum* values (ca. 20%) and slightly lower overall pollen concentrations, which may demonstrate a higher level of nutrient influx into Lake Kushu and increased biomass production leading to rising sedimentation rates. On the other hand, *Quercus*, *Ulmus*, and *Juglans* percentages further decrease throughout this zone, pointing to progressive cooling.

RK12-1b (181.5–76.5 cm; ca. 1100–410 cal BP, 850–1540 CE) reflects a phase of natural forest recovery and reduced human impact with arboreal taxa reaching average values (81%), almost as high as those of zones RK12-3–2 (ca. 84%). This change is mainly due to the spread of *Abies*, which reaches its highest abundance in this zone; although, *Alnus* and *Betula* also show increased percentages. The forest recovery is also reflected by lower values for *Artemisia* and Poaceae. The grass values drop markedly from 18%, at the end of the previous zone, to on average 5%. Unlike *Abies*, *Alnus*, and *Betula*, temperate deciduous tree and shrub percentages continue to decline in parallel to rising taiga biome scores, indicating gradual cooling. At the same time, *Lysichiton* prevails on relatively high levels, showing a slight increase (up to 8%) during the upper half of this zone. High values, comparable to the preceding interval, are also recorded for *Pediastrum*.

The uppermost subzone RK12-1a (76.5–50.5 cm; ca. 410–270 cal BP, 1540–1680 CE) is characterised by a distinct decrease in forest cover, evidenced by a drop in AP values to as low as 55% and a fourfold rise in Poaceae values (ca. 20%). *Artemisia* proportions similarly increased from 3% in RK12-1b to 9%. The spread of herbaceous taxa mainly occurred to the expense of *Abies* and *Betula*, which were likely depleted by deforestation. As in the previous zones RK12-3–1b, temperate deciduous tree values follow a gradually decreasing trend. The short-term peak in *Lysichiton* abundances (ca. 11%) at the beginning of this zone is noteworthy. Together with slightly increasing values of *Myriophyllum*, it may point to a lowering of the lake level.

5.3. Macrobotanical assemblages from Hamanaka 2

For the Final Jomon, Epi Jomon, and Ainu cultural layers we have identified 28, 44, and 10 charred seeds and seed fragments from the flotation samples, respectively, that were arranged into seven taxonomic categories (Table 2). Identified wild plant seeds belong to *Actinidia* sp., *Aralia* sp., *Phellodendron amurense*, *Sambucus* sp., *Rhus/Toxicodendron* sp., and *Vitis* sp. All these taxa comprise plant parts or produce fruits, which are edible or may be used for medical purposes, and we assume that they reflect a foraging component of the local people. In addition, six caryopses of domesticated six-rowed naked barley (*Hordeum vulgare* var. *nudum*) were identified, of which two are associated with Epi Jomon and four others with Ainu cultural contexts. Morphometric measurements for the six barley caryopses (Supplemental Table S3) show a variation in length and width from 3.0 to 5.8 mm and from 2.4 to 3.8 mm, respectively. The degree of compactness, which may be expressed as a length/width ratio, is in a range (1.25–1.65) typical for naked barley, previously identified in the Okhotsk cultural layers of Hamanaka 2 (Leipe et al., 2017).

To strengthen chronological assessment of the extracted archaeobotanical assemblages from Hamanaka 2 and to facilitate their correlation with palaeoenvironmental records, we have dated a set of 20 charred seeds and charcoal pieces (Table 1) supplementing the radiocarbon dating on archaeobotanical material presented in Müller et al. (2016) and Leipe et al. (2017). Results for the charred naked barley grains demonstrate that the calibrated ages do not always conform to the cultural layers they were extracted from pointing to redeposition processes such as bioturbation. Of the four grains (no. 1, 4, 12, and 18; Table 1) originating from Ainu layers II–I, two (no. 12 and 18) date to the Okhotsk culture period. This also applies to one (no. 30) out of two (no. 30 and 38) grains from layers VI–VII that are associated with the Epi Jomon culture based on archaeological assemblages. Regarding the other material dated, there is one sample of charcoal (no. 10) that was extracted from layers II–I, but also dates to the Okhotsk culture period.

6. Discussion

6.1. Regional vegetation and climate history with some notes to cultural dynamics

The RK12 pollen analysis results from Lake Kushu represent the only available confidently-dated pollen record of bi-decadal resolution, which documents Middle to Late Holocene vegetation and climate changes in northern Japan and the north-western Pacific region. The most prominent climate trend visible in the record is the overall gradual cooling throughout the last 6000 years. This is

Table 1
Radiocarbon dates and calibrated ages for the AMS-dated samples from the Final Jomon, Epi Jomon, and Ainu cultural layers of Hamanaka 2, Rebun Island. Conversion of radiocarbon dates to calendar ages was done using OxCal v4.2.3 (Bronk Ramsey, 2013) and the calibration curve Intcal13 (Reimer et al., 2013).

Lab ID	Sample ID	Dated material	AMS radiocarbon date, uncal BP	Calendar age (68% range)	Calendar age (95% range)	No. in Fig. 6
Poz-91178	F2015-023-01	*Vitis coignetiae*	2240 ± 30	377-215 BCE	390-205 BCE	39
Poz-91171	F2014-089-01	*Hordeum vulgare* var. *nudum*	2220 ± 30	361-210 BCE	375-203 BCE	38
Poz-91179	F2015-019-01	*Sambucus* sp.	2200 ± 30	357-204 BCE	366-192 BCE	37
Poz-73805	F2013-157	Charcoal piece	2220 ± 30	374-202 BCE	360-208 BCE	36
Poz-73806	F2013-177	Charcoal piece	2220 ± 30	374-202 BCE	360-208 BCE	35
Poz-91175	F2014-125-01	*Vitis coignetiae*	2170 ± 30	352-176 BCE	360-116 BCE	34
Poz-73804	F2013-083	Charcoal piece	2200 ± 35	370-178 BCE	356-202 BCE	33
Poz-73803	F2013-127	Charcoal piece	2195 ± 30	362-182 BCE	355-200 BCE	32
Poz-91177	F2014-091-01	*Toxicodendron* sp.	2115 ± 30	191-101 BCE	341-49 BCE	31
Poz-91170	F2014-055-01	*Hordeum vulgare* var. *nudum*	1555 ± 30	430-545 CE	421-570 CE	30
Poz-73802	F2013-097	Charcoal piece	1455 ± 30	555-650 CE	585-640 CE	27
Poz-91167	F2013-011-01	*Hordeum vulgare* var. *nudum*	1245 ± 30	687-800 CE	680-874 CE	18
Poz-91169	F2014-041-02	*Hordeum vulgare* var. *nudum*	1175 ± 30	777-890 CE	770-963 CE	12
Poz-73799	F2013-061	Charcoal piece	1165 ± 30	777-940 CE	772-966 CE	10
Poz-73797	F2013-025	Charcoal piece	215 ± 30	1649- … CE	1644- … CE	9
Poz-73798	F2013-047	Charcoal piece	210 ± 30	1651- … CE	1646- … CE	7
Poz-73801	F2013-065	Charcoal piece	170 ± 30	1668- … CE	1659- … CE	6
Poz-91165	F2014-003-01	*Hordeum vulgare* var. *nudum*	130 ± 30	1682-1936 CE	1675-1942 CE	4
Poz-73796	F2013-043	Charcoal piece	120 ± 30	1685-1927 CE	1678-1940 CE	3
Poz-91168	F2014-041-01	*Hordeum vulgare* var. *nudum*	80 ± 30	1697-1917 CE	1690-1926 CE	1

expressed by a continuous decrease in temperate and cool-temperate deciduous trees in favour of boreal trees (Fig. 3). The pollen percentage curve of *Quercus* (Fig. 5b) may be regarded as a reliable proxy for thermal conditions. This temperate deciduous plant (Prentice et al., 1996) is sensitive to climate cooling, and contemporary stands in northern Hokkaido are located close to the taxon's current northern distribution limit (i.e. the COMX/TAIG biome boundary in southern Sakhalin; Leipe et al., 2015). The long-term decrease in temperate/cool-temperate deciduous taxa progressed in favour of boreal tree taxa, which is mirrored by increasing TAIG biome scores (Fig. 5c). Both, the *Quercus* percentage and TAIG score curves parallel the summer solar radiation decline (Laskar et al., 2004, Fig. 5d) that is also well-reflected in the NGRIP ice $\delta^{18}O$ record from Greenland (Svensson et al., 2008, Fig. 5e). These correlations corroborate previous research, which identified orbital forcing as the main driver of Northern Hemisphere (NH) Middle to Late Holocene climate cooling (Wanner et al., 2008). A similar long-term development in thermal conditions is recorded in the temperate deciduous forest biome (TEDE) scores derived from a well-dated high-resolution pollen record from Sihailongwan Maar Lake (Stebich et al., 2015, Fig. 5f), which is representative of the neighbouring continental region of north-eastern China. In contrast to the *Quercus* percentage and TAIG score curves from Lake Kushu, the TEDE curve (Fig. 5f) shows stronger oscillations superimposed on the insolation-induced cooling trend, which could be explained by the more pronounced summer-winter temperature anomaly in the continental environment compared to maritime locations where seasonality is less distinct.

In addition to the long-term cooling trend, there is evidence for different climate transitions and short-term events. On a global scale, there is no clear agreement about the timing of Middle Holocene cooling (i.e. the onset of the Subboreal period or Neoglacial climate interval), which marks the termination of the Holocene Thermal Optimum. Comprehensive reviews of continental glacier advances identified a global-scale cooling trend with the beginning dated to around 5400 (Grove, 2004; Solomina et al., 2015) or 5300 (Denton and Karlén, 1973) cal BP. Based on studies of Holocene climate forcing mechanisms, Debret et al. (2007) argue for an earlier climate transition at ca. 5500 cal BP. However, other synoptic studies (Wanner et al., 2008, 2011) did not find significant evidence for a global 'Holocene Climate Transition'. Regarding the RK12 core, the observed continuous decline in *Quercus* percentages started ca. 5350 cal BP. Evidence for changing environmental conditions is also given by a phase of low pollen concentration (ca. 5540–5300 cal BP; Fig. 3), which peaks at 5400 cal BP. In combination, both findings indicate a cooling trend that started as early as 5540 cal BP, leading to less favourable growing conditions and, as a result, to lower pollen production rates. Consequently, from ca. 5350 cal BP, as cooling further progressed, oak population on the island decreased. For the first time, this climate shift can be established with confidence in the study region, suggesting it is broadly synchronous with the hemispheric cooling trend postulated in the above-mentioned summary studies. Wanner et al. (2008) relate the Late Holocene global trend of glacier advance to the highest magnitude interval of Bond cycle 4 (Bond et al., 2001, Fig. 5g), which took place around 5530 cal BP and may also be linked to the cooling trend registered in the RK12 pollen record. Although, the pronounced step-wise increase in the mass concentration of drift ice indicators (i.e. hematite-stained grains) associated with Bond cycle 4 started much earlier at ca. 6600 cal BP. Impact of solar changes and/or a cooler North Atlantic climate in regions influenced by the Asian monsoon system are also not recorded before ca. 5600 cal BP, when the onset of a phase of decreasing summer monsoon intensity is suggested by key stalagmite isotope records (Dykoski et al., 2005; Fleitmann et al., 2003). A swing towards lower annual temperatures, which apparently mark the Atlantic/Subboreal transition, is also evident from a quantitative pollen-based climate reconstruction from northern Sakhalin (Leipe et al., 2015), despite the chronological control for this record is much less robust than that in the current research. While, the linear age-depth model based on four radiocarbon dates for the entire Holocene (Leipe et al., 2015) places this climate shift around 5200 cal BP, it is likely to be synchronous with the registered drop in the RK12 *Quercus* pollen percentage curve ca. 5350 cal BP. Consequently, the RK12 pollen record denotes that the Early Jomon phase in Hokkaido (ca. 6000–5000 cal BP; Weber et al., 2013) roughly coincides with the final phase of the Holocene Thermal Optimum. Additionally, the Hokkaido Middle Jomon phase (ca. 5000–4000 cal BP; Weber et al., 2013), which, according to Abe et al. (2016), expresses the highest density of occupation sites ($n = 2757$; Fig. 5h), was established after the initiation of continuous cooling ca. 5350 cal BP. This peak in the regional archaeological site density (and likely a corollary demographic shift) deserves special attention and further investigation.

Table 2
Sample-specific total counts of charred macrobotanical remains and floated litres from the typologically defined Final Jomon, Epi Jomon, and Ainu cultural layers of Hamanaka 2.

Sample ID	Layer ID	Volume (litres)	*Actinidia* sp.	*Aralia* sp.	*Hordeum vulgare* var. *nudum*	*Pheollodendron amurense*	*Sambucus* sp.	*Rhus*/ *Toxicodendron* sp.	*Vitis* sp.	Unidentified Seed	Sum	Cultural layer
F2016-001	Ic	6	2								2	Ainu
F2016-003	Ic	6.5							1		1	Ainu
F2014-041	I	6			2						2	Ainu
F2013-011	IIa	18			1					1	1	Ainu
F2013-019	IIa	13						1			1	Ainu
F2014-003	IIc	10			1						1	Ainu
F2015-035	IIc	16							2		2	Ainu
F2013-073	VII	12	1							1	1	Epi Jomon
F2013-115	VII	12	1								1	Epi Jomon
F2013-119	VII	11	1				1				2	Epi Jomon
F2013-121	VII	5						1			1	Epi Jomon
F2013-165	VII	8					1				1	Epi Jomon
F2014-023	VII	5					1			1	1	Epi Jomon
F2014-035	VII	9	1								1	Epi Jomon
F2014-043	VII	6	1	1							2	Epi Jomon
F2014-055	VII	9.5			1						1	Epi Jomon
F2014-069	VII	14					1				1	Epi Jomon
F2014-083	VII	5							1		1	Epi Jomon
F2014-087	VII	10							1		1	Epi Jomon
F2014-089	VII	12			1				1		2	Epi Jomon
F2014-091	VII	12		2				1		2	3	Epi Jomon
F2014-097	VII	15				1					1	Epi Jomon
F2014-103	VII	15		1						1	1	Epi Jomon
F2014-117	VII	10	1								1	Epi Jomon
F2014-125	VII	15							2		2	Epi Jomon
F2014-129	VII	2					1				1	Epi Jomon
F2014-141	VII	8					1	1	1		3	Epi Jomon
F2014-155	VII	12					1		3	1	4	Epi Jomon
F2014-157	VII	12	1						2		3	Epi Jomon
F2015-005	VII	9					2	6	1	3	9	Epi Jomon
F2015-019	VIII	7	2					1			3	Final Jomon
F2015-023	VIII	29	7	1			7	7	3	3	25	Final Jomon

An exceptionally strong decline in *Quercus* values (8%) is registered at ca. 4130 cal BP. This event, which is represented by only one sample, does not necessarily indicate a reduction in oak tree population, but could be related to a drop in oak pollen productivity due to ecological stress caused by climate cooling. Although short-term, this drop coincides with the so-called ‘4.2 kiloyear event’, which is likely linked to Bond cycle 3 (deMenocal et al., 2000). This climate event has been detected in palaeoenvironmental records from different regions of the world, where it is mostly related to cooler/drier conditions (Roland, 2012), and is implicated in the decline of several ancient civilisations (Liu and Feng, 2012). However, the global pattern of this climate oscillation seems to be non-uniform and its underlying forcing mechanisms are complex and insufficiently understood (Booth et al., 2005; Roland, 2012). While various palaeoclimate records suggest a relatively short-lived (ca. 200–300 years) phase of climate change, others advocate the onset of a long-term cooling/drying trend (Roland, 2012), used by Walker et al. (2012) to defined the Middle–Late Holocene boundary. Further evidence for a short-lasting 4.2 kiloyear climate shift is found in the pollen record from Sihailongwan Maar Lake (Stebich et al., 2015). The lake record exhibits a short-term drop in TEDE scores (Fig. 5f), i.e. in pollen percentages of temperate deciduous trees including *Fraxinus*, *Ulmus*, *Tilia*, *Carpinus*, and *Quercus*, at 4120 cal BP synchronous with the RK12 record. Consequently, both pollen records, from Lake Kushu (this study) and Sihailongwan Maar Lake (Stebich et al., 2015), strongly suggest a particularly short (i.e. multi-decadal) shift towards cooler conditions in the wider study region. It is conceivable that this climate event may have triggered the cultural changes (e.g. in settlement structure and size, ritual practices) recorded during the late Middle Jomon, initiating the termination of this cultural stage around 4200 cal BP. This event, resulted in the formation of the Late Jomon (ca. 4000–3300 cal BP), associated with lower archaeological site numbers (Abe et al., 2016, Fig. 5h).

The following period, stretching from ca. 4000 to 1550 cal BP, is characterised by a slow decrease in *Quercus* percentages, suggesting a period of continuous climate cooling. The next more pronounced shift towards lower values is observed at ca. 1550 cal BP. This drop in oak densities, which coincides with the onset of Bond cycle 1 (Fig. 5g), is indicative of enhanced cooling and may point to another case of teleconnection between the North Atlantic and the study region. A similar drop is also documented in the annual precipitation reconstruction, which is based on the pollen record from Sihailongwan Maar Lake (Stebich et al., 2015). In addition, these findings support a rather weakly imprinted cold climate event at ca. 1500 cal BP in the Khoe pollen record from northern Sakhalin that Leipe et al. (2015) linked to the Holocene North Atlantic cold spells. The centuries around 1500 cal BP are often referred to as the 'Dark Ages Cold Period' (McDermott et al., 2001). This cold interval, which according to Wanner (2016) continued from ca. 1900 to 1050 cal BP, was characterised by several cooling peaks often related to major human migration waves affecting large parts of Europe (Collins, 2010). There, the main migration phase started in the late 4th century CE (1575 cal BP), with the incursion of the Huns. The Migration Period in Europe was paralleled by generally colder climate conditions, which were unfavourable for agriculture. However, scholars dispute the role climate change played during this time of major cultural and political upheaval. In our study region, the onset of enhanced cooling at 1550 cal BP (400 CE) corresponds with the southward migration of the Okhotsk culture and its spread over the north-eastern Hokkaido region (Ohyi, 1975) dated between ca. 400 (Hirasawa et al., 2017) and 500 CE (Hudson, 2004; Zhushchikhovskaya, 2010). This spread is well reflected by enhanced human activities on Rebun Island, documented in the RK12 pollen and archaeobotanical record from Hamanaka 2. Abe et al. (2016) briefly discussed linkages between the regional climate and Okhotsk migrations, based on available marine records of sea surface temperature from the Sea of Okhotsk. Here, we present the first robust terrestrial evidence for potential influence of climate change on the Okhotsk migration. The enhanced cooling may also highlight an East Asian 'Dark Ages Cold Period', which a number of available studies have suggested for different regions without an underlying consistent temporal pattern (Helama et al., 2017). The immigration of Okhotsk culture groups may have led to a population increase, which is reflected in a greater density of archaeological sites in the Hokkaido region after ca. 500 CE (Abe et al., 2016, Fig. 5h).

Following the significant drop in the *Quercus* pollen percentages at ca. 1550 cal BP, the values continue to slowly decrease until ca. 390 cal BP, roughly corresponding to the LPSZ RK12-2a/1a shift, when the next more significant change towards lower oak pollen frequencies is identified. This decline in *Quercus* percentages (and likely in oak population) is coeval with another globally recognised period of generally cold climate conditions known as the 'Little Ice Age' (LIA), which followed the relatively warm 'Medieval Climate Anomaly'. The transition between both phases appears to be asynchronous among different regions varying between the middle of the 13th and 16th century CE (ca. 700–400 cal BP) (Matthews and Briffa, 2005). As seen in the oak percentage curve (Fig. 5b), climate cooling in the study region was related to the parallel occurrence of the Maunder Minimum (Steinhilber et al., 2009), one of four Late Holocene Grand Solar Minima, and a phase of enhanced volcanic activity stretching between 400 and 230 cal BP (Wanner and Grosjean, 2014). In fact, two previous overlapping phases of major volcanic eruptions and weak solar irradiance (Wolf- and Spörer-Minimum) during ca. 700–600 and 550–450 cal BP (Wanner and Grosjean, 2014) seem to have had no significant effect on the pollen/vegetation record from Rebun Island and, therefore, on thermal conditions in the study region. However, a comparable development is registered in surface snow temperature reconstructions for Greenland, suggesting that values did not drop prior to ca. 400 cal BP (Kobashi et al., 2011). As occurred around 1550 cal BP, the relatively rapid shift to cooler climate conditions at 390 cal BP is paralleled by cultural changes, namely the transformation from the Formative (Prehistoric) to Classic (Historic) Ainu at the turn of the 17th century CE. The latter is characterised by increased trade with surrounding populations (Hudson, 1999; Walker, 2001; see also chapter 6.2). In this regard, it is also worth noting that the initial emergence of the Ainu (i.e. Formative Ainu), at the start of the 13th century CE (Hirasawa et al., 2017), coincides with the beginning of the LIA (i.e. a succession of different phases of enhanced volcanic activity and solar radiation minima) ca. 700 cal BP (ca. 1250 CE). Although, the *Quercus* pollen curve (Fig. 5b) suggests a relatively weak climate cooling trend, an influence on the Satsumon/Ainu cultural transformation could be considered. Archaeobotanical studies have demonstrated that the Satsumon culture, identified as at least one of the ancestors of the Ainu people, had a mixed subsistence economy not only based on hunting, fishing, and gathering, but also on crop cultivation, including barley, wheat (*Triticum aestivum*), foxtail (*Setaria italica*) and broomcorn millet (*Panicum miliaceum*), *Perilla* sp., soybean (*Glycine max*), and Japanese red bean (*Vigna angularis*) (Crawford, 2011). At some Satsumon culture sites, the macrobotanical assemblages of these plants were so extensive that different authors were convinced that their cultivation was associated with day-to-day activities (see Crawford, 2011 and references therein), thus was of significant importance. Given a substantial dependence on crop cultivation, it seems conceivable that progressive cooling was involved in the observed cultural changes at the Satsumon/Ainu transition, though the underlying mechanisms of the entire process are still poorly understood. The regional changes associated with the establishment of the Ainu culture comprise a reduction in archaeological site numbers in Hokkaido compared to the preceding Okhotsk and Satsumon culture periods (Abe et al., 2016, Fig. 5h) and evolvement of a rather complex hunter-fisher-gatherer economy, which possessed some agriculture but more strongly relied on trade of natural resources, such as marine products, animal furs, and eagle feathers (Hudson, 1999, 2017). Subsequently, at the onset of the LIA main stage (ca. 400 cal BP), further cooling may have led to the recorded intensification of resource exploitation during the

Classic Ainu phase.

6.2. Human activities on Rebun Island and their influence on the local environment

The earliest traces of human presence on the island date to the Late Palaeolithic (ca. 20,000 BCE) when the island and entire Hokkaido and Sakhalin were part of the continent (Inui, 2000). The oldest residential site is Uedomari (north-eastern Rebun Island) dating to the first half of the Middle Jomon (ca. 2950–2470 BCE) (Hokkaido Maizo Bunkazai Center, 1984), i.e. since Lake Kushu had turned into a freshwater lake. It appears that Rebun Island, and especially the Funadomari Bay, was a centre for shell bead production during the Middle and Late Jomon periods (Nishimoto, 2000a). While the number of Middle Jomon sites is five, there are ten Late Jomon sites and one Final Jomon site reported (Abe et al., 2016, Fig. 5i). The synopsis of the palynological analysis of RK12 and the AMS radiocarbon dates of charred terrestrial archaeobotanical remains from Hamanaka 2 provide insights into human activities on Rebun Island from the Final Jomon culture period onwards. Combining the previously obtained dates on plant macrofossils (Leipe et al., 2017; Müller et al., 2016) with the new (this study) radiocarbon dates (Table 1) from the Final Jomon, Epi Jomon, Okhotsk, and Ainu cultural layers (VIII–I) shows a trimodal distribution (Fig. 6). Given the 95% confidence intervals, the oldest registered occupation phase spans ca. 390–50 BCE, followed by a second phase temporally bounded between ca. 420 and 970 CE. The third phase starts ca. 1640 CE and may potentially stretch into recent times. This suggests three discontinuous occupational phases at the site. The oldest period temporally corresponds to the end of the Final Jomon and most of the Epi Jomon periods, as defined in the archaeological chronologies for Hokkaido (Hirasawa et al., 2017, Fig. 6). During this time, arboreal taxa (~84%) remained abundant. Hence there is no indication of human-induced disturbance of natural forests (Müller et al., 2016), although relatively high population numbers are at least suggested by an increase in the number ($n = 23$; Fig. 5i) of Epi Jomon archaeological sites (Abe et al., 2016; Inui, 2000). This may be explained by an occupation that was short-term or seasonal (e.g. during marine hunting season) rather than year-round as previously argued by Sakaguchi (2007). This occupational phase, stretching ca. 390–50 BCE, features a single charred grain of naked barley (ID: F2014-089-01, Table 1). Direct AMS ^{14}C dating of this grain revealed an age range of 375–203 BCE (95% confidence interval). This predates any other well-documented archaeobotanical remains of domesticated barley in the Hokkaido region by ca. 800 years (Leipe et al., 2017; Yamada, 1995). As indicated by the 2-sigma calibrated age range, this single barley grain may be associated with the Final Jomon culture. However, a connection to Epi Jomon culture activities seems more likely, since the grain was extracted from an Epi Jomon cultural context. To date, there is limited evidence for the use of domesticated crops by Epi Jomon groups, which, in addition to barley, also include the millets and rice (*Oryza sativa*) (D'Andrea, 1995). As for barley, only one caryopsis has previously been found in the Epi Jomon level (typologically dated to ca. 200–400 CE) of the K135–4 Chome site in Sapporo city (Crawford and Takamiya, 1990). The relatively few finds of domesticated crops from Epi Jomon cultural layers are likely the result of exchange and imported grains of low-level use with small-scale or no cultivation. Nevertheless, the incorporation of domesticated crops into the Epi Jomon diet characterises it as “complex” hunter–gatherers that, according to Smith's (2001) conceptual framework, belong to the so called ‘middle ground’ subsistence economy. Like the grains associated with the Okhotsk culture (Leipe et al., 2017 and this study), the so far oldest specimen F2014-089-01 represents compact naked barley (Fig. 4, Supplemental Table S3), thus probably also originated from the continental Russian Far East, rather than from the Japanese islands region south of Hokkaido (see discussion in Leipe et al., 2017).

For the period between 50 BCE and 420 CE there is no evidence of human activities at Hamanaka 2. The natural forest appears to have persisted on the island during this interval, which corresponds to the Susuya culture period (ca. 100 BCE–500 CE) that was long regarded as the initial stage of the Okhotsk (Proto-Okhotsk) but is now defined as a separate cultural unit (Zhushchikhovskaya, 2010). Both the Susuya and Okhotsk (ca. 500–1000 CE) cultures share similar traits in terms of material culture and subsistence economy (Zhushchikhovskaya, 2010). However, unlike the Okhotsk culture people, the Susuya culture people probably did not occupy this area. With 19 archaeological sites (Fig. 5i) in the database analysed by Abe et al. (2016), Rebun Island seems to have been an important location for people of the Okhotsk culture. The Hamanaka 2 area appears to have been especially attractive as a residential and hunting/fishing ground (Nishimoto, 2000b; Sakaguchi, 2007). According to the available datings, the next phase of human occupation at Hamanaka 2 is bounded sometime between 420 and 970 CE and apparently was related to the Okhotsk culture. This period is marked by more human-induced vegetation disturbance on the Island. As illustrated by the AP percentage curve of the Lake Kushu record, noticeable deforestation and opening of the landscape started at least ca. 480 CE and culminated around 640–715 CE. Regarding the increased *Pediastrum* percentages (Fig. 3), which may point to enhanced input of nutrients due to increased surface runoff within the open catchment, forest clearance might have started around Funadomari Bay and Lake Kushu as early as ca. 370 CE, corresponding to the onset of LPSZ RK12-1c. Since 715 CE, the pollen record from Lake Kushu shows rising AP proportions indicating a continuous decrease in human impact and a return to the natural forest-dominated vegetation by ca. 800 CE, roughly corresponding to the beginning of LPSZ RK12-1b. These trends suggest that ‘Early Okhotsk’ groups substantially disturbed the local vegetation on the island while the impact of groups of the ‘Late Okhotsk’ phase, which is represented by the Motochi stage (ca. 9th–10th century CE; Hudson, 2004; Deryugin, 2008), was rather weak. This may point to reduced human presence and lower activities of ‘Late Okhotsk’ populations, which corroborates models that propose an advance of Satsumon groups into northern Hokkaido in the 9th century CE. These population shifts supposedly led to warlike conflicts (Hudson, 1999) and the emigration of Okhotsk people to Sakhalin (Ohyi, 1975) and Kuril Islands. This phase may have been characterised by occasional or seasonal visits of humans and minor impact on local vegetation.

Natural forests on Rebun Island seem to have persisted without noticeable area loss throughout the Satsumon and Formative Ainu periods. The pollen record from Lake Kushu corroborates the absence of evidence for human activities at Hamanaka 2 during this phase. Decreasing human activities/presence is also suggested by a decline in archaeological site numbers to 12 for the Satsumon culture and 9 for the Ainu culture (Abe et al., 2016, Fig. 5i), although there is no separate information provided for both Ainu substages (i.e. Formative and Classic Ainu periods). This situation changed around 1540 CE (onset of LPSZ RK12-1a) when the AP percentages drop quickly reaching minimum levels by ca. 1600 cal BP, suggesting a new phase of pronounced human-induced disturbance of local forests. This enhanced pressure on the natural vegetation might be associated with the transition from the Formative (ca. 1200–1600 CE; Hudson, 2004) to Classic (ca. 1600–1868 CE; Hudson, 2004) Ainu culture. The re-occupation of the Hamanaka 2 area, as implied by the radiocarbon dating, supports a population increase and/or a shift towards annual presence of the (Classic)

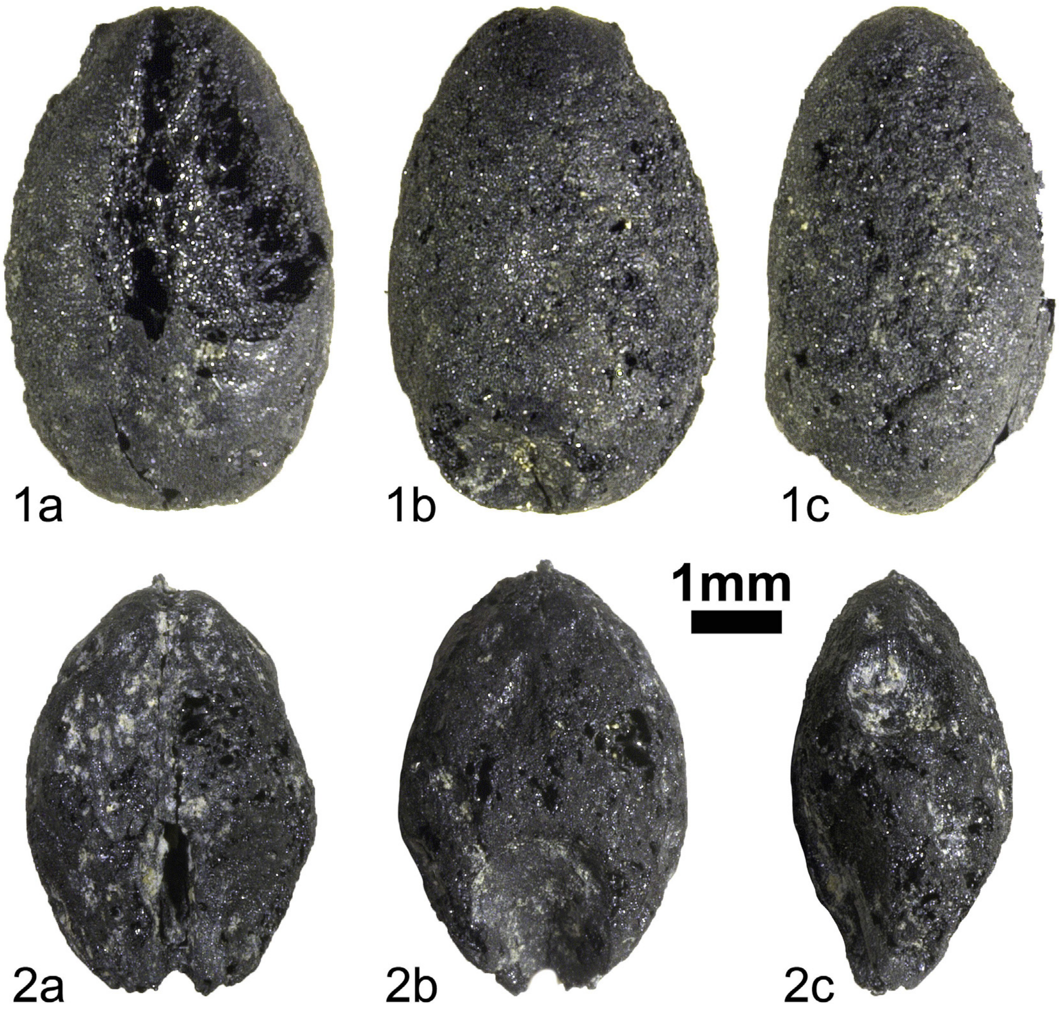
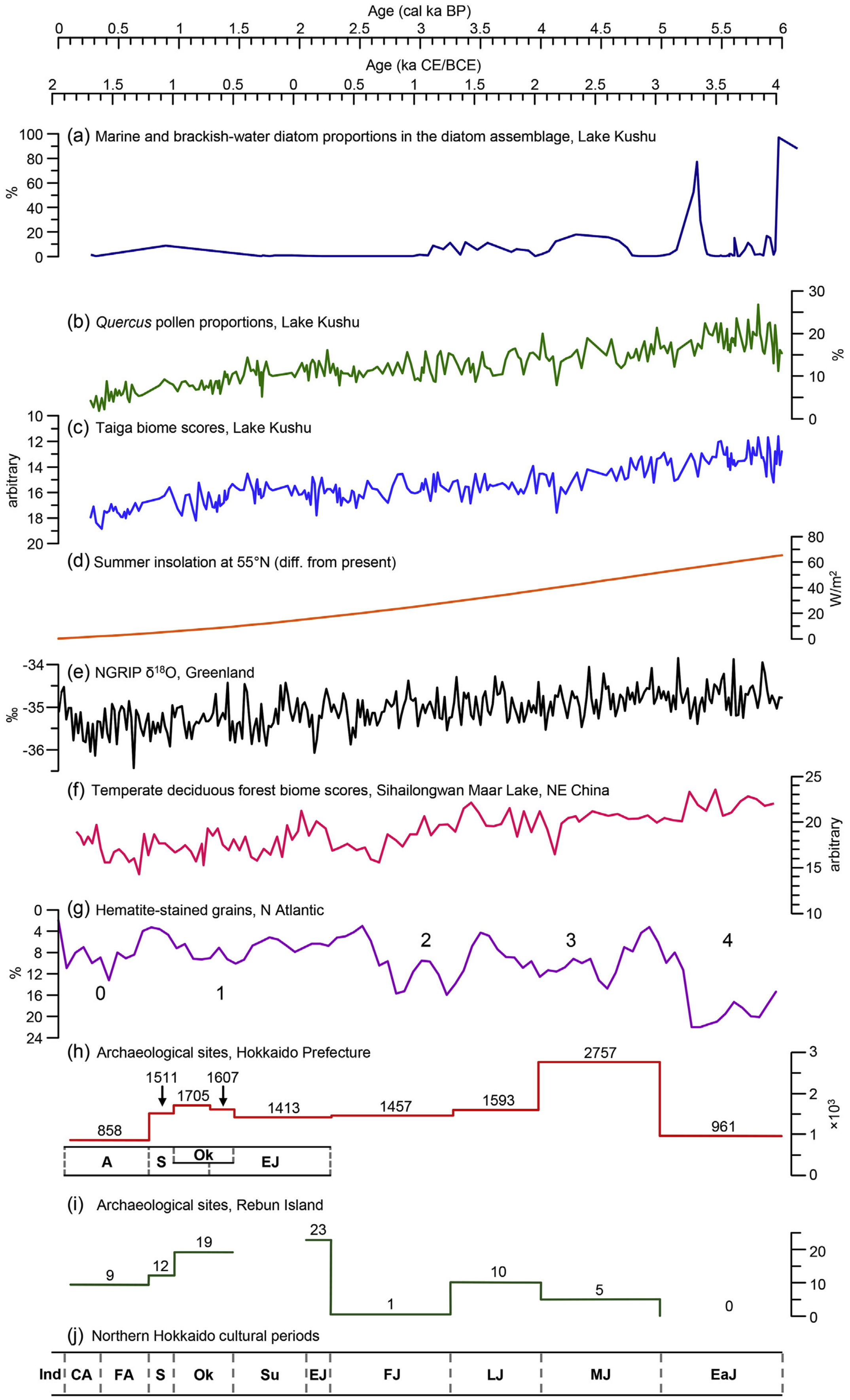


Fig. 4. Early naked barley grain (1a–c) from the site dating (375–203 BCE, 95% confidence interval, INTCAL13; Reimer et al., 2013) to the Final (ca. 1300–300 BCE) and Epi (ca. 300–100 BCE) Jomon culture periods in comparison to a naked barley grain (2a–c) representative for the naked barley assemblages extracted from Okhotsk cultural layers from the same site (Leipe et al., 2017). Both specimens are shown in ventral (a), dorsal (b), and lateral (c) views.

Ainu population on Rebun Island. In fact, there is evidence that trade between the Ainu and Japanese intensified after the 16th century CE (Hudson, 1999; Walker, 2001), indicating that the observed forest decline reflects enhanced exploitation of natural resources.

7. Conclusions

The securely dated high-resolution pollen record RK12 and archaeobotanical assemblages from the archaeological site of Hamanaka 2 allow insights into regional vegetation and climate dynamics and human-environmental interactions on Rebun Island in the NW Pacific during the last 6000 years. Results of the pollen analysis and pollen-derived biome reconstruction suggest a continuous long-term trend of climate cooling, which parallels the decline in the NH Holocene summer insolation. This development is superimposed by several phases of relatively quick transitions towards cooler climate conditions at ca. 5540/5350, 1550, and 390 cal BP, and one pronounced short-term cold event about 4130 cal BP. These cold events partly coincided with shifts in the prehistoric cultural sequence documented by archaeological records from Hokkaido, though, possible links between the environmental changes and prehistoric humans in the region require further investigations. These shifts are in line with major NH-wide to global-scale climate transitions/events (i.e. the ‘Holocene Climate Transition’, the onset of the ‘Dark Ages Cold Period’ main phase, the LIA, and the 4.2 kiloyear event, respectively) often linked to North Atlantic cold spells (i.e. Bond cycles 4, 3, 1, and 0, respectively). Although, some of the more pronounced shifts towards cooler conditions, including those at 5540/5350 and 1550 cal BP, coincide with Bond cycles 4 and 1, respectively, others (at ca. 4130 and 390 cal BP) do not. There is also no indication of vegetation and climate change during Bond cycle 2, which is often related to the 2.8 kiloyear event (Plunkett and Swindles, 2008) of which evidence was found in palaeoenvironmental proxy records from different regions of the Northern and Southern Hemisphere. Consequently, the presented results do not show teleconnection between the study region in the NW Pacific and the North Atlantic cold intervals (i.e. Bond cycles). In fact, our data reflect spatial variation in the intensity of these mostly hemispheric- to global-scale climate anomalies. These anomalies emphasise the complexity of combined external (e.g. solar activity) and internal (e.g. ocean–atmosphere systems) forcing, which require additional palaeoenvironmental studies for a better understanding. Another interesting feature of the current study is that warmer climate ‘reversals’ like the ‘Bronze Age Optimum’, the ‘Roman Warm Period’, or the ‘Medieval Warm Period’ are not pronounced in the RK12 pollen record. Instead, the pollen data signify intervals of


Age (cal ka BP)
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5 5 5.5 6
Age (ka CE/BCE)
2 1.5 1 0.5 0 0.5 1 1.5 2 2.5 3 3.5 4
(a) Marine and brackish-water diatom proportions in the diatom assemblage, Lake Kushu
%
100 80 60 40 20 0
(b) Quercus pollen proportions, Lake Kushu
30 20 10 0
%
(c) Taiga biome scores, Lake Kushu
arbitrary
10 12 14 16 18 20
(d) Summer insolation at 55°N (diff. from present)
80 60 40 20 0
W/m²
(e) NGRIP δ¹⁸O, Greenland
‰
-34 -35 -36
(f) Temperate deciduous forest biome scores, Sihailongwan Maar Lake, NE China
25 20 15 10
arbitrary
(g) Hematite-stained grains, N Atlantic
%
0 4 8 12 16 20 24
0 1 2 3 4
(h) Archaeological sites, Hokkaido Prefecture
858 1511 1705 1607 1413 1457 1593 2757 961
×10³
3 2 1 0
A S Ok EJ
(i) Archaeological sites, Rebun Island
9 12 19 23 1 10 5 0
20 10 0
(j) Northern Hokkaido cultural periods
Ind CA FA S Ok Su EJ FJ LJ MJ EaJ

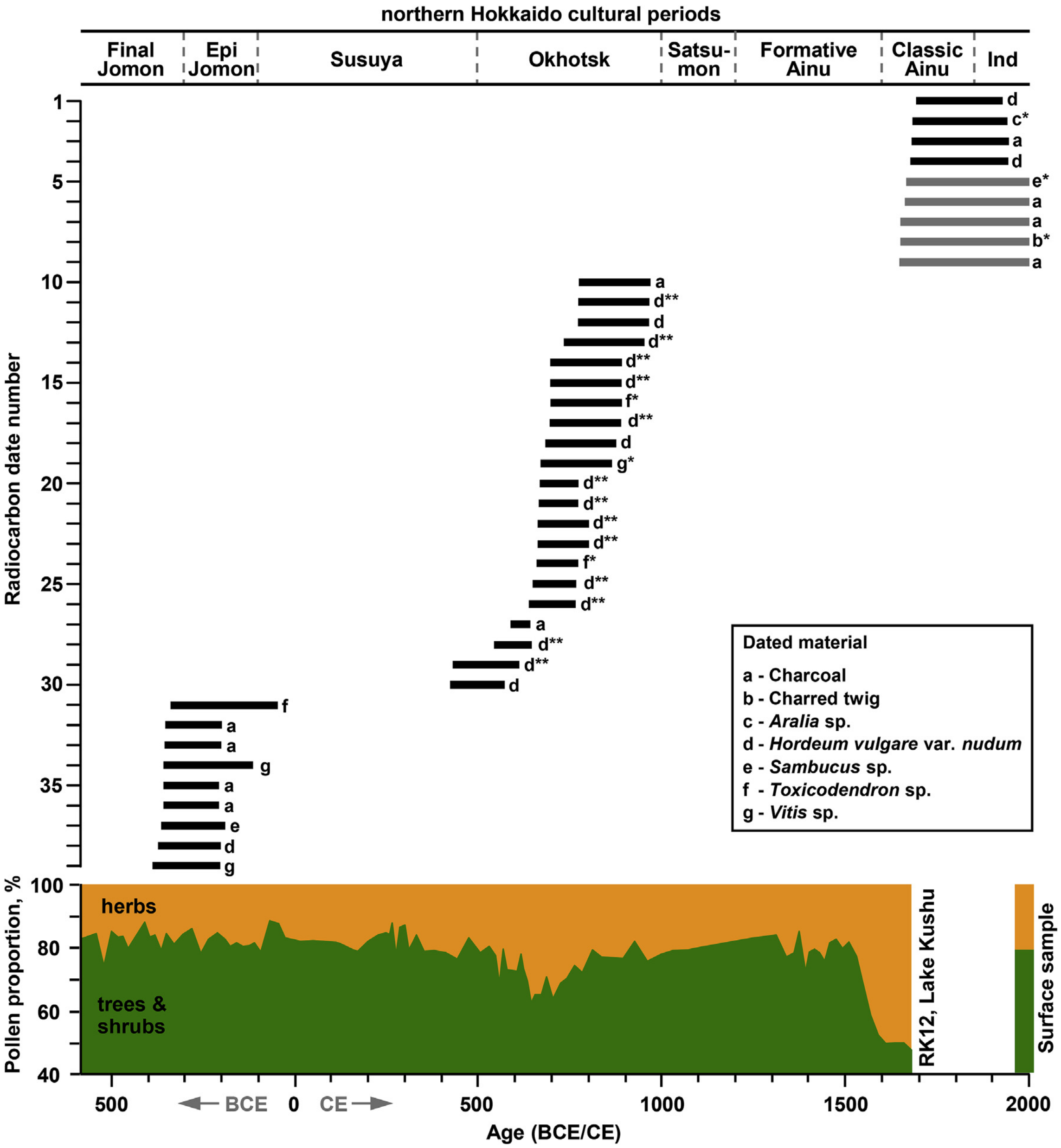


Fig. 6. Results of the AMS radiocarbon dating of macrobotanical remains from cultural layers of the archaeological site together with the terrestrial pollen sum diagram for the RK12 sediment core from Lake Kushu and the surface samples set (Fig. 2), based on average percentages. Black bars show the 95% confidence interval of INTCAL13 (Reimer et al., 2013) calibrated ages. Grey bars represent datings that have no upper confidence limit. One and two asterisks indicate datings previously published in Müller et al. (2016) and Leipe et al. (2017), respectively. Chronology of prehistoric and early historic cultures in northern Hokkaido comprises Final Jomon (ca. 1300–300 BCE), Epi Jomon (ca. 300–100 BCE), Susuya (ca. 100 BCE–500 CE), Okhotsk (ca. 500–1000 CE), Satsumon (1000–1200 CE), Formative (Prehistoric) Ainu (ca. 1200–1600 CE), Classic (Historic) Ainu (ca. 1600–1868 CE) cultures (according to Deryugin, 2008; Hudson, 2004, 2007; Weber et al., 2013), and Industrial Age (Ind).

progressive low-scale cooling. We argue that during these periods, temperature in our study region was in equilibrium with the major long-term forcing factors (i.e. the Holocene summer solar insolation) without significant influence from short-term driving forces (e.g. volcanism or solar variability). This has been demonstrated in a recent study (Bradley et al., 2016) for the ‘Medieval Warm Period’.

The comprehensive set of AMS radiocarbon dates of charred macrobotanical remains from the site suggests three discontinuous

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Fig. 5. Summary chart showing (a) marine and brackish-water diatom proportions in the diatom assemblage from Lake Kushu (Schmidt, 2018), (b) the *Quercus* pollen proportions and (c) taiga biome scores of the RK12 pollen sequence from Lake Kushu (Fig. 1), (d) calculated mean summer (June–August) insolation at 55°N (Laskar et al., 2004), (e) the NGRIP ice core (75.10°N, 42.32°W, 2917 m a.s.l.) $\delta^{18}O$ record (Svensson et al., 2008), (f) the temperate deciduous forest biome (TEDE) scores based on the pollen record from Sihailongwan Maar Lake (Stebich et al., 2015), (g) the hematite-stained grains record as a North Atlantic drift ice indicator with numbered Bond cycles (Bond et al., 2001), (h) the absolute number of archaeological sites in Hokkaido Prefecture per period (Abe et al., 2016) where cultural periods are indicated when differing from the chronology given in (j), (i) the absolute number of archaeological sites (note that Susuya sites are not contained in the dataset and the number for Ainu covers both Formative and Classic stages) on Rebun Island per period (Abe et al., 2016), and (j) the chronology of prehistoric and early historic cultures of northern Hokkaido including the Early (EaJ), Middle (MJ), Late (LJ), Final (FJ), and Epi (EJ) Jomon, as well as Susuya (Su), Okhotsk (Ok), Satsumon (S), Formative (FA) and Classic (CA) Ainu cultural periods, and Industrial Age (Ind) (see caption of Fig. 6 for details).

occupational periods ca. 390–50 BCE, 420–970 CE, and from 1640 CE that correspond to the Epi Jomon, Okhotsk, and Classic Ainu cultural phases, respectively. Given the RK12 arboreal/non-arboreal pollen ratios, the impact on natural environments (i.e. forest clearance) was marginal during the Epi Jomon phase. By contrast, deforestation was evident during the Okhotsk culture phase (especially during the early stage) and became even more intensive during the Classic Ainu occupation. This may point to population dynamics, changing degrees of mobility, and/or different patterns of natural resource exploitation and land use strategies, an interpretation supported by available archaeological and archaeobotanical studies. The earliest well-documented evidence for the use of naked barley in the Hokkaido region by Epi Jomon groups emphasises the complexity in subsistence economy of regional hunter–gatherer cultures. The domesticated grain also hints to early exchange between northern Hokkaido and regions to the north (Sakhalin Island) and west (continental Russian Far East) and/or to migration waves from the latter two regions.

Data availability

Datasets related to this article can be found online in the Open Access information system PANGAEA at https://doi.pangaea.de/10.1594/PANGAEA.890926.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.06.011.

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