

# Mathematisch-Naturwissenschaftliche Fakultät

Bastian Niemeyer | Ulrike Herzschuh | Luidmila Pestryakova

Vegetation and lake changes on the southern Taymyr peninsula, northern Siberia, during the last 300 years inferred from pollen and Pediastrum green algae records

Suggested citation referring to the original publication: The Holocene 25(4) (2015)
DOI https://doi.org/10.1177/0959683614565954
ISSN (print) 0959-6836
ISSN (online) 1477-0911

Postprint archived at the Institutional Repository of the Potsdam University in: Postprints der Universität Potsdam Mathematisch-Naturwissenschaftliche Reihe ; 421 ISSN 1866-8372

http://nbn-resolving.de/urn:nbn:de:kobv:517-opus4-404880



# Vegetation and lake changes on the southern Taymyr peninsula, northern Siberia, during the last 300 years inferred from pollen and *Pediastrum* green algae records

The Holocene 2015, Vol. 25(4) 596–606 © The Author(s) 2015 Reprints and permissions: sagepub.co.uk/journalsPermissions.nav DOI: 10.1177/0959683614565954 hol.sagepub.com

**\$**SAGE

# Bastian Niemeyer, Ulrike Herzschuh<sup>1,2</sup> and Luidmila Pestryakova<sup>3</sup>

#### **Abstract**

Siberian arctic vegetation and lake water communities, known for their temperature dependence, are expected to be particularly impacted by recent climate change and high warming rates. However, decadal information on the nature and strength of recent vegetation change and its time lag to climate signals are rare. In this study, we present a <sup>210</sup>Pb/<sup>137</sup>Cs dated pollen and *Pediastrum* species record from a unnamed lake in the south of the Taymyr peninsula covering the period from AD 1706 to 2011. Thirty-nine palynomorphs and 10 morphotypes of *Pediastrum* species were studied to assess changes in vegetation and lake conditions as probable responses to climate change. We compared the pollen record with *Pediastrum* species, which we consider to be important proxies of climate changes. Three pollen assemblage zones characterised by *Betula nana, Alnus viridis* and *Larix gmelinii* (1706–1808); herbs such as Cyperaceae, *Artemisia* or *Senecio* (1808–1879), and higher abundance of *Larix* pollen (1955–2011) are visible. Also, three *Pediastrum* assemblage zones show changes of aquatic conditions: higher abundances of *Pediastrum boryanum* var. *brevicorne* (1706–1802); medium abundances of *P. kawraiskyi* and *P. integrum* (1802–1840 and 1920–1980), indicating cooler conditions while less eutrophic conditions are indicated by *P. boryanum*, and a mainly balanced composition with only small changes of cold- and warm-adapted *Pediastrum* species (1965–2011). In general, compositional *Pediastrum* species turnover is slightly higher than that indicated by pollen data (0.54 vs 0.34 SD), but both are only minor for this treeline location. In conclusion, the relevance of differentiation of *Pediastrum* species is promising and can give further insights into the relationship between lakes and their surrounding vegetation transferred onto climatic conditions.

#### **Keywords**

morphotypes, Pediastrum, pollen, Siberia, treeline, vegetation

Received 28 July 2014; revised manuscript accepted 17 November 2014

# Introduction

Vegetation composition at the northern treeline is known for its strong ecological change in time and space and is sensitive to climate change. Numerous transect studies on modern vegetation (e.g. De Klerk et al., 2009; Pisaric et al., 2001a; Sidorova et al., 2013) and millennial-scale long-term studies (e.g. Andreev et al., 2002, 2004; Hahne and Melles, 1999; Pisaric et al., 2001b) have been made, but still the complex vegetation-climate feedback mechanisms (Bonan, 2008) related to the northward expansion of the boreal forests (MacDonald et al., 2008) are not fully understood. Palynological investigations of Holocene lake-sediment cores from northern Siberian lowlands indicate that vegetation changed markedly on millennial time-scales, most of them showing a long-term trend in forest decrease correlated with an insolation decline (Andreev et al., 2002; Hahne and Melles, 1997; Klemm et al., 2013; MacDonald et al., 2000; Pisaric et al., 2001b). However, similar studies on recent decadal changes in northern Siberia are lacking. Tracing the response of vegetation to recent climate change is of great importance for the understanding of future vegetation changes and related feedbacks because predicted rates of temperature increase for the Siberian lowland are among the highest worldwide (Serreze et al., 2000).

High-latitude vegetation transitions can be reflected in the chemical characteristics of lakes (Bennett et al., 2001; Biskaborn et al., 2012; Fritz et al., 2012; Radle et al., 1989; Sancetta et al., 1985). Recently, a causal relationship between larch forest density and ion content of thermokarst lakes of Siberian lowlands was proposed, based on parallel pollen and diatom analyses of sediment cores (Herzschuh et al., 2013). In contrast to diatoms that are regularly used as a proxy of aquatic conditions, the value

Periglacial Research Section, Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Germany

 $^{2} \mbox{Institute}$  for Earth and Environmental Science, University of Potsdam, Germany

<sup>3</sup>Department for Geography and Biology, Northeastern Federal University of Yakutsk, Russia

#### Corresponding author:

Bastian Niemeyer, Periglacial Research Section, Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Telegrafenberg A43, 14473 Potsdam, Germany. Email: bastian.niemeyer@awi.de

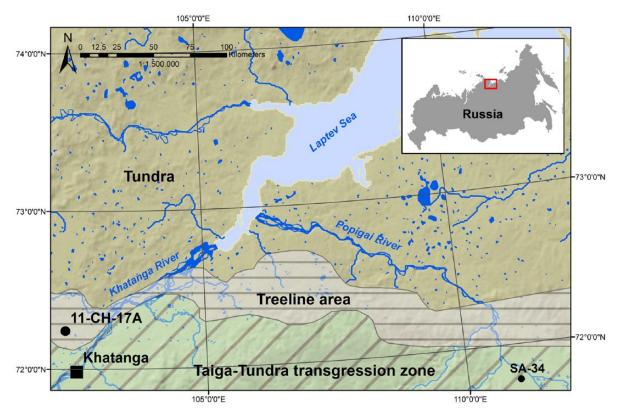


Figure 1. Overview of investigated area and position in northern Russia (detail). Sampled lake 11-CH-17A (left) is located approximately 300 km west of Lake SA-34 (Herzschuh et al., 2013). Tundra, treeline and taiga—tundra transgression zones following the Vegetation of the Soviet Union, 1990 (Stone and Schlesinger, 2003. Figure processed with ArcGIS 10.2.

of frequency changes of *Pediastrum* species and their morphotypes has seldom been investigated (Jankovská and Komárek, 2000) despite these green algae colonies being common components of high-latitude palynomorph records (Komárek and Jankovská, 2001; Nielsen and Sørensen, 1992).

Here, we present pollen and *Pediastrum* green algae records covering the last 300 years from a treeline lake on the southern Taymyr peninsula, in northern Siberia. Our objectives are (1) to reconstruct the vegetation changes with sub-decadal resolution, (2) to trace changes in the aquatic environment with the help of compositional changes of *Pediastrum* species and (3) to compare inferred ecological changes to independent proxy data on climate change.

# Study area

The study area (Figure 1) is located at the southern part of the Taymyr peninsula in northern Siberia within the administrative district of Krasnoyarsk territory (Russia). The area is dominated by lowlands and gentle hills. The soil has a locally varying active layer depth (range: 10-53 cm). Continuous permafrost causes the formation of thermokarst lakes in this region. The Last Glacial Maximum (LGM) left the northern Siberian lowlands ice free (Bigelow, 2003; Hahne and Melles, 1997; Möller et al., 1999), thus the landscape has not been overprinted by glacial deposits.

The climate is characterised by cold winters with a thin snow cover and moderately cold and wet summers. Climate observations (1962–2011) at the weather station in Khatanga (71.983°N, 102.466°E) give 12.6°C/–32.5°C as the mean July/January temperature (Polyakov et al., 2003). The coldest recorded mean January temperature occurred in 1979 (–41.6°C), while the warmest mean January temperature was recorded in 1981 (–20.3°C). The highest mean July temperature was recorded in 1984 (18.1°C) and the coldest in 1993 with 7.9°C. Mean annual precipitation is 257 mm. Precipitation occurs mainly in summer between June

and August (Duguay et al., 2012). Highest/lowest mean annual precipitation was recorded in 1967/1978 (352/154 mm). A long-term warming trend is visible for the winter months, but no trend is discernible for summer temperature.

The study area is located in the transition zone between tundra and larch forest-tundra as indicated by Matveyeva (1994) and Hahne and Melles (1999). The studied thermokarst lake is situated approximately 250 km north of the Arctic Circle and approximately 23 km west of the Khatanga River (Figure 1; 72.24454°N, 102.23571°E, 53 m.a.s.l.). The lake covers an area of approximately 0.036 km<sup>2</sup>. The maximum water depth is 3.40 m, and Secchi depth is 1.70 m. The lake water has a pH of 7.87, a conductivity of 64.2 µS/cm and an alkalinity of 0.3 mol/L. Vegetation surveys recorded sparse larch forest in the vicinity of the lake intermixed with polygonal tundra in wet depressions and forest-tundra in the uplands. The dominant taxa are Larix gmelinii (Rupr.) Rupr. (the only tree in the area) and shrubs such as Betula nana L., Alnus viridis subsp. fruticosa (Rupr.) Nyman, and Salix spp. L. and the herbaceous Ledum palustre Harmaja. Poaceae and Cyperaceae are also dominant in the polygonal tundra.

# Material and methods

The lake (field code: 11-CH-17) – selected from a topographic map and visually surveyed from helicopter – is surrounded by typical and relatively even forest-tundra and has a simple catchment hydrology, consisting of run-offs and melt-water intake. The catchment area is approximately  $1\,\mathrm{km^2}$ , and no direct connections to other lakes or streams are present.

## Sediment coring and dating

A 90-cm-long core (6 cm in diameter) consisting of homogenous gytja was obtained from the centre of the lake with a UWITEC gravity corer equipped with a hammer tool. To investigate the

recent years of the late Holocene, only the uppermost 27-cm samples were subsampled into 0.5 cm slices in the field and were stored cool and dark before being transported to the Alfred Wegener Institute in Potsdam, Germany, where the samples were stored at 4°C until further analysis. Four samples (10.5, 15.5, 20.5 and 25.5 cm) were accelerator mass spectrometry (AMS) radiocarbon dated at the Poznan Radiocarbon Laboratory at Adam Mickiewicz University, Poland. Furthermore, samples of the upper 11.75 cm were analysed for <sup>210</sup>Pb/<sup>137</sup>Cs by an Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detector at the Liverpool University Environmental Radioactivity Laboratory (Appleby and Piliposian, 2012).

#### Palynological analysis

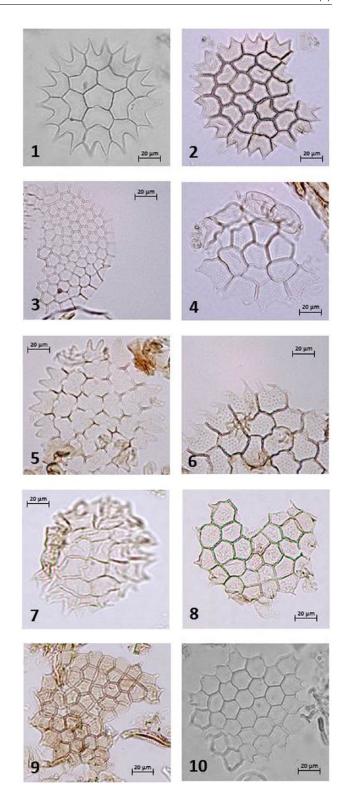
Sediment samples were probed in the laboratory, using a syringe taking 0.75 or  $1\,\mathrm{cm}^3$ , depending on the amount of material available. After adding a *Lycopodium* spore tablet (Batch nr. 1031; n=20,848), the subsamples were processed following standard procedures (Faegri and Iversen, 1989), including chemical treatment with HCl (10%), KOH (10%), NaOH (10%), hot HF (42%) and acetolysis treatment for 2 min. Ultrasonic bath (7  $\mu$ m) was done for a maximum of 1 min. The pollen material was finally stored in glycerine. It was analysed using a Zeiss Axioskop 40 light microscope at  $400\times$  magnification.

Identification of pollen grains was based on the relevant literature (Beug, 2004; Moore et al., 1991), and further indications for Siberian pollen taxa (e.g. Cassiope tetragona, Betula nana-type and Alnus viridis-type) were obtained from Savelieva et al. (2013). Also a pollen reference collection at the Alfred Wegener Institute in Potsdam was used for comparison. Nomenclature follows Beug (2004), identifying taxa mostly to genus level. Larix pollen grains were only counted if more than half of the pollen body was preserved. At least 300 pollen grains of terrestrial plants were identified per sample. The total pollen sum was taken as 100% and was calculated based on arboreal and non-arboreal pollen, not including submerged taxa such as Potamogeton. Percentages of non-pollen palynomorphs (NPP; e.g. Larix stomata) and spores (e.g. Equisetum or Pteridium) were also calculated based on the total sum of pollen. Taxa with occurrences in at least five samples are included in the pollen diagram.

In addition to pollen, different *Pediastrum* green algae species were counted using the same slides but during a second analysis run. Six different species had been discovered, whereof *Pediastrum* orientale shows two different morphotypes (P. orientale 1 and 2) and P. boryanum shows two morphotypes (P. boryanum 1 and 2) as well as two varieties (P. boryanum var. longicorne and P. boryanum var. brevicorne) as seen in Figure 2. The identification of Pediastrum taxa follows the descriptions of Komárek and Jankovská (2001) but was additionally verified by the descriptions of Kowalska and Wolowski (2010) and Nielsen and Sørensen (1992). An overview of the main features used to identify the 10 Pediastrum taxa is given in Table 1. P. boryanum var. longicorne and P. boryanum var. brevicorne can be unambiguously identified while one has to bear in mind the presence of transitional and difficult to recognise morphotypes of P. boryanum (Jankovská and Komárek, 2000). Frequencies of each taxon were calculated based on the total sum of Pediastrum. Diagrams of pollen and Pediastrum taxa were drawn using Tilia software (Grimm, 1991, 2004). The results of the pollen and *Pediastrum* analysis are available at http:// doi.pangaea.de/10.1594/PANGAEA.834488.

# Statistical analysis

All pollen and *Pediastrum* taxa with 0.5% abundance in at least five samples are included in the statistical analyses. Taxa which do not meet these criteria were excluded, and percentages were



**Figure 2.** Morphological appearance of different *Pediastrum* taxa: (1) *P. boryanum*-type 1, (2) *P. boryanum*-type 2, (3) *P. integrum*, (4) *P. boryanum* var. *brevicorne*, (5) *P. duplex*, (6) *P. boryanum* var. *longicorne*, (7) *P. angulosum*, (8) *P. orientale*-type 1, (9) *P. orientale*-type 2 and (10) *P. kawraiskyi*.

recalculated and square-root transformed prior to further statistical analyses as indicated in Grimm (1987). Age-constrained cluster analysis using the Constrained Incremental Sum of Squares (CONISS) algorithm (Grimm, 1987), together with a broken-stick model for zone number verification (Bennett, 1996; MacArthur, 1957), was applied to identify the Local Pollen Assemblage Zones (PAZs) of the pollen record according to West (1970) and the Local *Pediastrum* Assemblage Zones (PedAZs), likewise.

**Table 1.** Main features for identification of different *Pediastrum* green algae (Komárek and Jankovská, 2001; Kowalska and Wolowski, 2010; Nielsen and Sørensen, 1992).

Taxon	Lobus	Process	Surface	Holes	Comments
P. angulosum	Short, U-shaped, plane position	Missing or indistinct, abrupt or conical ended	Distinct net-like structure, forming polygonal meshes	No	
P. orientale	No incision, rounded, rotated position	Short, abrupt ending	Granular	No	Lower rotation of lobi and slighter granular cell wall than type 2
P. orientale 2	No incision, strongly rotated position	Short, abrupt ending	Very granular, thick cell walls	No	Higher rotation of lobi than type I and very granular cell surface
P. kawraiskyi	Massive, distinct, rotated position	Abrupt ending	Irregular, sometimes granular	No	
P. integrum	No incision	Very short or missing, often unequally long	Distinct granular	No	
P. duplex	Long V-shaped incision	Short	Smooth or fine granular, irregular net-like	Yes	
P. boryanum var. longicorne	Deep V-shaped incision	Very long, slightly curved	Granular	No	
P. boryanum var. brevicorne	Very small, shallow incision (U or V shape)	Shorter than cell diameter	Regular coarse granular	No	
P. boryanum var. boryanum 1	V-shaped incision, plane position	Narrow to long, abrupt ending	Distinct granular	No	More regular cell wall and slighter granular cell surface than type 2
P. boryanum var. boryanum 2	V-shaped incision, plane position	Narrow to long, abrupt ending	Highly granular, irregular cell wall	No	More irregular cell wall and cell surface than type I

Table 2. Results of the radiocarbon dating of bulk sediment from lake 11-CH-17.

Depth	Lab code	Material	Radiocarbon age (years)	Age without the 1626 years dead-carbon effect plateau	Calibrated age (yr AD)	Calibrated age (yr BP)
10.75	Poz-54102	Bulk	1665 ± 30	39	1917±66	33±66
15.75	Poz-54096	Bulk	2130±35	504	1416±14	534±14
20.75	Poz-54097	Bulk	1735 ± 25	109	1807 ± 96	143 ± 96
25.75	Poz-54099	Bulk	$2660 \pm 30$	1034	998±17	952±17

Principal Component Analysis (PCA; Bennett, 1996; Legendre et al., 2011; Ter Braak, 1983, 1994) was performed in the statistical software R version 3.0.3 (R Development Core Team, 2011) using the packages 'vegan' (Oksanen et al., 2011) and 'rioja' (Juggins, 2012), to display the main components of variance within the data and to reveal the relationships between taxa and PAZ/PedAZ and among taxa. Furthermore, a time-constrained Detrended Canonical Correspondence Analysis (DCCA; Hill and Gauch, 1980) using CANOCO 4.5 (Ter Braak and Šmilauer, 2002) was implemented with detrending by segments and nonlinear rescaling but without down-weighting of rare taxa, to estimate the strength of taxa reorganisation and change throughout the core, as turnover or standard deviation (SD) units of beta-diversity Smol et al. (2005).

# **Results**

# Dates and age-to-depth model

Radiocarbon analyses gave dates ranging between  $1665\pm30$  and  $2660\pm30$  radiocarbon years (Table 2) and are inconsistent due to age discrepancies between consecutive samples. The  $^{210}\text{Pb}/^{137}\text{Cs}$  dating of the 11.75-cm-long sediment core gave ages ranging between AD 2011 and 1898 (Table 3), which partially overlap the range of the radiocarbon dates.

To estimate a possible dead-carbon effect, a parallel dating of the 10.75-cm sample by  $^{14}\mathrm{C}$  AMS and  $^{210}\mathrm{Pb}/^{137}\mathrm{Cs}$  techniques was realised. The result of the  $^{14}\mathrm{C}$  AMS analysis is  $1665\pm30$  BP, which is equal to AD 285. This differs from the results of AD 1911 given by the  $^{210}\mathrm{Pb}/^{137}\mathrm{Cs}$  analysis. We assume this age discrepancy of  $1626\,\mathrm{years}$  as dead-carbon effect. Using this assumption, both age-to-depth models ( $^{14}\mathrm{C}$  AMS and  $^{210}\mathrm{Pb}/^{137}\mathrm{Cs}$ ) provide

similar results for two dated samples at 10.75 and 20.75 cm. The age-to-depth models indicate a basal age of 300 years for the core, while two other samples at 15.75 and 25.75 cm have dates older than the oldest extrapolated age of the <sup>210</sup>Pb/<sup>137</sup>Cs dating (Figure 3). The ages of the samples below 11.75 cm were estimated by extrapolating the mean sedimentation rate of the lowermost four <sup>210</sup>Pb/<sup>137</sup>Cs dated samples (Table 3) and give a date of AD 1706 for the 27-cm sample.

The <sup>210</sup>Pb/<sup>137</sup>Cs peaks are in good agreement with the 1963 fallout maximum (Appleby and Piliposian, 2012), and the sedimentation rate of the core varies between 0.21 cm yr<sup>-1</sup> in the uppermost samples and 0.08 cm yr<sup>-1</sup> in the lower samples. Thus, the samples have about a 6-year resolution on average. Despite the general fact that density of upper lake-sediment layers is usually less than lower sediments and, therefore, covering less years within same layer size, we think two of the <sup>14</sup>C dates are too old, probably because of thermo-erosional input of older organic carbon into the lake or redeposition in lakes as mentioned in Grimm (2011). The age-to-depth model based on <sup>210</sup>Pb/<sup>137</sup>Cs analysis is, therefore, considered as more reliable and has been used for the statistical analysis and interpretation of the results.

# Pollen data

In total, 36 pollen taxa were identified in the core; 18 of them met the criteria to be included in the pollen diagram and statistical analyses (Figure 4). Most abundant are *Betula, Alnus*, Poaceae, and Cyperaceae, which sum exceeds 80% in almost all samples. *Larix* percentages range between 0.3% and 12.7%. Fern spores (*Pteridium, Equisetum, Lycopodium clavatum*-type)

and submerged aquatics such as *Potamogeton* or *Rumex aquaticus* are present at low abundance. Based on the results of the age-constrained cluster analysis, the data set is divided into three local PAZs.

PAZ I is dominated by *Betula nana*-type and *Alnus viridis*-type, and *Larix* appears at moderate percentages. PAZ Ia (27–25.5 cm; AD 1706–1725) shows moderate values of *Alnus viridis*-type (up to 20%) and *Betula nana*-type, and *Larix* decreases from 10% to less than 5%. Compared to PAZ Ia, PAZ Ib (25.5–19 cm; AD 1725–1808) is characterised by low percentages of *Alnus viridis*-type (10%), while *Alnus glutinosa*-type appears

**Table 3.** Results of the <sup>210</sup>Pb/<sup>137</sup>Cs dating for lake 11-CH-17 (Appleby and Piliposian, 2012).

Depth	Date AD	±	Sedimentation rate (cmyr <sup>-1</sup> )	± (%)
0.00	2011	0	0	0
0.25	2010	- 1	0.21	2.7
0.75	2008	2	0.19	3.8
1.25	2005	2	0.17	4.8
1.75	2002	2	0.14	4.5
2.25	1998	2	0.12	4.2
2.75	1993	3	0.11	5.9
3.25	1988	4	0.10	7.5
3.75	1983	4	0.11	7.5
4.25	1979	4	0.11	7.5
4.75	1974	5	0.11	7.5
5.25	1969	5	0.11	7.5
5.75	1965	5	0.10	7.5
6.25	1960	6	0.10	7.5
6.75	1955	6	0.10	7.5
7.25	1950	7	0.10	7.5
8.00	1942	8	0.09	7.5
8.75	1934	9	0.09	7.5
9.25	1928	10	0.09	7.5
9.75	1922	11	0.09	7.5
10.25	1917	11	0.08	7.5
10.75	1911	12	0.08	7.5
11.25	1904	13	0.08	7.5
11.75	1898	14	0.08	7.5

with about 5% presence. *Larix* obtains <5% but stomata of larches were found in six samples.

Like PAZ I, PAZ II is characterised by high percentages of *Betula nana*-type and Cyperaceae becomes more abundant. In PAZ IIa (19–13.5 cm; AD 1808–1879), *Betula nana*-type and Cyperaceae reach about 30%. *Larix* has low percentages (<5%), and *Alnus glutinosa*-type (>8%) and *Betula pubescens*-type (>10%) have higher percentages compared to the other zones. A maximum of *Betula nana*-type (30% at 7.5 cm) is found in PAZ IIb (13.5–7 cm; AD 1879–1955), and Cyperaceae reaches a maximum (>30%) at the start of PAZ IIb (12 cm) but declines to 20% towards the upper part of PAZ IIb. *Alnus viridis*-type and *Larix* percentages increase from 11 cm upwards.

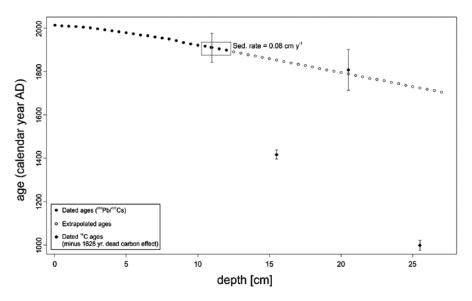
Betula nana-type and Alnus viridis-type increase from 10% to 20% at the transition to PAZ III (7–0 cm; AD 1955–2011). Larix attains maximum values (15%) of the entire record at 3.5 cm (~AD 1990). All three zones have Salix and Pinus at low abundance (~5%). Picea and Abies pollen were only rarely found in PAZ IIb and PAZ III.

The eigenvalues of the PCA calculations show that the first two axes (PC 1 and PC 2; Figure 5a), explain 65.5% of the pollen data variance. Samples of the individual PAZs, indicated by their year, are found in different parts of the PCA biplot. *Thalictrum, Vaccinium*-type, *Salix* and *Cassiope tetragona* are positively correlated with PC 1, while *Larix, Senecio*-type, *Betula pubescens*-type, *Betula nana*-type and *Alnus viridis*-type are positively correlated with PC 2. PAZ I, and in particular PAZ II, attain positive values on PC 1, whereas PAZ III is characterised by negative values on the first principal component and positive values on PC 2. The results of the pollen-based DCCA reveal a small turnover of 0.345 (inertia: 0.138) SD units of beta-diversity since 1706.

#### Pediastrum data

Pediastrum morphotypes show low (>1–5%; P. duplex, P. angulo-sum), moderate (5–15%; P. orientale 2, P. kawraiskyi, P. integrum, P. boryanum 1) or high (15–45%; P. orientale 1, P. boryanum 2) abundance within the core (Figure 6). Generally, our record is characterised by high short-term variability. CONISS and the broken-stick model revealed three significant PedAZs.

PedAZ I (27–19.5 cm; AD 1706–1802) is characterised by high abundances (20–30%) of *P. boryanum* var. *brevicorne* and *P.* 



**Figure 3.** Age–depth model of the core 11-CH-17 by <sup>14</sup>C and <sup>210</sup>Pb/<sup>137</sup>Cs dating. Beneath a depth of 11.75 cm, the <sup>210</sup>Pb/<sup>137</sup>Cs dates are extrapolated using the mean sedimentation rate (Sed. rate) of 0.08 cm yr<sup>-1</sup>. Two <sup>14</sup>C dates are too old, probably caused by input of older organic carbon due to thermo-erosional processes.

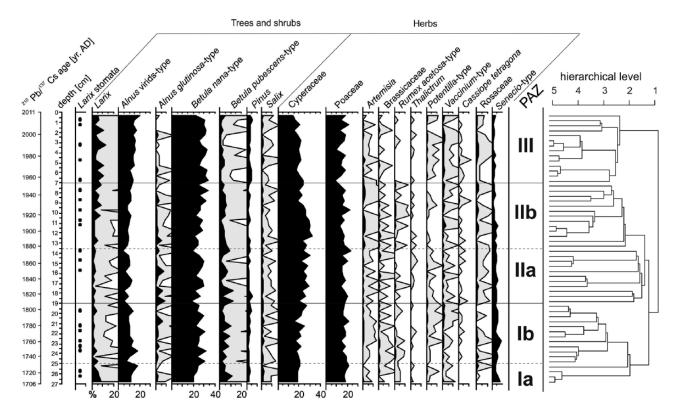


Figure 4. Pollen stratigraphy of lake 11-CH-17A. Only taxa with an abundance of >1% in at least five samples are shown. Original pollen abundance is represented by the black silhouettes; grey silhouettes show ×10 exaggeration. Samples containing Larix stomata are marked as black dots. Three pollen accumulation zones (PAZs) are shown, derived from the CONISS analysis (right).

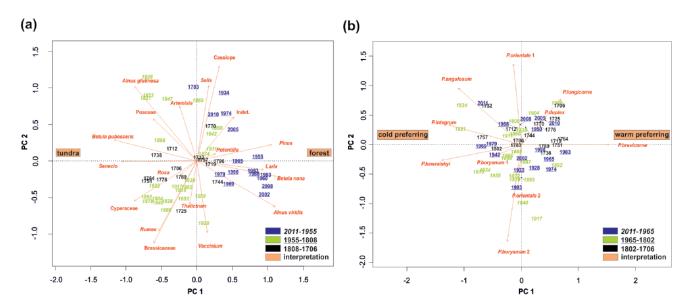


Figure 5. Results of the principal component analysis (PCA) for (a) pollen and (b) *Pediastrum*. Samples are coloured according to the years they represent (see legend) – note that they cover slightly different time periods.

boryanum var. longicorne and low abundances (<5%) of *P. kawraiskyi*, *P. duplex* and *P. angulosum*. *P. boryanum* var. longicorne and *P. boryanum* var. brevicorne decline abruptly at the transition to PedAZ IIa (19.5–16.5 cm; AD 1802–1840), while *P. integrum* attains its maximum for the entire record (~15%). At the transition to PedAZ IIb (16.5–6 cm; AD 1840–1965), *P. boryanum* var. longicorne increases again (from ~5% to 15%), and *P. boryanum* var. brevicorne attains its maximum (40%) for the entire record. *P. integrum* and *P. kawraiskyi* reach values of ~8%. *P. integrum* and *P. kawraiskyi* are missing in some samples of PedAZ III (6–0 cm; AD 1965–2011). *P. boryanum* var. brevicorne, *P. boryanum* var. longicorne and *P. boryanum* 1 and 2 show moderate to

medium abundances in PedAZ III. The fast increase of *P. orientale* 1 is accompanied by a simultaneous decrease of *P. boryanum* 1 and 2 at about AD 1980.

The first two principal components explain 42.3% of *Pediastrum* morphotype variance. The biplot in Figure 5b indicates that *P. boryanum* 2 and *P. orientale* 1 and 2 are strongly correlated to PC 1, and *P. kawraiskyi*, *P. integrum*, *P. boryanum* 1 and *P. boryanum* var. *brevicorne* are positively correlated to PC 2. PedAZ II mainly has positive values on axis 1. PedAZ I has positive values mainly on axis 2, while PedAZ II, and in particular PedAZ III, mostly have negative values. The DCCA of *Pediastrum* shows a small turnover of 0.542 SD (Inertia: 0154).

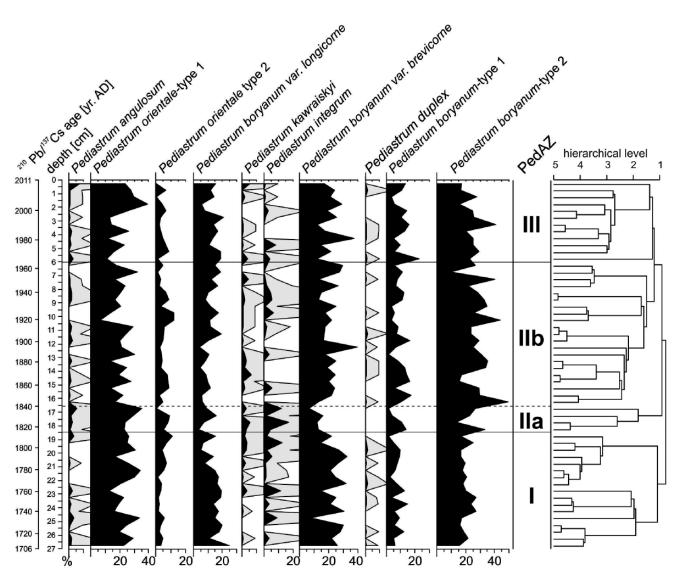


Figure 6. Pediastrum composition over time for lake 11-CH-17A. Pediastrum abundances are shown as black silhouettes and grey silhouettes as 10× exaggeration. Three Pediastrum accumulation zones (PedAZs) are shown, derived from the CONISS analysis (right).

# Discussion

# Vegetation history of the last 300 years

The sorting of pollen taxa of the fossil pollen data from core 11-CH-17 range from tundra elements, indicated by negative values on PC 1, to open forest elements with positive values, as seen in Figure 5a. A transition from one vegetation type (e.g. tundra or open vegetation) to another type (e.g. tree tundra or forest) forms the major trend in the pollen record. Pollen spectra from Siberian tundra vegetation are typically rich in various herb taxa. In particular, Poaceae, Cyperaceae and Asteraceae are common (Klemm et al., 2013), and all attain low scores on PC 1. It is known that openness (i.e. low shrub and tree cover) of regional vegetation and related low regional productivity cause over-representation of the far-distant transported pollen load (Broström et al., 2008; Cwynar, 1992; Klemm et al., 2013) which would explain why pollen grains of tree growth forms of birch (Betula pubescens-type) and alder (Alnus glutinosa-type) are correlated to typical tundra elements even though they are not part of the regional vegetation. An alternative explanation of the observed pattern in Betula and Alnus pollen types relates to the assumption that the two pollen types originate from pollen dimorphism known for arctic taxa (De Klerk et al., 2009, 2014), which in our case would be related to environmental conditions.

Alnus viridis-type, Betula nana-type (pollen types that are commonly related to shrubby growth forms of Alnus and Betula) and Larix have high taxa scores on PC 1. The occurrence of Larix-stomata throughout the entire record may indicate the presence of larch trees in the vicinity of the lake during the last 300 years, although Pisaric et al. (2001a) state far-distant transport as another possible stomata source. Tree cover may have changed as the threshold for the expansion of northern larch taiga, i.e., a Larix increase >2% in combination with an Alnus viridistype increase >10% (Klemm et al., 2013), was crossed several times.

If the first principal component reveals a trend in vegetation openness, the second principal component seems to be correlated with a moisture gradient, separating taxa characteristic of polygonal wetlands such as Cyperaceae or *Rumex* from those that are more abundant in dry tundra vegetation such as Poaceae, *Artemisia* and *Cassiope* (Bigelow, 2003; De Klerk et al., 2009).

Three local pollen zones reflect the major phases of local vegetation development. Within PAZ I (AD 1706–1725), medium amounts of *Larix* pollen indicate forest-tundra conditions, which is possibly a remnant of former closed larch forest (MacDonald et al., 2008; Tchebakova et al., 2005) with an understorey of *Betula nana* and *Alnus viridis*. The vegetation began to be more open by AD 1725 as indicated by a decrease in *Larix*, *Betula pubescens*-type and *Alnus glutinosa*-type. In contrast, Devi et al. (2008),

assuming a change in growth form, suggest a densification of larch stands over the last 250 years in the Polar Urals. PAZ II is inferred to reflect a phase of reduced vegetation cover, shown by herbs indicative of openness such as Artemisia, Potentilla and Vaccinium. PAZ IIa predominantly indicates the main phase of open vegetation cover, whereas the increase of Alnus viridis-type, Betula nana-type and Larix in PAZ IIb suggests the densification of the vegetation. The indications of openness are consistent with an observed Larix decline occurring between AD 1700 and 1800 in a pollen record from the upper Popigai River located ~300 km to the east (Herzschuh et al., 2013). High Cyperaceae values in PAZ IIb probably indicate extended polygonal wetlands (Stone and Schlesinger, 2003). PAZ III is characterised by the highest percentage of shrub and tree pollen (e.g. Alnus viridis, Betula nana, Larix) for the entire record, and dry tundra vegetation is inferred to have expanded. Even though slight changes in the relative vegetation cover become visible in the pollen record, the DCCA results only show a beta-diversity of 0.345 SD. This indicates that vegetation turnover is generally low, compared to values seen in Birks and Birks (2008), Smol et al. (2005) or Wischnewski et al. (2011). This underlines the relatively small changes in vegetation composition within our pollen record.

### Lake history during the last 300 years

Climate-driven changes of limnological conditions influence the Pediastrum composition during the course of a year. High summer temperatures cause blooms of warm-adapted Pediastrum species such as P. boryanum and P. boryanum var. brevicorne. If, due to colder water conditions, summer blooming events are absent or rare, the portion of cold-adapted species such as P. integrum or P. kawraiskyi increases. Temperature regimes influence the species composition, but the organic carbon content of the lake explains more variance of species composition (Weckström et al., 2010). These blooms, caused by the ability of *Pediastrum* to multiply rapidly, are reflected in our studied records by the abrupt changes in the Pediastrum composition. The PCA biplot indicates that certain species which have similar environmental requirements co-vary. For example, P. kawraiskyi and P. integrum, often regarded as indicators of cold conditions (Komárek and Jankovská, 2001; Nielsen and Sørensen, 1992), are negatively correlated with axis 1 (Figure 5). Thermophilic taxa such as *P. boryanum* var. *brevicorne* and P. boryanum, which also indicate eutrophic conditions (Komárek and Jankovská, 2001), are opposite P. kawraiskyi and P. integrum in the PCA biplot. The separation of the two morphotypes of P. orientale along the first principal component may indicate different ecological preferences of these taxa. Similar indications can be assumed for the morphotypes of P. boryanum. Thus, it seems necessary to differentiate these taxa in further investigations. PC 1 may, therefore, reflect the strength and frequency of *Pediastrum* blooms driven by summer temperatures.

The separation of water temperature effects from climate- and catchment-driven chemical effects on *Pediastrum* composition is challenging or even impossible due to inter-relationships among these environmental variables. For example, on one hand, high alkalinity may result from strong evapo(-transpi)ration at times of dense vegetation and warm summer climate (Herzschuh et al., 2013), but, on the other hand, humid conditions may support the input of ions via sea-spray (Abollino et al., 2004; Giblin et al., 1990) in times of high wind. Our records indicate opposing trends between group 1 (*P. boryanum* 2, *P. orientale* 1 and *P. boryanum* var. *brevicorne*) and group 2 (*P. kawraiskyi*, *P. integrum*, *P. orientale* 2 and *P. boryanum* var. *longicorne*). This reflects the varying ecological preferences of the individual species, specifically the preference of warmer (group 1) or colder conditions (group 2).

Pediastrum abundances at the beginning of PedAZ I indicate slightly warmer water conditions around AD 1706, compared to

the following decades. A cooling trend becomes visible from AD 1725 onwards with the increase of *P. kawraiskyi* and *P. integrum*, which have a maximum abundance between 1802 and 1840 (PedAZ IIa). The absence or low abundances of cold-adapted *P. kawraiskyi* and *P. integrum* from AD 1840 onwards until 1920 indicate warmer and eutrophic lake conditions. An increase of *P. boryanum* var. *brevicorne* and *P. boryanum* 1 between AD 1840 and 1915 (PedAZ IIb) also suggests slightly warmer and more eutrophic conditions, which are followed by a colder stage (AD 1915–1980) with alkaline water conditions indicated by an increase of *P. orientale* 2 and *P. boryanum* var. *longicorne*. PedAZ III is inferred to reflect a warm period indicated by the depression of *P. orientale* 1 and *P. boryanum* var. *longicorne* from 1980 onwards.

# Sensitivity of vegetation and lake aquatic conditions to climate change in northern Siberia

As long-term weather station records are lacking from the area, variations in our record can only be compared to climate proxy data derived from regional ice-core and tree-ring records spanning more than the last 300 years. Around AD 1806-1825, cold summer temperatures of 8.2°C have been reconstructed by tree-ring analyses (Naurzbaev and Vaganov, 2000) and  $\delta^{18}$ O ice-core analyses also indicate low temperatures (Fritzsche et al., 2005; Opel et al., 2013). Decreasing Alnus viridis-type and the simultaneous increase of Betula pubescens-type, Alnus glutinosa-type, P. kawraiskyi and P. integrum may reflect this cooling event. Further indications of a major cooling phase between AD 1800 and 1900 are proclaimed by tree-ring analysis by Jacoby et al. (2000) and also by isotope measurements (Sidorova et al., 2013). This matches with our finding of the dominance of cold-adapted Pediastrumtypes, as well as with vegetation openness as indicated by the comparison in Figure 7. A warmer climate between 1915 and 1970, as indicated in the tree-ring data and ice-core analyses (Naurzbaev and Vaganov, 2000; Opel et al., 2013), may have led to stronger Larix flowering and, over time, increased Larix establishment. Summer blooms of thermophilic P. boryanum 2 were also more frequent during 1915-1970. Our record reveals two short-term deteriorations in the vegetation and Pediastrum growing conditions at AD 1975 and 2002. The 1975 event at least is reflected in the tree-ring data as a cold depression (Jacoby et al., 2000; MacDonald et al., 2008; Naurzbaev and Vaganov, 2000) and is also present in  $\delta^{18}$ O analyses (Opel et al., 2013).

Compared to other palynological analyses from northern Siberia spanning longer time-scales (e.g. Andreev et al., 2002, 2004; Hahne and Melles, 1999; Kienel and Siegert, 1999; Pisaric et al., 2001b), the compositional reorganisation at the unnamed lake 11-CH-17 is small. Ecological change indicated by the pollenbased DCCA is similarly in a low range as noted by Wischnewski et al. (2011), suggesting little climatic influence on species composition. The finding of low compositional change during the last 100 years contradicts the record of a strong warming trend in the Arctic, as found by Serreze et al. (2000) and Kaufman et al. (2009). Even though our recorded vegetation change is minor, it hints at a minimum forest extent between AD 1755 and 1880 probably in response to a strong cooling as indicated by Opel et al. (2013). Later, our results suggest a slight forest re-expansion, which is still ongoing, reflecting the major warming trend that influences the treeline as described by Jacoby et al. (2000) and MacDonald et al. (2008). Although better climatic conditions may have favoured densification and the establishment of seedlings, a few years may pass before this change is fully reflected in the pollen record because of the comparatively long life cycles of shrubs and trees.

DCCA-based compositional turnover of *Pediastrum* records is, likewise, small. Compared to pollen, climate change seems to

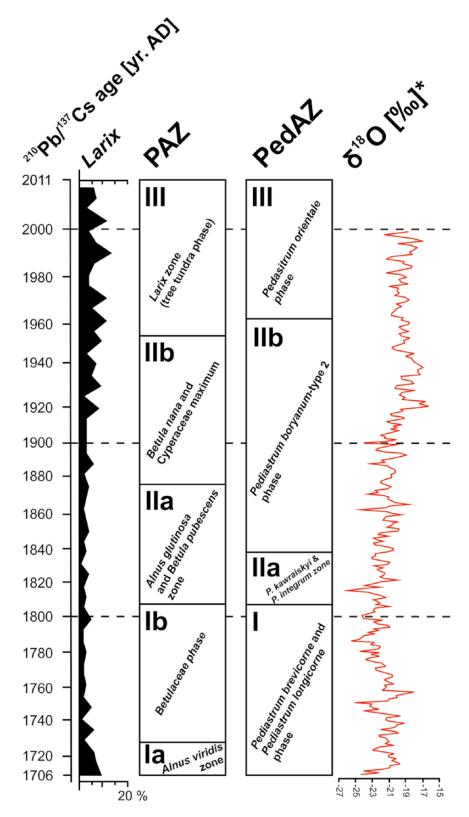


Figure 7. Comparison of vegetation and lake ecosystem changes given by pollen accumulation zones (PAZs), *Pediastrum* accumulation zones (PedAZs) and  $\delta^{18}$ O data.

have a greater influence on *Pediastrum* composition. Wischnewski et al. (2011) also note a greater influence on lake water communities than on pollen spectra. In comparison to other arctic aquatic records showing higher turnover mainly in the last 150 years (Smol et al., 2005), our DCCA results indicate a lower range of possible changes during the late Holocene. Comparison of *Pediastrum* and pollen records reveals generally similar variations throughout, although the pollen changes occur with some

short-term delay. If climate was the only trigger of planktonic changes of *Pediastrum*, near real-time changes could be expected owing to their short life cycles. Aside from summer temperature, lake water chemistry can drive *Pediastrum* composition, which in turn may reflect changes in the catchment vegetation that occurred as a response to climate (Herzschuh et al., 2013). Accordingly, the actual time lag of lake biota is affected by a complex interaction of various variables.

<sup>\*</sup>According to the Akademii Nauk (AN) core presented in Opel et al. (2013).

# Conclusion

Northern Siberian vegetation, as inferred from our pollen record of sub-decadal resolution from the southern Taymyr peninsula, changed only slightly during the last 300 years. The density of Larix forest was probably lowest between AD 1808 and 1879, and shrub abundance was also reduced then. Since that time, the vegetation became denser, but forest and shrub abundance did not or only slightly exceeded the 18th-century values. Accordingly, the strong warming known from climate proxy data and observations is only minimally reflected by the Siberian treeline vegetation. Changes in Pediastrum composition, recorded in the same core were also slight, but we assume that these compositional changes mainly reflect the number and strength of Pediastrum blooms related to warmer lake water during summer. We find that the period of forest retreat is paralleled by absent and/or weak blooms of thermophilic Pediastrum taxa. We also find a slight delay in the terrestrial vegetation signals in comparison to the aquatic changes, which seem to reflect climatic changes in near real time. Therefore, we consider *Pediastrum* to be a useful support for climate and vegetation reconstructions, especially if different taxa are tracked.

## **Acknowledgements**

We thank all participants of the joint Russian—German project for their support and effort, especially during the field campaign. We also thank the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research for financial support. Many thanks are directed to the helpful comments given by the editorial board and the annotations and revisions by the reviewers.

#### **Funding**

This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

#### References

- Abollino O, Aceto M, Buoso S et al. (2004) Distribution of major, minor and trace elements in lake environments of Antarctica. *Antarctic Science* 16(3): 277–291.
- Andreev AA, Siegert C, Klimanov VA et al. (2002) Late Pleistocene and Holocene vegetation and climate on the Taymyr Lowland, northern Siberia. *Quaternary Research* 57(1): 138–150.
- Andreev AA, Tarasov PE, Klimanov VA et al. (2004) Vegetation and climate changes around the Lama Lake, Taymyr Peninsula, Russia during the Late Pleistocene and Holocene. *Quaternary International* 122(1): 69–84.
- Appleby PG and Piliposian TG (2012) Radiometric dating of lake sediment cores from four sites in the vicinity of Chatanga, Northern Siberia. Dating report, p. 12. Liverpool: University of Liverpool.
- Bennett JR, Cumming BF, Leavitt PR et al. (2001) Diatom, pollen, and chemical evidence of postglacial climatic change at Big Lake, south-central British Columbia, Canada. *Quaternary Research* 55(3): 332–343.
- Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132: 155–170.
- Beug H-J (2004) Leitfaden der Pollenbestimmung. München: Verlag Dr. Friedrich Pfeil.
- Bigelow NH (2003) Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present. *Journal of Geophysi*cal Research 108(D19): 8170.
- Birks HJB and Birks HH (2008) Biological responses to rapid climate change at the Younger Dryas-Holocene transition at Krakenes, western Norway. *The Holocene* 18(1): 19–30.
- Biskaborn BK, Herzschuh U, Bolshiyanov D et al. (2012) Late Holocene thermokarst variability inferred from diatoms in a

- lake sediment record from the Lena Delta, Siberian Arctic. *Journal of Paleolimnology* 49(2): 155–170.
- Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320(5882): 1444–1449.
- Broström A, Nielsen AB, Gaillard M-J et al. (2008) Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: A review. *Vegetation History and Archaeobotany* 17(5): 461–478.
- Cwynar LC (1992) A Late-Quaternary vegetation history from Hanging Lake, northern Yukon. *Ecological Monographs* 52(1): 1–24.
- De Klerk P, Donner N, Joosten H et al. (2009) Vegetation patterns, recent pollen deposition and distribution of non-pollen palynomorphs in a polygon mire near Chokurdakh (NE Yakutia, NE Siberia). *Boreas* 38(1): 39–58.
- De Klerk P, Teltewskoi A, Theuerkauf M et al. (2014) Vegetation patterns, pollen deposition and distribution of non-pollen palynomorphs in an ice-wedge polygon near Kytalyk (NE Siberia), with some remarks on Arctic pollen morphology. *Polar Biology* 37(10): 1393–1412.
- Devi N, Hagedorn F, Moiseev P et al. (2008) Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. *Global Change Biology* 14(7): 1581–1591.
- Duguay C, Soliman A, Hachem S et al. (2012) Circumpolar and Regional Land Surface Temperature (LST) with Links to Geotiff Images and netCDF Files. Canada: University of Waterloo. Available at: http://dx.doi.org/10.1594/PAN-GAEA.775962.
- Faegri K and Iversen J (1989) *Textbook of Pollen Analysis*. Chichester: John Wiley & Sons.
- Fritz M, Herzschuh U, Wetterich S et al. (2012) Late glacial and Holocene sedimentation, vegetation, and climate history from easternmost Beringia (northern Yukon Territory, Canada). *Quaternary Research* 78(3): 549–560.
- Fritzsche D, Schütt R, Meyer H et al. (2005) A 275 year ice-core record from Akademii Nauk ice cap, Severnaya Zemlya, Russian Arctic. *Annals of Glaciology* 42: 361–366.
- Giblin AE, Likens GE, White D et al. (1990) Sulfur storage and alkalinity generation in New England lake sediments. *Limnology and Oceanography* 35(4): 852–869.
- Grimm EC (1987) Constrained cluster analysis by the methods of incremental sum of squares. *Computers & Geoscience* 13(1): 13–35
- Grimm EC (1991) *Tilia and Tilia-graph 1.7.16*. Springfield, IL: State Museum, Research and Collection Center.
- Grimm EC (2004) *TGView*. Springfield, IL: Illinois State Museum, Research and Collections Center.
- Grimm EC (2011) High-resolution age model based on AMS radiocarbon ages for Kettle Lake, North Dakota, USA. *Radiocarbon* 53(1): 39–53.
- Hahne J and Melles M (1997) Late- and post-glacial vegetation and climate history of the south-western Taymyr Peninsula, central Siberia, as revealed by pollen analysis of a core from Lake Lama. *Vegetation History and Archaeobotany* 6(1): 1–8.
- Hahne J and Melles M (1999) Climate and vegetation history of the Taymyr Peninsula since middle Weichselian time – Palynological evidence from lake sediments. In: Kassens H, Bauch HA, Dmitrenko IA et al. (eds) *Land- Ocean Systems in* the Siberian Arctic: Dynamics and History. Berlin: Springer, pp. 407–423.
- Herzschuh U, Pestryakova LA, Savelieva LA et al. (2013) Siberian larch forests and the ion content of thaw lakes form a geochemically functional entity. *Nature Communications* 4: 1–8.

Hill MO and Gauch HG (1980) Detrended correspondence analysis: An improved ordination technique. *Vegetatio* 42(1): 47–58

- Jacoby GC, Lovelius NV, Shumilov OI et al. (2000) Long-term temperature trends and tree growth in the Taymir region of northern Siberia. *Quaternary Research* 53(3): 312–318.
- Jankovská V and Komárek J (2000) Indicative value of Pediastrum and other coccal green algae in palaeoecology. Folia Geobotanica 35: 59–82.
- Juggins S (2012) rioja: Analysis of Quaternary science data, R package version 0.7–3. Available at: http://cran.r-project.org/ package=rioja.
- Kaufman DS, Schneider DP, McKay NP et al. (2009) Recent warming reverses long-term arctic cooling. Science 325(5945): 1236–1239.
- Kienel U and Siegert C (1999) Late Quaternary palaeoenvironmental reconstructions from a permafrost sequence (North Siberian Lowland, SE Taymyr Peninsula) – A multidisciplinary case study. *Boreas* 28(1): 181–193.
- Klemm J, Herzschuh U, Pisaric MFJ et al. (2013) A pollen-climate transfer function from the tundra and taiga vegetation in Arctic Siberia and its applicability to a Holocene record. Palaeogeography, Palaeoclimatology, Palaeoecology 386: 702–713.
- Komárek J and Jankovská V (2001) Review of the green algal genus Pediastrum; Implications for pollenanalytical research. *Bibliotheca Phycologica* 108: 1–127.
- Kowalska J and Wolowski K (2010) Rare *Pediastrum* species (Chlorophyceae). *Acta Societatis Botanicorum Poloniae* 79(3): 225–233.
- Legendre P, Oksanen J and ter Braak CJF (2011) Testing the significance of canonical axes in redundancy analysis. *Methods* in Ecology and Evolution 2(3): 269–277.
- MacArthur RH (1957) On the relative abundance of bird species. Proceedings of the National Academy of Science of the United States of America 43(3): 293–295.
- MacDonald GM, Kremenetski KV and Beilman DW (2008) Climate change and the northern Russian treeline zone. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 363(1501): 2285–2299.
- MacDonald GM, Velichko AA, Kremenetski CV et al. (2000) Holocene treeline history and climate change across northern Eurasia. *Quaternary Research* 53(3): 302–311.
- Matveyeva NV (1994) Floristic classification and ecology of tundra vegetation of the Taymyr Peninsula, northern Siberia. *Journal of Vegetation Science* 5(6): 813–828.
- Möller P, Bolshiyanov DY and Bergsten H (1999) Weichselian geology and palaeoenvironmental history of the central Taymyr Peninsula, Siberia, indicating no glaciation during the last global glacial maximum. *Boreas* 28: 92–114.
- Moore PD, Webb JA and Collinson ME (1991) *Pollen Analysis*. Oxford: Blackwell Scientific Publications.
- Naurzbaev MM and Vaganov EA (2000) Variation of early summer and annual temperature in east Taymir and Putoran (Siberia) over the last two millennia inferred from tree rings.

  Journal of Geophysical Research: Atmospheres 105: 7317–7326
- Nielsen H and Sørensen I (1992) Taxonomy and stratigraphy of late-glacial *Pediastrum* taxa from Lysmosen, Denmark A preliminary study. *Review of Palaeobotany and Palynology* 74(1–2): 55–75.
- Oksanen J, Blanchet F, Kindt R et al. (2011) vegan: Community Ecology Package. R package version 2.0–2. Available at: http://cran.r-project.org/package=vegan.
- Opel T, Fritzsche D and Meyer H (2013) Eurasian Arctic climate over the past millennium as recorded in the Akademii Nauk

- ice core (Severnaya Zemlya). *Climate of the Past* 9(5): 2379–2389.
- Pisaric MFJ, Macdonald GM, Cwynar LC et al. (2001a) Modern pollen and conifer stomates from north-central Siberian lake sediments: Their use in interpreting late Quaternary fossil pollen assemblages. *Arctic, Antarctic, and Alpine Research* 33(1): 19–27.
- Pisaric MFJ, MacDonald GM, Velichko AA et al. (2001b) The Lateglacial and Postglacial vegetation history of the northwestern limits of Beringia, based on pollen, stomate and tree stump evidence. *Quaternary Science Reviews* 20(1–3): 235–245.
- Polyakov IV, Bekryaev RV, Alekseev GV et al. (2003) Variability and trends of air temperature and pressure in the maritime Arctic, 1875. *American Meteorological Society* 16(12): 2067–2077.
- R Development Core Team (2011) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Available at: http://www.r-project.org.
- Radle N, Keister C and Battarbee R (1989) Diatom, pollen, and geochemical evidence for the palaeosalinity of Medicine Lake, S. Dakota, during the late-Wisconsin and early Holocene. *Journal of Paleolimnology* 2(3): 159–172.
- Sancetta C, Heusser L, Labeyrie L et al. (1985) Wisconsin-Holocene paleoenvironment of the Bering Sea: Evidence from diatoms, pollen, oxygen isotopes and clay minerals. *Marine Geology* 62: 55–68.
- Savelieva LA, Raschke EA and Titova DV (2013) *Photographic Atlas of Plants and Pollen of the Lena River Delta*. Saint-Petersburg: St. Petersburg State University.
- Serreze MC, Walsh JE, Osterkamp T et al. (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46: 159–207.
- Sidorova OV, Saurer M, Andreev A et al. (2013) Is the 20th century warming unprecedented in the Siberian north? *Quaternary Science Reviews* 73: 93–102.
- Smol JP, Wolfe AP, Birks HJB et al. (2005) Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences of the United States of America* 102(12): 4397–4402.
- Stone TA and Schlesinger P (2003) *RLC Vegetative Cover of the Former Soviet Union, 1990*. Oak Ridge, TN: Oak Ridge National Laboratory Distributed Active Archive Center. Available at: http://www.daac.ornl.gov.
- Tchebakova NM, Rehfeld GE and Parfenova EI (2005) Impacts of climate change on the distribution of Larix spp. and Pinus sylvestris and their climatypes in Siberia. *Mitigation and Adaptation Strategies for Global Change* 11(4): 861–882.
- Ter Braak CJF (1983) Principal components biplots and alpha and beta diversity. *Ecology* 64(3): 454–462.
- Ter Braak CJF (1994) Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* 1(2): 127–140.
- Ter Braak CJF and Šmilauer P (2002) CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Ithaca, NY: Microcomputer Power. Available at: www.canoco.com.
- Weckström K, Weckström J, Yliniemi L-M et al. (2010) The ecology of *Pediastrum* (Chlorophyceae) in subarctic lakes and their potential as paleobioindicators. *Journal of Paleolimnology* 43(1): 61–73.
- West RG (1970) Pollen zones in the Pleistocene of Great Britain and their correlation. *New Phytologist* 69: 1179–1183.
- Wischnewski J, Kramer A, Kong Z et al. (2011) Terrestrial and aquatic responses to climate change and human impact on the southeastern Tibetan Plateau during the past two centuries. *Global Change Biology* 17(11): 3376–3391.