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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

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Abstract In ice-wedge polygon mires, small-scaled microrelief of ridges enclosing small depressions results in a short-distance vegetation mosaic. The correct recognition of these landscape elements in palaeoecological studies of peat sections in order to reconstruct their patterns and dynamics requires insight in the short-distance relationship between vegetation and pollen deposition. This paper presents an analysis of pollen surface samples in a high-resolution (1 m) transect across an ice-wedge polygon near Kytalyk (NE Siberia), including a discussion on the morphology of some critical pollen types and non-pollen palynomorphs (NPPs). We found a strong correlation between vegetation and surface elevation and a fair correspondence between pollen deposition and vegetation. Distribution of NPPs reflects surface elevation well, with algal spores dominating deep spots and testate amoebae prevailing on higher spots. Peak pollen/spore values unrelated to high species coverages (e.g. of *Salix*, *Betula*, *Sphagnum*, Poaceae) indicate that single plants within a population may cause the bulk of the pollen production. The absence of pollen of taxa with an important presence in the vegetation (e.g. *Utricularia*) must be attributable to low pollen productivity. Distributional patterns point at pollen transport by water in the polygon troughs/depressions. Our study shows that Arctic pollen records mainly reflect short-distance vegetation patterns. Palaeosequences consequently allow accurate reconstruction of local microtopography and its dynamics, but should not be over-interpreted in terms of changing (over)regional vegetation patterns and associated drivers.

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Introduction

Ice-wedge polygons are typical landscape elements in the Arctic. They develop as a result of frost cracking and ice-wedge growth under permafrost conditions, leading to a pattern of ridges enclosing depressions of 10–30 m diameter (cf. Zoltai and Tarnocai 1975; Washburn 1979; Billings and Peterson 1980; Botch and Masing 1983; Chernov and Matveyeva 1997; Mackay 2000; Minke et al. 2007).

Polygon mires, i.e. ice-wedge polygon structures with peat formation (Minke et al. 2007), occur extensively in the vast coastal plains of the Lena Delta and the Yana-Indigirka and Kolyma lowlands in NE Russia and along the northern shores of Alaska and NW Canada (Fig. 1). They are common on flat watersheds, river terraces and flood-plains, and on the bottom of drained lakes (Boch 1974). Polygon mires cover some 250,000 km^2, being 3 % of the total Arctic land mass (Minke et al. 2007).
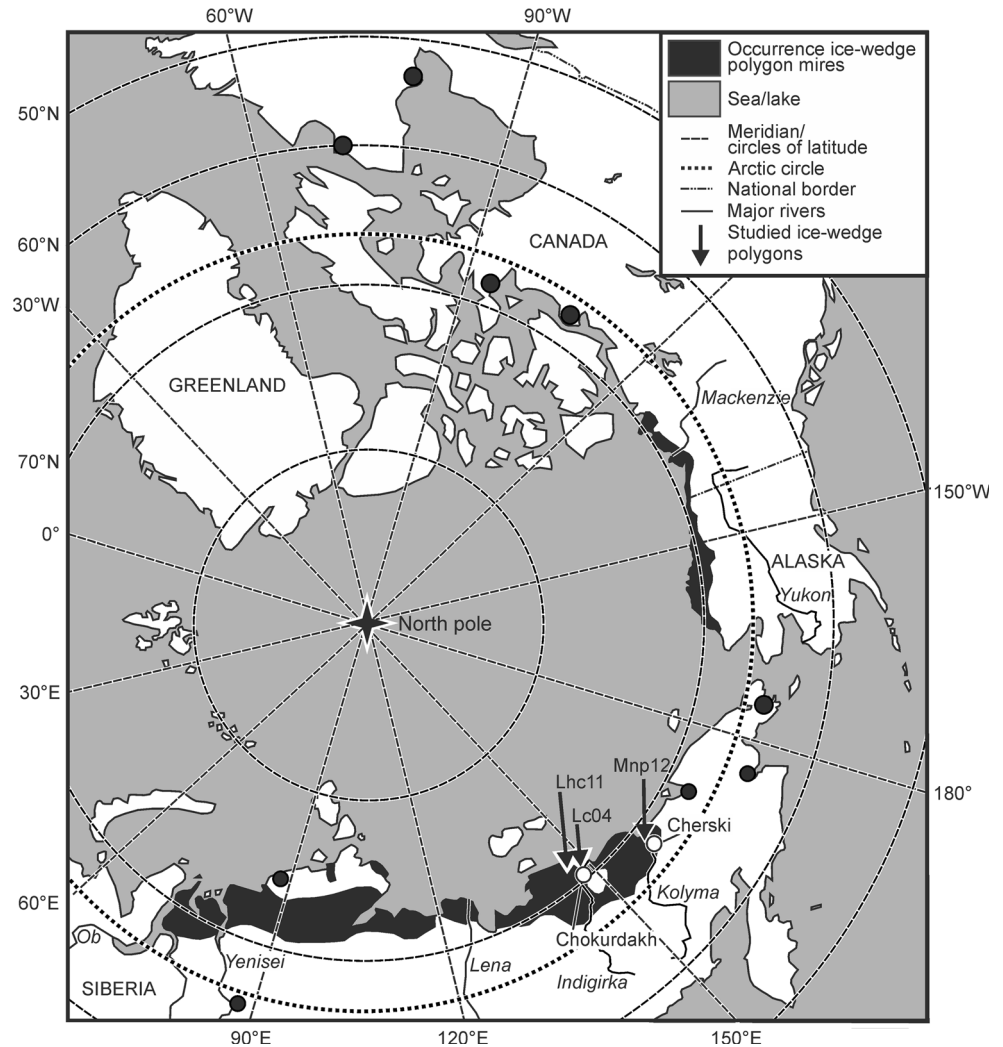
Fig. 1 Circumpolar distribution of ice-wedge polygon mires (after Minke et al. 2007), with the location of the polygons mentioned in the text. *Black circles* indicate areas with ice-wedge polygon mires outside their main distribution area

The Arctic is expected to experience intensive environmental changes in the near future as a result of global warming (Hinzman et al. 2005; McGuire et al. 2007; Koven et al. 2011). As the Arctic soils hold around 15 % of the world's soil carbon (Post et al. 1982; Billings 1987; Lal and Kimble 2000; Kuhry et al. 2010; Zhu et al. 2013; cf. Tarnocai et al. 2009), a melting of these soils may result in substantial greenhouse gas emissions that may feedback on global warming (cf. Tarnocai 1999; Dutta et al. 2006; Koven et al. 2011).

The complex interplay of external and internal forcing, direct and indirect effects, and positive and negative feedback mechanisms (Donner et al. 2012) complicates the understanding of how ice-wedge polygon mires will react to global warming. Palaeoecological studies may contribute to unravelling this complexity (De Klerk et al. 2011).

The palaeoecological reconstruction of ice-wedge polygon mire development must take the microrelief into account, i.e. the fine-scaled pattern of ridges, depressions and troughs. To reconstruct microtopographical

development from palaeoecological records realistically, it is necessary to have detailed insight in the relation between these small-scaled landscape elements, their actual vegetation, and the pollen signal of this vegetation (De Klerk et al. 2009, 2011). Various studies have indeed dealt with modern pollen deposition in (sub)Arctic environments (e.g. Birks 1977, 1980; Andrews and Nichols 1981; Lamb 1984; Van der Knaap 1990; Eisner and Peterson 1998a; Lozhkin et al. 2001; Whitmore et al. 2005), but few deal with NE Siberia (e.g. Savelieva et al. 2000; Bigelow et al. 2003; Vasil'chuk 2005; Klemm et al. 2013; Tarasov et al. 2013) and only one addresses the typical short-distance vegetation patterns in a low-centred ice-wedge polygon mire (De Klerk et al. 2009). Only one other paper presents surface samples from a transect crossing ten ice-wedge polygons (Eisner and Peterson 1998a), but as samples are only taken from the centres of the polygons that study does not address pollen deposition patterns within a single polygon.
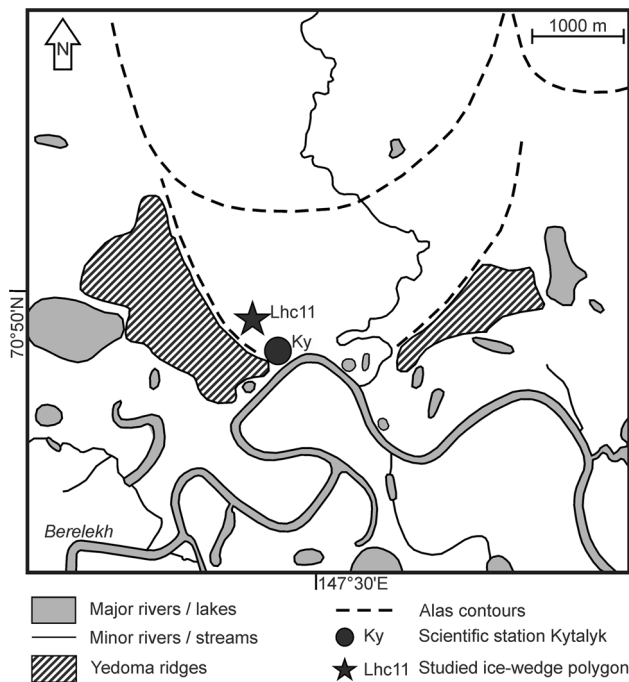
Fig. 2 Location of ice-wedge polygon Lhc11 near the research station Kytalyk along the Berelekh River; indicated are the most important landforms

The present paper expands the previous study by De Klerk et al. (2009) of a simple low-centred ice-wedge polygon mire by addressing short-distance vegetation patterns, pollen deposition and distribution of selected non-pollen palynomorphs (NPPs) in a more complex low–high-centred polygon.

Study area

The studied ice-wedge polygon mire Lhc11 (70,83069°N, 147,48115°E) is located near the Kytalyk scientific station, ca. 30 km north-west of Chokurdakh along the Berelekh River (Fig. 2). The landscape (cf. Van der Molen et al. 2007; Petrescu et al. 2008; Tumskoy and Schirrmeister 2012) consists predominantly of alluvial landforms near the river. Higher landscape elements include some hills composed of Middle to Late Pleistocene ice-rich silts and silty sands containing numerous large ice wedges ('yedoma', cf. Morgenstern et al. 2011, 2013; Schirrmeister et al. 2013). Furthermore, various alases (or alasses; singular: alas) result from major thermokarst melting during the Holocene (Morgenstern et al. 2011, 2013). Ice-wedge polygon mires with deposits of peat and silt are widespread in the alluvial landforms and alas depressions of the Kytalyk area, with those in alases having a more mature appearance and being supposedly older than those on the floodplains (Van der Molen et al. 2007).

Polygon Lhc11 (21 × 26 m) is positioned in an alas on a distance of 300 m to a yedoma ridge and 600 m to the Berelekh River bank (Fig. 2). The centre of the site consists of a small, shallow pool surrounded by ridges of different heights with a clear deeply thawed "hydrological window" (Minke et al. 2007, 2009; Donner et al. 2012) in the south-western corner. Deep and broad troughs separate the ridges of Lhc11 from those of neighbouring polygons (Figs. 3, 4).

We suppose that polygon Lhc11 constitutes an intermediate form between a standard low-centred and a typical high-centred polygon: whereas a water-filled depression still forms the centre of the polygon, the ice wedges seem to have partly collapsed to form wide troughs, while the ridges seemingly have migrated inward from their original position (Teltewskoi et al. 2012).

Methods

Field research was conducted in the summer of 2011. Vegetation and site parameters were mapped in a grid of 1 × 1 m quadrats, covering an area of 26 × 21 m. Ground surface elevation, frost table height (i.e. elevation) and open water level were determined in the centre of each quadrat relative to a horizontal reference level (Fig. 3). Ground surface was defined as the surface of living moss or the surface of unvegetated peat. Frost table position was measured by pushing a rod into the unfrozen soil down to resistance. Thaw depth is the difference between the two measures (Minke et al. 2009). A 3D model of the polygon (Fig. 3) was prepared with the computer program surfer 11 and modified with a drawing computer program.

Species coverage was estimated into 15 cover classes after Londo (1976) and summarised to seven classes. Vascular plants were identified with Polunin (1959), Tolmachev (1974) and Rothmaler (2002); their nomenclature follows Czerepanov (1995). *Sphagnum* species were identified and named after Frey et al. (1995) and Michaelis (2011). Vegetation maps (Fig. 4) were constructed using the software QGis version 1.8.0 "Lisboa" and modified with drawing software.

Surface samples of mosses or litter were collected in the centre of each 1 × 1 m plot. C/N ratios were determined by drying samples at 70–80 °C for 24 h, grounding in a mill (Pulverisette 14, Fritsch, Idar-Oberstein, meshes 0.2 mm), oven-drying at 80 °C for 2 h and analysing with a dry combustion C and N analyser (Vario-EL, elementar/ Hanau, WLF-Detektor).

All surface samples of transect j were palynologically analysed and are discussed in this paper. This transect crosses—west to east—a 10-m-wide trough area, which includes in quadrats j3 and j4 a still slightly emerging part

Fig. 3 Three-dimensional model of ice-wedge polygon Lhc11 (situation in late July 2011). Note that the software used interpolates the centres of the plots and that, thus, the marginal plots are not displayed up to their actual boundaries
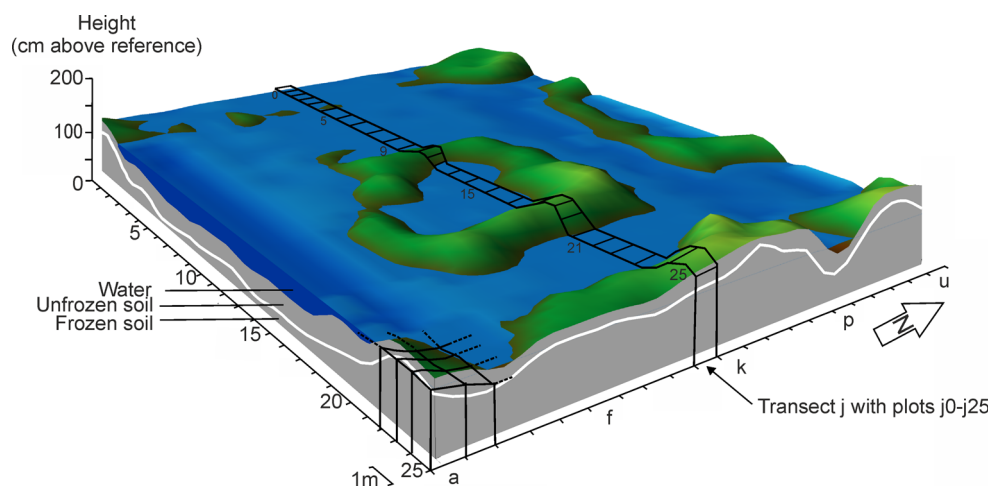
of a largely submerged ridge. The polygon ridges intersected by quadrats j11/12 and j18/19 surround a depression, which is shallow (maximum depth 14 cm in July 2011) compared to the troughs traversed by quadrats j5–j10 (maximum depth 31 cm) and j21–23 (maximum depth 28 cm), respectively. Quadrats j24 and j25 cover part of the ridge of an adjacent polygon.

Preparation of palynological samples (cf. Fægri and Iversen 1989) included treatment with KOH, sieving (mesh width 125 μm), treatment with HF and acetolysis (7 min). Preparation of reference pollen samples included only sieving and acetolysis (5 min).

Pollen counting was carried out with a Leitz Dialux 22 EB light microscope with 400× magnification; larger magnifications were used for identifying problematic pollen grains. Pollen clumps were counted as one entity, not as individual grains.

In order to distinguish unambiguously between taxonomical (i.e. taxa) and palynomorphological entities (i.e. pollen/spore and NPP types), the latter are displayed in SMALL CAPITALS (Joosten and De Klerk 2002; De Klerk and Joosten 2007). Pollen and spore types were identified and named after Fægri and Iversen (1989) (epitaph f in Fig. 5), Moore et al. (1991) (m), the Northwest European Pollen Flora (NEPF) (Punt 1976; Punt and Clarke 1980, 1981, 1984; Punt and Blackmore 1991; Punt et al. 1988, 1995, 2003) (p), and Beug (2004) (b). Testate amoebae were identified with Charman et al. (2000) (c), ASSULINA MUSCORUM types after Schönborn and Peschke (1990), and other NPPs (g) after Van Geel (1978), Pals et al. (1980) and Van Geel et al. (1981). Palynomorphs not identified with these references are marked (*) (described by De Klerk et al. 2008), or (**) (discussed in this paper).

Pollen values were calculated relative to a pollen sum including the pollen types PINUS UNDIFF., PINUS HAPLOXYLON T., PINUS DIPLOXYLON T., ARTEMISIA, ALNUS: ALNUS ALNOBETULA SYN. A VIRIDIS, ALNUS: ALNUS INCANA & A. GLUTINOSA and ALNUS UNDIFF., of which the producers do not grow in polygon Lhc11.

Combined pollen/vegetation diagrams (Fig. 5) display pollen type percentages with actual values (closed curves) and a 5-time exaggeration (open curves with sample lines). The cover of associated plant taxa is displayed in solid bars for transect j, and in dotted and open bars for the adjacent transects i and k, respectively. Pollen types omitted from Fig. 5 are listed in Table 1.

Interpretation of the distributional data follows the terminology of Janssen (1973) who distinguishes between 'local' pollen deposition directly under a pollen source, 'regional' deposition at greater distance with generally equal values over large areas and 'extralocal' pollen deposition in a transitional reach. The long-distance component is referred to as 'extraregional' pollen deposition. For trees with good pollen dispersal capacities, the extralocal trajectory may range up to several hundreds of metres (Janssen et al. 1985; Bos and Janssen 1996; De Klerk et al. 1997), but for Arctic herbs and dwarfshrubs, this trajectory seems to be very short and probably does not exceed one or two metres (De Klerk et al. 2009). This means that already at short distance to a specific plant regional pollen deposition values of the relevant pollen type are encountered.

Ordination was applied to characterise the relation between vegetation, pollen and NPP composition, using linear response models and applying PCA (function 'princomp' in the R package; R Development Core Team 2011) on log-transformed data.

Remarks on morphology and nomenclature of some pollen and NPP types

At present, no complete overview on the pollen morphology of Arctic plant species exist (cf. Hooghiemstra and Van Geel 1998). The recent atlas of Savelieva et al. (2013)

provides valuable photographs of pollen and plants in the Lena Delta, but has only been published in a limited number of 100 copies. Difficult to access are the pollen morphological descriptions (in Chinese) of 12 plant species of Barrow Island (NE Alaska) by Tang et al. (2003). Zhang et al. (2004) describe some further pollen morphological types from Barrow Island, and Yao et al. (2012) present useful information on the pollen morphology of several plant taxa on Svalbard.

The major European pollen morphological works (cf. "Methods" section) cover most pollen types produced by plants growing in northern Siberia. Some pollen types from NE Siberia, however, diverge from the pollen types described. Here, we provide some further remarks on the morphology of several types, which we base on a review of pollen morphological literature supplemented with the study of pollen reference samples from plant specimens collected during the 2011 field expedition.

BETULA PUBESCENS TYPE, BETULA NANA TYPE, BETULA UNDIFF

Attempts to distinguish between pollen produced by tree and shrub species of *Betula* have a long history (cf. Mäkelä 1996; De Klerk 2004), with separation between types based on various size-statistical methods or pollen morphological features. Size-statistical methods are very time-consuming and therefore hardly applied.

We follow Punt et al. (2003), who describe a BETULA PUBESCENS TYPE with prominently protruding pores (i.e. having a large vestibulum), which is assumed to be produced by tree birches only, and a BETULA NANA TYPE with slightly protruding pores assumed to be produced by birch shrubs only (Online Resource 1). Also Moore et al. (1991) and Beug (2004) note that the vestibula of pollen of shrubs are smaller than those of pollen of trees, but do not distinguish separate pollen types. Whereas such qualitative distinction may appear to be subjective, an experienced palynologist will be able to estimate the degree of pore protrusion by sight accurately. We categorise pollen grains with intermediate pore protrusion or of which the vestibulum size cannot be properly observed (because of corrosion, erosion or folding) under BETULA UNDIFF. (cf. De Klerk et al. 2008).

As in the Siberian Arctic only *B. exilis* occurs (syn. *B. nana* ssp. *exilis*; Czerepanov 1995), one would expect to find predominantly BETULA NANA TYPE pollen in this region. However, already in our earlier studies from this region (De Klerk et al. 2009, 2011), we noticed that BETULA PUBESCENS TYPE pollen also occurs prominently, together with BETULA UNDIFF., showing clear local deposition values connected to the actual presence of *B. exilis*, and we found the same in polygon Lhc11 (Fig. 5). This implies that *B. exilis* produces two distinct pollen types, i.e. pollen grains with clearly protruding and with less protruding pores. Also the photographs of Savelieva et al. (2013) show distinct differences in pore protrusion among pollen grains of *B. exilis* (Online Resource 1), whereas the same phenomenon has also been mentioned by A. Andreev (personal communication 2005) for other areas of NE Siberia. Apparently, this pollen dimorphism is widespread and needs further study to see whether the different pollen types are produced by different flowers/anthers, different plant specimens, or whether all *B. exilis* flowers produce both types.

ALNUS: ALNUS ALNOBETULA SYN. A VIRIDIS, ALNUS: ALNUS INCANA & A. GLUTINOSA, ALNUS UNDIFF

We found similar dimorphism among pollen grains attributable to "alder" species, of which in NE Siberia only *Duschekia fruticosa* occurs (also commonly named *Alnaster*, *Alnus fructicosa* or *A. viridis*, Czerepanov 1995). Punt et al. (2003) assume that pollen produced by (sub)species of green alder (including *Duschekia*) has only small vestibula and use—among others—this characteristic to define their ALNUS VIRIDIS TYPE. Furthermore, they describe prominent vestibula for their ALNUS GLUTINOSA TYPE. However, they describe for all pollen produced by alder (sub)species prominent arcus (i.e. the bands of thickened pollen grain wall, which connect the pores—note that the plural of arcus is arcus, not arci; Punt et al. 2007). Beug (2004), in contrast, mentions that the arcus of pollen produced by *A. viridis* (using the name *A. alnobetula* syn. *A. viridis*) are badly developed or just represented by a crinkle or fold. He also mentions the smaller pore protrusion of pollen of *A. viridis*, but does not define a separate pollen type and mentions these characteristics only as a variation within his ALNUS pollen type.

The three ALNUS pollen types distinguished by us are recognisable by their arcus or arcuslike structures, but often these are badly developed or present only between two and not all pores. Following the descriptions by Beug (2004), we distinguish two types ALNUS: ALNUS INCANA & A. GLUTINOSA, and ALNUS: ALNUS ALNOBETULA SYN. A VIRIDIS. Additionally, we distinguished ALNUS UNDIFF. pollen that could not be attributed to either of both types because pore protrusion was not clearly visible (cf. BETULA UNDIFF.)

In the Lhc11-surface samples, values of ALNUS: ALNUS INCANA & A. GLUTINOSA are low in comparison with those of ALNUS: ALNUS ALNOBETULA SYN. A VIRIDIS, and one may be inclined to ascribe the presence to long-distance pollen transport. However, in an unpublished surface sample from a *Duschekia* stand near Chokurdakh, we found 230 grains of ALNUS: ALNUS ALNOBETULA SYN. A VIRIDIS, 153 grains of ALNUS: ALNUS INCANA & A. GLUTINOSA, and 28 ALNUS
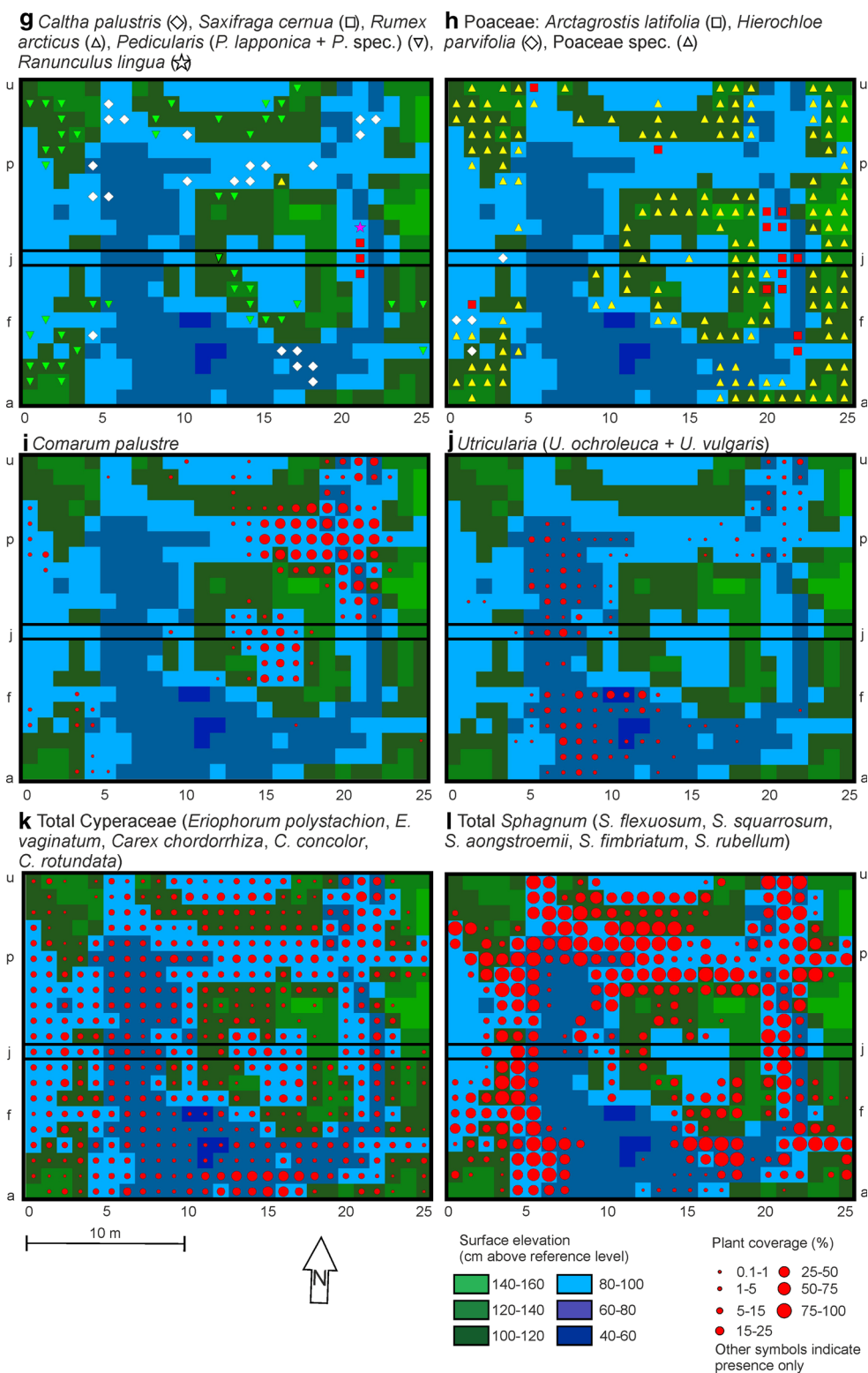
Fig. 4 Distribution maps of plant taxa growing in ice-wedge polygon Lhc11, with coordinates 0–25 (W–E axis) and a-u (N–S axis)
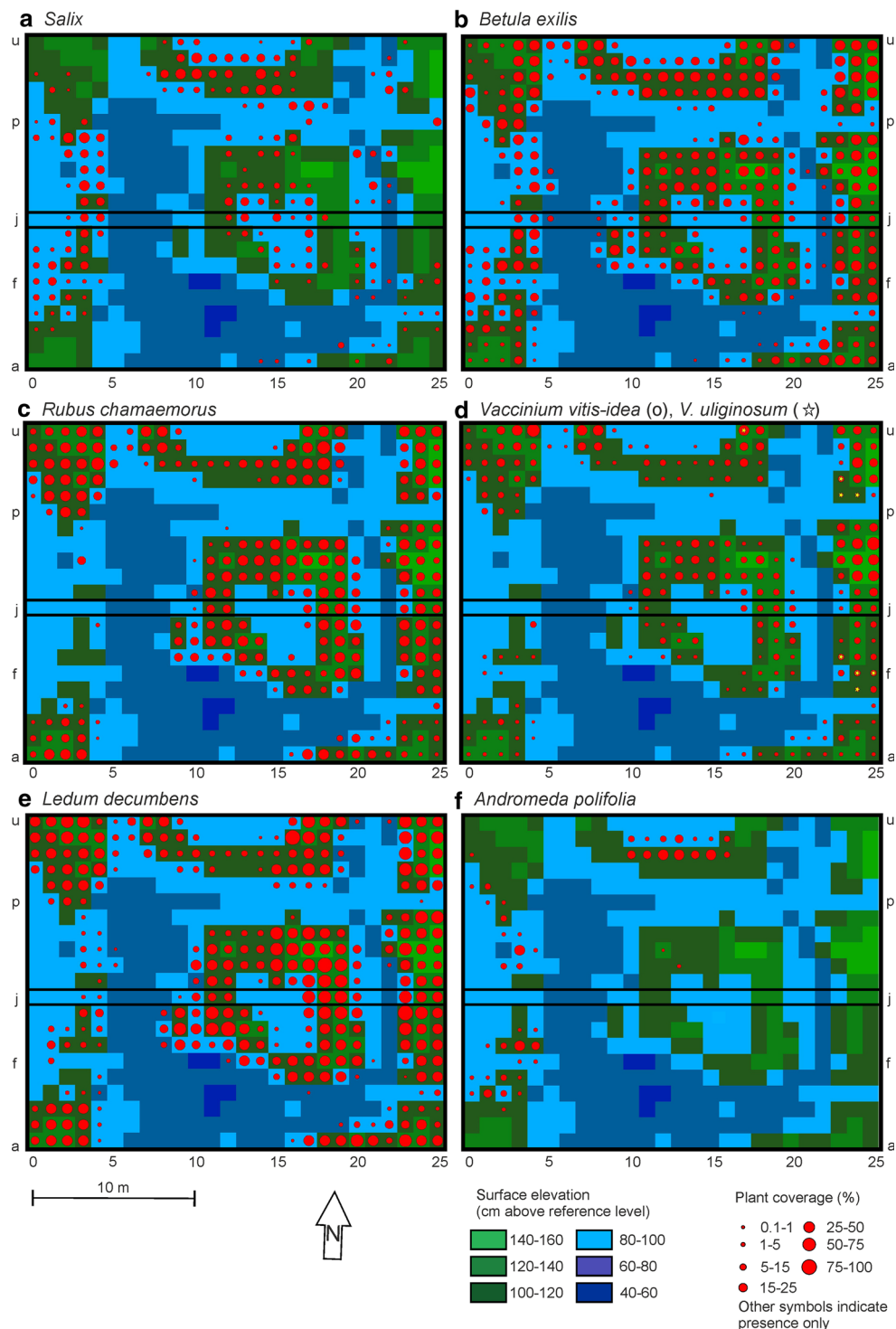
UNDIFF. grains (P. De Klerk et al. unpublished data), and in surface samples from polygon Mnp12 near Pokhodsk (cf. Fig. 1) ALNUS: ALNUS INCANA & A. GLUTINOSA reaches values up to ca. 20–25 %, being several hundreds of grains per sample (P. de Klerk et al. unpublished data). This can only mean that *Duschekia* in NE Siberia, similar to *Betula exilis*,

also produces pollen with diverse pore protrusion. The photographs of pollen of *Duschekia* (presented as *Alnaster fructicosus*) by Savelieva et al. (2013) also display both grains with clearly protruding and grains with only slightly protruding pores, as well as both clear and inconspicuous arcus or arcuslike structures (Online Resource 1).

Fig. 4 continued

g *Caltha palustris* (◇), *Saxifraga cernua* (□), *Rumex arcticus* (△), *Pedicularis* (*P. lapponica* + *P.* spec.) (▽), *Ranunculus lingua* (☆)

h Poaceae: *Arctagrostis latifolia* (□), *Hierochloe parvifolia* (◇), Poaceae spec. (△)

i *Comarum palustre*

j *Utricularia* (*U. ochroleuca* + *U. vulgaris*)

k Total Cyperaceae (*Eriophorum polystachion*, *E. vaginatum*, *Carex chordorrhiza*, *C. concolor*, *C. rotundata*)

l Total *Sphagnum* (*S. flexuosum*, *S. squarrosum*, *S. aongstroemii*, *S. fimbriatum*, *S. rubellum*)

10 m

N

Surface elevation
(cm above reference level)

140-160   80-100
120-140   60-80
100-120   40-60

Plant coverage (%)

0.1-1   25-50
1-5   50-75
5-15   75-100
15-25

Other symbols indicate presence only

cf. ANCHUSA ARVENSIS

The grain we named accordingly is similar to ANCHUSA ARVENSIS pollen as described by Moore et al. (1991), except for the endopori which we could not accurately see. Therefore, the identification remains insecure. Since *Anchusa* does not occur in NE Siberia (Tolmachev 1974), the type either results from long-distance transport or is produced by another taxon.

Table 1 Relative values of pollen types omitted from the pollen diagram (Fig. 5)

Pollen type: sample (percentage)
Group 2: Carpinus type (m) 3 (0.88), Fagus (m) 8 (0.9), Fraxinus (m) 8 (0.9), Tilia (m) 8 (0.9) 9 (0.87), Ulmus (m) 10 (0.92) 15 (0.91)
Group 3: Caryophyllaceae undiff. (*) 3 (0.88) 5 (0.97), Chenopodiaceae and Amarathaceae (m) 11 (0.9), Huperzia selago (m) 7 (1.82), Lycopodium clavatum (m) 1 (0.94), Polemonium (m) 8 (0.9) 20 (2.15), Polygonum bistora type (p) 12 (0.77), Sinapis type (m) 3 (0.88) 5 (0.97) 12 (0.77)
Group 4: cf. Anchusa arvensis type (p) 15 (0.91), cf. Castanea type (m) 12 (2.32) 16 (0.85), Indet. broken 18 (0.92), Monolete spores without perine (*) 13 (0.98) 15 (0.91) 24 (0.95)

cf. Caltha palustris type

The pollen grains named cf. Caltha palustris type resemble the Caltha palustris type of Punt and Blackmore (1991) well, but the shape of the microechinae could not be accurately distinguished.

cf. Castanea type

We found small tricolporate grains with a psilate wall that resemble the Castanea type or the Lotus type of Moore et al. (1991), with the exception that the shape of the en- dopori could not be accurately seen. Producers of these types, however, do not occur in the NE Siberian Arctic (Polunin 1959; Tolmachev 1974). Since the type was found several times, it probably does not represent long-distance transport, but most likely originates from a not yet identi- fied plant taxon in NE Siberia.

Cyperaceae

Earlier (De Klerk et al. 2009, 2011) we distinguished between pollen types that were attributed to various Cy- peraceae taxa (cf. Fægri and Iversen 1989). As such dis- tinction requires the pollen to be largely undamaged and unfolded, identification beyond the level of Cyperaceae is mostly not possible. Therefore, we now only present a Cyperaceae pollen type. Pollen of *Eriophorum* is included at a lower hierarchical level in the Carex type of Fægri and Iversen (1989), and our earlier conclusion (De Klerk et al. 2009) that *Eriophorum* pollen is absent from the surface samples from Lc04 appears unsupported by evidence.

Pollen of Ericales (Online Resource 1)

Identification and nomenclature of pollen types attributed to various Ericales species are not straightforward in the keys of Fægri and Iversen (1989) and Moore et al. (1991). The latter explicitly note that their Ericaceae, Empetraceae and Pyrolaceae subkey should only be taken as a guide to what to look for on reference type slides. We used the key of the Ericaceae/Empetrum-Gruppe of Beug (2004) that includes among others Empetrum/Ledum and Sammelgruppe: Vacci- nium typ. The nomenclature of Beug (2004) confusingly uses the terms group ("Gruppe" in German) and type on the same hierarchical level (cf. Joosten and De Klerk 2002), but his key provides better morphological descriptions than other pollen keys. Earlier (De Klerk et al. 2009, 2011) we distinguished a large tetrad pollen type (Vaccinium group ca. 50 μm), which we assumed to be produced by *Andromeda*, but in the present study, we no longer made this separation because of size-overlapping of the pollen within the Sam- melgruppe: Vaccinium type. Our reference samples revealed that *Cassiope tetragona* and *Vaccinium vitis-ideae* produce this pollen type, which is not surprising.

cf. Larix type

The pollen types Larix type (sensu Moore et al. 1991) and Larix, Pseudotsuga (sensu Beug 2004) are described as psilate, inaperturate (but having a long slit) and rather large. Both studies warn that the pollen outline in palynological samples might be modified by folds or damages. Moore et al. (1991) mention that various fungal, algal or animal NPPs may key-out as Larix type in their key. It is also conceivable that the wall patterns of some NPPs may be confused with corroded walls of Larix type pollen. Recent studies by B. Niemeyer (personal communication September 2013) show that pollen grains of *Larix* display a large variety in degree of preservation already in the tree cones prior to dispersal and that pollen wall structure, aperture, sizes and outline can often not be seen correctly (Online Resource 1). For these reasons, we added the "cf." to our pollen type name.

Pedicularis palustris type

Being syncolpate, this type can be easily distinguished from other pollen types (Online Resource 1). In our ref- erence samples of *Pedicularis* spec., however, we also observed that many grains were so degraded that they were hardly recognisable as pollen grains. The thin wall was, for example, often so damaged that the original psilate struc- ture was no longer recognisable. Furthermore, as the syn- colpus is so different from "normal" colpi, it may not be recognised as such if the palynologist is not aware of this.

Rubus chamaemorus

Moore et al. (1991) describe Rubus chamaemorus as echinate only, which would lead to erroneous identification

with their key since the pollen grains produced by *Rubus chamaemorus* also have conspicuous clavae (Beug 2004; Zhang et al. 2004). In our reference material as well as in the surface samples, we found predominantly pollen with clavae interspersed with less conspicuous echinae (Online Resource 1).

RUMEX AQUATICUS T

Only one *Rumex* species occurs in polygon Lhc11: *R. arcticus* which grows in plot o16 (Fig. 4g). The RUMEX AQUATICUS T. grains in our samples have a scabrate wall structure, and both tricolporate and tetracolporate grains occur (Online Resource 1). Whereas Punt et al. (1988), Moore et al. (1991) and Beug (2004) describe pollen of all *Rumex* species as reticulate only, Fægri and Iversen (1989) mention a scabrate wall structure for their RUMEX AQUATICUS T., but do not mention tetracolporate grains. The other pollen keys, however, mention that pollen produced by *Rumex* species may also often have four (or more) colpori.

Pollen of RUMEX ARCTICUS was not studied for the European pollen keys, but our reference sample indeed shows a scabrate wall structure. Tang et al. (2003) also describe pollen of *R. arcticus* as being tri- or tetracolporate and having a granulate (i.e. scabrate) wall structure. On the basis of the wall structure, we identified the encountered pollen grains as RUMEX AQUATICUS T. sensu Fægri and Iversen (1989), but note that—in deviation from that key— the pollen type may also have more than three colpori.

VALERIANA

Our pollen type VALERIANA does not completely correspond to pollen types described in the morphological literature available to us. The type occurs regularly in samples from transect j, and even more frequently in a fossil peat section of polygon Lhc11 (P. De Klerk et al. unpublished data), indicating that the producing plants will have grown in the studied polygon. Whereas the grains we found did not key-out at all using Moore et al. (1991), they key-out near the VALERIANA ELONGATA-GRUPPE of Beug (2004) (but our grains are slightly less ovalish) and near the VALERIANA OFFICINALIS TYPE of Punt and Clarke (1980). The microscope used by us did not allow unambiguous identification of the shapes or bases of the echinae, which is a distinctive criterion in the European pollen keys. For this reason, we just use the name VALERIANA.

The only Valerianaceae species in the Siberian Arctic is *Valeriana capitata* (Tolmachev 1974), of which the pollen was not studied for the European pollen keys. The species is currently not present in polygon Lhc11, but regularly grows in polygons in the region (De Klerk et al. 2009, personal observations). Our reference sample as well as a

photograph by Savelieva et al. (2013; Online Resource 1) illustrates that this species produces pollen similar to the pollen type we observed and that it is safe to assume that our pollen type is produced by *V. capitata*.

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Regularly, a type occurs with a faintly scabrate wall structure that does not key-out properly in the available pollen literature (Online Resource 1). Because of the similar wall structure, we identified such grains as CF. TEUCRIUM (m) in the peat-section samples of polygon Lc04 (De Klerk et al. 2011), although the variation in wall thickness described by Moore et al. (1991) is absent. Since *Teucrium* does not grow in the Siberian Arctic (Tolmachev 1974), it would have been an unlikely producer anyway. The best morphological fit is with the pollen morphological descriptions in the Trizonocolpate, scabrate-verrucate to microechinate subkey of Moore et al. (1991) up to exit 2a. The subsequent pollen types in that key can all be excluded, i.e. TEUCRIUM and ARTEMISIA (that normally is colporate and only deviate grains key-out here) because our type has no variation in wall thickness, and CALTHA TYPE and PAPAVER RHOAS TYPE because these types have smaller wall structure processes. With Beug (2004), no appropriate key exit can be reached.

The regular occurrence of the pollen type, especially in the peat sections of Lc04 and Lhc11 (De Klerk et al. 2011; unpublished data), would suggest the presence of the parent plant in the studied polygons. However, no species currently growing in polygons Lc04 or Lhc11 seems a likely producer. Some vague similarity exists with the pollen of *Papaver pulvinatum* ssp. *lenaense* displayed by Savelieva et al. (2013) and of *P. macounii* displayed by Zhang et al. (2004), but the habitat requirements of these taxa make them unlikely parents plant. The same accounts for other *Papaver* species. The faintly scabrate wall structure also reminds of pollen of some Ranunculaceae species, but no available pollen key describes a corresponding Ranunculaceae type. *Ranunculus gmelinii* and *R. pallasii* actually occur in ice-wedge polygon complexes in the region (personal observation), of which pollen morphological descriptions or reference material were not available to us.

ASSULINA

Tests of the genus *Assulina* are ovoid, flattened and covered with oval, regularly arranged plates (Grospietsch 1972; Charman et al. 2000; Clarke 2003). Whereas many publications mention differences in colour as a distinctive characteristic, this has no significance in pollen samples because the acetolysis procedure may result in artificial colouring of palynomorphs, although the actual extent of such colouring

effects on testate amoebae is still insufficiently studied. *A. seminulum* and *A. scandinavica* have test lengths of 60–105 and 80–120 μm, respectively (Grospietsch 1972; Charman et al. 2000; Clarke 2003; Lara et al. 2011). *A. muscorum* shell lengths range between 28–60 μm (Grospietsch 1972; Charman et al. 2000; Clarke 2003). Schönborn and Peschke (1988) pose that *A. collaris*, an assumed African species, may have been generally overlooked in other areas because its size overlaps with the longer specimens of *A. muscorum*, but *A. collaris* has a generally small collar surrounding the aperture.

Schönborn and Peschke (1990) distinguish four types of *A. muscorum* based on variation in shell width (Online Resource 1). Type 1 has the largest width in the top third of the shell, is narrow and has a small aperture. Type 2 also has its maximum width in the top third, but is broad and has a broad aperture. The largest width of Type 3 is in the centre, and the lower part of the test is narrower than the upper part. Type 4 also has the maximum width in the shell centre, but the upper and lower parts are equally wide. It is at present not clear whether these types have any taxonomic or ecological significance or whether they represent different developmental stages only. A related species *Valkanovia elegans* is mentioned to produce Type 4 tests as well, but these have a somewhat different aperture rim than *A. muscorum* (Schönborn and Peschke 1990).

As variation in colour is unsuitable for identification of *Assulina* during pollen analysis, distinction between shells of *A. muscorum*, *A. seminulum* and *A. scandinavica* in pollen samples can only be made by size. Size ranges of the species do not overlap, but such overlap may not be excluded for some exceptional shells as the upper length limit of *A. muscorum* reaches the lower length limit of *A. seminulum*.

Also differences in aperture shapes are often difficult to see since this requires a clear view on the front of the aperture, whereas in pollen samples, the tests lay on their side and the aperture can only be seen in cross-section.

In the pollen surface samples of polygon Lhc11, we did not encounter large Assulina tests, implying that *A. seminulum* and *A. scandinavica* do not play a major role in the testate amoebae populations. Regularly, however, tests were observed that range towards the upper length limits of *A. muscorum*, and theoretically, these may be *A. collaris* or small *A. seminulum*. For that reason, we present only a general Assulina curve. In a later stage of our research, we checked five selected samples for the four morphological types of Schönborn and Peschke (1990) which all occur in different proportions. Furthermore, we distinguish Assulina muscorum undiff. tests which are asymmetrical along their longest axis and, thus, do not display a single largest width.

Small reticulate *Spirogyra* spores

Reticulate spores were observed that resemble Type 132 (Pals et al. 1980), but are conspicuously smaller and probably originate from NE Siberian *Spirogyra* species that were not studied in the available reference literature.

Further information provided by the reference pollen samples

Study of pollen samples of locally collected taxa revealed that *Chrysoplenium alterniflorum*, *Comarum palustre*, *Dryas octopetala*, *Saxifraga foliolosa* and *Tofielda pusilla* produce similar morphological types as their European counterparts and key-out correctly in the keys used by us. In our reference sample of *Saxifraga cernua*, three-colpate pollen grains prevail with a somewhat irregular scabrate wall structure. Whereas Fægri and Iversen (1989) and Moore et al. (1991) include a Saxifraga cernua type in their Tricolpate rugulate–striate key for which they mention a diffuse or faint striation, Beug (2004) mentions only a scabrate wall structure for pollen of *S. cernua* and includes it in his Saxifraga hirculus-Typ. Punt and Clarke (1980) include the pollen of *S. cernua* in the Saxifraga granulata type for which they describe a scabrate wall structure with a lower sexine layer that is weakly striate or rugulate (cf. Zhang et al. 2004). In our reference sample, the striae or rugulae are hardly visible and the pollen should preferably be described as scabrate. Also the photograph of Savelieva et al. (2013) shows grains with a scabrate wall structure (Online Resource 1).

Of grasses that were not studied in the European pollen morphological works, *Arctagrostis latifolia* and *Hierochloë pauciflora* both seem to produce Wild grass group pollen. Most pollen grains of *Glyceria declinata* are relatively large, but sizes are variable between grains, and we observed in the reference samples several grains that range around the size boundaries between the Hordeum group and the Wild grass group (Online Resource 1). Of the European flora, *G. fluitans* and *G. notata* (under the old name *G. plicata*) produce Hordeum group pollen, whereas *G. maxima* produces Wild grass group pollen (Andersen 1979).

Results and discussion: patterns in vegetation and palynomorph distribution in polygon Lhc11

Groups 1–4: Regional and extraregional pollen types and pollen of unknown taxonomic affinity

Of the pollen sum types, Alnus: Alnus alnobetula syn. A. viridis displays the highest values (Fig. 5). The producing taxon *Duschekia* occurs only sporadically in the Kytalyk

area, specifically along streams that cross the alas depressions. In samples j0–j3, values of ALNUS: ALNUS ALNOBETULA syn. A. VIRIDIS are considerably lower, and those of PINUS DIPLOXYLON T. and ARTEMISIA higher than in the other samples. Since plant taxa producing these types do not grow in the immediate vicinity of polygon Lhc11, this phenomenon must relate to different capture of pollen grains at these plots and not to the proximity or remoteness of the parent plants of these types.

Pollen types in the surface samples of polygon Lhc11 that may result from long-distance transport include PICEA, ABIES, CARPINUS TYPE, QUERCUS, FRAXINUS, FAGUS, TILIA and ULMUS (Fig. 5; Table 1). In general, the taxa producing these grains occur at considerable distances up to some thousands of km from the Kytalyk area (Tolmachev 1974). Next to large long-distance transport, the presence of these types may perhaps also be attributed to contamination.

Pollen grains of other types, of which the known producers do not occur in the studied polygon but are present in NE Siberia, include ANTHEMIS TYPE, cf. LARIX TYPE, SINAPIS TYPE, CARYOPHYLLACEAE UNDIFF., EQUISETUM, HUPERZIA SELAGO, POLEMONIUM, CHENOPODIACEAE and AMARANTHACEAE, POLYGONUM BISTORTA TYPE, MONOLETE SPORES WITHOUT PERINE and LYCOPODIUM CLAVATUM (Fig. 5; Table 1). No *Lycopodium* tablets (Stockmarr 1971) have been added to our samples, and contamination with "spikes" during sample preparation in the laboratory would have been revealed by the deeper dark-brown/dark-red colour that is caused by the double acetolysis (during tablet preparation and during sample processing). Therefore, it is likely that LYCOPODIUM CLAVATUM originates from *Lycopodium* plants in the NE Siberian Arctic.

For various pollen types, the taxonomical affinity is still unclear (Group 4). These types include obviously the three "INDET." pollen curves, as well as several types discussed in text section "Remarks on morphology and nomenclature of some pollen types".

Group 5: Pollen types produced by plants at some distance to transect j

RANUNCULUS ACRIS TYPE occurs in four samples along transect j (Fig. 5). In Lhc11, the type is only produced by *Ranunculus lingua*, which grows with a coverage of 5 % in plot l21 (Fig. 4g).

cf. CALTHA PALUSTRIS TYPE was found with substantial values in various samples from the troughs and the polygon centre. *Caltha palustris* is present at various plots in the troughs (Fig. 4g). Likely the pollen grains in transect j originate from these plants, indicating pollen dispersal, possibly by water, over several metres. Also *Aquilegia vulgaris*—which grows on the nearby yedoma ridge (Fig. 2)—produces this pollen type, but input from there cannot be extensive because in that case cf. CALTHA

PALUSTRIS TYPE would also occur in the samples from the more elevated polygon parts.

Of the two pollen types attributable to *Rumex* species, RUMEX ACETOSA TYPE occurs incidentally, whereas RUMEX AQUATICUS T. was found regularly, especially in the troughs (Fig. 5). Considering the fact that *R. arcticus* grows in one plot only in low amounts, the regular occurrence of RUMEX AQUATICUS T. in the pollen samples indicates good extralocal pollen dispersal over several metres (possibly by water) or a considerable regional pollen deposition.

Group 6: Plants present in the polygon without registered pollen signal

Saxifraga cernua occurs in three plots, including j21 (Figs. 4, 5), but with low coverage (0.1–1 %) only. Its pollen type, i.e. the SAXIFRAGA GRANULATA TYPE sensu Punt and Clarke (1980) or the SAXIFRAGA HIRCULUS-TYP sensu Beug (2004), has not been found at all, which is easily explained by the very low abundance of the species.

Utricularia vulgaris and *U. ochroleuca* occur prominently in the troughs, including those along transect j, but as no UTRICULARIA pollen grains occur, pollen production or dispersal of *Utricularia* in polygon Lhc11 must be restricted. *Utricularia* species are often sterile (Beretta et al. 2014), and during our field research, we did not observe flowering specimens in Lhc11 or adjacent polygons. Furthermore, *U. ochroleuca* is reported to produce often numerous malformed pollen grains (Beretta et al. 2014), but it seems unlikely that these would have been overlooked during pollen analysis.

Group 7: Types produced by plants along transects i, j and k

Salix occurs predominantly on the ridges in polygon Lhc11, but also in the central depression and some trough parts (Fig. 4a). The specimens were identified as *S.* cf. *myrtilloides* and *S.* cf. *sphenophylla*, but because of imperfect fit of morphological characteristics and the frequent occurrence of *Salix* hybrids, this identification is ambiguous. Peak SALIX pollen values (Fig. 5) occur especially in the ridge samples j3 and j12 being plots where *Salix* actually grows. Presence of *Salix* in the depression quadrates j13–j17, however, is not accompanied by high SALIX pollen values. Since willow is dioecious, this phenomenon may relate to a specific distribution of male and female specimens within the polygon. In earlier studies, *Salix* was also found with higher densities on the ridges and with peak pollen values restricted to only few plots (De Klerk et al. 2009).

Betula exilis concentrates on the polygon ridges (Figs. 4b, 5), but the restriction of peak values of pollen

attributable to birches to sample j4 indicates that optimal pollen production is—similarly to earlier studies (De Klerk et al. 2009)—restricted to only one or few specimens.

Ledum decumbens and *Vaccinium vitis-idea* occur prominently in the elevated and intermediate plots (Fig. 4d, e). In general, high pollen values of EMPETRUM/LEDUM correspond well to actual occurrences of *Ledum*, and those of SAMMELGRUPPE VACCINIUM TYPE with the abundance of *V. vitis-idea*. However, both pollen types peak in sample j9, where *Vaccinium* and *Ledum* are absent. Whereas the high EMPETRUM/LEDUM value in sample j9 may reflect the high *Ledum* abundance in the adjacent plot i9, this does not apply for the SAMMELGRUPPE: VACCINIUM TYPE and *Vaccinium* specimens (Fig. 4d). Since j9 is located along a wet trough, again pollen transport by water to the plot is conceivable. Of the other species that produce SAMMELGRUPPE: VACCINIUM TYPE pollen, *V. uliginosum* occurs only sporadically in Lhc11 at some distance from transect j (Fig. 4d), whereas *Andromeda polifolia* occurs especially in lower-ridge plots in the eastern and northern part of the polygon, but is absent from transects i, j and k.

Rubus chamaemorus occurs with high abundances at the higher plots (Fig. 4c). RUBUS CHAMAEMORUS pollen occurs at all plots of the transect j, with peak values up to 300 % corresponding well to actual presence (Fig. 5). The species occurs hardly in plots j9/j10, but the high values of the pollen type in these plots coincide well with the presence of *R. chamaemorus* in the adjacent transects i and k. This indicates that the species has a high pollen production and a relatively good pollen dispersal up to several metres distance. In polygon Lc04, it was only found to grow with low coverage in some plots where RUBUS CHAMAEMORUS pollen was not found at all (De Klerk et al. 2009). This is probably attributable to generally lower ridges in Lc04 where the species is limited in height and may fail to flower.

Cyperaceae occur abundantly in polygon Lhc11 (Figs. 4k, 5), with *Carex concolor* (syn. *C. aquatilis* ssp. *stans*, cf. Czerepanov 1995) being only absent from some of the higher ridge parts. *C. chordorrhiza* and *C. rotundata* occur in low abundances in the deeper spots of the western and northern parts of the polygon, whereas the latter also occurs in the central depression. *Eriophorum vaginatum* occurs as single plants in moist plots and as tussocks in drier plots, whereas *E. polystachion* concentrates in the southern and eastern trough. CYPERACEAE pollen occurs with very high values in all surface samples. A clear peak in sample j2 corresponds to the combined presence of *C. concolor*, *C. chordorrhiza* and *C. rotundata* along the i, j and k transects. A peak in sample j5 corresponds to presence of *C. concolor*, whereas the high values between samples j13–j16 coincide with actual occurrences of *C. concolor* and *C. rotundata*. Low pollen values in samples j11/12 and j18/j19 reflect elevated ranges with sparse

Fig. 5 Combined diagram of pollen, vegetation, non-pollen palynomorphs and C/N values in the surface samples from transect j. Relative values of pollen types are displayed with actual values (*closed curve*) and a 5-time exaggeration (*open curves* with sample bars). Plant abundances are displayed in *black* (transect j), dotted (**i**) and white bars (**k**); *arrows* clarify presence of plant taxa in very low abundance. Groups of pollen types and plant taxa: *1* pollen sum types, *2* extraregional types, *3* types of plants that do not occur in ice-wedge polygon Lhc11, *4* types of unknown/unclear taxonomical affinity, *5* types produced by plants in Lhc11 at some distance to transects **i**–**k**, *6* plant species present in Lhc11 without observed pollen types, *7* pollen types and plant species present along transects **i**–**k**, *8* non-pollen palynomorphs (NPPs)—fungal remains, *9*: NPPs—algal remains; *10*: NPPs—testate amoebae

presence of *Carex*. Sample j20 with 200 % CYPERACEAE corresponds to the local presence of *E. vaginatum*. Apparently, Cyperaceae taxa in polygon Lhc11 produce much pollen and the local presence of Cyperaceae species corresponds well with the deposition of CYPERACEAE pollen. Similar observations were made by De Klerk et al. (2009).

PEDICULARIS PALUSTRIS TYPE pollen is present in several samples from the deeper parts of transect j, whereas *Pedicularis* specimens grow in low abundances only on somewhat higher spots (Fig. 4g), including one plot located along transect i. This indicates good pollen dispersal to the aquatic plots and within the pond, probably by water.

POTENTILLA TYPE pollen occurs in all samples of the transect j with values around 10 %, rising to ca. 20 % at plots in the depression where *Comarum palustre*—the only species in the polygon that produces POTENTILLA TYPE pollen—actually occurs. Similar good pollen dispersal was also inferred for POTENTILLA TYPE by De Klerk et al. (2009). The high relative values indicate a high pollen production of *C. palustre*.

The coverage of species of the Poaceae family in polygon Lhc11 does not exceed 5 % (Figs. 4h, 5), whereas WILD GRASS GROUP pollen was found in all pollen samples with values from 10 to 170 %. The relatively low values in j11–j19 probably reflect regional deposition values and indicate that the higher values in the other samples must be attributable to high pollen production of grasses growing in polygon Lhc11. A similar behaviour was noted for Poaceae by De Klerk et al. (2009).

Sphagnum flexuosum and *S. squarrosum* occur abundantly in polygon Lhc11, whereas the distribution of *S. aongstroemii*, *S. fimbriatum* and *S. rubellum* is more restricted and does not cover transects i, j and k (Fig. 5). Very high values of SPHAGNUM spores of ca. 300 and 1,000 % in samples j3 and j4 correspond to the presence of both *S. flexuosum* and *S. squarrosum* and may point to complete spore capsules having been caught in the surface samples. The values in all other samples range between 5
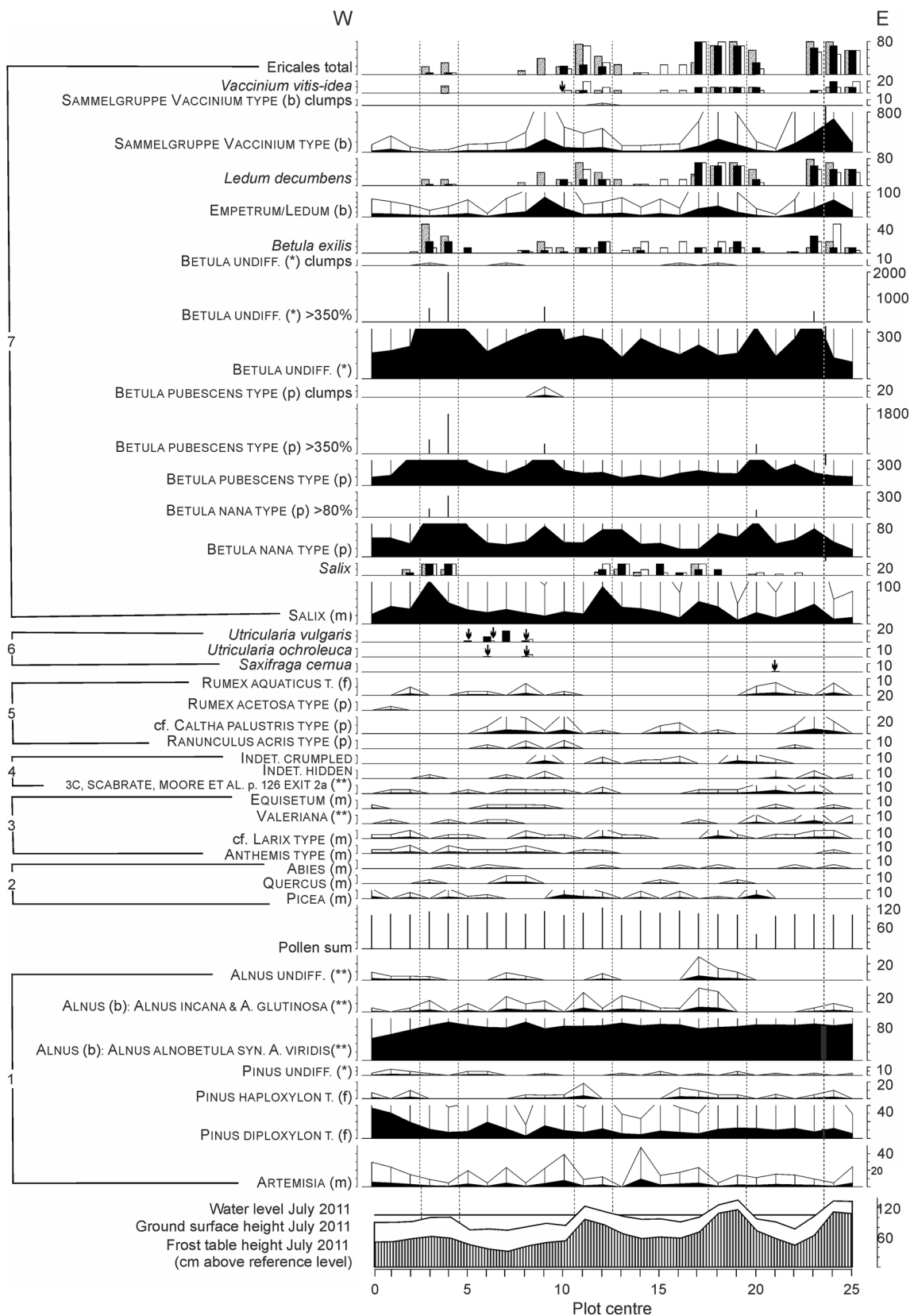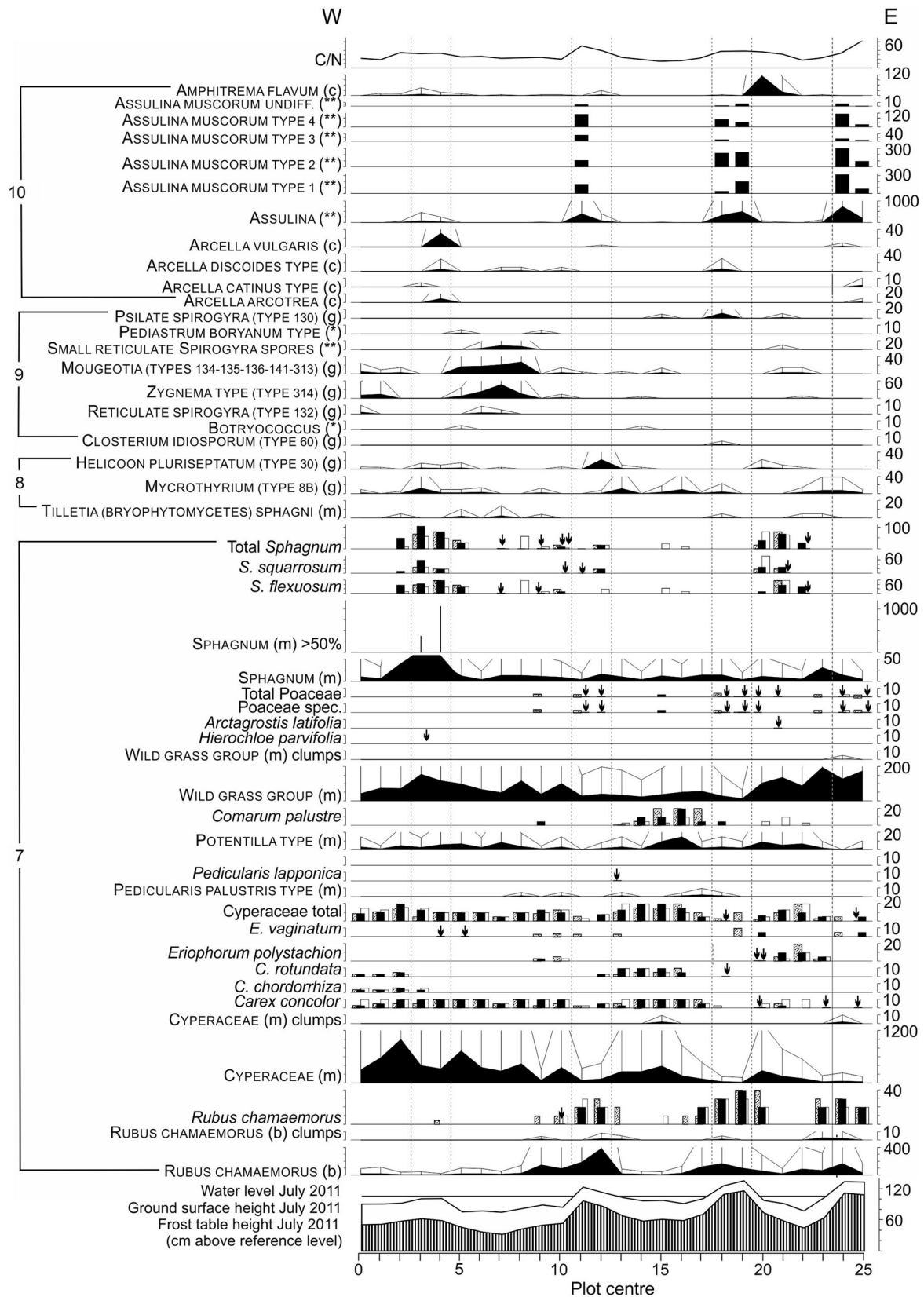
Fig. 5 continued

and 20 %, even if *Sphagnum* is prominently present (samples 12, 20, 21 and 22 of transects i, j and k). A peak of 30 % Sphagnum spores in sample j23 does not correspond to the presence of *Sphagnum*. Apparently, most *Sphagnum* specimens sporulate poorly, a conclusion likewise drawn for also other *Sphagnum* species by De Klerk et al. (2009).

Groups 8–10: Non-pollen palynomorphs (NPPs)

NPP analysis of Arctic sections is still uncommon, although various Arctic studies show their great value as ecological indicators, especially for dry or wet settings (Eisner and Peterson 1998a, b; Eisner et al. 2005; Andreev et al. 2008; De Klerk et al. 2009, 2011; Andreev et al. 2012; Zibulski et al. 2013).

Fungal remains (group 8) include fruit bodies of *Mycrothyrium* at both wet and dry plots. Remains of *Helicoon pluriseptatum* are also present in both wet and dry plots, but peak in the dry plot j12. Tilletia (bryophytomycetes) sphagni spores occur in various samples where *Sphagnum* grows, as well as in two samples from plots where *Sphagnum* is absent. A similar observation brought De Klerk et al. (2009) to the hypothesis that the Tilletia (bryophytomycetes) sphagni palynomorph possibly includes spores of other *Tilletia* species that parasite on other plant taxa.

The algal remains (group 9) are concentrated in wet plots and include Zygnema type (Type 314), Mougeotia (a complex of morphologically very similar spores of Types 134/135/136/141/313), reticulate Spirogyra (Type 132), and Small reticulate Spirogyra spores. These members of the Zygnemataceae family generally occur in shallow, stagnant, clean, oxygen-rich waters (Van Geel 1986; Van Geel and Grenfell 1996, 2001), which corresponds well with their distribution in Lhc11. The fact that they need relatively high temperatures for sporulation (Van Geel 1976, 1986, 2001) may seem to contradict their presence in an Arctic mire, but apparently the shallow humus-rich water in ice-wedge polygons warms sufficiently during the long Arctic summer days. Remains of *Pediastrum* and *Botryococcus* are sporadically present in samples from wet spots, whereas Closterium idiosporum (Type 60) zygospores show an incidental occurrence at the dry spot j18.

Most testate amoebae (group 10) do not withstand pollen sample processing (Charman et al. 2000; Payne et al. 2012), and consequently, only few species of the genera *Arcella*, *Assulina* and *Amphitrema* were found. Ecological studies of testate amoebae have predominantly focussed on the relation to moisture and water availability, and knowledge about other habitat preferences, e.g. with respect to pH, trophy, and other chemical parameters is still insufficient (Booth 2001; Mazei and Tsyganov 2007; Charman et al. 2007; Mieczan 2012). Qin et al. (2012) even found in a Chinese mire that

hydrology was not the main factor controlling testate amoebae distribution, without, however, being able to identify an alternative factor. It is plausible that ecological preferences are not identical in different geographic regions (Payne et al. 2006; Mitchell et al. 2008). Beyens et al. (1986) found, for example, that in the Arctic in northern direction *Assulina muscorum* increasingly occurs in lichens, whereas its presence in mosses diminishes. Another complication is that testate amoebae do not only live in the upper living mosses, but also somewhat deeper in the upper parts of dead mosses layers (Booth 2002; Mazei and Tsyganov 2007), with as consequence that not all tests found together in a peat layer represent the same time frame. *Amphitrema flavum* and *Assulina* species both prefer the upper ca. 5-9 cm of living *Sphagnum* (Booth 2002; Mazei and Tsyganov 2007) and, thus, will be largely synchronous with the peat layers in which they are found and with the respective pollen signal. In the palaeosequences of polygon Lc04, we found sharp boundaries in testate amoebae values (De Klerk et al. 2011), indicating that temporal mixing of fossils found in pollen samples is limited.

In Lhc11, the observed testate amoebae occur predominantly on the dry ridges with high C/N values. De Klerk et al. (2009) found a strong correlation with elevation, trophic status and the presence of *Sphagnum*. They furthermore found that *Arcella catinus* prominently occurred on spots with a lower pH than those where *Amphitrema flavum* was abundant. Whereas some authors describe *Arcella* and *Assulina* species as xerophilous (e.g. Beyens et al. 1986; Tolonen 1986; Beyens and Chardez 1995; Mazei and Tsyganov 2007; Mieczan 2012), others note that the taxa may also occur in wet habitats (Grospietsch 1972; Avel-Niinemets et al. 2011; Payne et al. 2012 [in their online appendix]). In the investigated polygons Lc11 and Lc04, *Arcella* and *Assulina* prefer rather dry habitats and do not occur in wet plots. Several authors also note that *Assulina* is sphagnophilous (Mazei and Tsyganov 2007; Bobrov et al. 2013), but such relation is not observable in Lhc11 where the genus occurs with high values in plots j11, j18 and j19 where *Sphagnum* is absent. Of the four morphological Assulina muscorum types of Schönborn and Peschke (1990), Type 1 and Type 2 are the most common ones. Values of Type 1 are considerably lower in j18 than in other samples, whereas here values of Type 2 do not show a similar decrease. This indicates that the distribution of these types may represent different requirements, but from this dataset, it is unclear what these requirements might be.

In Lhc11, *Amphitrema flavum* occurs with a clear peak in sample j20 at the transition from a ridge to a trough where peatmosses grow locally. Whereas the literature is somewhat ambiguous on what the moisture requirements of *A. flavum* (or under its new name *Archerella flavum*) are, most sources agree on its dependence on *Sphagnum* (e.g.

Fig. 6 PCA samples scores of vegetation (**a**), non-pollen palynomorphs (**b**) and pollen types (**c**) in relation to surface height (*bars*). Note that the pca samples scores of **a** and **c** are displayed in reversed order, with the lowest values to the *top* of the axis
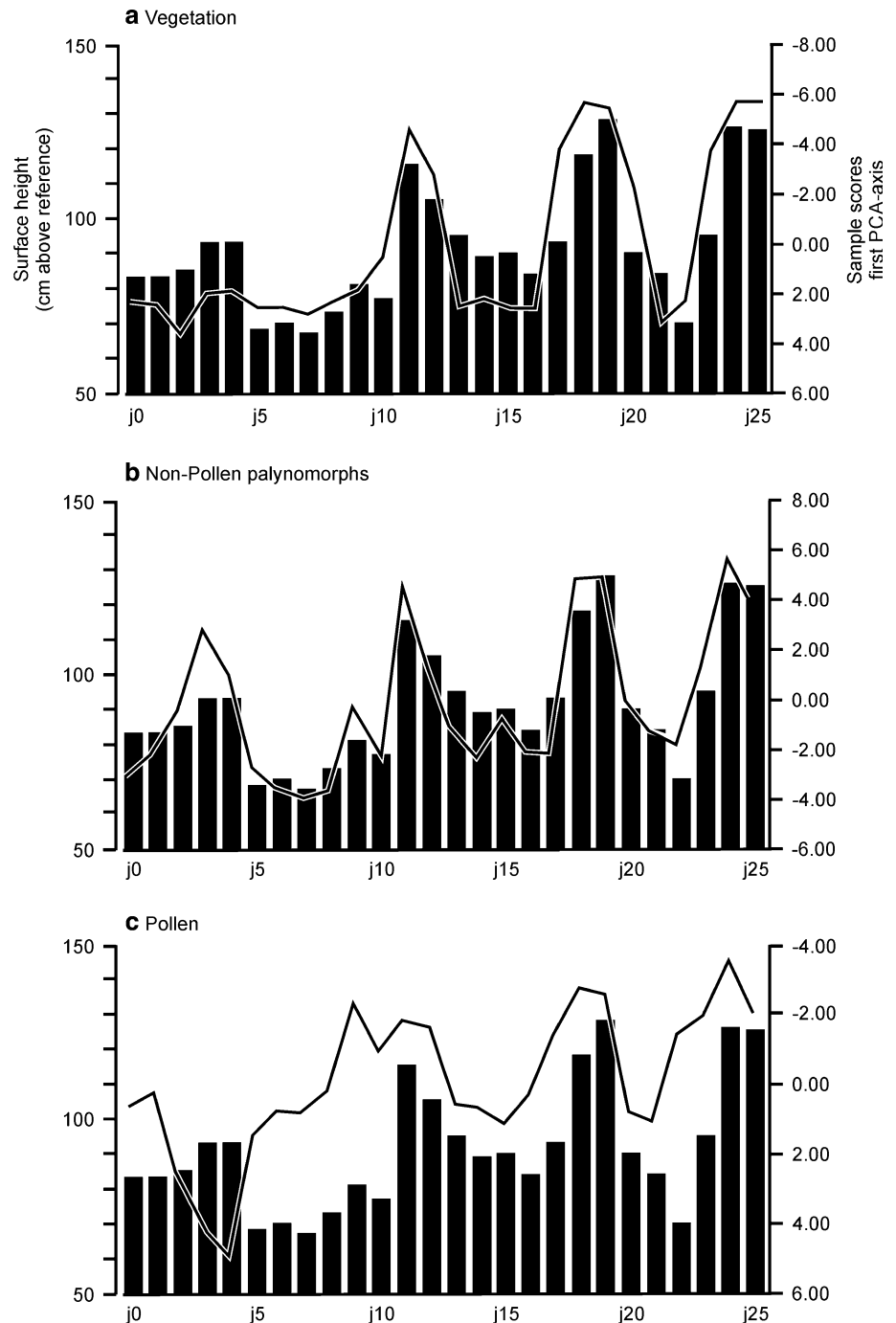
Grospietsch 1972; Mazei and Tsyganov 2007; Bobrov et al. 2013), although the cause for this dependence is still unknown (Avel-Niinemets et al. 2011).

Ordination

The gradient is short in the pollen data set (1.8) but longer in the NPP (3.1) and vegetation data (4.3). Ordination underlines the close relation between vegetation composition and surface elevation along the transect (Fig. 6a). Sample scores of vegetation on the first PCA axis (explaining 45 % of total variance) are lowest for the polygon ridges (j11, j18–19, j24/25) and highest for the low lying parts (j5–10, j13–15, j21/22). Ordination produces similar trends for the NPP data (with the first axis explaining 58 % of total variance; Fig. 6b), which mainly reflects that most NPPs represent organisms growing on either high dry (i.e. testate amoebae) or low wet spots

(algae). For pollen (Fig. 6c), sample scores of the first PCA axis (explaining 40 % of total variance) follow surface elevation between plots j5 and j25 but show a divergent trend in the western part of the transect. This less sharp signal in the pollen data is related to the fact that pollen deposition in each spots also includes pollen derived from longer distances (De Klerk et al. 2009).

Concluding remarks: implications for palaeopalynological research

The main factor influencing vegetation distribution in ice-wedge polygon Lhc11 is surface elevation, probably in combination with associated factors such as water table, trophic status (C/N) or depth of unfrozen soil.

In general, pollen deposition in polygon Lhc11 corresponds well with actual vegetation, but a perfect match does not exist. For several plant taxa, e.g. *Salix*, *Betula* and *Sphagnum*, high pollen or spore values are limited to only few specimens of the total population. This means that a change in pollen values in fossil records does not necessarily mean a decrease or increase of the actual population of the associated plant taxa. Low pollen production may prohibit detecting the presence of some prominently present species, as in our case *Utricularia*. On the other hand, high pollen values do not necessarily indicate the prominent presence of the producers, as our Poaceae example illustrates. Furthermore, we got the strong impression that in polygons with water-filled depressions and troughs, water transport may affect pollen distribution. In and around Lhc11 substantial water flow was observed during field work. The NPPs show very good correspondence to surface elevation, stressing their indicator value in Arctic conditions, although the ecological requirements of some testate amoebae are not yet completely clear. Differences in C/N values indicate that testate amoebae distribution may not only relate to hydrological conditions, but to trophic status as well.

Both detailed pollen/vegetation comparison and ordination demonstrate very good correspondence between palynomorphs and microtopography, allowing accurate reconstruction of local site conditions from fossil sequences, including reconstructing the dynamics of closely spaced microtopographical elements in polygon mires (cf. De Klerk et al. 2011).

Our studies also show that the distance to which inferences from fossil peat sections can validly be made is severely restricted. Arctic palaeosequences can thus only be interpreted with critical awareness. Single cores from a polygon landscape prohibit reconstructing the wider landscape and are of limited (palaeo)ecological value.

Some differences in recent pollen deposition patterns were observed between the Kytalyk polygon Lhc11 and the Chokurdakh polygon Lc04 located 30 km apart (De Klerk et al. 2009). These differences are attributable to dissimilar relief distinctiveness and wetness, but do not affect the correct interpretation of microrelief elements from palynological assemblages.

Some ambiguity arises from the fact that not all Arctic plant species have been studied pollen morphologically yet. Future progress in this discipline will contribute to a greater accuracy of palynological research in the Arctic.

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