



Floral evidence for high summer temperatures in southern Scandinavia during 15–11 cal ka BP

Frederik Schenk^{a, *}, Ole Bennike^b, Minna Väliranta^c, Rachael Avery^a, Svante Björck^d, Barbara Wohlfarth^a

^a Bolin Centre for Climate Research and Department of Geological Sciences, Stockholm University, Svante Arrhenius Väg 8, SE106-91, Stockholm, Sweden

^b Geological Survey of Denmark and Greenland, Øster Voldgade 10, Copenhagen K, DK 1350, Denmark

^c Environmental Change Research Unit (ECRU), Ecosystems and Environment Research Programme, University of Helsinki, PO Box 65, FI-00014, Helsinki, Finland

^d Department of Geology, Quaternary Sciences, Lund University, Box 117, SE221-00, Lund, Sweden

ARTICLE INFO

Article history:

Received 13 January 2020

Received in revised form

24 February 2020

Accepted 24 February 2020

Available online 4 March 2020

Keywords:

Deglaciation

Paleoclimatology

Scandinavia

Plant macrofossils

Summer temperatures

ABSTRACT

The global climate transition from the Lateglacial to the Early Holocene is dominated by a rapid warming trend driven by an increase in orbital summer insolation over high northern latitudes and related feedbacks. The warming trend was interrupted by several abrupt shifts between colder (stadial) and warmer (interstadial) climate states following instabilities of the Atlantic Meridional Overturning Circulation (AMOC) in response to rapidly melting ice sheets. The sequence of abrupt shifts between extreme climate states had profound impacts on ecosystems which make it challenging to reliably quantify state variables like July temperatures within a non-analogue climate envelope. For Europe, there is increasing albeit inconclusive evidence for higher stadial summer temperatures than initially thought. Here we present a comprehensive floral compilation of plant macrofossils from lake sediment cores of 15 sites from S-Scandinavia covering the period ~15 to 11 ka BP. We find evidence for a continued presence of plant species indicating high July temperatures throughout the last deglaciation. The presence of hemiboreal plants in close vicinity to the southern margin of the Fennoscandian Ice Sheet implies a strong thermal summer forcing for the rapid ice sheet melt. Consistent with some recent studies, we do not find evidence for a general stadial summer cooling, which indicates that other reasons than summer temperatures caused drastic setbacks in proxy signals possibly driven by extreme winter cooling and/or shorter warm seasons.

© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

The rapid climate shifts between unusually warm interstadials and setbacks to glacial-like conditions during stadials are particularly well documented in lake sediments south of the Fennoscandian Ice Sheet (FIS) during the deglaciation. Already more than 80 years ago (Nilsson, 1935), the re-emergence of cold tolerant plant species including the eponymous *Dryas octopetala* during the most recent stadial, the Younger Dryas (YD, ~12.8–11.7 ka BP), was interpreted as a return to glacial like conditions with open tundra-like vegetation in Denmark (Iversen, 1954) and S-Sweden (Nilsson, 1935). Subsequent studies over recent decades mostly confirmed

the narrative of cold stadial summers in Europe. For the Younger Dryas, a shift to lower July temperatures was inferred from chironomid-based reconstructions with a particularly strong cooling in NW-Europe (e.g. Heiri et al., 2014), but also in S-Sweden (Muschitiello et al., 2015a; Wohlfarth et al., 2017, 2018). The abrupt stadial cooling is generally attributed to a sluggish state of the Atlantic Meridional Overturning Circulation (AMOC) and a southward migration of the sea-ice front (e.g. Björck et al., 1996; Broecker, 1998; McManus et al., 2004; Stouffer et al., 2006).

However, some recent studies provide conflicting evidence for little to no summer cooling during the Younger Dryas across a large number of sites from NW-Europe (Birks and Birks, 2014) to central Europe (Schenk et al., 2018) and E-Europe (Magyari et al., 2019). Plant macrofossil and pollen records indicate that cold-tolerant boreal pine and birch woodland remained common during the Younger Dryas in Brandenburg (eastern Germany) (Kobe et al.,

* Corresponding author.

E-mail address: frederik.schenk@geo.su.se (F. Schenk).

2019) and that a pine forest survived the Younger Dryas at least locally in the Elbe/Jeezel valley in northern Germany (Turner et al., 2013). Preserved *in situ* remains of pine trunks indicate at least local presence of trees in north-central Europe during the Younger Dryas (Kaiser et al., 2018). These findings suggest that the cold stage vegetation patterns in central Europe experienced a stronger control by local soil and relief conditions (Theuerkauf and Joosten, 2012).

In light of a widespread inference of relatively high stadial July temperatures of ~14 °C in the Netherlands and NE-Germany (Birks and Birks, 2014), and >15 °C across central and E-Europe (Schenk et al., 2018) with up to 17 °C in the Pannonian Basin (Magyari et al., 2019), it has been suggested that other reasons than low summer temperatures *per se* are responsible for the strong environmental shifts during the YD (Birks and Birks, 2014; Schenk et al., 2018). It has been proposed that increased seasonality with severe winters dominated periods of abrupt climate shifts (Denton et al., 2005), which is consistent with recent climate model simulations (Schenk et al., 2018).

In addition to seasonal temperature changes, a shift to drier conditions at the Allerød-YD transition may have contributed to a widespread disappearance of forests. For the first half of the YD, a widespread hiatus in northern German lake sediments is indicative of very dry conditions (Usinger, 1981). Paleo-soils with sandy aeolian layers containing high amounts of charcoal, which extend from the Netherlands (Usselo soils) in the west to N-Germany and Poland in the east (Finow soils), indicate high fire activity mainly in the late Allerød (so even before stadial cooling) but notably also during the YD and to a lesser extent during the Preboreal (Kaiser et al., 2009). This is indicative of a shift to dry terrestrial conditions towards the end of the deglaciation. Under stadial conditions, hydroclimate reconstructions show a clear shift to even drier conditions during the YD e.g. in W-Germany (Rach et al., 2014, 2017) and in S-Sweden (Muschitiello et al., 2015a; Wohlfarth et al., 2017, 2018).

Owing to the extreme shifts in both, seasonal temperatures and aridity, it is challenging to conclude whether changes in seasonality, summer temperature and/or aridity were major drivers for bio(geo-)chemical shifts and related climate proxy signals under Lateglacial conditions.

Paleo-proxy studies have, during the past decades, moved from being predominantly descriptive/qualitative to providing quantified climate estimates that can be compared across spatial and temporal scales and used to evaluate climate model performance (e.g. Heiri et al., 2014; Renssen et al., 2015; Schenk et al., 2018). A major draw-back of most biological or geochemical proxies is, however, their restriction to the warm or growing season, which corresponds to spring/summer in high and low latitudes. As indicated by a numerical lake model simulation for Lateglacial conditions in S-Sweden (Ahmed et al., 2018), lakes under stadial conditions were probably ice-covered until early June even if peak summer air temperatures were high. This implies that seasonality changes may indeed dominate (Denton et al., 2005) over any other changes that may affect different proxies differently. Owing to the different seasonal sensitivities, it is hence crucial to analyse as many different proxies as possible to gain a complete picture of paleoclimatic changes.

The composition of plant and animal remains in lake sediments are generally limited by a number of (often unknown) factors such as lake size, water depth, water temperature, type and extent of the fringing vegetation, local soil and moisture conditions, exposure and topography, microclimate, predators and competition. Transport of terrestrial plant and animal remains into a lake, rapid embedding of the material and anoxic conditions at the sediment-water interface are furthermore crucial for the preservation of a

fossil assemblage. Biological proxy data used in lake sediment studies are therefore, by their nature, incomplete and only represent a fraction of the biota that lived at a certain time in and around the study site. Moreover, sampling location and sample size, preparation techniques and taxonomic issues add further uncertainties to the interpretation of fossil assemblages. A recent study, comparing pollen, plant macrofossil data and environmental DNA in lake sediments for example highlights some of these biases and shows that DNA allows detecting many more plant taxa than traditional paleoecological methods (Parducci et al., 2019) and that absence of certain taxa in a sample does not mean that they were not present in the local vegetation. Although the ancient flora and/or fauna preserved in lake sediment samples provide an incomplete view on the presence/absence of past biota, they are important means to obtain qualitative reconstructions of past climatic and environmental conditions.

The step from qualitative climatic and environmental parameters to obtaining quantified climate estimates involves the use of different techniques, such as the climate indicator species, mutual climate range or transfer functions methods (Atkinson et al., 1986; Thompson et al., 2012). Developed more than 100 years ago (Johansen, 1904; Iversen, 1954), the climate indicator species method is based on a species' present-day geographic distribution and summer temperature requirements. The method was later refined (Kolstrup 1979, 1980) and extended to include more plant species and has since been used for a range of plant macrofossil data sets (e.g. Brinkkemper et al., 1987; Isarin and Bohncke, 1999; Bos, 1998; Bos et al., 2004; Helmens et al., 2007). However, as pointed out by for example Iversen (1954), Iversen (1964) and Brinkkemper et al. (1987), the indicator species method has clear limitations, since some plants can remain in a vegetative state or be preserved in a seed bank also at the outer limit of their general optimal distribution area. The comparison between a plant's present-day distribution and its mean July temperature requirements can therefore lead to lower temperature estimates if the northern geographical distribution limit and its related thermal limit is based on sparse presence of a species. When transferred to a fossil assemblage, this will result in reconstructed temperatures that are too low. Recent studies have therefore moved towards defining thermal limits based on a common northern distribution limit rather than on sparse presence beyond any limits (Väliranta et al., 2015; Schenk et al., 2018). Moreover, environmental conditions today are considerably different from those during the past, when for instance competition, soil conditions, and shading were likely important additional factors (Iversen 1954, 1964). This implies that the absence of many species may be unrelated to climatic parameters like July temperature.

Since Iversen (1954, 1964)'s initial studies, other techniques have been developed to reconstruct past temperatures from fossil biota. One of these is the mutual climate range (MCR) method, which leans on Iversen (1954)'s approach and on the assumption that today's climatic tolerance range of a species can be applied to fossil assemblages (Atkinson et al., 1986). The method has mainly been applied to coleoptera assemblages (e.g. Atkinson et al., 1987; Lowe et al., 1995; Coope and Berglund, 1986; Coope and Lemdahl, 1995; Coope et al., 1998; Björck et al., 1996) to reconstruct winter and summer temperatures, but has also been used for other types of fossil biota.

The modern analogue technique (MAT) (Guiot, 1990; Jackson and Williams, 2004) is based on statistical comparisons of large modern pollen data sets to fossil samples in respect to analogies in taxa composition and abundance. The climate variables for the modern data set can then be transferred to the fossil assemblages. Various statistical calibration or transfer function techniques are in

use to reconstruct summer temperatures using fossil chironomids, diatoms and also pollen (e.g. Birks et al., 1995; Birks et al., 1998; Juggins, 2013). These build on extensive regional training sets, for which recent/sub-recent assemblages (e.g., chironomids, diatoms, pollen) were analysed from surface sediments of lakes across various altitudinal, latitudinal and ecological gradients and compared to mean ambient summer air temperatures. The statistical comparison between these training sets and the fossil assemblages allows estimating past summer temperatures (e.g. Birks et al., 1998; Bigler et al., 2002; Larocque and Bigler, 2004; Juggins, 2013; Heiri et al., 2014).

The climate indicator species method (Iversen, 1954) has recently experienced a revival (Väliranta et al., 2009, 2015; Schenk et al., 2018) with the employment of a unique temperature gradient data set from Finland. This data set is composed of detailed modern species-specific spatial plant distribution surveys (<http://www.luomus.fi/kasviatlas>) and long-term meteorological observations, both available for 10 × 10 km grid cells (Venäläinen et al., 2005; Lampinen and Lahti, 2019). The plant distribution database, which is based on continuous botanical surveys, can thus be directly compared to climate variables and allows the reconstruction of quantitative minimum mean July temperatures (Väliranta et al., 2015; Schenk et al., 2018). As part of this study we further extend the number of climate indicator plant species which are based on a systematic definition of their thermal limits estimated from a common northern distribution limit over the temperature gradient in Finland.

We then use these data sets and apply them to a compilation of 15 published and unpublished Lateglacial and Early Holocene plant macrofossil records from southern Sweden and Denmark. The plant macrofossil data sets are from multiple sites in different topographic settings, but within a confined region and covering the same time intervals, and provide a broad spectrum of Lateglacial and early Holocene plant taxa. It allows us to evaluate the reliability and consistency of the climate indicator species-based summer temperature reconstruction and provides minimum mean July temperature estimates that can be compared to climate simulations.

2. Study region

Parts of Denmark and all of southernmost Sweden were covered by the Fennoscandian Ice Sheet (FIS) during the Last Glacial Maximum. The region became ice free between 22 and 13 thousand years (ka) ago (Fig. 1) (Lundqvist and Wohlfarth, 2001; Houmark-Nielsen and Kjaer, 2003; Houmark-Nielsen et al., 2005; Hughes et al., 2016; Stroeven et al., 2016). Stagnant ice, however, remained in several areas (Björck et al., 1996; Wohlfarth et al., 2017, 2018) and led to delayed start of sedimentation in several of the lake basins for which we have compiled data.

During the last deglaciation, the region was influenced by the gradual waning of FIS in the north, the Baltic Ice Lake to the east and south-east (Björck, 1995; Andrén et al., 2011) and a North Sea area that was mostly above sea level to the west (Björck and Digerfeldt, 1991). Ice sheet melting, isostatic rebound, eustatic sea level rise and damming of the Baltic Ice Lake led to a complicated pattern with flooding of low-lying land areas and/or land bridges between Denmark and southernmost Sweden (Björck, 1995; Andrén et al., 2011).

A large number of Lateglacial lake sediment records have been analysed for a variety of paleo-proxy parameters (e.g., pollen, macro remains, coleoptera, oxygen isotopes) in Denmark and Sweden during the last 80–100 years (Iversen, 1954; Nilsson, 1935; Berglund, 1966; Berglund et al., 1994; Lowe et al., 1994; Berglund,

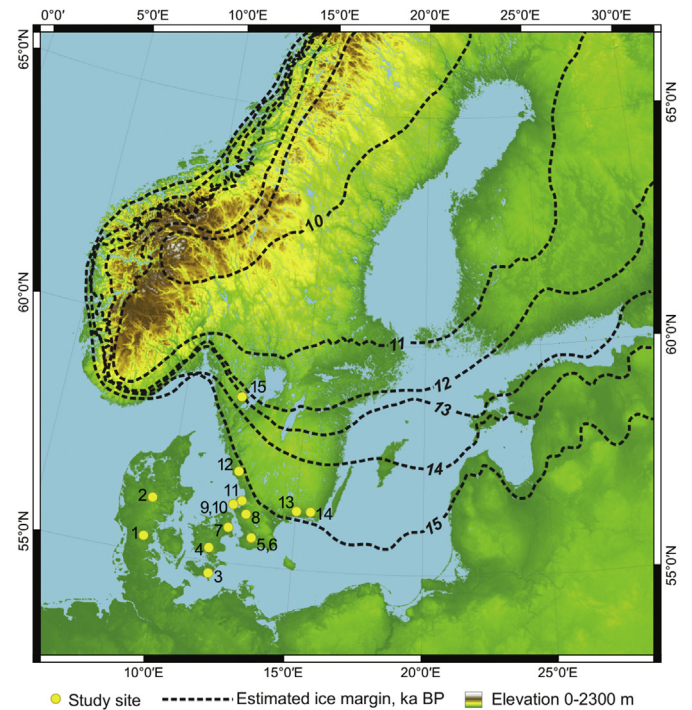


Fig. 1. Locations of study sites in Denmark and southern Sweden (dots) in the context of Fennoscandian Ice Sheet retreat from 15 to 11 ka BP. Ice margins at 1 kyr intervals are shown using the DATED-1 'most credible' estimates (Hughes et al., 2016). Note, that a present-day topography is shown here. For Lateglacial paleo-shorelines, see e.g. Wohlfarth et al. (2017, 2018).

1996), but a compilation and summary of all these and more recent studies has never been made.

In this study, we compiled available floral information from 14 published sites supplemented by so far unpublished plant macrofossil lake sediment records and, in addition, a compilation of published pollen and plant macrofossil records from Blekinge in southeast Sweden (Table 1). Our study region covers a north-south gradient of ~370 km and a maximum east-west distance of ~170 km. The sites are shown in Fig. 1 and information about the sites and references to the original data is provided in Table 1.

3. Materials and methods

Our data compilation (Schenk et al., 2020; Supplementary Data A) comprises six published (Atteköpsmosse, Björkerödsmosse, Håkullsmosse, Hässeldala Port, Korslättamossen, Toppeladugård) and three previously unpublished (Madtjärn, Mjällsjön, Torreberga) (Supplementary Data B) plant macrofossil data sets from southernmost Sweden, one compilation of pollen and plant macrofossil records from Blekinge (Berglund, 1966) and five published plant macrofossil records (Bølling Sø, Hasselø, Slotseng, Søndre Kobberdam, Trollesgave) from Denmark (Fig. 1, Table 1). All of the selected plant macrofossil diagrams were accompanied by a pollen stratigraphy and/or by a detailed radiocarbon chronology, which allows for inter-site correlations.

In a first step, we selected all terrestrial, telmatic and aquatic plant taxa that were determined below family level. These are listed in Schenk et al. (2020) and Supplementary Data A. To ensure that the samples were derived from within a pollen stratigraphic zone, we excluded samples closest to a pollen stratigraphic boundary. We also added very detailed pollen stratigraphic work from various sites in Blekinge, south-easternmost Sweden

Table 1
Sites with plant macrofossil records from southern Sweden and Denmark used for the compilation. Site locations are shown with their #ID in Fig. 1. The previously unpublished data by Bennike is provided as Supplementary Data B. The full compilation of plant species (Schenk et al., 2020) is available as Supplementary Data A.

#ID	Site name	Altitude [m a.s.l.]	Lat. [dec °]	Lon. [dec °]	References
1	Lake Madtjärn	135	58.62°N	12.33°E	Björck et al. (1996); Bennike, unpublished
2	Blekinge sites	–	56.15°N 56.30°N	15.32°E 15.87°E	Berglund (1966)
3	Hässeldala Port	63	56.27°N	15.02°E	Parducci et al. (2019)
4	Lake Mjällsjön	72	57.01°N	12.59°E	Björck et al. (1996); Bennike, unpublished
5	Atteköpsmosse	175	56.38°N	12.85°E	Wohlfarth et al. (2018)
6	Häkullsmosse	125	56.29°N	12.53°E	Liedberg Jönsson (1988)
7	Björkeröds mosse	125	56.28°N	12.53°E	Liedberg Jönsson (1988)
8	Körslättamossen	118	56.10°N	13.07°E	Hammarlund and Lemdahl (1994)
9	Søndre Kobberdam	–21	55.77°N	12.44°E	Bennike and Mortensen (2018)
10	Torreberga	7	55.62°N	13.23°E	Björck et al. (1996); Bennike, unpublished
11	Toppeladugård	35	55.60°N	13.37°E	Lemdahl (1988) Lieberg-Jönsson (1988)
12	Trollesgave	–	55.28°N	11.80°E	Fischer et al. (2013)
13	Hasselø	–	54.73°N	11.90°E	Mortensen et al. (2014a)
14	Bølling Sø	–	56.18°N	09.37°E	Bennike et al. (2004) Bennike, unpublished
15	Slotseng	40	55.33°N	09.27°E	Mortensen et al. (2011); Lemdahl et al. (2014)

(Berglund, 1966). For these latter records, we included macroscopic plant remains, taxa whose pollen are not transported over long-distances, taxa for which more than one pollen grain was reported and for which species identification was reliable according to (Berglund, 1966). To avoid false presence of indicator species in a given stratigraphic zone, we also excluded samples that were close to a pollen zone transition. We note, however, that we cannot rule out the possibility of minor Allerød (AL) macrofossil presence in YD sediments for some Danish lakes, in situations where AL macrofossils could be preserved outside the lake system during the drier early YD and re-enter the lake during the more humid later YD (Mortensen et al., 2014b). As we find indicator species with similarly high thermal requirements in other lakes and across much of Europe during the YD (Schenk et al., 2018), it is unlikely to affect the overall results.

For an age assignment to the Lateglacial and Early Holocene regional pollen zones, we followed the zonation published by the respective authors, but changed the transition between the Younger Dryas and Preboreal (PB) pollen zones in accordance with (Björck et al., 1996). This implies that the base of the YD/PB transition zone, which originally was a separate pollen zone between the YD and the PB pollen zones, now corresponds to the start of the Holocene.

In a second step, we compared the identified plant taxa (Schenk et al., 2020; Supplementary Data A) to plant distribution maps for Norden (Scandinavia) (Hultén, 1950; maps are also available online: <http://linnaeus.nrm.se/flora/>) to assure that the current range of the species is within the boreal to arctic vegetation zones. Because some plant species can reach their common northern distribution outside of Norden, we additionally evaluated Hultén's distribution maps for *Norra halvklotet* (northern hemisphere; Hultén and Fries, 1986) and excluded plants that are found in arctic regions like Greenland or Svalbard. This was e.g. the case for *Callitriche hermaphroditica* which appears to be sub-arctic in Norden with a tendency to brackish preference but which is clearly present at arctic conditions on Disko island, W-Greenland (Bennike, 1995). We then compared the remaining taxa to the very high-resolution species-specific spatial plant distribution data set for Finland (Venäläinen et al., 2005; Lampinen and Lahti, 2019; <http://www.luomus.fi/kasviatlas>), which covers the years 1971–2001. In accordance with Väiliranta et al. (2015) and Schenk et al. (2018), we

assume that anthropogenic pressure on plant distributions is negligible and distribution ranges represent a relatively natural state. Finland has a weak southwest (semi-oceanic) to northeast (semi-continental) oceanicity-continentiality gradient and a gradual precipitation gradient with a difference of ca. 200 mm a⁻¹ between southern and northern Finland. Importantly, Finland has a pronounced south-north temperature gradient with a mean July air temperature of ca. 17 °C in the south-southeast and of ca. 7.5 °C in the mountains of western Lapland. Finland therefore covers the hemiboreal, boreal and subarctic vegetation zones and many plant species reach their common northern distribution limits within Finland. Only in the northernmost part of the country are plant distributions limited by elevation-related climatic conditions.

In a third step, we selected those taxa, which are endemic to Fennoscandia and have a clear common northern distribution limit in Finland (Schenk and Väiliranta, 2020; Supplementary Data C). Taxa with rare occurrences or specific distribution patterns (e.g., only along the Baltic Sea shore, only on calcareous soils/bedrock), or taxa that are today common and not limited by temperatures reached in N-Finland were excluded from further analyses. The excluded taxa are, however, listed as “plants without quantification” in Schenk and Väiliranta (2020) and Supplementary Data C. We moreover excluded taxa that contain several species (e.g. *Ranunculus sect. Batrachium*.) with different distribution limits. Since *Nymphaea alba*, which has a clear distribution pattern, comprises several subspecies, which were not further determined in the respective macrofossil diagrams, we assigned the recorded macrofossil remains to *Nymphaea* sp. We also grouped *C. demersum* and *C. submersum* together as *Ceratophyllum* spp.; *C. submersum* is rare today, but we cannot exclude that it was more common during the Lateglacial/Early Holocene. Since *Callitriche* was not further identified to lower taxonomic level in Hasselø, we here use a conservative estimate of 13.7 °C.

Various plant species have changed names over time and are, in several of the older plant macrofossil records, shown with old names. The synonyms for the various plant species were added as comments in Supplementary Data C.

In a fourth step, we determined the grid points for the up to five common northern plant distribution locations for each taxon in Finland and compared these to average July temperatures for the same 10 × 10 km grid cells from the meteorological data set for the

years 1971–2001 (Venäläinen et al., 2005; Lampinen and Lahti, 2019). The coordinates and related July temperatures of the used grid points are included in Schenk and Väiliranta (2020) and Supplementary Data C. Although we only use climatological mean July temperatures for estimating thermal limits in this study, the dataset contains additional information about July temperatures of the coldest/warmest days/months during 1971–2001 accompanying the climatological mean value. Comparable mean July temperatures in a much more continental climate of the deglaciation (e.g. Schenk et al., 2018) or other periods may have experienced a much larger range of extreme temperatures which may be studied in the future e.g. with the help of climate model simulations. The full climatological data range over all thermal limits is visualized in Fig. 2.

It is important to note that the thermal limits for indicator plant species following Väiliranta et al. (2015) and Schenk et al. (2018) are defined based on their *common northern distribution limit* and not based on the coldest occurrence at an isolated location. This implies that the thermal limits are systematically higher than older definitions based on outpost individuals at unusually favourable locations.

Using a *common northern distribution limit* has two main advantages: First, the definition is more robust by omitting unusually favourable site localities which may be caused by local climatic or edaphic conditions (e.g. wind protected, south facing slope). In addition to usually small standard errors for the calculated thermal limits (Supplementary Data C), this is demonstrated by the high consistency of a near-zero difference between median vs. mean values in Fig. 2 despite the reliance on only very few locations. Second, the generally rare finds of plant macrofossils in lake sediments typically reflect a common and persistent presence of a given plant species rather than individual outpost plants. Ancient DNA analysis confirms that the *in situ* presence of plants reflects common presence at the lake site (Parducci et al., 2019). Based on this empirical probabilistic argument, it is not plausible to assume

that rare finds of plant macrofossils would represent individual rare outpost occurrence. Hence, it would be inconsistent to use a much colder thermal limit of outpost species when the plant species in the sediment reflect a common presence.

To document the typically found spatial distribution differences between regions with a common presence relative to areas with scattered presence, we accompanied the list of quantified T_{July} values in Supplementary Data C (Schenk and Väiliranta, 2020) with brief remarks about the common distribution (sub-polar, northern or central boreal, hemiboreal-temperate) and scattered occurrences like “scattered up to N-Finland, main distribution is boreal” etc. These generalized remarks are based on the distribution maps of Hultén (1950) and Hultén and Fries (1986). As can be inferred from these remarks, there is a clear tendency for scattered occurrences in the neighbouring climate zone, i.e. beyond the main population locus. This implies that e.g. species with a common northern distribution limit within the central boreal zone have typically a scattered occurrence in the northern boreal zone etc.

The spread between the common thermal limit and the coldest considered occurrence can be used as a taxa-specific uncertainty where a given July temperature may be overestimated (Väiliranta et al., 2015; Schenk et al., 2018). For the plant species used in our calibration dataset, the spread of the difference of mean thermal limit minus coldest limit along the common northern distribution limit ranges from 0.1 K to 2.7 K with a median (mean) difference of 0.6 (0.9) K. The individual taxa uncertainty is shown in Supplementary Data C (colour coded, green = as good as or better than 50% of the plant species, light green = best 5%, light orange = within 75%, darker orange 75–95%).

The standard error of the mean (σ/\sqrt{N}) for the common northern limits are generally small and indicate a small spread of the northern distribution grid points used to define the thermal limit. A comparison of the mean vs. median thermal limit based on up to five grid points yields almost no difference and confirms that the estimate of the climatological mean for the thermal limit is not biased/skewed by outliers (Fig. 2). As additionally shown in Fig. 2, this also applies to the estimate of warmest/coldest months and days for July in 1971–2001 related to the climatological mean of plant indicator species.

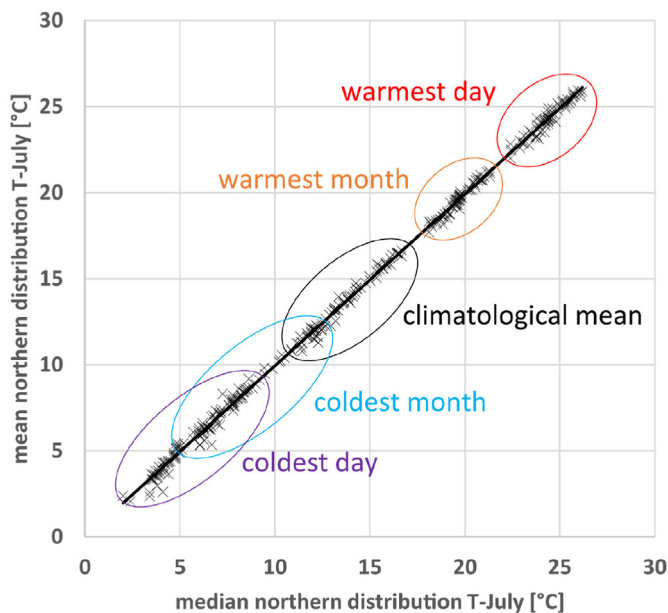


Fig. 2. Consistency of the common northern distribution limit definition and the relation of climatological mean July temperatures to the overall July climatology of Finland for the period 1971–2001. The almost perfect linear agreement of the median vs. mean northern July limit for all used plant indicator species shows that the definition of using up to five grid points as northern distribution limit is robust and unbiased relative to outliers which may be caused by complex terrain.

4. Results

4.1. Extended database for climate indicator plant species

In total, we were able to define thermal limits for $N = 62$ different climate indicator plant species (Fig. 3; Schenk and Väiliranta (2020); Supplementary Data C). For each plant taxa, the mean minimum July temperature [°C] is given based on the *common northern distribution limit* in Finland. The coordinates and July mean temperatures of the used grid points for the derivation of the thermal limits are provided in Schenk and Väiliranta (2020) and Supplementary Data C together with estimated July temperatures, the standard error of the mean [SE in °C] and the taxa uncertainty (the difference between the mean and the coldest location found at the common northern distribution). In addition, the dataset contains a list of 97 plant taxa for which we do not assign a thermal limit either because the taxa are currently not present in Finland or because they have a problematic distribution and/or cannot be reliably differentiated from other taxa with different thermal requirements. The reasons for refraining from quantifying are given as comments along with the taxa names in Schenk and Väiliranta (2020) and Supplementary Data C.

For the 62 indicator species, the taxa uncertainty, and hence a potential warm bias of the common northern distribution limit,

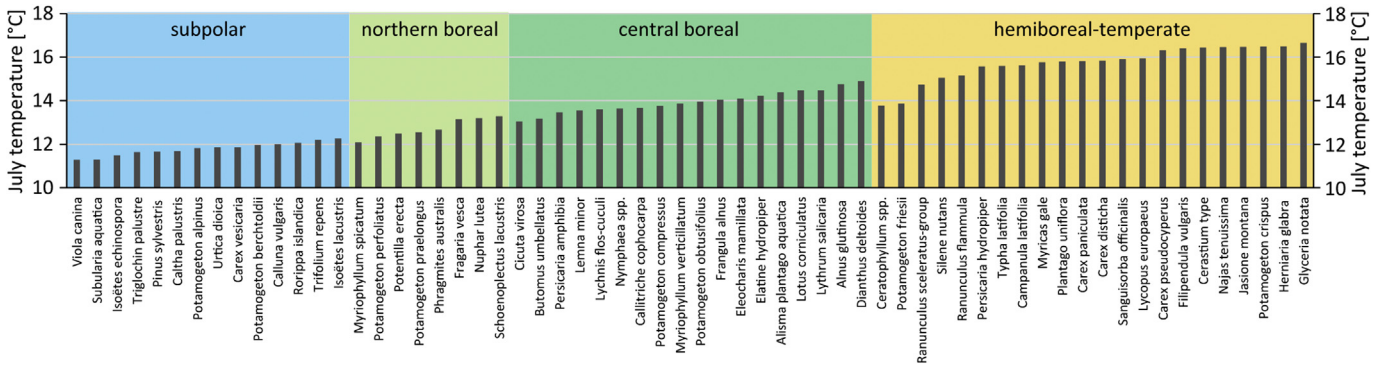


Fig. 3. Climate indicator plant species from modern Finland and their presence during the Lateglacial-Holocene transition in southern Scandinavia. The plant-specific July temperature limits are based on a common northern distribution limit in Finland (1971–2000). The climate zone classification represents the region in Finland where the indicator species reaches its common northern distribution limit following the distribution maps by Hultén (Hultén, 1950; Hultén and Fries, 1986). The standard error of the mean and taxa uncertainty for the thermal limits together with comments on the regions of scattered occurrence after Hultén are listed in Supplementary Data C.

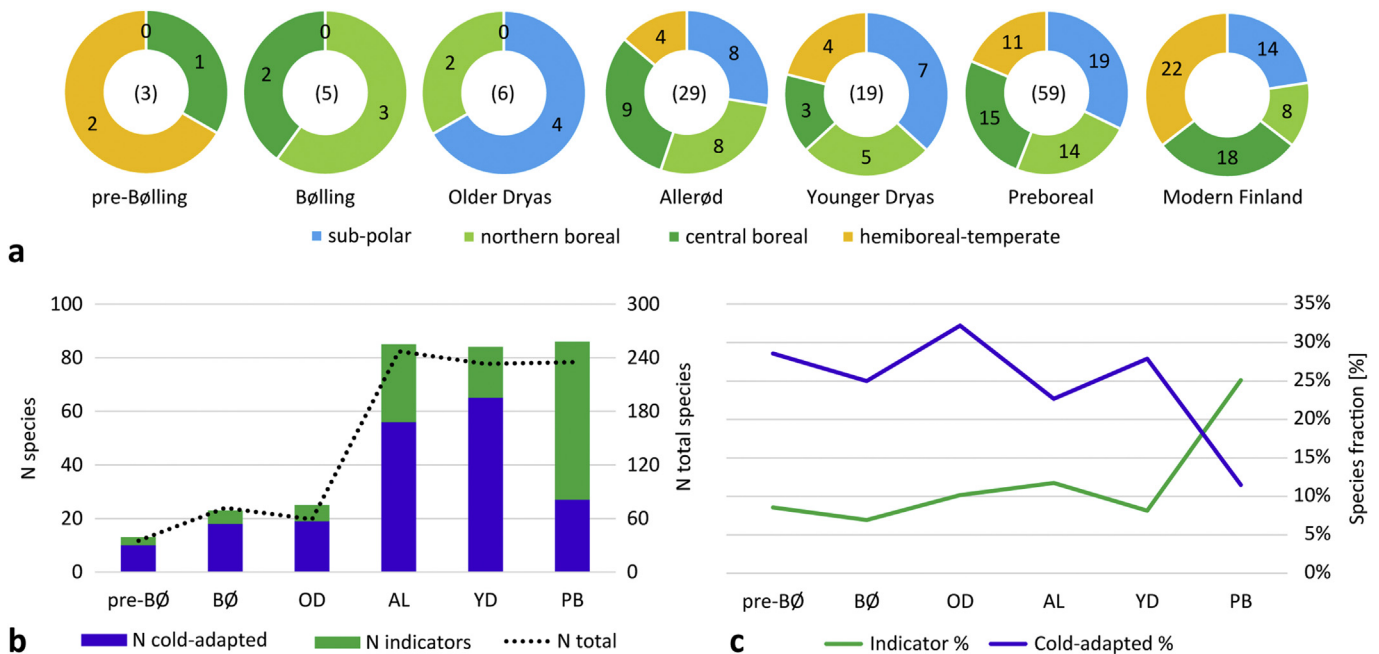


Fig. 4. Compilation and classification of climate indicator plant species based on 15 sites from southern Sweden and Denmark (~15 to 11 ka BP). a) Relative distribution of represented climate zones based on plant indicator species over time following the classification in Fig. 3 b) Absolute numbers [N] of cold-adapted plant species (blue) and number of quantified July indicator species (green) over time (left axis) and the total number of plant indicators found in sediments (dotted line, right axis). c) Relative fraction [%] of cold-adapted and quantified indicator species based on the total number of plant indicator species. Note that the total numbers in (a) for the past are based on the total number of species counted for all 15 sites while modern Finland displays only the list of N = 62 species as shown in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

ranges from 0.1 to 2.7 °C with a median (mean) of 0.6 °C (0.9 °C). With the exception of *Silene nutans*, indicator species with thermal requirements >12.5 °C tend to have a relatively small taxa uncertainty (<1.5 °C) while the thermal limits in colder regions are more uncertain. Over all 62 species, the uncertainty of thermal limits linearly decreases from colder to warmer limits with 0.26 °C per degree ($r^2 = 0.43$).

As introduced by Väiliranta et al. (2015) and used by Schenk et al. (2018), the taxa uncertainty is probably the only useful statistical uncertainty to estimate a potential warm bias of an indicator species in the past. As relying on rare presence of indicator plant species comes with a risk of false absence of even warmer taxa, there is no possibility to estimate a potential cold bias of the July estimate (for details see Väiliranta et al., 2015; Schenk et al., 2018). The best solution for increasing confidence in the July estimates is

hence to rely on the analysis of as many sediment cores and lake sites within a certain region as possible. Future studies using ancient DNA from lake sediments have a high potential to significantly reduce the false absence problem as ancient DNA allows for an extended identification of species growing at the lake site and their abundance (Parducci et al., 2019). This implies that the thermal limits from the climate indicator approach can increasingly be applied to plants identified through their ancient DNA.

In addition to the statistical uncertainty estimates for common thermal limits in Finland, we evaluated the general distribution maps of the selected plant indicators based on Hultén’s maps for Norden (Hultén, 1950) and the Northern Hemisphere (Hultén and Fries, 1986). Based on these maps, we added brief standardized descriptions to Schenk and Väiliranta (2020) and Supplementary Data C about the climate zones with scattered occurrence and the

northernmost zones where they reach their common distribution limit. We classified the climate zones containing the common northern distribution of indicator plants as sub-polar, northern or central boreal and hemiboreal-temperate for a distribution in southernmost Finland. Fig. 3 shows the common minimum July thermal limits of the 62 climate indicator plant species together with the climate zone where they reach their common northern distribution limit.

The dataset based on the temperature range of Finland does not allow for a quantification of some important indicator plants which grow at even colder temperatures outside of Finland. To at least partly account for this limitation when analysing sediment cores from the deglaciation, we also consider a (possibly non-conclusive) shortlist (Table 2) of plant indicator species which are known to be cold-adapted plants including e.g. the eponymous *Dryas octopetala*. Changes in the presence of these cold-adapted plants provide important additional information beyond the focus on the minimum July temperature of plant indicator species with the highest thermal limit. It should be noted though that cold-adapted plants are usually also heliophytes. It is therefore not possible to interpret the presence of cold-adapted plants as indicative of generally low, summer or growing season, temperatures.

4.2. Compilation of indicator plants for S-Scandinavia (~15–11 ka BP)

From the compilation of published and unpublished climate indicator plant species, we were able to select 96 samples which can be quantified for their July temperature requirements from 15 sites distributed across southern Sweden and Denmark (Fig. 1). The number of quantified indicator species is considerably lower than the overall identified plant fossil taxa in the sediment cores (Fig. 4b, Schenk et al., 2020; Supplementary Data A). As outlined in the methods, we excluded all samples, which were close to original chronological boundaries and could lead to a false presence in a wrong chrono-, climate- or bio-zone. In addition, we excluded taxa which consist of species which are difficult or impossible to distinguish from other species, which have different thermal requirements.

Fig. 4 provides an overview on the number and classification of the plant indicator compilation based on all 15 sites. The numbers in brackets in Fig. 4a give the total number of quantifiable indicator species for each time period while the pie charts display the relative distribution of climate zones represented by the indicator species counts from all 15 sites following the classification from Fig. 3. Although the pre-Allerød data are based on a low number of sites and samples, we note the remarkably early presence of hemiboreal and central boreal indicator species already in the pre-Bølling (pre-Bø). With exception of the short Older Dryas (OD) stadial, the compilation indicates a persistent presence of at least central boreal or even hemiboreal indicator species during the Lateglacial

including the YD stadial. As shown in Fig. 4b, the Lateglacial period hosts generally a high number of cold-adapted plants despite the presence of indicator species with relatively high thermal requirements (Fig. 4a). Although the fraction of cold-adapted indicator plants [%] relative to the total number of plant species is higher during stadials (OD, YD), their dominance persists also during the interstadials (Bø, AL) (Fig. 4c). Only with the onset of the Holocene do plant indicators with higher thermal requirements dominate over the presence of cold-adapted plants in the PB.

4.3. Local July temperature reconstructions

The compilation of climate indicator species from our 15 sites in Fig. 4 demonstrates the co-existence of plants with very different thermal requirements and tolerances throughout the Lateglacial and to a lesser extent even PB. Despite the dominance of cold-adapted plants/heliophytes and a notable presence of sub-polar species, a large fraction of species indicates that warm summer conditions as found today in southern to central Finland prevailed throughout the Lateglacial since ~15 ka BP. To determine the related minimum July temperatures for the different periods, Fig. 5 shows the July temperature estimates based on up to five indicator species with the highest thermal limits compiled from the 15 sites. Consistent with Fig. 4a, the minimum July temperature estimates cover a wide range owing to the co-existence of plants with very different northern distribution limits.

As was already shown in Fig. 4 for the total number of species, the more recent periods of the PB, YD and AL are well represented in terms of both number of sites and presence of indicator plants. In contrast, the OD and Bø are only based on three to four sites and pre-Bø is only available from Björkerödsosse. This makes it difficult to reliably infer July temperatures for OD, Bø and pre-Bø.

The comparison of sites indicates that the spatial distribution across Denmark and S-Sweden with a north-south transect of ~370 km and an east-west transect of ~170 km (Fig. 1) is rather heterogeneous without any systematic geographical differences. Due to the relatively low number of indicator species, it is not possible to estimate whether the heterogeneity is due to local site-specific edaphic differences or simply due to scarcity of data and/or false absence in the sediment core.

4.4. Regional July temperature reconstruction for S-Scandinavia

The heterogeneous site-specific results in Fig. 5 highlight the importance to form a regional compilation of sites within a region to determine the paleoclimate based on scarce indicator species. This is i.e. true for the YD where a widening of the distribution and large differences between different sites (Fig. 5) would lead to very different estimates of July temperatures if based on only one site.

Fig. 6 presents the overall statistics derived from merging all local sites from Fig. 5 into one regional sample representing the minimum July temperature estimates for S-Scandinavia for major climate periods during ~15–11 ka BP. The histogram in Fig. 6a presents an overview for the temperature distribution based on the total number of July estimates (black) and the distributions for the different (inter-)stadials and early Holocene (colours). With exception of the data-sparse OD and the PB, Lateglacial periods tend to have a skewed bi-modal distribution where a large number of estimates is concentrated around 12–13 °C (stadials) to 12–14 °C (interstadials) while a secondary peak around 16 °C contains several different species surrounding the species with highest thermal limits in the regional compilation.

As a result, there is a large temperate spread for the 3rd quartile (containing 25% of thermal limits above the median) towards

Table 2

List of cold-adapted indicator plants often found in Lateglacial sediments. Note that cold-adapted plants are usually also heliophytes and do not always imply low summer temperatures *per se* (cf. Fig. 4). Some of these taxa, such as *Betula nana*, occupy a wide range of climate zones.

<i>Arctostaphylos alpina</i>	<i>Papaver sect. Scapiflora</i>	<i>Saxifraga adscendens</i>
<i>Betula nana</i>	<i>Polygonum viviparum</i>	<i>Saxifraga aizoides</i>
<i>Cerastium alpinum</i>	<i>Potamogeton filiformis</i>	<i>Saxifraga oppositifolia</i>
<i>Dryas octopetala</i>	<i>Ranunculus hyperboreus</i>	<i>Selaginella selaginoides</i>
<i>Gentiana nivalis</i>	<i>Salix phylicifolia</i>	<i>Silene acaulis</i>
<i>Lychnis alpina</i>	<i>Salix herbacea</i>	<i>Thalictrum alpinum</i>
<i>Minuartia rubella</i>	<i>Salix polaris</i>	<i>Viscaria alpina</i>
<i>Minuartia stricta</i>	<i>Salix reticulata</i>	

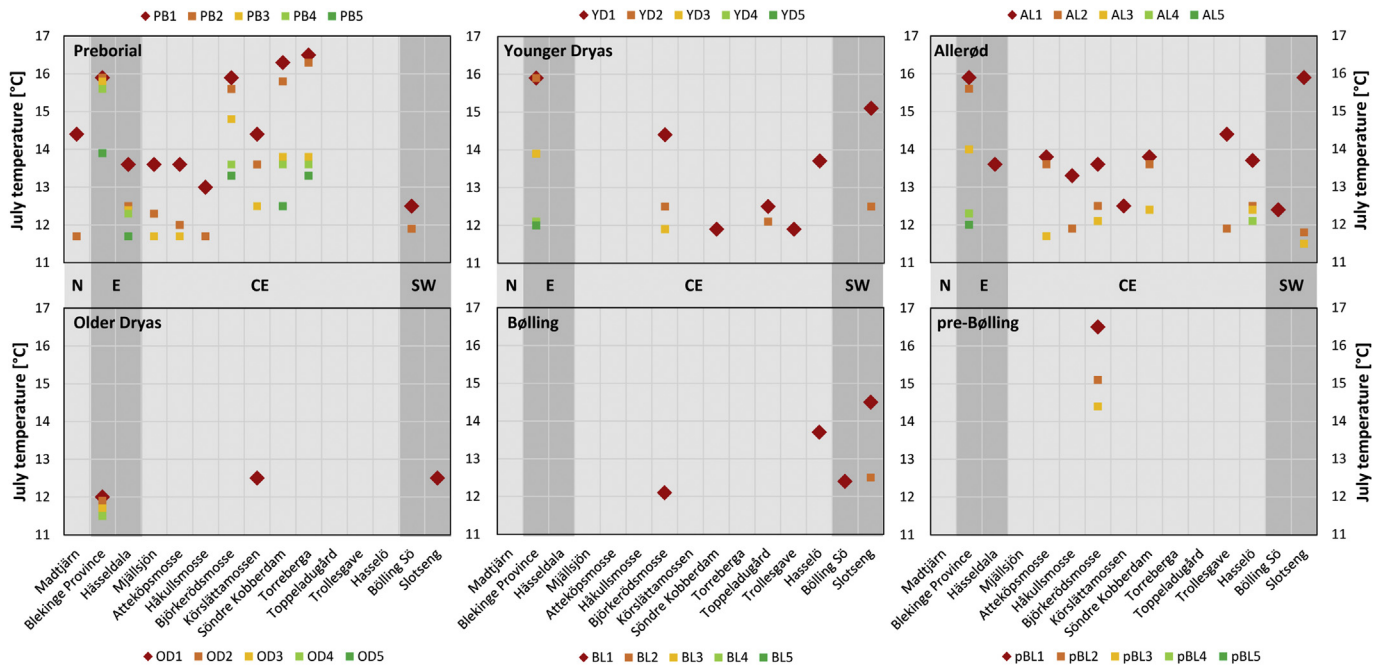


Fig. 5. Compilation of quantified climate indicator plant species for different locations from Denmark and S-Sweden (~15–11 ka BP). Note that the sites have been ordered from north (N) via east (E), central (CE) to southwest (SW) from left to right. Where available, the up to five warmest indicator species values are shown for each site. The warmest indicator value of each site is highlighted with a red diamond. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

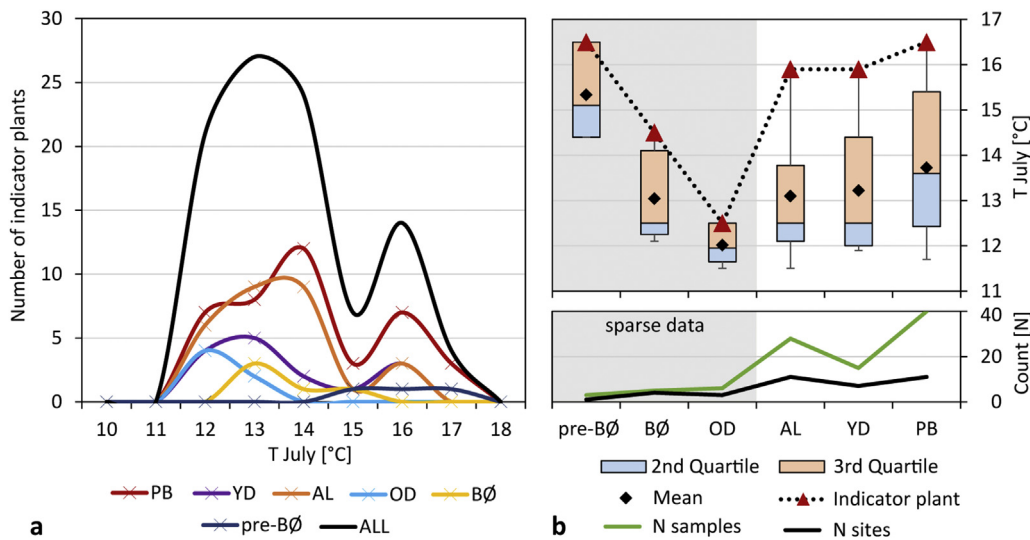


Fig. 6. Statistical distribution of quantified climate indicator plant species for southern Sweden and Denmark. A) Histogram for the number of quantified indicator plants and their T_{July} values for a given time period. B) Relative statistical distribution of T_{July} values for a given time period together with absolute sample counts and number of sites. Note that only the warmest indicator plant(s) (red triangle) would typically be used to represent the minimum July temperature of each climatic period. The time period before OD is based on sparse data only. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

warmer July estimates and a very small spread for the 2nd quartile towards cooler estimates surrounding the median July estimate for the different time periods (Fig. 6b). The high values for the warmest minimum July temperature estimates for AL, YD and PB are clearly above the mean or median July estimate which highlights the importance of using individual indicator species with the highest thermal requirements as climate indicator species for the minimum July temperatures rather than much colder mean or median values.

This is also clearly reflected in the relative distribution of July temperatures in Fig. 6b. Here, the median located between the 2nd

and 3rd quartile indicates a higher number of cold-adapted plant species during the YD including cold-tolerant plants (*Betula nana*, *Empetrum*, *Dryas octopetala*) which are absent during other time periods. The YD also contains several indicator plants with much higher thermal requirements. The comparison of the median, mean and quartiles of available July temperature estimates indicates notable differences in results if they are based on the number or abundance of plants rather than on the warmest indicator species (red triangles). Interestingly though, and despite the widening of the distribution during the YD, the overall mean (black diamonds)

July temperatures calculated over all samples within a time period appears to follow the general transient evolution of the warmest climate indicator plant species (red triangles).

The warmest indicator species (Fig. 6b) from our compilation indicate that with the exception of BØ and OD ($T_{\text{July}} \geq 14$ °C), July temperatures in S-Scandinavia were surprisingly high with ~ 16 °C during the pre-BØ, AL, YD and PB. The presence of plants with a modern northern distribution limit in S-Finland implies high hemiboreal summer temperatures throughout the deglaciation south of the retreating Fennoscandian Ice Sheet.

We have, however, low confidence in the robustness of the pre-AL estimates owing to the sparse data and low number of sites. Both, the BØ and OD, were relatively short climatic periods and are only captured by three to four sites. It is therefore uncertain if the cooler estimates are realistic or simply due to false absence of warmer plant indicators during these short time intervals. The most remarkable results are the presence of unusually warm indicator species already during the pre-BØ. The warmest indicator species of the pre-BØ appears to be as warm as the PB (*Herniaria glabra*, $T_{\text{July}} \geq 16.5$ °C). Relatively high July temperatures for the pre-BØ are supported by the presence of two additional indicator plants (*Silene nutans*, *Alisma plantago-aquatica*) with thermal limits around 14–15 °C. The sparse presence of these plants implies that hemiboreal conditions may already have been reached ~ 15 ka BP. However, more evidence is required to support these results, which are based on a few species only.

Overall, it is interesting to note that the spread of minimum July temperature estimates within the same site and between sites (Fig. 5) is smaller for PB and AL, while the YD stadial shows a widening of the distribution containing both low and high July temperature estimates. This is consistent with the increased relative and absolute presence of cold-adapted plants during stadials (Fig. 4b and c) despite the continued presence of warm indicator species. This implies that rather a change in seasonality (Denton et al., 2005; Schenk et al., 2018) or other factors (Birks and Birks, 2014) define harsh stadial conditions while peak summer temperatures remain high.

5. Discussion

The availability of sites and hence the number of plant macrofossils decreases back in time over the deglaciation. In some cases, the delayed lake formation was due to bodies of stagnant ice (Björck et al., 1996) (Wohlfarth et al., 2017), (Wohlfarth et al., 2018). It is also likely that unstable catchment soils and higher run-off during the early lake development phase delayed the establishment of dense vegetation (Kylander et al., 2013). Turbid waters during this phase were not beneficial for submerged aquatic plant taxa. It is therefore important to note the very early presence of plant indicator species with remarkably high thermal requirements, which are already found in the pre-Bølling at Björkeröds mosse with *Herniaria glabra* ($T_{\text{July}} \geq 16.5$ °C), *Silene nutans* (15.1 °C) and *Alisma plantago-aquatica* (14.4 °C). It should be noted that additional macrofossils at Slotseng have been dated to be pre-Bølling, namely *Lotus corniculatus* (14.5 °C) and *Potamogeton praelongus* (12.5 °C) (Mortensen et al., 2011). These were not included in our study following our strict protocol to exclude samples too close to (inter-)stadial boundaries. Although based on sparse data, this implies that summer temperatures in S-Sweden in the late Pleniglacial around 15 ka BP were already high and close to modern temperatures in the region as soon as the lakes evolved near the southern margin of the Fennoscandian Ice Sheet.

Although more sites across a larger spatial area are required to confirm the pre-Allerød results from this study, it appears that July

temperatures were already high as soon as the lakes started to form. Similar results are known for the deglaciation around Greenland where remarkably high summer temperatures ~ 4 – 7 °C warmer than today were reconstructed as soon as melt waters did no longer reach the lake with the Early Holocene (McFarlin et al., 2018; Axford et al., 2019). As already found by Björck et al. (2002) for southern Greenland, it appears that summer temperatures were high even during the YD in close vicinity to the Greenland ice sheet as well as south of FIS (this study). The high T_{July} estimates for stadial conditions of the pre-BØ and YD found here do also support recent evidence for enhanced surface melting of FIS during stadial cooling in the North Atlantic e.g. during Heinrich Stadial 1–3 (Toucanne et al., 2015; Boswell et al., 2019) or the Baltic Ice Lake drainage at the onset of the YD stadial (Muschitiello et al., 2015b).

Based on high resolution climate model simulations, the high summer temperatures south of FIS and over Eurasia can be explained by atmospheric blocking of westerly winds by FIS during summer (Schenk et al., 2018; Schenk and Vinuesa, 2019). According to these simulations, the blocking is enhanced by an increasing high-pressure ridge over the British Isles in response to strong North Atlantic cooling during the YD (Schenk et al., 2018). The high T_{July} directly south of FIS reconstructed from this study confirms such a mechanism. The overall proxy-model evidence also lends support to the proposed demise of Scotland's last ice fields within the YD stadial (Bromley et al., 2014, 2018), which the authors attribute to warm stadial summers. There is, however, an ongoing debate about the age estimates and time of disappearance of Scotland's last ice fields where a recent study by Lowe et al. (2019) suggests a termination after the YD.

Although more accurate age estimates for ice sheets margins are required, the evidence for high stadial July temperatures in this and previous studies (e.g. Björck et al., 2002; Birks and Birks, 2014; Schenk et al., 2018; Kobe et al., 2019) imply at least a high potential for stadial ice melting in agreement with increased stadial sediment discharge through the British Channel (Toucanne et al., 2015; Boswell et al., 2019). The extreme seasonality with very short stadial warm seasons (Schenk et al., 2018) may however limit the overall decrease in glacial mass balance independent from high peak summer temperatures.

The continued and widespread presence of warm climate indicator species during the YD is inconsistent with the July cooling inferred from some chironomid studies (Heiri et al., 2014; Renssen et al., 2015; Muschitiello, 2015; Wohlfarth, 2017, 2018). However, recent studies show that chironomids infer considerably higher stadial July temperatures of ~ 15 °C for the YD in agreement with our climate indicator species (Fig. 6b) when chironomid reconstructions are based on a continental rather than oceanic training set (Pióciennik et al., 2011). This is consistent with the multi-training set comparison of recent studies (Engels et al., 2014; Pliik et al., 2019; Luoto et al., 2019; Kotrys et al., 2019) which show that chironomids yield considerably higher temperatures when they are inferred from continental training sets.

Because July temperatures are already high with up to ~ 16 °C during AL and YD in our compilation, there is only a small additional warming for the onset of the Holocene in the PB. There is, however, clear evidence that most sites now shift to indicator species with high temperature requirements during the PB with an abrupt decrease in the number of cold-adapted plants compared to the YD (Fig. 4b). This could imply that site-specific factors became less important possibly due to longer rather than warmer summers with the onset of the Holocene.

There is, however, still a debate as to what extent the Preboreal in the region had already reached full interglacial conditions since the FIS was still present around 11 ka BP (Fig. 1) (Hughes et al.,

2016). It has been hypothesized that the onset of warming in the early Holocene was delayed by around one and a half millennia in NW-Russia and the eastern Baltic region possibly due to continued anticyclonic blocking of westerly winds over the retreating FIS bringing cooler air with ^{18}O -depleted precipitation from the Barents Sea (Subetto et al., 2008; Wohlfarth et al., 2002, 2007; Lauterbach et al., 2011). The continental rather than westerly dominance of regional wind systems appears to have extended as far west as southern Sweden as a similarly delayed ^{18}O -signal has also been found in southern Sweden (Hammarlund et al., 2003) for the early Holocene. Based on plant indicator species from the Blekinge Province in SE-Sweden, T_{July} were unusually warm throughout the Lateglacial and the Preboreal. It is hence likely that the delayed ^{18}O -signal either reflects winter to spring precipitation (thermal fractionation) or that the continued dominance of blocking with easterly winds advected generally more ^{18}O -enriched precipitation than westerly winds during summer (source region effect).

The comparison of 15 sites within a region, as done here, provides additional useful information beyond focusing only on the warmest indicator species. The widening of the species distribution with a relative increase of cold-adapted heliophytes during stadials coincides with a continued presence of warm indicator plants and can be interpreted as a shift to an overall colder stadial climate but with short warm summers. This is consistent with the hypothesis (Denton et al., 2005) and climate modelling results (Schenk et al., 2018) of increased seasonality and a shift to a more continental climate during the YD, and possibly other stadials. The heterogeneous presence or absence of indicator plants during the YD at sites within a small region could imply that site-specific factors play a crucial role during extreme stadial climate states. Such a shift to a continental climate with extreme seasonality with site-specific heterogeneity could also explain recent evidence for divergent constraints and debate on the (de-)glaciation of Scotland during the YD: On the one hand, warm summers during the YD appear to have triggered the demise of Scotland's last ice fields within the YD stadial (Bromley et al., 2014, 2018) while on the other hand spatially restricted plateau ice fields may have re-emerged locally (Chandler et al., 2019).

6. Conclusion

In the first part of this study, we extended the list of minimum July temperature proxies based on climate indicator plant species following the procedure of previous work (Väliranta et al., 2015; Schenk et al., 2018). We define the minimum July temperature for a given indicator species based on their *common northern distribution limit* in Finland. As part of the update, we applied a strict selection process and removed problematic indicator species that have no clear distribution limit or that cannot be distinguished from other species with different thermal requirements. In total, we provide $N = 62$ different indicator species that cover a minimum July temperature range from $11\text{ }^{\circ}\text{C}$ to $16.7\text{ }^{\circ}\text{C}$ with a median (mean) potential warm bias of $0.6\text{ }^{\circ}\text{C}$ ($0.9\text{ }^{\circ}\text{C}$). Our covered temperature gradient is comparable to the Finnish lake training set for chironomids which covers $11.3\text{--}17.1\text{ }^{\circ}\text{C}$ (Luoto et al., 2010, 2019). A strong limitation of the indicator approach remains the scarcity of samples typically found in sediment cores. There is, however, a strong potential for future studies to make use of the definition of minimum thermal limits to plant species identified by ancient DNA analysis of lake sediments (Parducci et al., 2019) in addition to traditional plant micro- or macrofossils.

In the second part of this study, we compiled and quantified $N = 96$ climate indicator plant species from 15 sites that allowed us

to reconstruct minimum July temperatures in Denmark and S-Sweden for ~ 15 to 11 ka BP. Although the number of sites and hence indicator species is very low during the pre-BØ, BØ and OD, the presence of indicator species with high thermal requirements such as *Herniaria glabra* ($T_{\text{July}} \geq 16.5\text{ }^{\circ}\text{C}$), *Silene nutans* ($15.1\text{ }^{\circ}\text{C}$) or *Alisma plantago-aquatica* ($14.4\text{ }^{\circ}\text{C}$) at Björkerödsmosse and possibly *Lotus corniculatus* ($14.5\text{ }^{\circ}\text{C}$) at Slotseng, indicates near-modern July temperatures even by ~ 15 ka BP in close vicinity to the FIS margin at that time. We also find clear evidence for equally high July temperatures during the YD stadial of at least $\sim 14\text{ }^{\circ}\text{C}$ and possibly up to $\sim 16\text{ }^{\circ}\text{C}$ consistent with high summer temperatures found in previous studies (e.g. Birks and Birks, 2014; Schenk et al., 2018).

Overall, our results of an surprisingly early emergence of high Lateglacial summer temperatures together with high stadial summer temperatures underline the clear need to more thoroughly analyse and discuss the problem of how extreme seasonality or other parameters may affect various July proxy-reconstructions differently during the last deglaciation and in particular during stadial conditions. While climate simulations can provide strong evidence for a shift to extreme seasonal changes and quantify temperatures for long-lasting severe winters with a narrow window for short warm stadial summers (Schenk et al., 2018), the simulation's validity is dependent on a reliable quantification of peak summer temperatures from proxy data. We suggest that climate indicator plant species can play an important role in identifying suitable training sets for chironomids and other proxies during the Lateglacial regarding peak summer temperatures.

Data availability

All datasets used or constructed in this study are publically available. For the compilation of paleo-vegetation and July temperature reconstructions, see Schenk et al. (2020) and Supplementary Data A. Previously unpublished macrofossils by O. Bennike are provided in Supplementary Data B. The list of climate indicator plant species with their July temperatures at the common northern distribution limit are accessible from Schenk and Väliranta (2020) and Supplementary Data C.

Declaration of competing interest

The authors declare no competing financial interests.

CRediT authorship contribution statement

Frederik Schenk: Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Validation, Formal analysis, Investigation, Visualization. **Ole Bennike:** Validation, Investigation, Data curation, Writing - review & editing. **Minna Väliranta:** Methodology, Validation, Investigation, Writing - review & editing. **Rachael Avery:** Visualization, Writing - review & editing. **Svante Björck:** Writing - review & editing. **Barbara Wohlfarth:** Conceptualization, Methodology, Investigation, Validation, Writing - original draft.

Acknowledgements

We are very grateful to the many colleagues who have, over many decades, collected and identified plant macrofossils which form the basis of our study. This work was supported by the Swedish Research Council (VR 2015-04418). The work contributes to the Swedish-Finnish *Arctic Avenue* spearhead project, a collaboration between Stockholm University and the University of Helsinki.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2020.106243>.

References

- Ahmed, E., et al., 2018. Archaeal community changes in Lateglacial lake sediments: evidence from ancient DNA. *Quat. Sci. Rev.* 181, 19–29. <https://doi.org/10.1016/j.quascirev.2017.11.037>.
- Andrén, T., et al., 2011. In: Harff, J., Björck, S., Hoth, P. (Eds.), *The Development of the Baltic Sea Basin during the Last 130 Ka. The Baltic Sea Basin*. Berlin/Heidelberg, Springer, pp. 75–97.
- Atkinson, T.C., et al., 1986. In: Berglund, B.E. (Ed.), *Handbook of Holocene Paleocology and Paleohydrology*. Wiley, J. & Sons Ltd., Chichester.
- Atkinson, T.C., et al., 1987. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325, 587–592.
- Axford, Y., et al., 2019. Holocene temperature history of northwest Greenland – with new ice cap constraints and chironomid assemblages from Deltasø. *Quat. Sci. Rev.* 215, 160–172. <https://doi.org/10.1016/j.quascirev.2019.05.011>.
- Bennike, O., Mortensen, M.F., 2018. A multi-disciplinary macrofossil study of late glacial to early Holocene sediments from Sønder Kobberdam, Hareskovene, Denmark. *Bull. Geol. Soc. Den.* 66, 113–122.
- Bennike, O., 1995. Palaeoecology of two lake basins from Disko, West Greenland. *J. Quat. Sci.* 10, 149–155.
- Bennike, O., et al., 2004. Reinvestigation of the classic late-glacial Bølling Sø sequence, Denmark: chronology, macrofossils, Cladocera and chydorid ephippia. *J. Quat. Sci.* 19, 465–478.
- Berglund, B.E., 1966. Late-Quaternary vegetation in eastern Blekinge, south-eastern Sweden. *Opera Bot.* 12 (1), 5–180.
- Berglund, B.E., et al., 1994. Late Weichselian environmental change in southern Sweden and Denmark. *J. Quat. Sci.* 9 (2), 127–132.
- Berglund, B.E., et al. (Eds.), 1996. *Palaeoecological Events during the Last 15,000 Years*. Wiley & Sons, Chichester.
- Bigler, C., et al., 2002. Quantitative multiproxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. *Holocene* 12 (4), 481–496.
- Birks, H.H., et al., 1998. Numerical tools in palaeolimnology - progress, potentialities, and problems. *J. Paleolimnol.* 20, 307–332.
- Birks, H.J.B., 1995. *Quantitative palaeoenvironmental reconstructions. Statistical Modelling of Quaternary Science Data*. D. Maddy and J. S. Brew Cambridge, Quat. Res. Assoc. 161–254.
- Birks, H.H., Birks, H.J.B., 2014. To what extent did changes in July temperature influence late glacial vegetation patterns in NW-Europe? *Quat. Sci. Rev.* 106, 262–277.
- Björck, S., Digerfeldt, G., 1991. Allerød- Younger Dryas sea level changes in southwestern Sweden and their relation to the Baltic Ice Lake development. *Boreas* 20, 115–133. <https://doi.org/10.1111/j.1502-3885.1991.tb00301.x>.
- Björck, S., 1995. A review of the history of the Baltic Sea 13.0 to 8.0 ka BP. *Quat. Int.* 27, 19–40.
- Björck, S., et al., 1996. Synchronised terrestrial-atmospheric deglacial records around the North Atlantic. *Science* 274, 1155–1160.
- Björck, S., et al., 2002. Anomalously mild Younger Dryas summer conditions in southern Greenland. *Geology* 30, 427–430.
- Bos, H., 1998. Aspects of lateglacial-early Holocene vegetation development in western Europe, 10, 240. Faculty of Biology, Utrecht, University of Utrecht. LPP Contribution Series.
- Bos, J.A.A., et al., 2004. Flora, fauna and climate of Scotland during the Weichselian Middle Pleniglacial - palynological, macrofossil and coleopteran investigations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 204, 65–100.
- Boswell, S.M., et al., 2019. Enhanced surface melting of the fennoscandian ice sheet during periods of North Atlantic cooling. *Geology* 47 (7), 664–668. <https://doi.org/10.1130/G46370.1>.
- Brinkkemper, O., et al., 1987. Palaeoecological study of a middle-pleniglacial deposit from tilligte, The Netherlands. *Rev. Palaeobot. Palynol.* 51, 235–269.
- Broecker, W.S., 1998. Paleocirculation during the last deglaciation: a bipolar seesaw? *Paleoceanography* 13, 119–121.
- Bromley, G.R.M., et al., 2014. Younger Dryas deglaciation of Scotland driven by warming summers. *Proc. Natl. Acad. Sci. Unit. States Am.* 111, 6215–6219.
- Bromley, G.R.M., et al., 2018. Interstadial rise and younger Dryas demise of Scotland's last ice fields. *Paleoceanogr. Palaeoclimatol.* 33 (4), 412–429. <https://doi.org/10.1002/2018PA003341>.
- Chandler, B., et al., 2019. A spatially-restricted Younger Dryas plateau icefield in the Gaick, Scotland: reconstruction and palaeoclimatic implications. *Quat. Sci. Rev.* 211, 107–135. <https://doi.org/10.1016/j.quascirev.2019.03.019>.
- Coope, G.R., 1986. *Coleoptera Analysis. Handbook of Holocene Paleocology and Paleohydrology*. B. E. Berglund. Wiley & Sons, Chichester, pp. 703–714.
- Coope, G.R., Lemdahl, G., 1995. Regional differences in the Lateglacial climate of northern Europe based on coleopteran analysis. *J. Quat. Sci.* 10 (4), 391–395.
- Coope, G.R., et al., 1998. Temperature gradients in northern Europe during the last glacial-Holocene transition (14-9 kyr BP) interpreted from coleopteran assemblages. *J. Quat. Sci.* 13 (5), 419–433.
- Denton, G., et al., 2005. The role of seasonality in abrupt climate change. *Quat. Sci. Rev.* 24, 1159–1182.
- Engels, S., et al., 2014. A comparison of three Eurasian chironomid-climate calibration datasets on a W-E continentality gradient and the implications for quantitative temperature reconstructions. *J. Paleolimnol.* 2014 (51), 529–547. <https://doi.org/10.1007/s10933-014-9772-8>.
- Fischer, A., et al., 2013. Dating the Trollesgave site and the Bromme culture e chronological fix-points for the Lateglacial settlement of Southern Scandinavia. *J. Archaeol. Sci.* 40 (12), 4663–4674. <https://doi.org/10.1016/j.jas.2013.06.026>.
- Guiot, J., 1990. Methodology of palaeoclimatic reconstruction from pollen in France. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 80, 49–69.
- Hammarlund, D., Lemdahl, G., 1994. A Late Weichselian stable isotope stratigraphy compared with biostratigraphical data: a case study from southern Sweden. *J. Quat. Sci.* 9 (1), 13–31.
- Hammarlund, D., et al., 2003. Holocene changes in atmospheric circulation recorded in the oxygen-isotope stratigraphy of lacustrine carbonates from northern Sweden. *Holocene* 12 (3), 339–351.
- Heiri, O., et al., 2014. Validation of climate model-inferred regional temperature change for late-glacial Europe. *Nat. Commun.* 5, 4914.
- Helmens, K.F., et al., 2007. Present-day temperatures in northern Scandinavia during the last glaciation. *Geology* 35, 987–990.
- Houmark-Nielsen, M., Kjaer, K.H., 2003. Southwest Scandinavia, 40-15 kyr BP: palaeogeography and environmental change. *J. Quat. Sci.* 18, 1–18.
- Houmark-Nielsen, M., et al., 2005. De seneste 150.000 år i Danmark. *Geovidden - Geologi og geografi* 2, 1–20.
- Hughes, A.L.C., et al., 2016. The last Eurasian ice sheets – a chronological database and time-slice reconstruction, DATED-1. *Boreas* 45, 1–45.
- Hultén, E., Fries, M., 1986. *Atlas of North European Vascular Plants: North of the Tropic of Cancer*, vols. 1–3. Königstein, Koeltz.
- Hultén, E., 1950. *Atlas Över Växternas Utbredning I Norden : Fanerogamer Och Ormbunksväxter = Atlas of the Distribution of Vascular Plants in Northwestern Europe. Generalstabens Litografiska Anstalt, Stockholm*, p. 512.
- Isarin, R.F.B., Bohncke, S.J.P., 1999. Mean July temperatures during the Younger Dryas in northwestern and central Europe as inferred from climate indicator plant species. *Quat. Res.* 51, 158–173.
- Iversen, J., 1954. The Late-Glacial flora of Denmark and its relation to climate and soil. *Danmarks Geologiske Undersøgelse II* (80), 87–119.
- Iversen, J., 1964. Plant Indicators of Climate, Soil, and Other Factors during the Quaternary. *Warsaw Report VI: 421–428. International Quaternary Association (INQUA) Congress*.
- Jackson, S.T., Williams, J.W., 2004. Modern analogues in quaternary paleoecology: here today, gone tomorrow? *Annu. Rev. Earth Planet. Sci.* 32, 495–537.
- Johansen, A.C., 1904. *Om Den Fossile Kvarterare Molluskfauna I Danmark Og Dens Relationer Til Forandringer I Klimaet, Land- Og Ferskvandsmolluskfaunaen. Gyldendalske Boghandel, Copenhagen*, p. 136.
- Juggins, S., 2013. Quantitative reconstructions in palaeolimnology: new paradigm or sick science? *Quat. Sci. Rev.* 64, 20–23.
- Kaiser, K., et al., 2009. Palaeopedological marker horizons in northern central Europe: characteristics of lateglacial ussello and finow soils. *Boreas* 38 (3), 591–609. <https://doi.org/10.1111/j.1502-3885.2008.00076.x>.
- Kaiser, K., et al., 2018. A submerged pine forest from the early Holocene in the Mecklenburg Lake District, northern Germany. *Boreas* 47 (3), 910–925. <https://doi.org/10.1111/bor.12314>.
- Kobe, F., et al., 2019. Lateglacial and early Holocene environments and human occupation in Brandenburg, eastern Germany. *Geo. Environ. Sustain.* 12 (2), 132–147. <https://doi.org/10.24057/2071-9388-2018-50>.
- Kolstrup, E., 1979. Herbs as July temperature indicators for parts of the pleniglacial and late-glacial in The Netherlands. *Geol. Mijnbouw* 58, 377–380.
- Kolstrup, E., 1980. Climate and stratigraphy in northwestern Europe between 30,000 B.P. and 13,000 B.P., with special reference to The Netherlands. *Meded. Rijks Geol. Dienst* 32–15, 181–253.
- Kotrys, B., et al., 2019. Expanding the Swiss-Norwegian chironomid training set with Polish data. *Boreas* 49 (1), 89–107. <https://doi.org/10.1111/bor.12406>.
- Kylander, M.E., Klaminder, J., Wohlfarth, B., Löwemark, L., 2013. Geochemical responses to paleoclimatic changes in southern Sweden since the late glacial: the Hässeldala Port lake sediment record. *J. Paleolimnol.* 50, 57–70. <https://doi.org/10.1007/s10933-013-9704-z>.
- Lampinen, R., Lahti, T., 2019. *Kasviatlas 2018. - Helsingin Yliopisto, Luonnontieteellinen Keskusmuuseum. Levinneisyyskartat osoitteessa, Helsinki*. <http://koivu.luomus.fi/kasviatlas>.
- Larocque, I., Bigler, C., 2004. Similarities and discrepancies between chironomid-diatom-inferred temperature reconstructions through the Holocene at Lake 850, northern Sweden. *Quat. Int.* 122, 109–121.
- Lauterbach, et al., 2011. Multi-proxy evidence for early to mid-Holocene environmental and climatic changes in northeastern Poland. *Boreas* 40, 57–72. <https://doi.org/10.1111/j.1502-3885.2010.00159.x>.
- Lemdahl, G., 1988. *Palaeoclimatic and Palaeoecological Studies Based on Subfossil Insects from Late Weichselian Sediments in Southern Sweden (Thesis). LUNDQUA*.
- Lemdahl, G., et al., 2014. Lateglacial insect assemblages from the Palaeolithic site Slotseng : new evidence concerning climate and environment in SW Denmark. *Quat. Int.* 341, 172–183.
- Lieberg-Jönsson, B., 1988. *Thesis. The Late Weichselian Macrofossil Flora in Western Skåne, Southern Sweden*, vol. 24. LUNDQUA.
- Lowe, et al., 2019. On the timing of retreat of the Loch lomond ("Younger Dryas") readvance icefield in the SW scottish highlands and its wider significance. *Quat.*

- Sci. Rev. 219, 171–186. <https://doi.org/10.1016/j.quascirev.2019.06.034>.
- Lowe, J.J., et al., 1994. Climatic changes in areas adjacent to the North-atlantic during the last glacial-interglacial transition (14-9 ka Bp) - a contribution to Igcp-253. *J. Quat. Sci.* 9 (2), 185–198.
- Lowe, J.J., et al., 1995. Direct comparison of UK temperatures and Greenland snow accumulation rates, 15,000 to 12,000 Years ago. *J. Quat. Sci.* 10 (2), 175–180.
- Lundqvist, J., Wohlfarth, B., 2001. Timing and east-west correlation of south Swedish ice marginal lines during the Late Weichselian. *Quat. Sci. Rev.* 20, 1127–1148.
- Luoto, T., et al., 2010. Temperature and effective moisture variability in southern Finland during the Holocene quantified with midge-based calibration models. *J. Quat. Sci.* 25 (8), 1317–1326.
- Luoto, T.P., Kotrys, B., Pióciennik, M., 2019. East European chironomid-based calibration model for past summer temperature reconstructions. *Clim. Res.* 77, 63–76. <https://doi.org/10.3354/cr01543>.
- Magyari, E.K., et al., 2019. Warm Younger Dryas summers and early late glacial spread of temperate deciduous trees in the Pannonian Basin during the last glacial termination (20-9 kyr cal BP). *Quat. Sci. Rev.* 225, 105980.
- McFarlin, J.M., et al., 2018. Pronounced summer warming in northwest Greenland during the Holocene and last interglacial. *Proc. Natl. Acad. Sci. Unit. States Am.* 115 (25), 201720420. <https://doi.org/10.1073/pnas.1720420115>.
- McManus, J.F., Francois, R., Gherardi, J.-M., Keigwin, L.D., Brown-Leger, S., 2004. Collapse and rapid resumption of Atlantic meridional circulation linked to deglacial climate changes. *Nature* 428, 834–837.
- Mortensen, M.F., et al., 2011. Late-glacial vegetation development in Denmark—new evidence based on macrofossils and pollen from Slotseng, a small-scale site in southern Jutland. *Quat. Sci. Rev.* 30, 2,534–3,550.
- Mortensen, M.F., et al., 2014b. Living on the good soil: relationships between soils, vegetation and human settlement during the late Allerød period in Denmark. *Veg. Hist. Archaeobotany* 23 (3), 195–205.
- Mortensen, M.F., Henriksen, P.S., Christensen, C., Petersen, P.V., Olsen, J., 2014a. Vegetation development in southeast Denmark during the Weichselian late Glacial – palaeoenvironmental studies close to the Palaeolithic site of Hasselø. *Danish J. Archaeol.* 3, 48–66.
- Muschitiello, et al., 2015a. Fennoscandian freshwater control on Greenland hydroclimate shifts at the onset of the Younger Dryas. *Nat. Commun.* 6, 8939. <https://doi.org/10.1038/ncomms9939>.
- Muschitiello, et al., 2015b. Timing of the first drainage of the Baltic Ice Lake synchronous with the onset of Greenland stadial 1. *Boreas* 45 (2), 322–334. <https://doi.org/10.1111/bor.12155>.
- Nilsson, T., 1935. Die pollenanalytische Zonengliederung der spät- und post-glazialen Bildungen Schonens. *GFF (Geol. Foren. Stockh. Forh.)* 57, 385–562.
- Parducci, L., et al., 2019. Shotgun environmental DNA, pollen, and macrofossil analysis of lateglacial lake sediments from southern Sweden. *Front. Ecol. Evol.* 7, 189.
- Pliik, A., et al., 2019. Chironomid-based temperature reconstruction for the Eemian Interglacial (MIS 5e) at Sokli, northeast Finland. *J. Paleolimnol.* 61, 355–371. <https://doi.org/10.1007/s10933-018-00064-y>.
- Pióciennik, M., et al., 2011. Chironomidae (Insecta: Diptera) succession in Żabieniec bog and its palaeo-lake (central Poland) through the late Weichselian and Holocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 307, 150–167. <https://doi.org/10.1016/j.palaeo.2011.05.010>.
- Rach, O., et al., 2014. Delayed hydrological response to Greenland cooling at the onset of the Younger Dryas in western Europe. *Nat. Geosci.* 7 (2), 109–112. <https://doi.org/10.1038/ngeo2053>.
- Rach, O., et al., 2017. A dual-biomarker approach for quantification of changes in relative humidity from sedimentary lipid D/H ratios. *Clim. Past* 13 (7), 741–757. <https://doi.org/10.5194/cp-13-741-2017>.
- Renssen, H., et al., 2015. Multiple causes of the Younger Dryas cold period. *Nat. Geosci.* 8, 946–949.
- Schenk, F., Vinuesa, R., 2019. Enhanced large-scale atmospheric flow interaction with ice sheets at high model resolution. *Results Eng.* 3, 100030. <https://doi.org/10.1016/j.rineng.2019.100030>.
- Schenk, F., et al., 2018. Warm summers during the Younger Dryas cold reversal. *Nat. Commun.* 9, 1634.
- Schenk, F., Bennike, O., Välranta, M., Avery, R., Björck, S., Wohlfarth, B., 2020. Compilation of Local Vegetation and July Temperature Reconstructions for Southern Scandinavia 15,000 to 11,000 Years Ago. *Bolin Centre Database*. <https://doi.org/10.17043/schenk-2020-paleovegetation>.
- Schenk, F., Välranta, M., 2020. Definition of Climate Indicator Plant Species and Their Common Minimum July Temperature Limits. *Bolin Centre Database*. <https://doi.org/10.17043/schenk-2020-indicatorplants>.
- Stouffer, R.J., et al., 2006. Investigating the causes of the response of the thermohaline circulation to past and future climate changes. *J. Clim.* 19, 1365–1387.
- Stroeven, A., et al., 2016. Deglaciation of Fennoscandia. *Quat. Sci. Rev.* 147, 91–121.
- Subetto, D.A., et al., 2008. Climate and environment on the Karelian Isthmus, northwestern Russia, 13000-9000 cal. yrs BP. *Boreas* 31 (1), 1–19. <https://doi.org/10.1111/j.1502-3885.2002.tb01051.x>.
- Theuerkauf, M., Joosten, H., 2012. Younger Dryas cold stage vegetation patterns of central Europe – climate, soil and relief controls. *Boreas* 41, 391–407.
- Thompson, et al., 2012. Quantitative estimation of climatic parameters from vegetation data in North America by the mutual climatic range technique. *Quat. Sci. Rev.* 51, 18–39. <https://doi.org/10.1016/j.quascirev.2012.07.003>.
- Toucanne, S., et al., 2015. Millennial-scale fluctuations of the European Ice Sheet at the end of the last glacial, and their potential impact on global climate. *Quat. Sci. Rev.* 123, 113–133. <https://doi.org/10.1016/j.quascirev.2015.06.010>.
- Turner, F., et al., 2013. Lateglacial/early Holocene fluvial reactions of the Jeetzel river (Elbe valley, northern Germany) to abrupt climatic and environmental changes. *Quat. Sci. Rev.* 60, 91–109. <https://doi.org/10.1016/j.quascirev.2012.10.037>.
- Unger, H., 1981. Ein weit verbreiteter Hiatus in spätglazialen Seesedimenten: mögliche Ursache für Fehlinterpretation von Pollendiagrammen und Hinweis auf klimatisch verursachte Seespiegelbewegungen. *Eiszeitalt. Ggw.* 31, 91–107.
- Välranta, M., et al., 2009. Early Weichselian interstadial (MIS 5c) summer temperatures were higher than today in northern Fennoscandia. *Quat. Sci. Rev.* 28, 777–782.
- Välranta, M., et al., 2015. Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northern Europe. *Nat. Commun.* 6, 6809.
- Venäläinen, A., et al., 2005. A Basic Climate Data Set 1961-2000—Description and Illustrations. Reports 5. Finnish Meteorological Institute.
- Wohlfarth, B., et al., 2002. Late-glacial and early Holocene environmental and climatic change at lake tambichozero, southeastern Russian Karelia. *Quat. Res.* 58 (3), 261–272.
- Wohlfarth, B., et al., 2007. Climatic and environmental changes in north-western Russia between 15,000 and 8000 cal yr BP: a review. *Quat. Sci. Rev.* 26, 1871–1883. <https://doi.org/10.1016/j.quascirev.2007.04.005>.
- Wohlfarth, B., et al., 2017. Hässeldala – a key site for Last Termination climate events in northern Europe. *Boreas* 46, 143–161.
- Wohlfarth, B., et al., 2018. Climate and environment in southwest Sweden 15.5-11.3 cal. ka BP. *Boreas* 47, 687–710.