



## Biotic turnover rates during the Pleistocene-Holocene transition



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### ABSTRACT

The Northern Hemisphere is currently warming at the rate which is unprecedented during the Holocene. Quantitative palaeoclimatic records show that the most recent time in the geological history with comparable warming rates was during the Pleistocene-Holocene transition (PHT) about 14,000 to 11,000 years ago. To better understand the biotic response to rapid temperature change, we explore the community turnover rates during the PHT by focusing on the Baltic region in the southeastern sector of the Scandinavian Ice Sheet, where an exceptionally dense network of microfossil and macrofossil data that reflect the biotic community history are available. We further use a composite chironomid-based summer temperature reconstruction compiled specifically for our study region to calculate the rate of temperature change during the PHT. The fastest biotic turnover in the terrestrial and aquatic communities occurred during the Younger Dryas-Holocene shift at 11,700 years ago. This general shift in species composition was accompanied by regional extinctions, including disappearance of mammoth (*Mammuthus primigenius*) and reindeer (*Rangifer tarandus*) and many arctic-alpine plant taxa, such as *Dryas octopetala*, *Salix polaris* and *Saxifraga aizoides*, from the region. This rapid biotic turnover rate occurred when the rate of warming was 0.17 °C/decade, thus slightly lower than the current Northern Hemisphere warming of 0.2 °C/decade. We therefore conclude that the Younger Dryas-Holocene shift with its rapid turnover rates and associated regional extinctions represents an important palaeoanalogue to the current high latitude warming and gives insights about the probable future turnover rates and patterns of the terrestrial and aquatic ecosystem change.

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## 1. Introduction

The Northern Hemisphere has warmed rapidly over the last century, with a mean warming trend of 0.2 °C per decade during the last 40 years (Smith et al., 2015). Comprehensive meta-analyses

of changes in plant, mammal, bird, fish, and invertebrate communities show that this warming is causing a massive reorganization of terrestrial and aquatic biota with rapidly changing species abundance, immigration, speciation, and extinctions resulting in emergence of communities with novel species compositions (Dawson et al., 2011; Dornelas et al., 2014). Associated with the ongoing state-shift has been an increasing interest in ecology to investigate and measure the species turnover rates. Biotic community turnover, a central concept in ecology since the seminal work by Whittaker (1960), reflects the changes in species abundance and composition over a spatial or temporal gradient. It thus corresponds with the beta diversity in Whittaker (1977) and many studies have focused on analyzing the spatial turnover rates, or beta

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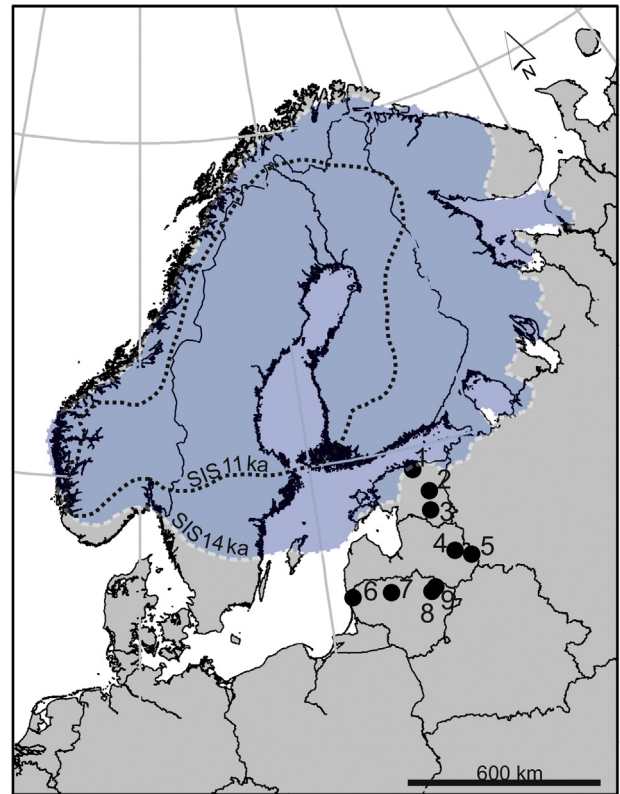
E-mail addresses: [normunds.stivrins@helsinki.fi](mailto:normunds.stivrins@helsinki.fi) (N. Stivrins), [janne.soininen@helsinki.fi](mailto:janne.soininen@helsinki.fi) (J. Soininen), [leeli.amon@ttu.ee](mailto:leeli.amon@ttu.ee) (L. Amon), [sonia.fontana@biologie.uni-goettingen.de](mailto:sonia.fontana@biologie.uni-goettingen.de) (S.L. Fontana), [grazyna.gryguc@geo.lt](mailto:grazyna.gryguc@geo.lt) (G. Gryguc), [majja.heikkila@helsinki.fi](mailto:majja.heikkila@helsinki.fi) (M. Heikkilä), [oliver.heiri@ips.unibe.ch](mailto:oliver.heiri@ips.unibe.ch) (O. Heiri), [kisieliene@geo.lt](mailto:kisieliene@geo.lt) (D. Kisieliene), [triin.reitalu@ttu.ee](mailto:triin.reitalu@ttu.ee) (T. Reitalu), [stancikaite@geo.lt](mailto:stancikaite@geo.lt) (M. Stančikaitė), [siim.veski@ttu.ee](mailto:siim.veski@ttu.ee) (S. Veski), [heikki.seppa@helsinki.fi](mailto:heikki.seppa@helsinki.fi) (H. Seppä).

diversity, of species assemblages (Arita and Rodríguez, 2002; Gotelli et al., 2009; Koleff et al., 2003; Mittelbach, 2012; Plotkin and Muller-Landau, 2002; Rodríguez and Arita, 2004).

In addition to spatial biotic turnover, temporal trends in biotic turnover have been empirically investigated using long-term observation-based species time series records for terrestrial (Aggemyr and Cousins, 2012; Evans et al., 2008; Pergl et al., 2012; White, 2004) and aquatic communities (Korhonen et al., 2010; Shurin et al., 2007). Such observation-based studies of temporal biotic turnover usually span only at most a few decades and can be insufficient to account for slow ecological processes, such as extinction debt or migration credit, that may influence the turnover rates over decadal or centennial timescales (Dornelas et al., 2014). Palaeoecological records are rich sources to investigate past changes in terrestrial plant and animal communities as well as aquatic plant and phytoplankton communities because they make it possible to reconstruct past biotic community changes and turnover rates over centuries or millennia (Cooper et al., 2015; Jackson and Sax, 2009). Furthermore, palaeoecological records are long enough to reflect regional and global extinction events, which in paleontological and palaeoecological context are often defined as major turnover events. In general, the fossil data unambiguously show that while the current global turnover may be extremely rapid periods of fast species turnover have occurred frequently in the history of the Earth, including periods of particularly massive extinctions (Barnosky, 2008; Barnosky et al., 2011; Plotnick et al., 2016). Palaeoecological studies further show that while the drivers of the turnover events are often ambiguous to detect, biotic turnover results from processes that ultimately trace back to alteration of the abiotic environment causing simultaneous response in multiple species (Blois and Hadly, 2009; Puzachenko and Markova, 2014).

For discerning the biotic turnover and its drivers from fossil and palaeoenvironmental data there are several requirements. Most importantly, precisely dated fossil datasets that reflect the dynamics of past communities and ecosystems are needed. Secondly, to elucidate the drivers of the turnover rates, quantitative data on climate and other environmental factors are necessary. The Pleistocene–Holocene transition (PHT) 14,000–11,000 years ago (14–11 ka BP), during which northern Europe became ice free in tune with the melting of the Scandinavian Ice Sheet (SIS), fulfils these criteria better than most other geological time periods. There exist abundant fossil records and independent quantitative palaeoclimate data over this transition period from various biotic, physical and chemical records. Moreover, independent palaeoclimate records, based for example on Greenland ice core data (Steffensen et al., 2008) and chironomid-based temperature reconstructions from Europe (Heiri et al., 2014), show that the PHT is characterized by rapid warming from the glacial conditions of the late Pleistocene to the interglacial temperature level in the early Holocene, with a general summer warming of 5–6 °C over few centuries. It thus represents the last natural abrupt warming event and provides a critically important opportunity to use fossil data to investigate the biotic response to high-magnitude warming.

Here, we focus on analysing the biotic turnover rates during PHT in the Baltic region (Lithuania, Latvia, and Estonia) in Europe (Fig. 1). This region became gradually ice free during the deglaciation of the SIS from 15 to 13 ka BP ago and we are therefore able to investigate the biotic patterns from the first deglacial colonization of plants and animals to the establishment of the forest in the early Holocene. This area is also special because of a long-lasting project of collecting terrestrial and aquatic fossil records, which now results in an exceptionally dense network of pollen, plant macrofossil and fossil phytoplankton data from sediment cores (Amon, 2012; Amon et al., 2010, 2012, 2014; Amon and Saarse, 2010; Heikkilä



**Fig. 1.** The study area is located in the Baltic region (Estonia, Latvia and Lithuania) that extends from 53 to 60°N and from 21 to 28°E. Location of the sites included in the study: (1) Lake Udriku; (2) Lake Prossa; (3) Lake Nakri; (4) Lake Lielais Svētīņi; (5) Lake Kurjanovas; (6) Lake Kašūciai; (7) Lake Ginkūnai; (8) Bog Juodonys; (9) Lake Petrašiūnai. During the last glaciation, the Baltic region was fully covered by the Scandinavian Ice Sheet (SIS) and became ice free about 15,000–13,000 BP. In the map the dotted lines show the SIS ice margin distribution at 14,000 and 11,000 BP (according to Hughes et al., 2016) that corresponds to the beginning and end of our study time frame.

et al., 2009; Stancikaitė et al., 2004, 2008, 2009, 2015; Stivrins et al., 2014, 2015; Veski et al., 2012). Our aim is to synthesize these data and use them to estimate temporal biotic turnover rates of the terrestrial and aquatic communities and to establish to what extent the climate influenced turnover and regional extinctions of plants and animals during the PHT. We further make use of the recent quantitative summer (July) mean temperature reconstruction based on fossil chironomid remains (Heiri et al., 2014). This reconstruction covers the PHT period and is specifically constructed from our study area. It therefore allows us to directly compare the regional biotic turnover patterns and rates with regional summer temperature rate of change and provides thus a reference point to ongoing climatic warming and its biotic impacts.

## 2. Materials and methods

### 2.1. Data collection

The plant macrofossil, pollen and fossil phytoplankton data are obtained from sediment cores sampled from eight lakes and one bog in the Baltic region (Fig. 1, Supplementary material 1). The size range of selected sites is 2–160 ha. High-quality data are required in terms of consistent site selection, careful field sampling, laboratory and analytical procedures, and taxonomic precision for the use of fossil data for quantitative turnover and diversity analyses (Birks, 2014; Birks et al., 2016). There are tens of lake and bog study sites

available from the region, but many of them have been analyzed with low sample resolution or are too poorly dated to be useful in analyzing biotic turnover rates. After screening the records, nine sites covering the period from 14 to 11 ka BP with most reliable chronology were selected. Descriptions of these sites have been published previously (see Supplementary material 1). Pollen data are available from eight of these sites, plant macrofossil data from nine sites and fossil phytoplankton data from three sites. All cores have been dated using few conventional but mostly AMS radiocarbon datings. The original radiocarbon dates were recalibrated utilizing the IntCal13 calibration dataset (Reimer et al., 2013) with a two  $\sigma$  (95.4%) confidence level and the age-depth models of each sequence were developed using software Bacon 2.2 (Blaauw and Christen, 2011) in the R environment (version 3.0.3) (R Core Team, 2014). In addition, biostratigraphic correlation was used to define the boundaries of major stratigraphic changes between Bølling-Allerød-Younger Dryas and Younger Dryas-Holocene. These levels were identified in pollen, plant macrofossil and lithological features and the ages derived from the Greenland ice core records were assigned to them (Lowe et al., 2008; Rasmussen et al., 2014).

Plant macrofossils are presented as concentration data. The weakness of the plant macrofossil record is scarcity of plant remains in the sediment cores, which results in discontinuous occurrence of the plant taxa in the diagrams. It is likely that such discontinuous occurrence does not reflect real changes in presence of a given taxa in the vicinity of the study site, but is an artefact associated with low concentration of the macrofossils (Birks, 2014). We minimized this effect by pooling together all plant macrofossil data into one composite plant macrofossil diagram for the Baltic countries. To do that, a known age was set for each macrofossil sample. The resulting composite plant macrofossil diagram includes 102 taxa. Such a composite record should come from the same vegetation type in a rather restricted and small region. In our case, this requirement is mostly fulfilled because the dominant vegetation was fairly uniform over the Baltic region during the Late Glacial (Amon, 2012; Amon et al., 2014; Stancikaitė et al., 2009, 2015; Veski et al., 2012).

The percentages of terrestrial pollen taxa for eight sites were calculated using arboreal and non-arboreal pollen sums, excluding pollen and spores of aquatic and wetland plants. Tree pollen that were considered exotic, such as *Alnus*, *Corylus*, *Tilia*, *Quercus*, *Ulmus*, *Fraxinus* and *Carpinus*, were excluded from the data earlier than 11.7 ka BP. Sporadic grains of these pollen types occur in the highly inorganic sediment in the basal part of the cores and are mostly likely washed into the lake from the unvegetated terrain during and after the deglaciation as suggested by Reitalu et al. (2015) and Veski et al. (2012). Occurrence of such redeposited pollen grains is a common problem in the earliest post-glacial sediment sequences in the glaciated regions in eastern and northern Europe.

In addition of using pollen and plant macrofossil data for measuring biotic turnover rates, the evaluation of the regional extinctions of the plant taxa during the PHT was carried out by analysing all published plant macrofossil diagrams in the region. The regional extinctions of terrestrial vascular plant species were defined on the basis of the last occurrence of plant macrofossils of such species which are at present absent in the Baltic region.

The animal communities of the study period can be reconstructed using the fossil bone and dental records from the Baltic region. Such records are too scattered and biased by preservation factors to attempt any detailed or quantitative analysis of turnover patterns. However, there exist tens of bone findings of reindeer (*Rangifer tarandus*) (Ukkonen et al., 2006) and few bone and tooth findings of woolly mammoth (*Mammuthus primigenius*) (Ukkonen et al., 2011) in the region, presumably representing *in situ* findings of these species. These two mammal species went regionally

extinct in the study region and we compare their records to explore whether their Late Glacial occurrences show features which can be related to plant community turnover and rapid climate changes.

To analyse the turnover rates of aquatic biota, we used fossil phytoplankton percentage data. Phytoplankton are primary producers in lakes and their abundance and composition is generally determined by light conditions, temperature and nutrient concentration of a lake (De Senerpont Domis et al., 2013). Hence fossil phytoplankton community reflects aquatic ecosystem changes in the past. The types of phytoplankton remains that can be preserved in the lake sediment cores include chlorophyta (*Botryococcus*, *Pediastrum*, *Scenedesmus* and *Tetraëdron*) and cyanobacteria (*Anabaena*, *Glaucoispira* and *Gloeotrichia*). Diatom valves are generally among the most common fossil phytoplankton types in lake sediments. However, in contrast to Lithuania where majority of the sediment sequences contain diatoms, in Estonia and Latvia diatom remains are rare or absent during the PHT, possibly due to high alkalinity of the lakes (Veski et al., 2012). Due to this preservation issue, diatom data were not included in this study.

Chironomid-based mean July temperature reconstruction ( $T_{July}$ ) for the Baltic region published by Heiri et al. (2014) was used as independent climate proxy to characterize the overall climatic change. Reconstruction of  $T_{July}$  uses a modern chironomid-temperature calibration data set consisting of records from 274 lakes in Norway and Switzerland (Heiri et al., 2011).  $T_{July}$  was reconstructed based on fossil chironomid assemblages from two sites Lake Nakri and Kurjanovas (Fig. 1) using weighted-averaging partial least-squares regression and calibration procedure. As chironomid data can be affected by site-specific factors, a stacked  $T_{July}$  curve was produced to summarize the temperature trends of the Baltic region (Heiri et al., 2014). Dating errors in radiocarbon-dated Late Glacial lake sediment records amount from several decades to a few centuries in most cases. For the Kurjanovas and the Nakri records the situation for individual radiocarbon dates is similar (Amon et al., 2014; Heikkilä et al., 2009). Based on  $T_{July}$  data, we estimated the rate of temperature change per decade without any smoothing or interpolation of the data prior or later. This was done by dividing the temperature difference between two successive data points with the time difference in years and by averaging to decades.

## 2.2. Data analyses

For quantifying local vegetation turnover, we used Sørensen dissimilarity index. Along with the Jaccard index, Sørensen index is one of the most widely used (dis)similarity indices and it is regarded as one of the most effective presence/absence measures (Magurran, 2004). We used Sørensen index also because it allows us to partition total beta diversity ( $\beta_{SOR}$ ) into turnover and nestedness components following Baselga (2010). Sørensen dissimilarity index is calculated by  $\beta_{SOR} = 1 - (2a/(2a + b + c))$ , where 'a' indicates the total number of species present in both samples, 'b' refers to the number of species present only in sample one and 'c' to the number of species present only in sample two. The index ranges from zero to one, where zero indicates that the communities have identical species composition while one indicates that two communities have no shared species and thus full turnover.

Although nine sites contain a record of plant macrofossils, only five of them (Nakri, Lielais Svētīņu, Kurjanovas, Ginkūnai and Kašučiai) have continuous record that covers the whole study period from 14 to 11 ka BP. Data from these five sites were utilised further in the statistical analyses. For the statistical analyses, the data were organized into 300-year bins. Defining the bins is critically important. If the bins are too few and cover a too long time period, important details can be lost; conversely if the bins are



many and short, they contain too few samples and the random fluctuations in the data may be obscured (Birks, 2014). We used 300 years as our bin length as in this way we were able to include all three subregions (Lithuania, Latvia, Estonia) at the same time into the analyses and to ensure an even number of samples (eight) per bin which is important for reliable Sørensen index calculation. To unravel whether the variation in species composition between two successive bins was due to species turnover (i.e., species replacement between samples) or nestedness (i.e., species loss between samples), we used beta diversity partitioning proposed by Baselga (2010). This method partitions the total community dissimilarity into turnover and nestedness components. Three pairwise dissimilarity metrics were calculated: i) Sørensen dissimilarity index ( $\beta_{\text{SOR}}$ ) measures the total variation in species composition between samples accounting for both turnover and nestedness; ii) Simpson dissimilarity index ( $\beta_{\text{SIM}}$ ) accounts for changes in community composition due to species turnover only; and iii) nestedness component ( $\beta_{\text{NES}}$ ), calculated as  $\beta_{\text{SOR}} - \beta_{\text{SIM}}$ , captures community variation due to nestedness. Using presence-absence data, the dissimilarity metrics were calculated using function *beta.pair* in R package *betapart* (Baselga and Orme, 2012). In addition, we calculated Sørensen index and beta diversity partitioning separately for terrestrial and aquatic plant macrofossil data, but the results were not statistically significant (not presented here) probably due to low number of samples or taxa per bin, hence we used the combined macrofossil (terrestrial and aquatic) data that was statistically significant.

Palynological and phytoplankton turnover were estimated by Detrended Canonical Correspondence Analysis (DCCA) with time as the constraining variable. The reason of using DCCA instead of Sørensen index is that the pollen records differ from the plant macrofossil records in some fundamental ways. Unlike the plant macrofossil data, pollen percentages provide relative abundance data. In addition, the source area of pollen is larger, with pollen transported by wind to the sites from tens of kilometres. Thus the pollen records provide a general picture of the vegetation composition, but do not reliably reflect the presence of the plant taxa directly around the study sites. Contrary to plant macrofossil samples which are commonly analyzed continuously throughout the sediment sequence, pollen samples are analyzed within intervals that may vary. Because of this, the number of the pollen samples per time unit at each site can differ, leading to uneven number of pollen samples per given time interval. For DCCA, we used 500-year time intervals that ensured the adequate number of samples within a time interval while we were still able to estimate turnover for relatively short climatic periods. DCCA expresses turnover results in standard deviations (SD) and the turnover can be estimated as the difference between the highest and lowest values for each time sequence (Birks, 2007; Birks and Birks, 2008). A complete turnover of species, with no species in common at either end of the gradient, would have a gradient length of 4 SD (Hill and Gauch, 1980) or 100% of the total changes in sequence. Prior to the analysis, we square-root transformed the datasets, and detrended by segments with no down-weighting of rare taxa and non-linear rescaling. The DCCA was performed individually for each subregion and the results were combined to generate an average palynological and phytoplankton turnover curves for the whole study region. CANOCO 5.04 (ter Braak and Šmilauer, 2012) was used for DCCA.

### 3. Results

The study period begins at 14 ka BP. This dates to the Bølling-Allerød interstadial, a warm period (Fig. 2) during which a rapid post-glacial migration of tree species and forest development in the

southern Baltic region began (Fig. 3) while the northern part remained treeless (Amon, 2012; Amon et al., 2014; Heikkilä et al., 2009). The  $T_{\text{July}}$  increased to  $\sim 14^\circ\text{C}$  at 13.8 ka BP, and remained at this level until a sudden cooling at 12.9–12.7 ka BP to about  $\sim 11^\circ\text{C}$ . This cooling represents the beginning of the Younger Dryas stadial, a cold period which lasted about 1200 years and ended with rapid warming of  $T_{\text{July}}$  to above  $12^\circ\text{C}$  around 11.7 ka BP (Fig. 2a). This warming corresponds with the beginning of the Holocene interglacial, and on the basis of our data, during the first centuries of the Holocene  $T_{\text{July}}$  was still rising, and reached  $15^\circ\text{C}$  by 11.2 ka BP. The change of temperature rate was highest,  $\sim 0.3^\circ\text{C}$  per decade, from 12.85 to 12.5 ka BP, during the Bølling-Allerød-Younger Dryas shift (Fig. 2b). The transition from Younger Dryas to Holocene at 11.7 ka BP was marked by temperature change of  $0.17^\circ\text{C}$  per decade.

Based on DCCA results, the palynological turnover showed generally similar trends in all subregions (Fig. 4). It decreased from 14 to 13.5 to 13–13.5 ka BP and increased at 13–12.5 ka BP, during the Bølling-Allerød-Younger Dryas shift. The values remained low during the Younger Dryas and reached the maximum in two subregions (Estonia and Lithuania) at 11.5–12 ka BP, i.e. during the Younger Dryas-Holocene shift (Fig. 4, Supplementary material 2).

Fossil phytoplankton turnover rates were roughly similar with the palynological turnover trends, with fairly high values during the Bølling-Allerød interstadial from 14 to 13.5 ka BP, lower values at 13.5–12 ka BP, and a minimum during the Younger Dryas (Fig. 5). An increase occurred during the Younger Dryas-Holocene shift at 11.7 ka BP (Supplementary material 3) and the highest turnover rate occurred in the early Holocene at 11.3 ka BP. In the early Holocene, the phytoplankton turnover was comparable to that during the Bølling-Allerød interstadial. Thus the aquatic community turnover during the Younger Dryas-Holocene shift was less marked than the terrestrial one.

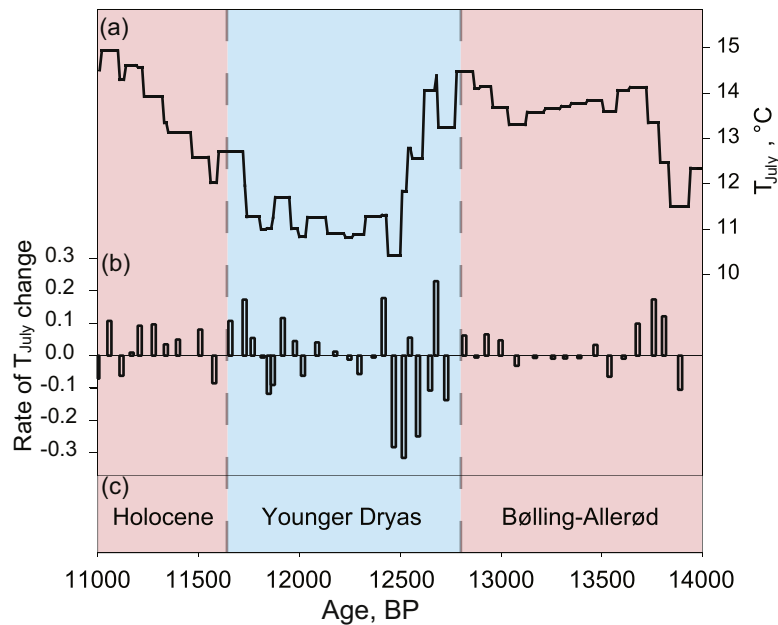
The Sørensen dissimilarity index suggests relatively stable terrestrial plant communities (range 0.43–0.48) from 14 to 13 ka BP (Fig. 5d). No notable increase in the terrestrial vegetation turnover can be observed during the cooling at the Bølling-Allerød-Younger Dryas shift at 13–12.7 ka BP. The turnover rose to a maximum of 0.55 during the Younger Dryas-Holocene shift at 12–11.5 ka BP and decreased afterwards. Thus the highest turnover in the local terrestrial plant communities occurred during the warming of the Younger Dryas-Holocene shift. Beta diversity partitioning analyses using combined data of terrestrial and aquatic taxa revealed that turnover was the dominant beta diversity component ( $r = 0.317$ ;  $p = 0.001$ ), whereas nestedness was negligible ( $r = 0.121$ ;  $p = 0.073$ ) (Supplementary material 4).

## 4. Discussion

### 4.1. The use of palaeoecological data

Before interpreting the results in terms of biotic turnover rate and its drivers, it is necessary to explore the special characteristics of different types of fossil data in biotic turnover analyses. Critical features of the types of fossil data used here are a) the spatial representation of the data, b) the questions of true and false presence and true and false absence of species, c) taxonomical resolution, d) temporal resolution of the data, e) and whether the data should be considered as binary or quantitative data.

Pollen data are generally stratigraphically more detailed than plant macrofossil data. Pollen data are also quantitative, making it possible to investigate the turnover based not only on species presence/absence but on relative abundance. However, the difficulty with the pollen data is that pollen grains are carried by wind and especially in the open, non-forested environment, such as much of the Late Glacial in the Baltic region a part of the fossil



**Fig. 2.** Climate data and the geochronological periods: (a) chironomid based July temperature reconstruction ( $T_{July}$ ) for Baltic region from Heiri et al. (2014); (b) rate of  $T_{July}$  change per decade (based on curve (a)); (c) the geochronological periods Bølling-Allerød, Younger Dryas and the Holocene (Lowe et al., 2008; Rasmussen et al., 2014) and age at the bottom (BP).

pollen do not represent local vegetation, but some pollen grains can be transported by wind over tens or hundreds of kilometres. This phenomenon is reflected in the modern pollen samples, e.g. from N Scandinavia or Svalbard, where tree taxa such as *Pinus* are present in the pollen diagrams with values up to 5–25% although these species are not present (Birks et al., 2016; Seppä, 1998). In pollen data these pollen types can be termed as “false richness” (Birks et al., 2016), similarly as redeposited pollen grains. Consequently, the pollen values of many wind-pollinated plant taxa, for example *Pinus*, *Betula*, and *Alnus* in our diagrams may be partly or fully arrived by long-distance transport and thus do not represent the abundance of such taxa in our study region (Birks, 2008). In general, pollen data from Late Glacial environment provide an approximate picture of the structure and composition of vegetation on regional or landscape-ecological scale, but do not provide firm evidence of the presence of plant species in the catchment or vicinity from where the sediment cores are collected.

To overcome the problem of false presence that would induce misleading turnover results, we used the plant macrofossil data to provide a more local picture of plant communities, as plant macrofossils generally reflect the presence of plant in the catchment or vicinity (few km) from the lakes and bogs reliably. In principle, a plant macrofossil record provides a time series record of plant community composition comparable with a permanent vegetation plot monitored over certain time period and permits analysing temporal plant community turnover around the bogs or lakes. However, there are some important caveats also in plant macrofossil data. First, plant macrofossil data are binary data, as they reflect the presence of plant species but not their abundances (Birks, 2014). In the case of plant macrofossils, the non-zero values almost certainly reflect true presence of a plant species in the local vegetation in contrast to fossil pollen where non-zero values may reflect the presence of the relevant taxon locally or regionally (true presence) or far-distance extra-regional pollen (false presence) (Birks et al., 2016). However, zero values in macrofossil data do not necessarily indicate true absence of species, because zero values in macrofossil data may result either from the macrofossil of the taxon in question not being found in the sediment sample examined

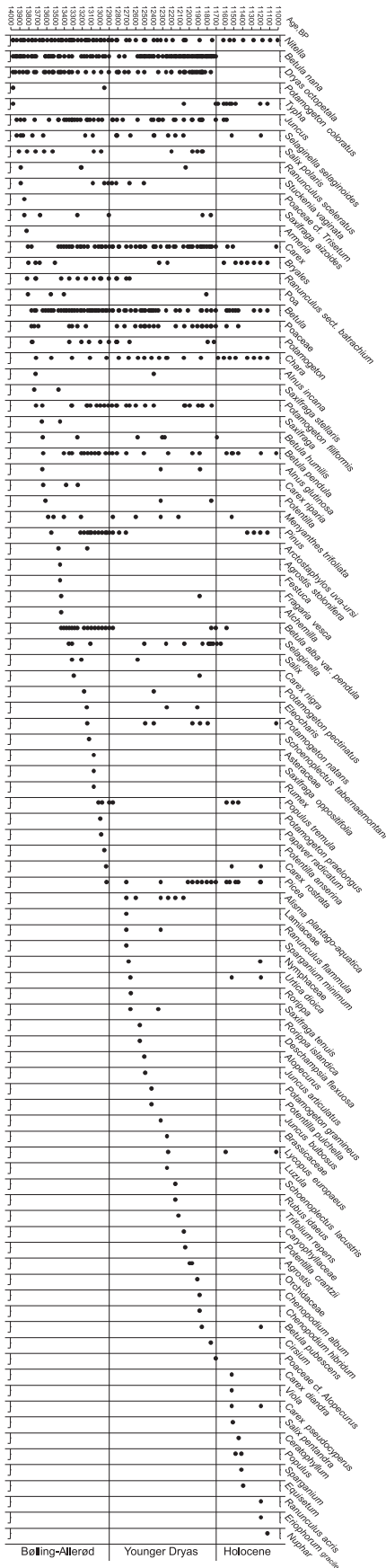
(false absence) or from the genuine absence of the taxon near the site of deposition (true absence). False absences are common in both macrofossil and pollen data whereas false presences are rare in macrofossil data but can be common in pollen data (Birks, 2014; Birks and Birks, 2014).

Associated with the false absence of macrofossils is the scarcity of plant remains in the sediment cores, which results in the discontinuous occurrence of the plant taxa in the diagrams. It is very likely that such discontinuous occurrence does not reflect a real presence-absence variation of a given taxa in the vicinity of the study site, but is an artefact associated with low concentration of the macrofossils. We minimized this effect by stacking all plant macrofossil data into one composite plant macrofossil diagram to generate a more complete and reliable record of occurrence of the plant species in the study region (Fig. 3). While such stacked composite diagrams are rarely used in macrofossil-based studies, they may be the most realistic way to use macrofossil data for calculating turnover rates and can be seen as equivalents to the practise of analysing a number of vegetation plots from one vegetation zone and averaging their results in modern spatial vegetation turnover studies.

Fossil phytoplankton percentage data were included in the study to examine the biotic turnover rate of the aquatic communities and to compare them with terrestrial communities. As with the terrestrial plant macrofossils and pollen, fossil phytoplankton records from the sediment samples do not reflect the entire taxonomic diversity. Several ways with different taxonomical resolution exist to recover past information on phytoplankton, including fossil representatives recovered from pollen slides (Stivrins et al., 2015; Turner et al., 2014), through diatom analysis (Rühland et al., 2015), by measuring algal pigments and by determining ancient DNA (Pal et al., 2015). Nevertheless, fossil records of phytoplankton have been successfully used to evaluate climate impact on phytoplankton turnover rates over the last 150 years (Smol et al., 2005).

#### 4.2. Biotic turnover during the Pleistocene-Holocene transition

Both terrestrial and aquatic biotic turnover rates indicate



periods of marked change and stability during the PHT. The periods of lowest turnover and hence stable communities date to 13.5–13 ka BP and 12.5–12 ka BP (Fig. 5b–c). The former period represents the Bølling-Allerød interstadial when the study region was mostly covered by pine-birch forest except for the northernmost part where the tundra remained (Amon et al., 2014). The latter period represents the Younger Dryas stadial, characterized by low temperature and the predominance of the tundra or steppe-tundra ecosystems in our study region. These two periods of community stability correspond with periods of low rates of the temperature change. For example, there was a period of practically no summer temperature change from 13.5 to 13.1 ka BP and this period was characterized by the lowest turnover rates in the pollen data in all three subregions (Fig. 4). We therefore conclude that the Bølling-Allerød and Younger Dryas were periods of little climatic and biotic change in the region, at least at the multidecadal to centennial time scales captured by our sediment records.

The Younger Dryas-Holocene shift at 11.7 ka BP represents the most abrupt turnover event in both terrestrial and aquatic communities in our study region. It is obvious that the underlying reason for this rapid turnover was the rapid climate warming. In the chironomid-based  $T_{July}$  reconstruction this warming begins at 11.7 ka BP and continues during the several centuries in the early Holocene. The same fast warming can be seen in the Greenland ice core data. Steffensen et al. (2008) argued that this warming was triggered by an abrupt change in atmospheric circulation which initiated a warming over about 50 years and lasted about 60 years (Steffensen et al., 2008). In the European lake sediment records, the same abrupt warming can be seen, for example in the high-resolution records from United Kingdom, Norway and Switzerland (Bakke et al., 2009; Birks et al., 2012; Heiri et al., 2015).

Arctic lakes are responsive to climate change, because even slight warming results in decreased ice cover and, hence, longer growing seasons for algae and other organisms (Douglas and Smol, 1999; Rouse et al., 1997; Smol et al., 2005). As the summer temperatures during the PHT in the study region were comparable to modern arctic and boreal regions, it is not surprising that the DCCA results show that the trends in the phytoplankton turnover rates in general followed rates of temperature change and were hence mostly consistent with the turnover rates of the terrestrial communities (Fig. 5). In a comparable study of the recent community change in the arctic lakes, Smol et al. (2005) used DCCA to analyse compositional turnover in diatom community rates over the last 150 years and discovered that many arctic freshwater ecosystems have experienced dramatic and unidirectional regime shifts within the last 150 years.

An intriguing aspect is that while the Younger Dryas-Holocene shift is characterized by rapid  $T_{July}$  warming and higher turnover, an even more pronounced temperature change is indicated during the Bølling-Allerød–Younger Dryas shift, when there was a rapid  $T_{July}$  cooling with a rate of 0.31 °C per decade (Fig. 5a). This is the fastest rate of temperature change in our dataset, but it had relatively muted effect on biotic turnover (Fig. 5b–d). There may be a number of reasons explaining this difference. Our July mean temperature record differs from other high-resolution temperature reconstructions from Europe. For example, in the high-resolution records from Kråkenes from western Norway (Bakke et al., 2009; Birks and Birks, 2008), from Scotland (Brooks et al., 2016) and from the NGRIP ice core data from Greenland (Buizert et al., 2014) the amplitude of warming at the Younger Dryas-Holocene shift is

Fig. 3. Composite Baltic plant macrofossil diagram from 14,000 to 11,000 BP with a 102 taxa from nine sites organized according their first appearance from left to right. Three chronozones indicated: Bølling-Allerød, Younger Dryas and the Holocene.

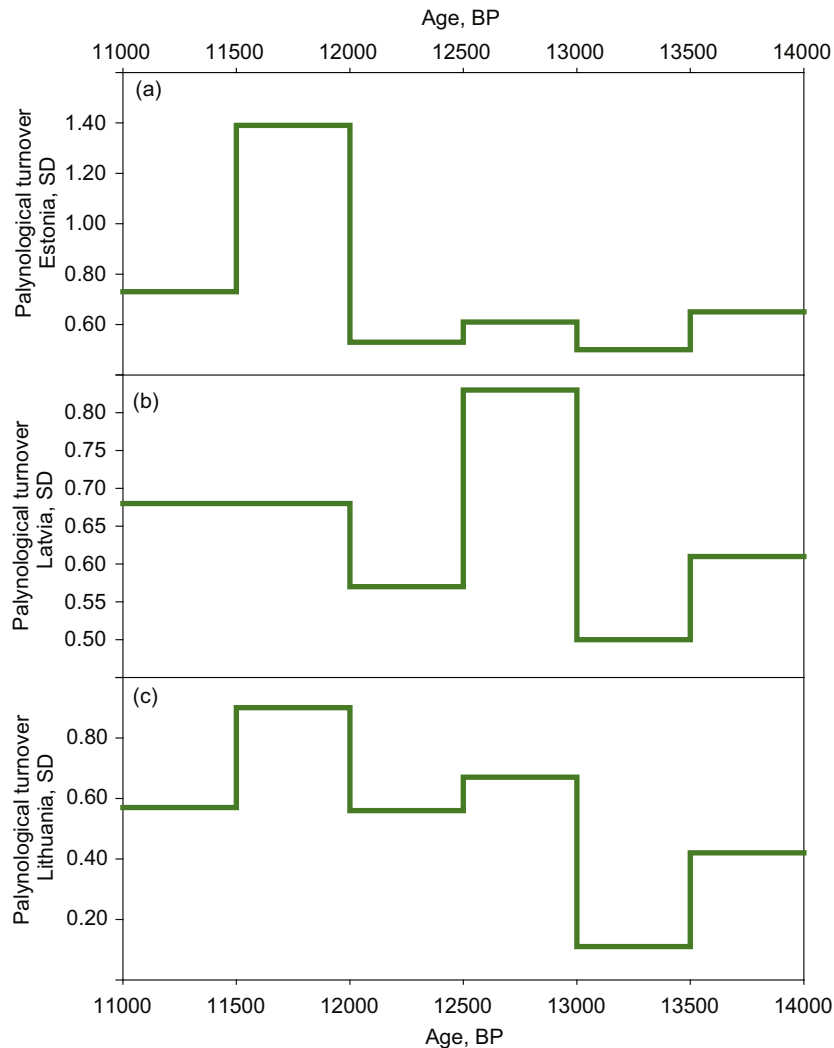


Fig. 4. Palynological turnover for Baltic from 14,000 to 11,000 BP in SD units: (a) Estonia, (b) Latvia and (c) Lithuania.

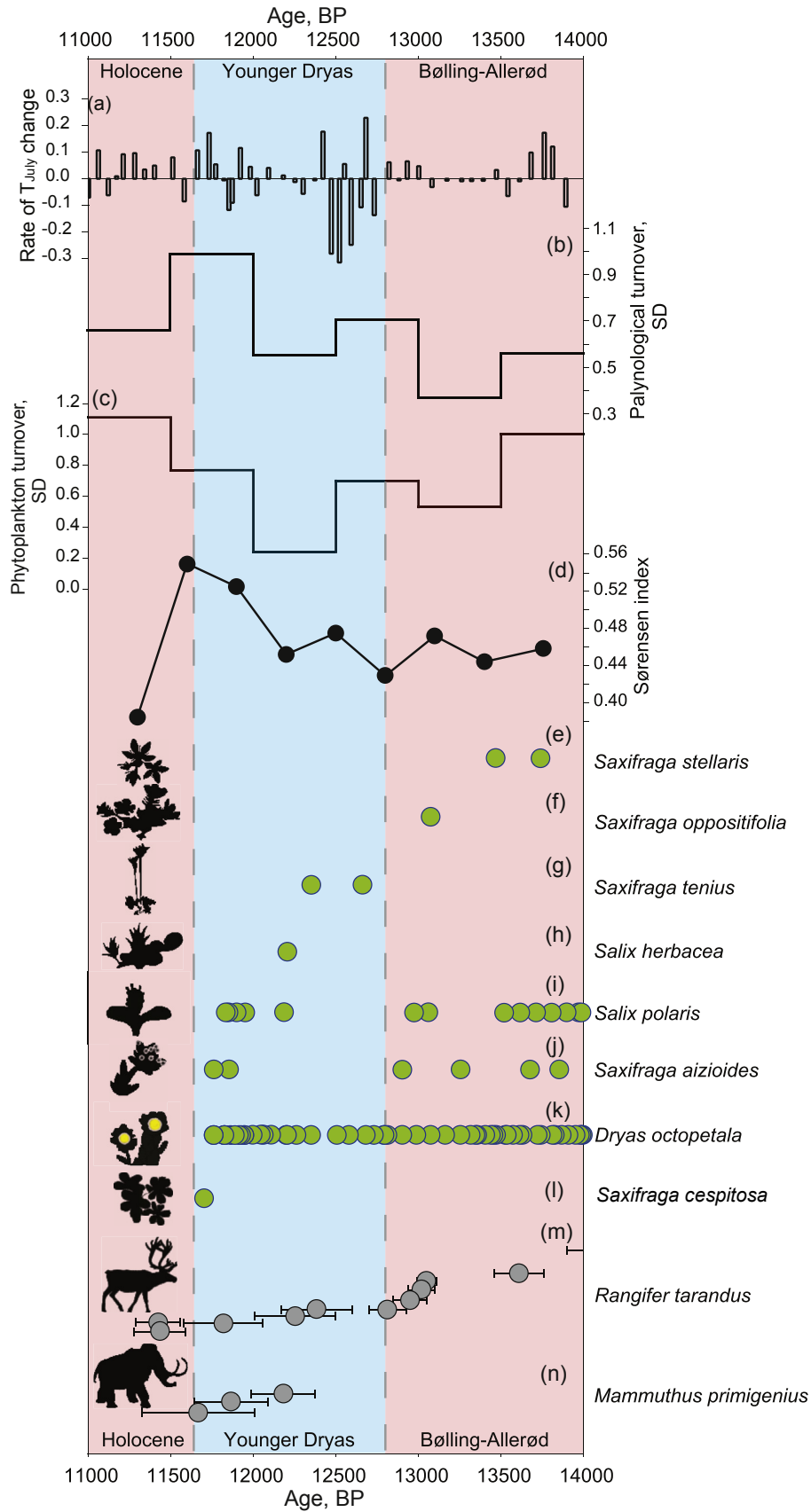
faster than during the cooling at the Bølling-Allerød-Younger Dryas shift. It is thus possible that the Baltic chironomid-based temperature record during the Younger Dryas-Holocene shift is smoother than the real temperature change, possibly because of bioturbation that can occur in non-varved lakes and can cause sediment mixing, thus blurring the palaeoclimatic signal.

Another potential explanation is that other climatic variables may have influenced the biotic responses and turnover rates. Summer or July mean temperatures are strong predictors of distribution and abundance for a plant or algal species that require some minimum of consecutive frost-free days to complete their growth and reproductive cycles (Woodward, 1987). However,  $T_{\text{July}}$  might serve as a poor predictor of range or population shifts for other species, which are more dependent on long growing season. Winter temperature can be another important variable, as it can limit beginning and length of growing season (Alfano et al., 2003; Cooper, 2014). Similarly, mean temperatures and temperature extremes during spring or autumn may have a significant effect on terrestrial biota and changes in these temperature variables will not have been captured in our temperature reconstruction. Moisture availability is another important variable for terrestrial plants, and it is often expressed as mean annual or seasonal precipitation or as actual or potential deficit. Birks and Birks (2014) showed that  $T_{\text{July}}$

does not explain all changes in vegetation and argued that precipitation was an important climatic component during the Late Glacial. No independent quantitative winter temperature or precipitation data exist for the PHT from Europe yet, but climate simulations suggest higher temperature changes during the Younger Dryas-Holocene shift in winter than in summer (Buizert et al., 2014).

#### 4.3. Rapid turnover and regional extinctions

An important part of the biotic turnover was the regional extinction of the arctic-alpine plant and animal species. Fig. 5 highlights the occurrence and disappearance of the plant taxa which are considered regionally extinct in the region. These plants comprise arctic-alpine plants, such as *Saxifraga aizoides*, *S. cespitosa*, *S. oppositifolia*, *S. stellaris*, *S. tenuis*, *Salix herbacea*, *Salix polaris* and *Dryas octopetala*. Macrofossils show that all these plant species were locally present in the Baltic region during the study period. *Dryas octopetala*, which is usually abundantly present in plant macrofossil records (Birks, 2008; Godwin, 1975), is present from 14 ka BP to the Younger Dryas-Holocene shift at 11.7 ka BP. Given the continuous nature of the record, it is likely that its fossils represent reliably its presence and regional extinction in the region.



**Fig. 5.** Biological turnover of Baltic region from 14,000 to 11,000 BP: (a) rate of  $T_{July}$  change, (b) mean palynological turnover in SD units, (c) mean phytoplankton turnover in SD units, (d) Sørensen dissimilarity index for plant macrofossil 300-year bins, and plant macrofossils (e) *Saxifraga stellaris*, (f) *Saxifraga oppositifolia*, (g) *Saxifraga tenuis*, (h) *Salix herbacea*, (i) *Salix polaris*, (j) *Saxifraga aizoides*, (k) *Dryas octopetala* and (l) *Saxifraga cespitosa*. Information on mammals (m) *Rangifer tarandus* (reindeer) and (n) *Mammuthus primigenius* (mammoth) obtained from Ukkonen et al. (2006, 2011).



The plant macrofossils of other now extinct plant taxa are more scattered. It is certain that the macrofossil records of these species underestimate the presence of these taxa regionally and temporally. For example, it is not likely that *Saxifraga cespitosa* would have been present in the Baltic region only during the end of the Younger Dryas, as indicated by the only found macrofossil of this species in the Baltic region (Fig. 5). It is more likely that these species that are common in modern arctic, as well as other arctic-alpine plant species, were early colonizers of the deglaciated terrain during the Late Glacial and may have been present throughout the Bølling-Allerød and Younger Dryas in the Baltic region. The disappearance of these taxa seems to have happened either during the Younger Dryas-Holocene shift or few decades after this shift at the latest.

The impact of Younger Dryas-Holocene shift on the disappearance of the arctic-alpine plants can be seen elsewhere in northern Europe as well. In Denmark and Scania in southernmost Sweden, the Late Glacial presence of *Dryas octopetala* has been well documented by pollen and plant macrofossils records, which indicate its disappearance during the Younger Dryas-Holocene shift (e.g. Bennike et al., 2004; Fischer Mortensen et al., 2011; Liedberg-Jönsson, 1988). Other arctic-alpine species which went regionally extinct during the Younger Dryas-Holocene shift include *Salix polaris* and *S. herbacea*, *S. reticulata* (Berglund and Malmer, 1971; Liedberg-Jönsson, 1988), *Arctostaphylos alpina* (Berglund and Digerfeldt, 1970; Liedberg-Jönsson, 1988), *Selaginella selaginoides* (Fischer Mortensen et al., 2011; Liedberg-Jönsson, 1988) and *Potentilla nivea* (Fischer Mortensen et al., 2011). Hence the strong impact of the Younger Dryas-Holocene warming on terrestrial plant communities can be observed widely in northern Europe, although direct comparison with our results cannot be done due to lack of quantitative turnover rate calculations elsewhere in Europe.

The fossil bone records give evidence of the mammal community change and regional extinctions of the mammal species during the PHT (Fig. 5m–n). Although they are too sparse to quantify the animal community turnover during the PHT. Reindeer and woolly mammoth, the two mammalian species for which bone records exist from the study region, show different population dynamics during the PHT. There are no bone findings of woolly mammoth during the Bølling-Allerød 14–12.8 ka BP, and the species may indeed have been absent fully or mostly from the Baltic region, as the boreal forest that covered most of the region during this period was poorly suitable for it. Its appearance during the Younger Dryas 12.8–11.7 ka BP may thus represent its return to the Baltic from northern Russia where the open habitats remained throughout the PHT (Stuart et al., 2002; Ukkonen et al., 2011). It went regionally extinct at the Younger Dryas-Holocene shift at 11.7 ka BP, thus simultaneously with the most rapid terrestrial vegetation turnover phase. In contrast, the reindeer has been present in the Baltic region possibly since the deglaciation throughout the PHT to its regional extinction at about 11.2 ka BP. However, there is a gap in its bone record at 13.4–13.2 ka BP, during the Bølling-Allerød period when the  $T_{July}$  was about 14 °C and most of the region was covered by pine-birch forest. It is therefore possible that during this short period reindeer was absent or restricted to northern Estonia, where predominantly open tundra prevailed even during the Bølling-Allerød interstadial (Amon et al., 2014).

To sum up, it is clear that although the PHT included a number of rapid climate changes, the most fundamental turnover in terrestrial and aquatic plant and animal communities occurred during the Younger Dryas-Holocene shift at 11.7 ka BP. It is likely that this fundamental change in the terrestrial and aquatic plant and animal community structure was not caused only by the direct impact of warming. Many arctic-alpine species can tolerate warm temperature and can grow and regenerate under controlled conditions such as gardens (Dahl, 1998). They succumb to competition, but if the

habitat remains open, they can survive in the lowlands (Birks, 2008). Hence the indirect influences of the warming can be more important. Pollen and plant macrofossil data suggest that during the Younger Dryas-Holocene shift the typical boreal species, such as birch and pine, suddenly became common species in the study area (Amon et al., 2014; Heikkilä et al., 2009). Their expansion had a major impact on the flora of the tundra or steppe-tundra vegetation which prevailed during the Younger Dryas, and influenced the interspecific competition by reducing light and nutrient availability, eventually causing development of the boreal forest and the regional extinction of the arctic-alpine plant species in the region. Moreover, there is evidence that the permafrost prevailed in northern Europe, including the Baltic region, during the Younger Dryas and started to melt during the rapid warming at the Younger Dryas-Holocene shift (Isarin, 1997; Lamsters and Zelcs, 2014; Vandenberghe and Pissart, 1993). The permafrost and associated periglacial soil processes, such as cryoturbation and other soil disturbances, would have promoted the occurrence of the arctic-alpine plants, which can utilize the seasonally thawed soils above the permafrost and survive in such unstable conditions (Peterson, 2014).

The fossil evidence is not precise enough to assess whether the disappearance of the arctic-alpine elements happened during the fast warming of the Younger Dryas-Holocene shift or more gradually with the development of the dense boreal forest, but the evidence points to fairly rapid disappearance, rather in decades than in centuries. The indirect influences are likely the cause of the regional extinction of the woolly mammoth as well. A typical dietary pattern during the Younger Dryas probably consisted of grasses, sedges and small-leaved dwarf willow (*Salix* sp.) twigs and decayed plants during winter (Schwartz-Narbonne et al., 2015; van Geel et al., 2008). With the reduction of suitable habitat and the replacement of herbaceous and grassy plants, its key dietary plants, by the pine and birch forest during the Younger Dryas-Holocene shift woolly mammoth was unable to survive.

Unlike the arctic-alpine plants and mammoth, reindeer survived a few hundreds of years into the Holocene both in the Baltic region and in southern Sweden, where it went extinct as late as 10.3 ka BP (Sommer et al., 2011). Although reindeer was a common mammal species in the cold, open environments of the PHT and is at present mainly confined to tundra, it can occur in northern boreal forests too and is thus not exclusively confined to an open or semi-open habitats. In any case, the fundamental trigger of its regional extinction in the Baltic countries and southern Scandinavia was the warming from the Late Glacial to the Holocene interglacial (Sommer et al., 2011) and its regional extinction therefore represents a palaeoecological example of the time-delayed impact of habitat loss or “extinction debt” (Hanski and Ovaskainen, 2002; Tilman et al., 1994).

## 5. Conclusions

The impact of rapid climate changes during the Pleistocene-Holocene transition (PHT) 14–11 ka BP on the biotic turnover rates of terrestrial and aquatic communities were investigated in the Baltic region using pollen, plant macrofossil, and fossil phytoplankton data from lake and bog sediment cores. In general, the terrestrial and aquatic communities showed comparable trends in their biotic turnover rates. Periods of low turnover and hence stable communities dated to Bølling-Allerød interstadial 13.4–13.1 ka BP and to the Younger Dryas stadial 12.9–11.7 ka BP. During both stable periods the rate of summer temperature change was minimal. The highest biotic turnover rates occurred during the Younger Dryas-Holocene shift at 11.7 ka BP. This rapid turnover event included significant regional extinctions as the arctic-alpine and

glacial elements of the flora and fauna in the Baltic region.

Over the last decades, the Northern Hemisphere has warmed by a rate of 0.2 °C/decade. Associated with this rapid warming are accelerated biotic turnover and extinction rates, and fundamental ecosystem reorganizations. One of the most important results of the study is that the rapid biotic turnover during the Younger Dryas-Holocene shift occurred when the rate of warming was 0.17 °C/decade, thus slightly lower than the current Northern Hemisphere warming. This can be combined with the fact that the summer temperature values during the PHT in the Baltic region were 11–14 °C, thus comparable to the modern summer temperature values of the southern arctic zone. We therefore conclude that the Younger Dryas-Holocene shift with its rapid turnover rates and associated regional extinctions represents an important palaeoanalogue to the current high latitude warming and gives insights about the probable future turnover rates and patterns of the terrestrial and aquatic ecosystems change in the arctic.

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### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2016.09.008>.

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