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Biotic turnover rates during the Pleistocene-Holocene transition

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A B S T R A C T

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 on 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.

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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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 et al., 2009; Stančikaitė 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.

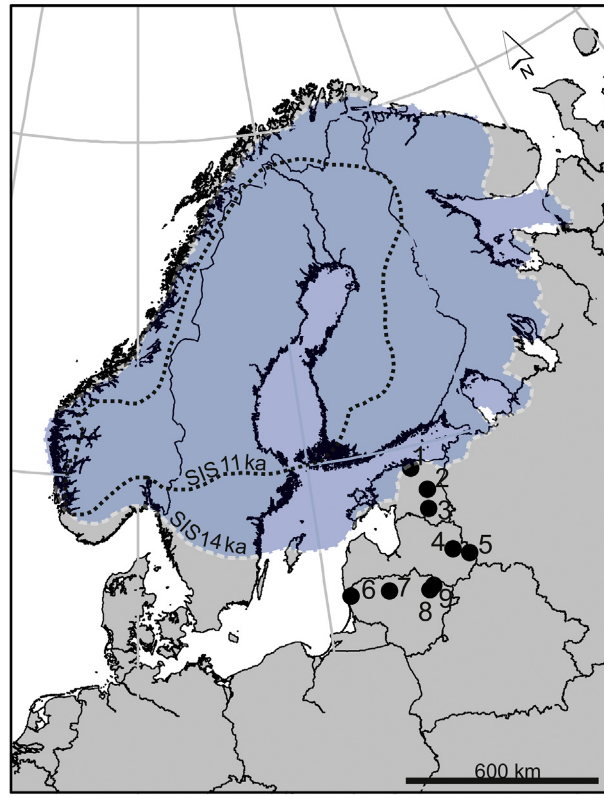

Fig. 1. The study area is located in the Baltic region (Estonia, Latvia and Lithuania) that extends from 53 to 60°N and from 21 to 28°E. Location of the sites included in the study: (1) Lake Udriku; (2) Lake Prossa; (3) Lake Nakri; (4) Lake Lielais Svētiņu; (5) Lake Kurjanovas; (6) Lake Kašučiai; (7) 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.

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