Quaternary Science Reviews 263 (2021) 107006

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Environmental drivers and abrupt changes of phytoplankton community in temperate lake Lielais Svētiņu, Eastern Latvia, over the last Post-Glacial period from 14.5 kyr

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ARTICLE INFO

Article history:
Received 15 February 2021
Received in revised form
26 May 2021
Accepted 28 May 2021
Available online 9 June 2021

Handling Editor: Yan Zhao

Keywords:
Holocene
Paleolimnology
Eastern Europe
Statistical modelling
Ecological disturbance
Phototrophs
Fossil pigments
Ancient sedimentary DNA
Generic anthropogenic influence
Land-use change
Regime shift

ABSTRACT

Understanding the long-term dynamics of ecological communities on the centuries-to-millennia scale is important for explaining the emergence of present-day biodiversity patterns and for predicting possible future scenarios. Fossil pigments and ancient DNA present in various sedimentary deposits can be analysed to study long-term changes in ecological communities. We analysed recent compilations of data, including fossil pigments, microfossils, and molecular inventories from the sedimentary archives, to understand the impact of gradual versus abrupt climate changes on the ecosystem status of a regional model lake over the last ~14.5 kyr. Such long and complete paleo-archives are scarce in North-Eastern Europe. The study site lies in a sensitive area, both climatically and in respect to vegetation. Namely the maritime-continentality line runs west to east in the central Baltic area to NE Europe and its south-north transect lies within the gradual decay of the nemoral forest into a boreal environment. Therefore, the selected location is an ideal sampling point to decipher long term environmental changes in the temperate climate zone. The main objective of the present study was to find out external factors influencing phototroph dynamics at temperate Lake Lielais Svētiņu over the post-glacial period (~14.5 kyr). We were able to model climate change together with vegetation change and the appearance of anthropogenic forcing, either as a gradual change or as abrupt events that influenced the phototrophs, which are keystone groups within the lacustrine ecosystem. Most interestingly, the gradual increase of species richness of phototrophs was linked to similar increase in fungal parasites of the same group — phototrophs. Abrupt climate change in the Late Glacial period caused abrupt events in the ecosystem but equally abrupt events were caused by gradual changes during the stable period of the Holocene Thermal Maximum (HTM). In addition, we highlight the increased frequency and degree of perturbation in pristine lakes due to low impact human activity over a larger region. Both observations demonstrate an impaired relationship between gradual external drivers and ecosystem response and apply to future scenarios of climate warming and increased human impact in north-eastern Europe.

1. Introduction

Regime shift has been recently shown to be a process of paramount importance for the functioning of present-day lakes. Our understanding of how aquatic ecosystems respond to gradual external forcing (i.e., environmental change) with a non-linear

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https://doi.org/10.1016/j.quascirev.2021.107006
0277-3791/

response has improved in recent years (Andersen et al., 2009; Williams et al., 2011; Randsalu-Wendrup et al., 2016). Such process is called regime shift because aquatic ecosystems are often resilient until an internal threshold is passed, leading to an abrupt shift in ecosystem state (Andersen et al., 2009). Regime shifts often result in large and persistent changes in biodiversity, and energy flows through food webs (Randsalu-Wendrup et al., 2016). Moreover, once a threshold is passed, recovery back into the original regime can be difficult due to numerous feedback effects that maintain the ecosystem in an alternative stable state (also called hysteresis; Randsalu-Wendrup et al., 2016). Almost all ecosystems are under constant pressure from changing climatic drivers, which can be either gradual or abrupt. One of the most studied lake ecosystem changes that follow a critical threshold is the sudden shift of clear water lakes to the turbid status due to nutrient loading together with submerged vegetation loss (Scheffer et al., 2001; Ravelo et al., 2004). Abrupt (threshold-like) responses in ecosystems can be driven by both abrupt and gradual changes in the environment (Andersen et al., 2009; Randsalu-Wendrup et al., 2016). Lakes are usually closely influenced by the surrounding catchment via nutrient income whether it originates from wet or dry climates or from human agricultural activity. Therefore, the response of lake ecosystems to outer physical (i.e., climate change) or anthropogenic forcing could be indirect, mediated through processes in the catchment (Schindler, 2009; Rolighed et al., 2016). Current climate change is a rapid process and is equally prone to cause immediate abrupt changes and to pave the way for much faster breakdown of the resilience of ecosystems more so than any other process in the recent past (Fischer et al., 2018). The term ‘resilience’, common in contemporary ecology, is becoming more and more popular in paleoecology studies (reviewed by Davies et al., 2018) and means the ability of a system to retain its current state via tolerating or resisting disturbance without rearranging into a structurally different state.

It is possible to reconstruct past changes in ecological states and the variability of ecosystem characteristics during stable climatic periods (or gradual successions with gradual responses) (Randsalu-Wendrup et al., 2016). Disentangling how lakes responded to climate change in the past is important, because ongoing warming will lead to warmer waters. This can increase the risk of nutrient input and intensify the process of eutrophication in lakes (Jeppesen et al., 2010; Bastviken et al., 2011). Under various forcing scenarios, the global mean surface temperature will increase from 0.3 to 4.8 °C by the end of the 21st century, relative to the period 1986–2005. In Northern Europe, the average air temperature will increase between 2 °C and >6 °C for the forcing scenarios RCP 4.5 and RCP 8.5 (IPCC, 2014; de Coninck et al., 2018).

Primary producers are the base of most aquatic food webs, therefore variability in their biomass and productivity leads to predominant control over the whole ecosystem (Jeppesen et al., 2014). Several primary producers in a lake are short–living benthic or pelagic algae that can respond rapidly to changing environmental conditions such as water temperature, humification, nutrient load and eutrophication/oligotrophication (Anderson et al., 1996; Fietz et al., 2007; Tõnno et al., 2013, 2019). Naturally, the lake responds to a warmer climate with increased water temperature, so thermophilic bloom-forming cyanobacteria could gain a competitive advantage over other algal groups in the near future (Paerl and Huisman, 2008; Havens and Paerl, 2015) in temperate regions. However, there is no detailed information on how broad biodiversity, i.e. overall species richness and diversity, will change. Gradual climate warming has occurred previously in the eastern part of North Europe, i.e. Holocene Thermal Maximum (HTM) from ~8.0 to 4.0 kyr when average temperatures in the region were about 2.5–3.5 °C higher than today (Antonsson and Seppä, 2007). However, several abrupt changes occurred in the Post-Glacial period (Veski et al., 2015; Shala et al., 2017) followed by more gradual changes over most of the Holocene (Heikkilä and Seppä, 2003; Antonsson and Seppä, 2007), allowing a relationship between forcing and ecological responses to be identified with predictive power. However, the gaps in understanding of the relationships between past climate changes and biological community changes in lakes does not allow us to deconstruct the mechanism behind these associations. Thus, in the present paper we study the dynamics of fossil pigment concentration, together with data from algal microfossils and sedaDNA from the lake Lielais Svētiņu in Eastern Latvia. This model lake serves well as a proxy to analyse changes in the community of phototrophs covering exceptionally long (last ~14.5 kyr) and continuous lacustrine sediment sequence in North-Eastern Europe. Moreover, the lake is a perfect reference site because it was in the natural state throughout the entire Holocene with relatively late and gradual human intervention (Stivrins et al., 2014, 2015). However, a low impact but direct (~2.0 kyr) human footprint is clear and an important driver in the area (Stivrins et al., 2015), making Lielais Svētiņu a valid model for studying both natural and human-related external forcing of aquatic ecosystems. Previous paleoresearch on Lielais Svētiņu focused on phototroph composition by using non-pollen palynomorphs. These studies reveal that the climate warming significantly affected the dynamics of the phototroph community in Late Glacial and favoured cyanobacteria over other phytoplankton taxa in the HTM period (Stivrins et al., 2015, 2016, 2018). Ancient sedimentary DNA (sedaDNA) studies indicate lower turnover rates of phototroph community during the Late Glacial but higher turnover rates during the Holocene (Stivrins et al., 2018; Kisand et al., 2018). Paleostudies of sediment organic matter (OM) and geochemical composition from Lielais Svētiņu demonstrated that carbon to nitrogen ratio (C/N), a proxy for terrestrial:aquatic OM in lakes, is closely related with climate change but also with landscape vegetation development and hydrological conditions (Liiv et al., 2019). Food web study report an abrupt rise in the contribution of CH_4-derived carbon to chironomid (Diptera, Chironomidae) biomass in Lielais Svētiņu since ~3.5 kyr. The driver for this could be the infilling process of the lake leading to the shallowing of lake water depth to around 7 m (Belle et al., 2018). Furthermore, climate reconstructions using pollen data from Lielais Svētiņu sediments to reconstruct past climate and vegetation history in the North-Eastern Europe revealed that in the Late Glacial, the climate fluctuated between warmer and colder periods while in the Holocene a remarkable climate warming followed (Veski et al., 2012, 2015; Stivrins et al., 2014, 2015). The accumulated data about this lake enables stronger generalisations to be made and allows ecological theories about the response of lacustrine ecosystems to climate change to be tested.

The aim of this study was to identify the response of the phototroph community in a temperate lake to changing external forcing over the last ~14.5 kyr. We compiled a comprehensive multiproxy dataset study, including fossil pigments, algal microfossils, and sedaDNA (richness of algae and algae parasitic fungi) to study phototroph communities. The new proxy, fungal DNA, was added to the analysis focusing on algae parasitic fungi (Talas et al., 2021). As several algal taxa do not preserve well as fossils (Riddick et al., 2017), the fungal DNA and their ecophysiological roles would also be useful proxy providing information about past communities (Bellemain et al., 2013; Talas et al., 2021) because fungi are the common residents in lake sediments (Kisand et al., 2018). Many aquatic fungi are closely connected with algae, playing a crucial role in organic matter turnover (i.e., “mycoloop”; Kagami et al., 2014). We considered model fitting and statistical anomalies as an indicator of ecological thresholds (perturbation periods and change points). In model fitting, the dynamics of fossil pigment concentration was modelled as a response variable to climate (i.e., temperature), pollen and non-pollen microfossil-based paleoecological proxies and richness of taxon-like molecular operational taxonomic units (mOTUs) from sedaDNA. We hypothesised that although the underlying gradual climate change causes mostly smooth successions in phototroph communities and thus in the whole ecosystem, the strong abrupt climate changes are reflected by abrupt responses. Threshold-type ecological changes (regime shifts) have occurred several times over the Post-Glacial period in lakes of Northern Europe such as Younger Dryas cooling (~12.7–11.65 kyr; Veski et al., 2015), ~8.2 kyr cooling event (Randsalu-Wendrup et al., 2012), ~5.8–5.1 kyr period cooling and Little Ice Age in period ~0.5–0.1 kyr (Seppä et al., 2009). These change points were responses to gradual forcing. In addition, we hypothesize that the richness of phototroph organisms change most rapidly during complex forcing periods, e.g. due to anthropogenic impact.

2. Study site

Lake Lielais Svētiņu (LS; mean depth 2.9 m; maximum depth 4.9 m) is a drainage lake in the Eastern Latvian lowland with an area of 18.8 ha and an altitude of 96.2 m above sea level (Fig. 1a; 56°46′N; 27°08′E). LS bedrock consists of Devonian dolomite covered by Quaternary deposits with a thickness of 5–10 m consisting of peat, sand, silt, clay, and till. The deposits have been greatly paludified during the Holocene (Stivrins et al., 2014). Its catchment area (~19.7 km^2) is mostly forested with some fields south-east of the lake and peatlands in the north-western part with relatively low impact and recent human disturbance (Kisand et al., 2018). According to our present knowledge, there is no monitoring data available about the present water chemistry and phytoplankton composition dynamics of LS. The climate in the area is a combination of continental (Eurasia) and maritime (Atlantic Ocean), therefore the annual frequency of arctic and sub-polar air masses is fairly high (Draveniece, 2009). Currently, the lake is mesotrophic-dystrophic (with brown, humic waters) and has three small inlets and one outlet. Although Latvia has been inhabited by humans since the Paleolithic, the continuous presence of forests in the vicinity of LS suggests that this boggy area was not a suitable location for human settlement or activities before ~1.5 kyr (Kisand et al., 2018).

3. Materials and methods

3.1. Coring and chronology

Lielais Svētiņu was sampled from the ice in March 2009 and 2013 using a Russian-type peat corer with a diameter of 10 cm. The detailed description and lithology of the 11.3 m long sediment core sampled in 2009 is given in Stivrins et al. (2015). In order to work with fresh sediment material, LS was sampled again for paleopigments and DNA extraction in 2013 and a 10.4 m sediment core was retrieved close to the earlier coring location (Fig. 1a). Chronology was obtained by cross-correlating lithological changes and loss-on-ignition (LOI) with the well-dated core from 2009, described more detailed in Kisand et al. (2018). The ages in the text are expressed in thousand calibrated years before the present (kyr) where AD 1950 corresponds to ~0 kyr.

3.2. Microfossils and paleoproxies

In the present study, pollen-based reconstructed mean summer temperatures (T_{sum}) and mean winter temperatures (T_{wint}) from Stivrins et al. (2015) were used to characterise the climate as a main driver of the length and intensity of the productive season and as a proxy for possible ice conditions (Fig. 1b; Table 1). To reveal the combination of environmental changes in the lake ecosystem and the surrounding landscape (regional changes) we used microfossil data and paleoproxy variables calculated using the abundance and diversity of those microfossils (Fig. 1b; Table 1). The accumulation rate (AR) of *Botryococcus* (Botry; green algae) microfossils (Stivrins et al., 2015) and the AR of *Picea* (spruce) pollen (Stivrins et al., 2014) were used as the proxies describing humification level. The sum of *Secale cereale* (rye), *Hordeum vulgare* (barley), *Triticum aestivum* (wheat) and *Avena sativa* (oat) pollen-based ARs (human-related pollens; HRP) from Stivrins et al. (2014) was used as a proxy for increased anthropogenic impact. In the present study we used

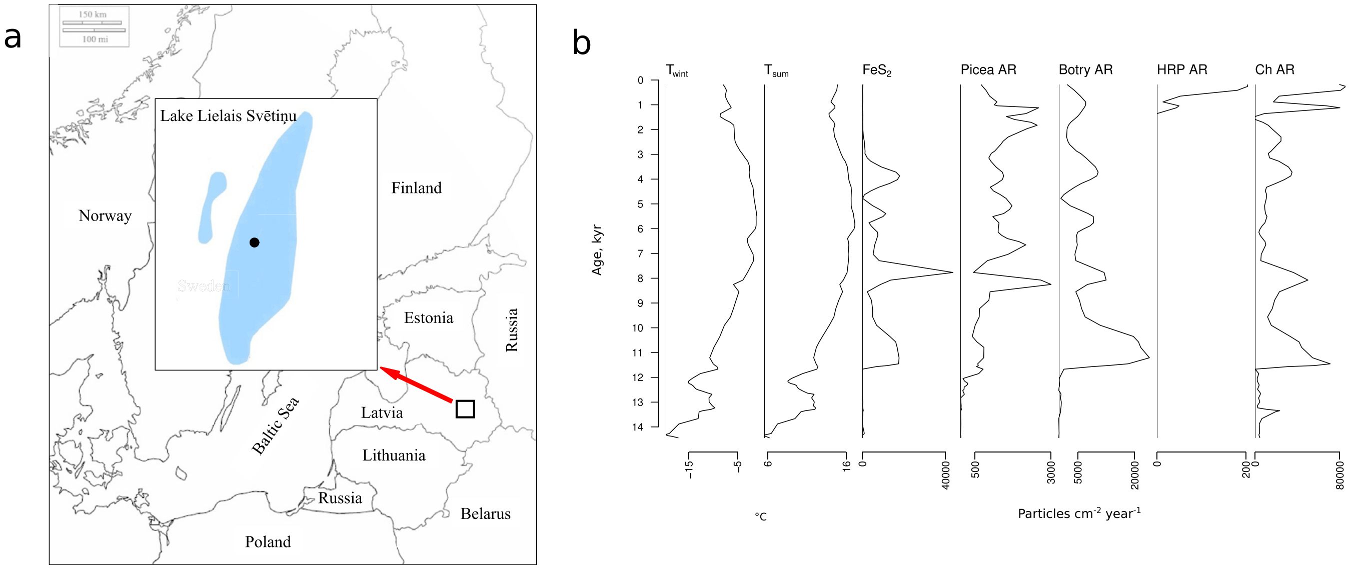

Fig. 1. Sampling location (A), and stratigraphy diagram of basic paleoproxy variables (B) used in the study. Winter temperature – T_{wint}; summer temperature – T_{sum}; Pyrite – FeS_2; *Botryococcus* accumulation rate – Botry AR (Stivrins et al., 2015); human-related pollen accumulation rate – HRP AR (Stivrins et al., 2014); charcoal particle accumulation rate – Ch AR (Stivrins et al., 2015).

Table 1
Lielais Svētiņu paleoproxies used for statistics.

Used proxies						Statistical analysis		
Proxy	**Paleoindicator origin**	**Paleoindication**	**Reference**	**Core**	**Core resolution**	**PCA**[a]	**Stepwise RDA**[b]	**GAM**[c]
Loss On Ignition (LOI)	sediment	organic matter (OM), mineral matter (MM), carbonate matter (CM)	Stivrins et al. (2015); Kisand et al. (2018)	2009; 2013	1 cm	NO	EXPLAN	
mean summer temperatures (Tsum)	pollen	ice conditions and climate change	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	Model A
mean winter temperatures (Twint)	pollen	ice conditions and climate change	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	
continential climate (Tsum - Twin)	pollen	climate change	this study	2009	5–20 cm	NO		
Botryococcus accumulation rate (AR of Botry)	microfossil	humification levels	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	Model B
Picea accumulation rate (AR of Picea)	pollen	humification levels	Stivrins et al. (2014)	2009	5–20 cm	NO	EXPLAN	
human related pollens (HRP)	pollen ARs of Secale cereale, Hordeum vulgare, *Triticum aestivum*, Avena sativa	anthropogenic impact	Stivrins et al. (2014)	2009	5–20 cm	NO	EXPLAN	
shade tolerance (Stol)	pollen	density of the vegetation	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	Model A
relative openness (Ropen)	pollen	density of the vegetation	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	
charcoal particles (Ch)	charcoal	fire dynamics	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	Model B
pyrite (FeS_2)	pyrite	anoxic conditions	Stivrins et al. (2015)	2009	5–20 cm	NO	EXPLAN	Model B
paleopigments consentrations	pigments	dynamics of primary producers	Stivrins et al. (2018)	2013	5 cm	YES	DEPEND	
degradation index of pigments (DI)	pigments	pigments preservation conditions	this study	2013	5 cm	NO	NO	
phytoplankton richness as number of mOTUs	sedaDNA, 18S rRNA region	phytoplankton dynamics	subset from Kisand et al. (2018)	2013	5–20 cm	NO	NO	Model C/D
algae parasitic fungi richness as number of mOTUs	sedaDNA; ITS2 region	dynamics of algae related fungi	subset from Talas et al. (2021)	2013	5–20 cm	NO	NO	Model E

[a] Variables included into PCA (YES/NO).
[b] Variables included into stepwise RDA as initial explanatory variables (EXPLAN) to constrain the ordination space of pigments (DEPEND).
[c] Variables/proxies selected for GAM.

calculated estimates of shade tolerance (S_{tol}) and relative openness (R_{open}) from Stivrins et al. (2015) to characterise the density of the vegetation in the lake catchment area (Table 1; Fig. S1). Charcoal (Ch) particle AR (Fig. 1b) identified from the pollen slides in Stivrins et al. (2015) were used to infer the fire dynamics in region around the lake, which could have influenced the vegetation in the region directly and therefore affected the lake ecosystem indirectly. Pyrite (FeS_2) from Stivrins et al. (2015) was used to indicate anoxic conditions at the bottom of the lake (Fig. 1b; Table 1).

3.3. *Paleopigment proxies*

Paleopigments from Stivrins et al. (2018) were used to follow the phototroph dynamics and composition in present study (Table 1). Analysis of paleopigments followed the recommendations of Leavitt and Hodgson (2001). The pigments were separated by reversed–phase high–performance liquid chromatography, using a Shimadzu Prominence (Japan) series binary gradient system with a photodiode array and fluorescence detector (see Tamm et al., 2015). The concentrations of paleopigments studied were expressed as nanomoles per gram organic matter (nmol g^{-1} OM). Altogether 12 paleopigments were separated and identified from the studied sediment core. Chlorophyll *a* (Chl *a*), it's general derivative pheophytin *a* (Phe *a*) and β, β–carotene (β–car) were applied as indicators of the total algal abundance and primary production (Leavitt and Hodgson, 2001; Waters et al., 2013). Diatoms were represented by complex pigment formed by carotenoids diadinoxanthin and diatoxanthin (D + D) as in their xanthophyll cycle diadinoxanthin could be transformed to diatoxanthin under excessive light (Roy et al., 2011). Zeaxanthin (Zea), canthaxanthin (Cantha) and echinenone (Echi) was selected to indicate the abundance of cyanobacteria (DreBler et al., 2006; Romero-Viana et al., 2009). More specifically Cantha and Echi represent colonial and filamentous cyanobacteria and N_2-fixing filamentous cyanobacteria, respectively (Waters et al., 2013; Desphande et al., 2014). Previous study by Tamm et al. (2015) indicates a good correlation between zeaxanthin and cyanobacteria. Lutein (Lute) and chlorophyll *b* (Chl *b*) were analysed to track the dynamics of green algae, while alloxanthin (Allo) and peridinin (Perid) were selected to identify the dynamics of *Cryptophyta* and *Dinophyta*, respectively. In the present study, the Chlorophyll *a*/Pheophytin *a* (Chl *a*/Phe *a*) ratio (degradation index – DI) was used to follow the preservation conditions of paleopigments in the lake sediments (Ady and Patoine, 2016). The ratio of the paleopigments/DI was used in statistical analyses in order to compensate the effect of degradation on the marker pigment dynamics.

3.4. *SedaDNA proxies*

The two sub-datasets (phototroph and algae-parasitic fungal mOTUs) of total sedaDNA sequencing datasets from Kisand et al. (2018) and Talas et al. (2021), respectively, recovered from 2013 core samples were used to evaluate the dynamics of phototroph and algae related fungal taxa in relation with other paleo-proxies (Table S1, S2). Both sequencing sub-datasets, richness of eukaryotic phototroph (20% of total mOTUs from Kisand et al., 2018) and algae-parasitic fungi (16% of total mOTUs from Talas et al., 2021), were described and analysed comprehensively in this study. In brief, clean equipment/tools, UV light exposure to surfaces were used to avoid contamination in sub-sampling, DNA extraction and amplification as described in Kisand et al. (2018). A total of 252 collected samples covered the range from ~0.05 to 12.0 kyr (taken with 2.5 cm intervals; Kisand et al., 2018). Phototroph richness, i.e. number of mOTUs affiliated to any known phototroph taxa, was determined using PCR-based amplicon sequencing (Illumina) of the universal 18S rDNA gene V4 region fragment (~300–350 bp; Kisand et al., 2018). Algae-parasitic fungal richness was recovered using fungal specific ITS2 region fragment (~300–400 bp) amplified with multiplex primer pairs (forward primers ITS3-Mix1-tag, ITS3-Mix2-tag, ITS3-Mix3-tag, ITS3-Mix4-tag, ITS3-Mix5-tag and reverse primer ITS4mod-tag; Talas et al., 2021). The same DNA extracts were used for 18S (Kisand et al., 2018) and ITS2 (Talas et al., 2021) barcoding. The negative controls (no added DNA) were used for each PCR run, mixed and sequenced to avoid cross-contamination from reagents. The amplicon libraries were purified using PCR Kleen (Bio-Rad), tags added and sent to FIMM (University of Helsinki, Finland) for Illumina sequencing (2 × 250 bp) using the PE250 chemistry. All demultiplexed raw reads were quality trimmed (<Q30), paired, de-replicated, chimeras removed and clustered (97% of similarity threshold) to obtain mOTUs (molecular operational taxonomic units) against SILVA and UNITE database as described detail in Kisand et al. (2018) and in Talas et al. (2021). A few surviving reads in negative controls did not include any mOTUs we are presenting in this study.

Ecological roles assigned to fungal mOTUs (Table S2) were used to determine the possible relationship between the algae and identified algae related fungi. All fungal mOTUs described as possible or obligate parasites of algae, hyperparasites of zootrophic fungi on phytoplankton, parasites of zoo- and phytoplankton, or found connected to algal hosts, were assigned to the group “possible algae parasites”.

3.5. Statistical analysis

Principal component analysis (PCA) was used for unconstrained ordination of individual fossil pigment concentrations. PCA scores (axes 1 and 2) were considered as indicators of sedimentary pigment temporal variability. A constrained ordination analysis, the stepwise redundancy analysis (RDA) was used to select relevant paleoproxies as predictor variables to the pigment concentration ordination space (Table 1; Oksanen et al., 2019). This analysis allows to figure out the statistical relationships between the explanatory variables and response variables such as individual fossil pigment concentrations. Thereafter, general additive modelling (GAM) was used as a continuous-time, first-order autoregressive process to account for temporal autocorrelation to describe the statistical relationship between paleoproxies selected by stepwise RDA (Simpson and Anderson, 2009) (Table 1). Different paleoproxy variables were used to model PC1 or PC2 temporal variability (Table 1; Table S3, S4). In addition, the richness of algal and fungal mOTUs were used as predictors to model dynamics of PC2 scores as response variables (Table S5). The fitted values of various GAMs were compared with observed PC score values to reveal periods of perturbation and these periods were defined as non-predictable periods which did not follow the gradual changes in climate and catchment conditions. Thereafter, in order to validate the perturbation periods, Bayesian change point probability analysis was applied to the PC1 scores as a proxy (Table 1) to the temporal variability of fossil pigment concentrations mostly driven by climate change. We expected to find a greater difference between model predictions and the observed PC scores during periods of perturbation, which are characterised by more frequent regime shifts or change points; they were obtained from Bayesian model selection, which identifies the strongest association of the linear regression splines of covariates (Erdman and Emerson, 2007).

4. Results

4.1. Stratigraphy of fossil pigments

Degradation index (DI) fluctuated on a large scale during the Late Glacial indicating variable preservation conditions during this period (Fig. 2). The contents of the investigated paleopigments and their ratio to DI (hereafter DI ratio) during the Late Glacial (~14.5–11.65 kyr) were relatively low and fluctuated somewhat, with a considerable increase during the Allerød warming period (~13.3–12.7 kyr) and a sharp decrease thereafter during the Younger Dryas cooling (~12.7–11.65 kyr; except Cantha). Within the Holocene period, DI steadily decreased from the older to the younger sediment layers. During the Early Holocene (~11.65–7.5 kyr) the content of some of the paleopigments (D + D, Zea, Lute, Allo) and their DI ratios gradually increased while the contents of Cantha, Echi, Chl *b*, Perid and their DI ratios remained relatively stable (Fig. 2). The values of the studied paleopigments and their DI ratios were maximal at ~6.0 kyr, in the Mid Holocene. Thereafter, the contents of paleopigments and their DI ratios decreased, followed by another increase after ~2.0 kyr, except in Chl *a* and β–car.

4.2. Richness of eukaryotic algae in sedaDNA

In total, 257 eukaryotic phototroph mOTUs (subset of phototroph data from Kisand et al., 2018) were identified over the whole sediment core, the richest taxon being *Chlorophyta* followed by *Chrysophyta*, *Dinoflagellata*, and *Bacillariophyta* (Table S1). The richness of phototrophs showed no trends until the last ~2.0–2.5 kyr, ranging from a few to several tens of individual mOTUs per analysed layer (Fig. S1). The overall maximum number of mOTUs per layer was 69 (mean = 10). During the last ~2.0 kyr there was a trend of increasing richness. The main difference between the last ~2.0 kyr and the earlier Holocene periods was the greater richness of *Chlorophyta* in the older samples. The richness of all other phyla was greater during the last ~2.0 kyr. Identification of various phototrophs using 18S rDNA fragment did not allow very high resolution of taxonomy, therefore only few mOTUs (n = 3) were possible affiliate at genus level, which both belonged to *Dinoflagellata* (two *Ceratium* spp and one *Woloszynskia* sp mOTUs). The rest of the mOTUs remained classified at higher taxonomic resolution. The negative controls included only a small number of possibly fungal mOTUs with few reads (Kisand et al., 2018) that were distinct from other detected species.

4.3. Richness of possible fungal parasites of eukaryotic algae in sedaDNA

The sub-dataset of 180 mOTUs from ITS analysis (Talas et al., 2021) assigned as fungi possibly parasitic on algae (Table S2) were recovered from the whole sediment core. The used extraction negative controls contained only 2 mOTUs (*Ascomycota* and unidentified fungi with ~4 reads). Most of the possible fungal parasites of algae identified belonged to the phylum *Rozellomycota* (162 mOTUs) and *Chytridiomycota* (17 mOTUs). While most mOTUs were affiliated with a low taxonomic level, some mOTUs could only be assigned at high levels (Table S1). According to ITS analysis a very small number of mOTUs were represented by phylum *Ascomycota* (1 mOTU) and *Chytridiomycota* (17 mOTUs). At the same time, 17 mOTUs were assigned at the order level (*Lobulomycetales* (2

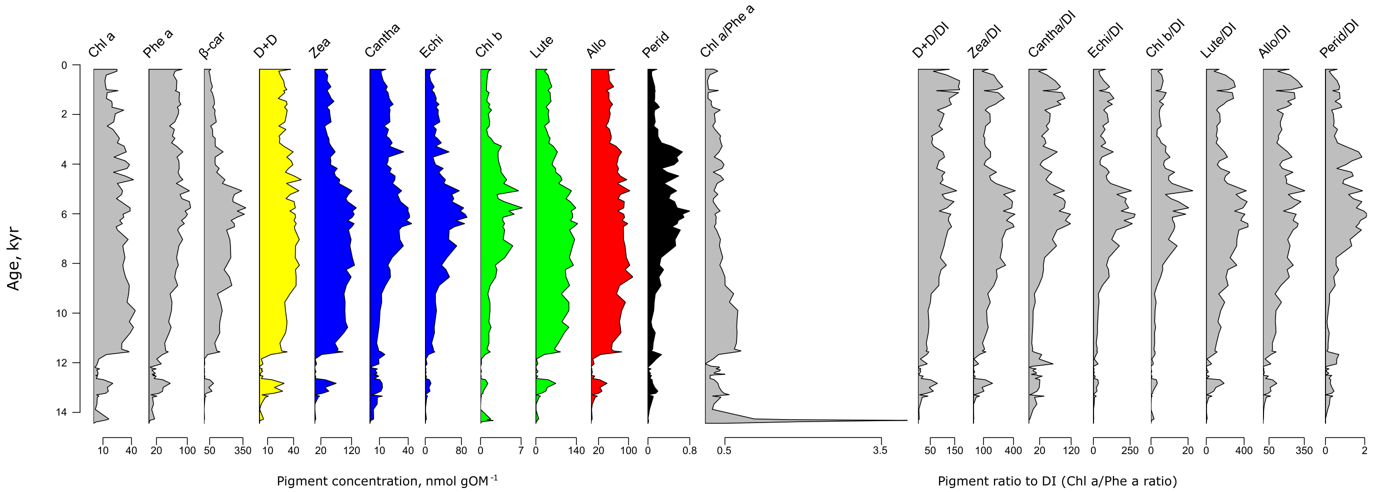

Fig. 2. Dynamics of fossil pigment concentration and ratio to degradation index (DI). Chlorophyll *a* – Chl a; Pheophytin a – Phe a; β, β–carotene – β–car; Diadinoxanthin + Diatoxanthin – D + D; Zeaxanthin – Zea; Canthaxanthin – Cantha; Echinenone – Echi; Chlorophyll *b* – Chl b; Lutein – Lute; Alloxanthin – Allo; Peridinin – Perid; DI corresponds to the Chl a/Phe a ratio.

mOTUs), *Rhizophydiales* (9 mOTUs), *Chytridiales* (6 mOTUs) in phylum *Chytridiomycota* and 1 mOTU at the family level (*Halosphaeriaceae*, phylum *Ascomycota*). The greatest richness of fungi possibly parasitic on algae was discovered in the last ~2.0 kyr with a maximum of 50 mOTUs per layer (mean = 20). The mean richness in the Late Holocene (~4.0–2.0 kyr) was six mOTUs per layer with a maximum of 12. The richness in all other periods (Mid and Early Holocene) was very low (mean two mOTUs and maximum five per layer). Most of the mOTUs of fungi possibly parasitic on algae detected (88%) were located in the last 3.5 kyrs (*Rozellomycota* and *Chytridiomycota*). However, the only species detected in the phylum *Ascomycota* positioned in the Mid Holocene (~4.7 kyr).

4.4. Environmental drivers, disturbance periods, and change points

Most of the variation in PCA space of fossil pigment concentration is associated with PC1 (Fig. S2a). The RDA revealed that such variation might be driven by major climate and climate-dependent vegetation changes in the region (Table S3; Fig. S2b), monotonous climate warming (T_{sum}) and continentality (T_{sum} - T_{win}) peaking in Holocene Thermal Maximum (~8.0–4.0 kyr) followed by monotonous cooling. This reversion was distorted around ~2.5 kyr, associated with HRP accumulation rate and increased charcoal particle AR in the RDA (Fig. S2b; Table S3).

To address the potentially non-linear response of phototrophs biomass (i.e., paleopigment concentration; and the lake ecosystem in general) to the environmental paleoproxy changes (i.e. T_{sum}, S_{tol}, Ch AR, *Botry* AR, FeS_2), the GAM approach was applied to the PCA sample scores of individual pigments/DI (Table S4). PC1 is strongly related to T_{sum} (Table S4, model GAM A; Fig. S3), while PC2 is related to charcoal (Ch AR), pyrite (FeS_2), and humification proxies (i.e., AR of *Botryococcus* (Botry); Table S4, model GAM B; Fig. S4). Comparing the fitted predictions of PC1 to real scores, three disturbance periods deviating from gradual change were identified when GAM A (model using climate and vegetation as predictor variables) explained the observed dynamics of phototroph biomass poorly (Fig. 3a); prediction of PC2 scores was better using GAM B (Table S4, model GAM B). The association of perturbation periods with possible regime shifts was confirmed by Bayesian change point analysis, that increased the difference between observed and predicted PC1 scores associated with the high frequency of changes probability (Fig. 3b).

Further, the discrepancy between modelled and observed PC2 scores is associated with the increase in the richness of phototrophs (number of mOTUs). I.e., model GAM C (Fig. 4; Table S5) indicates that PC2, which describes a remaining variability not included in PC1, is significantly related to increased total richness (S.obs), and specifically to the mOTUs affiliated with *Chlorophyta* (Table S5, model D; Fig. S5). This association is most pronounced for the last ~2.5 kyr (Fig. 4). The non-linear change of richness of parasitic fungi during past millennia was associated most strongly (R2 = 0.479, $p < 0.001$) with changes in the potentially additive effect of climate change and human activity.

5. Discussion

As revealed from earlier studies, development of lake ecosystems was predominantly modulated by gradual climate changes (i.e., average temperatures; Fig. 1b) over the period after ice-recession (from ~14.5 kyr to present) from the area (Seppä and Poska, 2004; Heikkilä and Seppä, 2010; Veski et al., 2015). The phototroph community, which is a keystone functional group of lake ecosystems (Jeppesen et al., 2014), became gradually more abundant in biomass when both average winter and summer temperatures rose (Fig. 1b), and most probably formed blooms during the HTM (~8.0–4.0 kyr; Tõnno et al., 2019). Thereafter, following climate cooling, the phototroph biomass decreased (Fig. 2). In addition, abrupt temperature changes – strong perturbations to all lifeforms, especially in the Post-Glacial (Stivrins et al., 2016) - caused immediate high-amplitude variability in phototroph biomass (Fig. 2). Nevertheless, we were able to identify several perturbation periods leading to change points when the apparently smooth relationship between driver and ecosystem status yielded to a threshold-type response of the phototroph community (i.e., richness) and biomass (i.e., paleopigment concentration; Fig. 3a). There were no drastic changes of mOTU richness of algae before ~2.5–3.0 kyr when the increase in richness boosted (Fig. 4). The fungal mOTUs of possible algal parasites appeared at low abundance after the Post-Glacial period and showed a concerted boost in richness within the Late Holocene (Fig. 4). This change in organismal richness can be identified as the appearance of a novel external forcing, i.e. anthropogenic pressure. Human impact caused diversification of the eco-niches, leading to higher species richness but also to greater competition (Fig. 4b).

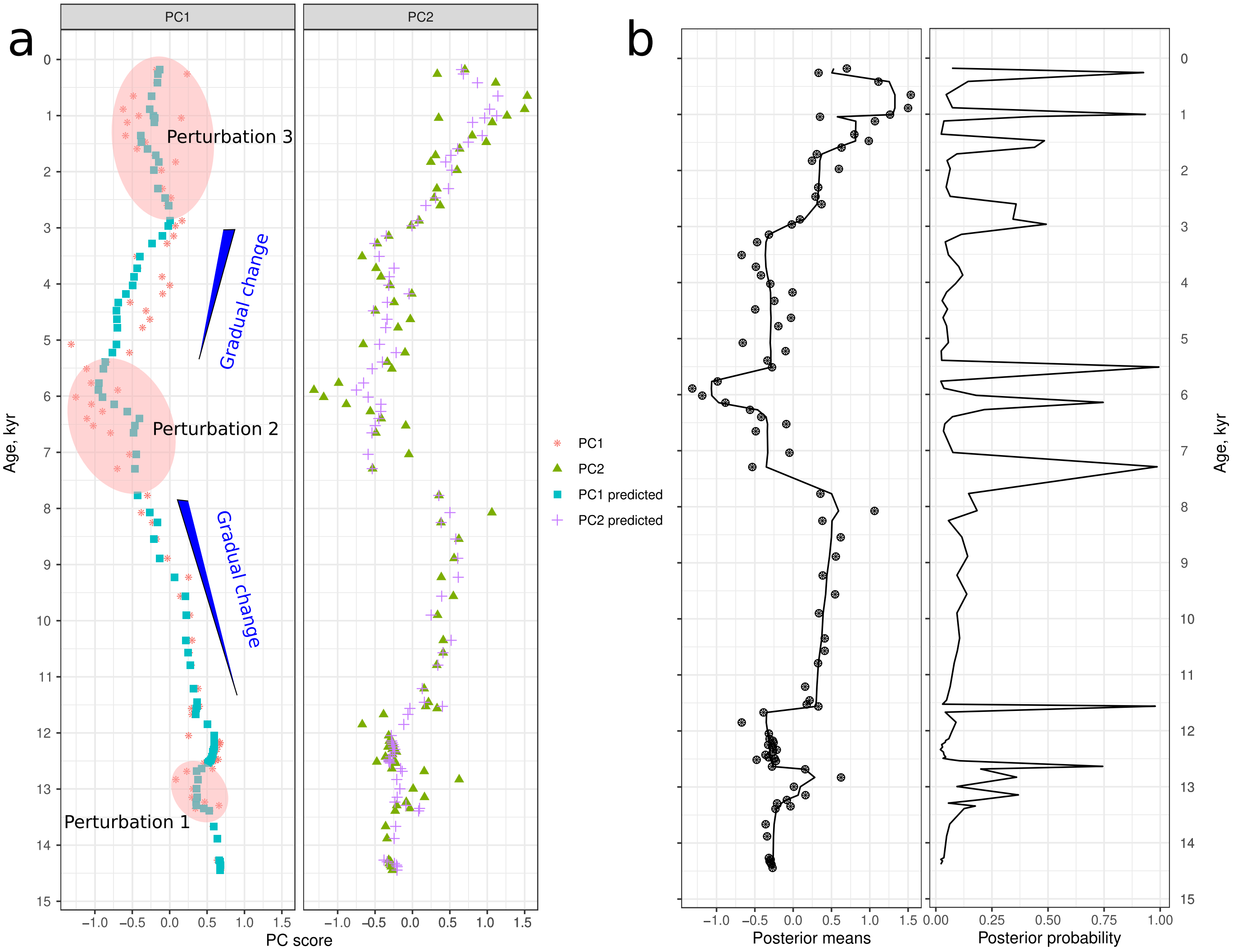

Fig. 3. Comparison of dynamics of PC scores of pigment:DI data. (**A**) Fitted values of these PC scores by GAM using explanatory variables indicated in Table S4. PC1 scores are modelled with T_{sum} and S_{tol}; PC2 scores with Ch AR and Botry (*Botryococcus*) AR. Blue lines indicate the gradual changes due to temperature change. Red ellipses denote perturbation periods from 1 to 3, which are the time periods used for fitting PC1 to climate (T_{sum}) divergence (statistical anomalies) and are better explained by PC2 scores fitted to Ch AR and Botry AR. (**B**) Bayesian change point analysis of PC1 scores, Posterior Means: location in the sequence versus the posterior means over the iterations (left), location in the sequence versus the relative frequency of iterations that led to a change point - posterior probability (of a change) (right). Indication of regime shifts is highly probable during disturbance periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

5.1. *Gradual change periods due to gradual climate change*

We observed two major extensive, multi-millennia gradual change periods mediated by temperature regime change in the Holocene. Gradual changes are characterised by readily-predictable dynamic changes in the concentration of fossil pigments described by PC1 (Fig. 3). From the onset of the Holocene the climate begun to warm (Veski et al., 2015), which obviously favoured the increase of phototroph biomass. This is in line with Stivrins et al. (2018) who revealed a higher turnover rate of phototrophs in the warmer Holocene period compared with the Late Glacial. Warming also favoured forest expansion in areas surrounding Lielais Svētiņu (Veski et al., 2012), which is clearly reflected in the increase of shade tolerance and decrease in the relative openness indices (Fig. S1; Stivrins et al., 2015). Changes in sediment composition (increase of OM) and prevailing anoxic conditions (increase of FeS_2) indicate enhanced production of autochthonous OM, possibly originating from the phototroph biomass and nutrient-rich allochthonous material inflow to the lake, which favoured natural eutrophication process. Indeed, rapid warming resulted in soil instability due to the melting of previously frozen catchment area which favoured terrestrial material inflow to water bodies enriched with nutrients (Liiv et al., 2019). During the ~8.2 kyr cooling event (Veski et al., 2004), the T_{win} dropped by 2–3 °C and the OM content in Lielais Svētiņu sediment decreased (Stivrins et a., 2015; Fig. S1). Surprisingly, no abrupt response could be identified in the present study to this cooling event. The concentrations of some fossil pigments slightly decreased (~8.2 kyr, Fig. 2), but no drastic changes in phototroph community structure (i.e., perturbation) were observed (Fig. 3b). This can be explained by the possibly high resilience of the phototroph community, which had enough time to develop into a well-balanced and diverse community as all major phyla of phototrophs (mOTUs) appeared at the beginning of the Holocene (Fig. 4). According to the study by Stivirins et al. (2018) phototroph turnover happened before and after but not within the ~8.2 kyr cooling event. Also, the increase of algal richness (mainly *Chlorophyta*) during the Early Holocene is confirmed by microfossil analysis (Stivrins et al., 2015).

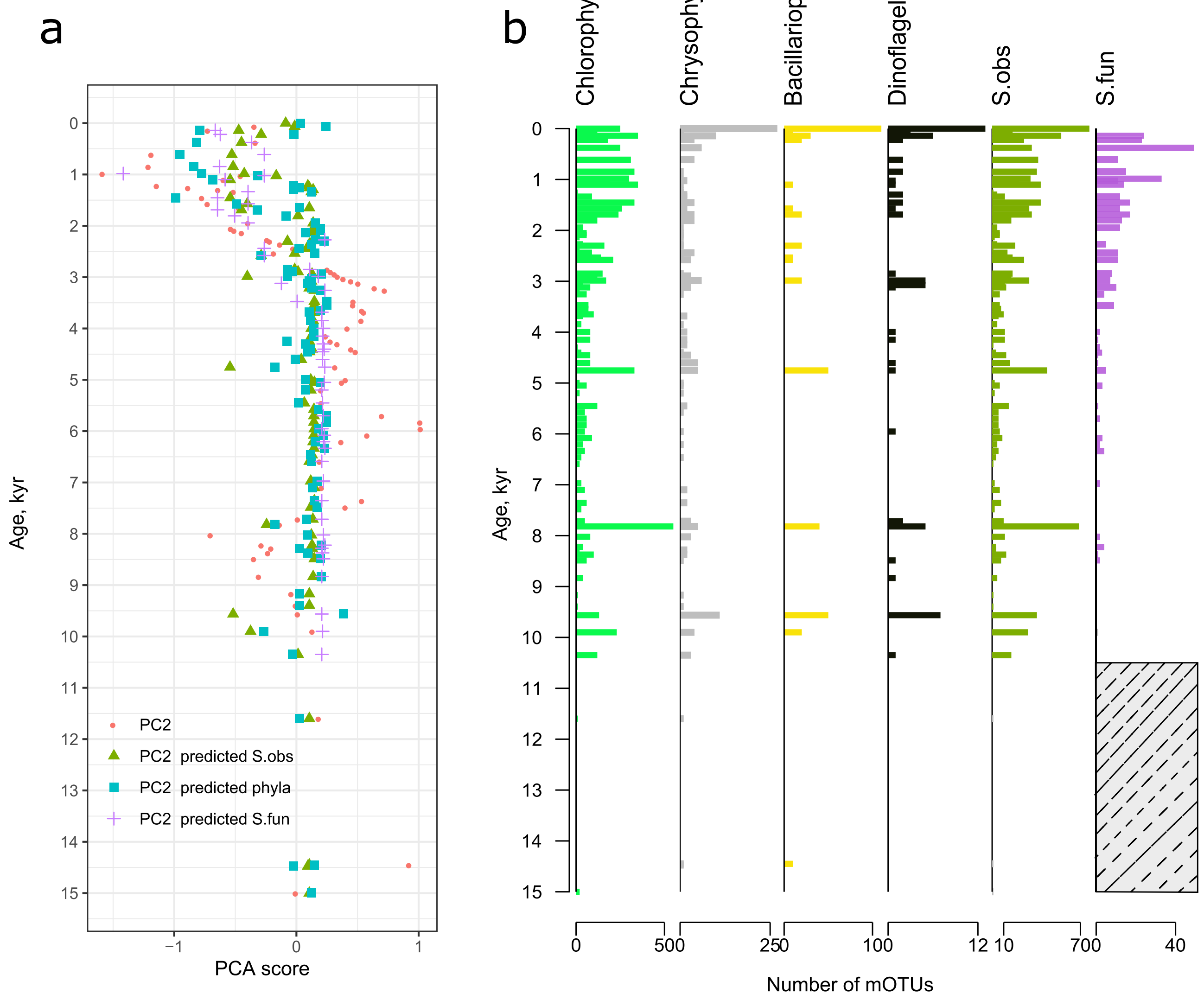

Fig. 4. Comparison of GAM fitted values with PC2 scores from analysis using the subset of pigment ratios (pigment:DI). (**A**) Variables used in the modelling are explained in Table S5. (**B**) Stratigraphy of richness of major phototroph taxon, total richness of phototrophs (S.obs) and fungal parasites/pathogens of algae (S.fun, times series shorter: <10.5 kyr). S.fun not measured in gray area.

The second period of smooth driver–status relationship with a cooling climate (decreasing average summer temperatures and increasing continentality) was shorter, strictly lasting only about 2.5 kyr, from ~5.5 to 3.0 kyr (Fig. 3a). During this gradual change period, the conifer forest developed in areas surrounding LS (revealed by *Picea* pollen and stomata data) and also the peat decomposition decreased after ~5.0 kyr. The latter observation suggests increased soil moisture levels (Stivrins et al., 2015), and in combination with shallowing of the lake water due to sedimentary filling processes (Belle et al., 2018), possibly led to lower light intensity in the lake water column. According to Fritz and Anderson (2013) the presence of a peatland and conifers can lead to acidification of catchment soils which can increase dissolved organic carbon fluxes and cause a decrease of pH in a lake. Indeed, remains of *Botryococcus* in LS sediment point to the presence of incoming dystrophic waters (Jankovská and Komárek, 2000), that can be associated with the paludification processes around the LS (Stivrins et al., 2015). Moreover, the development of conifer forests is generally accompanied by lower soil N, leading to a gradual loss of N from the lake and hampering of in-lake productivity (Fritz and Anderson, 2013) resulting with natural oligotrophication process in Lielais Svētiņu. Such natural climate-driven processes dominated until a new external forcing appeared (see below). The results of the RDA analysis, variability in PC2 (Figs. 3a and 4a), and absorbed covariation of several other environmental proxies (Table S4) revealed an intense association of phototroph dynamics with both in-lake and catchment processes.

5.2. Perturbation periods and their association with change points

Perturbation periods were primarily indicated by the lack of fit between the PC1 scores dynamics and the scores predicted by GAM (Fig. 3a). During the Late Glacial (~14.5–11.65 kyr), the “young”, less resilient (low ecological resilience) and low diverse phototroph community responded abruptly (high biomass versus very low biomass) with no sign of high ecological resilience on the scale of data resolution in the study (interval of a few hundreds of years). Unfortunately, we have no solid mOTU data from the Late Glacial period (Fig. 4b). In the few layers we detected *Chlorophyta*, *Chrysophyta* and *Bacillariophyta* using 18S rDNA fragment analysis. This can be due to poor DNA preservation conditions or high degree of DNA degradation in deeper layers (older samples than ~11.0 kyr) which also showed low amplification success.

More striking is a perturbation during the HTM (~8.0–4.0 kyr), which is considered a stable period in North-Eastern Europe in respect of the surrounding terrestrial ecosystems (Feurdean et al., 2017). In the phototroph community there was a relatively high variability of fossil pigment concentrations from around ~7.5 kyr–5.0 kyr (Fig. 2). Increase of fossil pigments accumulation within HTM was also noticed by Stivrins et al. (2018). The change points most probably fall into the same period (Fig. 3b), though there is a stable period between the first and second change points lasting over ~0.5 kyr. The turnover of phototrophs was lower in period ~6.3–4.7 kyr probably due to that the cyanobacteria blooms indicating prolonged thermal stratification of LS water column (Stivirins et al., 2018). Proposed triggers of the environmental processes behind this perturbation are humification and changed ice-conditions – as a single driver for different change points, or a combination of these processes. Humification in LS was already beginning from the early Holocene (Fig. S2). Indeed, the acid water-tolerant genera *Cryptophyta* (Allo) and *Dinophyta* (Perid) became relatively more abundant than planktonic cyanobacteria (Fig. 2; Reynolds, 2006). This is supported by the appearance of several low pH-tolerant green algae species among the mOTUs affiliated with the genera *Scherffelia*, *Choricystis*, *Desmodesmus* and *Woloszynskia* (Fig. S6; Kessler et al., 1997). Ice-conditions are directly related to climate conditions. The HTM is a period when weak or missing ice-conditions could occur (T_{wint} around −1.5 to −1 °C). Ice cover conditions respond to small changes in temperature in a threshold fashion (Weyhenmeyer et al., 2004), so relatively subtle temperature changes can cause dramatic changes in the lake state. A shorter ice cover duration with no light shading snow on top of the ice can cause a prominent increase in the length of the growing season (Catalan et al., 2013). Therefore, even a tiny recession from the trend could form the basis for the change points in period ~7.5–5.0 kyr.

Earlier studies have demonstrated that rapid threshold-like responses to increased external driver force are often anthropogenic (Randsalu-Wendrup et al., 2016). The first minor human farming activity in the landscape immediately surrounding LS started ~2.0 kyr (Fig. 1b, appearance of HRP) with intensification ~0.6 kyr (Stivrins et al., 2015, 2019). Despite the relatively late immediate anthropogenic forcing, a low impact effect clearly coinciding with the increase of R_{open} (Fig. S1) can be assumed in the region (several thousand km^2) after ~3.5 kyr (Kalnina et al., 2006), best described by the dynamics of PC2 on fossil pigments. Anthropogenic forcing is manifested through the cultivation of forests (an increase of R_{open}), enriching lakes with nutrients and leading to the eutrophication (Stivrins et al., 2015, 2018, 2018). This is mirrored by several observations: a prominent increase in phototroph species and their fungal parasites (number of mOTUs as species proxy; Fig. 4b; Table S5), and an increased frequency of change point posterior probabilities (Fig. 3b). According to Stivrins et al. (2018) increase of phototroph turnover rate from ~1.0 kyr coincides with agricultural activities in Lielais Svētiņu surroundings. There has been a similar increase in the number of species and diversity due to low impact human activity, which we call generic human impact, in large scale areas of vegetation (Reitalu et al., 2015, 2019). Whilst the low impact human activity increased the patchiness of the boreal and semi-boreal forest, offering more niches for various terrestrial species, a similar increase in plant pathogenic fungi and plankton parasites was detected in the lake ecosystem (Talas et al., 2021). The community change of plankton parasitic fungi (~2.0 kyr) has been suggested to be associated with human induced plant material transfer into the lake and therefore richness rise of planktonic organisms (Kisand et al., 2018; Talas et al., 2021). While the biomass of the phototroph community has crashed below the level attained during the HTM, the increase in species richness means capturing new niches or greater competition between phototroph species for the same resources. Because of such competition leads to suboptimal growth conditions, the increased parasite attack rate is obvious (Ibelings et al., 2004 and references therein).

Also, the DNA fragmentation analysis has been performed to the Lielais Svētiņu samples (Talas et al., 2021) to consider the effect of DNA degradation in deeper sediment layers. It showed expected higher degradation in deeper layers (until 9 m), but no bias for the targeted amplicon sizes enabling the successful amplification of the studied regions (18S and ITS2 fragments). Besides, our robust bioinformatic analysis discarding all rare taxa with very low number of reads, will enable us to assess as realistic richness as possible using only the abundant taxa. Furthermore, the high richness of some eukaryotes have been shown also in deeper sediment layers of lake Lielais Svētiņu (Kisand et al., 2018; Talas et al., 2021) suggesting that degradation is not the main factor influencing the richness at least for the first ~10.0 kyr. Still, the amplification success rate was very low in the last ~11.0–15.0 kyr (as mentioned before; Fig. 4b) which could be the result of inefficient DNA extraction or high DNA degradation in these layers.

6. Conclusions

The gradual climate change and gradual development of ecosystems have modulated the changes in aquatic ecosystems of North-Eastern Europe. Gradual climate warming or cooling can induce natural eutrophication or oligotrophication processes in the lake, respectively. Threshold-like responses occur when climate, lake ontogeny, or novel forcing such as human activity disrupts in-lake phototroph communities and climate relationships. The latter forcing can act as generic influencer over larger (thousands of km^2) regions, or direct forcing via traditional agricultural activity near the lake. Low impact disruption can lead to increased microbial biodiversity including various fungal parasites of phototrophs, which could serve as a signature of future perturbation (Pace et al., 2015) leading to future changes in ecological status.

Data availability

Raw sequencing data were deposited at the European Nucleotide archive under project PRJEB17781 (252 samples). The data that support the findings of this study are available from the corresponding author upon reasonable request.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors acknowledge Dr Anne Bjune from University of Bergen and Prof Heikki Seppä for their general comments on the study design.

Funding

Ilmar Tõnno and Rene Freiberg were supported by the Estonian Research Council (ETAg) IUT21-2, PRG705, PRG709 and PRG1167. Veljo Kisand was supported by grants PUT134 and PUT1389 (ETAg) and Institute of Technology, University of Tartu basic funding grant. Siim Veski was supported by IUT1-8 and PRG323 (ETAg). Normunds Stivrins was additionally financially supported by the Latvian Council of Science project No. LZP-2020/2–0060.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.107006.

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