# The Effect of Climate Change on the Palaeohydrology of Subarctic Permafrost Peatlands in Kola Peninsula, Russia

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**Ilona Latsa**

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|---|---|---|
| Ilona Latsa | | |

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Tiivistelmä - Referat - Abstract

Pohjoisilla soilla on merkittävä vaikutus globaaliin hiilen kiertoon suuren hiilivarastonsa sekä vuosittaisten hiilidioksidin ($CO_2$) ja metaanin ($CH_4$) virtausten myötä. Ihmisen aiheuttama ilmastonmuutos voi vaikuttaa soiden hiilidynamiikkaan muuttamalla esimerkiksi perustuotantoon liittyviä prosesseja ja kosteusoloja sekä sulattamalla ikiroutaa. Näiden muutosten vaikutusta pohjoisten soiden kykyyn toimia tulevaisuuden hiilinieluina ei vielä tarkoin tunneta, mutta erityisesti soiden kosteusolojen muutoksilla voi olla merkittävä vaikutus hiilinielun tehokkuuteen.

Tässä pro gradu -tutkielmassa tarkastelen viime vuosisatojen paleohydrologiaa ja turpeen kertymistä Lovozeron ikiroutasuoalueella Kuolan niemimaalla Venäjällä. Käytän kuoriamebojen fossiileja historiallisten kosteusmuutosten indikaattoreina. Muita tutkimusmenetelmiä ovat detrended correspondence – analyysi sekä radiohiili $^{14}$C ja lyijyisotoopin $^{210}$Pb ajoitukset. Muiden tutkimusryhmän jäsenten tuottamat kasvimakrofossiili- ja hiilikertymäaineistot toimivat omia tuloksiani tukevina aineistoina.

Tulokset osoittavat, että eri tutkimusalueiden hydrologiset muutokset ja turpeen kertymisen nopeus erosivat toisistaan menneiden ilmastovaihteluiden aikana. Tämä viittaa siihen, että muutokset johtuvat enemminkin soiden sisäisistä prosesseista kuin ilmastosta. Kuitenkin kaikissa kolmessa suokohteessa oli havaittavissa kuivumista ja turpeen kertymisen kiihtymistä viimeisen vuosisadan aikana. Lisäksi kaikissa kohteissa on tapahtunut muutos kosteampiin olosuhteisiin viimeisen vuosikymmenen aikana. Tämä kosteuden lisääntyminen voi mahdollisesti johtua ikiroudan sulamisen kiihtymisestä. Kuoriameba-aineistossa havaittiin myös miksotrofisten kuoriamebojen määrän lisääntyminen pintakerroksissa. Tämä on saattanut edistää nopeaa turpeen kertymistä suon pintaosissa.

Lovozeron soiden toisistaan poikkeavat historiat sekä viime vuosisadan kehityskulku kohti kuivempia olosuhteita vastaavat muilta pohjoisilta soilta saatuja tuloksia. Viimeaikainen muutos kosteampiin olosuhteisiin poikkeaa kuitenkin muualta pohjoisilta alueilta tehdyistä havainnoista. Vaikuttaa siis siltä, että ilmastonmuutoksen aiheuttamat muutokset soiden hydrologiaan ja/tai turpeen ja hiilen kertymiseen eivät välttämättä ole kaikkialla yhteneviä. Näin ollen lisätutkimuksia edelleen tarvitaan erilaisten suovasteiden tarkempaan selvittämiseen.

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Tiivistelmä - Referat - Abstract

Northern peatlands have a major role in the global carbon cycle due to their carbon stocks and fluxes of carbon dioxide ($CO_2$) and methane ($CH_4$). Anthropogenic climate change may affect peatland carbon dynamics through changes in e.g. primary production, hydrology, and permafrost dynamics. It is uncertain whether these changes will lead to northern peatlands becoming significant sources of carbon to the atmosphere. Changes in moisture conditions especially can be an important factor in determining the carbon sink potential of northern peatlands.

In this thesis I examine the palaeohydrology and peat accumulation over the past centuries in a permafrost peatland complex in Lovozero, Kola Peninsula, Russia. I used testate amoebae as a proxy of past changes in moisture conditions. Other study methods used here are detrended correspondence analysis (DCA) and $^{14}C$ and $^{210}Pb$ dating. The results were also supplemented with plant macrofossil and carbon accumulation data provided by other members of the research team.

The results show varying responses of the peatland hydrology and peat accumulation to the past climatic shifts, suggesting that the changes have been driven more by autogenic factors rather than climate. However, all three sites indicated a drying trend and an increased peat accumulation for the last century. Yet, the last decade is characherised by a wet shift. The wet shifts suggest that the peatlands may have crossed a threshold where increased evapotranspiration is exceeded by increased moisture due to thawing permfrost. The surface peat layers of all three sites were dominated by mixotrophic testate amoebae, which may have contributed to the high peat accumulation.

The inconsistency of past successional pathways identified at Lovozero peatlands and the drying trend over the past century correspond to the previous studies from northern peatlands elsewhere. However, the most recent surface wetting during the last decade differs from what has been reported for the other northern sites. This suggests that the response mechanisms of peatlands to the anthropogenic climate change may not be uniform. Thus, further research is inevitably needed to increase our understanding of peatland-climate intercations.

Keywords
palaeohydrology, testate amoebae, peatland, permafrost, carbon dynamics, climate change

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# 1 Introduction

Northern peatlands play a significant role in the global carbon cycle due to their extensive carbon stocks and the annual fluxes of carbon dioxide ($CO_2$) and methane ($CH_4$) to the atmosphere (Loisel et al. 2014). The carbon dynamics of northern peatlands may change with anthropogenic climate change, as the increase of annual temperatures is projected to be over two times higher than the global average in the Arctic latitudes north of 67.5°N (Collins et al. 2013). Permafrost peatlands in the sporadic and discontinuous permafrost areas at the southern limits of the permafrost zone are especially sensitive, and increased permafrost temperature, increased active layer thickness, permafrost thaw and degradation have already been reported in several locations around the circumpolar north (Schuur et al. 2015; Jones et al. 2016; AMAP 2017).

It is still uncertain how anthropogenic climate change will affect peatland carbon dynamics, and whether the net effect will mitigate the temperature increase or further intensify it (Charman et al. 2013; Gallego-Sala et al. 2018). Carbon dynamics in peatlands are determined by the balance between production and decomposition, which are affected by various allogenic and autogenic factors, such as climate, permafrost dynamics, hydrology and peatland succession (Tuittila et al. 2007; Turetsky et al. 2007; Gallego-Sala et al. 2018). Recent studies have highlighted the heterogeneity of peatland responses to past climatic shifts (Gałka et al. 2017; Zhang et al. 2018b), which complicates predictions of how anthropogenic climate change will affect peatlands and their role as a carbon sink. As a result, more detailed studies are needed to form a more complete understanding of future peatland responses to climate change.

## 1.1 Northern peatlands in the global carbon cycle

When the productivity of peat forming plants exceeds decomposition, peat starts to accumulate. Peat consists of plant and animal remains, and it accumulates in water saturated low oxygen conditions where decomposition is slow (Clymo 1984; Rydin & Jeglum 2006). Accumulated peat retains water creating anoxia, which further slows down decomposition and accelerates peat accumulation. In biology, a peatland is defined by the occurrence of specific peat forming plants, such as sedges and mosses (Korhonen & Vasander 1998). In geology, on the other hand, peatlands are defined by a minimum depth of peat, and generally 30 cm depth is required (Rydin & Jeglum 2006). A widely used model of peatlands portrays a two-layered structure with distinct differences between the

two layers (Clymo 1984). The upper acrotelm is aerobic with a relatively fast decomposition rate, whereas decomposition is slow in the deep, anoxic catotelm (Clymo 1984). Although this model is useful in its simplicity, it ignores the horizontal and spatial heterogeneity that is common in peatlands (Morris et al. 2011).

Peatlands can be categorised based on their water source, since this regulates other peatland qualities, such as primary production, nutrient content and acidity. Ombrotrophic bogs are isolated from the surrounding environment due to their elevated dome shape and only receive water from precipitation, which results in poor nutrient status, low pH and low production (Rydin & Jeglum 2006). Minerotrophic fens, on the other hand, have their surface below the surrounding environment and receive water from mineral soils and ground water (Rydin & Jeglum 2006). This creates more nutrient rich ecosystems with higher production rates (Rydin & Jeglum 2006).

Furthermore, permafrost formation affects peatland dynamics. Permafrost can form when the ground temperature remains below 0°C for a minimum of two years (Harris et al. 1988). Peatlands cover ca. 19% of the northern circumpolar permafrost region (Tarnocai et al. 2009). Permafrost peatlands consist of bog-type frozen hummocks patterned with more minerotrophic, fen-type depressions (Vitt 2006, p. 13). The expansion of volume as water freezes raises the peat surface, forming palsas or peat plateaus (Seppälä 2011). Permafrost aggradation can also limit primary production and change peatland hydrology by desiccating the surface of peat mounds (Christensen et al. 2004; Seppälä 2011; Treat et al. 2016).

Palsa peatlands are common features at the southern limits of the discontinuous permafrost zone (Seppälä 2011). In Northern Europe, palsa formation was extensive during colder periods around 2000 and 600-100 years ago (Oksanen & Väliranta 2006). However, in northern Norway in 1950-2010, a significant decrease of 33-71% in the area of peat plateaus and palsas has been observed (Borge et al. 2017). While the reasons behind this loss of area are uncertain, the reduction in the areal extent has coincided with increases in air temperature, precipitation, and snow depth in the area (Borge et al. 2017)

The accumulation of organic material as peat over thousands of years has turned northern peatlands into significant carbon stores, but the estimates of the total carbon stock vary. For areas north of 45°N, the peatland carbon stock is approximated to be ca. 400-600 Pg with the uncertainty mainly stemming from unevenly distributed data, or a lack of data (Yu et al. 2010; Yu 2012; Loisel et al. 2014). Of this stock, ca. 277 Pg, i.e.

more than 50%, is stored in permafrost peatlands (Schuur et al. 2008). A recent study suggests almost a doubling of the previous estimations with a storage of 1055 Pg (Nichols & Peteet 2019). However, the methodology used in this paper, such as the same carbon density value used in all sites, has been questioned by the authors of the previous estimates (Yu et al. 2019).

While there are variations and uncertainties in the estimations, the carbon storage in the northern peatlands is nevertheless significant when compared with the ca. 800 Pg carbon stock of the atmosphere (Ciais et al. 2013). Thus, the potential release of this carbon back to the atmosphere could create a positive feedback to anthropogenic climate change. In one estimation, the thawing of sporadic and discontinuous permafrost areas alone by the end of the century could release up to 24 Pg of carbon from permafrost stores (Jones et al. 2017). However, the northern peatlands could also help to mitigate climate change due to their potential for further carbon storage, and it is estimated that northern peatlands could remove up to $328 \pm 74$ Pg of carbon from the atmosphere before the end of the current interglacial (Alexandrov et al. 2020).

Peatlands are a part of the global biogeochemical cycle by sequestering $CO_2$ via photosynthesis and by emitting both $CO_2$ and $CH_4$ back to the atmosphere through respiration and decomposition (Moore & Knowles 1989; Gorham 1991). The radiative forcing effect of peatlands can partly depend on the ratio of these gases, as $CH_4$ has a 25-times higher warming potential than $CO_2$ in a 100-year period (Whiting & Chanton 2001; Forster et al. 2007). Over time, the forcing effect typically changes with the autogenic succession and lateral expansion of the peatland (Frolking & Roulet 2007; Mathijssen et al. 2014). During the Holocene in the last 11 500 years, the net forcing effect of the northern peatlands has been cooling, even though initially they had a warming impact due to large emissions of $CH_4$ during peatland formation (Frolking & Roulet 2007). The average carbon accumulation (CA) rate of northern peatlands has been ca. 23 g $C/m^2$/year over the Holocene (Loisel et al. 2014). In permafrost peatlands, CA rate has varied in the range of 10.80–32.40 g $C/m^2$ /year (Zhang et al. 2018a), and it has generally been lower than in non-permafrost areas (Treat et al. 2016).

## 1.2  Drivers of peatland carbon dynamics

### 1.2.1  Climate

Climate has varied significantly over the whole interglacial period and in the past 2000 years, and several decadal and centennial scale temperature fluctuations have occurred in the Northern Hemisphere (Ljungqvist 2010; Wilson et al. 2016). Two time periods especially differ considerably from long-term average temperatures (Wilson et al. 2016). During the Medieval Climate Anomaly (MCA) in AD 900-1250, temperatures were above average in the Northern Hemisphere (Mann et al. 2009; Wilson et al. 2016). This was followed by a cold period, the Little Ice Age (LIA), from AD 1450-1850 (Mann et al. 2009; Ljungqvist 2010; Wilson et al. 2016). Since the LIA to the present, climate has warmed, and lately especially due to anthropogenic climate change (Wilson et al. 2016). A synthesis of both simulations and different hydroclimate proxies around the Arctic suggests wetter conditions for the MCA and drier for the LIA, but the variation between different regions is considerable (Linderholm et al. 2018). For example in Fennoscandia, multiple proxies indicate a drier MCA and a wetter LIA (Linderholm et al. 2018; see also Väliranta et al. 2007)

Similarly to climate, the carbon accumulation rates of both permafrost and non-permafrost peatlands have varied considerably over the Holocene (Yu et al. 2009; Loisel et al. 2014; Gałka et al. 2017; Zhang et al. 2018a). These historical variations in carbon accumulation and their link to climate can help to constrain the factors that most effectively influence peatland carbon dynamics. During the Holocene, the highest CA rates have generally coincided with warmer temperatures, such as the Holocene Thermal Maximum (HTM) ca. 9000-5000 years ago (Yu et al. 2009; Loisel et al. 2014). In addition, some of the lowest CA rates have occurred during cooler periods, such as the LIA (Lamarre, Garneau & Asnong 2012). This suggests a strong climatic forcing on peatland carbon accumulation rates (Loisel et al. 2014). Indeed, some studies have found photosynthetically active radiation to be the most significant factor affecting carbon accumulation due to its positive effect on primary production (Charman et al. 2013; Gallego-Sala et al. 2018).

Thus, it seems that climate has a significant influence on peatland carbon dynamics. With anthropogenic climate change and projected temperature increases, carbon uptake in peatlands may also increase (Charman et al. 2013; Loisel et al. 2014). Increased CA rates have already been observed at certain locations, but CA dynamics

have not been regionally consistent despite the recent increase in temperatures (Zhang et al. 2018a). Furthermore, it is important to treat modern accumulation values with caution as accumulation rates often appear higher in the surface layers due to the incomplete decomposition of peat (Lamarre et al. 2012; Zhang et al. 2018a; Piilo et al. 2019; Young et al. 2019).

During the Holocene, CA rates were not always universally compatible with temperature patterns. For example, Gao & Couwenberg (2015) noted the highest CA rates in North Eastern Russia during the cold period LIA. Furthermore, CA rates remained very low during the warm mid-Holocene period in a subarctic fen in Finnish Lapland (Mathijssen et al. 2014). Varying CA rates have also been observed in studies that applied multiple-core approach: adjacent sampling points from the same peatland indicate that other drivers than climate have determined carbon accumulation (Zhang et al. 2018a). The ultimate effect of climatic change can also depend on the vegetation composition of the peatland, as fens seem to be more sensitive to environmental changes than bogs (Kokkonen et al. 2019).

These variations in carbon accumulation rates show that carbon dynamics are complicated, and climate is not the only factor influencing carbon accumulation. The effect of climate can be indirect and mediated through changes in e.g. hydrology, permafrost and local topography (Belyea & Malmer 2004; Yu et al. 2009). In addition, many autogenic factors, such as peatland succession, regulate carbon accumulation (Gao & Couwenberg 2015; Zhang et al. 2018b). Consequently, the response of peatland CA rates to anthropogenic climate change cannot be assumed to be straightforward.

### 1.2.2 Hydrology

The significance of peatland hydrology on $CO_2$ and $CH_4$ fluxes is well established. Experimental studies have shown that lowering of the water table increases $CO_2$ release almost linearily (Moore & Knowles 1989; Silvola et al. 1996; Nykänen et al. 1998; Laine et al. 2019). In their experiments, Laine et al. (2019) also noted that temperature increase alone did not affect $CO_2$ dynamics, but when combined with drying of the peatland, $CO_2$ emissions increased significantly due to increased respiration. For methane emissions, water table fluctuations have the opposite effect. As water table is lowered, there may be an initial increase in $CH_4$ release from soil pores (Moore & Roulet 1993), but eventually the release of methane decreases significantly (Moore & Knowles 1989; Moore & Roulet

1993; Natali et al. 2015). Thus, the drying of a peatland increases $CO_2$ release but decreases $CH_4$ emissions, while wet surfaces emit more $CH_4$ which has higher warming potential than $CO_2$.

The effect of hydrology on peatland carbon storage can be complex. Occasionally, carbon accumulation seems to be influenced more by other factors than moisture, as high or stable CA rates have occurred during both wetter and drier periods (Loisel & Garneau 2010; Lamarre et al. 2012; Gao & Couwenberg 2015; Gallego-Sala et al. 2018). Gallego-Sala et al. (2018) suggested that when the moisture level of a peatland is sufficient to decrease decomposition, further increases in moisture do not impact carbon accumulation. This would indicate that moisture acts as an on-off switch: while an increase in moisture may not have a significant effect, a substantial drying of the peatland could impact carbon dynamics by accelerating decomposition and respiration.

### 1.2.3 Vegetation and peatland succession

Peatland hydrology is closely connected to the autogenic succession of peatlands and it determines the vegetation composition (Tuittila et al. 2007). As the peat layer thickens, the autogenic succession of peatlands usually follows a transition from wet, minerotrophic fen to drier, ombrotrophic bog (Väliranta et al. 2017). With the succession, the dominating vegetation shifts from sedges and forbs to *Sphagnum* mosses (Tuittila et al. 2013; Väliranta et al. 2017). These changes in water table position and vegetation composition affect the carbon dynamics of peatlands.

Minerotrophic fens emit significantly more $CH_4$ than ombrotrophic bogs, mainly due to the higher water level and the dominance of graminoid species (Nykänen et al. 1998; Turetsky et al. 2014). Thus, as a consequence of the autogenic succession, the $CH_4$ emissions from peatlands tend to decrease over time (MacDonald et al. 2006). The reduced $CH_4$ emissions of bogs may be partly due to the methane-consuming bacteria that live with *Sphagnum* (Larmola et al. 2010). *Sphagnum* and graminoids also differ in other qualities. For example, *Sphagnum* litter decomposes more slowly than sedge litter due to their recalcitrant structure, enhancing peat accumulation in bogs (Turetsky et al. 2008). On the other hand, sedges have higher rates of photosynthesis than *Sphagnum* contributing to the higher production rates of fens (Leppälä et al. 2008). All of these factors impact the carbon fluxes and carbon accumulation rates of peatlands, and

ombrotrophic bogs have been found to generally have higher carbon accumulation rates than fens (Tolonen & Turunen 1996; Turunen et al. 2002).

### 1.2.4 Permafrost thaw dynamics

In permafrost peatlands, the aggdaration and thawing of permafrost can significantly affect the carbon dynamics. The presence of surface permafrost tends to slow carbon accumulation and reduce $CH_4$ emissions in peatlands (Turetsky et al. 2007; Turetsky et al. 2014), while permafrost thaw has the opposite effect (Camill et al. 2001; Turetsky et al. 2007; Treat et al. 2016). Thus, climate change could increase the carbon sequestration in peatlands following permafrost thawing. However, also more complex response scenarios exist to permafrost thaw. While permafrost thaw can lead to higher carbon sequestration at the surface, simultaneously the organic matter in the deeper layers may start to decompose faster (O'Donnell et al. 2012; Jones et al. 2017). Another view is that permafrost thaw leads to net loss of carbon initially, but that the peatland ecosystem retains its sink function in about a decade after thaw (Jones et al. 2017). In any case, permafrost thaw and the decomposition of deeper layers could lead to increased carbon release from permafrost peatlands.

Permafrost thaw likely impacts peatland hydrology. Zhang (2018) compiled several different scenarios of how peatland hydrology and carbon dynamics could be affected following permafrost thaw. As warmer temperatures can both thaw permafrost and increase evapotranspiration, the balance between these two components determines whether the peat surface will get drier or wetter. In the case of increased moisture, production and therefore carbon accumulation may increase, whereas dryness can limit production. More minor permafrost thaw may lead to surface drying, if thaw waters are drained from the peatland or if evapotranspiration is high. However, according to a model by Swindles et al. (2015c), a more significant permafrost thaw can cause the peat surface to collapse leading to water-saturated conditions and the development of a fen ecosystem with both higher primary production and $CH_4$ emissions.

The carbon emissions and resulting positive forcing impact on the climate seem to be higher from dry, aerobic permafrost peatlands than from wet, anaerobic conditions, even when accounting for the higher forcing effect of $CH_4$ from water-saturated soils (Schuur et al. 2015; Schädel et al. 2016). Increase in temperature also enhances ecosystem respiration and thus more carbon is released under dry conditions than wet conditions

(Oberbauer et al. 2007; Laine et al. 2019). Thus, whether northern peatlands will become drier or wetter due to climate change may have a significant impact on their future carbon sink function and their climatic forcing impact.

## 1.3  Past changes in peatland hydrology in the north

As peatland hydrology is one of the factors that drives carbon dynamics, it is important to assess how anthropogenic climate change might alter peatland moisture conditions. To improve estimations, it is useful to trace how past climatic shifts have affected peatland hydrology. Many reconstructions of past peatland hydrology have been conducted in various regions, and their conculsions and results also vary. During the warm MCA, there were several shifts towards wetter conditions in peatlands in Canada, Finland and Russia, but the Finnish and Russian sites also experienced some drier shifts (Loisel & Garneau 2010; Zhang et al. 2018b). On the other hand, the cold LIA coincided with dry conditions in many Russian and Fennoscandian peatlands (Väliranta et al. 2007; Gałka et al. 2017; Zhang et al. 2018b), whereas western Europe and Canada were generally wetter (Charman et al. 2006; Loisel & Garneau 2010). Thus, it is challenging to determine any general hydrological trend for northern peatlands as a whole for the past climatic shifts.

Peatland hydrology is affected by various factors in addition to climate. Periodically, climate can be the dominant factor causing drying due to increased evapotranspiration or permafrost aggradation, or wetter conditions due to permafrost thaw (Swindles et al. 2015c; Zhang et al. 2018b). However, the various hydrological developments in different locations during similar climatic conditions indicate that changes in moisture can often be controlled more by local topographical and autogenic factors than climate (Väliranta et al. 2007; Loisel & Garneau 2010; Lamarre et al. 2012; Gałka et al. 2017). Furthermore, climatic influence can initially cause an effect, which is then enhanced by autogenic factors. A model constructed by Ise et al. (2008) suggests that as warmer temperatures lead to higher evapotranspiration and decomposition, the water holding capacity of the soil is reduced leading to more significant drying than by evapotranspiration alone.

Despite the complicated climate-peatland relationships in the past, recent data show more consistency. Several permafrost peatland ecosystems and peatlands without permafrost in Northern Europe and Canada have become drier in the recent decades with the rising average temperatures (Väliranta et al. 2007; Lamarre et al. 2012; Swindles et

al. 2015c; Gałka et al. 2017; Zhang et al. 2018b). Some peatlands at later stages of permafrost degradation have had wet shifts (Swindles et al. 2015c), while in other permafrost peatlands the drying trend is visible, even when thawing initially led to increase in moisture and higher water tables (Gałka et al. 2017; Zhang et al. 2018b). Furthermore, a pan-European analysis of 31 peatlands shows significant drying in 69% of the sites and wetter shifts only in 7% of the sites in the last ca. 300 years due to both climatic and human influence (Swindles et al. 2019).

## 1.4 Testate amoebae as indicators of hydrology

A traditional method to reconstruct past peatland hydrology is testate amoeba analysis (Charman 2001; Booth 2008). Testate amoebae are small (20-300µm), single-celled protists that live on surface vegetation and are common in minerotrophic and ombrotrophic peatlands (Charman 2001; Mitchell, Charman & Warner 2008). Many of the known ca. 2000 species have a cosmopolitan distribution (Charman et al. 2007; Mitchell et al. 2008). Testate amoebae produce a shell, i.e. a test, with an aperture through which they use pseudopodia to move and feed (Charman 2001). Based on whether the amoeba itself produces the material for the test or it uses material from its environment for test construction, testate amoebae can be defined as idiosomic and xenosomic, respectively (Charman 2001). The shape and position of the aperture(s), test shape and material can thus be used in taxonomic identification (Charman et al. 2000).

Since the tests are preserved in peat layers, fossilized testate amoebae shells form biological archives that can be utilized for palaeoecological reconstruction. Especially in bog environments, testate amoeba distribution is most prominently affected by moisture conditions, so they can serve as a useful proxy for reconstructing past hydrology of peatlands and the past climate (Tolonen, Warner & Vasander 1994; Charman 2001; Mitchell et al. 2008). Moisture has been found to be the dominant factor controlling testate amoebae distribution also in permafrost peatlands, though their tolerance ranges may be more constricted in permafrost areas due to more extreme conditions (Swindles et al. 2015a; Zhang et al. 2017). An advantage of testate amoebae as hydrological indicators over the plant assemblage analyses is that amoebae seem to react to changes in moisture conditions faster, and thus they are better suited to reconstruct short-term changes in moisture conditions (Loisel & Garneau 2010; Väliranta et al. 2012; Secco et al. 2016). However, pH and nutrient availability seem to be strong controls of testate

assemblages in fen environments complicating the data interpretation in these ecosystems (Zhang et al. 2018c). Furthermore, peatlands with varying nutrient conditions, such as bogs and fens, may exhibit different testate amoebae assemblages (Payne 2011).

In palaeoecology, transfer functions are used to make quantitative reconstructions of past environmental variables (Birks et al. 1990). With transfer functions, fossil testate data are transferred into quantitative measures of water table depth (WTD) or moisture content on the basis of modern testate amoebae assemblages and their ecology (Amesbury et al. 2016; Zhang et al. 2017). However, the quantitative reconstruction values should not be interpreted as very accurate (Swindles et al. 2015b; Amesbury et al. 2016). To improve the reliability of the interpretation, residual or standardized values (z-scores) are used instead to indicate more robust directional changes in hydrology (Swindles et al. 2015b; Amesbury et al. 2016). Some of the inaccuracy of the reconstructions stems from the fact that dry taxa have wider habitat ranges than wet taxa, which complicates reconstructing dry periods especially (Charman et al. 2007; Amesbury et al. 2016; Zhang et al. 2017). Despite these challenges, testate amoebae have been demonstrated to be a robust proxy for hydrological shifts (Swindles et al. 2015a; Amesbury et al. 2016). In addition, using multiple proxies, such as combined testate amoebae and plant assemblages, increases the reliability of the reconstructions (Loisel & Garneau 2010; Väliranta et al. 2012).

## 1.5 Hypotheses

As results from previous studies have shown great variety in the resposes of northern peatlands to past climatic shifts, the future responses of these peatlands to the anthropogenic climate change are difficult to estimate and may be equally variable. The developments in hydrology can determine whether northern peatlands will mostly remain carbon sinks or become carbon sources. Further research, especially in the form of site-based studies, is needed to form a better picture of the responses of different peatland types to climate change.

To provide more insight about site specific developments in peatland hydrology, in this thesis I examine how permafrost peatland moisture conditions have varied in the past in a peatland complex in Lovozero, Kola Peninsula, Russia. The study period focuses on the Little Ice Age (1850s) and the subsequent warming, but some data was also obtained from earlier periods. I studied three peat sections from the same peatland

complex (Figure 1) to obtain a replicate, more representative, dataset. I used testate amoebae analysis to reconstruct past changes in moisture conditions.

The Lovozero peatland complex is located at the zone of sporadic permafrost and is thus sensitive to changes in climate (cf. Zhang et al. 2018b). It is expected that the Lovozero peatlands would have followed a similar recent drying trend found in other nearby permafrost peatlands (e.g. Gałka et al. 2017; Zhang et al. 2018b). Based on this, my hypotheses are:

1) past shifts in climate have resulted in changes in Lovozero peatland moisture conditions,
2) moisture shifts are reflected as changes in testate amoeba communities,
3) recent warming since the ca. 1980's has resulted in surface drying.

I had plant macrofossil data and carbon accumulation data produced by other team members available for comparison. The plant macrofossil data was used to verify the changes in WTD indicated by testate amoebae data. Furthermore, Ahonen (2019) from the same research team had conducted testate amoebae analyses in Northern Sweden in her Master's Thesis, and these unpublished data were also available for comparison. My work is tightly linked to an on-going project coordinated by docent M. Väliranta, where the response of northern peatlands to climate change is investigated using a multiproxy approach. The project is funded by the Academy of Finland, and my study will provide data to this project.

# 2 Material and methods

## 2.1 The study sites

The three study sites (Figure 1) are in the sporadic permafrost zone of Kola Peninsula, in Lovozero, Murmansk. The Lovozero peatland complex expands over 3,000 ha on the shore of Lake Lovozero and consists mainly of palsa and aapa peatlands (Elina, Lukashov & Yurkovskaya 2010, p. 104). Over the time period 1966-2015, the mean annual temperature at Lovozero was -1.2 °C and mean annual precipitation was 479 mm (Marshall, Vignols & Rees 2016). In this 50-year period, the Kola Peninsula region has experienced statistically significant warming of 2.3°C ± 1°C (Marshall et al. 2016).



*Figure 1 a) A general view of the study region b) The locations of the LOV1, LOV2 and LOV3 coring sites.* Google Earth, *earth.google.com/web/.*

Three ca. 50 cm long peat cores were collected with a box corer from three sections of the peatland complex in August 2018. One core from each peatland section is analyzed in this thesis. The cores were collected from plateaus between higher hummocks and lower wet areas. In the three cores used in this thesis, the corer did not reach permafrost. Local member of the group, Dr. Natalia Koroleva, had visited the site ca. a decade earlier and they had observed permafrost. Thus, the permafrost may have partly thawed since then or seasonal frost may have remained longer the year of the previous visit.

The core LOV1 was collected from a *Spagnum* lawn of an aapa mire at location 67°68'N, 35°04'E (Figure 2a, d, g). Even though the corer did not reach permafrost, permafrost occurred at 55 cm depth in an adjacent core from this same peatland section. The forest edge was ca. 30 meters from the coring site. Vegetation was characterized by the moss *Sphagnum fuscum*, accompanied by several dwarf shrub species, such as *Rubus*

*chamaemorus*, *Andromeda polifolia*, *Empetrum nigrum*, *Betula nana, Vaccinium uliginosum* and *V. oxycoccos*.

During sample collection the peatland was dry with a water table depth, hereafter WTD, of 35 cm. The dry conditions may be partly influenced by the exceptionally hot and dry July in 2018. In Lovozero, the average temperature was 19 °C and precipitation 14.07 mm with only 6 days of rain in July 2018, when the 2009-2017 July averages have been 13.11 °C, 40.45 mm precipitation, and 17.78 days of rain (World Weather Online 2019).
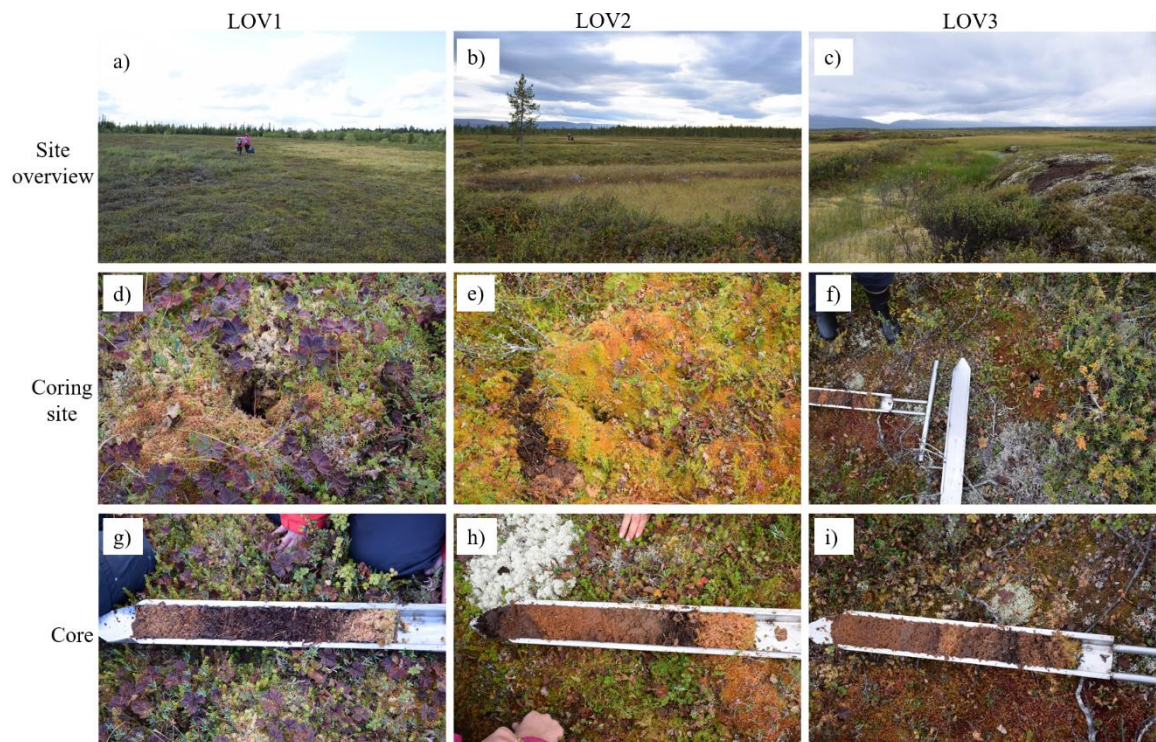


*Figure 2a) LOV1 aapa peatland b) LOV2 aapa peatland c) LOV3 palsa peatland d) LOV1 coring site e) LOV2 coring site f) LOV3 coring site g) LOV1 core h) LOV2 core i) LOV3 core. © Sanna Piilo*

The second sample, LOV2, was collected from the *Sphagnum* lawn of an aapa mire located at 68°01'N, 34°58'E (Figure 2b, e, h). Permafrost depth was not reached at any of the three cores collected from this peatland section. LOV2 has been influenced by human activity as it is situated near a road. This site was also dry with WTD of 30 cm. The vegetation was dominated by the *Sphagnum* mosses *S. fuscum* and *S. capillifolium*. The vegetation also included sedges *Eriophorum* spp. The dwarf shrub species were very similar to those identified at LOV1: *Rubus chamaemorus*, *Andromeda polifolia*, *Empetrum nigrum, Betula nana*, *Vaccinium uliginosum* and *V. oxycoccos*, with the addition of *Rhododendron tomentosum*.

The third core, LOV3, was collected from a *S. fuscum* lawn at the edge of a palsa mound at 67°60'N, 35°01'E (Figure 2c, f, i). Permafrost depth was not reached at any of the cores collected from this site. Like the other two sample locations, this site was also dry with WTD of 32 cm. The vegetation at this site resembled that of LOV1 and LOV2. The dominant moss species were *Sphagnum fuscum* and *Mylia anomala*. The dwarf shrubs included four *Vaccinium* species *V. uliginosum*, *V. oxycoccos, V. myrtillus* and *V. vitis-idaea,* as well as four other dwarf shrub species *Rubus chamaemorus*, *Andromeda polifolia*, *Empetrum nigrum*, and *Betula nana*. The details of all three coring sites are compiled in Table 1.

*Table 1 Basic information of the sampling sites LOV1, LOV2, and LOV3. Coordinates, peatland type, elevation (m), water table depth (WTD) (cm), pH, coring microtype, and permafrost.*

| Sampling site | Coordinates | | Peatland type | Elevation (m) | WTD (cm) | pH | Coring habitat type | Permafrost |
|---|---|---|---|---|---|---|---|---|
| | N | E | | | | | | |
| LOV1 | 67°58.764` | 35°03.826` | Aapa | 158 | 35 | 4 | Lawn | 55 cm |
| LOV2 | 68°01.174` | 34°58.260` | Aapa | 179 | 30 | 4 | Lawn | unknown |
| LOV3 | 67°59.641` | 35°01.105` | Palsa | 160 | 32 | 4 | Lawn | unknown |

## 2.2 Establishing chronology

The peat samples estimated to be older than AD 1950 were dated using radiocarbon ^{14}C dating developed by Libby (1961). Plants take up $CO_2$ with photosynthesis, and some of the carbon atoms are radioactive isotopes, such as [14]C. These isotopes occur in organic matter in roughly the same concentration as in the atmosphere. When plants die, the amount of ^{14}C begins to decrease at a known rate, and for ^{14}C the half-life is 5,730 ± 40 years (Godwin 1962). The age of peat samples can be determined based on their remaining ^{14}C content. Radiocarbon dating can be used on samples that are up to 50,000 years old (Taylor 2000). In radiocarbon dating, the modern reference year is AD 1950.

The samples from the top of the peat sections were dated with lead ^{210}Pb dating. This method can be used for peat samples at maximum 150-200 years of age (Turetsky, Manning & Wieder 2004). The method utilizes the decay of radioactive uranium [238]U to ^{210}Pb via several daughter isotopes (Appleby & Oldfield 1978; Turetsky et al. 2004). The half-life of one of the daughter isotopes, radon [222]Rn to ^{210}Pb, is 22.3 years (Appleby & Oldfield 1978). Uranium-238 is a primordial element that has deposited in all soils (Turetsky et al. 2004).

Three samples from each peat section were $^{14}$C dated by the Accelerator Mass Spectrometry (AMS) method in the Laboratory of Chronology at the University of Helsinki (Table 2). The $^{210}$Pb dating was conducted with the Constant Rate of Supply (CRS) model developed by Appleby and Oldfield (1978) using alpha spectrometry at the the University of Exeter, UK. The $^{210}$Pb dating was done at 2 cm resolution from the top sections of the cores (Table 2). The laboratory work for the $^{14}$C and $^{210}$Pb dating was conducted by other members of the research team.

Based on the $^{14}$C and $^{210}$Pb dating methods, age-depth models were constructed using the BACON v.2.3.3 package in R version 3.4.3 (R-Core-Team 2017), which is based on Bayesian statistics and it estimates weighted mean ages in 1 cm resolution (Blaauw & Christen 2011). Before running the model, $^{14}$C ages younger than AD 1950 were converted to $^{14}$C BP ages using the NH Zone 1 post bomb curve (Hua, Barbetti & Rakowski 2013). Based on the age-depth models, peat accumulation rates (mm/y) were calculated at 1 cm resolution by dividing the peat thickness (mm) with the difference of the weighted mean ages (years) between the layers.

*Table 2 The samples used in $^{210}$Pb and $^{14}$C dating methods. For the $^{210}$Pb dating, the table shows the range from which analysis was conducted at 2 cm resolution.*

| LOV1 | LOV2 | LOV3 | Dating method |
|--------|--------|--------|---------------|
| 1-27cm | 1-17cm | 1-23cm | $^{210}$Pb |
| 20cm | 13cm | 17cm | $^{14}$C |
| 35cm | 30cm | 31cm | $^{14}$C |
| 50cm | 47cm | 45cm | $^{14}$C |

## 2.3 Testate amoebae analysis

From the peat cores, the testate amoebae assemblages were analyzed at 2 cm resolution. The preparation of the chosen peat samples for the testate amoeba analysis followed a modification of the method by Booth et al. (2010). 1-2 cm$^3$ of the peat samples were boiled with a Lycopodium spore tablet in ca. 100 ml distilled water for 10-15 minutes stirring occasionally. After boiling, the samples were sieved through 300 µm and 15 µm sieves. The material left in the 15 µm sieve was washed with distilled water into centrifuge tubes. The samples were centrifuged at 3000 rpm for 5 minutes.

The samples were analyzed under a light microscope with 200-400x magnification. From each sample, 50-100 testate amoebae taxa or 'types' were counted

and identified using the key by Booth & Sullivan (2007, updated by Amesbury 2019) with help from the online source www.arcella.nl. If a minimum count of 50 amoebae could not be reached with a reasonable effort, the samples were discarded from the analysis.

For the WTD reconstructions, the absolute numbers of identified taxa or 'types' were transformed to percentages of the total number of tests identified in each sample. The WTD reconstruction and a cluster analysis with the Bray-Curtis similarity measure (e.g. Michie 1982) were conducted in R version 3.6.0 (R-Core-Team 2019) using the package rioja (Juggins 2017). The reconstruction was performed with the pan-European transfer function developed by Amesbury et al. (2016). The performance of the reconstruction was also tested by running the model with only the local data of northern Sweden from the pan-European dataset. The tests conducted by Amesbury et al. (2016) show the model performance to be at a similar level to other available models. In addition, most of the taxa in the model had a pan-European distribution, suggesting that this model is applicable to individual sites within the region (Amesbury et al. 2016). The model was run using tolerance-downweighted weighted averaging with inverse deshrinking as recommended by Amesbury et al. (2016) and cross-validated by leave-one-out. The model was then applied to our fossil data. The reconstruction was run with standard errors that were based on 1000 bootstrapping cycles. The z-scores, i.e. standardized residuals, were calculated with the R Basic package.

To form a more detailed picture of the structure of the species assemblages, detrended correspondence analysis (DCA) (Hill & Gauch 1980) was also conducted with the R package vegan (Oksanen, J. et al. 2019) using testate amoebae data with rare taxa (with <5% abundance) removed.

# 3 Results

## 3.1 Age-depth models

The age-depth models show differences in peat accumulation rates over time (Figure 3). Based on the models, the two peat sections LOV1 and LOV3 have had rather similar developments, while LOV2 differs significantly from the other two. According to the age-depth model, the basal age for LOV1 (at 50 cm) is 985 cal BP and 935 cal BP for LOV3 (at 45 cm). The basal age of LOV2 is almost 3000 years older, i.e. 3860 cal BP at 47 cm depth.

For LOV1, between 985 and 630 cal BP, the peat accumulation rate is ca. 0.28 mm/y. After that the accumulation slows down to ca. 0.20 mm/y until AD 1780. Then the peat accumulation rate accelerates again and between AD 1810 and 1980 the rate ranges from 0.71 to 1 mm/y. From the AD 1980s, the accumulation rate increases significantly, and it has been around 10 mm or more per year for the last 10 years. Due to the very high accumulation rate over the last decade, the average accumulation rate for the whole peat section, 2.77 mm/y, is the highest of the three sections.

In LOV2, peat accumulation rate is significantly lower throughout the collected peat section. Over the time period from 3860 cal BP to AD 1830, the average peat accumulation rate is 0.08 mm/y, with the lowest rate of 0.04 mm/y occurring between 1895 and 980 cal BP. After AD 1830 until 1980, the accumulation accelerates averaging 0.60 mm/y. From the AD 1980s to the present, accumulation has further increased ranging from 1.08 mm/y in the 1980s to 5.88 mm/y over the last few years. Out of the three sections, LOV2 has the lowest total average accumulation rate, i.e. 0.98 mm/y due to the very slow accumulation rates at the base of the peat section.

For LOV3, the accumulation rate increases quite steadily from 935 cal BP to the AD 1880s, with an average accumulation rate of ca. 0.20 mm/y between 935 and 445 cal BP, 0.34 mm/y between 415 and 180 cal BP, and ca. 0.56 mm/y from AD 1790 to 1880. Between AD 1885 and 1910, the accumulation rate is higher, i.e. 1.43 mm/y on average, but subsequently slows down to 0.68 mm/y between AD 1930 and 1975. Similarly to the other two sections, the accumulation rate starts to significantly increase after the 1980s, ranging from 1.06 mm/y in AD 1985 to 3.57 mm/y over the last few years. Even though the accumulation rate increases in the top layers, it remains much lower than the very high rates detected for LOV1. Thus, the average accumulation rate 1.04 mm/y for the whole LOV3 section is much lower than that of LOV1.
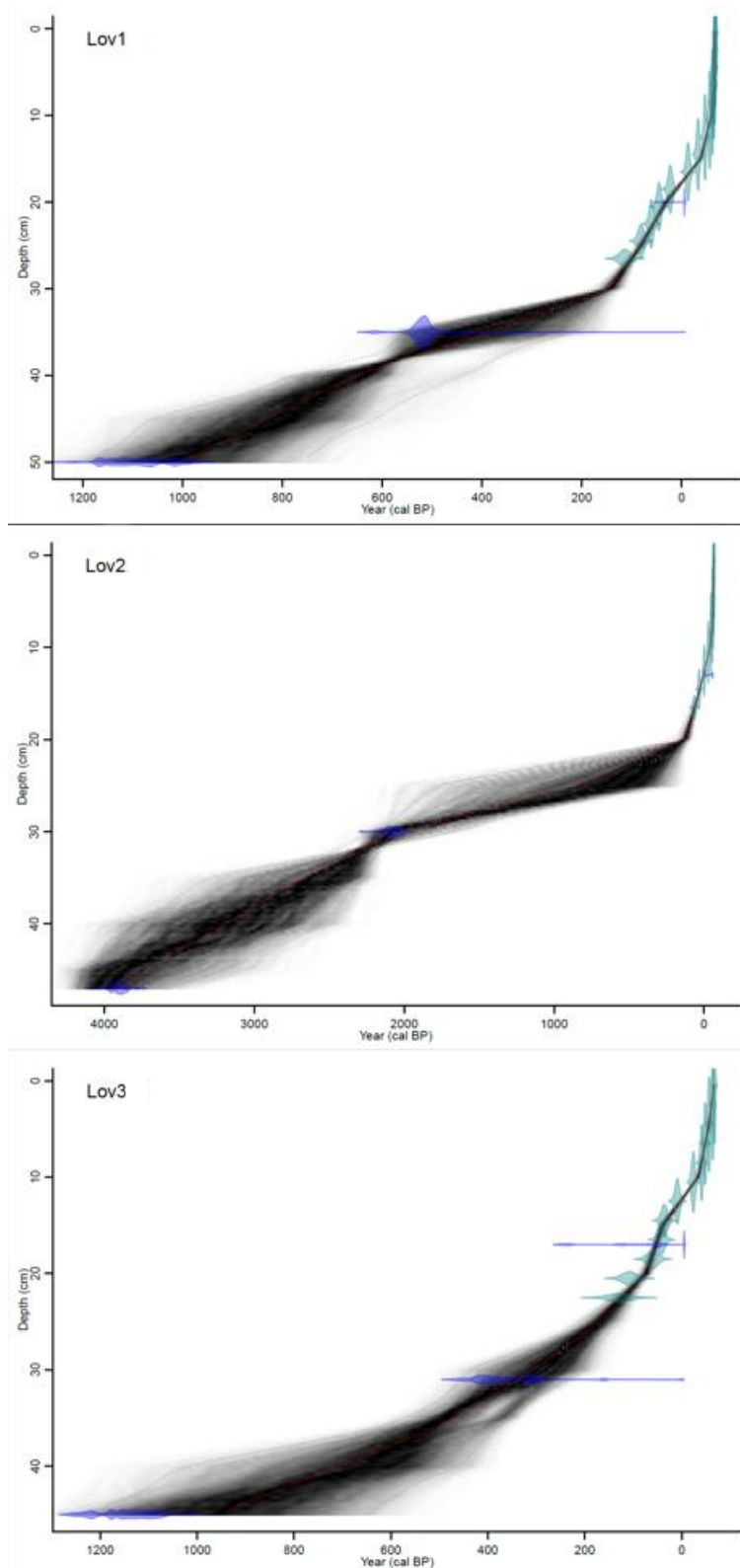
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*Figure 3 Age-depth models for all three peat sections constructed with BACON. Horizontal blue lines refer to the uncertainty ranges in $^{14}C$ dating, and light blue to uncertainty ranges in $^{210}Pb$ dating. The grey shading shows different possibilities for the age-depth model. The darker the grey, the more likely the*

*calendar age is. The red line shows the closest fit calculated based on the weighted mean ages of each depth. (Blaauw & Christen 2013)*

## 3.2 Testate amoebae analysis

### 3.2.1 Taxa assemblages

For data interpretation, testate amoebae taxa were divided into three categories (Table 3) based on their WTD optimas reported in Amesbury at al. (2016), where the WTD optimum range of all taxa was ca. 0-30 cm. In this thesis, testate amoebae taxa with WTD optima <10 cm were included in the wet category, taxa with WTD optima in the range 10-20 cm in the intermediate category, and taxa with WTD optima >20 cm in the dry category. Most of the species found in the Lovozero peat records were intermediate indicators with 10-15 cm WTD optimas.

*Table 3 Selected taxa identified at Lovozero divided into three categories. Wet includes taxa with WTD optima <10 cm, intermediate in the range 10-20 cm, and dry >20 cm. The taxa are ordered in each category from wetter to drier. As the taxa in the intermediate group was so numerous, it was further divided into two subgroups.*

| Wet | Intermediate | | Dry |
|---|---|---|---|
| *WTD <10 cm* | *10 ≤ WTD < 15 cm* | *15 ≤ WTD ≤ 20 cm* | *WTD > 20 cm* |
| *Amphitrema wrightianum* | *Difflugia lucida* type | *Euglypha tuberculata* type | *Nebela tincta* |
| *Arcella discoides* type | *Difflugia pristis* type | *Euglypha strigosa* type | *Alabasta militaris* |
| *Archerella flavum* | *Pseudodifflugia fulva* type | *Heleopera sylvatica* | *Assulina muscorum* |
| *Placocista spinosa* type | *Hyalosphenia papilio* | *Euglypha rotunda* type | *Bullinaria indica* |
| *Argynnia dentistoma* type | *Cyclopyxis arcelloides* type | *Assulina seminulum* | *Corynthion - Trinema* type |
| *Physochila griseola* type | *Phryganella acropodia* type | *Arcella catinus* type | *Trigonopyxis arcula* type |
| | *Hyalosphenia elegans* | | *Trigonopyxis minuta* type |
| | *Difflugia pulex* | | |
| | *Hyalosphenia minuta* | | |

In LOV1, a total of 31 testate amoebae taxa or types were identified. The most common types in this record were the intermediate indicators *Difflugia pristis* type (abundance range across all samples 0-48.0%) and *Hyalosphenia elegans* (0-55.8%), the drier indicators *Trigonopyxis minuta* type (0-38.0%), and *Alabasta militaris* (0-40.8%), as well as the wetter indicator *Archerella flavum* (0-53.0%). Testates were counted for the top 39 cm of the core, after which counting was stopped due to low concentrations of testate amoebae in the samples.

There are several shifts in the species assemblages along the peat section, and the data was divided into four zones based on the cluster analysis (Figure 5). In zone 1, from

575-470 cal BP (39-37 cm), the wet indicator *A. flavum* is the most dominant (18-44%) with additions from the intermediate taxa *D. pristis* type (14-26%) and *Difflugia pulex* (22%). In zone 1, species diversity is low at <10 taxa identified (Figure 4). At the beginning of the zone two in 370 cal BP (35 cm), *A. flavum* disappears from the assemblages and there is a shift towards drier and intermediate indicators. Until the end of zone 2 in AD 1940 (19 cm), the intermediate indicator *D. pristis* type (16-48%) and the dry indicator *T. minuta* type (ca. 30%) are the most common taxa. Other common taxa in zone 2 are *Difflugia lucida, Trigonopyxis arcula, Pseudodifflugia fulva,* and *Arcella catinus*. Towards the year AD 1940 (19 cm), the abundance of *D. pristis* gradually decreases while the abundance of *T. minuta* and the species diversity increase.

In zone 3, after AD 1940 until ca. AD 2007 (17-11 cm), the assemblage shifts towards drier habitat conditions. *D. pristis* is no longer found while *T. minuta* remains relatively abundant and *A. militaris* becomes the most common species (22-41%). In this time period, there is also a wide variety of amoebae taxa with e.g. *A. catinus, Assulina muscroum, A. seminulum, Euglypha tuberculata, E. strigosa, Nebela tincta* and *Placocista spinosa* present and 15-20 different taxa identified per peat sample.

The zone 4 begins ca. AD 2011 (9 cm) with a shift where the driest indicators become rarer with e.g. *A. militaris* decreasing while the intermediate indicator *Hyalosphenia elegans* becomes the most common (27-56%). The top 3 cm of the core from years ca. AD 2017-2018 have a high abundance of the wet indicators *A. flavum* and *P. spinosa* and a lower diversity of taxa (9-12 identified per peat sample).
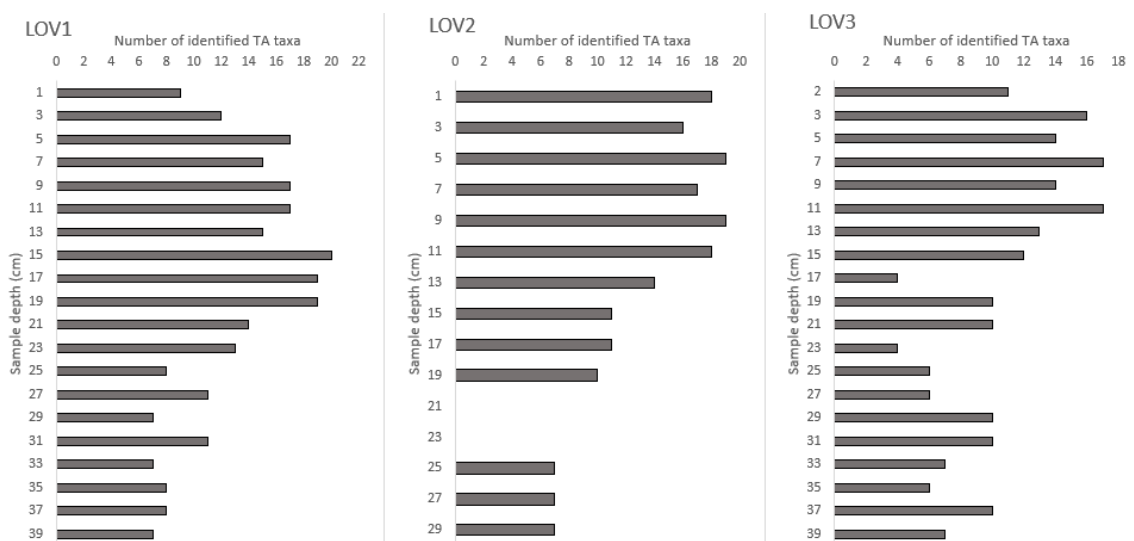


*Figure 4 The number of identified testate amoebae taxa at sample depths (cm) in the Lovozero peat sections.*
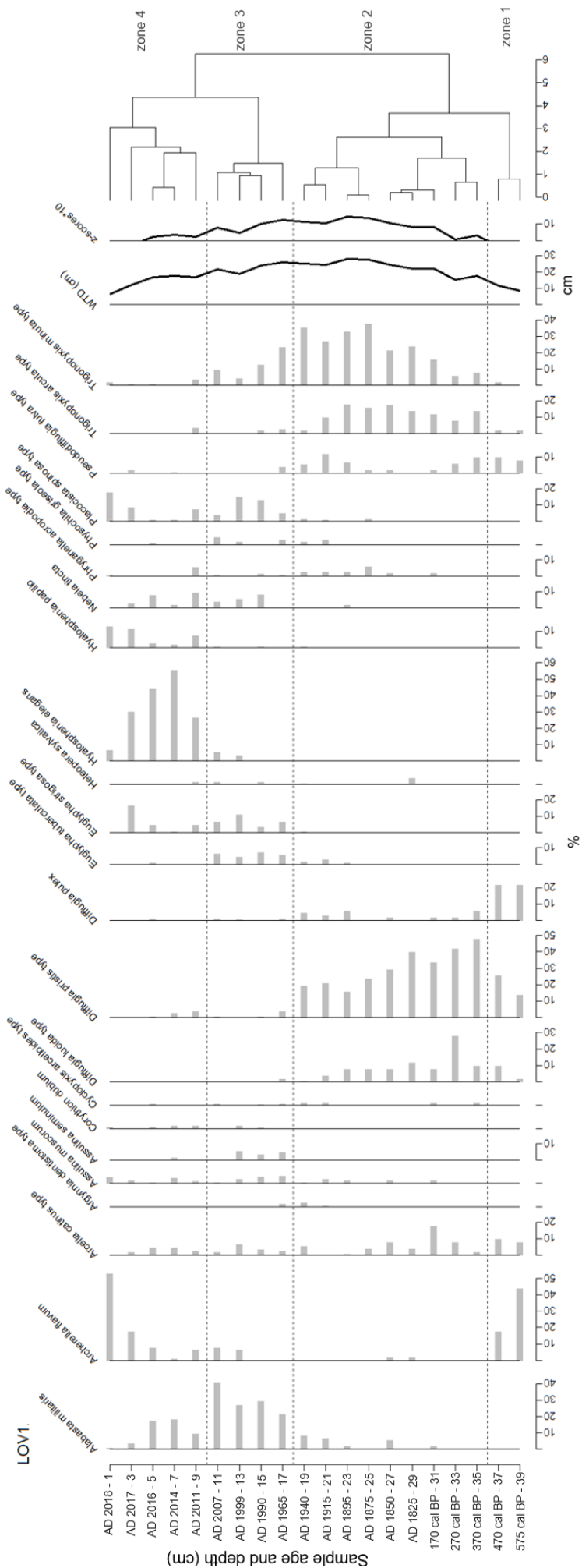
*Figure 5 LOV1 The abundances (%) of selected testate amoebae, the water table depth reconstruction (cm), and the z-score (z<0 indicating wetter and z>0 indicating drier than average conditions) are plotted against sample age and depth (cm). The cluster analysis dendrogram is on the right, and the horizontal lines mark the four zones from the cluster analysis.*

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In LOV2, 32 testate amoebae taxa or types were identified. The most common types were the intermediate indicators *Difflugia pulex* (0-57.0%), *D. pristis* type (0-40.0%), *D. lucida* type (0-42.0%), *P. fulva* type (0-40.0%), and *H. papilio* (0-38.0%), the dry indicator *A. militaris* (0-42.6%), as well as the wetter indicator *A. flavum* (0-24.8%). The samples 21-23 cm were discarded from the analysis due to very high density of mineral material that severely inhibited counting, after which counting continued until 29 cm depth. Due to the missing data, cluster analysis could not be conducted on this peat section.

Despite the missing data, some shifts in taxa assembalages are visible (Figure 6). Between the time period from 1665 to 795 cal BP (29-25 cm), the intermediate indicator types *D. pristis*, *D. lucida*, and *P. fulva* are the most common, each taxon with > 20% abundance. In addition, *D. pulex*, *Physochila griseola* type, and *T. minuta* are present in moderate concentrations. The taxa diversity is low with only 7 taxa identified (Figure 4). After this, there is the gap in testate amoebae data between 25 and 19 cm, which corresponds to a ca. 700-year period from 795 cal BP to AD 1850. Such a long time period in only a 6-cm section of peat combined with the high density of mineral grains in the peat samples suggests a hiatus or very slow peat accumulation rate possibly associated with landscape erosion or instability in the surroundings. According to the age-depth models, peat accumulation was the slowest of the whole core at 29-21 cm.

After the data gap in AD 1850, similar TA assemblages are present than before the gap. However, the relative taxa abundances changed, as *D. pristis* is the most abundant (~ 40%), while the proportion of *P. fulva* has decreased significantly. In the AD 1880s (17 cm), *D. pulex* becomes very dominant with over 50% abundance, accompanied by moderate abundances of *D. pristis*, *P. fulva* and *Phryganella acropodia* type. Ca. AD 1980, *D. pulex* decreases significantly, while *A. militaris* becomes the most abundant taxon (22-43%), with also some *D. pristis*, *H. elegans*, *H. papilio*, *E. tuberculata*, *P. spinosa,* and *A. flavum* present. The taxa diversity increases and remains high (11-19 identified taxa per sample) for the top 17 cm of the peat section.

Recently, since AD 2010, the taxa shift towards wetter indicators. The top 3 cm of the peat surface is dominated by *A. flavum* (16-25%) and *H. papilio* (32-38%). The taxa *A. muscorum*, *H. elegans*, *H. minuta*, and *P. spinosa* are also present with each taxon under 10% abundance.
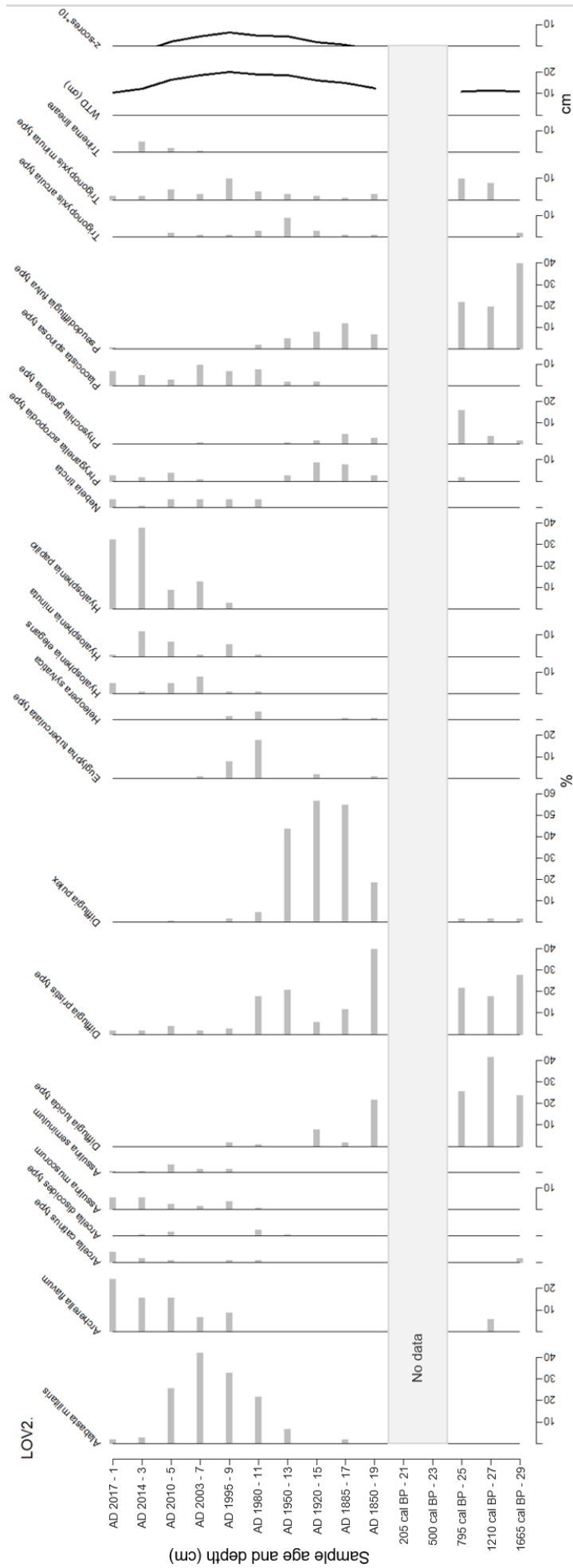
*Figure 6 LOV 2.2 The abundances (%) of selected testate amoebae, the water table depth reconstruction (cm), and the z-score (z<0 indicating wetter and z>0 indicating drier than average conditions) are plotted against sample age and depth (cm).*

In LOV3, 29 testate amoebae taxa or types were identified. In this peat section, the wet indicator *A. flavum* is by far the most common taxon, with up to 90.0% abundance in some samples and with its abundance averaging ca. 32% along the whole record. The more intermediate WTD indicator *D. pulex* also reaches 90% abundance once in the record but is overall less abundant than *A. flavum* with average abundance of ca. 19%. *H. elegans* is also common with abundance across all samples in the range 0-44.6%, with *A. militaris* (0-32.7%), *A. discoides* type (0-32%), and *P. fulva* type (0-29.0%). Testates were counted until the depth of 39 cm, after which counting was stopped due to the low concentrations of testate amoebae.

Based on the cluster analysis, LOV3 was also divided into four zones (Figure 7). Zone 1 from 630 cal BP to AD 1885 (39-19 cm) lasts ca. 500 years, and the abundance of *A. flavum* ranges from 24% to 90% remaining > 40% for most of this period. For the first ca. 300 years and for the last few decades of this period, the abundance of *D. pulex* is also high (20-50%). Between AD 1685 and 1830, the abundance of *D. pulex* is low, while the wet indicator *A. discoides* is more abundantly present, ca. 30% of the ammeblages. Other relatively common amoebae taxa over this period are *A. catinus* and *P. fulva.* In zone 1, the taxa diversity remains relatively low (≤10) due to the very high dominance of both *A. flavum* and *D. pulex* (Figure 4).

Zone 2 between ca. AD 1900 and 1950 (17-13 cm) is dominated by *D. pulex* starting with 90% abundance and decreasing to 20% by the AD 1950s. In addition to *D. pulex*, *A. militaris* and *P. fulva* are also present, while, interestingly, the usually common *A. flavum* is absent. In zone 3 between ca. AD 1975 and 1990 (11-9 cm), *D. pulex* disappears while *A. militaris* becomes the most dominant taxon, accompanied by moderate amounts of *A. flavum*, *A. muscorum*, *E. strigosa*, *H. papilio*, and *N. tincta.* For the top 15 cm of the record, taxa diversity remains relatively high with 11-17 taxa identified per peat sample.

The zone 4 is marked since AD 1998 to the present (top 7 cm), as *A. militaris* decreases and *H. elegans* becomes the most common with the average abundance of 43%, and *A. flavum* is also common averaging ~19% abundance. Moderately abundant taxa in this period are for example *A. militaris*, *E. strigosa*, *N. tincta*, and *P. spinosa*.
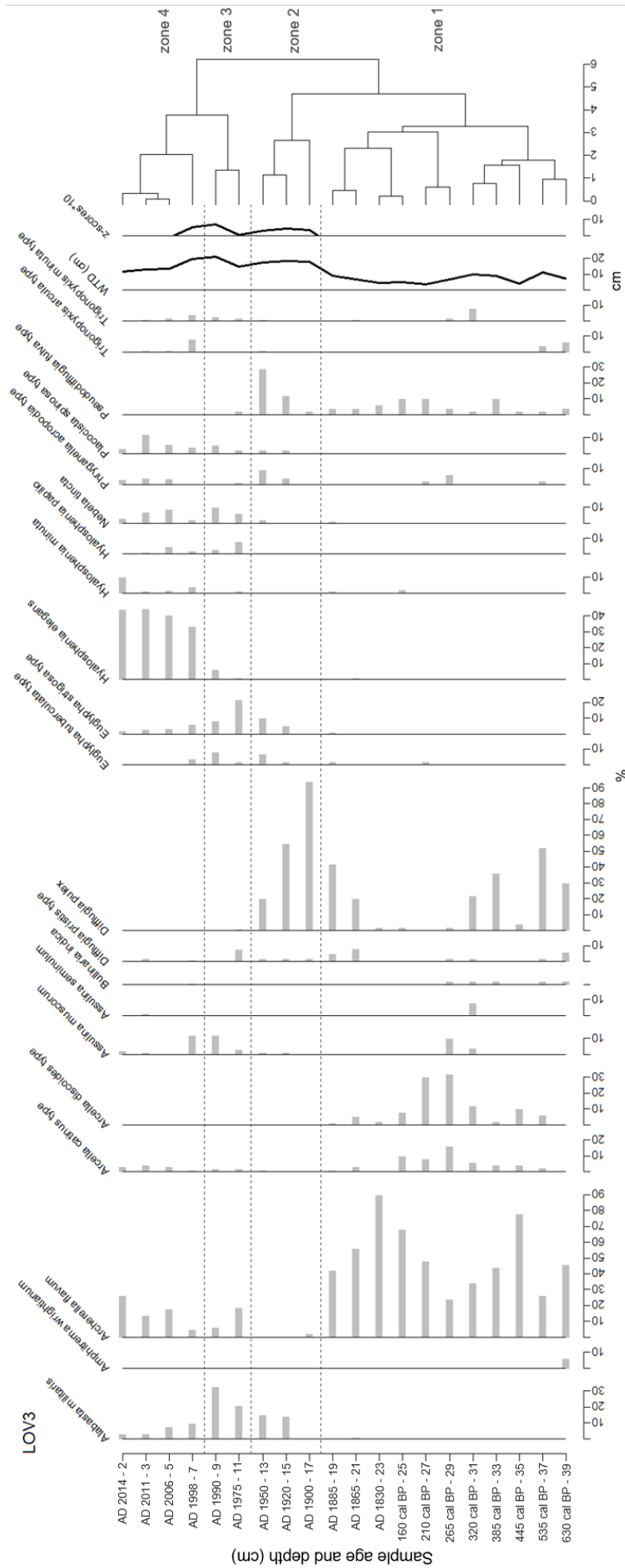
*Figure 7 LOV3 The abundances (%) of selected testate amoebae, the water table depth reconstruction (cm), and the z-score (z<0 indicating wetter and z>0 indicating drier than average conditions) are plotted against sample age and depth (cm). The cluster analysis dendrogram is on the right, and the horizontal lines mark the four zones from the cluster analysis.*

When comparing the Lovozero testate amoebae assemblages, in all three cores, similar taxa typical for ombrotrophic peatlands are generally present while their abundances vary. For example, *D. pulex* is present in high abundances in both LOV2 and LOV3 but in LOV1 only in small amounts. On the other hand, LOV1 has high abundance of the dry indicators *Trigonopyxis* spp., while their abundances are low in the other two records. Notably, the wettest taxa with WTD optima <5 cm were absent in Lovozero, except for *Amphitrema wrightianum* in one sample at the bottom of the LOV3 peat section. Curiously, all three records indicate a significant increase in the dry indicator *A. militaris* proportions since ca. AD 1950s but a subsequent decrease over the recent decade. Another similarity for the three records is that the taxa of the topmost samples is dominated by mixotrophic taxa with endosymbiotic algae such as the wet to intermediate indicators *A. flavum*, *H. elegans*, *H. papilio*, and *P. spinosa* that can feed on other organisms and also photosynthesize (Gomaa et al. 2014).

### 3.2.2  The water table depth reconstruction

The water table depth reconstructions based on the pan-European dataset and the local dataset from northern Sweden yielded very similar results (Figure 8). The local data set lacked three taxa identified at Lovozero, so the taxa had to be removed from the fossil data set in order to run the local reconstruction. The three removed taxa were *Argynnia dentistoma*, *Heleopera rosea*, and *Heleopera sylvatica*. However, all of these taxa were found in Lovozero only in a few samples and in low abundances ($< 3\%$), so their removal did not notably impact the local reconstruction. The only point where the reconstructions slightly differed (Figure 8) is in the core LOV1 between AD 1940 and 1965 where the abundance of *A. dentistoma* is 2-3% and that of *H. sylvatica* is ca. 1%.

There are some differences in the performance statistics of the two models. The local model has a higher coefficient of determination $R^2$=0.632 but also a higher root mean square error RMSE=9.431, suggesting a higher proportion of the variance was accounted for but with larger errors in the local model than in the pan-European model ($R^2$=0.585 and RMSE=7.725). As both of the models yielded similar reconstruction outcomes and z-scores, the interpretation of the shifts in water table depth will be the same regardless of the model used. Further analysis of the directional shifts in the water table depth at Lovozero is based on the z-scores yielded from the pan-European training

set. Negative z-scores suggest wetter and positive z-scores suggest drier than average conditions.
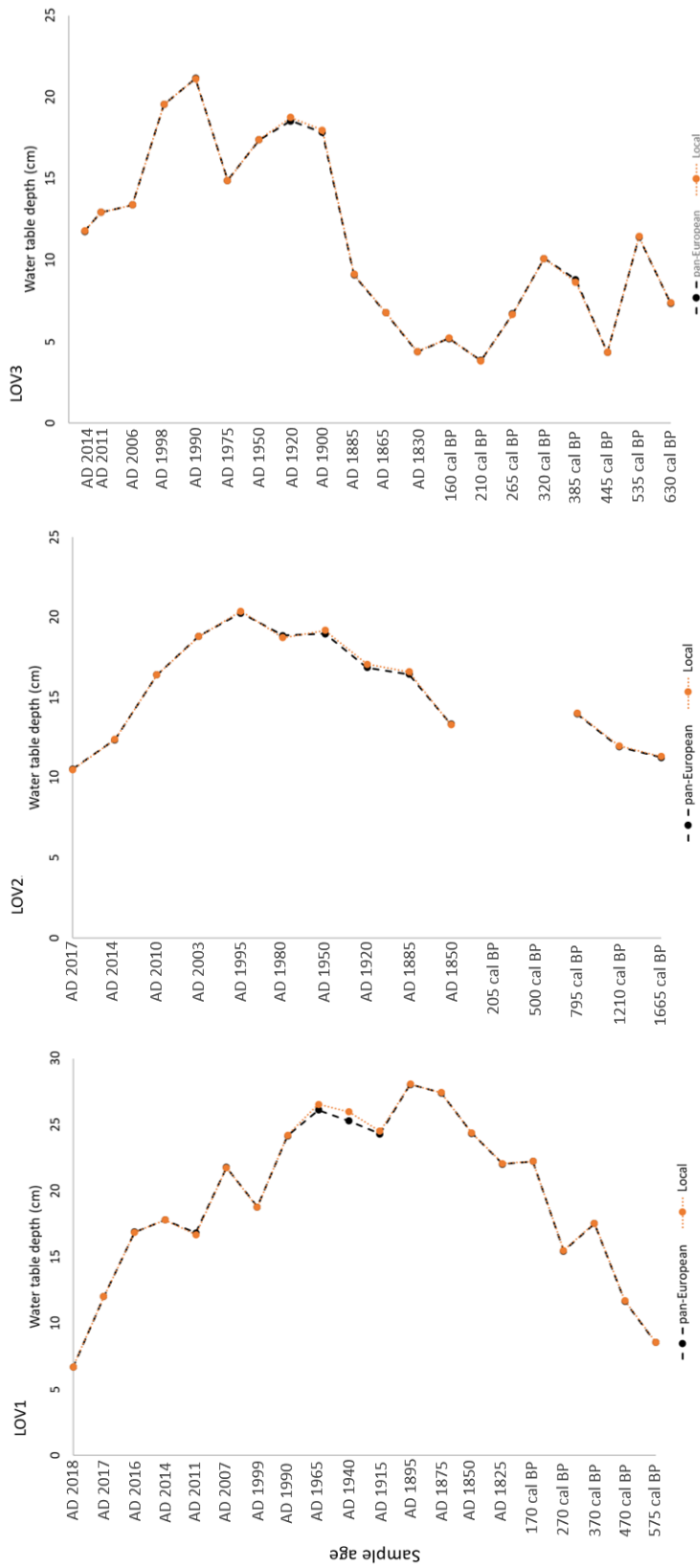


*Figure 8 Water table depth (cm) reconstructions of the three Lovozero cores based on the pan-European data set (black) and the local (northern Swedish) dataset (orange) by Amesbury et al. (2016).*

In the LOV1 reconstruction, the WTD ranges between 6.67 – 28.05 cm ±7.8 cm (Figure 8). Between 575 and 470 cal BP, the z-score is negative indicating wetter than average habitat conditions (Figure 9). This reflects the high abundance of *A. flavum* in the samples. In 370 cal BP *A. flavum* disappears and dry indicators become abundant, consequently the WTD increases and the z-score turns positive suggesting a change to drier conditions. The dry conditions remain ca. 400 years, until AD 2016. Although this period includes changes in the taxonomic composition and diversity, the dominant taxa are dry indicators such as *T. minuta* and *A. militaris*. A change in the assemblages indicates a wet shift a few years prior to AD 2016 already in AD 2011 when *A. militaris* decreases and *H. elegans* becomes dominant. However, as *A. militars* still remains relatively abundant between AD 2011 and 2016, the habitat conditions seem to become wetter only around AD 2017-2018 when the abundances of *A. flavum* and *P. spinosa* increase and the z-score turns negative.
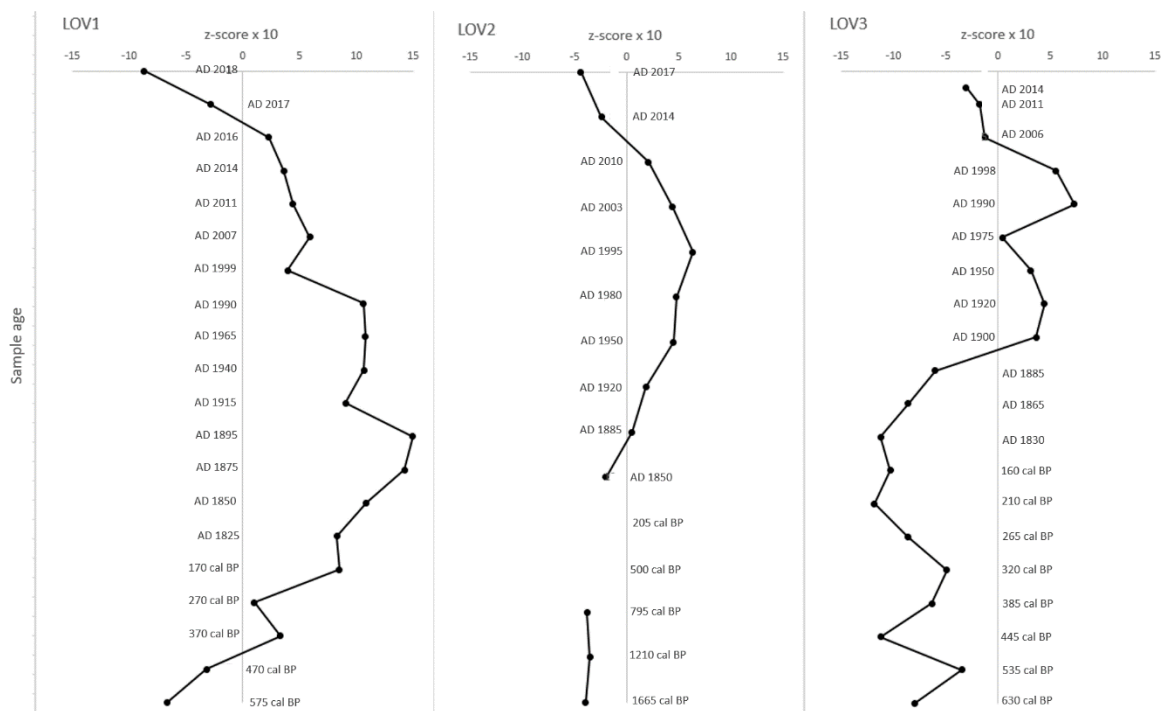


Figure 9 The z-scores (multiplied by 10 for visibility) of the three Lovozero cores from the pan-European reconstruction. z<0 suggests wetter and z>0 drier than average conditions.

The pan-European training set-based reconstruction for the LOV2 section estimates a WTD range of 10.5 – 20.3 cm ±7.8 cm. Between 1665 and 795 cal BP and after the data gap in AD 1850, the z-score is negative suggesting a wetter than average habitat (Figure 9). In these wetter periods the assemblages are dominated by intermediate indicators with WTD optimas of 10-15 cm. A dry shift occurs in ca. AD 1885 as *D. pulex*

becomes very dominant turning the z-score positive and increasing the reconstructed WTD. These dry conditions remain until ca. AD 2010 suggesting an over 100-year drier period. During this period, *A. militairs* replaces *D. pulex* as the dominant taxon. Like in LOV1, there is a recent wet shift, as the WTD decreases and z-score turns negative in ca. AD 2013 when the dominant taxa shift to *A. flavum* and *H. papilio.*

In the LOV3 reconstruction, the WTD ranges between 3.8-21.2 cm ± 7.8 cm (Figure 8). From 630 cal BP to AD 1885, the z-score is negative suggesting a wet period that lasted over 500 years. The WTD increases and the z-score turns positive in AD 1900 as *A. flavum* disappears and *D. pulex* becomes dominant. These drier conditions remain until AD 1998 indicating a 100-year dry period. The WTD starts to decrease and the z-score shifts back to negative in ca. AD 2006 as *A. militaris* has decreased and *H. elegans* and *A. flavum* become dominant suggesting a shift to wetter conditions in the surface layers.

### 3.2.3   Detrended correspondence analysis

The detrended correspondence analysis (DCA) examines the associations between different taxa and arranges them on different axes of variability. The variables that drive the ordination along these axes are not known. However, as moisture is usually the strongest control of testate amoebae distributions (Tolonen et al. 1994; Charman 2001), it could be hypothesized that the axis 1 depicts the water table gradient. pH and nutrient status are two other common controls of testate amoebae distribution (Tolonen et al. 1994; Charman 2001), but as the taxa identified in the Lovozero cores are all common to ombrotrophic peatlands suggesting similar nutrient and pH status between the cores, these two variables may not be significant drivers in this case. Other variables that have been found to affect testate amoebae distributions are e.g. depth of the sample, dissolved organic carbon (DOC) content, and C:N ratio (Tolonen et al. 1994).

The DCA of LOV1 shows the taxa found at similar depths grouped together (Figure 10). In the top right are the common mixotrophic species of the top peat layers (e.g. *A. flavum*), while the common species at 5-17 cm depths are in the bottom right. These groups are roughly at the same point along the hypothesized water table gradient (axis 1), even though some of the taxa are known to thrive in wet conditions, such as *A. flavum* and *P. spinosa*, as well as in intermediate to dry conditions, such as *A. militaris*, *Assulina* spp., and *Euglypha* spp.. At the same time, these groups lie roughly on the

opposite sides of the axis 2. Thus, the ordination of the taxa along axis 2 seems to better reflect the existing knowledge about the WTD optimas of these taxa, suggesting that axis 2 may actually reflect the water table gradient.

The distribution of taxa along axis 1 quite closely follows the division between idiosomic and xenosomic testate amoebae, with mainly idiosomic (e.g. *Hyalosphenia* spp., *Euglypha* spp., *Assulina* spp.) and intermediate between idiosomic and xenosomic taxa (e.g *A. militaris*) on the right and xenosomic (*Difflugia* spp., *Trigonopyxis* spp.) on the left. In general, idiosomic shells do not preserve as well in peat as xenosomic shells (Charman 2001), which may partly explain why the idiosomic amoebae are mainly contentrated in the top 17 cm of the peat core while xenosomic taxa dominate the bottom 20 cm. In addition, the dominance of the mixotrophic taxa in the surface layers could be connected to factors that benefit photosynthesis, such as the increased $CO_2$ concentration in the atmosphere, which has been shown to increase photosynthesis and growth in plants and algae (Ainsworth & Rogers 2007; Singh & Singh 2014). Thus, as the mixotrophic taxa can utilize photosynthesis, it is possible that they also benefit from $CO_2$ fertilization. However, this connection to increased $CO_2$ is speculative, and there may be other factors that benefit mixotrophic taxa causing them to dominate the top layers of peat.
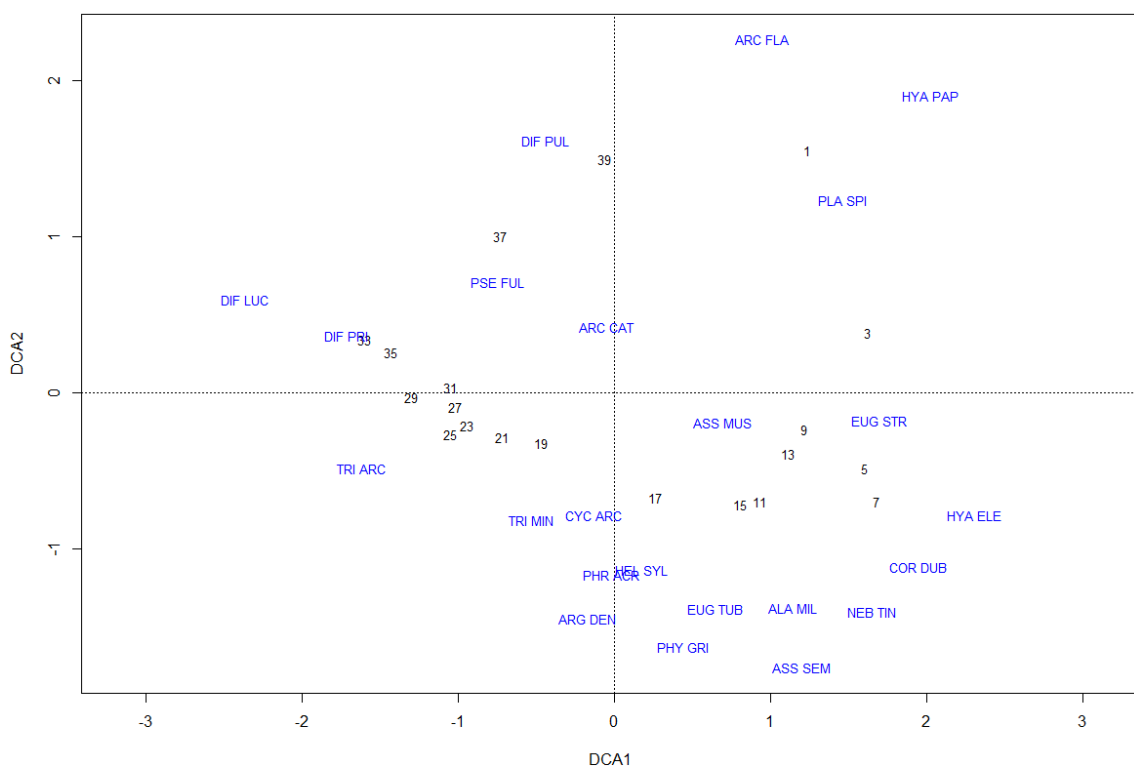


*Figure 10 LOV1 Detrended Correspondence Analysis (DCA) plot with the testate amoebae species marked as 3-3 letter abbreviations and samples by the sample depth (cm).*

Also in the case of LOV2, axis 1 of the DCA (Figure 11) does not seem to depict the water table gradient, as wet, intermediate and dry taxa (e.g. *P. spinosa*, *A. militaris*) are very mixed along the axis. However, the ordination of the taxa does not seem to clearly follow moisture gradients along axis 2 either. Like in the LOV1, the distribution of taxa along axis 1 seems to some extent follow the division between idiosomic and xenosomic testate amoebae, with idiosomic taxa (e.g. *Hyalosphenia* spp., *Assulina* spp., *A. flavum*) on the far right and xenosomic (*Difflugia* spp., *Trigonopyxis* spp.) on the far left. The dominant mixotrophic taxa of this core (*A. flavum*, *H. papilio*) are also positioned at the right edge of axis 1, indicating that environmental factors benefiting mixotrophic taxa, such as atmospheric $CO_2$ concentration, could possibly be one of the drivers on this axis similarly to LOV1. Along axis 2, only the taxa that were present in the highly decomposed or slowly accumulated peat section at 19-29 cm are on the negative side of the values. Thus, this axis may depict environmental variables related to slow production or high decomposition rates. However, as the taxa seem somewhat randomly positioned along the DCA axes, it is very difficult to determine the exact drivers.
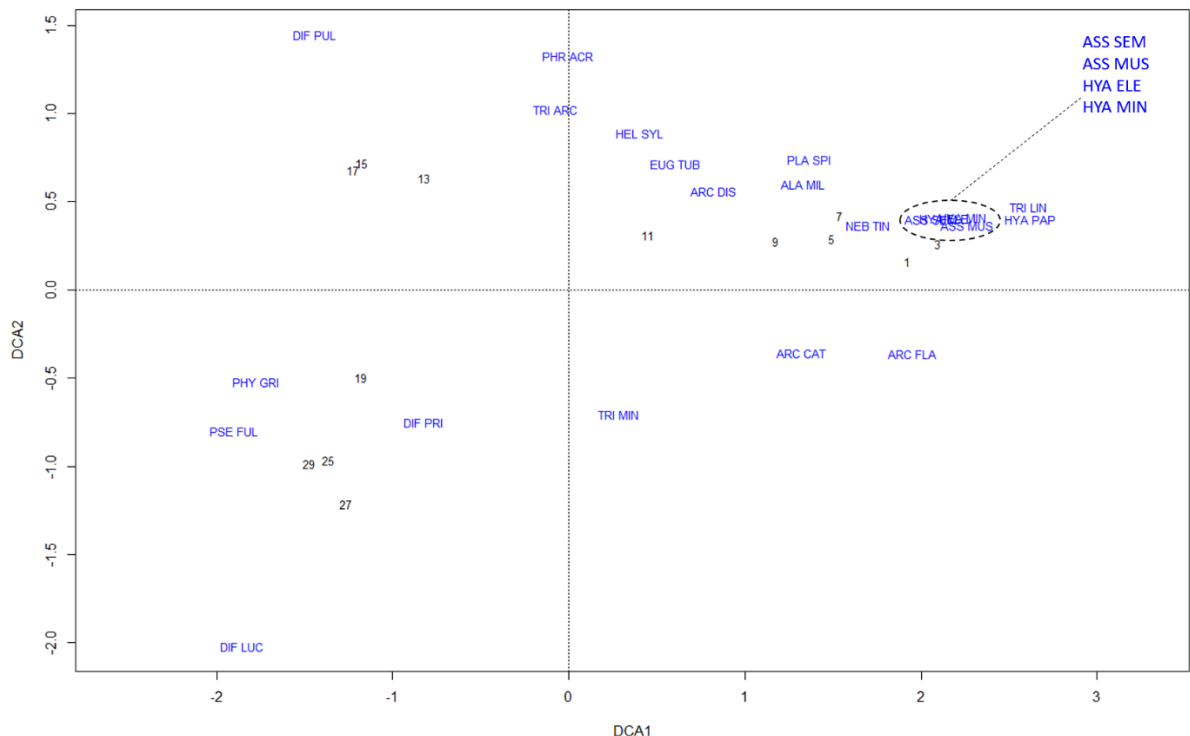


*Figure 11 LOV2 Detrended Correspondence Analysis (DCA) plot with the testate amoebae species represented by 3-3 letter abbreviations and samples by the sample depth (cm).*

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Similarly to the other two peat sections, the ordination of taxa along axis 1 of the LOV3 DCA does not seem to follow the assumed water table gradient (Figure 12). Here, the water table gradient or moisture conditions could be the primary driver of the distribution along axis 2 with the wetter taxa on the negative side and the dry indicators on the positive side. However, not all taxa are consistent with this pattern, as the intermediate indicators *Hyalosphenia* spp. are lower on the axis than the wet indicators *A. flavum* and *A. wrightianum*. Along the axis 1, the ordination of taxa follows the division of idiosomic and xenosomic in some aspects, with e.g. *Hyalosphenia* spp., *P. spinosa*, and *Euglypha* spp. on the right, and *D. pulex* on the far left. However, many idiosomic and xenosomic taxa are also fairly mixed in the middle of the plot, suggesting that this factor may not be a dominant driver along the axis 1. The most dominant mixotrophic taxon of the surface layers in this core, *H. elegans*, is the furthest to the right along axis 1, indicating that factors benefiting mixotrophy could be one driver behind the ordination along axis 1. However, the drivers behind the ordinations along the axes 1 and 2 remain unresolved.
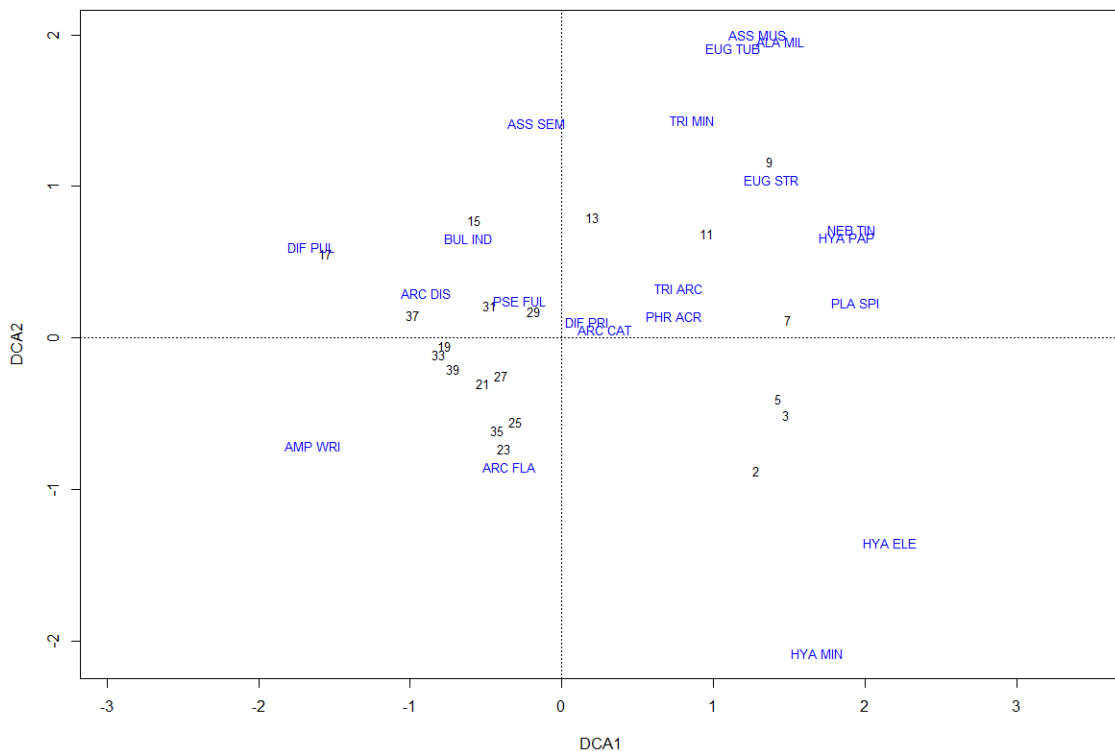


*Figure 12 LOV3 Detrended correspondence analysis plot plot with the testate amoebae species represented by 3-3 letter abbreviations and samples by the sample depth (cm).*

As the three Lovozero peat sections were collected close to each other from the same peatland complex, it could be hypothesized that the main drivers are the same for all the sites. To examine this, the data from all three cores were combined and the DCA analysis was run with a combined dataset. The taxa ordinations in the combined DCA plot (Figure 13) are quite similar to the LOV1 DCA plot, with the common mixotrophic species of the top layers (e.g. *A. flavum, H. papilio*) in the top right, dry to intermediate and idiosomic taxa bottom right, and many xenosomic taxa on the left and in the center. Thus, the hypothesized drivers for LOV1 distributions, such as water table gradient and the preservation of idiosomic and xenosomic tests, as well as factors benefiting mixotrophic taxa are probably valid for all of the three cores.
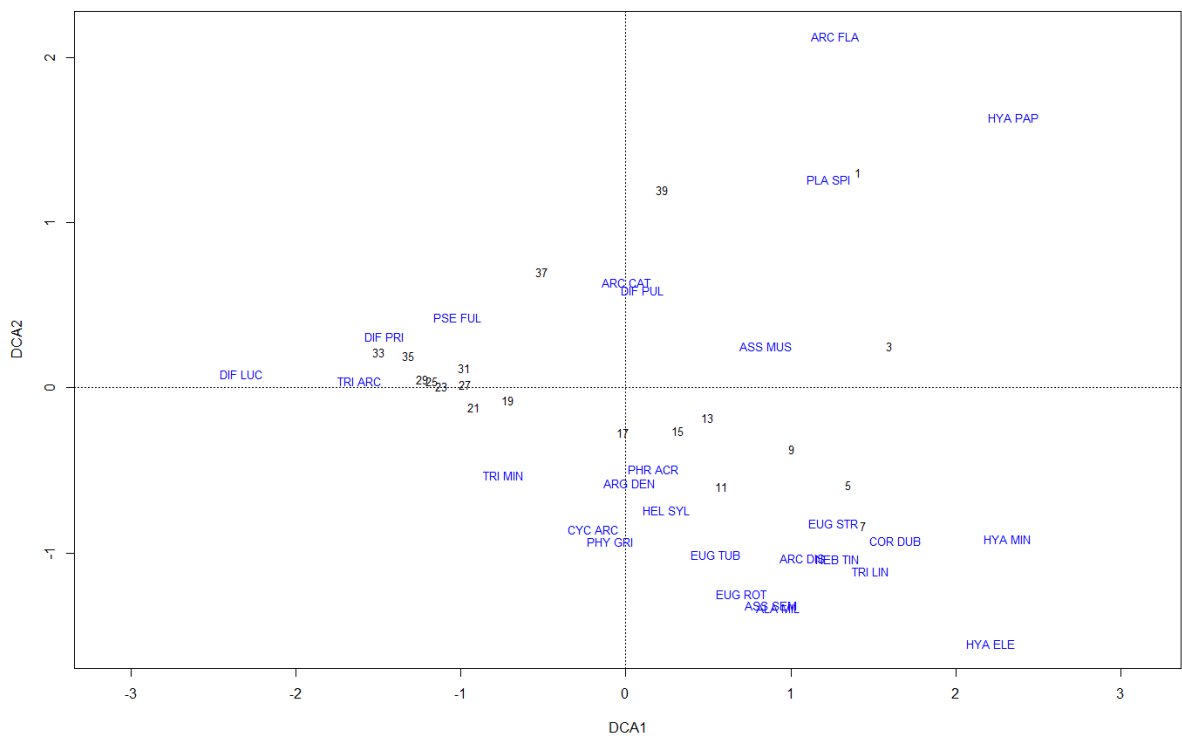


*Figure 13 Detrended correspondence analysis plot with the data stacked from all three cores. Testate amoebae taxa are represented by 3-3 letter abbreviations and peat samples by sample depth (cm).*

## 3.3 Carbon accumulation and plant macrofossils

The carbon accumulation measurements (Figure 14) and the plant macrofossil analyses (Figures 15, 16, 17) were conducted by other members of the research team. The results are only presented here as graphs to enable comparison of the peat accumulation patterns and testate amoebae data in the discussion.



Figure 14 The apparent carbon accumulation rates (ACAR g C/m²/y) of the Lovozero cores.

*Figure 15 LOV1 selected plant macrofossil taxa/types shown as percentages (%) in each sample.*

*Figure 16 LOV2 selected plant macrofossil taxa/types shown as percentages (%) in each sample.*

*Figure 16 LOV3 selected plant macrofossil taxa/types shown as percentages (%) in each sample.*

# 4 Discussion
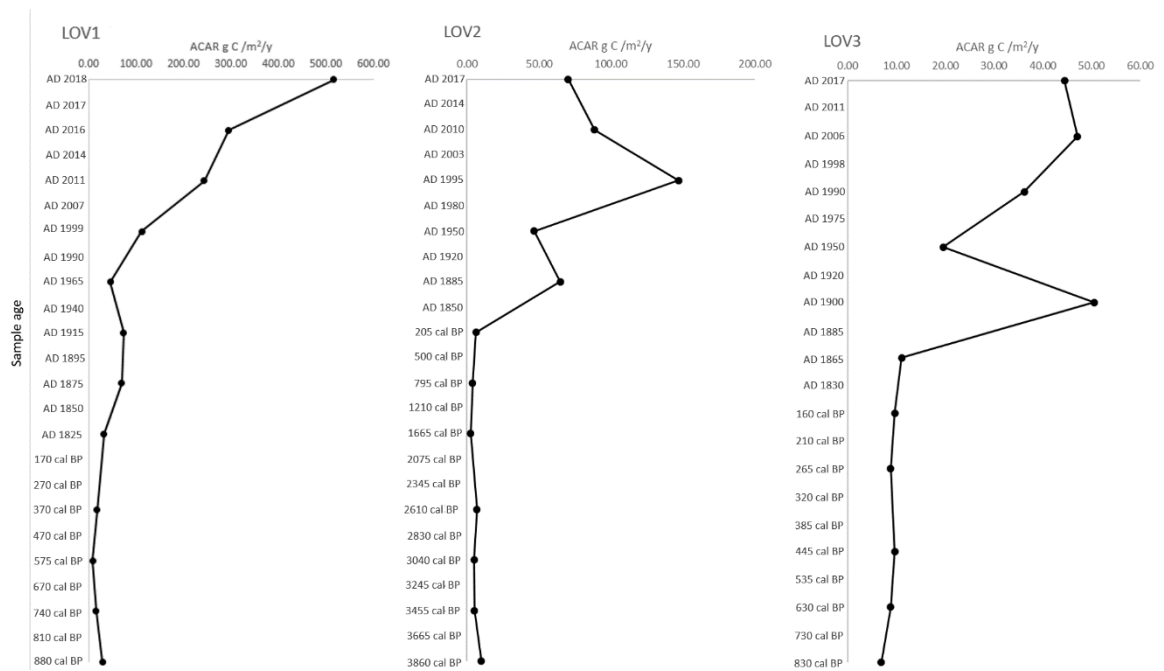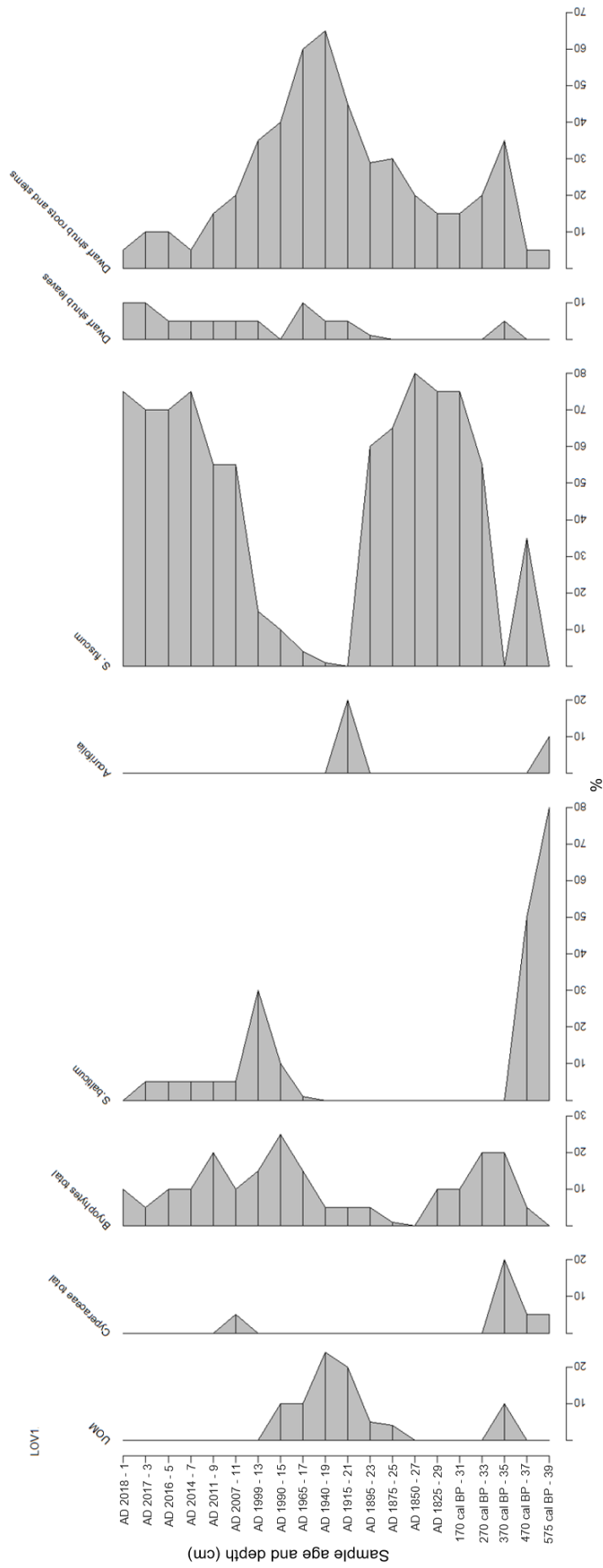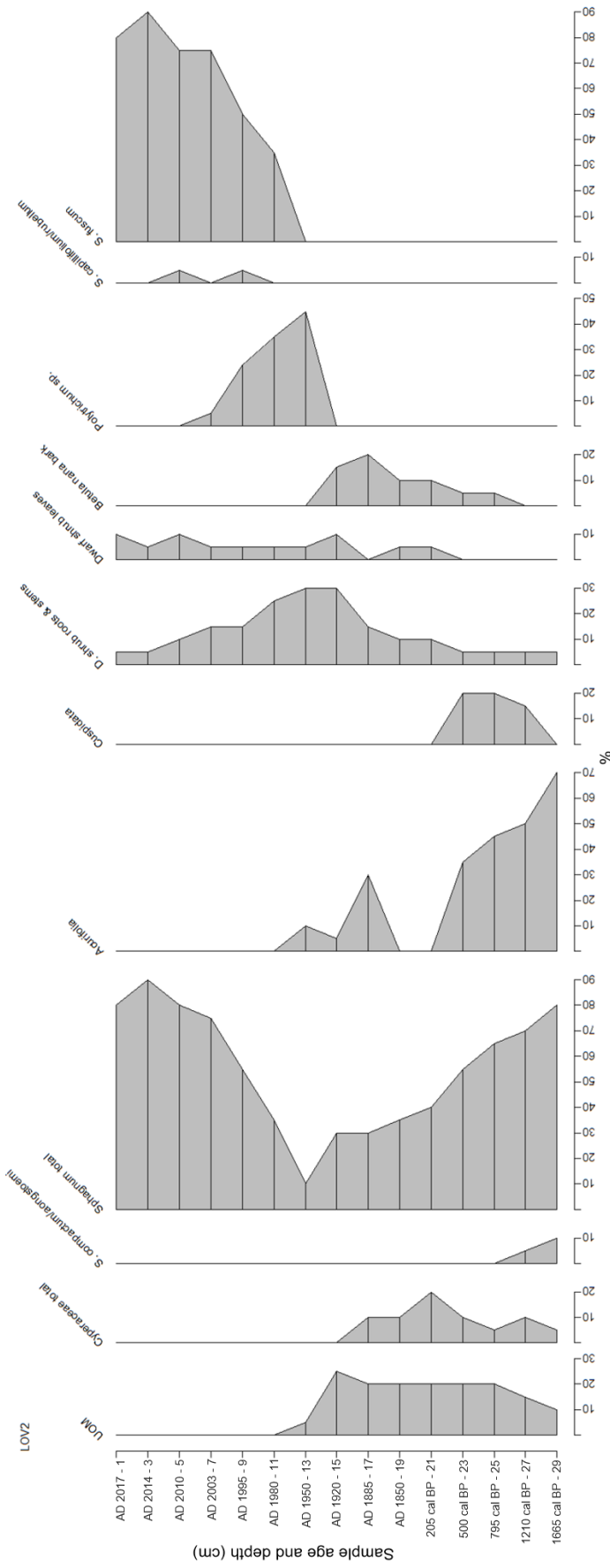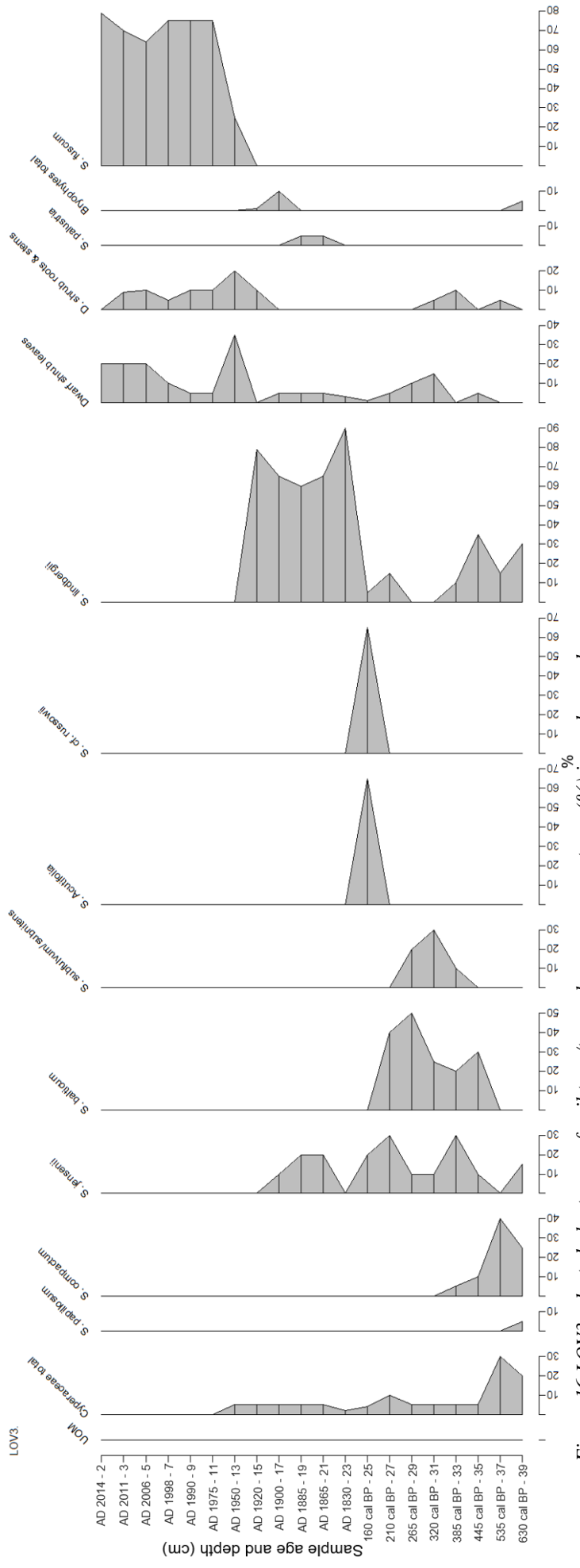
## 4.1 Peat and carbon accumulation

Overall, the mean peat accumulation rates of the Lovozero sites (0.98-2.77 mm/y) are higher than those found in other sites in northern Sweden, Finland and Russia (0.14 – 0.67 mm/y) (Gałka et al. 2017; Sannel 2018; Zhang et al. 2018a). The recent rates of accumulation are comparable to the high peat and carbon accumulation rates found in northwestern Canada, where peat accumulation ranged between 1.6-5.4 mm/y in the last 200 years (Piilo et al. 2019).

All three Lovozero sites have had varying peat and carbon accumulation patterns during the past climatic shifts. In LOV1, peat and carbon accumulation rates were relatively high during the warm MCA, while in LOV2 and LOV3 both peat and carbon accumulation rates remained low (see Figure 14). Low accumulation rates during the MCA have been common in other nearby sites in northern Fennoscandia (Table 4) (Gałka et al. 2017; Sannel 2018; Zhang et al. 2018a). The lowest carbon accumulation rates occurred during the cold LIA for LOV1 (< 10 g $C/m^2/y$) and especially so for LOV2 (< 3 g $C/m^2/y$). These low accumulation rates could have been connected to low primary production in the colder climate. In addition, the high number of mineral grains in the LOV2 record could have been influenced by a drier climate as well as erosion in the surrounding landscape. However, in LOV3, accumulation rates increased throughout LIA. Notably, LOV3 had higher moisture during LIA, which may have contributed to the increasing carbon accumulation. Both low and increasing accumulation rates have been observed during the LIA in the nearby sites in northern Fennoscandia (Table 4) (Gałka et al. 2017; Sannel 2018; Zhang et al. 2018a).

There is a pattern of accelerating peat and carbon accumulation rates towards the top layers of peat in all the Lovozero sites and this pattern has been widely observed in the circumpolar north (Gałka et al. 2017; Sannel 2018; Zhang et al. 2018a; Piilo et al. 2019). Peat and carbon accumulation rates start to increase in all of the Lovozero sites during the 1800s, with significant acceleration since ca. 1950s. It is normal for surface layers to have higher apparent accumulation rates due to the incomplete decomposition of the peat material (Yu et al. 2009). However, Zhang et al. (2018a) attempted to control for the incomplete decomposition of the surface layers by applying different models for young and old peat sections, but still observed increased accumulation rates for the recent decades. As the acceleration in the accumulation rates coincides with the recent

temperature increase and is visible in most of the peatlands in this area, it can be suggested that at least partly the increase in carbon accumulation rate is attributed to the climate.

*Table 4 The trends in apparent carbon accumulation during different climatic phases (Medieval Climate Anomaly, Little Ice Age, Recent Warming) at the Lovozero sites and nearby sites from Abisko (Gałka et al. 2017) and Tavvavuoma (Sannel 2018) in northern Sweden as well as from Kevo and Kilpisjärvi in northern Finland (Zhang et al. 2018a).*

| | Site | Kola peninsula | | | Northern Sweden | | | Northern Finland | |
|---|---|---|---|---|---|---|---|---|---|
| | | LOV1 | LOV2 | LOV3 | Abisko 1 | Abisko 2 | Tavvavuoma | Kevo | Kilpisjärvi |
| **Climatic phase** | **MCA** | High | Low | Low | Decreasing | Low | Low/hiatus | Low | Low |
| | **LIA** | Low | Low/ Hiatus | Increasing | High | Low /increasing | Low/hiatus | Low | Increasing |
| | **RW** | High | High | High | - | High | High | High | High |

The high carbon accumulation rates of the top layers may also be connected to the testate amoebae assemblages. All three Lovozero sites had high abundances of mixotrophic testate amoebae in the top few centimeters. Mixotrophic taxa can influence carbon dynamics in peatlands, as they both sequester carbon through photosynthesis and can slow decomposition due to them predating on decomposers (Jassey et al. 2015). Thus, mixotrophic taxa could be one factor explaining the high accumulation rates in the top layers. In LOV1, recent accumulation has been especially rapid, as the top ca. 9 cm of peat has accumulated in about 8 years during 2011-2018 and the carbon accumulation rate reaches over 500 g C/m²/y in 2017-2018, suggesting high primary production. However, experimental results suggest that mixotrophic taxa are less tolerant to an increase in temperatures than other testate amoebae taxa (Jassey et al. 2015). This effect was not visible yet in the Lovozero sites, but it is possible that the mixotrophic taxa will be negatively affected as climate change progresses in the future.

## 4.2 Hydrology

### 4.2.1 Comparison of plant macrofossils and testate amoebae

Most of the hydrological shifts indicated by testate amoebae communities are also visible in the plant macrofossil assemblages. In LOV1 the wetness during 575-470 cal BP is visible in both proxies, as high abundance of the wet indicator *Sphagnum balticum* and the family Cyperaceae dominated the plant assemblages (see Figure 15) and *A. flavum* was dominant in the testate amoebae assemblages. In addition, the subsequent dry shift around 370 cal BP is also shown in both proxy records, as the dry indicator *S. fuscum* became dominant and the abundance of dwarf shrubs also increased at the same time

when the drier indicators *D. pristis* and *T. minuta* became abundant in the amoebae communities. Similarly to the testate amoebae assemblages, the dry conditions persisted for several hundred years also in the vegetation composition.

In LOV2, the identification of plant macrofossils was somewhat inhibited in the highly decomposed peat, which was reflected in the high portion of unidentified organic matter (UOM) in the samples in 1665 cal BP – AD 1920 (see Figure 16). The oldest peat from ca. 1665 cal BP to AD 1850 was dominated by the dry *Sphagnum* section Acutifolia, but wetter indicators Cyperaceae and *Sphagnum* from the section Cuspidata were also relatively abundant suggesting moderate moisture conditions. This corresponds to the testate amoebae assemblages relatively well, since even though the z-score here was negative indicating wetter than average conditions, the taxa included only intermediate indicators and no wet indicator taxa were present. The testate amoebae data suggest a dry shift in AD 1880 with the increase of *D. pulex*, but the plant assemblages were difficult to identify from this period due to the high humification. However, the increase of *Polytrichum* sp. and *S. fuscum* in the AD 1950s when *A. militaris* increases in the testate assemblages show the shift to drier conditions in plant assemblages, although occurring slightly later.

In LOV3, the plant macrofossils also show the over 500-year wet period from 630 cal BP to AD 1880s, when the site was dominated by *Sphagnum* from the wet section Cuspidata, with e.g. *S. jensenii*, *S. balticum* and *S. lindbergii* in the assemblages while the wet indicator *A. flavum* dominated the testate amoebae assemblages. However, similarly to the case of LOV2, the timing of the subsequent dry shift slightly differs between the two proxies. As testate amoebae data show a dry shift in ca. AD 1900 due to high abundance of *D. pulex*, in plant assemblages this is visible only after ca. AD 1950 when the proportions of *S. fuscum* and dwarf shrubs increase and *A. militaris* becomes abundant in testate assemblages. The similar patterns in LOV2 and LOV3 with high abundance of *D. pulex* prior to a dry shift indicated by plant assemblages could suggest *D. pulex* to be somewhat of a "transition" taxon, and it has been suggested that *D. pulex* could be an indicator of fluctuating water table levels (Loisel & Garneau 2010). In any case, both proxies of LOV3 and LOV2 show a dry shift somewhere between AD 1900-1950.

The recent wet shift visible in testate amoebae in LOV3 since ca. AD 2006 and in LOV1 and LOV2 in the last few years is not visible in the plant assemblages of any of the Lovozero sites. Instead, the plant composition remains very much dominated by *S.*

*fuscum* up to the top layers. This may be due to the slower response times of plant assemblages to shifts in moisture conditions (Väliranta et al. 2012). In addition, *S. fuscum* may be quite resistant to fluctuations in moisture, and vegetation can remain dominated by *S. fuscum* through varying shifts in water table levels (Hughes et al. 2006). Furthermore, as the DCA shows, it is also possible that the increase in the mixotrophic taxa of the surface layers is partly caused by other factors that benefit their ability to photosynthesize, and the shift in moisture conditions may not be as significant as the WTD optimas of the testate amoebae taxa might suggest. Even the two wettest mixotrophic taxa found in Lovozero, *A. flavum* and *P. spinosa*, can tolerate water table levels up to 15 cm depth, although the exact value of the tolerance range is somewhat uncertain (Amesbury et al. 2016). Nevertheless, the significant decrease of the dry indicator *A. militaris* in the surface layers suggests at least some shift towards higher moisture conditions, but the shift may not have been enough to trigger change in the vegetation composition.

### 4.2.2 Hypotheses

In my first hypothesis, past shifts in climate have resulted in changes in Lovozero peatland moisture conditions. However, the moisture conditions of the Lovozero sites do not show consistent responses to previous climatic shifts. LOV1 had wetter conditons during the early part of the Little Ice Age, but a dry shift occurred ca. AD 1470 and the site remained dry for the rest of the cold period. On the contrary, the site LOV3 remained wet for the whole of LIA. During the LIA, both dry and wet shifts have also occurred in other nearby locations in Fennoscandia (Gałka et al. 2017; Zhang et al. 2018b) and in the unpublished testate amoebae data by Ahonen (2019) from Northern Sweden (Table 5). The drier conditions may have been caused by permafrost aggradation during the colder climate, while the wetter conditions or periodical wet shifts could have been influenced by the wetter climate in Scandinavia during the LIA (Linderholm et al. 2018). Thus, despite the differing moisture conditions in the Lovozero peatlands during the LIA, both wet and dry shifts could have been influenced by climatic factors in line with the first hypothesis. However, since these peatland sections are located in such close proximity, they could be expected to respond to similar climatic drivers. As the sites still exhibited opposite moisture conditions, autogenic influence may have been a significant factor contributing to the moisture shifts.

For LOV2, the gap in testate amoebae data covers most of the LIA. The testate data from ca. AD 1850 at the end of LIA, shows slightly wetter than average conditions. However, the somewhat limited plant plant macrofossil analysis shows a mixture of dry and wet taxa suggesting intermediate moisture conditions for this period as well as the warmer period MCA. There also is no major change in the vegetation composition between these two periods. Mainly dry conditions have been reported for the warm MCA period for northern Fennoscandian peatlands, but some sites had wet interruptions (Gałka et al. 2017; Zhang et al. 2018b; Ahonen 2019). As there are such differing results from nearby peatlands and no notable change occurred between MCA and LIA in the LOV2 vegetation, autogenic influence may have impacted moisture conditions more than climate in LOV2 as well.

*Table 5 Average hydrological conditions during climatic phases (Medieval Climate Anomaly, Little Ice Age, Recent Warming since ca. AD 1900s) at Lovozero and nearby peatland sites in northern Sweden (Abisko 1 & 2 by Gałka et al. (2017), unpublished data from Abisko 3 and Tavvavuoma 1 & 2 by Ahonen (2019)) and northern Finland (Kevo & Kilpisjärvi by Zhang et al. (2018b)).*

| | | Kola peninsula | | | Northern Sweden | | | | | Northern Finland | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Site | LOV1 | LOV2 | LOV3 | Abisko 1 | Abisko 2 | Abisko 3 | Tavva 1 | Tavva 2 | Kevo | Kilpisjärvi |
| Climatic phase | MCA | - | Intermediate? | - | Dry | Dry | - | Wet | Dry | Dry | Wet (fen) |
| | LIA | Dry | Intermediate? | Wet | Wet with brief dry shift | Dry | Wet | Dry | Wet | Dry | Dry |
| | RW | Dry & very recent wet shift | Dry & very recent wet shift | Dry & very recent wet shift | Drying | Drying | Dry & very recent wet shift | Dry & very recent wet shift | Dry & very recent wet shift | Drying | Drying |

According to my second hypothesis, moisture shifts are reflected as changes in the testate amobae communities. As most of the hydrological shifts indicated by the plant macrofossil assemblages are also visible in the testate amoebae communities, the testate amoebae assemblages seem to mostly follow moisture shifts in line with the hypothesis 2. However, as the DCA shows, the ordination of testate amoebae taxa does not always consistently reflect the moisture gradient suggesting that other drivers in addition to moisture, such as the preservation of tests or factors impacting mixotrophic taxa, may have also affected the fossil testate amoebae assemblages.

In my third hypothesis, recent warming since the 1980's has resulted in surface drying. The hydrological patterns since the AD 1900s are similar between the Lovozero peatlands, suggesting a stronger climatic influence. All three sampling sites indicate a drying trend during the latest century similarly to many peatlands around the circumpolar

north (Lamarre et al. 2012; Gałka et al. 2017; Swindles et al. 2015c; Zhang et al. 2018b; Swindles et al. 2019). In LOV1, the dryness is a continuation from the LIA, while in LOV2 and LOV3 the dry shifts occured later in ca. 1900s. Markedly around the AD 1950s in all three sites, the dry indicators *A. militaris* and *S. fuscum* increased suggesting continued drying following my hypothesis 3, but three decades earlier than was estimated. The increase in dryness could be due to the rise in temperatures causing increased evapotranspiration, which has also been observed in other drying peatland sites (Zhang et al. 2018b).

However, contrary to the results from many other sites and to hypothesis 3, all three Lovozero sites also had a wet shift in the last decade based on the change in testate amoebae communities. In Abisko, Sweden, two peatlands have also had abrupt wet shifts after a drying trend due to permafrost thaw, but there the wet shifts occurred earlier than in Lovozero before the 2000s (Swindles et al. 2015c). In addition, similar changes in testate amoebae communities towards wetter indicators have also been observed in the surface samples of the unpublished data from northern Sweden (Ahonen 2019). Thus, it is possible that permafrost thaw dynamics are beginning to show in Lovozero and in nearby peatlands in Sweden. The warming may have crossed a threshold where permafrost thaw and release of melting waters exceed the impact of increased evapotranspiration leading to wetter conditions (Swindles et al. 2015c; Zhang 2018).

## 4.3 The future of the northern peatland carbon sink

There are varying estimations of how the future northern peatland carbon sink will develop, and these estimates are complicated by the many interacting factors that influence peatland carbon dynamics. Anthropogenic climate change could enhance primary production more than it increases decomposition, thus increasing the sequestration of carbon in northern peatlands (Frolking & Roulet 2007; Charman et al. 2013; Gallego-sala et al. 2018). Permafrost thaw may also increase primary production enough to compensate for the increased carbon release (Lamarre et al. 2012; Swindles et al. 2015c).

However, some estimations suggest the increase in primary production may not be enough to compensate for the increase in emitted carbon (Ise et al. 2008; Schuur et al. 2008; Dorrepaal et al. 2009; Koven et al. 2011; Schuur et al. 2015). In particular, the underestimation of future carbon release from the deeper peat layers and permafrost thaw

may have yielded too optimistic predictions (Ise et al. 2008; Schuur et al. 2008; Dorrepaal et al. 2009; Koven et al. 2011; Schuur et al. 2015).

In Lovozero, despite the proximity of the studied peatlands, the sites have had varying developments during past climatic shifts suggesting that autogenic factors and local variability may have had a significant role in their moisture and carbon accumulation dynamics. However, as the recent trends show more consistency, the Lovozero sites seem to be responding to a common driver, presumably anthropogenic climate change. Peat and carbon accumulation appear to have increased during the recent decades. In addition, despite the longer drying trend over the last century, the testate amoebae indicate a sudden shift towards wetter conditions in the last decade, suggesting that permafrost melting may be at a threshold where the increased thaw waters exceed the drying effects of increased evapotranspiration (Swindles et al. 2015c).

If this development should continue, the Lovozero peatlands could become even stronger carbon sinks due to higher primary production and carbon sequestration (Zhang 2018). If the moisture content would significantly increase, it could slow down decomposition but also increase $CH_4$ emissions (Zhang 2018). However, as the vegetation composition has not yet shifted towards wetter taxa, it is uncertain whether the wetting will continue and eventually lead to a significant change in the peatland ecosystem. It is possible that the increased moisture is only short-lasting or not strong enough to cause shifts in the vegetation composition. If the Lovozero peatlands continued to dry, decomposition could increase and the dryness could also become a limiting factor for primary production hindering the carbon sink function of the ecosystem (Zhang 2018). In all of these scenarios, permafrost thaw could also lead to higher than expected carbon release from deeper peat layers (Schuur et al. 2015).

The effect of increased mixotrophic testate amoebae on the future carbon sink function of the Lovozero peatlands is uncertain. As stated, mixotrophic taxa can increase carbon accumulation by photosynthesis and through predating on decomposers (Jassey et al. 2015). However, their poor tolerance of increased temperatures in experimental settings suggests that climate change could reduce their abundance (Jassey et al. 2015). More research is needed to determine how the combination of increased temperatures and $CO_2$ concentration in the atmosphere affect these taxa. In addition, further studies would form a clearer picture on how important these taxa are on peatland carbon dynamics. More research is also needed to determine whether the recent trend of increased

mixotrophic taxa in the surface layers of peatlands is a widespread trend in the northern peatlands or just a local phenomenon.

## 4.4  Possible sources of error

One of the major possible error sources relates to the testate amoebae analysis. Some previous reconstruction studies have revealed issues related to identification of fossil tests. The identification of taxa from fossil samples can be challenging due to various reasons, such as the wide variety in test morphology even within the same taxon, and problems in identifying critical features with light microscopy (Charman 1999). Thus, exact identification may sometimes fail. This combined with my inexperience with testate amoebae identification at the beginning of my analysis may have affected the results. However, I had important support for my identifications from my second supervisor M. Amesbury, who is an expert in fossil testate amoeba analyses. Big uncertainties relate to the lower parts of the peat columns where tests were poorly preserved, i.e. broken or otherwise disfigured, and the peat was overall more humified, hindering optic quality. This problem was especially pressing in LOV2 where test identification was very challenging after 15 cm depth.

There may also be differences in test preservation between taxa, but some evidence suggests that this does not have a significant impact on reconstruction outcomes (Charman 1999; Mitchell, Payne & Lamentowicz 2008). Based on the ordination of the taxa in the DCA results, xenosomic taxa dominated the deeper peat sections with few idiosomic taxa present. Thus, the results may be biased towards xenosomic taxa in the deeper peat samples. Again, especially the lower half of the LOV2 core was significantly older than the other two sites increasing the possibility that idiosomic taxa have decomposed.

The reliability of the transfer function results depends on the reliability of the testate amoebae analysis as well as the quality of the available modern training set. As Amesbury et al. (2016) tested their model, it yielded similar performance values as many other commonly used models. However, issues can arise if moisture is not the strongest driver of testate amoebae taxa composition. The DCA here suggested that many other factors may have been strong drivers of the assemblages in addition to moisture gradient, which could affect the realiability of the reconstruction. However, as most of the moisture shifts

were also shown in the plant macrofossil analysis, the transfer function results can be assumed fairly reliable.

The study is also limited due to only analyzing one peat core from each peat section. As results from many studies have shown, even adjacent peat samples can have very varying developments (see e.g. Mathijssen et al. 2014; Zhang et al. 2018a; Piilo et al. 2019). Thus, one peat core may not be representative of the peatland as a whole. To be able to more reliably differentiate autogenic influence from allogenic, multiple samples are needed. However, master's level thesis constraints the quantity of the analyses, but as this thesis is a part of a larger research project, additional peat sections will be analyzed in the project to obtain more reliable results.

There are also uncertainties related to the age-depth analysis. Despite all precautions, when the samples are collected and analyzed, peat can be contaminated with modern carbon affecting the ^{14}C dating. In addition, the sample ages are always an estimation based on the weighted mean ages (Blaauw & Christen 2013). As the error ranges in especially the ^{14}C ages are large, uncertainties remain. However, as there were no visible inconsistencies in the data, such as a deeper peat sample being more modern than a sample higher up in the core, the age depth model seems fairly reliable. Moreoever, in contrast to many other studies, two different dating methods were applied in parallel, which lends support for robust chronologies.

# 5 Conclusions

Studies from northern peatlands have shown that peatland carbon dynamics and hydrology have responded in various ways to past climatic shifts. In addition, carbon dynamics and hydrology have sometimes been more driven by autogenic factors instead of climate. The past developments of Lovozero peatland hydrology and peat accumulation showed no consistent response to past climatic shifts. While LOV1 was dry with slowed peat and carbon accumulation during the LIA, LOV3 experienced wetter conditions with increasing accumulation rates. In LOV2, peat accumulation was extremely slow, while moisture conditions seem to have remained more intermediate. As the studied peatlands are closely located, these different trends suggest that the hydrology and carbon accumulation dynamics of the Lovozero peatlands have been affected by autogenous factors in addition to climate.

The northern peatland response to the anthropogenic climate change seems more consistent with widespread drying and increased carbon accumulation. The Lovozero sites have also had a drying trend and accelerating peat accumulation in the last century. However, contrary to most other previously studied peatlands, a recent wet shift over the last decade was identified at the Lovozero peatlands based on the testate amoebae composition. As this shift is not yet reflected in the vegetation composition, it is uncertain whether the wetting will be significant enough to trigger a more comprehensive change in the ecosystem. However, the increased moisture can be an indication that Lovozero peatlands have reached a treshold in permafrost thaw were the thawing and associated wetting exceeds the drying effects of evapotranspiration. But, the future development of the Lovozero peatland hydrology and carbon sink remains uncertain.

Another interesting observation at Lovozero is that the wetter testate amoebae taxa dominating the surface layers are mixotrophic. Their dominance could be partly connected to factors that stimulate photosynthesis, such as increased atmospheric $CO_2$ concentration. Their increased abundance may also have contributed to the increased carbon accumulation of the surface layers. More research is needed of the effects of mixotrophic testate amoebae on peatland carbon dynamics as well as their response to climatic shifts. In addition, further research will show whether this dominance of mixotrophs occurs around the circumpolar north or whether it is spatially more restricted.

To conclude, the inconsistency of past trends identified at Lovozero peatlands is similar to previous research. The recent wetting trend has not yet been widely observed at other sites, which indicates that the responses of peatlands to the anthropogenic climate change may not be uniform. The varying responses of peatlands to climatic shifts complicates the estimation of their future as anthropogenic climate change progresses. More research is needed to increase our understanding on climate-peatland interactions.

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