# Stable Isotopes ($^{13}C$, $^{15}N$) and biomarkers as indicators to assess drainage history of European peatlands

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# Abstract

Degradation of peatlands by land use changes and anthropogenic climate change produces climate-active gases, reduce biodiversity and flood prevention functions. Therefore, substantial effort is put into peatland restoration projects. However, the methods that are currently available to assess peatland hydrology are expensive and time consuming and require expert knowledge.

The aim of this thesis was to establish a cost- and time-efficient approach to assess peatland hydrology (undrained, drained, rewetted). We used a combination of stable isotopes ($^{13}C$, $^{15}N$) and microbial-derived membrane fatty acids (mFAs). Microbial communities and substrate cycling adapt to a changing hydrology. These activities should be imprinted in stable isotope bulk values as a result of specific isotopic fractionation by different microbial groups, their metabolic pathways, and nutrient sources. As the measurement of stable isotopes is a routine technique today, it could act as a tool to efficiently obtain reliable information about the hydrological regime.

In a first study, we investigated five nutrient-poor peatlands. Here we hypothesized that typical depth patterns of stable isotopes ($^{13}C$, $^{15}N$) exist and that they differ significantly depending upon hydrological regime. We found for all drained sites a distinct peak ("turning point") of the $\delta^{15}N$ bulk values in the center of the drained layer. To support our results and link them to specific microbial groups (fungi, bacteria), we conducted a mFA analysis on a few samples. Our results suggest a switch of fungal- to bacterial-forced metabolism in the drained layers. This switch is reflected by the $\delta^{15}N$ depth trend. The highest diversity of microbial-derived mFAs was indicated by the $\delta^{15}N$ turning point. Below the $\delta^{15}N$ turning point, oxygen is increasingly limited and concentrations of all microbial-derived mFAs decreased down to the onset of the permanently waterlogged anaerobic layer. Hence, we concluded that $\delta^{15}N$ stable isotope bulk values reflect microbial community composition, which differs between undrained and drained peatlands.

In the second study, we performed two sampling campaigns in two nutrient-poor peatlands to investigate (i) how microbial - especially bacterial - groups are shifting with changing hydrology and how they are linked to stable isotope depth pattern ($\delta^{15}N$, $\delta^{13}C$) and (ii) whether rewetting is also imprinted in mFA quantities and stable isotope bulk values. We integrated a mFA analysis related to various microbial groups that are

common in peatlands with stable isotope bulk values. Under waterlogged conditions, overall levels of microbial-derived mFAs were low. Drained layers showed simultaneous changes in mFA quantities and stable isotope bulk values. We found decreasing fungal-derived mFA quantities and increasing bacterial-derived, particularly acidobacterial-derived, quantities with depth. Interestingly, cores from recent rewetted peatlands show no depth trend of $\delta^{15}N$ in the layers grown under rewetting conditions; this is congruent with relatively low microbial-derived mFA quantities. Hence, we concluded that stable isotope bulk values, especially $\delta^{15}N$, reflect changing microbial metabolic processes, which differ between drained and undrained - and especially for rewetted - peatlands.

In a third study, we sampled nutrient-rich fens in an east-west transect across Europe (14 peatlands; Belgium to Poland) and conducted the same stable isotope ($\delta^{13}C$, $\delta^{15}N$) and combined mFA analysis that we used previously in nutrient-poor sites. The aim was to prove that the influence on isotopic fractionation by microbial communities and their metabolic pathways also exists in nutrient-rich fens. We found also for these sites' consistent changes in microbial-derived mFA quantities and stable isotope bulk values corresponding to the hydrological regime. In the uppermost layers, the highest quantities of microbial-derived mFAs were measured in undrained sites, and the lowest were found in drained sites. Fungal-derived mFA quantities were especially decreased in drained sites and deeper layers. Simultaneously, $\delta^{15}N$ stable isotope bulk values were the highest in drained sites and in the uppermost layer and lowest in undrained sites and deeper layers. These trends contrast with what we found previously in nutrient-poor peatlands. We hypothesized that this discrepancy is due to the higher nutrient levels and, therefore, difference in the fungal abundance. For $\delta^{13}C$ bulk values the patterns were similar to those of nutrient poor sites. The $\delta^{13}C$ bulk values for all hydrological regimes increased with depth, especially in drained sites. In rewetted sites, the mFA quantities and stable isotope bulk values shifted from values similar to drained sites (less than 10 years of rewetting) toward the values of undrained sites (more than 25 years of rewetting). We concluded that stable isotope bulk values reflect specific microbial metabolic processes that differ with hydrological regime and, thus, could signal both drainage and rewetting also in nutrient-rich fens.

The findings of this thesis enable us to obtain reliable information on the hydrological regime in a more cost- and time-efficient manner with the help of stable isotope measurements.

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# Abbreviations

| | |
|---|---|
| **C** | Carbon |
| **N** | Nitrogen |
| **mFA** | membrane fatty acids |
| **BD** | Bulk density |
| **CN** | Carbon-to-Nitrogen Ratio |
| **HI** | Humification Index |
| **TP** | Turning Point |
| **normD** | normalized Depth |
| **FB** | Fungi-to-Bacteria Ratio |

# 1

# Introduction

## 1.1. Peatlands

Peatlands cover only 3 % of the global land surface, but, in addition to oceans and forests, they are an enormous store of carbon. They store 30% of the global carbon in soil because they consist mostly of the less decomposed remains of peat-forming plants such as peat moss, sedges, and reeds, which are accumulated over thousands of years (Joosten et al., 2016). As a result, peatlands remove carbon dioxide from the atmosphere and, thus, have a cooling effect on the climate (Joosten et al., 2016).

Furthermore, peatlands provide a high number of other ecosystem processes. They have a dominant role in the landscape water balance for example by the filtration of groundwater and the prevention of flooding (Bedford and Godwin, 2003). Also, peatlands accommodate a high number of endangered and unique plant and animal species (Bedford and Godwin, 2003). Hence, it should be of high global interest to protect these unique ecosystems for extinction.

Peatlands are water-dependent ecosystems that develop where plant input exceeds plant decomposition. This commonly occurs where waterlogged, anoxic conditions hinder the degradation of plant material (Grover and Baldock, 2013).

Peatlands can roughly be divided by their water origin and, therefore, the differences of the degree of mineral soil water influence (minerotrophy; Heinselmann 1970). In the temperate zone of Europe, Asia, and North America, fens are the dominant peatland type (Joosten and Clarke, 2002). Fens are groundwater fed and therefore base rich. Hence, fens are classified as minerotrophic. The vegetation in fens is mostly comprised of species of *Cuspidata*, *Ericaceae,* and *carex,* as well as by *Eriophorum angustifolium* and mosses (*Sphagnum* and brown mosses; Szumigalski and Bayley, 1996). According to their evolution, fens are divided into silting, flooding, flow-through, sloping, swamping, and spring fens.

In contrast, rainwater-fed peatlands are called bogs. They are raised above the surrounding landscape and have no contact to the groundwater; therefore, no ion exchange takes place with the mineral soil (Grootjans et al., 2006). Hence, they are naturally depleted in bases, have a low pH value (3–4.8), and are called ombrotrophic. Their vegetation is mainly built up by *sphagnum* mosses, *Eriophorum angustifolium*,

*carex* species, and *Trichophorum cespitosum*; bogs are largely free of trees, especially in the center (Grootjans et al., 2006).

A transitional bog/fen is a third peatland type, which is in between the two previously mentioned types. They can be built up in both directions from fen to bog and vice versa. For example, in fens in a late stage of peat development, the inflow of groundwater can become locally insufficient to sustain groundwater-fed fen vegetation and a bog can start to develop in the center of the former fen (Grootjans et al., 2006). The vegetation in a transitional bog/fen is composed of a mosaic-like mixture of typical representatives of both types of biotopes (Grootjans et al., 2006).

### 1.1.1. Peatland soils

Peat is mainly composed of organic matter and water (Grove and Baldock, 2013). Peat soils are classified as Histosols (H; IUSS, 2015; organic soils). Histosols are characterized by a high amount of organic matter (> 30%), and a high-water content. In peatland soils, the amount of organic matter accumulation is higher than the amount of mineralization, which leads to a net production of organic matter and a storage of carbon.

From a hydrological perspective, peat—especially bog—soils can be divided into three different layers. Most biological metabolism and nutrient cycling occur in the acrotelm (uppermost aerobic peat layer with living vegetation; Asada et al., 2005a; Artz, 2009; Morris et al., 2011). In the water-saturated catotelm (deeper, anaerobic layer), organic substrates are decomposed at much lower rates due to anoxic conditions (Asada et al., 2005a; Artz, 2009; Lin et al., 2014). In the mesotelm, the peat layer situated between the acrotelm and catotelm, water table levels and oxygen content fluctuate, resulting in shifting aerobic and anaerobic conditions and shifting metabolic processes (Asada et al., 2005a; Artz, 2009; Lin et al., 2014). Clymo and Bryant (2008) therefore defined the mesotelm as a “transition layer”. In degraded peatlands, the mesotelm is expanded and formerly preserved organic substrate is decomposed (Zedler and Kercher, 2005). In an expanded mesotelm, conditions differ from the aerobic and warm conditions in the upper mesotelm to the semioxic, dark and cold conditions in the lower mesotelm (Artz, 2009; Lin et al., 2014). The conditions in the former mesotelm will be anaerobic, and microbial activity will be inhibited with rewetting (Andersen et al., 2006; Asada et al., 2005b; Thormann et al., 1999).

### 1.1.2. Biochemical processes in peatlands

Most carbon is stored in peatland soils in the anaerobic, water saturated deep layers. With increasing dryness, the hydrology, vegetation composition, and biogeochemical processes change, which also affects the carbon balance (Malmer et al., 2005). The decomposition of primary plant material in peat to products like $CO_2$, $CH_4$, and dissolved organic carbon is the result of a microbial metabolism and physically controlled transport processes of electron acceptors and nutrients (Limpens et al., 2008). The decomposition processes are regulated by the quality of the organic matter (Blodau, 2008). Changes in the environmental conditions can either directly or indirectly affect microbial activity through changes in vegetation and soil physical structure (Limpens et al., 2008). In the case of nitrogen, fixation has been reported to only occur in the surface layers of peat (Lin et al. 2014). However, the $N_2O$-producing, microbial-mediated nitrification and denitrification of organic matter, as well as other chemical processes, also occur in deeper layers (Palmer and Horn, 2015; Bremner, 1997). For peatlands, Palmer et al. (2010) report denitrification of organic matter as the main $N_2O$ source. Denitrification causes a reduction of nitrate and nitrite by converting them to nitric oxide (NO) and $N_2O$ and, ultimately, to dinitrogen ($N_2$; Novák et al., 1999). Especially for the deep, anaerobic layer, Lin et al. (2014) reported extremely low values for denitrification and other N-cycling processes and, therefore, a conservation of the substrate.

## 1.2. Peatland degradation

Peatlands are increasingly degrading due to climate change and drainage for agricultural and forestry use. As a result, peat is oxygenated, which increases microbial metabolism processes and leads to a breakdown of the organic matter (Limpens et al., 2008). These processes release considerable amounts of carbon dioxide and, in some cases, nitrous oxide (Limpens et al., 2008). Together with the compaction of peat, this leads to the subsidence of the bog surface: While undisturbed bogs grow about 1 mm per year (Succow and Joosten 2001), drained bogs lose about 0.5 to 5 cm in height per year (Tiemeyer, 2019).

### 1.2.1. Current methods to evaluate peatland degradation

Currently, the measurements that are available to indicate peatland hydrology involve some difficulties. In summary, they are time consuming and expensive, require expert knowledge, and do not provide information of dynamics and drainage history, or they exhibit a combination of these problems.

One current method entails an indirect detection of degradation by the measurement of greenhouse gas emissions (e.g., $CO_2$, $N_2O$ and $CH_4$; Bubier et al., 2013). Undrained peatlands with a high water-table are characterized by low values of carbon dioxide emissions and higher values of methane emissions (Blodau 2008). Drained peatlands with low water tables are associated with higher carbon dioxide emissions (Blodau, 2008). These emissions can be measured with the eddy covariance method. In doing so, the net balance of the emissions is determined by balancing the uptake of carbon dioxide by the plants via photosynthesis and the outgassing by degradation of organic matter (Bubier et al., 2013). These measurements are expensive and labor intensive and do not give information on drainage history and process dynamics beyond the specific measurement time.

A second method is the measuring of vegetation communities and growth. This method is connected to the following problems: (i) the sole growth of moss material not indicates peat growth, the balance of growth and degradation is important (how much vegetation material enters the catotelm and is therefore stored under anaerobic conditions); (ii) peat shrinks and swells with water supply (hence, measuring peat height at different water table heights would lead to different assumptions for peatland growth; Clymo, 1970); and (iii) peat growth, also in a natural hydrological regime, is slow and has an unambiguous effect on the success of restoration efforts, which might require decades of measurements (Clymo, 1970; Fenton, 1980).

Another method is to conduct an analysis of plant residuals and assess the degree of humification with the von Post scale (Baran, 2002). The von Post scale is designed for a description of peat soils in the field. It describes peat soils by three characteristics: (1) the type of the liquid expressed on squeezing, (2) the proportion of peat extruded between fingers and (3) the texture of plant residues is analyzed (Grover and Baldock, 2013). The von Post scale classifies peat soil in 10 classes: H1 to H10. With increasing decomposition, the number rises from H1 to H10. Von Post indices between H1 and H3 indicate undecomposed plant residuals or material with a low degree of decomposition. Classes from H4 to H6 indicate partly decomposed materials, and

classes from H7 to H10 indicate well-decomposed peat soil (Baran, 2002). The von Post scale is a field method and provide rapid characterization of peat soil (Baran, 2002).

Also, biogeochemical data as bulk density (BD) and the carbon:nitrogen ratio (C/N) are used as proxies for the degree of decomposition (Grover and Baldock, 2013). BD acts as an indicator for decomposition because decomposition processes lead to higher compaction of the peat soil, which leads to increased BD values (Novak et al., 2008). The C/N ratio indicates the degree of decomposition (Malmer and Holm, 1984; Kuhry and Vitt, 1996). With increasing decomposition, a preferential loss of C over N takes place, and the C/N ratio decreases.

As the previous methodological examples indicate, a time- and cost-efficient method is needed to obtain reliable data on current peatland hydrology and drainage history.

## 1.3. New approach to assess peatland hydrology

### 1.3.1. Stable isotopes

Elements often exist in more than one stable isotope version. For carbon and nitrogen, two stable isotopes exist. On earth, 98.89% of the naturally occurring carbon is in the form of $^{12}C$ and 1.11% in form of $^{13}C$ (Fry, 2007). The natural ratio for nitrogen is a combination of 99.64% $^{14}N$ and 0.36% $^{15}N$ (Fry, 2007). Stable isotope ratios are usually presented as a ratio and reported as parts per million (‰) comparing it to the Vienna Pee Dee Belemnite (VPDB) reference standard for carbon and the atmospheric nitrogen for nitrogen (Krüger et al., 2016).

$$\delta^{13}C_{sample} = \left(\frac{R_s}{R_{std}} - 1\right) x100$$

$R_s$ and $R_{std}$ are the ratios of $^{13}C/^{12}C$ in the sample and the VPDB standard ($R_{std}$ = 0.011182).

Nitrogen stable isotopes were expressed relative to atmospheric nitrogen and reported in delta notation (‰):

$$\delta^{15}N_{sample} = \left(\frac{R_s}{R_{std}} - 1\right) x100$$

$R_s$ and $R_{std}$ are the ratios of $^{15}N/^{14}N$ in the sample and atmospheric nitrogen ($R_{air}$ = 0.0). The stable isotopes of carbon and nitrogen are used in soil science as an indicator of biogeochemical processes and soil degradation (Krull and Retallack, 2000; Robinson, 2001; Schaub and Alewell, 2009; Conen et al., 2013; Meusburger et al., 2013). In general, decomposition of organic matter and cycling of elements leads to fractionation

processes that change the natural signature (Biester et al., 2014). Each metabolism process has an individual fractionation ratio (Lerch et al., 2011). For peat soil, the ratio and a changing ratio for different hydrological regimes is relevant because drainage induces an increasing decomposition of plant residuals and, therefore, also induces a changing fractionation rate of stable isotopes (Krüger et al., 2016). As decomposition induces an enrichment of heavy isotopes ($^{15}N$ and $^{13}C$), vegetation is mostly more deficient in $^{15}N$ and $^{13}C$ than microbial and recycled substrate (Biester et al., 2014).

#### 1.3.1.1. Carbon stable isotopes

Stable isotopes of carbon are known indicators of peatland hydrology (Alewell et al., 2011; Krüger et al., 2016; 2020; Kohl et al., 2015). For δ13C, Alewell et al. (2011), Krüger et al. (2016), Novak et al. (1999), Hobbie et al. (2017) and Biester et al. (2014) report an enrichment of $^{13}C$ with depth due to an increasing degree of organic matter decomposition. Substrates have a natural and specific range of $^{13}C$ values (Lerch et al., 2011). As lignin, cellulose, and lipids are known to be depleted in $^{13}C$, glucose, amino acids, pectin, and hemicellulose are enriched in $^{13}C$ (Lerch et al., 2011). In undrained wetlands, the combination of these substrates is mostly preserved due to the waterlogged conditions. If drainage takes place, the original bulk soil $\delta^{13}C$ value is changed by degradation and microbial metabolism processes. Kohl et al. (2015) state that an increasing $\delta^{13}C$ depth trend is a consequence of a switch in dominant microbial decomposition, which has stronger effects than the residual enrichment of recalcitrant compounds such as lignin. Kohl et al. (2015) also indicate that fungi are the main decomposer in the uppermost soil layers and bacteria are more prominent in deeper layers. With this switch of dominant microbial groups, the decomposed material also switches and, therefore, the $^{13}C$ bulk values change.

#### 1.3.1.2. Nitrogen stable isotopes

Fractionation of stable isotopes during microbial metabolism of nitrate and ammonium occurs, since most organisms prefer the lighter and more frequently occurring $^{14}N$ (Kohzu et al., 2003; Robinson et al., 1998). As a result, plants incorporate and translocate the lighter $^{14}N$ upwards to stem and foliar, which leads to an enrichment of heavier $^{15}N$ in the remaining bulk material (Högberg et al., 1996). Additionally, the mycorrhizal uptake of lighter $^{14}N$ into plants increases the $\delta^{15}N$ values of bulk material (Hobbie and Högberg, 2012). Furthermore, with ongoing microbial metabolic

processes in peat, the $\delta^{15}N$ values increase when microbial metabolism occurs, and lighter $^{14}N$ will be leached, translocated or lost via outgassing (Novák et al., 1999; Damman, 1988; Niemen, 1998). In 2010, Goldberg et al. showed that increasing oxygen concentrations in drained fens leads to higher $N_2O$ release by nitrification, which is followed by increasing $\delta^{15}N$ values in the remaining substrate. Thus, microbial abundance and stable isotope ratios are closely linked, especially for some microbial groups that are more active in nitrogen cycling than others and, therefore, play a greater role (Tfaily et al., 2014). Fungi have a low demand for nitrogen, making them less likely to be a main driver of increasing $\delta^{15}N$ values (Thormann, 2005). In contrast, acidobacteria are one of the main bacterial groups in peat and are highly active in nitrogen cycling; in particular, they are involved in denitrification and N fixation (Ward et al., 2009). Accordingly, their abundance can be expected to have a close link to carbon and nitrogen stable isotope depth trends (Weijer et al., 2010).

### 1.3.2. Membrane fatty acids

MFAs are valid markers to indicate the abundance of specific microbial communities. Sundh et al. (1997) and Torres and Pancost (2016) demonstrated that mFAs are persistent and, to a high degree, insoluble compounds in peat soil. Membrane fatty acids vary based on their origin (plants, specific microbial groups, etc.; Bajerski et al., 2017; Finotti et al. 1993; Piotrowska-Seget and Mrozik, 2003; Reiffarth et al., 2016; Willers et al., 2015). Therefore, based on an analysis of the quantity of mFAs present, the relative abundance of certain microbial communities might be assessed (Torres and Pancost, 2016; Piotrowska-Seget and Mrozik, 2003). We tested the existence of four bacterial markers and one fungal marker:

- i-C15:0 and C16:1ω7c, which, in combination, are indicative of acidobacteria (Damasté et al., 2011; Dedysh and Damsté, 2018; Myers and King, 2016);
- C14:0 and C17:0, which are generally indicative of bacteria (Willers et al., 2015; Zelles, 1997); and
- C18:2ω6c, which is indicative of saprotrophic fungi (Sundh et al., 1997; Elvert et al., 2003; Willers et al., 2015).

## 1.4. Goals of the thesis

The overall goal of this thesis was to strengthen the idea of stable isotopes as a cost- and time-efficient method to assess peatland hydrology. In previous studies, distinct

depth patterns for carbon stable isotopes were found in drained and undrained peatlands in different climate zones. Furthermore, differences in nitrogen stable isotope depth patterns have been documented in drained and undrained sites. Following this, this study combines an analysis of stable isotope bulk values ($\delta^{13}C$, $\delta^{15}N$) in bogs and fens and provides a supporting analysis of microbial-derived membrane fatty acids to elucidate the connection between the observed stable isotope depth trends and the underlying processes. Furthermore, we included rewetted peatland sites in our analysis to use stable isotopes as tool to indicate rewetting success.

The combination of biogeochemical measurements (stable isotope measurements, bulk density, carbon:nitrogen ratio), vegetation analyses, and microbial-derived membrane fatty acid analysis enables us to identify the influence of specific microbial groups to fractionation processes. This gives us the opportunity to confirm stable isotopes a as reliable indicator for peatland hydrology.

The first study presented in **Chapter 2** was published by Groß-Schmölders et al. (2020). In this study, we were examining the influence of changing dominant microbial groups (determined by microbial-derived mFAs of some exemplary samples) on nitrogen stable isotope depth patterns. We studied five nutrient-poor peatlands in a north-south transect through western Europe: Degerö Stormyr (northern Sweden), Lakkasuo (central Finland), and three mires in the Black Forest (southern Germany). At all locations, cores were taken from adjacent drained and undrained sites. We found that there are specific stable isotope depth trends for the different hydrological regimes, which correlate to a switch from fungal to bacterial dominated metabolism with depth.

To investigate the microbial groups (e.g. occurrence of specific biomarkers) and their influence on stable isotope depth patterns ($\delta^{13}C$, $\delta^{15}N$) in depth, we performed detailed sampling campaigns in two of the investigated peatlands from the first study (Degerö Stormyr, Lakkasuo) as part of a second study (**Chapter 3**) published by Groß-Schmölders et al. (2021).We analyzed stable isotope data ($\delta^{13}C$, $\delta^{15}N$) and membrane fatty acids of different microbial groups that are known to be common in peatlands. We found that a switch from fungi to acidobacteria is responsible for a distinct $\delta^{15}N$ depth trend and that $\delta^{15}N$ values are valid to indicate not only drainage but also rewetting. Furthermore, we determined that the $\delta^{13}C$ depth trend could be linked to drainage and abundance of specific microbial groups.

The third study was done in nutrient-rich peatlands in a west-east gradient (**Chapter 4**). The goal was to see if the connection between stable isotope depth trends and microbial abundance is also valid for nutrient-rich peatlands. Therefore, we investigated 14 nutrient-rich fens in mid-Europe. We performed the same analysis of stable isotopes ($\delta^{13}C$, $\delta^{15}N$) and membrane fatty acids. For each site, samples from an undrained, a drained, and a rewetted site were analyzed. We also found for these nutrient-rich sites that there is a correlation between stable isotopes ($\delta^{13}C$, $\delta^{15}N$) and membrane fatty acids. This study has been submitted for publication.

In **Chapter 5**, the conclusions of this thesis are presented, and an outlook is given in **Chapter 5.4**.

# 2

# Switch from fungal to bacterial degradation in natural, drained and rewetted oligotrophic peatlands reflected in $\delta^{15}N$ and fatty acid composition[1]


## Abstract

For centuries European peatlands have been degrading along with drainage, land use and climate changes. Increasing pressure on peatland ecosystems calls for a more cost-efficient method to indicate the current state of peatlands and the success of restoration efforts. Metabolic pathways in peatland soils are imprinted in stable isotope compositions due to differences in microorganism communities and their metabolic pathways. Therefore, we hypothesize that depth profiles of nitrogen stable isotope values provide a promising opportunity to detect peatland decomposition or restoration. We studied five peatlands, namely Degerö Stormyr (northern Sweden), Lakkasuo (central Finland) and three mires in the Black Forest (southern Germany). At all locations, cores were taken from adjacent drained (or rewetted) and natural sites to identify $\delta^{15}N$ trends that could indicate changes due to drainage and restoration. At all drained (and rewetted) sites we found a distinct peak ("turning point") of the $\delta^{15}N$ values in the center of the drained layer. We did a fatty acids (FAs) analysis to link our results to microbial community composition. As markers, we distinguished between one fungal-derived FA (C18:2ω6c) and four bacterial-derived FAs. For bacteria, we looked for one general bacterial-derived FA (C14:0), two FAs for gram-positive bacteria (i-C15:0; a-C15:0), and one FA for gram-negative bacteria (C16:1ω9c). In accordance with other studies, our results suggest that fungi dominate the microbial metabolism in the upper aerobic peat layer. This is reflected by depleted $\delta^{15}N$ values. Moving downwards, the drained layer conditions slowly switch to oxygen limitation. Consequently, fungal-derived FAs decrease whereas bacterial-derived FAs rise. The


[1] Study published as Groß-Schmölders, M, von Sengbusch, P., Krüger, J. P., Klein, K., Leifeld, J. and Alewell, C.: *Switch of fungal to bacterial degradation in natural, drained and rewetted oligotrophic peatland reflected by $\delta^{15}N$ and fatty acid composition. Soil, 6, 299-313, DOI: 10.5194/soil-6-299-2020, 2020.*

highest diversity of microbial-derived FAs is indicated by the $\delta^{15}N$ turning point. Below the $\delta^{15}N$ turning point, oxygen is increasingly limited, and concentrations of all microbial-derived FAs are decreasing down to the onset of the permanently waterlogged anaerobic layer. Peatland cores with restoration successes again show, above the formerly drained layer, no depth trend of the isotopic values. Hence, we conclude that $\delta^{15}N$ stable isotope values reflect microbial community composition, which differs between drained and natural peatlands.

## 2.1. Introduction

In Europe 70% of the peatlands are degraded (Joosten and Couwenberg, 2001). Leifeld and Menichetti (2018) reported that degraded peatlands account for 5% of the anthropogenic $CO_2$ emissions. Despite this dramatic peat decline, we lack reliable and transferable tools that provide time- and cost-efficient information of the peatland hydrological regime, as we define it.

We determine natural, drained and rewetted hydrological regimes of peatlands, derived by the average thickness of the aerobic layers and the resulting degree of decomposition. From a hydrological perspective, peatland soils can be divided in three different layers. Most biological metabolism and nutrient cycling take place in the acrotelm (uppermost aerobic peat layer with living vegetation; Asada et al., 2005a; Artz, 2009; Morris et al., 2011). In the water-saturated catotelm (deeper, anaerobic layer) organic substrates are decomposed at much smaller rates owing to anoxic conditions (Asada et al., 2005a; Artz, 2009; Lin et al., 2014). In the mesotelm, the peat layer situated between acrotelm and catotelm, water table levels and oxygen content fluctuate, resulting in shifting aerobic and anaerobic conditions and shifting metabolism processes (Asada et al., 2005a; Artz, 2009; Lin et al., 2014). Clymo and Bryant (2008) therefore defined the mesotelm as a “transition layer”. In degraded peatlands the mesotelm is expanded and former preserved organic substrate is decomposed (Zedler and Kercher, 2005). In an expanded mesotelm conditions differ from aerobic, light and warm conditions in the upper mesotelm to semioxic, dark and cold conditions in the lower mesotelm (Artz, 2009; Lin et al., 2014). The conditions in the former mesotelm will be anaerobic, and microbial activity will be inhibited with rewetting (Andersen et al., 2006; Asada et al., 2005b; Thormann et al., 1999).

We determined the hydrological regime by a vegetation analysis, the humification index (HI) after von Post (Silc and Stanek, 1977), the measurement of the water table

height, and historical data of the installation of drainage channels. Natural and rewetted sites have a high-water table near the surface and are mainly formed by Sphagnum mosses with low humification indices. Drained sites are characterized by low water tables, higher grades of humification, less Sphagnum and more of other moss species. However, determination of macro residuals and their humification degree in more or less degraded peat is time consuming, needs highly specialized expert knowledge and is thus limited to a small number of samples.

Other common methods to measure peatland hydrology currently are gas emission measurements and measurement of growth heights of peatland vegetation. Gas measurements (e.g., $CO_2$, $N_2O$ and $CH_4$) provide an indirect measurement of ongoing decomposition processes (Baldocchi et al., 1988). The method is expensive and labor intensive and does not to give information on drainage history and process dynamics beyond the specific measurement time (Bubier et al., 2003). Measuring vegetation growth is connected to the following problems: (i) not only does the sole growth of mosses indicate peat growth but also the balance of growth and degradation (it is important how much vegetation material enters the catotelm and is therefore stored under anaerobic conditions); (ii) peat shrinks and swells with water supply (hence, measuring peat height at different water table heights would lead to different assumptions for peatland growth; Clymo, 1970); and (iii), peat growth, also in a natural hydrological regime, is slow and an unambiguous effect on the success of restoration efforts might need decades of measurements (Clymo, 1970; Fenton, 1980).

As such, and in search of practical indicators, we measured bulk density (BD), the carbon:nitrogen ratio (CN) and bulk stable isotope values. BD acts as an indicator for decomposition because decomposition processes lead to higher compaction of the peat soil and therefore increasing BD values (Novak et al., 2008). The CN ratio indicates the degree of decomposition (Malmer and Holm, 1984; Kuhry and Vitt, 1996). With increasing decomposition, a preferential loss of C over N takes place and the C:N ratio decreases. Stable isotope depth patterns of $\delta^{13}C$ and $\delta^{15}N$ in peat have been found to be specific for peatland hydrology (drained, rewetted or natural) in previous studies (e.g., Krüger et al., 2016; Alewell et al., 2011), but the studies were unable to find an explanation for these depth patterns. As degradation is mostly connected to drainage, we hypothesized that an increase of microbial activity is responsible for the change in isotope patterns.

Stable C and N isotopes are correlated with vegetation composition and microbial decomposition processes. As decomposition induces an enrichment of heavy isotopes ($^{15}N$ and $^{13}C$), vegetation is mostly more depleted in $^{15}N$ and $^{13}C$ than microbial and recycled substrate. Alewell et al. (2011) and Krüger et al. (2014) reported distinct changes in $\delta^{13}C$ values for palsa peat with the onset of the decomposition of hummocks. Various authors observed the same trend with decomposition in peatlands of other climate conditions (Krüger et al., 2016; Novak et al., 1999; Hobbie et al., 2017; Biester et al., 2014). The distinct $\delta^{13}C$ depth pattern is a consequence of the use of different sources by fungi and bacteria, as investigated by Kohl et al. (2015) for peat profiles. They conclude that an increasing $^{13}C$ signal is caused by differences in biomass synthesis and carbon sources used by fungi and bacteria, which was also reported by Lichtfouse et al. (1995) and Baumann et al. (2013). We also found distinct changes in $\delta^{15}N$ with drainage. It is known that plants preferentially incorporate the lighter $^{14}N$ (Högberg, 1997), an effect that is strongly enhanced by mycorrhizal uptake of nitrogen into plants (Hobbie and Högberg, 2012). Plant rooting and the existence of mycorrhiza leads to enriched 1 $\delta^{15}N$ values in the remaining bulk material (Högberg et al., 1996) because plants and mycorrhiza preferentially process lighter $^{14}N$ (Adams and Grierson, 2001; Asada et al., 2005a; Hög berg et al., 1996; Kohzu et al., 2003; Robinson et al., 1998). However, our study sites are open peatlands with a low occurrence of vascular plants and mycorrhiza. Hence, we assume that these mechanisms cannot be the main drivers of our observed $\delta^{15}N$ depth patterns. Tfaily et al. (2014) reported that changing microbial abundance and metabolic pathways are correlated with $\delta^{15}N$ values. Conversely, this would mean that $\delta^{15}N$ values could reflect the hydrological regime. Therefore, we assume $\delta^{15}N$ values allow us to draw conclusions about whether the observed peatlands have a natural, drained or rewetted hydrological regime.

Following previous studies, we use specific terms for the points of change in the stable isotope depth pattern. The points where the stable isotope signals undergo a sudden directional shift with depth are called “turning points”, according to Alewell et al. (2011). Furthermore, the bottom of the mesotelm and the onset of the underlying catotelm are marked by the $\delta^{13}C$ turning point.

To test the idea of changing dominant microbial communities as drivers for isotope depth patterns, we did a fatty acid (FA) analysis of four investigated sites, namely two drained and two natural sites in Degerö Stormyr (central Sweden; 70 km from Umea)

and Lakkasuo (southern Finland; 14 km north of Orivesi). FAs are valid markers for indicating the abundance of specific microbial communities in the peat because they are specific and persistent compounds of cell membranes of different species (Bajerski, Wagner and Mangelsdorf, 2017; Finotti et al., 1993; Piotrowska-Seget and Mrozik 2003; Reiffarth et al., 2016). Therefore, FAs enable us to make qualitative and quantitative statements about the relative abundance of different microbial communities. We will test the existence of four bacterial markers (namely C14:0 as general marker; i-C15:0 and a-C15:0 indicative for gram positive; and C16:1ω9c indicative for gram negative; Vestal and White 1989; Willers et al., 2015; Zelles, 1997) and one fungal marker (C18:2ω6c); Sundh et al., 1997; Elvert et al., 2003; Willers et al., 2015).

We hypothesize that microbial abundance and diversity are the drivers for the distinct observed $\delta^{15}N$ depth pattern in natural, drained or rewetted peats. We assume the $\delta^{15}N$ depth pattern can therefore be used as an inexpensive and less time-consuming tool to obtain reliable information of peatland hydrology.

## 2.2. Study site

We studied five oligotrophic peatlands (Tables 2.1/ 2.2). All investigated sites are classified as fibric Histosols (HSf; IUSS, 2015; organic soils). Fibric Histosols are classified as soils with a cumulative organic layer and an organic matter amount of 35% or higher in at least half of the uppermost 80 – 100 cm and with a high amount (two-thirds) of little decomposed plant residuals (IUSS, 2015). In addition, all investigated peatland soils are Sphagnum peat because of their mean annual temperatures (between 1.2°C and 7°C) and their annual precipitation between 523 mm and 1600 ppm (Eurola et al., 1984; Vitt, 2006).

**Table 2.1:** *Labeling of all drilling sites*

| Location | Labeling |
|---|---|
| Degerö | |
| natural mire | DN |
| drained | DD |
| Lakkasuo | |
| minerotrophic natural | $LN_m$ |
| minerotrophic drained | $LD_m$ |
| ombrotrophic natural | $LN_o$ |
| ombrotrophic drained | $LD_o$ |
| Breitlohmisse | |
| natural mire | BN |
| natural dry | $BN_d$ |
| drained | $BD_1$ |
| near the mire edge | $BD_2$ |
| Rotmeer | |
| natural mire | RN |
| drained, with Sphagnum | $RD_1$ |
| drained, without Sphagnum | $RD_2$ |
| Ursee | |
| natural mire | UN |
| drained | UD |

Degerö Stormyr (200 m above sea level – a.s.l.) is situated in northern Sweden, at the Kulbäcksliden Experimental Forest near Vindeln, between the rivers Umeälven and Vindelälven (Eurola et al., 1984). It is an acidic mire with minerotrophic conditions and consists of interconnected small mire patches divided by ridges of glacial till. Degerö Stormyr is classified as northern eccentric peatland (Eurola et al., 1984). The climate is characterized as cold, with no dry seasons and cold summers (Dfc zone, based on the Köppen – Geiger climate classification; Peel et al., 2007). In Degerö Stormyr, ditches were installed at the beginning of the 20$^{th}$ century, were closed in 2017 and a natural reestablishment of Sphagnum took place afterwards. The water table is at the surface in the natural part (DN; Nilsson et al., 2008) and in around 10–15 cm depths at the drained location (DD).

Lakkasuo (150 m a.s.l.), central Finland, is a northern eccentric peatland complex (Eurola et al., 1984) with two parts. In the southern part the conditions are ombrotrophic, whereas the northern part is minerotrophic (Minkkinen et al., 1999). Lakkasuo is also located in the cold climate zone, with no dry seasons and cold summers (Dfc zone, based on the Köppen– Geiger climate classification; Peel et al., 2007). The ditches that were installed in 1961 (70 cm depth; spacing of 40–60 m) affect approximately 50% of the peatland (Minkkinen et al., 1999). In the ombrotrophic natural site ($LN_o$) the water table was around 13 cm below ground surface. The ombrotrophic drained site ($LD_o$) had a water table with a ±26 cm depth, whereas the water table is near the surface at the minerotrophic natural site ($LN_m$) and at depth of ±36 cm in the minerotrophic drained site ($LD_m$; Minkkinen et al., 1999; Tables 1–2).

In the Black Forest three mires were investigated, namely Breitlohmisse, Ursee and Rotmeer. They are located in the temperate climate zone with no dry seasons and warm summers (Cfb zone, based on the Köppen – Geiger climate classification; Peel et al., 2007). In the mires of the Black Forest, ditches were installed in the middle of the 20th century. Breitlohmisse (810 m a.s.l.; 50 km southeast of Baden-Baden) is minerotrophic and is located in the northern part of the Black Forest. The mire is mostly lanced with ditches for hunting ($BN_d$). The ditches are naturally refilled with Sphagnum. The water table is at ±15 cm in the natural center (BN; $BN_d$) and is found at lower depths near the degraded edges of the mire ($BD_1$; $BD_2$). Rotmeer (960ma.s.l.; 40 km southeast of Freiburg im Breisgau) and Ursee (850 m a.s.l., 45 km southeast of Freiburg im Breisgau) are both in the southern Black Forest. Rotmeer consists of an ombrotrophic center (RN; water table at the surface), surrounded by a minerotrophic part with signs of decomposition ($RD_1$; water table around 12 cm depth) and without mosses at the edges ($RD_2$; water table below 12 cm depth). Urmeer is minerotrophic. A quaking bog forms the center with the water table at the surface (UN), whereas the edges had a lower water table (UD; Tables 2.1 – 2.2).

**Table 2.2:** *Overview of studied mires; coordinates (lat./long.); mean annual temperature (MAT); annual precipitation (P); Sphagnum mosses (Sph.) (Laine et al., 2004; Nielsson et al., 2008; DWD, 2018; Alexandersson et al., 1991; Armbruster et al., 2003)*

| Country | Mire | lat/long.. | MAT | P | Main vegetation on top | |
|---|---|---|---|---|---|---|
| | | | [°C] | [mm] | natural | drained |
| Sweden | *Degerö Stromyr* | 64°11'lat., 19°33'long. | +1.2 | 523 | Sph. majus | Sph. balticum |
| Finland | *Lakkasuo* | 61°48'lat., 24°19'long. | +3 | 700 | Sph. angustifolia | Sph. angustifolia |
| Germany (Black Forest) | *Breitlohmisse* | 48°41'lat., 8°25'long. | +7 | 835 | Sph. capillifolium | Sph. capillifolium |
| | *Ursee* | 47°51'lat., 8°25'long. | +7 | 1600 | - | - |
| | *Rotmeer* | 47°52'lat., 8°6'long. | +7 | 1600 | Sph. rubellum | Sph. rubellum patches |

## 2.3. Material and methods

### 2.3.1. Soil sampling and bulk analyses

In May 2012 (Breitlohmisse), June 2012 (Rotmeer), July 2012 (Ursee) and September 2013 (Degerö Stormyr and Lakkasuo) three volumetric peat cores were drilled per site with a Russian peat corer (Eijkelkamp, the Netherlands) at a medium stage of small-scale topography. In Degerö Stormyr cores were sampled in the assumed natural center of the mire (DN) and a 1 m distance from a drainage ditch (1m depth; DD). In Lakkasuo we took cores at the natural sites (ombrotrophic natural – $LN_o$; minerotrophic

natural – $LN_m$) and the drained locations (ombrotrophic drained – $LD_o$; minerotrophic drained – $LD_m$). For Ursee two cores were taken, namely one in the natural center (UN) and one at the drained edge of the mire (UD). In Breitlohmisse and Rotmeer we took cores in a transect from natural (BN and RN) to strong drained ($BD_2$ and $RD_2$) sites. Each core has a composite length of 1 m. Here, we focus on the uppermost 60 cm because this part included the drained layer, and no major changes in isotopic composition were observed at the natural sites below the mesotelm. In all investigated peatlands, the catotelm starts in the natural sites below a 10 cm depth and varied in drained sites but was always visible below a 40 cm depth. Directly after drilling, HIs were determined for each layer with the von Post scale. The von Post scale has a range from 1 to 10. HI 1 indicates natural condition with undecomposed, completely visible vegetation residuals. HI 10 represents a strongly decomposed layer without visible vegetation residuals (Silc and Stanek, 1977). The cores were encased in plastic shells and covered with plastic wrap, stored in coolers, and transported to the laboratory. The cores were sliced in 2 cm sections and every second layer was analyzed, giving a 4 cm depth resolution. Samples were oven dried at 40 _C for 72 h and homogenized with a vibrating ball mill (MM400; Retsch GmbH, Haan, Germany). Stable C and N isotopic compositions were measured with an elemental analyzer combined with an isotope ratio mass spectrometer (EA–IRMS; Inegra2, Sercon Limited, Crewe, UK). Carbon isotopic composition ($^{13}C$:$^{12}C$) was expressed relative to the Vienna Pee Dee Belemnite (VPDB) standard and reported in delta notation (‰); stable nitrogen isotopes were expressed relative to the atmospheric nitrogen standard and reported in delta notation (‰). CN was determined with the mass relationship of the measured bulk content of C and N. Bulk density was measured with volumetric samples, which were weighted before and after drying. In Degerö Stormyr tree rings of seven individual trees were analyzed (Pinus sylvestris) to obtain information of growth conditions and, therefore, to enhance our knowledge of drainage history.

### 2.3.2. Fatty acid Analysis

Four cores (per site; one drained and one natural core) were selected to do a fatty acid analysis, namely two sites in Lakkasuo ($LDo_1$ and $LNo_3$) and two sites for Degerö Stormyr ($DD_3$ and $DN_1$). We took subsamples from all cores in the acrotelm (respectively, at the end of the mesotelm in DD) and in the catotelm. At the drained sites of $DD_3$ and $LDo_1$, we also took samples in the middle and at the end of the

mesotelm. We processed 0.2–1.1g of sample for the lipid extraction with a mixture of $CH_2Cl_2$:MeOH (9:1v/v) in an accelerated solvent extractor (Dionex ASE 350; Thermo Fisher Scientific, Waltham, Massachusetts, USA). A total of 50µL of an internal standard (0.4mg $mL^{-1}$; nonadecanoic acid) was added before processing each sample. The total lipid extracts (TLEs) were saponified by adding 2mL of KOH dissolved in MeOH (12%) and putting it in the oven for 3 h at 80°C. Following the method of Elvert et al. (2003), TLEs were pooled afterwards with 1mL KCl (0.1mol), and the neutral fraction was extracted by agitating three times with hexane. Neutral fraction in the supernatant was separated, dried under a stream of $N_2$ and stored in the fridge for later analysis. We acidified the rest of the TLEs with fuming hydrochloric acid to a pH of 1. The acid fraction was extracted by agitating again three times with hexane. The acid fraction in the supernatant was separated and hexane was reduced to near dryness under a stream of $N_2$. Then the acid fraction was methylated by adding 1mL boron trifluoride ($BF_3$) in MeOH (12% –1 4%) and putting it in the oven for 1 h at 60°C. Afterwards the resulting fatty acid methyl esters (FAMEs) fraction was pooled with KCl (0.1mol) extracted by agitating again three times with hexane and transferred in 2mL vials. The FAMEs were quantified with a gas chromatograph (Trace Ultra GC) equipped with a flame ionization detector (FID; Thermo Fisher Scientific, Waltham, Massachusetts, USA). The carrier gas (helium) had a constant flow of 1.2mL per minute and the GC–FID was set to splitless mode. Detector temperature was 320°C and the samples (dissolved in hexane) were injected by 300°C. The starting temperature of the oven was 50°C. The temperature was increased by 10°C per minute to 140°C. The temperature was held for 1 min before it was increased up to 300°C. This temperature was held for 63min. To identify the fungal and bacterial markers, we used the bacterial acid methyl esters (BAMEs) standard (Supelco, Inc, Pennsylvania, USA). The standard includes the following FAs as markers for bacteria: C14:0 (general bacterial marker; Willers et al., 2015, Zelles, 1997); i-C15:0 and a-C-15:0 (for gram-positive bacteria; Zelles, 1997; O'Leary and Wilkinson, 1988; Tunlid and White, 1992); and C16:1ω9c (for gram-negative bacteria; Willers et al., 2015; Zelles, 1997). For fungi, the standard includes C18:2ω6c (Andersen et al., 2010; Sundh et al., 1997; Zelles, 1997; O'Leary and Wilkinson 1988; Vestal and White, 1989). Quantification of the FAs was done using the internal standard, C19:0 FA, after correcting for the methyl group added during methylation reaction.

### 2.3.3. Data evaluation and statistical analysis

As we were interested in comparing the depth trends of all single profiles with each other, we first normalized the depths of the cores. This was done using the depth of the $\delta^{15}N$ turning point (see Section 2.4.3) in each drained profile as the anchor point serving as normalized depth (normD). The normalized depth of this anchor point was set to a 20cm depth (normD 20cm; Figure 2.1) in each single core. In the corresponding natural cores, we transferred the values from the same depth related to the drained core into the same norm depth. For example, the values of the natural site (DN) in a depth of 13cm (depth of the turning point of $\delta^{15}N$ in the corresponding DD core) were set to 20cm normD. In a second step, because we were mainly interested in trends and not the absolute values, we normalized the isotopic values themselves because the range of $\delta^{15}N$ varied considerably between the sites, whereas the trends show consistent patterns (Figure 2.1). Therefore, to be able to do a meaningful comparison we set the value of $\delta^{15}N$ at the turning point to zero in each profile as follows:

normalized $\delta^{15}N$[‰] = $\delta^{15}N$[‰] - $\delta^{15}N$[‰] at turning point.

Using the same procedure, all other parameters ($\delta^{13}C$, CN and BD) were normalized using the same anchor point (e.g., $\delta^{15}N$ turning point) as follows:

normalized value ($\delta^{13}C$[‰], CN, BD) = value ($\delta^{13}C$[‰], CN, BD) - value ($\delta^{13}C$[‰], CN, BD) at $\delta^{15}N$ turning point.

We used the above procedures' means to decide on the depth of the $\delta^{15}N$ turning points, which we backed up statistically with a t test ($p < 0:05$) and an integrated change point analysis with the software package "changepoint" in R (version 1.0.153). These analyses were done for each of the drained sites separately and also with an average of all the locations. For the t test, we analyzed if $\delta^{15}N$ values in the drained layer are of the same population as the values of the natural sites for each depth (H0 – drained and natural values are of the same population). For the changepoint analysis, the variance of $\delta^{15}N$ was evaluated with a linear gradient over the whole drained peat profile against the variance of three or four separated linear gradients (rewetted part, if present, upper mesotelm, lower mesotelm and catotelm). Here, we define the starting point of the drained layer with the onset of a shift in the $\delta^{15}N$ values upward and the end of this layer with the stabilization of the $\delta^{15}N$ values towards the surface. We also determined the slopes of each single core to acquire information on the strength of the differences of the isotopic values with depth. First, the whole peat profile of each

drained core was analyzed as one trend (called “overall profile”). Second, profiles were separated into the following different layers: (i) rewetted layer (if present), (ii) upper mesotelm, (iii) lower mesotelm and (iv) catotelm. If the values were clearly changing with depth, then the slopes were closer to zero. In layers with stabilized values, the slopes were distinctly higher or lower than zero. In the following we present only the normalized data.
Raw data without normalization are available in the Supplement A.

### 2.3.4. Tree ring width and microscope analysis of peat

The investigation of the tree ring width of seven surrounding trees (Pinus sylvestris) in Degerö Stormyr was done with a hand-operated wood drill (Djos Increment Borers, Haglöf Sweden, Västernorrland, Sweden; 5mm diameter). Samples were fixed on wooden carriers. The tracheids (elongated cells of the xylem of vascular plants) were cut with a sharp carbon blade and analyzed with an impinging light binocular (60x–160x amplification). Peat samples of four study sites were analyzed using an impinging light binocular (60x–160x amplification) to obtain an overview of the vegetation assemblages and to differentiate layers. For detailed information (and the distinction of the Sphagnum species) the samples were elutriated with water, pigmented with methyl blue and analyzed under a transmitted light microscope (100x–640x amplification).

## 2.4. Results and discussion

### 2.4.1. Depth profile of vegetation assemblage and water table defining the hydrological regimes

Following our indicators (HI and vegetation assemblages), we defined the following three types of hydrological regimes: (a) natural, (b) drained up to the surface and (c) profiles with a rewetted layer above the drained layer (Figure 2.1).

**Table 2.3:** *Description of vegetation of four of the study sites; Sphagnum mosses (Sph.)*

| Site | Layer | Main species | Description |
|---|---|---|---|
| **Degerö (DD)** | rewetted layer | *Sph. balticum* | Yellow, good preserved Sph.-turf, detached Sph. cymbifolia, *Vaccinium oxycoccos Eriophorum vaginatum, Andromeda polifolia* & *Cladopodiella fluitans* |
| | mesotelm | *Sph. balticum* | Darker, grayish*;* Sph.-turf, some *Eriophorum vaginatum,* detached Sph. cymbifolia, *Vaccinium oxycoccos, Andromeda polifolia* |
| | catotelm | *Sph. balticum* | Yellow; Sph.-turf, more Sph. cymbifolia, some *Eriophorum vaginatum,* detached, *Vaccinium oxycoccos, Andromeda polifolia* |
| **Lakkasuo ($LD_o$)** | upper mesotelm | *Sph. rubellum* | Dark brown; Sph.-turf, mostly *Sph. rubellum* with *Pleutrozium schreberi* in the uppermost part |
| | lower mesotelm | *Sph. rubellum* | Dark brown, grayish; Sph.-turf, mostly *Sph. rubellum* and *Sph. balticum* |
| | catotelm | *Sph. rubellum* | Light brown, yellow; Sph.-turf, mostly *Sph. rubellum* |
| **Breitlohmisse ($BN_d$)** | upper meostelm | *Sph. capillifoliu m* | Brown; Sph.-turf mostly *Sph. capillifolium* and *Sph. cymbifolia*, much *Ericaceous roots* and some *Eriophorum vaginatum* stems |
| | mesotelm | *Sph. cymbifolia* | Dark brown; Sph.-turf mostly *Sph. capillifolium* and *Sph. cymbifolia*, some *Ericaceous roots* and *Eriophorum vaginatum* |
| | catotelm | *Sph. cymbifolia* | Lighter, reddish; Sph.-turf mostly *Sph. capillifolium* and *Sph. cymbifolia*, some *Sph. acutifolia* |
| **Rotmeer ($RD_1$)** | upper mesotlem | *Sph. acutifolia* | Brown-reddish, yellow; Sph.-turf, mostly *Sph. acutifolia*, some *Sph. rubellum,* detached *Eriophorum vaginatum* |
| | mesotelm | *Sph. cymbifolia* | Dark brown, grayish; Sph.-turf, mostly *Sph. cymbifolia*, and *Sph. acutifolia*, some *Sph. rubellum,* detached *Eriophorum vaginatum* |
| | catotelm | *Sph. cymbifolia* | Reddish, yellow; Sph.-turf, mostly *Sph. cymbifolia*, some *Sph. acutifolia,* detached *Eriophorum vaginatum* |

All sites, which we attributed as “natural” (type a), had a water table near the surface (< 10cm), macro residuals were highly visible throughout the profile, HIs were low, and the main living vegetation was Sphagnum spp. (Table 2.3). All drained sites had higher HIs even if no direct modifications in the vegetation assemblage could be documented. For type (b), there was little or no Sphagnum visible at the surface and the water table was found at lower depths (Sect. 2.2.2). Macro residuals were more strongly affected by decomposition and HIs were high up to the surface. Especially the ombrotrophic-drained site ($LD_m$) was influenced by drainage. Here, mosses of drier environments replaced Sphagnum species or mosses were completely absent (Table 2.3).

For type (c), vegetation assemblages were mainly composed of Sphagnum spp. and the water table was near the surface. HIs were low in the rewetted layer and macro residuals were preserved well (Table 2.3). With the onset of the upper mesotelm, HIs and decomposition of macro residuals was high. In the lower mesotelm, the HIs were decreasing and more macro residuals were visible. In the catotelm, the quality of macro residuals was higher than in the mesotelm and the HIs were even lower (Table 2.3).

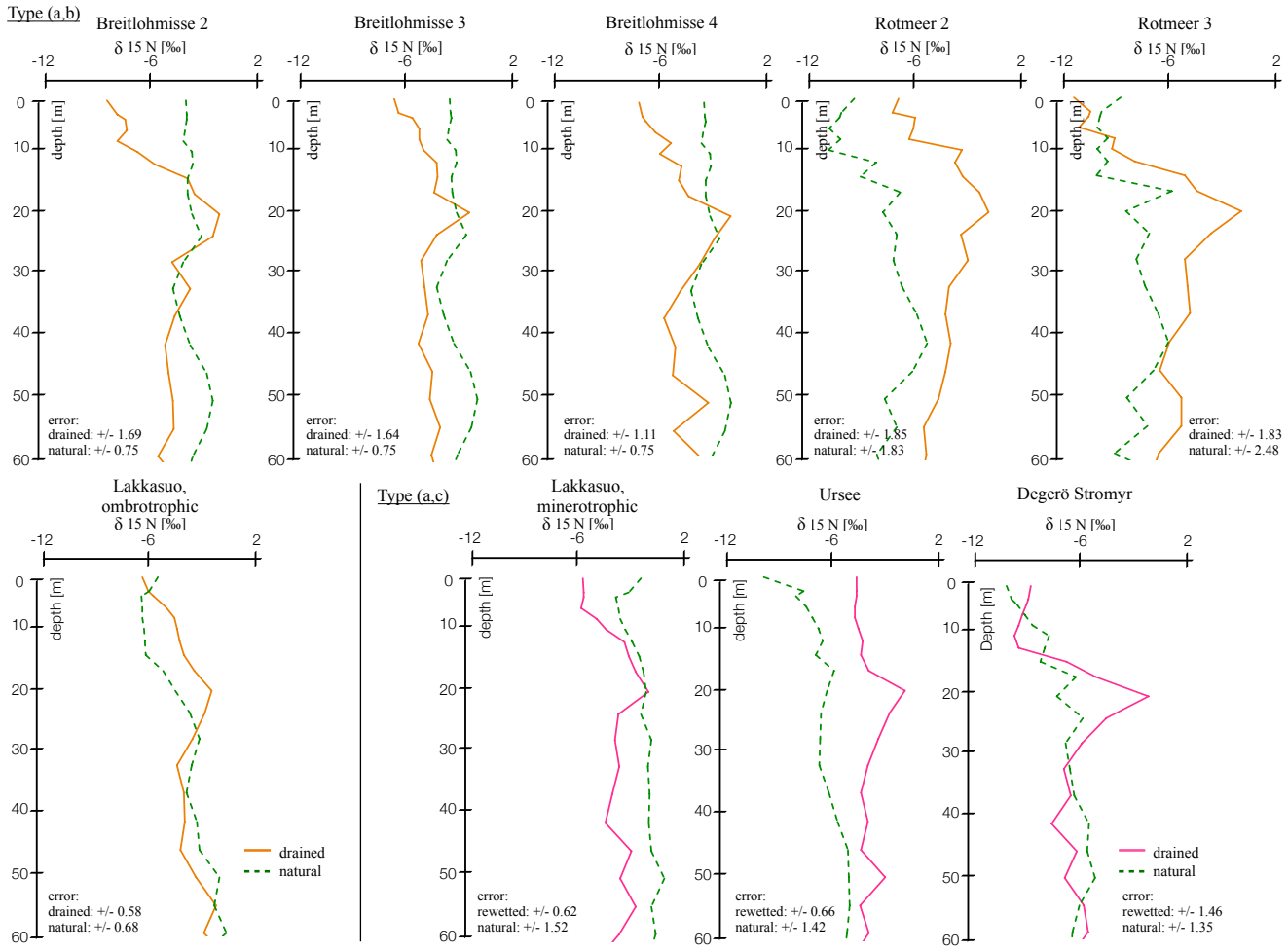


**Figure 2.1:** *$\delta^{15}N$ depth profiles in all natural and drained (or rewetted) sites; with normalized depth and normalized $\delta^{15}N$ values (see chapter 2.4); trend types: (a) natural (green), (b) drained up to the surface (orange) and (c) rewetted above drainage (pink) (For single, non-normalized values see supplementary information).*

### 2.4.2. Tree ring widths are verifying the rewetted hydrological regime of Degerö Stormyr

Tree ring width is a marker for the wellbeing and/or growth rate of trees. Young trees have a small circumference, coupled with high growth rates, which leads to thicker tree rings. Tree rings get smaller with the increasing age of the tree. If there are no environmental stressors like heat, increasing wetness or drought, tree rings are bigger, and the cell lumen is higher compared to trees at sites with environmental stress. With increasing environmental stress, tree ring width decreases (Stoffel et al., 2010). Before 1992, tree rings at the drained site (DD) site showed only a slightly decreasing trend, which could be due to aging (±1.3mm width in the 1930s to ±0.9mm in the late 1980s). The draining ditches in Degerö Stormyr were established at the beginning of the 20$^{th}$ century, which supports these results, with dryer and therefore better growth conditions

for trees. From 1992 onwards tree ring widths decreased, reaching 0.2mm in 1998 and thereafter. These results suggest a restoration to a wetter, i.e., more natural hydrological regime. Rewetted hydrological conditions are not favorable for tree growth and thus lead to smaller tree ring width.

### 2.4.3. Biogeochemical parameters and hydrological regime

Biogeochemical composition of peatlands strongly reflects the related hydrological regime (Moore and Basiliko, 2006). As is typical for oligotrophic peatlands, our investigated natural sites have a CN ratio of ±57 (Table A3). This is in line with results from Malmer and Holm (1984) and Kuhry and Vitt (1996) who found the CN ratio in the acrotelm of oligotrophic peatlands to be higher than 35 (mostly between 50 and 90). The values in the mesotelm were lower compared to both acrotelm and catotelm, most likely due to higher decomposition rates and the release of $CO_2$ (Table A3). As is typical for peatlands, BD in our peatlands is low due to the high amount of plant residuals in the soil and low values of mineralization (Novak et al., 2008), with 0.02kgm$^{-3}$ at the surface and increased with increasing decomposition and compaction of plant material downwards to 0.04kgm$^{-3}$ in the mesotelm (Table A4). BD was also increasing in the catotelm (±0.05kgm$^{-3}$; Table A4), following the increased gravimetric pressure. In contrast, the biogeochemical parameters of drained sites have a very different pattern. The lower CN ratio in the acrotelm (±41; Table A3) and the mesotelm (±35; Table A3) indicates higher mineralization rates with gaseous release of carbon and nitrogen (Krüger et al., 2017). In the catotelm with natural, anaerobic conditions, the CN ratio was in the same range as in the natural sites (±49; Table A3). BD of the acrotelm and mesotelm (±0.07kgm$^{-3}$; Table A4) also increased as a consequence of the enhanced decomposition processes. These results are in line with the hydrological regimes indicated by the vegetation analysis (Sect. 2.4.1).

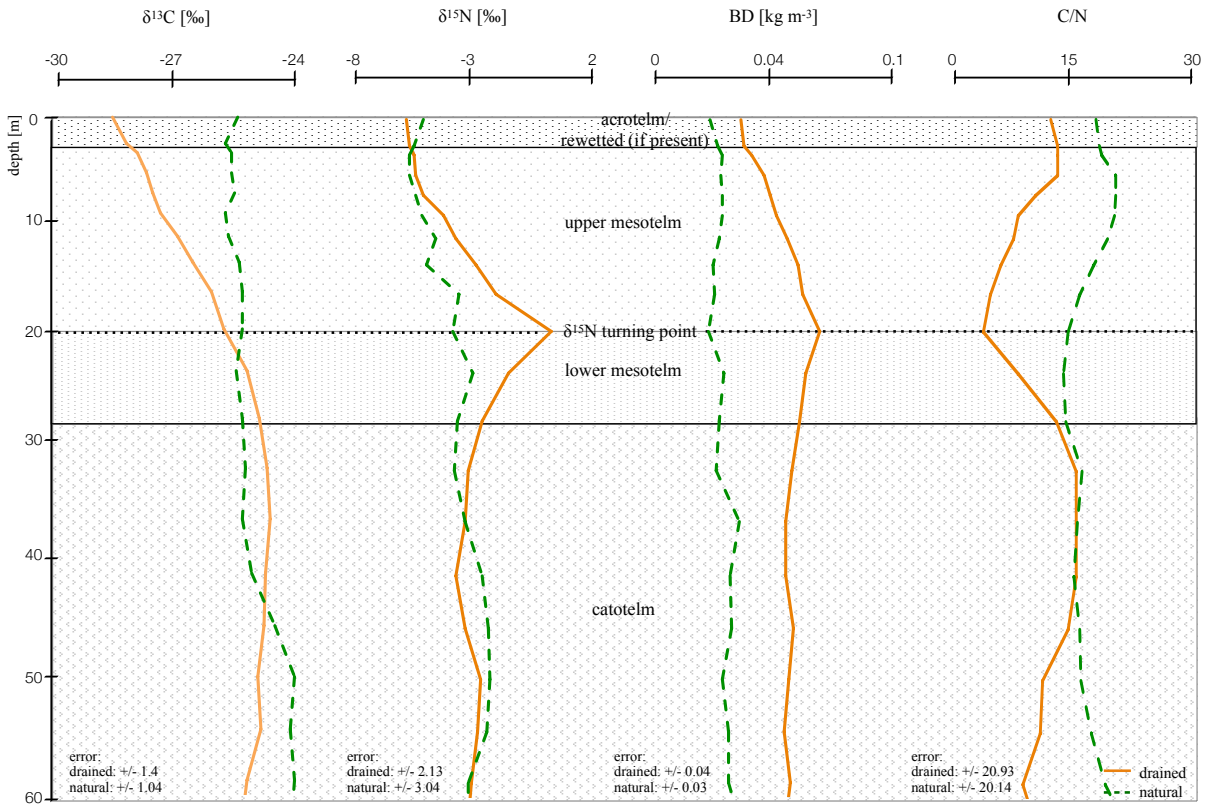


**Figure 2.2:** *Mean depth trends ($\delta^{15}N$, $\delta^{13}C$, C/N and BD) of natural and drained sites of all nine investigated peatlands with normalized depth and normalization based on $\delta^{15}N$ compositions (see chapter 2.4; For single $\delta^{13}C$, C/N and BD values of all peat cores see supplementary information).*

### 2.4.4. Stable nitrogen isotope depth trends as indicators for the hydrological regime

While mineral soils have been shown to have continuous increasing values of $^{15}N$ (Nadelhoffer et al., 1996; Högberg et al., 1997), we found increasing $\delta^{15}N$ and $\delta^{13}C$ values with depth down to particular isotopic-specific turning points in drained peatland soils (Figure 2.1). The trends of the single eight out of nine studied drained peatlands and the average trend confirm the existence of a $\delta^{15}N$ turning point. We determined a significant difference with $p < 0:05$ between $\delta^{15}N$ in the center of the mesotelm compared to the $\delta^{15}N$ values in undrained layers (Table A2), with a nonsignificant difference for one drained site, namely Breitlohmisse ($BD_1$). The latter was most likely related to generally higher $\delta^{15}N$ values of the natural site in Breitlohmisse (BN) compared to a smaller increase in $^{15}N$ at the related drained site ($BD_1$). The depth of $\delta^{15}N$ turning point (center of the mesotelm) differs from $\delta^{13}C$ turning point (end of the mesotelm) for all investigated sites (Figure 2.2). Changed slope values of the separated layers indicate significant trend changes (Table A1). In anaerobic conditions (natural and catotelm) with stabilized isotopic values with depth, slopes were distinctly different to 0 ($cm‰^{-1}$). $\delta^{15}N$ values seem to change rapidly within the mesotelm and

slope values were closer to zero. Most interesting was a switch to negative trend values at the $\delta^{15}N$ turning point in all investigated drained sites, which marks the beginning of the lower mesotelm (Table A2). In a natural hydrological regime – type (a) – all investigated parameters had a low variability and indicated a natural, wet mire hydrological regime (Figure 2.1). There were two exceptions, namely Breitlohmisse natural (BN; 40–60cm normD) and Rotmeer natural (RN; 30–50cm normD), with trend instabilities of $\delta^{15}N$. This might indicate some minor drainage or disturbance in the wetland sites we classified as "natural" (Figure 2.1). In contrast, the values of the drained sites showed significant trends. We found two different trend types in the drained sites, namely type (b) and (c; Figure 2.1). For type (b) we distinguished six sites, namely Lakkasuo ombrotrophic drained ($LD_o$); Breitlohmisse natural dry ($BN_d$); Breitlohmisse drained 1 ($BD_1$); Breitlohmisse 4 ($BD_2$); Rotmeer drained 1 ($RD_1$); and Rotmeer drained 2 ($RD_2$) with clear signs of decomposition up to the surface. Type (c) was visible in three sites, namely drained site Degerö Stormyr (DD), minerotrophic drained site Lakkasuo ($LD_m$), and Ursee 1 (UD). At type (c) sites the isotopic values, CN and BD, were stabilized again above the mesotelm. Therefore, they are assumed to be in a "new" natural status (Figures 2.1/ 2.2). Below 8 cm (normD; average profile) all drained profiles showed the typical signs of the upper mesotelm with increasing values of $\delta^{15}N$, $\delta^{13}C$ and BD down to the $\delta^{15}N$ turning point and decreasing CN. Below the $\delta^{15}N$ turning point, in the lower mesotelm, $\delta^{15}N$ values were decreasing. In this layer, $\delta^{13}C$ values, CN and BD were increasing. The end of the lower mesotelm was mostly linked to a clear shift in $\delta^{13}C$ trend to either stable values or a slow decreasing trend; hence, we called this point $\delta^{13}C$ turning point (28 cm normD; average profile; e.g., Krüger et al., 2014). Constant CN, BD and $\delta^{15}N$ values below the $\delta^{13}C$ turning point also served as indicators for reduced compaction and decomposition. Most likely the $\delta^{13}C$ turning point marked the onset of permanent waterlogged anaerobic conditions (e.g., Krüger et al., 2016). The similarity of the trends in these deeper parts of the drained sites to those of the catotelm in the natural sites supported the assumption of an intact catotelm below the $^{13}C$ turning point (Figures 2.1/ 2.2; for the single $\delta^{13}C$, CN and BD values of all peat cores see the Supplement A).

### 2.4.5. Changing microbial FAs and nitrogen stable isotope depth pattern

Fungal-derived FAs (80%of all microbial-derived FAs) were the dominant fraction near the surface. In the catotelm the microbial-derived FA values decreased down to 30%, compared to the acrotelm and the mesotelm, with a clear dominance of bacterial-derived FAs (98%), as a consequence of the anaerobic conditions (Figure 2.3). The latter is congruent with the results of Thormann et al. (1999); fungi will be outcompeted by bacteria with increasing depth and changing hydrological conditions (darker, less oxygen). In the acrotelm of the natural sites, 70% less microbial-derived FAs, compared to the acrotelm of the drained sites, confirmed the clear link between microbial abundance and the hydrological regime. In contrast, we found similar values of microbial FAs in the catotelm for drained and natural sites. This suggests that drainage did not affect the catotelm. In the drained sites the enhanced microbial-derived FAs, abundance could be caused by the improved conditions for metabolic processes by drainage, i.e., enhanced oxygen abundance and relatively high nutrient availability of the prior conserved plant material (Peltoniemi et al., 2009). In the acrotelm and the upper mesotelm fungal-derived FAs were dominating (77%). At the $\delta^{15}N$ turning point, lower values of fungal markers (23%) and increased bacterial-derived FAs (67%) could be found. In the lower mesotelm, the abundance of microbial-derived FAs was generally decreased and 69% of the detected FAs were bacterial derived (Figure 2.3).

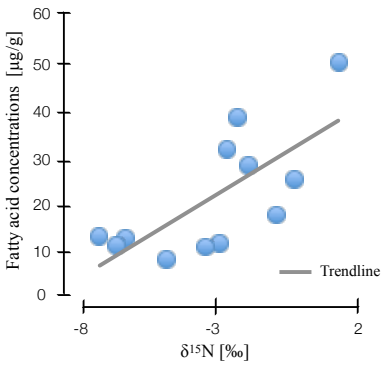


**Figure 2.3:** *Correlation of nitrogen stable isotope values and microbial fatty acid concentrations in natural and drained wetlands in Lakkasuo and Degerö Stormyr*

### 2.4.6. Microbial metabolism mirrored by stable isotope patterns

Our findings suggest that nitrogen stable isotope values are linked to microbial abundance and diversity. We found a clear correlation for stable isotope depth patterns and microbial-derived FAs in all sites ($r^2$ = 0.4; Figure 2.3), with high values of nitrogen stable isotopes being linked to high amounts of microbial-derived FAs.

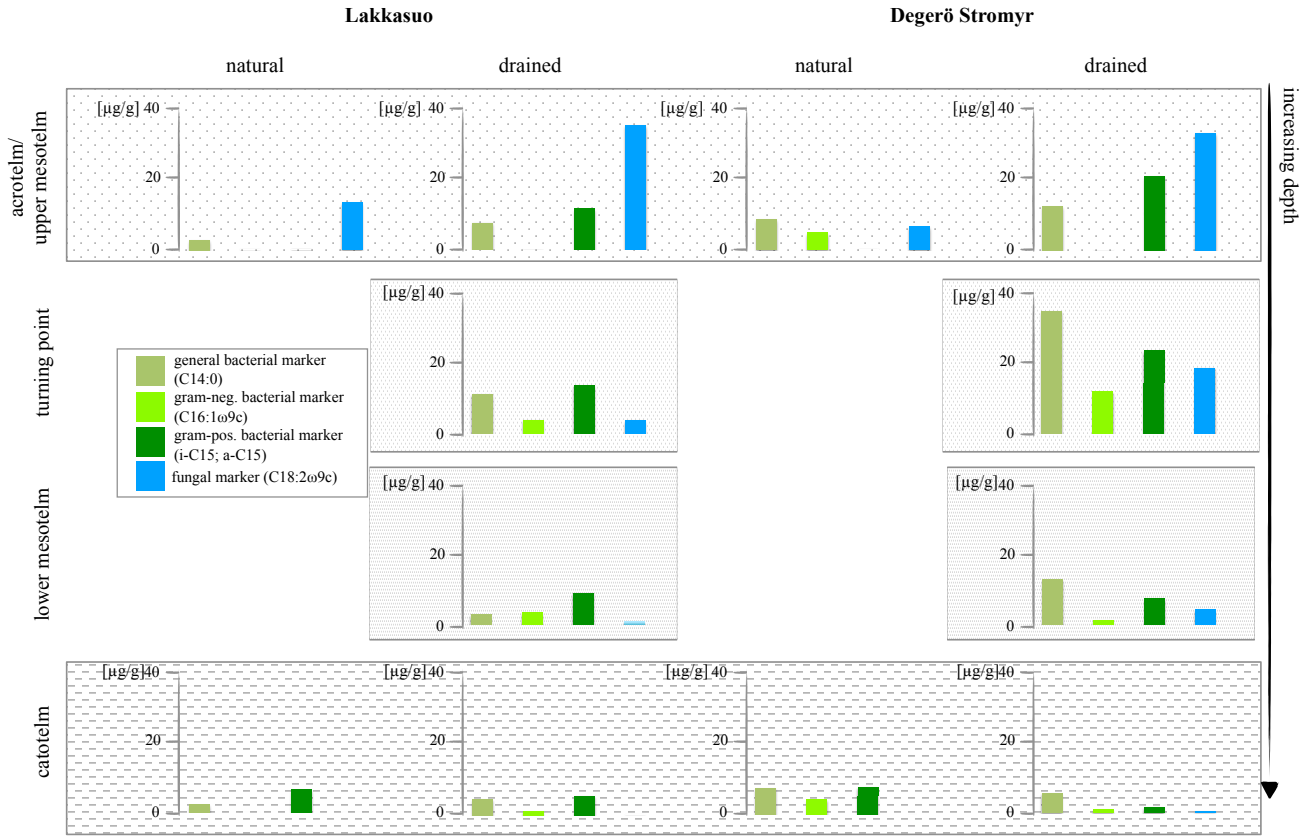


**Figure 2.4:** *Fatty acid concentrations of bacterial and fungal marker in natural and drained wetlands Lakkasuo and Degerö Stormyr in different layers*

Generally, plants are depleted in $^{15}N$ compared to atmospheric nitrogen (which is, by definition, 0‰ because air is used as the nitrogen isotopic standard) due to the general preference of plants for the lighter isotope $^{14}N$. As such, the average signal of the relatively undecomposed peat (e.g., the acrotelm of the natural/rewetted sites; the catotelm) is -10‰ to -4‰. These plant signals are imprinted in the acrotelm (±-6.09‰; Table A2). Furthermore, $^{15}N$ values of plants (here mostly Sphagnum mosses) are lower than the values of microbes and bulk material (Aldous, 2002; Lichtfouse et al., 1995). Microbes prefer to mineralize the lighter $^{14}N$ and plants incorporate (and therefore extract) the microbial mineralized lighter nitrogen (Dijkstra et al., 2006; Novák et al., 1999). Contrary to plants, microbial biomass is enriched in $^{15}N$, probably as the result of processing and releasing the lighter $^{14}N$ during mineralization and hence sequestering the remaining heavier $^{15}N$ (Roswell, 1976). In addition, as caused by the

preferential mineralization of lighter nitrogen, the heavier $^{15}N$ might be also enriched in the remaining humic substances (Novák et al., 1999). The effect of the latter on $\delta^{15}N$ bulk values is probably also enhanced due to the loss of $^{15}N$-depleted material during leaching (Damman, 1988; Niemen, 1998), denitrification and the release of gaseous nitrogen (Kohzu et al., 2003; Niemen, 1998). Our values confirm these reported patterns, with highest $\delta^{15}N$ values in the mesotelm (±-3.63‰; Table A2) and the correspondence of high microbial activity (reflected by the highest values of microbial-derived FAs) to the $\delta^{15}N$ turning point (Figures 2.4/ 2.5). In acid bogs under aerobic conditions, fungi will dominate the general metabolism in upper peat soils (Thormann et al., 2003). This is pictured by the highest amount of fungal-derived FAs in the acrotelm and the upper mesotelm (Figures 2.4). Fungi are the preferred decomposers of primary plant material (Wallander et al., 2009; Thormann et al., 2004); hence, the depleted plant isotopic signal is relatively preserved in the upper most aerobic layers. Furthermore, fungi have a relatively low nitrogen demand compared to bacteria (Myers et al., 2012). With increasing depth and increasing oxygen limitation, fungal metabolism decreases (Thormann, 2011). In parallel, the amount of bacterial-derived FAs increases (Figure 2.4) as Lin et al. (2014), Hu et al. (2011) and Bauersachs et al. (2009) also reported. They found evidence for bacterial-dominated decomposition in hypoxic conditions. This is in line with the findings of Kohl et al. (2015) and Schmidt and Bölter (2002), who also reported a switch from fungal to bacterial dominance in the mesotelm. Andersen et al. (2013), Wallander et al. (2009), Winsborough and Basiliko (2010) and Myers et al. (2012) also stated that fungal biomass is decreasing in peatland soils with depth. In addition, bacterial metabolism is generally faster than fungal metabolism and needs higher amounts of nitrogen (Brunner et al., 2013). We assume that bacteria and fungi compete most over decomposable substrates (not only nitrogen) at the $\delta^{15}N$ turning point, resulting in the highest turnover rates with an enrichment of $\delta^{15}N$ in the remaining peat, similar to reports from mineral soils with aerobic decomposition (Alewell et al., 2011; Nadelhofer et al., 1996). As such, we assume that besides the highest microbial activity, the diversity of microbial metabolism also peaks at the $\delta^{15}N$ turning point (Figure 2.5). This would also be related to the highest $\delta^{15}N$ values because (1) different microbial communities prefer different sources (Dijkstra et al., 2006; Drollinger et al., 2019) and (2) with increasing bacterial abundance, fungi have to also use recalcitrant (isotopically lighter) sources because bacterial metabolism will outcompete fungi for the easily degradable substances

(Rousk and Bååth, 2007; Winsborough and Basiliko, 2010). Hence, with increasing microbial diversity, the diversity of the mineralized organic fractions also increases (Thormann, 2006). To summarize, with an increased diversity of utilized nitrogen sources, more release of lighter $^{14}N$ is possible and the $\delta^{15}N$ values in the remaining substrate should increase (Dijkstra et al., 2008; Figures 2.3/ 2.4). However, because of the faster and more complete decomposition with increasing microbial activity (Damman, 1988), metabolism of $^{15}N$ increases as well and fractionation will be less (Lerch et al., 2011). These contrasting patterns must lead to only small increases in the $\delta^{15}N$ values of the bulk material, because if all nitrogen is used, fractionation will be lower at the $\delta^{15}N$ turning point. In the lower mesotelm, oxygen limitation increases, leading to a general decrease in microbial metabolism and related concentrations of microbial-derived FAs (Figure 2.4). The decreasing microbial metabolism leads to simultaneously decreasing $\delta^{15}N$ values because an increasing amount of intact vegetation (with low $\delta^{15}N$ values) will be conserved (Figures 2.4/ 2.5).

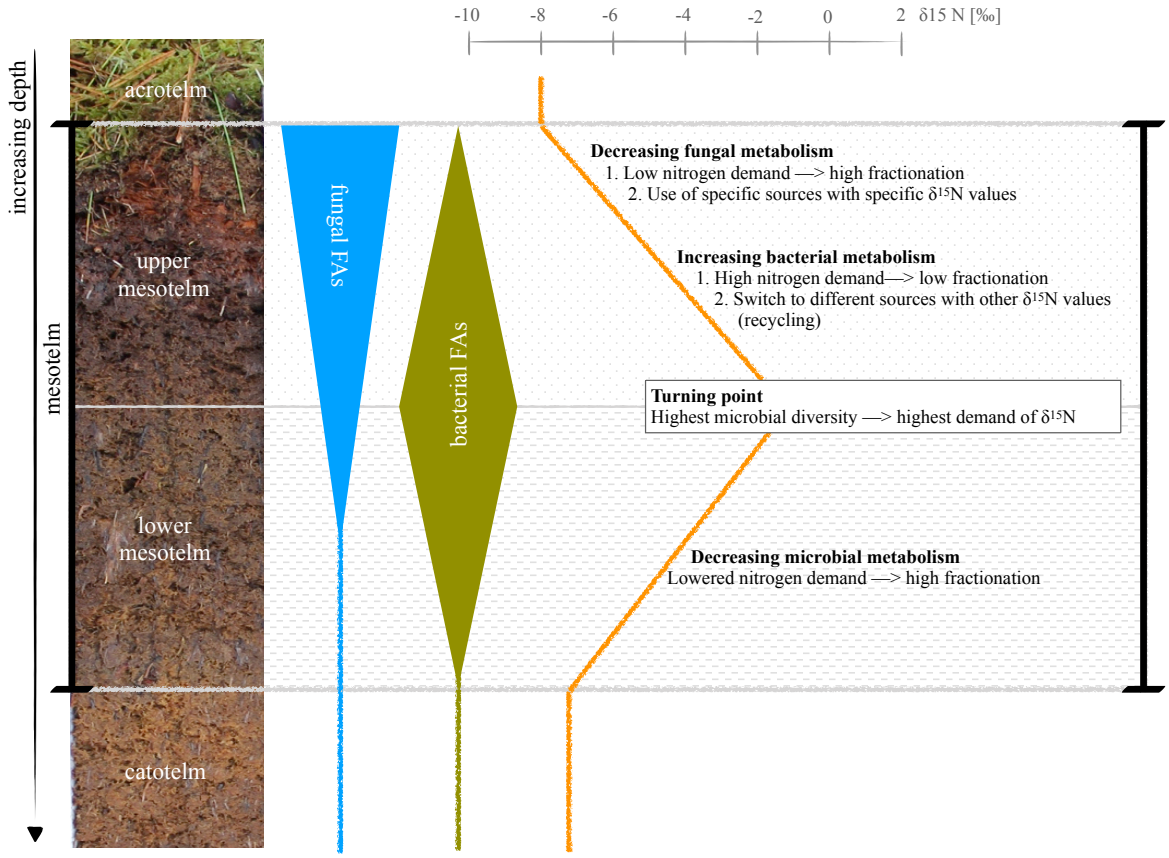


**Figure 2.5:** *Hypothesis of a microbial switch (fungi to bacteria) with depth, reflected by specific FAs, and its influence of the $\delta^{15}N$ depth trend; example photo and $\delta^{15}N$ values of the ombrotrophic, drained site in Lakkasuo ($LD_o$) (note all isotope values are normalized to zero at turning point).*

Finally, with the establishment of permanently waterlogged anaerobic conditions in the catotelm (also indicated by the $\delta^{13}C$ turning point), FA concentration decreases sharply to near-zero values. Here, decomposition processes are largely inhibited, which leads to stable $\delta^{15}N$ and $\delta^{13}C$ values, close to the original vegetation signals (Alewell et al., 2011; Krüger et al., 2015; Figure 2.1/ 2.4).

## 2.5. Conclusion

Our results confirmed that the nitrogen isotopic depth trends of peatlands are suitable indicators of the natural, drained or rewetted hydrological regime. We validated our isotopic hypothesis with microscope analysis of the vegetation remains in the cores and the investigation of tree rings as indicators for changed hydrological regime in the past. An analysis of gram-positive and gram-negative bacterial-derived FAs versus fungal-derived FAs underpinned our hypothesis with the expected changes in microbial abundance with depth. The aerobic acrotelm was characterized by a high fungal abundance with low nitrogen demand and turnover. The upper mesotelm was the transition to a mixture of decreasing fungal and increasing bacterial abundance, competing for organic substrates, and resulting in an enrichment of $\delta^{15}N$ values. In the lower mesotelm microbial decomposition generally decreased but was dominated by bacterial abundance, and finally, microbial metabolism was strongly impeded and $\delta^{15}N$ values were stabilized in the anaerobic catotelm. Carbon isotope compositions were also changed with drainage, but they are neither a suitable indicator for a switch in microbial abundance within the drained layer nor for the trend induced by the rewetting of the peatland. In summary, $\delta^{15}N$ depth profiles in peat might give more insights into a switch of microbial metabolism because they reflect more precisely different microbial abundance than carbon isotope compositions. Therefore, we conclude that $\delta^{15}N$ depth profiles could act as a reliable and efficient tool to obtain fast and easy information about the hydrological regime, restoration success and drainage history.

**Acknowledgements**

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# 3

# Rewetting and drainage of nutrient-poor peatlands, indicated by specific bacterial membrane fatty acids and a repeated sampling of stable isotopes ($\delta^{15}N$, $\delta^{13}C$)[2]


## Abstract

Peatland degradation impairs soil functions such as carbon storage and the existence of biodiversity hotspots. Therefore, and in view of the ongoing climate change, an efficient method of evaluating peatland hydrology and the success of restoration efforts is needed. To understand the role of microbial groups in biogeochemical cycling, gaseous loss and isotopic fractionation that lead to specific isotopic depth patterns ($\delta^{13}C$, $\delta^{15}N$), we integrated previously published stable isotope data with a membrane fatty acid (mFA) analysis related to various microbial groups that are known to be common in peatlands. We performed two sampling campaigns to verify the observed stable isotope depth trends in nutrient-poor peatlands in Northern Europe. Cores were taken from adjacent drained (or rewetted) and undrained sites. Fungal-derived mFA abundance was highest in the uppermost part of the drained layer. We found increasing bacterial-derived mFA concentrations with depth peaking in the middle of the drained layers, which correlates with a $\delta^{15}N$ peak of bulk material. The results support our hypothesis that changing peatland hydrology induce a shift in microbial community and metabolism processes and is therefore also imprinted in stable isotope values. Under waterlogged conditions overall levels of microbial-derived mFAs were generally low. Drained layers showed simultaneous changes in microbial abundance and composition and depth trends in stable isotope bulk values. Bacteria, particularly acidobacteria, can be expected to dominate increased denitrification with low oxygen content accompanied by increased $\delta^{15}N$ bulk values in the remaining substrate. Interestingly, cores from recent rewetted peatlands show no depth trend of $\delta^{15}N$ in the layers grown under rewetting conditions; this is congruent with relatively low


[2] Study published as Groß-Schmölders, M., Klein, K., Birkholz A., Leifeld J., and Alewell C.: *Rewetting and Drainage of Nutrient-Poor Peatlands Indicated by Specific Bacterial Membrane Fatty Acids and a Repeated Sampling of Stable Isotopes (δ15N, δ13C). Frontiers in Environmental Science 9, DOI:10.3389/fenvs.2021.730106, 2021*

concentrations of microbial-derived mFAs. Hence, we conclude that stable isotopes, especially $\delta^{15}N$ values, reflect changing microbial metabolic processes, which differ between drained and undrained - and especially also for recent rewetted – peatlands. As today stable isotope measurements are routine measurements, these findings enable us to get cost- and time efficient reliable information of drainage and restoration success.

## 3.1. Introduction

A unique biodiversity, slow rates of decomposition and the storage of significant quantities of carbon characterize wetland soils; this is especially true for nutrient-poor peatlands (Moore and Basiliko, 2006). The protection of biodiversity and successful peatland restoration could save 1.91 (0.31–3.38) gigatons (Gt) of $CO_2$-equivalent greenhouse gas emissions (Leifeld and Menichetti, 2018). Furthermore, 6% of the greenhouse effect is contributed by $N_2O$ (Schulze et al., 2009), which is also released by degraded peatlands due to impaired soil functioning (Palmer and Horn, 2015). For other ecosystems, microbial communities and their major role in biochemical cycling of carbon and nitrogen in soil are well documented, but little is known of the microbial community and its function in peatlands (Elliott et al., 2015). In particular, information about microbial community structures in different layers and their influence on biochemical processes under rewetting conditions is widely unknown (Elliott et al., 2015). Thus, more reliable information about peatland degradation and restoration success is needed.

Peat soil can be divided into three layers. In the uppermost part, the acrotelm, most biological metabolism and nutrient cycling takes place (Asada et al., 2005; Artz, 2013). In the lower layer, the anaerobic, water-saturated catotelm, microbial metabolism is suppressed due to the lack of oxygen (Asada et al., 2005; Artz, 2013; Lin et al., 2014). In between, the mesotelm is characterized by a fluctuating water table and facultative anaerobic conditions, which therefore leads to shifting levels of microbial abundance and activity (Asada et al., 2005; Artz, 2013; Lin et al., 2014). Drainage of peatlands expands the mesotelm, wherein formerly preserved organic substrates can be decomposed (Zedler and Kercher, 2005). If rewetting occurs, the former mesotelm will become anaerobic again, and aerobic microbial activity will be inhibited (Andersen et al., 2010; Asada et al., 2005).

Whereas microbial metabolism of carbon is discussed in several papers (see review of Blodau, 2002), nitrogen cycling in peatlands is less well studied. Nitrogen fixation has been reported to only occur in surface layers of peat, (Lin et al. 2014). However, the $N_2O$ producing microbial mediated nitrification and denitrification of organic matter as well as other chemical processes occur also in deeper layers (Palmer and Horn, 2015; Bremner, 1997). For peatlands, Palmer et al. (2010) report denitrification of organic matter as the main $N_2O$ source. Denitrification causes a reduction of nitrate and nitrite by converting them to nitric oxide (NO) and $N_2O$ and, ultimately, to dinitrogen ($N_2$; Novák et al., 1999). Especially for the deep, anaerobic layer, Lin et al. (2014) reported extremely low values for denitrification and other N-cycling processes and, therefore, a conservation of the substrate.

Stable isotopes of carbon and nitrogen are known indicators of peatland hydrology (Alewell et al., 2011; Krüger et al., 2016; Groß-Schmölders et al., 2020; Kohl et al., 2015). For $\delta^{13}C$, Alewell et al. (2011), Krüger et al. (2016), Novak et al. (1999), Hobbie et al. (2017) and Biester et al. (2014) report an enrichment of $^{13}C$ with depth due to an increasing degree of organic matter decomposition. Substrates have a natural and specific range of $^{13}C$ values (Lerch et al., 2011). As lignin, cellulose and lipids are known to be depleted in $^{13}C$, glucose, amino acids, pectin and hemicellulose are enriched in $^{13}C$ (Lerch et al., 2011). In undrained wetlands, the combination of these substrates is mostly preserved due to the waterlogged conditions. If drainage takes place, the original bulk soil $\delta^{13}C$ value is changed by degradation and microbial metabolism processes. Kohl et al. (2015) state that an increasing $\delta^{13}C$ depth trend is a consequence of a switch in dominant microbial decomposition, which has stronger effects than the residual enrichment of recalcitrant compounds such as lignin. Kohl et al. (2015) stated out, that fungi are main decomposer in the uppermost soil layers and bacteria are more prominent in deeper layers. With this switch of dominant microbial groups, also the decomposed material switches and therefore the $^{13}C$ bulk values change.

Additionally, a positive correlation between increased microbial metabolism and $\delta^{15}N$ was previously presented (Groß-Schmölders et al., 2020). Fractionation of stable isotopes during microbial metabolism of nitrate and ammonium occurs, since most organisms prefer the lighter and more frequently occurring $^{14}N$ (Kohzu et al., 2003; Robinson et al., 1998). As a result, plants in particular incorporate and translocate the lighter $^{14}N$ upwards to stem and foliar, which leads to an enrichment of heavier $^{15}N$ in

the remaining bulk material (Högberg et al., 1996). Additionally, the mycorrhizal uptake of lighter $^{14}N$ into plants increases the $\delta^{15}N$ values of bulk material (Hobbie and Högberg, 2012). Furthermore, with ongoing microbial metabolic processes in peat, the $\delta^{15}N$ values increase as long as microbial metabolism occurs, and lighter $^{14}N$ will be leached, translocated or lost via outgassing (Novák et al., 1999; Damman, 1988; Niemen, 1998). In 2010, Goldberg et al. showed, that increasing oxygen concentrations in drained fens leads to higher $N_2O$ release by nitrification, which is followed by increasing $\delta^{15}N$ values in the remaining substrate. Thus, microbial abundance and stable isotope ratios are closely linked, especially for some microbial groups that are more active in nitrogen cycling than others and therefore play a greater role (Tfaily et al., 2014). Fungi have a low demand for nitrogen, making them less likely to be a main driver of increasing $\delta^{15}N$ values (Thormann, 2005). In contrast, acidobacteria are one of the main bacterial groups in peat and are highly active in nitrogen cycling; in particular, they are involved in denitrification and N fixation (Ward et al., 2009). Accordingly, their abundance can be expected to have a close link to carbon and especially nitrogen stable isotope depth trends (Weijer et al., 2010).

To examine microbial abundance, we measured the concentrations of specific membrane fatty acids (mFAs). Membrane fatty acids are valid markers to indicate the abundance of specific microbial communities. Sundh et al. (1997) and Torres and Pancost (2016) demonstrated that mFAs are persistent and, to a high degree, insoluble compounds in peat soil. Membrane fatty acids vary based on their origin (plants, specific microbial groups, etc.; Bajerski et al., 2017; Finotti et al. 1993; Piotrowska-Seget and Mrozik, 2003; Reiffarth et al., 2016; Willers et al., 2015). Therefore, based on an analysis of the quantity of mFAs present, the relative abundance of certain microbial communities might be assessed (Torres and Pancost, 2016; Piotrowska-Seget and Mrozik, 2003). We tested the existence of four bacterial markers and one fungal marker:

- i-C15:0 and C16:1ω7c, which, in combination, are indicative of acidobacteria (Damasté et al., 2011; Dedysh and Damsté, 2018; Myers and King, 2016);

- C14:0 and C17:0, which are generally indicative of bacteria (Willers et al., 2015; Zelles, 1997);

- C18:2ω6c, which is indicative of saprotrophic fungi (Sundh et al., 1997; Elvert et al., 2003; Willers et al., 2015).

To differentiate between wetland soil functioning as carbon storage and biodiversity hotspots in undrained, rewetted and drained sites, we investigate the influence of drainage and rewetting on microbial-derived mFA abundance and stable isotopic values. We studied two peatlands with different drainage histories, using a high spatial resolution of 4 cm in the uppermost 50 cm of the peat columns. In both investigated peatlands' ditches were installed to drain the sites for agricultural use (Mikkenen et al.m, 1999; Nielsson et al., 2008). In Lakkasuo, Southern Finland, we located a site that had experienced continuous drainage since 1961 (Minkkinen et al., 1999). In the Swedish Degerö Stormyr, ditches were installed at the beginning of the 20th century (Nielsson et al., 2008). They have filled up naturally with sphagnum over the last 20 years and sites are thus rewetting. We compared undrained with drained sites in Lakkasuo and undrained with rewetted sites in Degerö Stormyr. Furthermore, to verify our previous results regarding stable isotopes as markers for peatland hydrology and drainage history (Minkkinen et al., 1999), we investigated depth trends at two points in time (2013 and 2017) to verify pattern stability over time.
We define a sudden directional change in the stable isotope depth patterns as "turning points," according to Alewell et al. (2011) and Groß-Schmölders et al. (2020). The $\delta^{15}N$ turning point is located in the middle of the mesotelm, where $\delta^{15}N$ values are highest. In contrast, the $\delta^{13}C$ turning point marks the bottom of the mesotelm and the onset of the underlying catotelm, above which the $\delta^{13}C$ values start to decrease continuously up to the surface.

The contribution of this paper is to examine the microbial composition of peat soil with respect to stable isotope fractionation and test the persistence of stable isotope depth trends with a repeated sampling approach.
We hypothesize the following:

- Bacterial abundance, especially that of acidobacteria, is highest in the mesotelm.

- Bacterial abundance is the main driver of the nitrogen stable isotope depth trend in nutrient-poor peatlands.

- Stable isotope depth patterns are persistent over a time span of four years (2013–2017) and are therefore reliable indicators of drainage and rewetting.

## 3.2. Study site

We investigated two nutrient-poor peatlands in northern Europe, both classified as fibric Histosol (HSf; IUSS, 2015; Table 3.1).

**Table 3.1:** *Detailed information for the acrotelm/ former mesotelm (only for Degerö rewetted) of the drained, rewetted and undrained sites of Degerö Stormyr and Lakkasuo at the surface (Nielsson et al., 2008; Mikkenen et al., 1999; Groß-Schmölders et al., 2020); av.: average, WT: water table below surface, C: carbon, N: nitrogen, CN: carbon:nitrogen ratio, BD bulk density [k m$^{-3}$], von Post Indices (vP)*

| location | av. WT [cm] | av. pH | av. C [kg m$^{-2}$] | av. N [kg m$^{-2}$] | CN | BD | vP |
|---|---|---|---|---|---|---|---|
| Lakkasuo | | | | | | | |
| undrained | 5 | 4.1 | 44.8 | 0.7 | 65.6 | 0.02 | H2 |
| drained | 26 | 3.8 | 48.1 | 1.0 | 44.2 | 0.06 | H3-H4 |
| Degerö Stormyr | | | | | | | |
| undrained | 0 | 4.8 | 42.9 | 0.4 | 88.8 | 0.02 | H1-H2 |
| rewetted | 10 | 4.8 | 45.2 | 0.7 | 58.8/ 41.1 | 0.02/0.06 | H1-H2 |

Degerö Stormyr (64°11'lat., 19°33'long.; 200m above sea level (a.s.l.)) is situated in Northern Sweden, at the Kulbäcksliden Experimental Forest near Vindeln, between the rivers Umeälven and Vindelälven (Eurola et al., 1984). It is an acidic bog and consists of interconnected small mire patches divided by ridges of glacial till. The climate is characterized as cold with no dry seasons and cold summers (Dfc-zone after Köppen-Geiger classification; Peel et al., 2007). Mean annual temperature is +1.2°C and the annual precipitation is ±523mm (Alexandersson et al., 1991). Ditches were installed in Degerö in the beginning of the 20$^{th}$ century but a natural reestablishment of sphagnum took place over the last few decades (>20years). Therefore, we define this site as rewetted. In the undrained part the main moss species is *Sphagnum majus* (Nielsson et al., 2008) and the water table is near the surface (Table 3.1). The humification index (HI) after von Post is low (H1-H2) and macro residuals are highly visible (Table 3.1; Groß-Schmölders et al., 2020). Also, biochemical parameters indicate undrained conditions. The carbon-to-nitrogen ratio (CN) in the acrotelm is 89, and the bulk density (BD) is low (0.02kg m$^{-3}$), both is typical for undrained nutrient poor peatlands (Table 3.1; Groß-Schmölders et al., 2020). For the rewetted site the main moss species is *Sphagnum balticum* (Nielsson et al., 2008). The water table is near the surface, HI is low (H2) and macro-residuals are preserved well in the upper layer (Table 3.1; Groß-Schmölders et al., 2020). In contrast the values of the former mesotelm indicate degradation: HI is higher (H3), less macro-residuals are visible, CN

decreased to 41 and the BD increased (0.06kg $m^{-3}$; Table 3.1; Groß-Schmölders et al., 2020).

Lakkasuo (150m a.s.l.) in Central Finland is an eccentric peatland complex with two parts. The southern part is a bog with ombrotrophic conditions; whereas the northern part is a fen (Minkkinen et al., 1999). Only samples of the ombrotrophic bog are included for this study. Lakkasuo is also located in the cold climate zone, with no dry seasons and cold summers (Dfc-zone after Köppen-Geiger classification; Peel et al., 2007). Mean annual temperature is +3°C and the precipitation is ±700mm (Laine et al., 2004). Lakkasuo is still drained. Ditches installed in 1961 (70 cm depth, spacing of 40m–60m) affected approximately 50% of the peatland (Minkkinen et al., 1999). The main current moss species in undrained sites is *Sphagnum angustifolia* (Laine et al., 2004). HI is low (H2), a high number of macro-residuals is visible, and the water table is near the surface (<5cm) (Table 3.1; Groß-Schmölders et al., 2020). Also, the biochemical parameters indicate undrained conditions: high CN (66) and low BD (0.02kg $m^{-3}$; Table 1; Groß-Schmölders et al., 2020). In the drained site *Pleurozium spp.,* a moss species of drier environments, is the main moss species and a high number of pine trees is abundant. Macro-residuals are strongly affected by decomposition, HI (H3-H4) and BD (0.06kg $m^{-3}$) are high and CN (44) is low (Table 3.1; Groß-Schmölders et al., 2020).

## 3.3. Material and methods

### 3.3.1. Soil sampling and bulk analyses

We drilled three volumetric peat cores per site in September 2013 and one in June 2017. Cores were drilled with a Russian peat corer (Eijkelkamp, The Netherlands). Per site three Cores were taken (1-3). Cores were taken in the undrained parts (Degerö Stormyr ($DU_{13}$1-3, $DU_{17}$); Lakkasuo ($LU_{13}$1-3, $LU_{17}$)), and in one-meter distance to a drainage ditch (to one-meter depth) (Degerö Stormyr rewetted ($DR_{13}$1-3, $DR_{17}$); Lakkasuo drained ($LD_{13}$1-3, $LD_{17}$)). We drilled the cores in 2017 close to the location of 2013, with a GPS accuracy of 1.3m, to monitor possible hydrological changes, which could be mirrored by stable isotope depth patterns and microbial FA abundance.

The cores were encased in hard plastic shells, stored in coolers, and transported to the laboratory. The cores were sliced in 2cm sections for the isotope analyses. Every second section was analyzed, giving a 4cm depth resolution. Samples were oven-dried at 40°C for 72h, and homogenized with a vibrating ball mill (MM400, Retsch, Germany).

Stable C and N isotopic signatures were measured an elemental analyzer combined with an isotope ratio mass spectrometer (EA-IRMS) (Inegra2, Sercon, Crewe, UK). Carbon isotopic composition ($^{13}C/^{12}C$) was expressed relative to Vienna Pee-Dee Belemnite (VPDB) standard and reported in delta notation (‰):

$$\delta^{13}C_{sample} = \left(\frac{R_s}{R_{std}} - 1\right) x100$$

$R_s$ and $R_{std}$ are the ratios of $^{13}C/^{12}C$ in the sample and VPDB standard ($R_{std}$ = 0.011182).

Nitrogen stable isotopes were expressed relative to atmospheric nitrogen and reported in delta notation (‰):

$$\delta^{15}N_{sample} = \left(\frac{R_s}{R_{std}} - 1\right) x100$$

$R_s$ and $R_{std}$ are the ratios of $^{15}N/^{14}N$ in the sample and atmospheric nitrogen ($R_{air}$ = 0.0).

### 3.3.2. Fatty acid analyses

We aimed to extract total membrane FAs to distinguish between FAs of different bacterial groups, fungi, and plants. We processed 0.2–1.1g of sample for the lipid extraction with a mixture of $CH_2Cl_2$: MeOH (9:1 v/v) in an Accelerated Solvent Extractor (Dionex ASE 350). 0.1 µg/ml of an internal standard with nonadecanoic acid was added before processing each sample.

The total lipid extracts (TLE) were saponified by adding 2ml of KOH dissolved in MeOH (12%) and putting it in the oven for 3 hours at 80°C.

Following the method of Elvert et al. (2003), the TLE were polarized with 1ml KCl (0.1mol), and the neutral fraction was extracted by rinsing three times with hexane, dried under a stream of $N_2$, and stored in the refrigerator for later analysis. We acidified the rest of the TLE with fuming hydrochloric acid to a pH of 1. The acid fraction was extracted by rinsing again three times with hexane dried under a stream of $N_2$. They were methylated by adding 1 ml Boron-Trifluoride ($BF_3$) in MeOH (12-14%) and putting it in the oven for 1 hour at 60°C. Afterwards the FA fraction was polarized with KCl (0.1mol) and transferred in 4 ml vials by rinsing three times with hexane. After one day, in which residues could settle, we transferred the upper part with hexane in 2ml vials to measure the FAs. The FAs were quantified with a Trace Ultra gas chromatograph (GC) equipped with a flame ionization detector (FID) (Thermo Scientific, Waltham, MA, USA). The carrier gas (helium) had a constant flow of 1.2ml per minute and the GC-FID was set to splitless mode. Detector temperature was set to 320°C and the samples

(dissolved in hexane) were injected at 300°C injector temperature. The starting temperature of the oven was 50°C and hold for 2 minutes. Then temperature was increased by 10°C per minute to 140°C. The temperature was held for 1 minute before it was increased up to 300°C. This temperature was held for 63 minutes.

To identify the fungal and bacterial markers, we used the Bacterial Acid Methyl Esters standard (BAME, Supelco Mix). For bacteria, it includes the FAs C14:0 and C17:0 as general bacterial markers (Zelles, 1997; Willers et al., 2015), i-C15:0 and C16:1ω7c for acidobacteria (Damasté et al., 2011; Dedysh and Damsté, 2018; Myers and King, 2016). The fatty acid C18:2ω6c was used as a marker for fungi (Andersen et al., 2010; Sundh et al., 1997; Zelles, 1997, O`Leary and Wilkinson, 1988; Vestal and White, 1989). All these markers are valid for overall membrane fatty acids and can be used to detect different microbial groups in soil (Bajerski et al., 2017; Finotti et al. 1993; Piotrowska-Seget and Mrozik, 2003). Quantification of the FAs was done using the injected internal standard C19:0 FA, after correcting for the methyl group, added during methylation reaction, normalized to dry weight of bulk material.

### 3.3.3. Statistical analysis

For the FA analysis and the comparison of spatial variations for drained vs. rewetted sites, we were interested in comparing the depth trends of all single profiles with each other. This was done by using the depth of the $\delta^{15}N$ turning point in each drained profile as the anchor point serving as normalized depth (normD) and set them to 17cm depth (normD = 17cm) in each single core. Using the same procedure, $\delta^{13}C$ trends were normalized using the same anchor point (e.g., $\delta^{15}N$ turning point) (for more detailed information, please see Groß-Schmölders et al., 2020).

For the cores of 2013 (3 replicates), variance, standard deviations, and spearman correlation coefficient (R) were calculated with the software R (version 1.0.153). We define an R-value above 0.4 as a strong correlation following McGrew and Monroe (2000) and define significance with $p < 0.05$ (McCune and Grace, 2002).

In the following we present only the normalized data. Raw data without normalization are available in the supplementary information.

## 3.4. Results

### 3.4.1. Microbial-derived membrane fatty acids

Microbial-derived mFA abundance was found to be low over the whole profile in undrained sites, with ±16.05µg/g (±7.4) in Lakkasuo (undrained; LU) and 14.74µg/g (±4.7) in Degerö Stormyr (undrained; DU). In the acrotelm, the quantity is higher (LU: 21.8 µg/g; DU: 27.7 µg/g) than in the catotelm (LU: 13.5µg/g, ±4.4; DU: 13.28µg/g, 3.4; Figure 3.1).

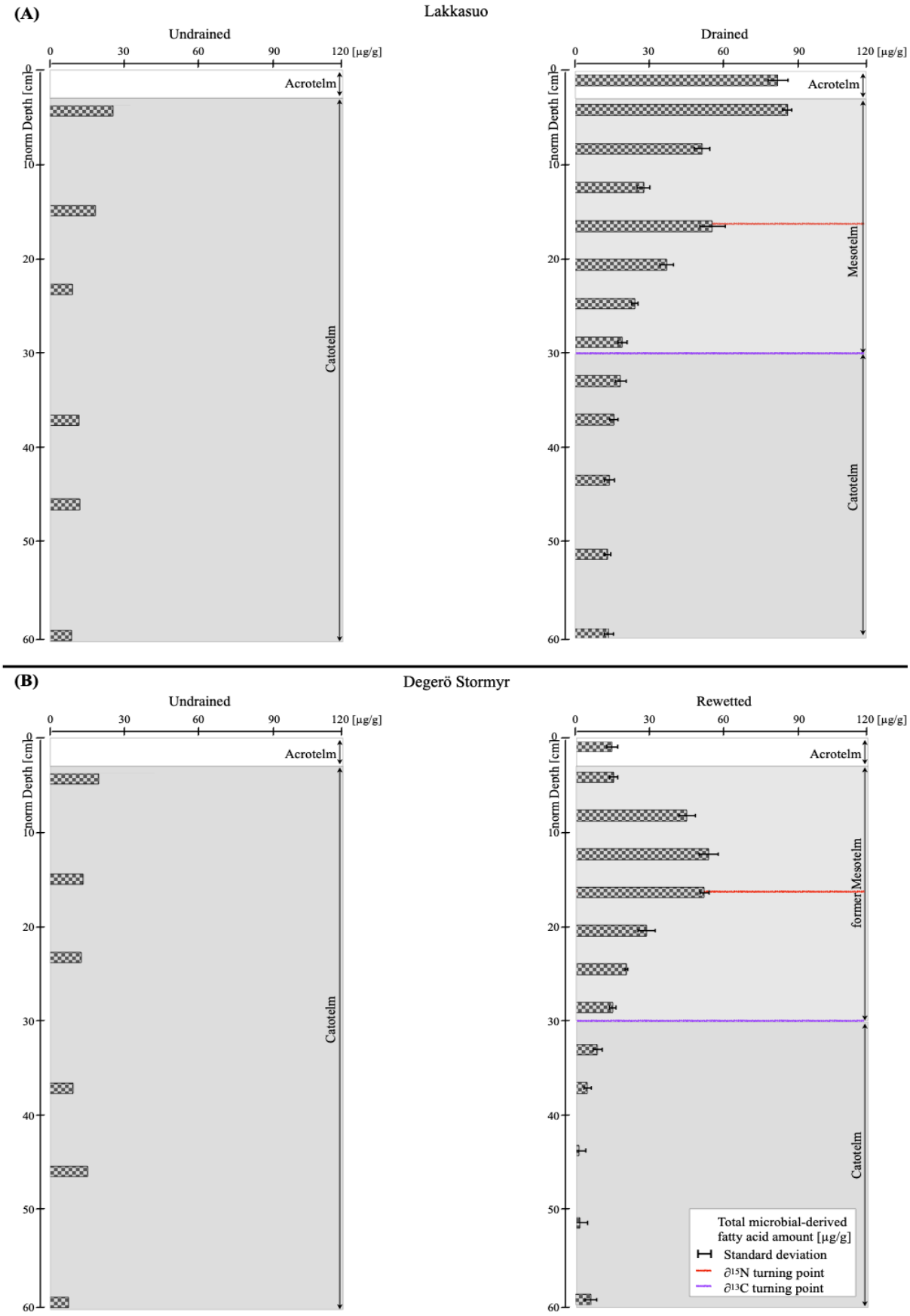


**Figure 3.1:** *Average values of total microbial-derived membrane fatty acid concentrations [µg/g]; (A) Lakkasuo: undrained (LU1-3) and drained ($LD_{13}$1-3); (B) Degerö Stormyr: undrained (DU1-3) and rewetted ($DR_{13}$1-3); Red reference line gives the $\delta^{15}N$ turning, purple reference line gives the $\delta^{13}C$ turning point*

In the drained site at Lakkasuo (LD), we discovered a large quantity of microbial-derived mFAs in the acrotelm ($LD_{13}$1-3: 108.7µg/g (mean, ±5.5 [standard deviation of n=3]; Figure 3.1) and the mesotelm (62.27µg/g [±3.7]; all results from the 2013 sampling). The highest microbial-derived mFA concentration was found at the $\delta^{15}N$ turning point (73.73µg/g, ±6.74; Figure 3.1). In the catotelm, the values of mFAs were low in the LD sites (21.01µg/g, ±2.4). The concentration of fungal-derived mFAs is decreasing from 40.33µg/g (±11.7; Figure 3.2) in the acrotelm of $LD_{13}$1-3, to very low values at the end of the mesotelm and in the catotelm (2.88 µg/g, ±1.4µg/g; Figure 3.2). Also, the percent of fungal-derived mFAs are decreasing from 49% of all microbial-derived mFAs in the acrotelm to 14% in the catotelm. Contrary to the continually decreasing trend in depth of the fungal-derived mFAs under drained conditions, the bacterial-derived mFA concentration is highest in the middle of the mesotelm and peaks parallel to the $\delta^{15}N$ turning point (mean 60.17µg/g, ±10.2; Figure 3.2). Bacterial-derived mFAs comprise up to 85% of total microbial-derived mFAs at this depth.

For the rewetted site in Degerö Stormyr ($DR_{13}$1-3), we detected low values of microbial-derived mFAs in the acrotelm and in the uppermost part of the former mesotelm (20.61µg/g [±2.6]). This is expected, because of the wet conditions which are not suitable for high microbial abundance. Below, in the deeper part of the former mesotelm microbial-derived mFA quantities increases (53.44µg/g [±2.93]). As in Lakkasuo, the microbial-derived mFA quantity also peaks at the $\delta^{15}N$ turning point in the middle of the formerly drained layer (71.55µg/g, ±2.48; Figure 3.1). In the below catotelm, values were low for DR sites (8.80µg/g, ±2.7; Figure 3.1).

In the rewetted cores $DR_{13}$1-3, we found that fungal-derived mFAs have the highest percentage of the mFAs detected in the acrotelm (35%) and in the upper part of the former mesotelm (32%, Figure 3.3). The highest total quantity of fungal-derived mFAs is in the upper mesotelm (16.75µg/g, ±3.82; Figure 3.2). In the catotelm, the percentage (16%) and the total quantity of fungal-derived mFAs (2.42µg/g, ±2.17; Figure 3.2/ 3.3) is low. With decreasing fungal-derived mFA percentage, the bacterial-derived mFA percentage increases, from 65% in the acrotelm to 84% in the catotelm (Figure 3.3). Overall, bacterial-derived mFA abundance is highest at the $\delta^{15}N$ turning point (62.15µg/g, ±5) and low in the catotelm (7.45µg/g, ±3; Figure 3.2).

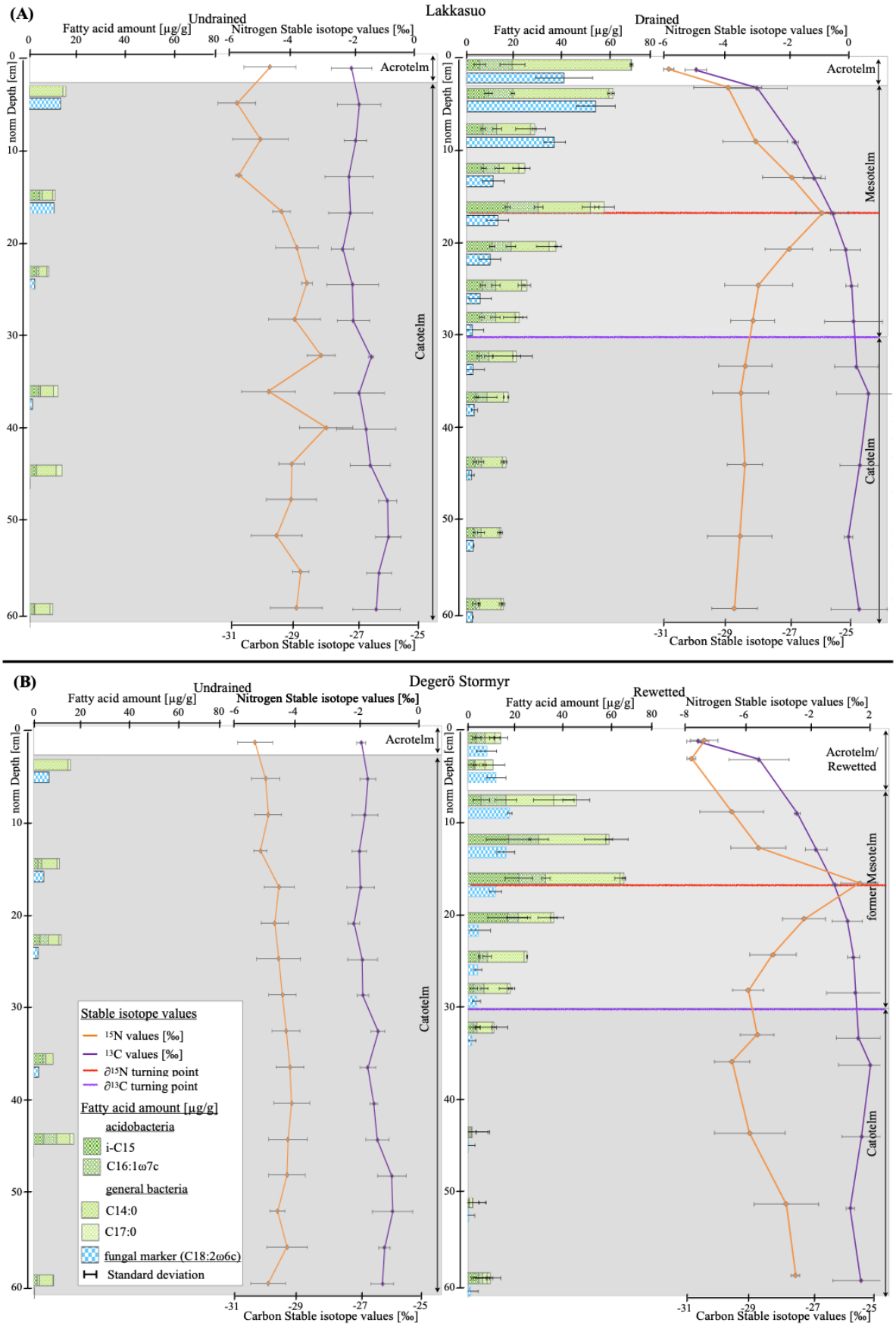


**Figure 3.2:** *Stable isotope depth trends [‰] (orange: $\delta^{15}N$, purple: $\delta^{13}C$) and fatty acids marker concentrations [µg/g], separated by different microbial groups; (A) Lakkasuo: undrained (LU1-3) and drained ($LD_{13}1$-3); (B) Degerö Stormyr: undrained (DU1-3) and rewetted ($DR_{13}1$-3); Red reference line gives the $\delta^{15}N$ turning point, purple reference line gives the $\delta^{13}C$ turning point*

### 3.4.2. Stable isotope values

Carbon and nitrogen isotope values in undrained sites in Lakkasuo ($LU_{13}$1-3, $LU_{17}$) and Degerö Stormyr ($DU_{13}$1-3, $DU_{17}$) show no depth trend, whereas carbon isotope values vary less than nitrogen stable isotope values (Figure 3.2).

In $LU_{13}$1-3 and $LU_{17}$, carbon isotope values range between -24.47‰ and -28.36‰ with a mean of -26.43‰ (±0.85). Nitrogen stable isotope values in these cores are between 0.51‰ and -6.56‰ (mean -3.15‰, ±1.78).

In $DU_{13}$1-3 and $DU_{17}$, carbon stable isotope values are between -22.84‰ and -27.38‰ (mean -24.52‰, ±0.94). For nitrogen, the values range between -0.71‰ and -9.31‰ (mean -3.99, ± 2.27).

In the drained site in Lakkasuo ($LD_{13}$1-3, $LD_{17}$) and the rewetted site in Degerö Stormyr ($DR_{13}$1-3, $DR_{17}$), values show a distinct depth pattern and vary more than in undrained sites (Figure 3.2). In both sites (LD and DR), carbon stable isotope values show a decreasing trend in the upper layers (above 30 cm normD, Figure 3.2). In $LD_{13}$1-3, carbon isotope values range between -24.53‰ and -31.04‰ (mean -26.67‰, ±1.23), and in $DR_{13}$1-3, between -23.30‰ and -29.74‰ (mean -26.33, ±1.33).

Nitrogen values in drained and rewetted sites show a peak in the mesotelm (17 cm normD, Figure 3.2). In $LD_{13}$1-3, $\delta^{15}N$ values are between 0.94‰ and -5.73‰ (mean 2.40, ±1.50). In $DR_{13}$1-3, $\delta^{15}N$ values are between 1.83‰ and −10.64‰ (mean -3.42, ±2.38).

## 3.5. Discussion

### 3.5.1. New insights to microbial abundance in undrained, rewetted and drained sites, identified by membrane fatty acids

In the undrained sites LU and DU, microbial-derived mFA concentrations were highest in the acrotelm, which is in line with other studies (Asada et al., 2005; Artz, 2013). It is the result of environmental conditions in this layer (aerobic, rich of primary plant material). But the values of the acrotelm in the undrained sites are low compared to those of the drained sites, which is a sign of the intact carbon storage function of peat soils and could be the result of (i) the overall nutrient-poor conditions of the investigated sites (Minick et al., 2019) with a reduced quantity of nutrients and (ii) the incorporation of C in living vegetation (Artz et al., 2008; Figure 3.1).

The highest microbial-derived mFA concentration discovered in the drained site of Lakkasuo is in line with our previous study (Groß-Schmölders et al., 2020) and Peltoniemi et al. (2009), as the facultative aerobic mesotelm, with its high content of available organic matter, provides optimal conditions for microbial metabolism and thus contains the highest microbial-derived mFA concentrations (Figure 3.1). This is also in line with the findings of Wang et al. (2019), who showed that the mesotelm is a hot spot for microbial communities, with the highest microbial diversity.

For the rewetted site in Degerö Stormyr, we assumed that the highest mFA concentration in the former mesotelm (the newly established catotelm after rewetting; Figure 3.1) could be the result of former microbial metabolism preserved from the past aerobic conditions that occurred due to drainage. This correlation was also reported by Torres and Pancost (2016). The low microbial-derived mFA quantities in the uppermost part of DR1-3, similar to concentrations of DU (Figure 3.1) are likely a result of the recovery of undrained conditions.

Regarding microbial community assemblage, our results are congruent with previous studies (Groß-Schmölders et al., 2020; Thormann, 2004) demonstrating that fungal-derived mFA concentrations are dominant in the upper layers of drained sites (LD, Figure 3.2). This is congruent with the ecological niche for fungi being located near the surface, where there are large quantities of primary plant material and aerobic conditions (Wallander et al., 2009; Strickland and Rousk, 2010; Thormann et al., 2004). Here, fungal metabolism has a competitive advantage (De Boer et al., 2005; Thormann et al., 2003; Thormann, 2011).

In contrast to fungi, bacteria are better adapted to the facultative anaerobic conditions lower in the profile, (Winsborough and Basiliko, 2010). They are able to make use of a wider spectrum of substrates, which leads to an increase in ratios of bacterial-derived mFAs as depth increases within the mesotelm (Figure 3.2; Kohl et al., 2015).

The group of acidobacteria is of special interest here, as acidobacteria are highly abundant in soil, especially in peatlands (Hausmann et al., 2018; Damsté et al., 2015). They comprise 30% of all bacteria in nutrient-rich fens and up to 80% in pristine bogs (Serkebaeva et al., 2013). Acidobacteria are known to have a slow growth rate and are tolerant to depleted sites, which supports their abundance in nutrient-poor peatlands (Wang et al., 2019). Because of their capability to metabolize in facultative anaerobic to anaerobic conditions, acidobacteria are particularly visible in the mesotelm (Urbanova and Barta, 2014). Acidobacteria are always gram-negative and exhibit a

group of specific membrane compounds (Dedysh and Damsté, 2018). In particular acidobacteria mainly produce glycerol dialkyl glycerol tetraethers (Weijers et al., 210) and the membrane lipids i-C15:0, C16:1ω7c and 13,16-dimethyl octacosanedioic acid (Damasté et al., 2011; Dedysh and Damsté, 2018). The concentrations of these were linked to low pH values and decreasing oxygen availability (Weijers et al., 2010), which are typical conditions of the mesotelm. Our results are in line with these findings, as we found an increasing abundance of the mFAs i-C15:0 and C16:1ω7c near the $\delta^{15}N$ turning point (Figures 3.2/ 3.3).

### 3.5.2. Microbial-derived membrane fatty acid quantities and isotopic values

In undrained sites, we saw no depth trend in the isotopic values compared to the strong decrease of microbial-derived mFA concentration in sublayers (Figure 3.2). We conclude that this is caused by the extreme environment of the catotelm, with low temperatures and anaerobic conditions. Hence, metabolism and decomposition processes are strongly inhibited, the mFA quantities and the isotopic fractionation rates are extremely low, and organic substrates are stored (Clymo, 1984; Frolking et al., 2001; Krüger et al., 2015).

#### 3.5.2.1. Microbial-derived membrane fatty acid quantities and carbon isotopic values

Carbon stable isotope values increase with depth in all investigated drained sites by ~2.48‰ from the acrotelm to the catotelm (Figure 3.2). This increase was also found previously (Alewell et al. 2011; Krüger et al., 2014) and is in the same range of what other studies have found for peatland soils (Kohl et al. 2015, Hobbie et al., 2017). Wynn et al. (2006) reported, that this trend is caused by the microbial communities involved and their preference for substrates. If more enriched substrates are degraded, the $\delta^{13}C$ values in the remaining substrate could decrease due to the enhanced gaseous loss of $^{13}C$ enriched $CO_2$ (Wynn et al., 2006). For example, glucose, pectin and hemicellulose, which are enriched in $^{13}C$, are some of the preferred substrates for microbial metabolism and are processed in the uppermost peat soil layers. As a result, $\delta^{13}C$ values are low in the uppermost peat layers of degraded sites, as we see in LD (Figure 3.2). In contrast to the enriched $\delta^{13}C$ values of $CO_2$, methane ($CH_4$) is depleted in $\delta^{13}C$, which could balance the effect of enriched $CO_2$ in the remaining substrate. But as methane production mainly occurs in anerobic conditions, the effect of gaseous loss

of depleted $CH_4$ is expected to play a minor role in drained peatlands (Yang et al., 2019). In addition, Hornibrook et al. (1997) reported that the $\delta^{13}C$ values of $CH_4$ are increasing with decreasing depth in peatlands, which could also minor the effect of depleted $CH_4$ in our sites. That the depleted $\delta^{13}C$ values in top layers of peat are caused by the preferred cycling and therefore gaseous loss of heavy $^{13}C$ isotopes can be verified by studies that reported that there is no preferred loss of lighter $^{12}C$ during microbial metabolism (Lerch et al., 2011). Increasing values of $\delta^{13}C$ in peat soil with depth are therefore related to a change in the processed substrates and their specific $\delta^{13}C$ values (Kohl et al., 2015). With increasing depth, recalcitrant, $\delta^{13}C$-depleted substrates such as lignin are also processed, which leads to increasing mobilization of lighter $^{12}C$ and further increasing $\delta^{13}C$ values in the remaining bulk soil with depth (Lerch et al., 2011). Further Boström et al. (2007) assume that the $^{13}C$ enrichment in drained soils with depth is a result of the increased contribution of microbial derived C with depth.

With regard to specific microbial groups, Kohl et al. reported in 2015 that a high fungi-to-bacteria ratio (FB) in the microbial community is negatively correlated with $\delta^{13}C$ values in the remaining substrate; this is caused by changes in processed substrates and their carbon isotopic signals. Hence, FB is decreasing, and $\delta^{13}C$ values are increasing due to a change in microbial metabolism processes and substrates used (Kohl et al., 2015). As Kohl et al. (2015) showed, the $\delta^{13}C$ values of bacteria (-40.1 to -30.6‰) and fungi (-31.1 to -24.6‰) stay the same in different depths of peat, but their ratios are changing, and with them, the $\delta^{13}C$ values of the bulk material. This is in line with our data of a decreasing FB and increasing $\delta^{13}C$ values with depth (Figure 3.2).

With regard to acidobacteria, Weijers et al. (2010) found that acidobacterial-derived mFAs have enriched $\delta^{13}C$ values compared to plants and in the same range then bulk. The reason for that could be the preferred cycling of glucose and pectin, which are enriched in $\delta^{13}C$ (Pankratov et al., 2008; Lerch et al. 2011). As the highest quantity of acidobacterial-derived mFAs is found in the mesotelm (Figures 3.2/ 3.3), we found that the increasing metabolism rate of acidobacteria could be linked to the increasing $\delta^{13}C$ values (Figure 3.2). An increase in acidobacterial-derived mFAs is expected because acidobacteria are known to be autotrophs and are therefore able to assimilate $CO_2$ from the soil (Weijers et al., 2010). As soil $CO_2$ is enriched in $^{13}C$ (Weijers et al., 2010), the increasing metabolism by acidobacteria increases the $\delta^{13}C$ values in the remaining substrate further.

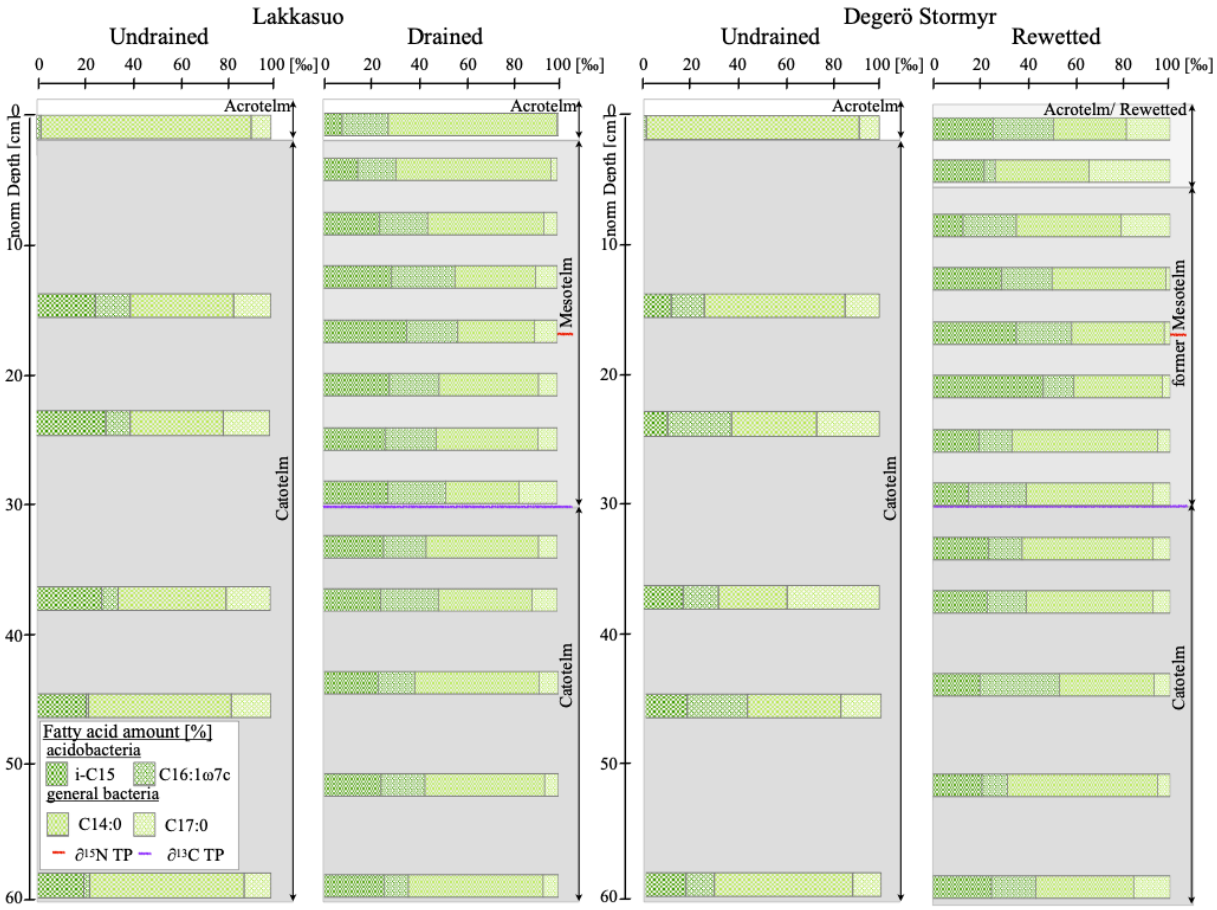


**Figure 3.3:** *Relative amount of bacterial-derived membrane fatty acids, separated for general and acidobacterial markers Lakkasuo (undrained, drained) and Degerö Stormyr (undrained, rewetted) in the cores of 2013; Red reference line gives the $\delta^{15}N$ turning*

### 3.5.2.2 Microbial-derived membrane fatty acid quantities and nitrogen isotopic values

Considering the parallel depth trend of the concentrations of bacterial-derived mFAs and $\delta^{15}N$ values (Figure 3.4), we conclude that nitrogen stable isotope values appear to be linked more closely to bacterial abundance than to overall microbial abundance. This interpretation is supported by a higher Spearman correlation index of R = 0.54 for bacteria compared to R = 0.30 for all microbes. Peaks in bacterial-derived mFA abundance and at $\delta^{15}N$ values occur in tandem and are visible for both sites investigated (Figure 3.2). The correlation is clear if we consider that the quantity of N in microbial biomass is a substantial part of N in bulk substrate of poor peatlands (Lin et al., 2014), and thus, isotopic fractionation by microbes will influence the bulk isotopic value significantly.

We differentiated between acidobacterial and general bacterial markers. For both bacterial groups, the mFA concentrations increased towards the $\delta^{15}N$ turning point and were lowest in the catotelm (Figure 3.2).

For both peatland sites, we found the highest concentration of acidobacterial-derived mFAs reaching approximately 50% of all bacterial-derived mFAs in the mesotelm (Figure 3.3). In the upper mesotelm and the catotelm, the percentage is approximately 40% (Figure 3.3). Hence, our results are congruent with the results of Artz in 2013, which point to a characteristic depth trend with a peak in the mesotelm of acidobacterial populations in nutrient-poor peatlands (Figures 3.2/ 3.3).

Acidobacteria are closely involved in nitrogen cycling (Eichhorst et al., 2018; Kalam et al., 2020; Urbanova and Barta, 2014). For example, they are involved in denitrification processes (Urbanova and Barta, 2014) They reduce nitrate, nitrite and possibly nitric oxide (Kalam et al., 2020; Eichhorst et al., 2018; Ward et al., 2009). As Eichhorst et al. (2018) reported, there are also evidence for the mobilization of ammonium by acidobacteria and the gaseous loss of $N_2O$. All these cycling processes are known to increase $\delta^{15}N$ values in bulk material (Denk et al., 2017) and are observed predominantly in the mesotelm (Palmer and Horn, 2015; Oshiki et al., 2016). Thus, acidobacteria could be the key to forming the $\delta^{15}N$ depth trends in nutrient-poor peatlands. We assume that as the occurrence of acidobacteria increases, more nitrogen will be processed. Lighter $^{14}N$ will be released in a gaseous state, leached or mineralized and then incorporated by plants and translocated upwards within the plants. These processes should lead to increasing $\delta^{15}N$ values in the remaining substrate (Hausmann et al., 2018). This correlation is illustrated by our data. Acidobacterial-derived mFA markers, shown in absolute concentrations (Figure 3.2) and in relation to other microbial markers, are highest at the $\delta^{15}N$ turning point (Figures 3.2/ 3.3). At the $\delta^{15}N$ turning point, the relative abundance of acidobacterial-derived mFAs in relation to all bacterial-derived mFAs is highest, with 49.92% for LD and 55.64% for DR (Figure 3.3). Overall investigated sites, $\delta^{15}N$ values and the acidobacterial-derived mFAs are highly significantly correlated ($R = 0.66$, $p < 0.05$; Figure 3.4).

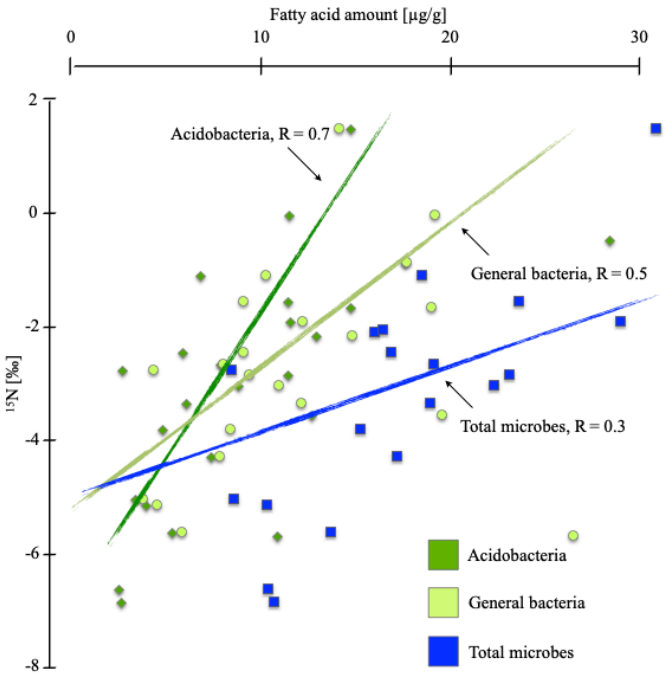


**Figure 3.4:** *Spearman correlation index (R) and correlation of δ$^{15}$N[‰] and microbial, general bacterial and acidobacterial membrane fatty acid marker amount [µg/g], for the rewetted site in Degerö Stormyr and the drained site in Lakkasuo*

### 3.5.2.3 Depth trend of stable isotopes in drained and rewetted sites

The comparison of stable isotope depth trends (δ$^{15}$N, δ$^{13}$C) revealed specific differences between undrained, drained, and rewetted sites, which remained stable over both years. Regardless of the sampling year, none of the cores of undrained sites ($DN_{13}$1-3, $DN_{17}$, $LN_{13}$1-3, $LN_{17}$) showed any depth trend of stable isotopes (Figure 3.5). The cores of the drained site Lakkasuo ($LD_{13}$1-3, $LD_{17}$) showed trends within the drained layer (acrotelm and mesotelm). δ$^{13}$C values increased throughout the drained layer, and a peak of $^{15}$N values (the δ$^{15}$N turning point) was visible in the mesotelm, which both is indicative for the ongoing loss of typical peatland soil functioning (e.g. carbon storage). In the rewetted site Degerö Stormyr ($DR_{13}$1-3, $DR_{17}$), no depth trends in δ$^{15}$N values were observed in the layer likely formed during rewetting conditions above the layer formed during former drainage (Figure 3.5). Below the rewetted layer, the δ$^{15}$N depth trend of the former mesotelm was preserved in the newly established (>20 years of rewetting) catotelm. The decreasing trend of δ$^{13}$C values in DR also seems to have slowed down in the rewetted core in 2017 (Figure 3.5).

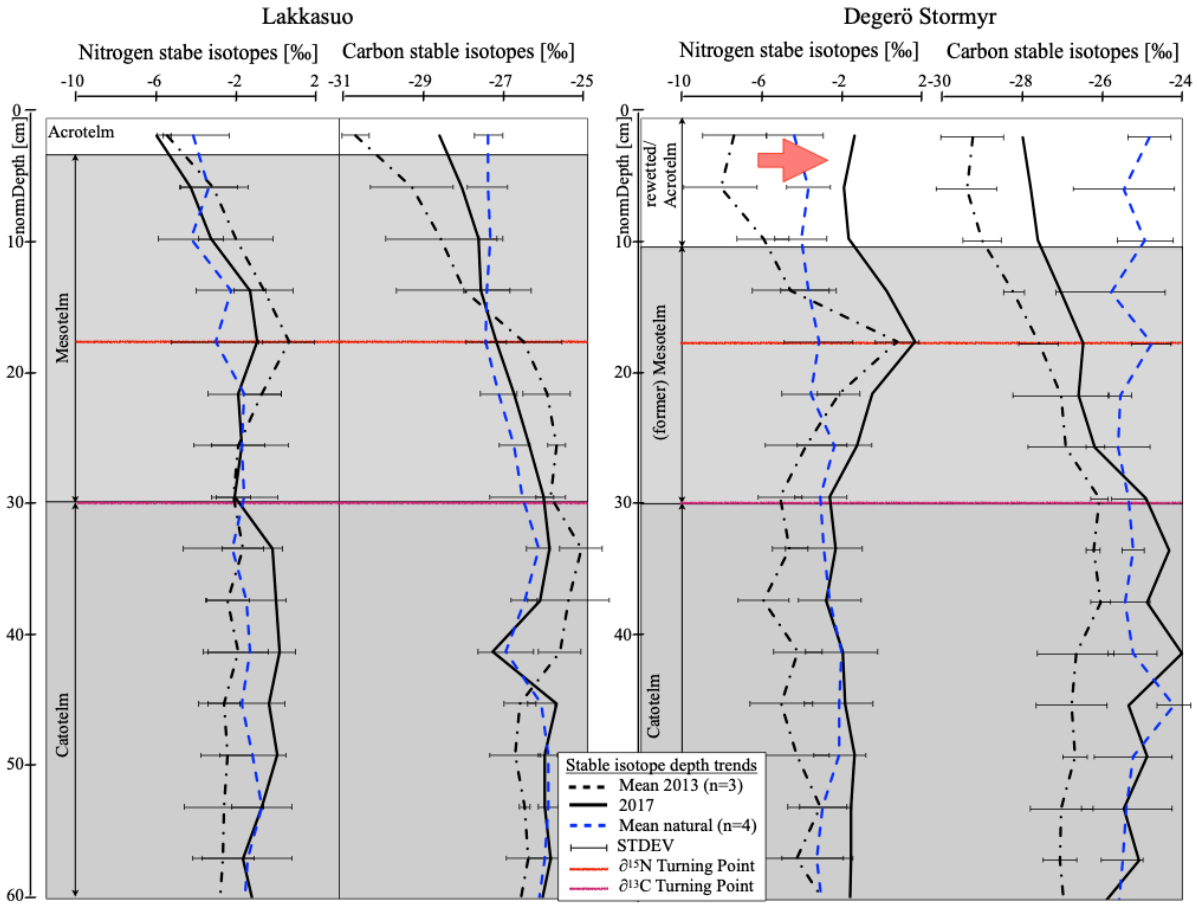


**Figure 3.5:** *Depth-normalized stable isotope trends (nitrogen, carbon) for Degerö Stormyr and Lakkasuo, separated for drained sites (2013 (black dotted) and 2017 (black)) and undrained sites (blue dotted) ; Red reference line gives the $\delta^{15}N$ turning point, purple reference line gives the $\delta^{13}C$ turning point; Note the shift between the nitrogen isotope depth trend from 2013 to 2017 in the rewetted Degerö Stormyr (marked with red arrow)*

The time-dependent sampling was devised to test the robustness of the stable isotope depth pattern as an indicator for peatland hydrology in relation to the onset, duration and ending of a drainage event. With one exception, nitrogen stable isotope depth trends in both years - 2013 and 2017 - are very similar, confirming our hypothesis (Figure 3.5). The exception is the $\delta^{15}N$ depth trends in Degerö Stormyr, the site that was rewetted in recent decades, where a shift in the rewetted layer in 2017 towards more undrained depth trends compared to 2013 most likely indicates a successful restoration.

The changes in stable isotope values with rewetting occur simultaneously with changes in microbial-derived mFA quantities. This indicates that the changed environmental conditions lead to changing microbial community compositions and therefore changed metabolism processes (Asada et al., 2005). This is in line with the findings of Elliott et al. (2015), who also found distinct changes in microbial communities with rewetting. In drained peat sites, they also found increased values of acidobacteria, which we also found in our sites (Figures 3.2/ 3.3). Elliott et al. (2015)

also indicated that changes in microbial communities are rapid after rewetting and could therefore also indicate relatively short rewetting times and the recovery of typical peatland soil functioning.

## 3.6. Conclusion

Our results confirm that the existence of specific microbial groups is correlated to stable isotope depth trends ($\delta^{15}N$, $\delta^{13}C$) of nutrient-poor peatlands, particularly that of nitrogen isotopes. An analysis of mFA markers for general bacteria as well as specific mFA markers for acidobacteria, and fungi revealed a high abundance of fungal-derived mFAs in the aerobic acrotelm. The upper mesotelm showed a transition to decreasing fungal-derived and increasing bacterial-derived mFA abundance (especially that of acidobacteria). As such, the $\delta^{15}N$ turning point seems to be driven in particular by the nitrogen cycling of bacterial metabolism, most prominently by acidobacteria. Downwards along the (former) mesotelm, $\delta^{15}N$ values decreased, likely due to low microbial metabolic rates. Finally, in the permanent anaerobic catotelm, where microbial metabolism is strongly impeded, $\delta^{15}N$ values show no further depth trend. Stable isotope depth trends ($\delta^{15}N$, $\delta^{13}C$) from two different years were able to confirm the persistence of these trends as indicators for ongoing drainage and therefore impaired soil functioning, e.g. as storage of carbon. Furthermore, $\delta^{15}N$ seems to indicate former drainage followed by rewetting processes. In summary, we conclude that microbial abundance as indicated by group specific biomarkers can be confirmed as key for stable isotope depth trends and that differences in $\delta^{15}N$ depth profiles may be indicative for drainage and rewetting.

**Acknowledgements**

We are very thankful to the editor and the reviewers for their valuable suggestions and comments which improved this paper.

# 4

# Stable isotopes ($\delta^{13}C$, $\delta^{15}N$) and biomarkers as indicators of the hydrological regime of fens in a European East–West transect[3]


## Abstract

Peatland degradation is tightly connected to hydrological changes and microbial metabolism. To better understand these metabolism processes, more information is needed on how microbial communities and substrate cycling are affected by changing hydrological regimes. These activities should be imprinted in stable isotope bulk values ($\delta^{15}N$, $\delta^{13}C$) due to specific isotopic fractionation by different microbial communities, their metabolic pathways and nutrient sources. We hypothesize that stable isotope values and microbial abundance are correlated and act as indicators of different hydrological regimes. We sampled an East–West transect across European fens in 14 areas and conducted a stable isotope ($\delta^{13}C$, $\delta^{15}N$) and membrane fatty acid (mFA) analysis. Within each area an undrained, drained and rewetted site was selected. Rewetted sites were separated based on when rewetting occurred. We found differences in the upper layers of all sites in microbial-derived mFAs and stable isotope values corresponding to hydrological regimes. The highest and lowest quantities of microbial-derived mFAs were measured in undrained and drained sites, respectively. Fungal-derived mFAs were especially lower in drained sites. Simultaneously, $\delta^{15}N$ stable isotope values were highest in drained sites. In addition, stable isotope values and microbial-derived mFAs showed distinct depth trends. In undrained sites stable isotopes values slightly increased with depth. In drained sites, $\delta^{15}N$ values decreased downwards, whereas $\delta^{13}C$ values increased. Overall microbial-derived mFAs decreased with depth. These patterns presumably result from anoxic conditions and high peat recalcitrance in the deeper layers. In sites with short time of rewetting, the microbial-derived mFAs and stable isotope values were similar to values of drained sites, while with increasing rewetting time values shifted to those of undrained sites. We conclude that biomarkers indicate that stable isotope values reflect specific


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microbial metabolic processes, which differ with hydrological regimes, and thus could signal both drainage and rewetting in fens.

## 4.1. Introduction

Groundwater-fed peatlands ("fens") in the temperate zones of Europe, North America, and Asia and are typically characterized by high biodiversity (Lamers et al., 2015). Because fens are influenced by groundwater and/or surface water flow (Grootjans, et al., 2006), they are generally more base-rich and often also nutrient-richer than rainwater-fed bogs (Joosten and Clarke, 2002). In Central and Western Europe, the majority of fens have been affected by drainage and subsequent agricultural use (Grootjans, et al., 2006), turning them from sinks to sources of carbon (C; Paul et al, 2021). Recently drained peatlands account for an estimated 5% of global atmospheric greenhouse gas (GHG) emissions, mostly as $CO_2$ (Leifeld and Menichetti, 2018). Furthermore, ecosystem services such as C sequestration are absent in drained fens due to shifts in microbial communities and altered metabolic processes (Bedford and Godwin, 2002; Philippot et al., 2013; Wagg et al., 2014).

In fens, the highest metabolic rates are found in the upper peat layer, on the oxic-anoxic interface (Artz, 2013; Asada et al., 2005; Morris et al., 2011). With increasing depth, the overall decrease in redox potential correlates with decreased metabolic rates, with the lowest rates in the deepest and always waterlogged peat layers (Artz, 2013; Asada et al., 2005; Lin et al., 2014).

Because microbial-induced metabolic processes such as denitrification and nitrification lead to isotopic fractionation, stable isotope values can be used as indicators for peatland hydrological regimes (Alewell et al., 2011; Groß-Schmölders et al., 2020; Krüger et al., 2015). For $\delta^{13}C$, Alewell et al. (2011), Biester et al. (2014), Hobbie et al. (2017), Krüger et al. (2014) and Novak et al. (1999) reported increasing values with depth and enhanced recycling with drainage. In drained sites they reported also a switch to the cycling of other substrates in peat with depth. As Kohl et al. (2015) demonstrated, this distinct $\delta^{13}C$ depth pattern is a consequence of changing microbial metabolism. Additionally, a significant negative correlation between the fungal-to-bacterial ratio and $\delta^{15}N$ values was reported in nutrient-poor peatlands (Groß-Schmölders et al., 2020). Microbial metabolic processes in fens are often constrained by a limited supply of nitrogen (N) and oxygen (O) (Lin et al., 2014). During microbial incorporation of N and metabolic processing, a fractionation of stable isotopes occurs,

as most organisms prefer the lighter and more frequently occurring $^{14}N$ (Adams and Grierson, 2001; Asada et al., 2005; Högberg et al., 1996; Kohzu et al., 2003). The preferential incorporation and translocation upwards to stem and foliar of the lighter $^{14}N$ by plants result in the enrichment of heavier $^{15}N$ in the remaining bulk substrate (Högberg et al., 1996). Additionally, the mycorrhizal uptake of lighter $^{14}N$ into plants increases the $\delta^{15}N$ values of mycorrhizal biomass and therefore increases the values of the substrate even more (Hobbie and Högberg, 2012). Furthermore, microbial metabolic processes in deeper peat layers increase the $\delta^{15}N$ values as long as microbial metabolism of organic substrate (mainly dead plant residues) occurs and lighter $^{14}N$ is leached, translocated, or lost via outgassing during denitrification (Damman, 1988; Niemen, 1998; Novák et al., 1999). If microbial activity decreases in the deeper peat layers, enrichment with $\delta^{15}N$ isotopes due to this isotopic fractionation being comparably lower than in a parallel system with high metabolic rates. As microbial abundance is higher in aerobic layers, microbial abundance and stable isotope values can be linked to peatland hydrological regimes (Groß-Schmölders et al., 2020; Groß-Schmölders et al., 2021; Tfaily et al., 2014). Some microbial groups are more active in N cycling than others and, therefore, play a greater role in N isotopic fractionation (Groß-Schmölders et al., 2021; Tfaily et al., 2014). For example, saprotrophic fungi have a low demand for N, making them unlikely to be a primary driver of increasing $\delta^{15}N$ values (Thormann, 2005).

Microbial community composition is, among other factors, driven by substrate quality (Emsens et al., 2020; Thormann et al., 2005). The C:N ratio, which indicates the degree of decomposition (Kuhry and Vitt, 1996; Malmer and Holm, 1984; Thormann, 2005), can be used as an indicator of substrate quality. With increasing levels of decomposition, a preferential loss of C over N takes place and the C:N ratio decreases. Sundh et al. (1997) and Torres and Pancost (2016) demonstrated that membrane fatty acids (mFAs) are persistent and largely insoluble compounds of specific cell membranes (microbial communities, living and dead) in peat soils. Because mFAs vary based on their origin (plants, specific microbial groups; Bajerski et al., 2017; Finotti et al., 1993; Piotrowska-Seget and Mrozik, 2003; Reiffarth et al., 2016; Willers et al., 2015), the relative abundance of specific microbial communities can be determined based on an analysis of the occurrence and quantities of mFAs present (Piotrowska-Seget and Mrozik, 2003; Torres and Pancost, 2016).

In our study, we investigated 14 fen regions across Europe, and each region comprised three fen sites that differed in the hydrological regime (undrained, drained, and rewetted sites).

We used stable isotope and two mFA analyses to obtain reliable information on the hydrological regime of the fen sites. We hypothesized that:

(i) Stable isotope depth trends differ between undrained, drained, and rewetted fen sites,

(ii) Microbial community composition, as indicated by mFAs, differs between undrained, drained, and rewetted fen sites,

(iii) Stable isotopic patterns correlate with microbial mFAs.

The verification of these hypotheses would enable us to assess restoration projects with higher precision and, thus, lend support to peatland conservation policies.

## 4.2. Study site

Peat soil was sampled in 14 lowland fen regions across a gradient from western to eastern Europe (United Kingdom, Belgium, Netherlands, Germany and Poland) in June 2013 (region Cuxhaven) and in May and June 2017 (the remaining 13 regions, as described by (Emsens et al. 2020; Table 4.1).

All regions were located in the temperate climatic zone and more or less within the same latitudinal range (N49.65° - N54.35°). Because the regions covered a wide longitudinal gradient (> 1500km), there is a climatological gradient from an oceanic (west, with mild winters and mild summers) to a more continental (east, with cold winters and warm summers) climate.

In each fen region, except for the Cuxhaven region, we collected samples in three fen sites with different hydrological regimes (undrained, drained and rewetted). In Cuxhaven, only samples of drained and undrained sites were available. The classification of the hydrological regime was made by observations in the field (presence of drainage ditches, groundwater table) and an analysis of vegetation composition (Table C1). The undrained sites were covered with typical fen species (e.g., Carex spp., brown mosses) and had a groundwater table near the peat surface for most of the year. The groundwater table was below 50cm (annual average (av.)) in the drainage-affected sites and the vegetation mainly consisted of moist or wet grassland species. Rewetting and high levels of groundwater (10-15cm below surface) was caused either by restoration projects or beaver dam building and had a fen

vegetation (e.g. Carex spp and brown mosses). Water table depths in the rewetted sites did not differ from the undrained sites (Emsens et al., 2020; Krüger et al., 2014). All sites had near neutral to slightly acidic pore water (mean pH=6.45, +/-0.33; min=5.6, max=7.1, measured in the field, WTW Multi 340i, WTW, Weilheim, Germany; Emsens et al., 2020; Krüger et al., 2014).

**Table 4.1:** *Site description of all investigated sites; coordinates [longitude (long.)/latitude (lat.).]; mean annual temperature (MAT) [°C]; precipitation (P) [mm]; time since rewetting (TsR) [years]; (Emsens et al., 2020; CustomWeather, 2020; Krüger et al., 2016)*

| Country | Site name | Long/ Lat. | MAT | P | TsR |
|---|---|---|---|---|---|
| Belgium | Arlon | 5.7/ 49.7 | +9 | 489 | >25 |
| | Zwarte Beek | 5.3/ 51.1 | +11 | 476 | >25 |
| Netherlands | Binnenveld | 5.6/ 52.0 | +11 | 569 | 10-25 |
| | Drentse Aa | 6.7/ 53.0 | +11 | 387 | 10-25 |
| Germany | Gützkow | 13.4/ 53.9 | +10 | 187 | 10-25 |
| | Peene mouth | 13.7/ 53.8 | +10 | 187 | <10 |
| | Kiel | 10.1/ 54.3 | +10 | 442 | <10 |
| | Recknitz | 12.6/ 54.2 | +10 | 439 | <10 |
| | Cuxhaven | 8.5/ 53.4 | +9 | 766 | - |
| Poland | Biebrza | 23.3/ 53.7 | +7 | 616 | <10 |
| | Rospuda | 22.6/ 53.8 | +7 | 623 | >25 |
| | Suwalszczyzna | 22.7/ 54.3 | +7 | 623 | <10 |
| | Mazury | 21.5/ 53.7 | +9 | 362 | <10 |
| United Kingdom | Anglesey | -4.3/ 53.3 | +10 | 2280 | 10-25 |

The rewetted sites were separated in three major “time since rewetting (TsR)” classes, following Emsens et al. (2020; Table 4.1): (1) less than 10 years of rewetting, (2) 10 to 25 years of rewetting, and (3) more than 25 years of rewetting. The classes were used to assess the effect of rewetting time on stable isotope values and mFAs. For each rewetting class an undrained and drained fen were also investigated. This, in the following all three hydrological regimes are assigned to the rewetting time of the respective rewetted fen.

## 4.3. Material and methods

### 4.3.1. Soil sampling and bulk analysis

At each site three to five subsamples were taken at three depths (0 - 5cm; 15 – 20cm and 45 - 50cm) and mixed into one composite sample per depth. All samples were individually packed in plastic bags and aluminum foil, cooled immediately after collection, and deep-frozen at the end of each day.

Samples were oven-dried at 40°C for 72h, and homogenized with a vibrating ball mill (MM400, Retsch, Germany). Stable C and N isotopic values were measured in an elemental analyzer combined with an isotope ratio mass spectrometer (EA-IRMS)

(Inegra2, Sercon, Crewe, UK). C isotopic composition ($\delta^{13}C$) was expressed relative to Vienna Pee-Dee Belemnite (VPDB) standard and reported in delta notation (‰), stable nitrogen isotopes were expressed relative to the atmospheric N standard and reported in delta notation (‰). C:N was determined with the mass relationship of the measured bulk content [mg/g] of C and N.

### 4.3.2. Fatty acid analysis

The mFA analysis of the soil samples were conducted by using two different methods, A and B (please see below for definition). The mFA at all areas except Cuxhaven were analyzed with method A. Cuxhaven data originated from a different project and samples were analyzed with method B. The reason for this difference is that the analysis was performed by two different laboratories with different analytical standard methods: The Ceske Budejovice Lab used method A and Basel Lab used method B.

Phospholipid fatty acid measurement Ceske Budejovice (method A):

Phospholipid fatty acids (PLFAs) were extracted from 0.5g of lyophilized subsamples. All samples were extracted with a chloroform:methanol:phosphate buffer mixture (1:2:0.8), after which the extracted lipids were separated using solid-phase extraction cartridges (LiChrolut Si 60, Merck). The samples were eluted in three fractions containing neutral lipids, glycolipids and phospholipids with 2mL of chloroform, 6mL of acetone and 2mL of methanol, respectively (Oravecz et al., 2004). The first and third fractions were then subjected to mild alkaline methanolysis (Šnajdr et al., 2008). The free methyl esters of the PLFAs were analyzed by gas chromatography-mass spectrometry (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA). The GC instrument was equipped with a split/splitless injector, and we used a DB-5MS column for separation (60m, 0.25mm i.d., 0.25µm film thickness). The temperature program began at 60C° and was maintained for 1min in splitless mode. Next the splitter was opened, and the oven was heated to 160C° at 25C°min-1. The second temperature ramp was up to 280C° at 2.5C°min-1, which was maintained for 10min. The solvent delay time was set at 8min. The transfer line temperature was set at 280C°. Mass spectra were recorded at 1scan s-1 under electron impact at 70eV, with mass range 50-350amu. We identified methylated fatty acids according to their mass spectra using a mixture of chemical standards from Sigma-Aldrich (Prague, Czech Republic) and Matreya LLC (Pleasant Gap, PA, USA).

Membrane fatty acid measurement Basel (method B):

We aimed to extract total mFAs to distinguish between mFAs of different bacterial groups, fungi and plants. We processed 0.2–1.1g of sample for the lipid extraction with a mixture of CH2Cl2:MeOH (9:1v/v) in an Accelerated Solvent Extractor (Dionex ASE 350). 0.4µg/µl of an internal standard with nonadecanoic acid was added before processing each sample.

The total lipid extracts (TLE) were saponified by adding 2ml of KOH dissolved in MeOH (12%) and putting it in the oven for 3 hours at 80°C.

Following the method of Elvert et al. (2003) TLE was afterwards polarized with 1ml KCl (0.1mol) and the neutral fraction was extracted by rinsing three times with hexane. Neutral fraction in the supernatant was separated, dried under a stream of $N_2$, and stored in the refrigerator for later analysis. We acidified the rest of the TLE with fuming hydrochloric acid to a pH of 1. The acid fraction was extracted by rinsing again three times with hexane. The acid fraction in the supernatant was separated and hexane dried under a stream of $N_2$. Then the acid fraction was methylated by adding 1ml Boron-Trifluoride (BF3) in MeOH (12-14%) and putting it in the oven for 1 hour at 60°C. Afterwards the mFA fraction was polarized with KCl (0.1mol) and transferred in 2ml vials by rinsing three times with hexane. The mFAs were quantified with a Trace Ultra gas chromatograph (GC) equipped with a flame ionization detector (FID) (Thermo Scientific, Waltham, MA, USA). The carrier gas (helium) had a constant flow of 1.2ml per minute and the GC-FID was set to splitless mode. Detector temperature was 320°C and the samples (dissolved in hexane) were injected by 300°C. The starting temperature of the oven was 50°C. The temperature was increased by 10°C per minute to 140°C. The temperature was held for 1 minute before it was increased up to 300°C. This temperature was held for 63 minutes.

To identify the fungal and bacterial markers, we used the Bacterial Acid Methyl Esters standard (BAME, Supelco Mix). For bacteria, it includes the mFAs C17:0 as general bacterial marker (Willers et al., 2015; Zelles, 1997), a-C-15:0 for gram-positive bacteria (Zelles, 1997; O`Leary and Wilkinson, 1988; Vestal and White, 1989) and C16:1ω9c for gram-negative bacteria (O`Leary and Wilkinson, 1988; Vestal and White, 1989; Zelles, 1997). The membrane fatty acid C18:2ω6c was used as a marker for saprotrophic fungi (Andersen et al., 2010; O`Leary and Wilkinson, 1988; Sundh et al., 1997; Vestal and White, 1989; Zelles, 1997). All these markers are valid for overall membrane fatty acids and can be used to detect different microbial groups in soil

(Bajerski et al., 2017; Finotti et al. 1993; Piotrowska-Seget and Mrozik 2003). Quantification of the mFAs was done using the internal standard, C19:0 mFA, after correcting for the methyl group, added during methylation reaction.
To combine the results of both methods and test whether it was possible to correlate the mFA results of different laboratories, we also tested method B in the Zwarte Beek site. The correlation of both methods showed the same range of absolute quantities for all hydrological regimes and depth (Table C3). In addition, the ratio of fungal-derived and bacterial-derived mFA (F:B) showed the same pattern (Table C4). These results suggested that the results of both methods could be combined.

### 4.3.3. Statistical analysis

We calculated variance and standard deviation (SD) of stable isotope values of the three hydrological regimes. We did a t test to analyze if microbial-derived mFAs are in the drained peat layers of the same population as the values of the undrained and rewetted sites (H0 – drained, rewetted and undrained quantities are of the same population, $p \leq 0.05$). To test whether stable isotope values and mFAs differed between drained, rewetted and undrained sites and with depth, we used two factor analysis of variance (ANOVA; $\alpha=0.05$) with hydrological regime and soil depth as fixed factors; separated for the different time classes (Girden, 1992). We calculated the statistical distribution of both stable isotopes, grouped by the rewetting time and separated for each hydrological regmie and depth.
In addition, we calculated the Pearson correlation coefficient (R) for the nitrogen stable isotopes values and the different groups of microbial-derived mFAs.
All analyses were done using R (version 1.0.153).

## 4.4. Results

### 4.4.1. Carbon-to-Nitrogen ratio

The C:N ratios for the deepest sampling depths (45–50cm) were similar (mean (± SD) = 17±3) between the hydrological regimes (Table C5), indicating similar degree of decomposition across the respective fens. The C:N ratio of the 0-5cm layer was highest in the undrained sites (21±5), intermediate in the rewetted sites (17±4), and lowest in the drained sites (13±2). The C:N ratio of the top layer of the rewetted sites increased from 14±3 to 22±2 with increasing time since rewetting (Table C5).

### 4.4.2. Stable nitrogen isotope bulk values

For the deepest sampling depth (45–50cm), $\delta^{15}N$ values were similar (-1.2‰±1.0 of dry weight) between the hydrological regimes (Figure 4.1, Table C2).

However, $\delta^{15}N$ values followed different depth trends under different hydrological regimes and were significantly different for the hydrological regimes ($p<0.01$) as well as for the interaction between depth and the hydrological regime ($p<0.01$, Table 4.2). In undrained sites, the $\delta^{15}N$ values were lowest in the 0-5cm peat layer (−1.2‰±0.8) and slightly increased with depth (Figure 4.1a, Table C2). In contrast, in drained sites, $\delta^{15}N$ values were highest in the 0-5cm peat layer (2.8‰±0.8; Table C1) and decreased with depth (Figure 4.1a). The $\delta^{15}N$ values of rewetted sites were in between the values of undrained and drained sites (2.2‰±1.0). The δ15N values of rewetted sites increased with depth (Figure 4.1a).

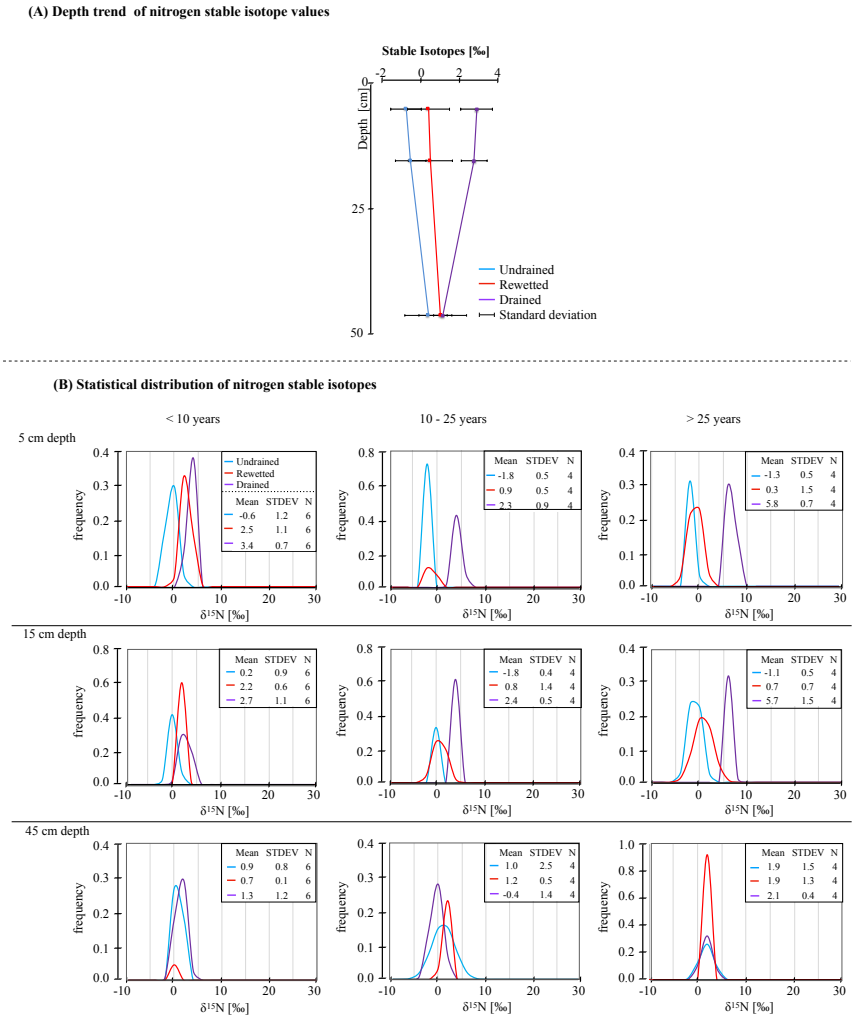


**Figure 4.1:** *Nitrogen stable Isotope values (A) average depth pattern, (B) statistical distribution of values (groups of fens are assigned to the time of rewetting of the respective rewetted fen), separated by the hydrological regime (undrained (blue), drained (purple), rewetted (red)).*

### 4.4.3. Stable carbon isotope bulk values

Similar to the $\delta^{15}N$ values, $\delta^{13}C$ values showed also very similar values (−28.3‰±0.6) in the 45-50cm peat layer (Figure 4.2, Table C2).

However, and in contrast to the $\delta^{15}N$ depth trends, the $\delta^{13}C$ values followed a similar trend with depth in all hydrological regimes and were significantly different for different depths ($p<0.01$, Table 4.2) in all three hydrological regimes. $\delta^{13}C$ values were lowest in the 0-5cm peat layer and increased with depth (Figure 4.2). Overall, $\delta^{13}C$ values were lowest at the undrained sites (−29.6‰±0.5) and highest at the drained sites (−28.8‰±0.8). The $\delta^{13}C$ values of the rewetted sites were also in between the values of the drained and undrained sites (−29.1‰±0.5) and did not differ significantly between hydrological regimes ($p=0.09$; Tables 4.2).

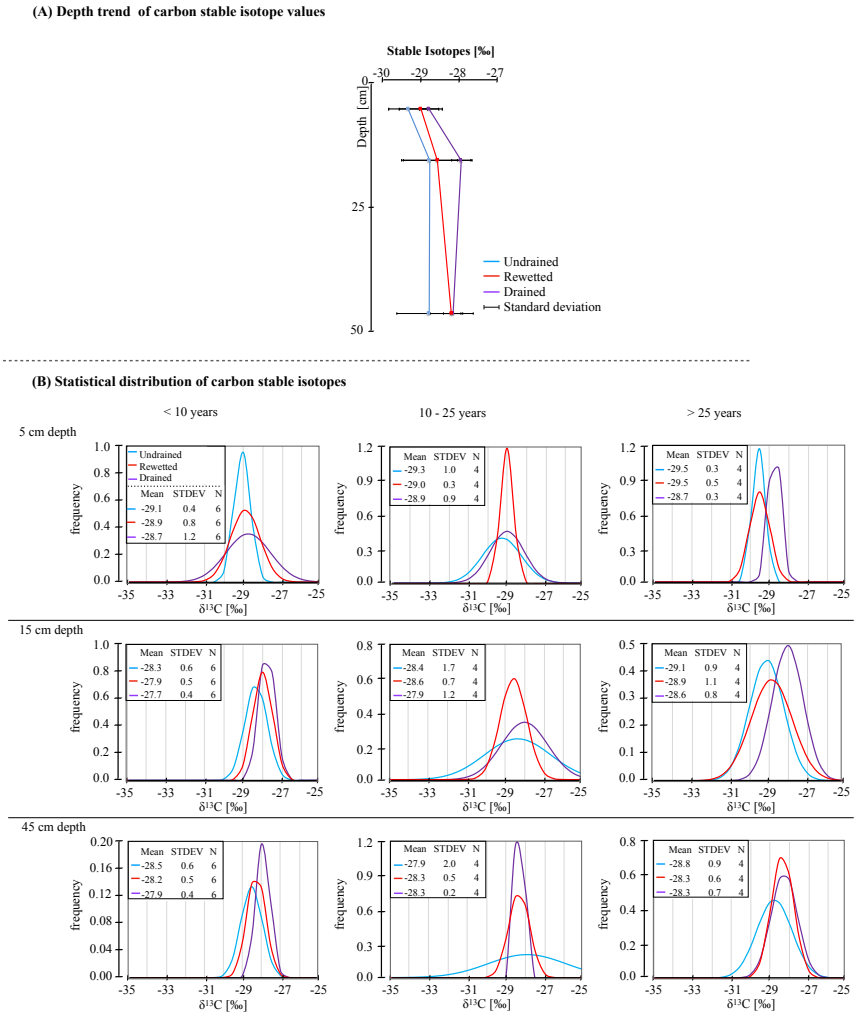


**Figure 4.2:** *Carbon stable Isotope values (A) average depth pattern, (B) statistical distribution of values (groups of fens are assigned to the time of rewetting of the respective rewetted fen), separated by the hydrological regime (undrained (blue), drained (purple), rewetted (red)).*

### 4.4.4. Stable isotope bulk values versus time since rewetting

We found a clear link between time since rewetting and stable isotope patterns for $\delta^{15}N$ values, with the depth profile of the longest rewetting class nearly similar to the depth profile of undrained sites (Figure 4.1/ 4.2). However, the latter was only marginally seen for $\delta^{13}C$ (Figure 4.2).

The $\delta^{15}N$ values at 0-5cm depth of undrained and drained sites differed significantly from each other between hydrological regimes, depth and for a combination of both ($p_{hydrological} < 0.00$, $p_{depth} = 0.02$, $p_{combination} = 0.00$; Table 4.2).

In the class up to 10 years of rewetting, the $\delta^{15}N$ values of rewetted sites (2.6‰±1.3) were between the $\delta^{15}N$ values of drained (3.4‰, ±0.7) and undrained sites (-0.6‰±1.2; Figures 4.1, Tables 4.2 and C2). The $\delta^{13}C$ values were similar at this depth across hydrological regimes (-29.2‰±0.6; p=0.07; Figure 4.2, Tables 4.2 and C2).

In the class of 10–25 years of rewetting, the stable isotope values in 0-5cm depth of rewetted sites ($\delta^{15}N$=0.9‰±0.5; $\delta^{13}C$=-29.0‰±0.3) shifted toward those of undrained sites ($\delta^{15}N$=-1.8‰±0.5; $\delta^{13}C$=-29.3‰±0.7; Figures 4.1 and 4.2, Table C2).

For the class of more than 25 years of rewetting, the $\delta^{15}N$ values of rewetted sites (-0.3±0.9) differed from those of drained sites (2.6‰±0.7) and were in the same range of the values of the undrained sites (-1.7‰±0.5; Figures 4.1 and 4.2). The detected differences were significantly different for $\delta^{15}N$ values, dependent on depth (p=0.03) and the hydrological regimes (p<0.01). Additionally, the $\delta^{13}C$ values of rewetted sites (-29.5‰±0.5) were equal to those of undrained sites (-29.5‰±0.3; Figure 4.2). The $\delta^{13}C$ values were not significant different for depth nor for the hydrological regime (Table 4.2).

**Table 4.2:** *F-, and p-values from a two factor ANOVA of all investigated sites for stable isotope ratios (nitrogen, carbon), with hydrological regime and soil depth as main factors; different time classes (<10, 10-25, > 25 years) were treated as independent; stable isotopes (ST); hydrological regime (HR); bold=significance (F - critical < F; p ≤ 0.05)*

| ST | Factors | <10 | | | 10-25 | | | >25 | | | all | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | p | F | F-crit | p | F | F-crit | p | F | F-crit | p | F | F-crit |
| $\delta^{15}N$ | | | | | | | | | | | | | |
| | depth | **0.02** | **4.2** | **3.2** | 0.46 | 0.8 | **3.6** | **0.03** | **4.3** | **3.6** | 0.58 | 0.5 | 3.1 |
| | HR | **0.00** | **28.5** | **3.2** | **0.00** | **22.5** | **3.6** | **0.00** | **19.3** | **3.6** | **0.00** | **49.6** | **3.1** |
| | Interaction of both | **0.00** | **6.7** | **2.6** | **0.01** | **9.2** | **2.9** | **0.01** | **4.7** | **2.9** | **0.00** | 12.0 | 2.5 |
| $\delta^{13}C$ | | | | | | | | | | | | | |
| | depth | 0.00 | 9.4 | 3.2 | 0.11 | 2.4 | 3.4 | 0.14 | 2.2 | 3.6 | 0.00 | 11.3 | 3.1 |
| | HR | 0.07 | 2.8 | 3.2 | 0.90 | 0.1 | 3.4 | 0.26 | 1.5 | 3.6 | 0.09 | 2.5 | 3.1 |
| | Interaction of both | 0.98 | 0.1 | 2.6 | 0.93 | 0.2 | 2.7 | 0.97 | 0.1 | 2.9 | 0.99 | 0.7 | 2.5 |

### 4.4.5. Microbial-derived mFA quantities

Across all sites total microbial-derived mFAs decreased from 30.97µg $g^{-1}$±8.7 in the 0-5cm peat layer to 3.91µg $g^{-1}$±2.3 in the 45-50cm peat layer, with very similar patterns across hydrological regimes (Figure 4.3, Table C6). This corresponds to a reduction of 87%. The mFA quantities differed significantly between different hydrological regimes ($p<0.01$; Table 4.3).

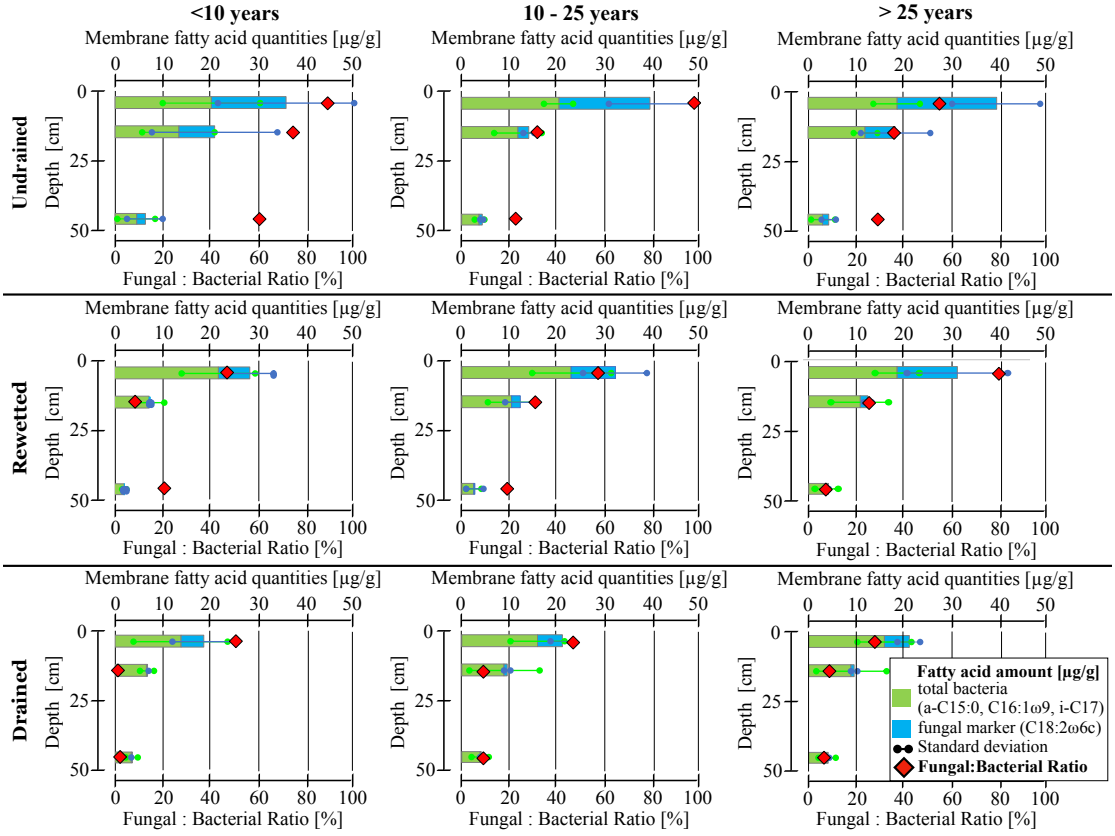


**Figure 4.3:** *Membrane fatty acid quantities (fungal- (blue) and bacterial- (green)) and Fungi-to-Bacteria Ratio (red diamonds), separated by the hydrological regime (undrained, drained, rewetted) and time since rewetting (<10 years (n=6), 10-25 years(n=4), >25 years (n=3))*

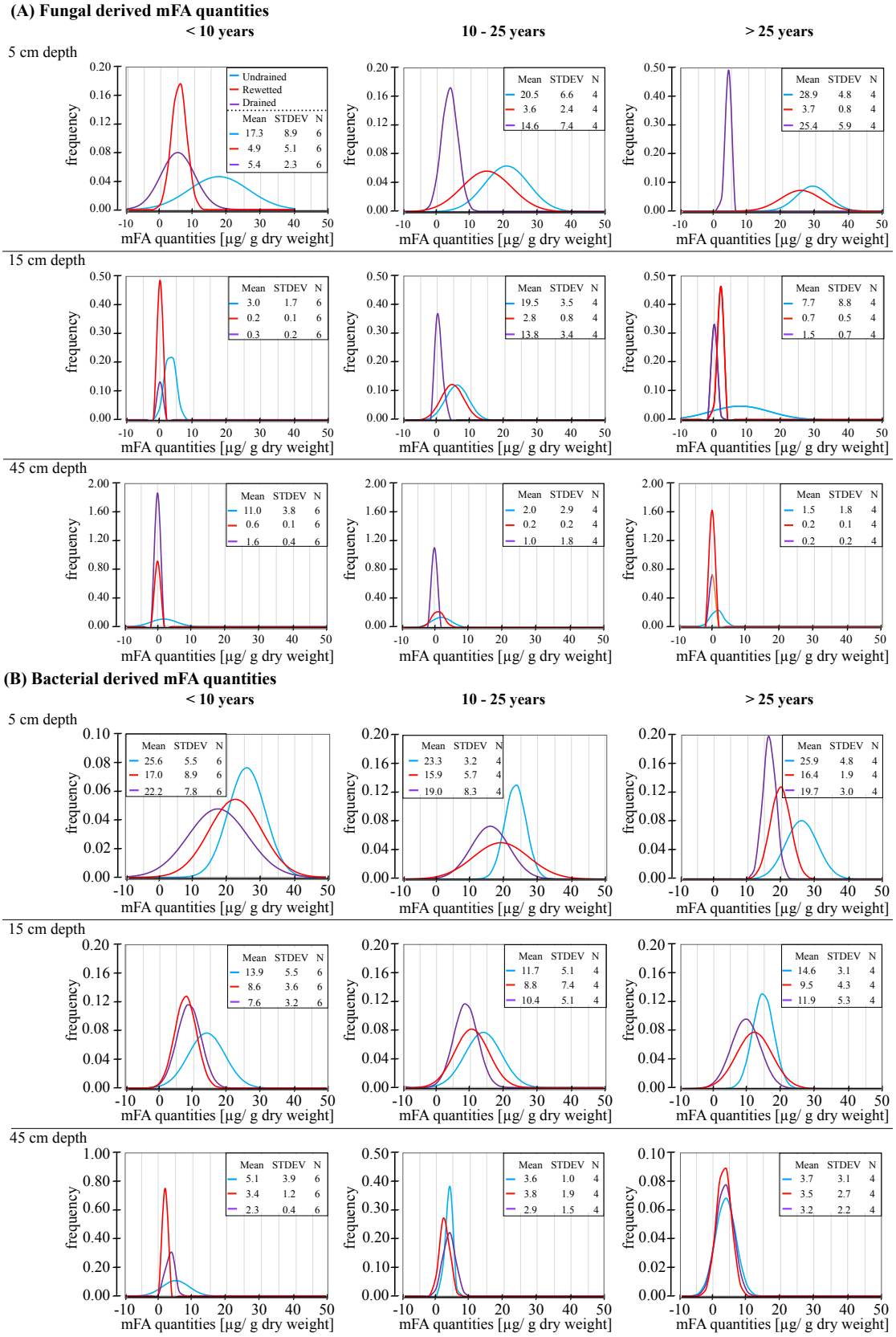


**Figure 4.4:** *Distribution of membrane fatty acids of (A) fungal-derived & (B) bacterial-derived membrane fatty acid quantities, (groups of fens are assigned to the time of rewetting of the respective rewetted fen), separated by the hydrological regime (undrained (blue), drained (purple), rewetted (red)).*

Fungal-derived mFAs decreased significantly ($p<0.01$; Table 4.3) with depth, from 11.62±10.5µg $g^{-1}$ to 0.55µg $g^{-1}$±1.7 (Table C5). This corresponds to a reduction of 95%.

Bacterial-derived mFAs were significantly ($p<0.01$, Table 4.3) reduced by 83% with increasing depth. Quantities ranged from 19.35µg $g^{-1}$±8.7 in the 0-5cm peat layer to 3.36µg $g^{-1}$±2.3 in the 45-50cm peat layer (Table C6).

With respect to different hydrological regimes, undrained sites had the highest quantities of microbial mFAs 41.33µg $g^{-1}$±9.0 in the 0-5cm peat layer. In contrast, drained sites had the lowest microbial-derived mFAs (21.71µg $g^{-1}$±5.6) in the 0-5cm peat layer (Table C6). The mFAs of rewetted sites ranged between those of drained and undrained sites (29.86µg $g^{-1}$±6.9; Table C6).

**Table 4.3:** *F-, and p-values from a two factor ANOVA of all investigated sites for membrane fatty acids (bacteria, fungi), with the hydrological regime and soil depth as the main factors; different time classes were treated as independent; hydrological regime (HR); bold = significance (F - critical < F; p ≤ 0.05)*

| mFAs | Factors | <10 | | | 10-25 | | | >25 | | | all | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | p | F | F-crit | p | F | F-crit | p | F | F-crit | p | F | F-crit |
| bacteria | | | | | | | | | | | | | |
| | depth | **0.00** | **51.7** | **3.2** | **0.00** | **32.9** | **3.4** | **0.00** | **52.8** | **3.6** | **0.00** | **137.8** | **3.1** |
| | HR | **0.02** | **4.8** | **3.2** | 0.40 | 0.9 | 3.4 | **0.02** | **4.98** | **3.6** | **0.00** | **8.6** | **3.1** |
| | Interaction of both | 0.30 | 1.3 | 2.6 | 0.54 | 0.8 | 2.7 | 0.28 | 1.38 | 2.9 | **0.04** | **2.67** | **2.5** |
| fungi | | | | | | | | | | | | | |
| | depth | 0.00 | 7.5 | 3.2 | 0.00 | 24.2 | 3.4 | 0.00 | 38.7 | 3.6 | 0.00 | 42.2 | 3.1 |
| | HR | 0.00 | 6.6 | 3.2 | 0.01 | 6.5 | 3.4 | 0.00 | 15.6 | 3.6 | 0.00 | 20.8 | 3.1 |
| | Interaction of both | 0.33 | 1.2 | 2.6 | 0.02 | 3.3 | 2.7 | 0.00 | 6.8 | 2.9 | 0.00 | 5.8 | 2.5 |
| microbes | | | | | | | | | | | | | |
| | depth | **0.00** | **26.1** | **3.2** | **0.00** | **39.2** | **3.4** | **0.00** | **67.7** | **3.6** | **0.00** | **101.9** | **3.1** |
| | HR | **0.00** | **7.0** | **3.2** | **0.03** | **4.1** | **3.4** | **0.00** | **15.2** | **3.6** | **0.00** | **19.7** | **3.1** |
| | Interaction of both | 0.44 | 1.0 | 2.6 | 0.12 | 2.0 | 2.7 | **0.00** | **5.7** | **2.9** | **0.00** | **4.8** | **2.5** |

With respect to hydrological regimes, fungal-derived mFAs showed the largest differences, especially in the 0-5cm peat layer (Figure 4.3). At this depth, fungal-derived mFAs were highest in the undrained sites (20.27µg $g^{-1}$±11.5) and lowest at the drained sites (5.61µg $g^{-1}$±4.0; Table C6). This means a significant reduction of 74% in fungal-derived mFAs between drained and undrained sites ($p<0.01$, Table C9). Additionally, bacterial-derived mFAs in the 0-5cm peat layer were significantly higher in undrained (21.06µg $g^{-1}$±6.5) sites than in drained sites (16.43$g^{-1}$µg±7.2; Table C6).

With increasing time since rewetting, mFAs in rewetted sites approached the abundance found in undrained sites in the 0-5cm peat layer (Figure 4.3). With less than 10 years of rewetting, microbial-derived mFAs (28.93µg $g^{-1}$±6.4; Table C7) were not

significantly different from those of drained sites (20.06µg $g^{-1}$±8.4, p=0.98; Tables C7 and C9) nor from undrained sites (36.03µg $g^{-1}$±12.3, p=0.06; Tables C7 and C9). With more than 25 years of rewetting, the quantities of microbial-derived mFAs (43.24µg $g^{-1}$±6.7 Table C7) were almost as high as those of undrained sites (48.25µg $g^{-1}$±6.1; Figure 4.5, Table C7). In this class, quantities were significantly different from drained (p=0.15) but not from undrained sites (p=0.04; Table C9).

Our results showed a higher F:B of the upper peat layers in undrained than drained sites. Whereas in the 0-5cm peat layer the F:B was 49 at undrained sites, and only 24 at drained sites and 31 at rewetted sites (Table C8). With increasing rewetting time, fungal-derived mFAs shifted towards the quantities of undrained sites. In the class of <10 years of rewetting, F:B accounted for 23 in the 0-5cm peat layer (Table C8). This increased to 40 with more than 25 years of rewetting (Table C8).

We found that fungal-derived mFAs decreased and $\delta^{15}N$ values increased from undrained to rewetted to drained in the 0-5cm peat layer. Fungal-derived mFAs and $\delta^{15}N$ values were significant negative correlated (r=−0.7; Figure 4.5).

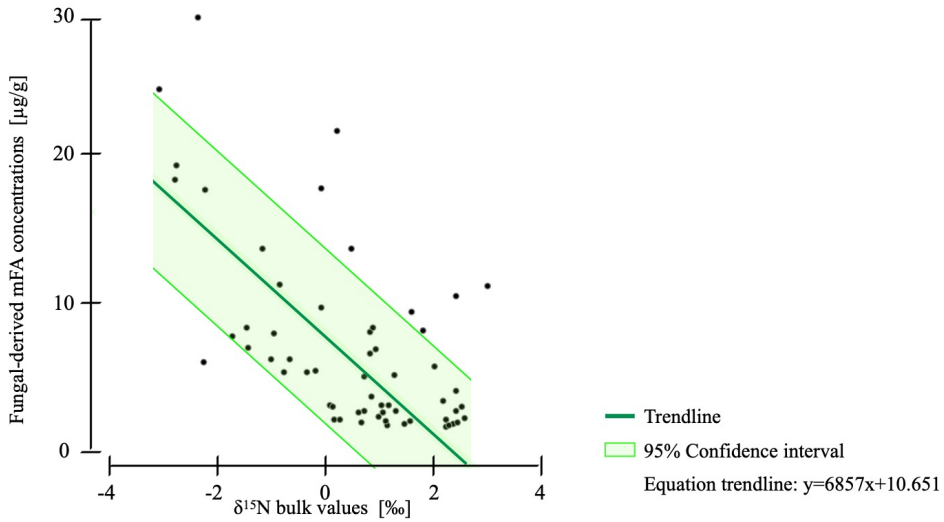


**Figure 4.5:** *Correlation between nitrogen stable isotopes values and fungal-derived membrane fatty acids (mFA) of all sites and all hydrological regime*

## 4.5. Discussion

### 4.5.1. Carbon-to-Nitrogen ratios across hydrological regimes

The C:N ratios of the undrained fen sites were similar to ratios reported by Bridgham et al. (1998). The C:N ratio is high in the top layer of undrained fens as a consequence of low N values in fen vegetation and low rates of decomposition (Malmer and Horn, 1984). The values for drained sites showed lower C:N ratios, most likely due to higher

decomposition rates and as a consequence of preferential C loss compared to N (Malmer and Horn, 1984). For rewetted sites, the ratio increased depending on the time since rewetting, which could be linked to the decreasing decomposition rates of plant residues (Malmer and Horn, 1984).

### 4.5.2. Stable isotope bulk values across hydrological regimes

The $\delta^{15}N$ and $\delta^{13}C$ values of the 45–50cm peat layers were similar across hydrological regimes. This result indicates a relatively undisturbed deeper peat layer with low metabolic rates for all investigated sites (Artz, 2013; Asada et al., 2005).

In contrast, $\delta^{15}N$ values of the upper peat layers (0–5cm and 15–20cm) differed significantly between the hydrological regimes. They were lowest in the undrained sites and significantly higher ($p < 0.01$) in drained sites. These results are in line with those from Denk et al. (2017) and Groß-Schmölders et al. (2020). In bogs, Groß-Schmölders et al. (2020) found no depth trends in the water-saturated peat layers of undrained and rewetted sites, while, at drained sites, $\delta^{15}N$ values changed with depth. The depth patterns in ombrotrophic peatlands contrast with the drained and rewetted sites of the groundwater fed fens investigated here. For ombrotrophic drained sites, $\delta^{15}N$ values increased with depth down to a $\delta^{15}N$ turning point and decreased below that point down to the onset of the anaerobic peat layer. In fens studied here, $\delta^{15}N$ decreased at the drained sites and showed only slightly increasing trends at water-saturated sites (undrained and rewetted). Such differences in ombrotrophic and minerotrophic sites could be driven by the different microbial abundances (see below in Section 4.5.3).

For $\delta^{13}C$, we found no difference in depth trends between three hydrological regimes, as the $\delta^{13}C$ values increased with depth for all hydrological regimes. This observation is in line with the findings of other studies that also reported increasing $\delta^{13}C$ values with depth in peatland soils (Krüger et al., 2015, Nadelhoffer and Fry, 1988). We saw the highest $\delta^{13}C$ values in drained sites and the lowest in undrained sites. With increasing drainage, recalcitrant and $\delta^{13}C$-depleted substrates such as lignin are also processed, which leads to increased mobilization of lighter $^{12}C$ and further increasing $\delta^{13}C$ values in the remaining bulk soil with depth (Lerch et al., 2011). Furthermore, Boström et al. (2007) assumed that the $^{13}C$ enrichment in drained peat soils with depth is a result of the increased contribution of microbial-derived C with depth (see below in Section 4.5.3).

### 4.5.3. Microbial-derived mFA quantities and composition dependent on the hydrological regime

Overall, the highest quantities of total microbial-derived and fungi-derived mFAs were found in the 0-5cm peat layers of the undrained sites. This is in line with the findings of Fisk et al. (2003), who found highest microbial abundance in sites with highest water saturation. A plausible explanation is the higher quantity and quality (less decomposed) of bulk C in combination with low N supply in the undrained sites, which favors higher fungal metabolic rates (Fisk et al., 2003; Scanlon and Moore, 2000).

While bacterial-derived mFAs changed less for different hydrological regimes in the 0–5cm peat layer, fungal-derived mFAs were significantly lower in drained sites compared to undrained sites. This is presumably related to the different ecological niches and adaptability to changing conditions of fungi vs. bacteria (Gilbert et al., 1998; Winsborough and Basiliko, 2010). Fungal metabolic processes may be more important than bacterial metabolic processes in the uppermost part of undrained minerotrophic fens (Thormann, 2005). Their abundance is closely linked to environmental conditions, such as moisture, O and N availability. Therefore, fungi are far more sensitive to hydrological changes in the 0–5cm peat layers than bacteria, mainly because of the nitrogen supply (Thormann, 2005). With a decreasing C:N ratio in drained sites, fungal abundance is known to decrease, whereby bacteria have a competitive advantage over fungi in these areas (Thormann and Bayley, 1997). Hence, fungal metabolism and abundance decreased with increasing drainage corresponding to a decreased C:N ratio in the 0–5cm peat layers in drained minerotrophic fens (Gilbert et al., 1998; Winsborough and Basiliko, 2010).

In the rewetted sites, the water table increased again. Therefore, with changing environmental conditions (increasing C:N ratio, moss growth), bacteria have less competitive advantages over fungi and fungal abundance and metabolism could rise in the 0–5cm peat layer (Figure 4; Fenner et al., 2005; Thormann, 2005; Winsborough and Basiliko, 2010).

### 4.5.4. Stable isotopes reflect microbial abundance – fungi make the difference

We found parallel changes between microbial-derived mFAs and stable isotope values, especially for $\delta^{15}N$ values. With lower water tables, $\delta^{15}N$ values increased, and microbial-derived mFAs decreased in the upper peat layers. The reason for such a

parallel trend is that isotope fractionation is shaped by microbial metabolic processes in the soil, which are more present in aerobic conditions (Dijkstra et al., 2006; Dröllinger et al., 2019; Kohl et al., 2015).

For bogs, previous studies have shown that microbial metabolism is a driver of stable isotope values. For $\delta^{13}C$, Krüger et al. (2015) stated that microbial metabolic processes increase $\delta^{13}C$ values with depth in drained peatlands. Kohl et al. (2015) reported the same trend and linked it to a shift in the dominant microbial groups. Each microbial group focuses on a specific metabolic process and uses specific substrates, which leads to a typical fractionation rate for each microbial group. Hence, a shift from fungal metabolism to bacterial metabolism will also lead to changes in stable isotope values (Kohl et al., 2015).

For $\delta^{15}N$ values, a correlation between increasing $\delta^{15}N$ values with drainage was reported to be due to changes in microbial metabolism (Carrell et al., 2019). Moreover, Gundale et al. (2011) hypothesized that increasing $\delta^{15}N$ values in drained peatland sites were the result of higher recycling rates of N and less incorporation of $^{14}N$ by microorganisms (and thus preferential release of the lighter $^{14}N$).

We found evidence that a changing F:B could also be responsible for the specific $\delta^{15}N$ values in our study sites. The pattern of simultaneously changing $\delta^{15}N$ values and microbial abundance was also observed in fens studied by Preston and Basiliko (2015). They reported that the $\delta^{15}N$ pattern was linked more to the microbial community composition (e.g., the relative abundance of different microbial groups) than to overall microbial activity. This observation fits with the correlation between a specific $\delta^{15}N$ depth trend and a changing F:B in drained bogs (Groß-Schmölders et al., 2020).

Therefore, we suggest that the influence of fungi on cycling processes is highest under undrained, wet conditions in our study. Fungi are a prominent microbial group in the 0–5cm peat layers of undrained fens as decomposers of primary plant material under aerobic conditions (Tfaily et al., 2014; Thormann 2005). The combination of naturally low $\delta^{15}N$ values in primary plant material and low demand (and, therefore, low recycling rate) of N for fungal-induced recycling processes leads to a low enrichment of $\delta^{15}N$ in fungal-dominated layers (Strickland and Rousk, 2010; Thormann et al., 2004; Wallander et al., 2009). Fungi are known to be especially vulnerable to changing substrate quality and, therefore, show clearer reactions to changing environmental conditions than other microbial groups (Peltoniemi et al., 2009; Preston and Basiliko, 2015), especially at higher N levels (Carrell et al., 2019). Brunner et al. (2013) reported

that bacterial-forced cycling increases with drainage in fens. Bacterial metabolism is generally faster than fungal metabolism and requires more available N (Brunner et al., 2013, Tunlid et al., 1992). Hence, fungi lose their competitive advantage with drainage and lower C:N ratio, and a shift to bacterial-induced cycling occurs, resulting in increased $\delta^{15}N$ values in the upper peat layer with drainage (Rousk and Bååth, 2007; Winsborough and Basiliko, 2010).

### 4.5.5. Reestablishment of undrained conditions with time

With increased rewetting time, microbial-derived mFAs and stable isotope values of rewetted sites shifted towards the values of undrained sites. This result is in line with the findings of Urbanovà and Bàrta (2020), who also reported a reestablishment of microbial communities after a longer period of rewetting.

With increased time since rewetting, fungal mFAs and, with them, $\delta^{15}N$ values in rewetted sites were no longer significantly different from those of undrained sites but differed significantly from those of drained sites. Hence, with increasing rewetting time, the microbial community structure and dominant metabolic processes changed and shifted towards the community composition of undrained sites, indicating a recovery of ecosystem functioning (Urbanovà and Bàrta, 2020).

However, we observed not at all rewetted sites a reestablishment of the stable isotope values and microbial-derived mFAs towards those of undrained sites. Differences in soil organic matter quantity and quality, as discussed by Emsens et al. (2020) and Fenner et al. (2005), could explain this. A major change in soil organic matter quality with drainage could impede the reestablishment of microbial communities that are typically found in undrained sites (Peltoniemi et al., 2009). Because stable isotope values depend on specific microbial metabolic processes, the absence of certain microbial groups and a low overall microbial community size will lead to values different from those of undrained sites, even after decades of rewetting (Emsens et al., 2020).

## 4.6. Conclusions

By combining microbial-derived mFA and stable isotope values ($\delta^{15}N$, $\delta^{13}C$) analyses, we were able to differentiate between the hydrological regimes (undrained, drained, and rewetted) of fens. With increasing time since rewetting, the stable isotope values of rewetted fens approached those of undrained sites.

The combination of stable isotopes and microbial mFAs indicated that changing $\delta^{15}N$ values, in particular, were a result of a change in microbial communities.

In summary, our findings support our hypotheses

(i) that stable isotope values, especially $\delta^{15}N$, differ between different hydrological regimes,

(ii) that mFA profiles change with the hydrological regime in parallel to $\delta^{15}N$ values, and

(iii) that $\delta^{15}N$ values in peat are negatively correlated to the fungal-derived mFA quantities.

Thus, we conclude that soil $\delta^{15}N$ values are valid markers for microbial metabolic processes and the hydrological regime of fens. Furthermore, we found that time since rewetting was the primary driver for restoration success of the microbial community in the investigated sites, and thus biomarkers and bulk stable isotope values are suitable indicators of rewetting success.

# 5

# Conclusion

In this thesis, we were able to strengthen the idea of a close link between stable isotope depth patterns and peatland hydrology via the investigation of the relative microbial proportion. Hence, we could successfully show that stable isotopes are a reliable tool to assess peatland degradation and restoration. The conclusions regarding typical depth trends of stable isotope bulk values ($\delta^{13}C$, $\delta^{15}N$) are summarized in **Chapter 5.1**. The main results of a connection between stable isotope bulk values ($\delta^{13}C$, $\delta^{15}N$) and specific microbial groups (fungi, acidobacteria, gram-positive, gram-negative bacteria) with respect to peatland hydrology are summarized in **Chapter 5.2**. The main conclusions for specific trends regarding nutrient and hydrological regimes are summarized in **Chapter 5.3**. **Chapter 5.4** explores possible future investigations that would support this approach to assessing peatland hydrology and further applications for stable isotope depth trends.

## 5.1. Stable isotopes indicative of hydrological regimes of peatlands

Our results confirm the hypothesis that stable isotope depth trends ($\delta^{13}C$, $\delta^{15}N$) are significantly different in different hydrological states, independent of the nutrient status. For nutrient-poor peatlands, distinct differences were found in all five investigated peatland sites corresponding to the hydrological regime (**Chapter 2 and 3**). Moreover, the 14 investigated nutrient-rich sites showed significant differences between the stable isotope depth trends ($\delta^{13}C$, $\delta^{15}N$) of undrained, drained, and rewetted sites (**Chapter 4**). Our studies revealed differences between the depth trends of both stable isotopes in accordance with the nutrient status, and we discovered that nitrogen stable isotope bulk values show different trends in nutrient-poor and nutrient-rich sites.

For the nutrient-poor sites, the bulk values of nitrogen showed no depth trend in undrained sites. However, the values of all investigated drained sites showed a distinct depth pattern with an increasing trend from the surface down to a peak in the mesotelm, followed by decreasing $\delta^{15}N$ bulk values. From the beginning of the anaerobic catotelm downwards, the $\delta^{15}N$ bulk values showed no depth trend, just as the undrained sites. Likewise, there was no depth trend visible for the rewetted layers in the layer build-up during rewetting (**Chapter 2**). In contrast, our research in nutrient-

rich sites, described in **Chapter 4**, revealed a slightly increasing trend for $\delta^{15}N$ bulk values with depth in the undrained sites and a decreasing trend downwards for the drained sites. Here, rewetted sites showed $\delta^{15}N$ bulk values in between the values of drained and undrained sites.

For carbon stable isotopes, all investigated sites, independent of the nutrient status, expressed increasing bulk values with depth (**Chapter 3 and 4**). For undrained sites, the increase, especially for nutrient-poor sites, was less strong than for drained sites (**Chapter 2**).

The informative value for the two stable isotopes was different. In the case of carbon, the bulk values showed significant differences between different hydrological regimes in nutrient-poor sites (**Chapter 2 and 3**), but not in nutrient-rich sites (**Chapter 4**). In contrast, nitrogen stable isotope depth patterns show significant differences between the different hydrological statues for nutrient-rich and nutrient-poor sites (**Chapter 2 and 4**).

In addition, as described in **Chapter 3**, we could confirm our hypothesis of a persistence of the stable isotope depth trends ($\delta^{13}C$, $\delta^{15}N$) by the repeated sampling in two years at the same undrained, drained, and rewetted locations. We were also able to confirm stable isotope depth trends as indicators for ongoing drainage and, therefore, impaired soil functioning, for example as storage of carbon, in nutrient-rich fens. Furthermore, this study strengthens the hypothesis that $\delta^{15}N$ seems to indicate former drainage followed by rewetting processes.

## 5.2. Stable isotopes reflecting microbial abundance

To support our idea of switching microbial abundance as a key factor for specific isotope bulk values, we implemented the membrane fatty acid analysis for specific groups that are known to be common in peatlands (fungi, gram-positive bacteria, gram-negative bacteria, acidobacteria). The results revealed two main linkages:

1. A strong negative correlation of the FB with nitrogen stable isotope bulk values: In layers with a high FB, the bulk values of nitrogen stable isotopes were low compared to those with a low FB ratio (**Chapter 3 and 4**). As described in Chapter 3, this mechanism is mainly determined by two parameters. First, fungi are known to be decomposer of primary plant material, which is naturally low in $^{15}N$. Consequently, fungal abundance is highest in layers with a high amount of primary plant material, where the $\delta^{15}N$ bulk values are low. Second, the metabolism of fungi

is characterized by a low demand of nitrogen, which leads to less recycling and hence low values of $\delta^{15}N$ values in the bulk material (Figure 5.1).

2. A negative correlation of microbial abundance and carbon stable isotope bulk values (**Chapter 2 and 3**). In layers where $\delta^{13}C$ bulk values were lowest, the microbial-derived membrane fatty acid quantities were highest. This is also a result of microbial metabolism as microbes prefer to metabolize specific substrates that are high in $\delta^{13}C$. Hence, with a high microbial metabolism, a high amount of $\delta^{13}C$ is processed and lost, as in the example of the gaseous loss of enriched $CO_2$ (Figure 5.1, **Chapter 3**).

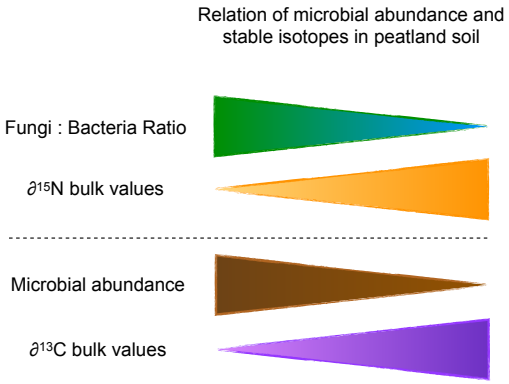


**Figure 5.1:** *Correlation of stable isotope bulk values and microbial communities in peatland soils*

## 5.3. Different trends in different peatlands?

The observed different trends in different hydrological and nutrient statuses become comprehensible, when we compare them to the mFA quantities. Firstly, with a look to the undrained sites there is no or just slightly increasing trends with depth visible. In these sites the water table is near the surface, which leads to waterlogged, anaerobic conditions. These environments are not favorable for microbial metabolism, hence only low values of microbial-derived membrane fatty acids are visible. Here, only small rates of metabolism take place, hence, stable isotope values also do not change considerably with depth because there is no fractionation during metabolism (Figure 5.2, **Chapter 3 and 4**). A small increase could be forced by small rates of microbial, mainly bacterial, degradation.

For drained sites, we saw differences in carbon and nitrogen stable isotope patterns. Whereas carbon isotopes show the same pattern in both nutrient conditions, the nitrogen stable isotopes showed different patterns (Figure 5.2).

Carbon stable isotope values show for both nutrient conditions an increasing trend with depth. These increasing $\delta^{13}C$ values are the result of the overall microbial metabolic

processes (**Chapter 3 and 4**). In the uppermost layers of the peat soil, the conditions are aerobic and favor microbial metabolism processes. As compounds, which are naturally enriched in $\delta^{13}C$ as glucose, pectin, and hemicellulose, are initially processed, a high gaseous loss of $\delta^{13}C$ take place. With increasing depth, recalcitrant, $\delta^{13}C$-depleted substrates such as lignin are also processed, which leads to increasing mobilization of lighter $^{12}C$ and further increasing $\delta^{13}C$ values in the remaining bulk soil with depth (Figure 5.2, **Chapter 4**).

For $\delta^{15}N$, we saw different patterns in nutrient-poor and nutrient-rich sites. As shown in **Chapter 2 and 3**, in nutrient-poor sites, microbial-derived membrane fatty acids were highest in drained sites. These sites showed an interesting depth pattern for fungal- and bacterial-derived membrane fatty acids. The values of fungal-derived fatty acids were highest near the surface and decreased with depth. In contrast, bacterial-membrane fatty acid quantities were highest in the mesotelm of drained sites. We conclude that this is caused by the different ecological niches. Whereas fungi have a competitive advantage in aerobic, nutrient-poor conditions with a high amount of primary plant material, they are outcompeted by bacteria with increasing depth and changing conditions. As bacterial metabolism is characterized by a higher demand on nitrogen and lower fractionation, the $\delta^{15}N$ bulk values increase with depth in these sites, down to a turning point (Figure 5.2, **Chapter 2**). Acidobacterial-derived membrane fatty acid quantities increase significantly to the turning point. This supported our hypothesis because they are closely involved in nitrogen cycling and, therefore, able to increase $\delta^{15}N$ bulk values significantly (**Chapter 3**). Below the overall microbial metabolism decreases because the conditions become more anaerobic and are unsuitable for overall microbial metabolism.

In contrast, $\delta^{15}N$ values in nutrient-rich sites are decreasing downwards the drained profiles and are significantly higher in these sites than in the corresponding undrained sites. This is in line with a different composition of the abundant microbial groups. In the nutrient-rich sites especially, fungal abundance is highest in undrained sites and significantly decreases in drained sites. This is evidenced by the highest $\delta^{15}N$ bulk values in drained sites, with a low FB ratio (Figure 5.2). The reason for the different patterns in nutrient-poor and nutrient-rich sites is forced by the environmental conditions. As fungi outcompete bacteria in drained nutrient-poor sites, they become the most vulnerable group in nutrient-rich fens. Hence, in these sites, their abundance must be highest in the undrained sites (**Chapter 4**).

Summing up, the investigations within the scope of this thesis showed that information of peatland hydrology could be evaluated without a high need of expert knowledge by examining stable isotope bulk values. Undrained sites showed overall no significant depth trends while drained sites exhibit distinct patterns, which depend on the sites nutrient content (Figure 5.2).

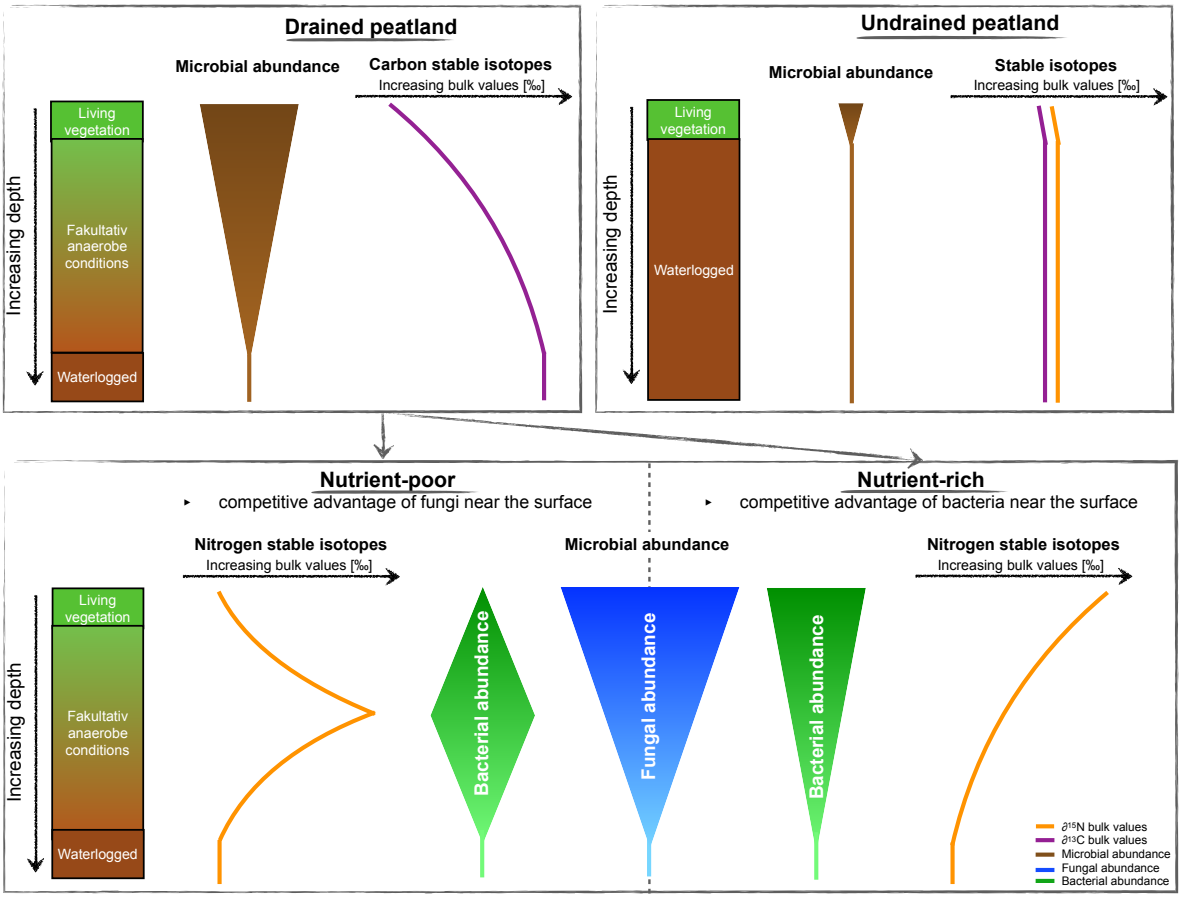


**Figure 5.2:** *Graphical conclusion of the correlation between microbial abundance and stable isotope depth pattern in peatland soils*

## 5.4 Outlook

Looking ahead into future implications, the findings of this thesis can provide a basis for creating a tool that enables a wider range of stakeholders to evaluate the hydrological regime of peatlands without the need of high expert knowledge. The received information about the renaturation success could then be used to adapt future renaturation actions in each restored peatland more efficiently. To get there, more investigations should be made to strengthen the presented correlation of stable isotopes and peatland hydrology. For example, the measurement of hydrogen-stable isotopes could give additional information about microbial activity as it is known that

microbes preferentially process lighter hydrogen from pore water and incorporate it. Hence, with a high microbial metabolism rate, hydrogen-stable isotope values of pore water should be depleted, whereas bulk values must be enriched (McAllan et al., 2017). Additionally, an analysis regarding the microbial activity would be interesting, like for example substrate-induced respiration analysis (SIR). SIR provides information about the current activity of different microbial groups (fungi-to-bacteria-ratio; Bailey et al., 2002), therefore, if a SIR would be done with samples of different hydrology and nutrient statuses, information about current microbial activity could confirm our investigated relationship between the abundance of mFAs, microbial abundance and therefore also to stable isotope bulk values. These analyses could strengthen our findings of specific microbial communities as a key to stable isotope depth patterns.

The results of this thesis should also be implemented in a larger model system to estimate biogeochemical processes in peat soils. For example, the Py-GC/MS data from Kristy Klein's partner project and further studies on vegetation assemblages and residues as well as the biogeochemical data from previous research studies (e.g. Krüger et al., 2016) can be combined to obtain an insight into how different parameters in peatland soils interact with each other during hydrological changes.

# A

# Supplemental Material: Switch from fungal to bacterial degradation in natural, drained and rewetted oligotrophic peatlands reflected in δ $^{15}$N and fatty acid composition

**Table A1:** *Carbon Stable Isotope Values for all investigated Peatlands; NM: Natural site Degerö Stormyr; DC: Drained site Degerö Stormyr; UR: Ursee Moor sites 1 and 2; Lakkasuo ombrotrophic, natural: ON; Lakkasuo ombrotrophic, drained: OD; Lakkasuo minerotrophic, natural: MN; Lakkasuo minerotrophic, drained: MD; BR: Breitlohmisse 1 – 4; RO: Rotmeer Moor 1-3*

| Depth [cm] | Degerö Stormyr | | | | | | Ursee Moor | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NM1 | NM2 | NM3 | DC1 | DC2 | DC3 | UR2-1 | UR-2-2 | UR2-3 | UR1-1 | UR1-2 | UR1-3 |
| 1 | -23.29 | -23.16 | -23.56 | -29.11 | -27.43 | -28.63 | -27.72 | -27.94 | -27.18 | -28.43 | -29.67 | -29.54 |
| 5 | -23.06 | -23.90 | -24.15 | -29.63 | -27.90 | -28.79 | -27.49 | -27.93 | -27.13 | -28.46 | -29.76 | -29.29 |
| 9 | -23.39 | -23.84 | -24.00 | -29.74 | -28.18 | -28.81 | -27.31 | -27.76 | -27.13 | -28.33 | -29.67 | -29.34 |
| 13 | -24.09 | -23.54 | -24.76 | -27.27 | -27.85 | -27.80 | -27.40 | -27.71 | -27.16 | -28.44 | -29.45 | -29.36 |
| 17 | -24.64 | -24.46 | -24.98 | -25.43 | -27.63 | -27.33 | | -27.56 | -26.96 | -28.12 | -28.39 | -29.52 |
| 21 | -24.01 | -23.88 | -25.09 | -25.11 | -27.13 | -27.76 | -26.95 | -27.31 | -27.18 | -27.81 | -27.98 | -28.92 |
| 25 | -24.23 | -24.05 | -24.56 | -25.26 | -25.94 | -26.79 | -27.04 | -26.50 | -27.98 | -27.50 | -27.57 | -28.31 |
| 29 | -24.06 | -24.61 | -24.58 | -25.69 | -25.31 | -25.63 | -27.25 | -26.26 | -27.13 | -27.41 | -27.71 | -28.09 |
| 33 | -23.76 | -24.41 | -24.31 | -25.10 | -25.26 | -25.59 | -26.14 | -26.18 | -27.39 | -26.77 | -27.74 | -27.58 |
| 37 | -23.88 | -23.82 | -24.12 | -26.94 | -25.34 | -25.40 | -25.56 | -25.21 | -27.06 | -26.66 | -26.75 | -27.78 |
| 41 | -22.84 | -23.63 | -23.80 | -26.17 | -25.58 | -24.98 | -25.29 | -25.23 | -26.56 | -25.96 | -26.65 | -27.41 |
| 45 | -22.96 | -24.06 | -24.08 | -25.89 | -26.05 | -25.18 | -24.72 | -24.67 | -25.86 | -26.29 | -26.18 | -26.37 |
| 49 | -23.26 | -24.85 | -23.32 | -26.90 | -26.98 | -25.79 | -25.22 | -25.53 | -25.59 | -26.04 | -26.58 | -26.11 |
| 53 | -24.15 | -24.62 | -24.20 | -26.21 | -26.35 | -25.43 | -25.48 | -23.69 | -25.38 | -26.82 | -26.42 | -26.04 |
| 57 | -24.00 | -24.86 | -24.02 | -26.81 | -26.73 | -26.09 | -25.19 | -25.54 | -25.14 | -27.00 | -26.51 | -25.67 |
| 61 | -22.62 | -24.34 | -26.11 | -26.58 | -26.88 | -25.77 | -24.93 | -24.54 | -25.62 | -27.09 | -26.70 | -25.83 |
| 65 | -23.70 | -24.54 | -24.08 | -26.92 | -26.78 | -26.28 | -25.95 | -25.49 | -25.52 | -27.81 | -26.77 | -26.29 |
| 69 | -24.09 | -23.98 | -24.63 | -27.09 | -27.10 | -26.70 | UR2-1 | UR-2-2 | UR2-3 | -28.43 | -29.67 | -29.54 |
| 73 | -24.64 | -24.93 | -24.44 | -26.89 | -27.05 | -26.78 | -27.72 | -27.94 | -27.18 | -28.46 | -29.76 | -29.29 |
| 77 | -23.97 | -24.70 | -25.08 | -27.26 | -27.18 | -26.83 | -27.49 | -27.93 | -27.13 | -28.33 | -29.67 | -29.34 |
| 81 | | -25.79 | -25.27 | -27.37 | -26.18 | -26.44 | -27.31 | -27.76 | -27.13 | -28.44 | -29.45 | -29.36 |
| 85 | | -25.88 | -25.61 | -27.30 | -26.96 | -26.51 | -27.40 | -27.71 | -27.16 | -28.12 | -28.39 | -29.52 |
| 89 | | | | -27.05 | -27.53 | -27.31 | | -27.56 | -26.96 | -27.81 | -27.98 | -28.92 |
| 93 | | | | -26.36 | -27.46 | -26.77 | -26.95 | -27.31 | -27.18 | -27.50 | -27.57 | -28.31 |

| Depth [cm] | Lakkasuo, ombrotrophic | | | | | | Lakkasuo, minerothropic | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ON1 | ON2 | ON3 | OD1 | OD2 | OD3 | MN1 | MN2 | MN3 | MD1 | MD2 | MD3 |
| 1 | -27.18 | -27.91 | -26.38 | -31.04 | -30.36 | -30.73 | -29.13 | -29.67 | -28.24 | -30.14 | -30.33 | -30.73 |
| 5 | -27.63 | -26.98 | -26.02 | -28.18 | -29.85 | -28.19 | -29.31 | -29.60 | -29.22 | -29.75 | -30.03 | -28.19 |
| 9 | -27.09 | -27.38 | -26.57 | -27.41 | -27.60 | -27.54 | -29.30 | -29.87 | -29.14 | -28.65 | -30.00 | -27.54 |
| 13 | -27.22 | -28.47 | -26.08 | -26.60 | -26.40 | -25.92 | -28.87 | -29.58 | -28.66 | -27.76 | -28.70 | -25.92 |
| 17 | -27.01 | -28.10 | -26.49 | -25.98 | -25.88 | -25.84 | -27.47 | -27.77 | -28.06 | -28.04 | -28.04 | -25.84 |
| 21 | -27.01 | -27.76 | -27.71 | -25.23 | -26.20 | -25.67 | -27.96 | -27.57 | -28.18 | -27.33 | -27.98 | -25.67 |
| 25 | -26.81 | -26.34 | -28.22 | -25.44 | -25.68 | -25.81 | -28.25 | -27.35 | -27.83 | -27.82 | -27.77 | -25.81 |
| 29 | -27.63 | -25.29 | -28.36 | -25.45 | -26.52 | -24.67 | -28.14 | -27.52 | -27.58 | -27.39 | -27.76 | -24.67 |
| 33 | -26.46 | -26.50 | -26.31 | -24.85 | -25.97 | -24.67 | -28.06 | -27.77 | -27.70 | -27.61 | -27.94 | -24.67 |
| 37 | -26.28 | -26.30 | -27.95 | -25.11 | -26.71 | -24.53 | -28.01 | -27.69 | -27.78 | -27.72 | -28.00 | -24.53 |
| 41 | -26.28 | -25.59 | -27.98 | -24.99 | -26.75 | -25.82 | -28.06 | -27.25 | -27.82 | -28.22 | -27.55 | -25.82 |
| 45 | -26.11 | -25.96 | -27.32 | -26.14 | -27.36 | -26.91 | -27.89 | -27.59 | -27.92 | -28.26 | -27.87 | -26.91 |
| 49 | -25.67 | -26.21 | -25.58 | -27.45 | -26.47 | -26.25 | -28.11 | -27.96 | -28.08 | -27.94 | -28.23 | -26.25 |
| 53 | -25.74 | -26.27 | -25.34 | -26.50 | -26.58 | -26.32 | -27.96 | -27.54 | -27.94 | -28.02 | -27.81 | -26.32 |
| 57 | -25.78 | -26.66 | -25.97 | -26.73 | -26.68 | -25.72 | -28.14 | -27.54 | -27.91 | -27.76 | -27.91 | -25.72 |
| 61 | -27.38 | -26.03 | -25.29 | -27.59 | -26.53 | -25.78 | -27.73 | -27.85 | -27.77 | -27.99 | -27.99 | -25.78 |
| 65 | -26.32 | -25.77 | -25.49 | -26.66 | -26.56 | -25.98 | -28.49 | -28.15 | -28.05 | -28.01 | -28.31 | -25.98 |
| 69 | -26.13 | -25.91 | -25.81 | -26.14 | -26.18 | -26.26 | -28.25 | -27.93 | -28.01 | -27.84 | -28.29 | -26.26 |
| 73 | -26.40 | -26.00 | -24.82 | -26.38 | -26.68 | -26.22 | -28.11 | -27.99 | -28.11 | -27.64 | -28.42 | -26.22 |
| 77 | -26.36 | -25.89 | -24.47 | -25.94 | -26.42 | -26.39 | -28.01 | -28.19 | -28.27 | -27.65 | -28.06 | -26.39 |
| 81 | -25.83 | -25.58 | -26.25 | -26.16 | -26.83 | -25.96 | -28.21 | -28.35 | -28.06 | -27.89 | -28.29 | -25.96 |
| 85 | -26.88 | -26.53 | -25.94 | -26.75 | -27.26 | -26.07 | -28.17 | -28.27 | -28.49 | -27.62 | -28.38 | -26.07 |
| 89 | -25.26 | -25.68 | -26.13 | -26.76 | -26.76 | -26.81 | -28.43 | -28.28 | -27.96 | -28.02 | -28.44 | -26.81 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 93 | -26.06 | -25.80 | -26.53 | -26.75 | -26.67 | -26.36 | -28.33 | -28.06 | -28.15 | -28.19 | -28.28 | -26.36 |

| Depth [cm] | Breitlohmisse | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **BR1-1** | **BR1-2** | **BR1-3** | **BR2-1** | **BR2-2** | **BR2-3** | **BR3-1** | **BR3-2** | **BR3-3** | **BR4-1** | **BR4-2** | **BR4-3** |
| 2 | -25.93 | -24.77 | -28.85 | -28.78 | -30.04 | -29.74 | -27.80 | -27.05 | -28.46 | -29.11 | -28.49 | -30.09 |
| 4 | -27.12 | -25.27 | -29.23 | -28.54 | -29.05 | -29.62 | -26.85 | -26.62 | -27.53 | -28.95 | -28.46 | -28.70 |
| 6 | -26.83 | -25.53 | -27.69 | -28.44 | -29.39 | -29.56 | -27.23 | -26.02 | -26.85 | -29.39 | -28.48 | -27.75 |
| 8 | -26.45 | -25.36 | -27.32 | -27.93 | -29.22 | -29.52 | -26.59 | -26.12 | -26.60 | -28.60 | -28.67 | -28.60 |
| 10 | -26.98 | -26.69 | -27.26 | -28.85 | -29.17 | -29.29 | -25.99 | -25.84 | -26.80 | -28.74 | -27.93 | -28.12 |
| 12 | -26.13 | -26.93 | -27.76 | -28.64 | -28.65 | -29.32 | -25.65 | -25.56 | -26.89 | -28.08 | -27.33 | -27.05 |
| 14 | -25.64 | -26.88 | -26.14 | -28.79 | -26.58 | -29.14 | -24.75 | -24.49 | -26.01 | -27.91 | -27.41 | -26.99 |
| 16 | -25.97 | -26.93 | -26.16 | -27.92 | -26.05 | -28.10 | -25.16 | -24.41 | -26.08 | -27.32 | -27.10 | -25.71 |
| 18 | -25.83 | -26.73 | -26.13 | -27.35 | -26.25 | -26.99 | -25.06 | -25.27 | -25.14 | -26.38 | -27.17 | -26.15 |
| 20 | -25.63 | -26.66 | -26.14 | -26.98 | -25.66 | -26.61 | -25.66 | -25.02 | -25.90 | -26.15 | -27.42 | -25.29 |
| 24 | -25.93 | -27.71 | -26.01 | -25.88 | -25.06 | -25.55 | -24.47 | -24.50 | -26.12 | -25.31 | -26.85 | -24.50 |
| 28 | -25.77 | -27.67 | -26.08 | -27.18 | -26.24 | -26.40 | -24.55 | -24.48 | -26.53 | -26.35 | -26.40 | -24.64 |
| 32 | -25.87 | -27.39 | -27.14 | -26.53 | -26.40 | -25.98 | -24.05 | -24.60 | -25.75 | -26.11 | -26.40 | -24.25 |
| 36 | -26.07 | -27.68 | -26.71 | -25.01 | -24.80 | -25.49 | -25.55 | -24.98 | -26.63 | -26.25 | -26.44 | -24.89 |
| 40 | -26.05 | -27.37 | -26.18 | -24.74 | -24.91 | -24.69 | -26.61 | -25.72 | -26.83 | -25.36 | -26.25 | -24.86 |
| 44 | -25.26 | -25.82 | -24.54 | -25.06 | -24.69 | -24.83 | -25.73 | -26.01 | -26.75 | -27.53 | -26.47 | -25.49 |
| 48 | -24.40 | -23.98 | -24.64 | -24.61 | -24.47 | -24.81 | -25.99 | -25.80 | -26.90 | -27.17 | -27.18 | -26.12 |
| 52 | -24.49 | -24.84 | -25.55 | -25.44 | -24.53 | -24.86 | -25.26 | -26.22 | -26.99 | -27.18 | -26.90 | -26.08 |
| 56 | -24.86 | -24.68 | -24.80 | -26.52 | -24.10 | -26.38 | -26.68 | -26.29 | -27.49 | -27.19 | -27.20 | -26.28 |
| 60 | -25.12 | -26.12 | -23.95 | -24.82 | -25.42 | -25.87 | -26.79 | -25.88 | -27.44 | -26.73 | -26.56 | -26.47 |
| 64 | -25.04 | -26.96 | -26.02 | -24.90 | -25.39 | -25.26 | -25.40 | -24.43 | -26.83 | -26.46 | -26.39 | -26.40 |
| 68 | -25.49 | -26.83 | -25.76 | -25.95 | -25.23 | -26.05 | -26.06 | -24.80 | -26.80 | -26.13 | -26.06 | -26.59 |
| 72 | -25.52 | -26.31 | -26.10 | -26.12 | -25.07 | -26.03 | -25.96 | -25.89 | -26.81 | -26.23 | -26.17 | -26.68 |
| 76 | -24.79 | -26.64 | -25.97 | -26.45 | -25.71 | -26.74 | -25.69 | -24.79 | -26.36 | -25.80 | -25.20 | -26.49 |
| 80 | -25.67 | -27.29 | -26.45 | -25.95 | -25.61 | -26.08 | -24.86 | -24.46 | -26.47 | -25.99 | -24.78 | -25.33 |
| 84 | -25.18 | -27.04 | -25.68 | -26.66 | -25.56 | -26.60 | -24.99 | -24.17 | -26.29 | -26.36 | -25.24 | -26.04 |
| 88 | -26.75 | -27.22 | -26.01 | -26.94 | -26.13 | -26.67 | -24.95 | -24.03 | -26.04 | -26.24 | -24.60 | -25.63 |
| 92 | -26.19 | -26.17 | -26.59 | -26.67 | -26.39 | -26.89 | -25.55 | -24.78 | -25.78 | -25.24 | -25.13 | -25.37 |
| | | | | | | | | | | | | |
| 96 | -26.42 | -24.85 | -26.43 | -26.30 | -26.31 | -26.10 | -25.59 | -22.37 | -25.25 | -25.93 | -24.88 | -25.09 |
| 100 | -26.63 | -24.84 | -26.85 | -27.40 | -26.05 | -26.93 | -25.31 | -24.29 | -25.44 | -25.80 | -24.90 | -25.49 |
| 104 | -24.93 | -24.06 | -26.35 | -27.26 | -26.21 | -27.13 | -24.90 | -23.43 | -24.80 | -25.96 | -24.58 | -26.00 |
| 108 | | -24.65 | -25.95 | -26.27 | -26.14 | | -24.73 | -24.00 | -26.43 | -25.10 | -24.70 | -25.50 |
| 112 | | | -25.86 | -26.43 | -26.48 | | | -24.23 | | | | |

| Depth [cm] | Rotmeer Moor | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **RO1-1** | **RO1-2** | **RO1-3** | **RO2-1** | **RO2-2** | **RO2-3** | **RO3-1** | **RO3-2** | **RO3-3** |
| 1 | -26.93 | -27.77 | -26.16 | -27.64 | -28.44 | -28.24 | -30.70 | -29.64 | -29.61 |
| 3 | -27.52 | -28.09 | -26.75 | -28.02 | -28.31 | -29.26 | -30.11 | -29.66 | -29.59 |
| 5 | -27.46 | -27.73 | -26.80 | -27.85 | -28.34 | -29.27 | -29.21 | -29.41 | -29.31 |
| 7 | -26.79 | -27.82 | -26.59 | -28.00 | -27.86 | -29.86 | -29.03 | -28.97 | -29.27 |
| 9 | -27.07 | -27.82 | -26.50 | -28.83 | -27.78 | -29.00 | -29.07 | -29.18 | -29.07 |
| 11 | -27.13 | -27.57 | -26.86 | -29.19 | -27.66 | -28.05 | -28.19 | -29.29 | -28.81 |
| 13 | -27.08 | -27.91 | -27.22 | -28.93 | -28.03 | -27.60 | -26.94 | -28.87 | -27.36 |
| 15 | -27.64 | -28.59 | | -28.01 | -28.18 | -27.25 | -26.15 | -26.74 | -26.55 |
| 17 | -27.47 | -27.70 | -26.87 | -28.09 | -28.27 | -27.85 | -26.58 | -26.51 | -26.91 |
| 21 | -27.31 | -27.42 | | -26.81 | -27.89 | -26.62 | -26.60 | -26.78 | -26.79 |
| 27 | -27.33 | -27.70 | -27.33 | -26.30 | -27.44 | -26.66 | -26.32 | -26.64 | -26.64 |
| 29 | -27.27 | | | -26.42 | -26.81 | -27.03 | -26.59 | -26.77 | -26.88 |
| 33 | -27.21 | -27.84 | -27.30 | -25.52 | -26.12 | -27.05 | -26.67 | -25.96 | -26.36 |
| 37 | -27.30 | -26.30 | -26.88 | -24.59 | -26.15 | -26.66 | -26.03 | -25.97 | -26.39 |
| 41 | -26.36 | -26.01 | -25.81 | -25.38 | -26.54 | -27.25 | -25.12 | -26.08 | -26.61 |
| 45 | -26.19 | -25.91 | -25.76 | -26.14 | -26.68 | -25.78 | -25.50 | -26.20 | -25.31 |
| 49 | -26.47 | -25.70 | -25.32 | -25.74 | -26.12 | -25.84 | -25.06 | -25.55 | -25.88 |
| 53 | -25.84 | -25.86 | -24.95 | -25.68 | -25.84 | -26.18 | -25.17 | -25.52 | -25.62 |
| 57 | -25.44 | -26.15 | -25.20 | -25.79 | -26.43 | -25.83 | -25.49 | -25.44 | -24.80 |
| 61 | -24.86 | -26.15 | -24.83 | -25.48 | -25.80 | -25.45 | -25.67 | -25.95 | -25.44 |
| 65 | -24.77 | -26.45 | -25.97 | -24.90 | -25.39 | -25.26 | -25.42 | -25.38 | -26.03 |
| 69 | -24.47 | -26.22 | -26.02 | -25.95 | -25.23 | -26.05 | -25.66 | -25.50 | -25.44 |
| 73 | -25.49 | -26.34 | -25.81 | -26.12 | -25.07 | -26.03 | -26.13 | -26.16 | -25.05 |

**Table A2:** *Nitrogen Stable Isotope Values for all investigated Peatlands; NM: Natural site Degerö Stormyr; DC: Drained site Degerö Stormyr; UR: Ursee Moor sites 1 and 2; Lakkasuo ombrotrophic, natural: ON; Lakkasuo ombrotrophic, drained: OD; Lakkasuo minerotrophic, natural: MN; Lakkasuo minerotrophic, drained: MD; BR: Breitlohmisse 1 – 4; RO: Rotmeer Moor 1-3*

| Depth [cm] | Degerö Stormyr | | | | | | Ursee Moor | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NM1 | NM2 | NM3 | DC1 | DC2 | DC3 | UR2-1 | UR-2-2 | UR2-3 | UR1-1 | UR1-2 | UR1-3 |
| 1 | -9.95 | -9.03 | -7.18 | -8.48 | -7.47 | -5.39 | -8.42 | -10.53 | -9.69 | -3.35 | -2.65 | -3.80 |
| 5 | -9.31 | -7.15 | -7.71 | -10.64 | -7.44 | -5.01 | -8.54 | -4.26 | -7.69 | -2.84 | -3.47 | -3.57 |
| 9 | -7.05 | -5.43 | -5.13 | -9.97 | -9.25 | -5.91 | -8.31 | -5.40 | -8.36 | -2.32 | -3.13 | -4.06 |
| 13 | -6.32 | -6.04 | -7.06 | -0.29 | -3.60 | -4.57 | -6.29 | -5.48 | -8.29 | -3.20 | -2.27 | -3.06 |
| 17 | -5.72 | -2.57 | -3.76 | -3.86 | -2.72 | -2.89 | | -5.81 | -7.87 | -1.12 | -0.62 | -3.40 |
| 21 | -7.07 | -5.32 | -3.68 | -5.49 | 1.07 | -0.32 | -1.29 | -6.98 | -8.46 | 0.96 | -0.83 | -2.67 |
| 25 | -5.14 | -3.83 | -1.74 | -4.83 | -2.29 | 1.83 | -5.14 | -7.10 | -5.87 | -0.95 | -1.03 | -1.94 |
| 29 | -5.93 | -5.72 | -2.57 | -4.13 | -3.81 | 0.17 | -4.12 | -6.12 | 4.17 | -1.81 | -1.77 | -0.33 |
| 33 | -7.20 | -4.80 | -1.34 | -5.68 | -5.97 | -1.53 | -6.45 | -7.34 | -3.26 | -2.56 | -1.82 | -1.14 |
| 37 | -6.81 | -4.59 | -1.04 | -4.93 | -5.37 | -3.81 | -3.48 | -9.18 | -4.66 | -1.21 | -3.80 | -1.75 |
| 41 | -4.53 | -4.63 | -0.40 | -7.68 | -6.96 | -3.69 | -2.03 | -8.07 | -3.56 | -0.06 | -4.03 | -3.09 |
| 45 | -3.94 | -4.41 | -1.55 | -3.85 | -4.37 | -4.47 | -27.98 | -12.97 | -3.75 | -2.29 | -3.70 | -3.81 |
| 49 | -4.29 | -2.49 | -1.45 | -2.34 | -3.69 | -2.67 | -4.22 | -1.14 | -5.82 | -0.31 | -1.55 | -7.30 |
| 53 | -4.13 | -4.13 | -3.13 | -5.21 | -5.77 | -3.03 | -4.86 | -2.69 | -4.71 | -2.74 | -3.56 | -2.94 |
| 57 | -6.07 | -3.90 | -2.94 | -3.07 | -4.68 | -0.97 | -4.72 | -7.27 | -6.83 | -0.63 | -3.33 | -2.06 |
| 61 | -6.79 | -4.25 | -2.08 | -5.39 | -5.46 | -2.56 | -5.20 | -6.49 | -6.18 | -0.69 | -5.64 | -15.82 |
| 65 | -6.25 | -5.28 | -3.87 | -4.63 | -2.76 | -1.74 | -4.46 | -9.65 | -5.91 | -3.37 | -3.75 | -3.37 |
| 69 | -5.53 | -4.86 | -2.71 | -3.85 | -2.93 | -1.46 | -8.42 | -10.53 | -9.69 | -3.35 | -2.65 | -3.80 |
| 73 | -9.70 | -3.85 | -4.03 | -5.68 | -4.17 | -1.44 | -8.54 | -4.26 | -7.69 | -2.84 | -3.47 | -3.57 |
| 77 | -6.82 | -4.18 | -3.12 | -4.48 | -4.57 | -2.28 | -8.31 | -5.40 | -8.36 | -2.32 | -3.13 | -4.06 |
| 81 | | -4.71 | -3.94 | -2.67 | -2.57 | -2.78 | -6.29 | -5.48 | -8.29 | -3.20 | -2.27 | -3.06 |
| 85 | | -6.03 | -4.03 | -3.23 | -2.09 | -4.39 | | -5.81 | -7.87 | -1.12 | -0.62 | -3.40 |
| 89 | -9.95 | -9.03 | -7.18 | -5.39 | -3.96 | -2.34 | -1.29 | -6.98 | -8.46 | 0.96 | -0.83 | -2.67 |
| 93 | -9.31 | -7.15 | -7.71 | -8.77 | -4.15 | -1.44 | -5.14 | -7.10 | -5.87 | -0.95 | -1.03 | -1.94 |

| Depth [cm] | Lakkasuo, ombrotrophic | | | | | | Lakkasuo, minerothropic | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ON1 | ON2 | ON3 | OD1 | OD2 | OD3 | MN1 | MN2 | MN3 | MD1 | MD2 | MD3 |
| 1 | -3.46 | -6.49 | -4.92 | -5.45 | -5.39 | -5.70 | -1.02 | -0.95 | -2.33 | -4.31 | -6.05 | -5.70 |
| 5 | -6.44 | -5.33 | -6.41 | -2.29 | -3.93 | -4.12 | -1.38 | -2.47 | -5.61 | -7.98 | -11.92 | -4.12 |
| 9 | -5.80 | -5.62 | -6.21 | -1.76 | -0.91 | -1.79 | -0.93 | -1.62 | -4.98 | -0.71 | -11.27 | -1.79 |
| 13 | -5.34 | -5.91 | -6.01 | -1.32 | -1.03 | -2.45 | -0.94 | -0.75 | -2.94 | 1.35 | -4.82 | -2.45 |
| 17 | -4.88 | -4.29 | -4.54 | 0.19 | -1.82 | -2.13 | -1.67 | -0.06 | -8.73 | -1.01 | -4.07 | -2.13 |
| 21 | -3.88 | -3.29 | -4.18 | -0.46 | -2.92 | -3.89 | -1.20 | -0.93 | -1.12 | -1.60 | -3.50 | -3.89 |
| 25 | -2.87 | -2.54 | -2.83 | -2.41 | -2.09 | -3.65 | -0.62 | -1.98 | -1.69 | -1.14 | -2.03 | -3.65 |
| 29 | -0.91 | -3.12 | -2.34 | -2.63 | -2.27 | -3.52 | -0.97 | 0.10 | -1.34 | -2.23 | -4.01 | -3.52 |
| 33 | -2.28 | -2.41 | -3.16 | -2.31 | -1.45 | -3.96 | -1.05 | -0.78 | -1.06 | -3.76 | -4.37 | -3.96 |
| 37 | -2.23 | -1.75 | -5.01 | -2.14 | -0.07 | -4.69 | -0.55 | -0.90 | -1.03 | -0.82 | -4.11 | -4.69 |
| 41 | -2.23 | -1.54 | -3.05 | -3.32 | 0.19 | -2.41 | -0.83 | -0.96 | -0.96 | -1.34 | -3.95 | -2.41 |
| 45 | -2.19 | -1.69 | -2.55 | -0.91 | -0.59 | -2.56 | -0.71 | -0.79 | -0.68 | -2.47 | -3.18 | -2.56 |
| 49 | 0.62 | -0.31 | 1.51 | 0.66 | -0.28 | 0.29 | -0.08 | 0.49 | 0.05 | -2.94 | -2.96 | 0.29 |
| 53 | -0.56 | -0.11 | -2.64 | -0.97 | -2.13 | -1.10 | -0.61 | -0.53 | -1.16 | -3.95 | -4.63 | -1.10 |
| 57 | 0.04 | -0.49 | -0.35 | -0.19 | -0.55 | -4.95 | -0.57 | -0.50 | -0.32 | -4.84 | -3.15 | -4.95 |
| 61 | -0.37 | -2.12 | -3.00 | 0.94 | -4.03 | -4.98 | -0.72 | -0.76 | -1.02 | -4.59 | -4.61 | -4.98 |
| 65 | -1.69 | -3.26 | -2.78 | -1.94 | -4.33 | -4.68 | -0.62 | -0.80 | -1.75 | -3.81 | -3.16 | -4.68 |
| 69 | -1.94 | -3.20 | -2.57 | -3.16 | -4.48 | -3.50 | -1.16 | -1.09 | -1.52 | -5.72 | -3.90 | -3.50 |
| 73 | -2.31 | -2.25 | -4.67 | -3.02 | -3.55 | -4.45 | -0.97 | -1.31 | -1.21 | -3.03 | -5.08 | -4.45 |
| 77 | -3.10 | -4.02 | -5.55 | -2.41 | -3.66 | -3.56 | -0.89 | -0.54 | -1.55 | -5.00 | -5.10 | -3.56 |
| 81 | -3.32 | -4.50 | -4.90 | -1.59 | -2.11 | -4.51 | -0.29 | -0.57 | -0.79 | -5.22 | -5.45 | -4.51 |
| 85 | -4.26 | -5.00 | -4.96 | -2.06 | -2.40 | -5.73 | -0.11 | -0.62 | -0.69 | -5.47 | -4.91 | -5.73 |
| 89 | -5.33 | -4.38 | -2.08 | -1.65 | -1.47 | -2.73 | -0.06 | -0.16 | -1.02 | -3.92 | -6.04 | -2.73 |
| 93 | -4.40 | -4.62 | -1.52 | -2.18 | -2.12 | -1.81 | -0.03 | -0.45 | -1.20 | -5.27 | -5.12 | -1.81 |

| Depth [cm] | Breitlohmisse | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BR1-1 | BR1-2 | BR1-3 | BR2-1 | BR2-2 | BR2-3 | BR3-1 | BR3-2 | BR3-3 | BR4-1 | BR4-2 | BR4-3 |
| 2 | -3.81 | -3.46 | -2.29 | -5.27 | -7.06 | -13.99 | -6.45 | -6.05 | -6.25 | -5.86 | -8.39 | -8.62 |
| 4 | -3.16 | -2.28 | -3.98 | -4.93 | -7.36 | -13.16 | -4.96 | -6.61 | -5.78 | -6.26 | -10.35 | -7.41 |
| 6 | -3.15 | -3.14 | -3.01 | -5.45 | -5.55 | -12.90 | -3.23 | -4.74 | -3.99 | -5.40 | -7.04 | -6.62 |
| 8 | -3.26 | -3.78 | -3.10 | -4.09 | -6.56 | -10.89 | -3.15 | -4.49 | -3.82 | -4.38 | -7.65 | -3.17 |
| 10 | -2.34 | -3.24 | -2.80 | -4.62 | -6.20 | -11.20 | -3.05 | -1.93 | -2.49 | -4.82 | -8.31 | -5.35 |
| 12 | -2.59 | -2.83 | -2.73 | -5.00 | -5.66 | -10.34 | -5.18 | -1.01 | -3.09 | -3.17 | -6.09 | -3.68 |
| 14 | -2.76 | -3.75 | -2.75 | -4.54 | -3.87 | -8.44 | -5.58 | -1.86 | -3.72 | -1.98 | -5.48 | -4.45 |
| 16 | -2.44 | -3.95 | -2.77 | -2.45 | -4.95 | -6.24 | -6.24 | -3.48 | -4.86 | -2.79 | -2.42 | -7.13 |
| 18 | -2.61 | -3.43 | -3.09 | -0.70 | -5.95 | -3.75 | -5.98 | -1.15 | -3.56 | -4.10 | -1.87 | -0.33 |
| 20 | -2.50 | -3.43 | -2.36 | -0.69 | -7.32 | -2.30 | -2.59 | -2.92 | -2.76 | -5.32 | -2.84 | -1.91 |
| 24 | -1.82 | -3.27 | -1.23 | 1.38 | -4.61 | -3.11 | -7.02 | -3.18 | -5.10 | -6.33 | -1.22 | -5.18 |
| 28 | -2.69 | -4.73 | -2.65 | 0.90 | -4.96 | -4.72 | -12.42 | -4.84 | -8.63 | -5.68 | -2.44 | -6.62 |
| 32 | -2.45 | -4.91 | -4.87 | -2.05 | -2.28 | -2.91 | -11.69 | -3.03 | -7.36 | -4.60 | -4.46 | -6.90 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 36 | -2.00 | -4.44 | -4.43 | -2.76 | -3.35 | -5.02 | -6.37 | -5.52 | -5.95 | -4.34 | -4.95 | -4.85 |
| 40 | -2.38 | -1.95 | -1.68 | -2.47 | -1.83 | -6.66 | -4.54 | -4.63 | -4.58 | -4.25 | -4.83 | -6.43 |
| 44 | -1.49 | -2.17 | -1.68 | -2.70 | -1.84 | -6.96 | -2.41 | -3.49 | -2.95 | -2.64 | -4.28 | -7.02 |
| 48 | -1.08 | -1.08 | -1.89 | -2.91 | -5.64 | -7.80 | -3.59 | -0.23 | -1.91 | -2.27 | -3.96 | -7.61 |
| 52 | -2.31 | -2.80 | -0.17 | -3.25 | -3.05 | -9.20 | -4.46 | -2.43 | -3.44 | -2.00 | -3.17 | -4.38 |
| 56 | -2.56 | -3.19 | -2.35 | -3.65 | -4.40 | -9.31 | -4.84 | -1.75 | -3.30 | -4.36 | -4.05 | -3.20 |
| 60 | -1.82 | -4.97 | -2.73 | -2.80 | -4.50 | -8.16 | -4.80 | -2.55 | -3.68 | -3.87 | -1.15 | -1.46 |
| 64 | -1.24 | -4.50 | -3.58 | -2.47 | -3.28 | -8.94 | -5.80 | -2.58 | -4.19 | -3.40 | -3.30 | -0.89 |
| 68 | -1.09 | -3.48 | -2.71 | -2.42 | -1.22 | -10.31 | -0.84 | -2.37 | -1.61 | -3.23 | -2.82 | -1.38 |
| 72 | -1.67 | -3.48 | -2.38 | -2.82 | 0.84 | -7.41 | -5.31 | -3.66 | -4.48 | -5.58 | -4.79 | -1.20 |
| 76 | -1.38 | -1.72 | -2.96 | -3.07 | -3.09 | -4.75 | -8.85 | -5.11 | -6.98 | -6.03 | -3.83 | -0.91 |
| 80 | -1.80 | 0.14 | -3.20 | -1.70 | -1.13 | -1.92 | -7.35 | -4.30 | -5.83 | -7.50 | -4.88 | -4.13 |
| 84 | -0.98 | 0.50 | -1.89 | -2.51 | -1.37 | -3.47 | -10.76 | -3.98 | -7.37 | -5.17 | -4.53 | -4.32 |
| 88 | -0.12 | 0.02 | -1.18 | -1.62 | -1.16 | -1.62 | -10.64 | -3.24 | -6.94 | -5.82 | -2.73 | -3.19 |
| 92 | -0.10 | -3.21 | -1.15 | -1.76 | -4.67 | -4.57 | -9.96 | -2.51 | -6.24 | -5.70 | -4.19 | -0.50 |
| | 1.81 | -3.55 | 0.08 | -0.36 | -1.68 | -3.95 | -13.52 | -4.47 | -8.99 | -6.62 | -4.40 | -5.59 |
| 96 | 0.79 | -2.16 | 1.52 | -1.17 | -2.72 | -5.80 | -11.05 | -5.07 | -8.06 | -4.33 | -3.88 | -5.04 |
| 100 | -1.81 | -3.63 | 0.42 | -1.05 | -2.70 | -3.71 | -9.23 | -5.54 | -7.39 | -5.42 | -4.27 | -5.35 |
| 104 | | -3.03 | -1.47 | -0.33 | -2.22 | | -11.88 | -6.40 | -9.14 | -4.43 | -5.29 | -3.83 |
| 108 | | | -1.82 | -0.94 | -0.61 | | -11.98 | | -11.98 | | | |
| 112 | | | -2.40 | | | | | | | -5.86 | -8.39 | -8.62 |

| **Depth [cm]** | **Rotmeer Moor** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **RO1-1** | **RO1-2** | **RO1-3** | **RO2-1** | **RO2-2** | **RO2-3** | **RO3-1** | **RO3-2** | **RO3-3** |
| 1 | -0.17 | -7.05 | -4.19 | -6.34 | -11.44 | -12.16 | -5.21 | -10.98 | |
| 3 | -14.40 | -11.46 | -8.22 | -7.86 | -11.62 | -4.13 | -9.71 | -13.66 | -13.02 |
| 5 | | -12.16 | -9.93 | -7.66 | -11.04 | -7.46 | -13.15 | -15.60 | -9.49 |
| 7 | | -6.82 | -12.72 | -5.32 | -10.94 | -9.52 | -10.75 | -16.06 | -12.62 |
| 9 | -15.11 | -8.08 | -13.48 | -6.71 | -10.98 | -9.50 | -8.14 | -12.43 | -9.82 |
| 11 | -13.53 | -6.85 | -6.64 | -9.21 | -9.64 | -7.29 | -7.66 | -12.44 | -7.11 |
| 13 | -13.71 | -7.68 | -8.79 | -4.80 | -4.44 | -6.15 | -4.43 | -10.96 | -3.59 |
| 15 | -12.45 | -5.13 | | -3.94 | -8.07 | -5.90 | -4.89 | -5.95 | -3.37 |
| 17 | -12.97 | -6.22 | -6.26 | -3.42 | -5.94 | -4.76 | -2.89 | -6.27 | -5.38 |
| 21 | -13.59 | -5.94 | | -2.02 | -5.18 | -3.44 | -3.43 | 1.07 | -6.04 |
| 27 | -14.53 | -7.25 | -8.03 | -1.68 | -3.89 | -4.57 | -4.78 | -3.06 | -7.29 |
| 29 | -4.00 | | | -2.46 | -7.33 | -3.33 | -3.68 | -6.56 | -4.56 |
| 33 | -10.24 | -6.32 | -9.59 | -3.47 | -4.21 | -3.08 | -3.37 | -5.88 | -7.08 |
| 37 | -11.02 | -10.74 | -6.32 | -4.68 | -4.31 | -4.45 | -5.89 | -8.43 | -6.50 |
| 41 | -8.57 | -5.51 | -7.03 | -4.54 | -2.72 | -5.22 | -6.65 | -8.16 | -3.50 |
| 45 | -11.22 | -6.56 | -6.37 | -6.06 | -3.03 | -7.67 | -8.32 | -7.89 | -4.78 |
| 49 | -11.82 | -9.59 | -14.53 | -6.05 | -4.30 | -10.07 | -7.05 | -9.78 | -9.24 |
| 53 | -12.23 | -6.98 | -10.89 | -8.83 | -3.26 | -7.32 | -7.07 | -6.46 | -9.70 |
| 57 | -10.56 | -5.71 | -9.33 | -7.55 | -3.79 | -7.07 | -8.33 | -6.35 | -8.87 |
| 61 | -12.13 | -10.48 | -10.19 | -6.49 | -5.71 | -6.71 | -6.61 | -6.87 | -9.64 |
| 65 | -5.43 | -7.65 | -10.34 | -6.89 | -3.98 | -10.41 | -7.82 | -6.58 | -8.99 |
| 69 | -9.05 | -6.78 | -5.51 | -9.03 | -5.44 | -9.12 | -7.96 | -8.72 | -8.68 |
| 73 | -5.78 | -6.19 | -7.75 | -5.21 | -7.50 | -11.17 | -6.13 | -3.37 | -8.52 |

**Table A3:** *Carbon:Nitrogen Ratio for all investigated Peatlands; NM: Natural site Degerö Stormyr; DC: Drained site Degerö Stormyr; UR: Ursee Moor sites 1 and 2; Lakkasuo ombrotrophic, natural: ON; Lakkasuo ombrotrophic, drained: OD; Lakkasuo minerotrophic, natural: MN; Lakkasuo minerotrophic, drained: MD; BR: Breitlohmisse 1 – 4; RO: Rotmeer Moor 1-3*

| Depth [cm] | Degerö Stormyr | | | | | | Ursee Moor | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NM1 | NM2 | NM3 | DC1 | DC2 | DC3 | UR2-1 | UR-2-2 | UR2-3 | UR1-1 | UR1-2 | UR1-3 |
| 1 | 114.11 | 77.81 | 76.79 | 89.57 | 66.10 | 53.12 | 44.31 | 49.94 | 46.95 | 47.07 | 17.63 | 17.23 |
| 5 | 138.08 | 65.62 | 100.04 | 101.25 | 84.49 | 49.71 | 59.28 | 55.79 | 61.34 | 58.80 | 16.09 | 17.17 |
| 9 | 102.49 | 42.80 | 81.47 | 75.59 | 81.81 | 57.69 | 55.53 | 62.28 | 63.96 | 60.59 | 15.59 | 18.99 |
| 13 | 68.16 | 54.92 | 86.03 | 69.70 | 26.04 | 43.36 | 48.38 | 58.47 | 63.82 | 56.89 | 17.20 | 19.30 |
| 17 | 50.56 | 37.01 | 44.48 | 44.02 | 42.35 | 22.76 | | 53.63 | 59.69 | 56.66 | 17.10 | 19.73 |
| 21 | 49.20 | 31.36 | 43.45 | 41.34 | 54.72 | 24.76 | 58.66 | 55.86 | 56.74 | 57.08 | 18.70 | 20.16 |
| 25 | 63.13 | 32.26 | 39.81 | 45.07 | 46.57 | 39.41 | 56.17 | 58.00 | 53.92 | 56.03 | 20.30 | 21.68 |
| 29 | 55.95 | 41.20 | 39.41 | 45.52 | 41.40 | 48.52 | 57.25 | 49.00 | 43.72 | 49.99 | 20.67 | 21.44 |
| 33 | 63.62 | 63.75 | 42.88 | 56.75 | 53.98 | 54.16 | 60.25 | 54.88 | 42.49 | 52.54 | 26.43 | 21.92 |
| 37 | 90.58 | 49.14 | 41.03 | 60.25 | 43.41 | 49.74 | 66.34 | 70.54 | 41.55 | 59.47 | 31.36 | 29.13 |
| 41 | 53.80 | 46.74 | 42.01 | 47.52 | 52.21 | 53.09 | 57.55 | 58.72 | 41.71 | 52.66 | 33.63 | 32.97 |
| 45 | 44.86 | 43.94 | 39.98 | 42.93 | 41.79 | 40.57 | 59.24 | 69.94 | 43.78 | 57.66 | 31.44 | 32.35 |
| 49 | 52.83 | 36.17 | 41.80 | 43.60 | 35.30 | 40.72 | 55.74 | 41.20 | 47.58 | 48.17 | 31.58 | 33.72 |
| 53 | 40.89 | 33.33 | 42.67 | 38.97 | 52.42 | 53.04 | 61.94 | 26.26 | 44.91 | 44.37 | 29.81 | 37.35 |
| 57 | 61.50 | 36.74 | 48.68 | 48.97 | 35.08 | 45.83 | 63.21 | 49.84 | 54.60 | 55.88 | 32.63 | 37.11 |
| 61 | 72.97 | 38.55 | 35.53 | 49.02 | 50.88 | 52.50 | 54.99 | 58.61 | 56.56 | 56.72 | 27.82 | 39.15 |
| 65 | 75.60 | 60.81 | 52.24 | 62.88 | 47.03 | 36.41 | 66.24 | 71.28 | 54.65 | 64.06 | 29.33 | 43.44 |
| 69 | 53.09 | 54.93 | 45.55 | 51.19 | 41.54 | 36.06 | 44.31 | 49.94 | 46.95 | 47.07 | 17.63 | 17.23 |
| 73 | 72.56 | 46.23 | 49.84 | 56.21 | 47.95 | 45.86 | 59.28 | 55.79 | 61.34 | 58.80 | 16.09 | 17.17 |
| 77 | 58.82 | 45.84 | 37.34 | 47.33 | 41.21 | 40.81 | 55.53 | 62.28 | 63.96 | 60.59 | 15.59 | 18.99 |
| 81 | | 53.95 | 39.70 | 46.83 | 33.30 | 36.18 | 48.38 | 58.47 | 63.82 | 56.89 | 17.20 | 19.30 |
| 85 | | 56.59 | 44.57 | 50.58 | 33.89 | 33.88 | | 53.63 | 59.69 | 56.66 | 17.10 | 19.73 |
| 89 | | | | | 45.26 | 35.47 | 58.66 | 55.86 | 56.74 | 57.08 | 18.70 | 20.16 |
| 93 | | | | | 61.05 | 34.33 | 56.17 | 58.00 | 53.92 | 56.03 | 20.30 | 21.68 |

| Depth [cm] | Lakkasuo, ombrotrophic | | | | | | Lakkasuo, minerothropic | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ON1 | ON2 | ON3 | OD1 | OD2 | OD3 | MN1 | MN2 | MN3 | MD1 | MD2 | MD3 |
| 1 | 57.70 | 50.13 | 54.36 | 54.07 | 43 | 39.12 | 43.34 | 39.12 | 49.89 | 44.12 | 49.14 | 49.24 |
| 5 | 60.52 | 66.98 | 63.25 | 63.59 | 41 | 39.04 | 40.67 | 39.04 | 57.42 | 45.71 | 34.14 | 37.61 |
| 9 | 94.99 | 78.96 | 63.09 | 79.01 | 31 | 35.00 | 31.30 | 35.00 | 62.30 | 42.87 | 45.00 | 37.94 |
| 13 | 91.41 | 90.94 | 62.93 | 81.76 | 31 | 25.29 | 31.03 | 25.29 | 43.63 | 33.32 | 54.59 | 41.47 |
| 17 | 87.83 | 87.67 | 69.10 | 81.53 | 23 | 18.78 | 23.44 | 18.78 | 38.03 | 26.75 | 52.51 | 50.05 |
| 21 | 72.34 | 61.57 | 52.48 | 62.13 | 15 | 19.76 | 15.01 | 19.76 | 20.99 | 18.59 | 63.64 | 56.40 |
| 25 | 56.85 | 49.48 | 41.29 | 49.21 | 16 | 20.47 | 15.75 | 20.47 | 18.43 | 18.21 | 80.33 | 66.69 |
| 29 | 40.31 | 66.99 | 35.03 | 47.44 | 18 | 15.23 | 17.98 | 15.23 | 17.39 | 16.87 | 81.14 | 57.42 |
| 33 | 42.53 | 66.29 | 55.39 | 54.74 | 20 | 18.05 | 19.77 | 18.05 | 17.17 | 18.33 | 60.41 | 50.00 |
| 37 | 39.29 | 50.78 | 65.72 | 51.93 | 21 | 18.72 | 21.00 | 18.72 | 19.28 | 19.66 | 59.73 | 39.15 |
| 41 | 39.29 | 57.82 | 50.76 | 49.29 | 22 | 20.44 | 22.33 | 20.44 | 20.20 | 20.99 | 79.61 | 27.68 |
| 45 | 36.06 | 50.96 | 45.83 | 44.28 | 23 | 21.59 | 22.63 | 21.59 | 20.27 | 21.50 | 35.17 | 32.10 |
| 49 | 46.45 | 45.45 | 24.78 | 38.89 | 23 | 22.72 | 22.91 | 22.72 | 23.52 | 23.05 | 24.52 | 45.09 |
| 53 | 40.18 | 37.25 | 49.59 | 42.34 | 24 | 22.41 | 24.12 | 22.41 | 23.19 | 23.24 | 40.27 | 43.53 |
| 57 | 32.44 | 31.60 | 29.33 | 31.13 | 23 | 21.88 | 22.80 | 21.88 | 19.13 | 21.27 | 33.66 | 30.70 |
| 61 | 21.29 | 55.51 | 43.35 | 40.05 | 24 | 23.47 | 24.44 | 23.47 | 22.93 | 23.61 | 22.87 | 47.73 |
| 65 | 43.90 | 61.56 | 33.13 | 46.19 | 22 | 22.94 | 22.49 | 22.94 | 24.20 | 23.21 | 35.35 | 56.05 |
| 69 | 38.24 | 51.00 | 22.90 | 37.38 | 26 | 23.25 | 26.06 | 23.25 | 24.38 | 24.56 | 49.74 | 60.13 |
| 73 | 42.73 | 46.73 | 36.36 | 41.94 | 25 | 22.50 | 24.76 | 22.50 | 22.45 | 23.24 | 48.29 | 56.59 |
| 77 | 56.07 | 64.54 | 45.60 | 55.40 | 23 | 23.70 | 23.37 | 23.70 | 21.99 | 23.02 | 52.29 | 59.11 |
| 81 | 71.76 | 70.19 | 45.09 | 62.34 | 22 | 22.50 | 22.14 | 22.50 | 23.09 | 22.57 | 44.21 | 43.67 |
| 85 | 68.16 | 73.71 | 53.65 | 65.17 | 23 | 25.77 | 23.44 | 25.77 | 24.81 | 24.67 | 50.67 | 45.69 |
| 89 | 87.74 | 62.66 | 33.67 | 61.36 | 23 | 23.19 | 23.46 | 23.19 | 24.36 | 23.67 | 50.26 | 44.08 |
| 93 | 78.69 | 75.25 | 26.26 | 60.07 | 23 | 25.42 | 22.53 | 25.42 | 27.10 | 25.02 | 54.25 | 47.87 |

| Depth [cm] | Breitlohmisse | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BR1-1 | BR1-2 | BR1-3 | BR2-1 | BR2-2 | BR2-3 | BR3-1 | BR3-2 | BR3-3 | BR4-1 | BR4-2 | BR4-3 |
| 2 | 45.66 | 47.75 | 87.52 | 60.31 | 73.39 | 46.93 | 57.87 | 59.40 | 33.09 | 25.86 | 36.39 | 31.78 |
| 4 | 31.90 | 32.63 | 40.08 | 34.87 | 103.19 | 59.65 | 80.31 | 81.05 | 24.31 | 22.78 | 26.66 | 24.59 |
| 6 | 48.00 | 37.11 | 36.75 | 40.62 | 105.01 | 48.48 | 72.11 | 75.20 | 23.45 | 24.35 | 24.05 | 23.95 |
| 8 | 46.75 | 43.18 | 43.64 | 44.52 | 95.43 | 49.69 | 68.84 | 71.32 | 23.47 | 33.50 | 28.56 | 28.51 |
| 10 | 39.87 | 57.13 | 44.50 | 47.16 | 83.03 | 47.00 | 66.75 | 65.59 | 28.40 | 41.62 | 33.55 | 34.52 |
| 12 | 32.39 | 63.59 | 55.78 | 50.59 | 89.24 | 41.29 | 64.81 | 65.11 | 34.10 | 39.68 | 41.83 | 38.54 |
| 14 | 39.49 | 74.59 | 52.05 | 55.38 | 68.24 | 45.18 | 57.34 | 56.92 | 45.11 | 47.63 | 45.23 | 45.99 |
| 16 | 34.24 | 67.04 | 56.88 | 52.72 | 39.93 | 65.60 | 41.07 | 48.87 | 52.55 | 56.74 | 47.02 | 52.11 |
| 18 | 39.38 | 60.93 | 54.18 | 51.50 | 36.21 | 74.82 | 30.23 | 47.09 | 54.85 | 66.31 | 59.14 | 60.10 |
| 20 | 35.92 | 64.84 | 62.29 | 54.35 | 38.71 | 80.76 | 33.21 | 50.90 | 60.39 | 75.90 | 64.81 | 67.04 |
| 24 | 54.24 | 42.93 | 63.06 | 53.41 | 35.27 | 78.57 | 46.26 | 53.37 | 68.00 | 92.06 | 95.53 | 85.20 |
| 28 | 50.06 | 57.26 | 59.03 | 55.45 | 31.63 | 42.63 | 45.27 | 39.84 | 73.96 | 96.56 | 107.07 | 92.53 |
| 32 | 47.27 | 65.26 | 53.03 | 55.19 | 53.90 | 27.81 | 57.98 | 46.56 | 81.54 | 96.87 | 112.62 | 97.01 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 36 | 46.28 | 68.04 | 45.67 | 53.33 | 77.92 | 40.87 | 58.57 | 59.12 | 72.06 | 53.49 | 80.83 | 68.79 |
| 40 | 49.79 | 53.56 | 73.76 | 59.03 | 81.63 | 55.43 | 63.25 | 66.77 | 51.35 | 50.17 | 72.21 | 57.91 |
| 44 | 56.15 | 55.25 | 89.26 | 66.89 | 79.15 | 63.70 | 67.17 | 70.01 | 46.43 | 36.95 | 60.35 | 47.91 |
| 48 | 52.70 | 56.72 | 83.84 | 64.42 | 96.83 | 72.13 | 80.30 | 83.09 | 42.32 | 40.17 | 49.09 | 43.86 |
| 52 | 55.10 | 81.66 | 72.57 | 69.78 | 100.85 | 61.47 | 106.00 | 89.44 | 31.60 | 38.95 | 43.68 | 38.08 |
| 56 | 47.97 | 93.03 | 79.84 | 73.62 | 79.95 | 65.74 | 75.80 | 73.83 | 28.44 | 45.38 | 33.73 | 35.85 |
| 60 | 44.28 | 75.23 | 79.96 | 66.49 | 108.19 | 63.26 | 62.86 | 78.10 | 34.45 | 56.11 | 35.52 | 42.02 |
| 64 | 58.81 | 62.80 | 64.52 | 62.04 | 99.57 | 58.81 | 91.45 | 83.28 | 45.55 | 62.23 | 44.86 | 50.88 |
| 68 | 56.16 | 59.41 | 72.97 | 62.85 | 94.80 | 62.85 | 110.74 | 89.47 | 43.96 | 59.01 | 55.33 | 52.77 |
| 72 | 43.97 | 44.14 | 82.13 | 56.75 | 94.00 | 66.90 | 81.06 | 80.65 | 54.29 | 50.47 | 81.12 | 61.96 |
| 76 | 45.03 | 32.37 | 69.81 | 49.07 | 75.61 | 44.12 | 47.52 | 55.75 | 55.17 | 66.11 | 77.61 | 66.30 |
| 80 | 40.48 | 33.76 | 56.77 | 43.67 | 62.81 | 42.87 | 38.82 | 48.17 | 58.71 | 63.34 | 55.88 | 59.31 |
| 84 | 40.11 | 37.96 | 41.19 | 39.76 | 52.12 | 45.22 | 36.19 | 44.51 | 67.97 | 81.58 | 62.52 | 70.69 |
| 88 | 26.33 | 34.22 | 41.41 | 33.99 | 48.94 | 38.72 | 37.68 | 41.78 | 68.33 | 91.25 | 75.06 | 78.21 |
| 92 | 27.13 | 46.38 | 37.09 | 36.87 | 35.19 | 46.55 | 45.14 | 42.29 | 52.44 | 69.96 | 87.60 | 70.00 |
| | 34.13 | 66.70 | 37.76 | 46.20 | 34.93 | 43.82 | 49.82 | 42.86 | 55.20 | 99.75 | 85.89 | 80.28 |
| 96 | 29.94 | 47.38 | 33.59 | 36.97 | 42.47 | 45.18 | 49.05 | 45.57 | 59.47 | 82.18 | 86.05 | 75.90 |
| 100 | 44.72 | 61.09 | 36.20 | 47.34 | 45.66 | 44.09 | 47.21 | 45.66 | 61.87 | 70.38 | 76.44 | 69.56 |
| 104 | | 80.85 | 47.83 | 64.34 | 43.89 | 42.09 | | 42.99 | 69.71 | 90.46 | 75.49 | 78.55 |
| 108 | | | 61.80 | 61.80 | 49.02 | 39.76 | | 44.39 | | 74.62 | | 74.62 |
| 112 | 45.66 | 47.75 | 87.52 | 60.31 | 73.39 | 46.93 | 57.87 | 59.40 | 33.09 | 25.86 | 36.39 | 31.78 |

| **Depth [cm]** | **Rotmeer Moor** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **RO1-1** | **RO1-2** | **RO1-3** | **RO2-1** | **RO2-2** | **RO2-3** | **RO3-1** | **RO3-2** | **RO3-3** |
| 1 | 42.10 | 62.97 | 41.27 | 48.78 | 50.63 | 54.84 | 49.06 | 51.51 | 39.25 |
| 3 | 65.65 | 82.73 | 77.08 | 75.15 | 71.77 | 64.44 | 50.14 | 62.11 | 51.43 |
| 5 | 102.05 | 73.72 | 82.61 | 86.13 | 67.59 | 60.81 | 48.07 | 58.82 | 57.42 |
| 7 | 87.11 | 49.12 | 76.91 | 71.05 | 62.30 | 65.23 | 35.95 | 54.49 | 39.68 |
| 9 | 70.26 | 52.60 | 65.41 | 62.76 | 52.23 | 63.37 | 33.27 | 49.62 | 36.01 |
| 11 | 58.63 | 33.78 | 52.15 | 48.19 | 36.47 | 57.45 | 34.44 | 42.78 | 36.43 |
| 13 | 57.43 | 37.32 | 47.32 | 47.35 | 24.28 | 61.07 | 37.11 | 40.82 | 28.45 |
| 15 | 55.38 | 39.28 | | 47.33 | 23.71 | 55.56 | 33.15 | 37.47 | 23.99 |
| 17 | 60.06 | 30.90 | 44.74 | 45.23 | 28.47 | 49.90 | 20.83 | 33.07 | 26.10 |
| 21 | 61.18 | 33.88 | | 47.53 | 23.94 | 38.83 | 20.17 | 27.65 | 30.43 |
| 27 | 54.72 | 37.94 | 47.75 | 46.80 | 27.36 | 26.66 | 24.36 | 26.13 | 34.31 |
| 29 | 57.08 | | | 57.08 | 21.98 | 40.82 | 21.84 | 28.21 | 28.80 |
| 33 | 53.95 | 27.87 | 36.41 | 39.41 | 30.92 | 41.93 | 23.22 | 32.02 | 26.54 |
| 37 | 52.20 | 60.04 | 30.23 | 47.49 | 28.19 | 31.24 | 32.30 | 30.58 | 38.69 |
| 41 | 52.71 | 51.20 | 49.24 | 51.05 | 35.99 | 27.41 | 27.10 | 30.17 | 51.10 |
| 45 | 67.78 | 46.13 | 62.26 | 58.72 | 31.34 | 27.48 | 44.93 | 34.58 | 48.13 |
| 49 | 58.39 | 104.24 | 79.08 | 80.57 | 38.59 | 25.12 | 56.82 | 40.18 | 48.27 |
| 53 | 75.64 | 73.60 | 69.67 | 72.97 | 49.65 | 32.12 | 41.10 | 40.95 | 54.97 |
| 57 | 68.64 | 70.46 | 85.70 | 74.93 | 51.27 | 31.69 | 42.71 | 41.89 | 55.12 |
| 61 | 90.21 | 125.13 | 81.18 | 98.84 | 51.69 | 0.00 | 47.84 | 33.18 | 47.96 |
| 65 | 63.90 | 111.19 | 55.00 | 76.70 | 45.41 | 32.14 | 63.91 | 47.15 | 48.88 |
| 69 | 65.70 | 47.50 | 49.82 | 54.34 | 52.33 | 43.44 | 62.69 | 52.82 | 52.23 |
| 73 | 74.73 | 74.96 | 52.87 | 67.52 | 56.40 | 57.54 | 65.21 | 59.72 | 57.79 |

**Table A4:** *Bulk Density for all investigated Peatlands; NM: Natural site Degerö Stormyr; DC: Drained site Degerö Stormyr; UR: Ursee Moor sites 1 and 2; Lakkasuo ombrotrophic, natural: ON; Lakkasuo ombrotrophic, drained: OD; Lakkasuo minerotrophic, natural: MN; Lakkasuo minerotrophic, drained: MD; BR: Breitlohmisse 1 – 4; RO: Rotmeer Moor 1-3*

| Depth [cm] | Degerö Stormyr | | | | | | Ursee Moor | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NM1 | NM2 | NM3 | DC1 | DC2 | DC3 | UR2-1 | UR-2-2 | UR2-3 | UR1-1 | UR1-2 | UR1-3 |
| 1 | 0.01 | 0.02 | 0.01 | 0.02 | 0.02 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.13 | 0.14 |
| 5 | 0.01 | 0.02 | 0.01 | 0.01 | 0.02 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.13 | 0.14 |
| 9 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.01 | 0.02 | 0.02 | 0.03 | 0.03 | 0.11 | 0.14 |
| 13 | 0.02 | 0.02 | 0.03 | 0.02 | 0.06 | 0.04 | 0.03 | 0.02 | 0.02 | 0.03 | 0.09 | 0.12 |
| 17 | 0.03 | 0.03 | 0.03 | 0.03 | 0.05 | 0.04 | 0.03 | 0.03 | 0.02 | 0.03 | 0.09 | 0.12 |
| 21 | 0.04 | 0.03 | 0.04 | 0.04 | 0.05 | 0.09 | 0.03 | 0.01 | 0.03 | 0.03 | 0.06 | 0.09 |
| 25 | 0.03 | 0.02 | 0.03 | 0.02 | 0.06 | 0.08 | 0.01 | 0.02 | 0.01 | 0.01 | 0.07 | 0.05 |
| 29 | 0.03 | 0.02 | 0.03 | 0.02 | 0.06 | 0.07 | 0.01 | 0.01 | 0.02 | 0.02 | 0.07 | 0.06 |
| 33 | 0.03 | 0.02 | 0.02 | 0.02 | 0.06 | 0.06 | 0.01 | 0.01 | 0.03 | 0.02 | 0.06 | 0.04 |
| 37 | 0.02 | 0.03 | 0.03 | 0.03 | 0.06 | 0.06 | 0.01 | 0.01 | 0.02 | 0.01 | 0.05 | 0.03 |
| 41 | 0.02 | 0.03 | 0.03 | 0.03 | 0.07 | 0.06 | 0.02 | 0.01 | 0.04 | 0.02 | 0.03 | 0.05 |
| 45 | 0.03 | 0.03 | 0.06 | 0.04 | 0.07 | 0.09 | 0.01 | 0.01 | 0.03 | 0.02 | 0.07 | 0.03 |
| 49 | 0.03 | 0.05 | 0.04 | 0.04 | 0.11 | 0.09 | 0.01 | | 0.02 | 0.02 | 0.05 | 0.03 |
| 53 | 0.04 | 0.06 | 0.05 | 0.05 | 0.06 | 0.08 | 0.01 | 0.01 | 0.05 | 0.02 | 0.03 | 0.07 |
| 57 | 0.02 | 0.05 | 0.05 | 0.04 | 0.11 | 0.11 | 0.01 | 0.02 | 0.05 | 0.03 | 0.02 | 0.04 |
| 61 | 0.02 | 0.05 | 0.09 | 0.05 | 0.10 | 0.12 | 0.01 | 0.01 | 0.06 | 0.03 | 0.02 | 0.03 |
| 65 | 0.02 | 0.04 | 0.05 | 0.04 | 0.13 | 0.17 | 0.02 | 0.02 | 0.02 | 0.02 | 0.13 | 0.14 |
| 69 | 0.03 | 0.05 | 0.04 | 0.04 | 0.13 | 0.16 | 0.02 | 0.02 | 0.02 | 0.02 | 0.13 | 0.14 |
| 73 | 0.02 | 0.06 | 0.04 | 0.04 | 0.13 | 0.11 | 0.02 | 0.02 | 0.03 | 0.03 | 0.11 | 0.14 |
| 77 | 0.02 | 0.05 | 0.05 | 0.04 | 0.15 | 0.14 | 0.03 | 0.02 | 0.02 | 0.03 | 0.09 | 0.12 |
| 81 | | 0.05 | 0.05 | 0.05 | 0.20 | 0.15 | 0.03 | 0.03 | 0.02 | 0.03 | 0.09 | 0.12 |
| 85 | | 0.04 | 0.04 | 0.04 | 0.20 | 0.21 | 0.03 | 0.01 | 0.03 | 0.03 | 0.06 | 0.09 |
| 89 | | | | | 0.13 | 0.17 | 0.01 | 0.02 | 0.01 | 0.01 | 0.07 | 0.05 |
| 93 | | | | | 0.13 | 0.19 | | | | | | |

| Depth [cm] | Lakkasuo, ombrotrophic | | | | | | Lakkasuo, minerothropic | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ON1 | ON2 | ON3 | OD1 | OD2 | OD3 | MN1 | MN2 | MN3 | MD1 | MD2 | MD3 |
| 1 | 0.01 | 0.02 | 0.01 | 0.02 | 0.02 | 0.04 | 0.01 | 0.02 | 0.01 | 0.03 | 0.02 | 0.02 |
| 5 | 0.02 | 0.03 | 0.02 | 0.06 | 0.03 | 0.09 | 0.02 | 0.03 | 0.02 | 0.04 | 0.06 | 0.07 |
| 9 | 0.02 | 0.04 | 0.02 | 0.05 | 0.10 | 0.11 | 0.02 | 0.04 | 0.02 | 0.04 | 0.05 | 0.07 |
| 13 | 0.02 | 0.03 | 0.02 | 0.07 | 0.08 | 0.07 | 0.02 | 0.03 | 0.02 | 0.14 | 0.10 | 0.15 |
| 17 | 0.03 | 0.03 | 0.03 | 0.06 | 0.07 | 0.07 | 0.03 | 0.03 | 0.03 | 0.19 | 0.21 | 0.20 |
| 21 | 0.02 | 0.03 | 0.03 | 0.06 | 0.07 | 0.07 | 0.02 | 0.03 | 0.03 | 0.10 | 0.16 | 0.13 |
| 25 | 0.03 | 0.05 | 0.03 | 0.06 | 0.07 | 0.07 | 0.03 | 0.05 | 0.03 | 0.10 | 0.12 | 0.11 |
| 29 | 0.03 | 0.04 | 0.03 | 0.05 | 0.07 | 0.05 | 0.03 | 0.04 | 0.03 | 0.09 | 0.11 | 0.10 |
| 33 | 0.04 | 0.04 | 0.03 | 0.05 | 0.08 | 0.07 | 0.04 | 0.04 | 0.03 | 0.07 | 0.08 | 0.09 |
| 37 | 0.04 | 0.05 | 0.02 | 0.06 | 0.09 | 0.06 | 0.04 | 0.05 | 0.02 | 0.08 | 0.09 | 0.08 |
| 41 | 0.04 | 0.05 | 0.03 | 0.05 | 0.11 | 0.11 | 0.04 | 0.05 | 0.03 | 0.11 | 0.09 | 0.08 |
| 45 | 0.06 | 0.05 | 0.04 | 0.09 | 0.07 | 0.08 | 0.06 | 0.05 | 0.04 | 0.09 | 0.09 | 0.08 |
| 49 | 0.04 | 0.05 | 0.07 | 0.11 | 0.07 | 0.08 | 0.04 | 0.05 | 0.07 | 0.08 | 0.09 | 0.07 |
| 53 | 0.04 | 0.08 | 0.05 | 0.05 | 0.09 | 0.08 | 0.04 | 0.08 | 0.05 | 0.06 | 0.10 | 0.09 |
| 57 | 0.07 | 0.07 | 0.07 | 0.09 | 0.11 | 0.06 | 0.07 | 0.07 | 0.07 | 0.05 | 0.10 | 0.11 |
| 61 | 0.08 | 0.07 | 0.07 | 0.09 | 0.11 | 0.06 | 0.08 | 0.07 | 0.07 | 0.09 | 0.11 | 0.10 |
| 65 | 0.07 | 0.09 | 0.07 | 0.08 | 0.09 | 0.07 | 0.07 | 0.09 | 0.07 | 0.10 | 0.10 | 0.09 |
| 69 | 0.07 | 0.10 | 0.04 | 0.07 | 0.08 | 0.09 | 0.07 | 0.10 | 0.04 | 0.09 | 0.11 | 0.08 |
| 73 | 0.09 | 0.11 | 0.07 | 0.08 | 0.09 | 0.07 | 0.09 | 0.11 | 0.07 | 0.09 | 0.09 | 0.07 |
| 77 | 0.07 | 0.07 | 0.07 | 0.09 | 0.09 | 0.09 | 0.07 | 0.07 | 0.07 | 0.09 | 0.12 | 0.08 |
| 81 | 0.08 | 0.07 | 0.05 | 0.09 | 0.07 | 0.06 | 0.08 | 0.07 | 0.05 | 0.09 | 0.13 | 0.07 |
| 85 | 0.06 | 0.07 | 0.07 | 0.09 | 0.09 | 0.06 | 0.06 | 0.07 | 0.07 | 0.09 | 0.12 | 0.06 |
| 89 | 0.05 | 0.05 | 0.06 | 0.10 | 0.08 | 0.07 | 0.05 | 0.05 | 0.06 | 0.08 | 0.12 | 0.09 |
| 93 | 0.05 | 0.05 | 0.07 | 0.08 | 0.05 | | 0.05 | 0.05 | 0.07 | 0.11 | 0.10 | 0.12 |

| Depth [cm] | Breitlohmisse | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BR1-1 | BR1-2 | BR1-3 | BR2-1 | BR2-2 | BR2-3 | BR3-1 | BR3-2 | BR3-3 | BR4-1 | BR4-2 | BR4-3 |
| 2 | 0.05 | 0.04 | 0.05 | 0.05 | 0.03 | 0.05 | 0.04 | 0.04 | 0.06 | 0.13 | 0.07 | 0.09 |
| 4 | 0.06 | 0.06 | 0.05 | 0.06 | 0.02 | 0.03 | 0.03 | 0.03 | 0.07 | 0.13 | 0.07 | 0.09 |
| 6 | 0.05 | 0.06 | 0.07 | 0.06 | 0.02 | 0.05 | 0.04 | 0.04 | 0.10 | 0.15 | 0.13 | 0.13 |
| 8 | 0.06 | 0.05 | 0.07 | 0.06 | 0.03 | 0.06 | 0.04 | 0.04 | 0.13 | 0.16 | 0.18 | 0.15 |
| 10 | 0.01 | 0.02 | 0.06 | 0.03 | 0.02 | 0.06 | 0.04 | 0.04 | 0.14 | 0.15 | 0.13 | 0.14 |
| 12 | 0.02 | 0.04 | 0.05 | 0.04 | 0.03 | 0.05 | 0.04 | 0.04 | 0.15 | 0.12 | 0.11 | 0.13 |
| 14 | 0.02 | 0.03 | 0.04 | 0.03 | 0.06 | 0.05 | 0.04 | 0.05 | 0.14 | 0.11 | 0.10 | 0.11 |
| 16 | 0.02 | 0.03 | 0.03 | 0.03 | 0.09 | 0.06 | 0.07 | 0.07 | 0.13 | 0.10 | 0.09 | 0.11 |
| 18 | 0.04 | 0.03 | 0.04 | 0.04 | 0.10 | 0.04 | 0.10 | 0.08 | 0.11 | 0.11 | 0.09 | 0.10 |
| 20 | 0.03 | 0.03 | 0.03 | 0.03 | 0.09 | 0.06 | 0.10 | 0.08 | 0.14 | 0.13 | 0.06 | 0.11 |
| 24 | 0.02 | 0.06 | 0.03 | 0.04 | 0.08 | 0.04 | 0.07 | 0.06 | 0.08 | 0.10 | 0.05 | 0.08 |
| 28 | 0.03 | 0.05 | 0.05 | 0.04 | 0.08 | 0.07 | 0.08 | 0.08 | 0.11 | 0.10 | 0.05 | 0.09 |
| 32 | 0.03 | 0.04 | 0.05 | 0.04 | 0.06 | 0.05 | 0.05 | 0.05 | 0.11 | 0.08 | 0.06 | 0.08 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 36 | 0.03 | 0.06 | 0.08 | 0.06 | 0.06 | 0.04 | 0.05 | 0.05 | 0.11 | 0.12 | 0.07 | 0.10 |
| 40 | 0.03 | 0.03 | 0.06 | 0.04 | 0.06 | 0.04 | 0.06 | 0.05 | 0.12 | 0.11 | 0.06 | 0.10 |
| 44 | 0.02 | 0.04 | 0.07 | 0.04 | 0.04 | 0.03 | 0.06 | 0.04 | 0.12 | 0.13 | 0.09 | 0.11 |
| 48 | 0.02 | 0.04 | 0.07 | 0.05 | 0.05 | 0.04 | 0.04 | 0.04 | 0.12 | 0.13 | 0.06 | 0.10 |
| 52 | 0.03 | 0.03 | 0.06 | 0.04 | 0.05 | 0.03 | 0.04 | 0.04 | 0.10 | 0.14 | 0.07 | 0.11 |
| 56 | 0.01 | 0.02 | 0.04 | 0.02 | 0.04 | 0.03 | 0.06 | 0.05 | 0.12 | 0.12 | 0.07 | 0.10 |
| 60 | 0.05 | 0.07 | 0.03 | 0.05 | 0.05 | 0.04 | 0.04 | 0.04 | 0.09 | 0.11 | 0.12 | 0.11 |
| 64 | 0.05 | 0.08 | 0.05 | 0.06 | 0.05 | 0.06 | 0.03 | 0.05 | 0.10 | 0.11 | 0.12 | 0.11 |
| 68 | 0.04 | 0.07 | 0.05 | 0.06 | 0.05 | 0.05 | 0.06 | 0.05 | 0.13 | 0.13 | 0.09 | 0.11 |
| 72 | 0.06 | 0.07 | 0.05 | 0.06 | 0.05 | 0.05 | 0.06 | 0.05 | 0.12 | 0.11 | 0.08 | 0.10 |
| 76 | 0.07 | 0.08 | 0.06 | 0.07 | 0.07 | 0.07 | 0.08 | 0.07 | 0.10 | 0.10 | 0.07 | 0.09 |
| 80 | 0.08 | 0.12 | 0.07 | 0.09 | 0.08 | 0.09 | 0.08 | 0.09 | 0.12 | 0.10 | 0.12 | 0.11 |
| 84 | 0.09 | 0.15 | 0.08 | 0.11 | 0.06 | 0.09 | 0.14 | 0.10 | 0.10 | 0.08 | 0.08 | 0.09 |
| 88 | 0.07 | 0.13 | 0.07 | 0.09 | 0.09 | 0.09 | 0.12 | 0.10 | 0.13 | 0.08 | 0.11 | 0.11 |
| 92 | 0.12 | 0.11 | 0.08 | 0.10 | 0.12 | 0.09 | 0.12 | 0.11 | 0.10 | 0.10 | 0.13 | 0.11 |
| | 0.10 | 0.11 | 0.11 | 0.11 | 0.12 | 0.11 | 0.11 | 0.11 | 0.09 | 0.09 | 0.10 | 0.09 |
| 96 | 0.08 | 0.13 | 0.13 | 0.11 | 0.11 | 0.08 | 0.13 | 0.11 | 0.09 | 0.10 | 0.08 | 0.09 |
| 100 | 0.05 | 0.08 | 0.09 | 0.07 | 0.09 | 0.09 | 0.11 | 0.10 | 0.08 | 0.08 | 0.09 | 0.08 |
| 104 | 0.04 | 0.08 | 0.08 | 0.06 | 0.09 | 0.08 | 0.13 | 0.10 | 0.07 | 0.09 | 0.06 | 0.07 |
| 108 | | | | | 0.06 | 0.05 | 0.09 | 0.07 | | | | |
| 112 | 0.05 | 0.04 | 0.05 | 0.05 | 0.03 | 0.05 | 0.04 | 0.04 | 0.06 | 0.13 | 0.07 | 0.09 |

| **Depth [cm]** | **Rotmeer Moor** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **RO1-1** | **RO1-2** | **RO1-3** | **RO2-1** | **RO2-2** | **RO2-3** | **RO3-1** | **RO3-2** | **RO3-3** |
| 1 | 0.00 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.00 |
| 3 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 |
| 5 | 0.03 | 0.02 | 0.01 | 0.02 | 0.01 | 0.01 | 0.03 | 0.02 | 0.04 |
| 7 | 0.03 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.04 | 0.02 | 0.04 |
| 9 | 0.03 | 0.03 | 0.02 | 0.03 | 0.03 | 0.01 | 0.03 | 0.02 | 0.05 |
| 11 | 0.02 | 0.02 | 0.02 | 0.02 | 0.04 | 0.02 | 0.03 | 0.03 | 0.04 |
| 13 | 0.02 | 0.01 | 0.01 | 0.01 | 0.06 | 0.02 | 0.09 | 0.06 | 0.04 |
| 15 | 0.02 | 0.02 | 0.01 | 0.02 | 0.05 | 0.04 | 0.10 | 0.06 | 0.08 |
| 17 | 0.02 | 0.02 | 0.01 | 0.02 | 0.05 | 0.05 | 0.10 | 0.07 | 0.10 |
| 21 | 0.02 | 0.01 | 0.01 | 0.02 | 0.06 | 0.06 | 0.08 | 0.07 | 0.13 |
| 27 | 0.03 | 0.02 | 0.02 | 0.02 | 0.09 | 0.06 | 0.11 | 0.09 | 0.12 |
| 29 | 0.02 | 0.02 | 0.03 | 0.02 | 0.09 | 0.06 | 0.12 | 0.09 | 0.12 |
| 33 | 0.03 | 0.02 | 0.03 | 0.02 | 0.10 | 0.09 | 0.15 | 0.11 | 0.10 |
| 37 | 0.04 | 0.02 | 0.02 | 0.03 | 0.09 | 0.08 | 0.13 | 0.10 | 0.11 |
| 41 | 0.03 | 0.01 | 0.04 | 0.03 | 0.12 | 0.12 | 0.16 | 0.13 | 0.13 |
| 45 | 0.04 | 0.02 | 0.03 | 0.03 | 0.13 | 0.13 | 0.11 | 0.12 | 0.08 |
| 49 | 0.04 | 0.03 | 0.02 | 0.03 | 0.11 | 0.19 | 0.10 | 0.13 | 0.07 |
| 53 | 0.03 | 0.05 | 0.03 | 0.04 | 0.10 | 0.13 | 0.07 | 0.10 | 0.07 |
| 57 | 0.02 | 0.02 | 0.02 | 0.02 | 0.07 | 0.10 | 0.07 | 0.08 | 0.06 |
| 61 | 0.02 | 0.02 | 0.02 | 0.02 | 0.07 | 0.08 | 0.06 | 0.07 | 0.05 |
| 65 | 0.02 | 0.01 | 0.01 | 0.02 | 0.07 | 0.05 | 0.05 | 0.05 | 0.06 |
| 69 | 0.01 | 0.01 | 0.01 | 0.01 | 0.06 | 0.08 | 0.06 | 0.07 | 0.06 |
| 73 | 0.02 | 0.01 | 0.02 | 0.02 | 0.06 | 0.07 | 0.05 | 0.06 | 0.06 |

# B

# Supplemental Material: Rewetting and drainage of nutrient-poor peatlands, indicated by specific bacterial membrane fatty acids and a repeated sampling of stable isotopes ($\delta^{15}N$, $\delta^{13}C$)

**Table B1:** *Nitrogen Stable Isotope Values for all investigated Peatlands in 2013 and 2017; DN: undrained site Degerö Stormyr, DR: Rewetted site Degerö Stormyr; LU: undrained site Lakkasuo, LD: drained site Lakkasuo*

| | Degerö Stormyr | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Depth [cm] | $DU_{17}$ | $DU_{13}1$ | $DU_{13}2$ | $DU_{13}3$ | $DR_{17}$ | $DR_{13}1$ | $DR_{13}2$ | $DR_{13}3$ |
| 1 | -2.58 | -9.95 | -9.03 | -7.18 | -1.21 | -8.48 | -7.47 | -5.39 |
| 5 | -2.72 | -9.31 | -7.15 | -7.71 | -1.74 | -10.64 | -7.44 | -5.01 |
| 9 | -1.84 | -7.05 | -5.43 | -5.13 | -1.50 | -9.97 | -9.25 | -4.57 |
| 13 | -1.58 | -6.32 | -6.04 | -7.06 | -0.40 | -0.29 | -2.72 | -2.89 |
| 17 | -1.93 | -5.72 | -2.57 | -3.76 | 0.35 | -2.86 | 1.07 | 1.83 |
| 21 | -1.39 | -7.07 | -5.32 | -3.68 | 1.75 | -4.43 | -2.29 | 0.17 |
| 25 | -0.83 | -5.14 | -3.83 | -1.74 | -0.35 | -4.78 | -3.81 | -1.53 |
| 29 | -1.05 | -5.93 | -5.72 | -2.57 | -1.12 | -5.13 | -5.97 | -3.81 |
| 33 | -1.05 | -7.20 | -4.80 | -1.34 | -2.45 | -4.68 | -5.37 | -3.69 |
| 37 | -0.71 | -6.81 | -4.59 | -1.04 | -2.15 | -4.93 | -6.96 | -4.47 |
| 41 | -0.48 | -4.53 | -4.63 | -0.40 | -2.61 | -7.68 | -4.37 | -2.67 |
| 45 | -0.71 | -3.94 | -4.41 | -1.55 | -1.79 | -3.85 | -3.69 | -3.03 |
| 49 | -1.17 | -4.29 | -2.49 | -1.45 | -1.70 | -2.34 | -5.77 | -0.97 |
| 53 | -1.74 | -4.13 | -4.13 | -3.13 | -1.20 | -5.21 | -4.68 | -2.56 |
| 57 | -1.82 | -6.07 | -3.90 | -2.94 | -1.39 | -3.07 | -5.46 | -1.74 |
| 61 | -1.24 | -6.79 | -4.25 | -2.08 | -1.42 | -5.39 | -2.76 | -1.46 |
| 65 | -2.41 | -6.25 | -5.28 | -3.87 | -1.06 | -4.63 | -2.93 | -1.44 |
| 69 | -3.00 | -5.53 | -4.86 | -2.71 | -2.00 | -3.85 | -4.17 | -2.28 |
| 73 | -2.23 | -9.70 | -3.85 | -4.03 | -2.60 | -5.68 | -4.57 | -2.78 |
| 77 | -2.29 | -6.82 | -4.18 | -3.12 | -1.03 | -4.48 | -2.57 | -4.39 |
| 81 | -2.16 | | -4.71 | -3.94 | -0.50 | -2.67 | -2.09 | -2.34 |
| | **Lakkasuo** | | | | | | | |
| Depth [cm] | $LU_{17}$ | $LU_{13}1$ | $LU_{13}2$ | $LU_{13}3$ | $LD_{17}$ | $LD_{13}1$ | $LD_{13}2$ | $LD_{13}3$ |
| 1 | -4.73 | -3.46 | -6.49 | -4.92 | -5.24 | -5.45 | -5.39 | -5.70 |
| 5 | -4.79 | -6.44 | -5.33 | -6.41 | -3.48 | -1.76 | -3.93 | -4.12 |
| 9 | -4.48 | -5.80 | -5.46 | -7.56 | -2.93 | -1.32 | -0.91 | -1.79 |
| 13 | -2.30 | -6.09 | -5.91 | -6.01 | -1.69 | 0.19 | -1.03 | -2.45 |
| 17 | -2.06 | -4.88 | -4.29 | -4.54 | -1.53 | -0.46 | -1.82 | -2.13 |
| 21 | -2.77 | -4.70 | -3.29 | -4.18 | -0.25 | -2.41 | -2.92 | -3.89 |
| 25 | -2.64 | -2.87 | -2.54 | -2.83 | -1.56 | -2.63 | -2.09 | -3.65 |
| 29 | -2.90 | -0.91 | -3.12 | -2.34 | -2.15 | -2.31 | -2.27 | -3.52 |
| 33 | -1.47 | -2.28 | -2.41 | -3.16 | -1.06 | -2.14 | -1.45 | -3.96 |
| 37 | -1.33 | -1.39 | -1.75 | -5.01 | -0.85 | -1.52 | -0.07 | -3.69 |
| 41 | -1.18 | -0.51 | -1.54 | -3.05 | -0.99 | -0.91 | -0.33 | -3.12 |
| 45 | -1.58 | -2.19 | -1.69 | -2.55 | -1.06 | -0.94 | -0.59 | -2.56 |
| 49 | -1.27 | 0.62 | -0.31 | 1.51 | -1.05 | -0.97 | -1.36 | -1.83 |
| 53 | -1.88 | -0.56 | -0.11 | -2.64 | -1.58 | -0.19 | -2.13 | -1.10 |
| 57 | -2.57 | 0.04 | -0.49 | -0.35 | -2.59 | -1.94 | -0.55 | -2.89 |
| 61 | -2.12 | -0.37 | -2.12 | -3.00 | -3.31 | -3.16 | -4.33 | -4.68 |
| 65 | -3.22 | -1.69 | -3.26 | | -3.56 | -3.02 | -4.48 | -3.50 |
| 69 | -4.21 | -1.94 | -3.20 | -2.57 | -3.08 | -2.41 | -3.55 | -4.45 |
| 73 | -3.50 | -2.31 | -2.25 | -4.67 | -3.26 | -1.59 | -3.66 | -3.56 |
| 77 | -4.37 | -3.10 | -4.02 | -5.55 | -3.05 | -2.06 | -2.11 | -4.51 |
| 81 | -3.77 | -3.32 | -4.50 | -4.90 | -2.08 | -1.65 | -2.40 | -5.73 |

**Table B2:** *Carbon Stable Isotope Values for all investigated Peatlands in 2013 and 2017; DN: undrained site Degerö Stormyr, DR: Rewetted site Degerö Stormyr; LU: undrained site Lakkasuo, LD: drained site Lakkasuo*

| | **Degerö Stormyr** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Depth [cm]** | **$DU_{17}$** | **$DU_{13}1$** | **$DU_{13}2$** | **$DU_{13}3$** | **$DR_{17}$** | **$DR_{13}1$** | **$DR_{13}2$** | **$DR_{13}3$** |
| 1 | -24.38 | -23.29 | -23.16 | -23.56 | -27.87 | -29.81 | -27.43 | -28.63 |
| 5 | -26.02 | -23.17 | -23.53 | -23.85 | -27.64 | -29.63 | -27.90 | -28.79 |
| 9 | -24.74 | -23.06 | -23.90 | -24.15 | -26.95 | -28.45 | -27.87 | -28.29 |
| 13 | -26.46 | -23.39 | -23.84 | -24.00 | -26.37 | -27.27 | -27.85 | -27.80 |
| 17 | -24.01 | -24.09 | -23.54 | -24.76 | -25.79 | -26.36 | -27.63 | -27.33 |
| 21 | -25.02 | -24.64 | -24.46 | -24.98 | -25.91 | -25.43 | -27.13 | -27.76 |
| 25 | -25.51 | -24.01 | -23.88 | -25.09 | -25.52 | -25.11 | -25.94 | -26.79 |
| 29 | -25.02 | -24.23 | -24.05 | -24.56 | -25.01 | -25.26 | -25.31 | -25.63 |
| 33 | -24.64 | -24.06 | -24.61 | -24.58 | -24.61 | -25.69 | -25.26 | -25.59 |
| 37 | -25.31 | -23.76 | -24.41 | -24.31 | -25.17 | -25.10 | -25.34 | -25.40 |
| 41 | -25.14 | -23.88 | -23.82 | -24.12 | -24.30 | -26.94 | -25.58 | -24.98 |
| 45 | -23.56 | -22.84 | -23.63 | -23.80 | -25.65 | -26.17 | -26.05 | -25.18 |
| 49 | -25.38 | -22.96 | -24.06 | -24.08 | -25.17 | -25.89 | -26.98 | -25.79 |
| 53 | -25.58 | -23.26 | -24.85 | -23.32 | -25.77 | -26.90 | -26.35 | -25.43 |
| 57 | -25.29 | -24.15 | -24.62 | -24.20 | -25.39 | -26.21 | -26.73 | -26.09 |
| 61 | -25.56 | -24.00 | -24.86 | -24.02 | -26.45 | -26.81 | -26.88 | -25.77 |
| 65 | -25.17 | -22.62 | -24.34 | -26.11 | -25.64 | -26.58 | -26.78 | -26.28 |
| 69 | -25.02 | -23.70 | -24.54 | -24.08 | -24.50 | -26.92 | -27.10 | -26.70 |
| 73 | -25.89 | -24.09 | -23.98 | -24.63 | -24.41 | -27.09 | -27.05 | -26.78 |
| 77 | -25.04 | -24.64 | -24.93 | -24.44 | -26.81 | -26.89 | -27.18 | -26.83 |
| 81 | -25.44 | -23.97 | -24.70 | -25.08 | -25.60 | -27.26 | -26.18 | -26.44 |
| | **Lakkasuo** | | | | | | | |
| **Depth [cm]** | **$LU_{17}$** | **$LU_{13}1$** | **$LU_{13}2$** | **$LU_{13}3$** | **$LD_{17}$** | **$LD_{13}1$** | **$LD_{13}2$** | **$LD_{13}3$** |
| 1 | -27.61 | -27.18 | -27.91 | -26.38 | -29.84 | -31.04 | -30.36 | -30.73 |
| 5 | -27.94 | -27.63 | -26.98 | -26.02 | -29.90 | -28.18 | -29.85 | -28.19 |
| 9 | -27.64 | -27.09 | -27.38 | -26.57 | -28.42 | -27.41 | -27.60 | -27.54 |
| 13 | -27.58 | -27.22 | -28.47 | -26.08 | -26.79 | -26.60 | -26.40 | -25.92 |
| 17 | -27.68 | -27.01 | -28.10 | -26.49 | -26.07 | -25.98 | -25.88 | -25.84 |
| 21 | -26.75 | -27.01 | -27.76 | -27.71 | -26.50 | -25.23 | -26.20 | -25.67 |
| 25 | -26.35 | -26.81 | -26.34 | -28.22 | -26.18 | -25.44 | -25.68 | -25.81 |
| 29 | -26.01 | -27.63 | -26.29 | -28.36 | -25.87 | -25.45 | -26.52 | -24.67 |
| 33 | -25.85 | -26.46 | -26.50 | -26.31 | -27.40 | -24.85 | -25.97 | -24.67 |
| 37 | -26.11 | -26.37 | -26.30 | -27.95 | -26.49 | -25.11 | -26.71 | -24.53 |
| 41 | -27.27 | -26.28 | -25.59 | -27.98 | -26.08 | -24.99 | -26.75 | -25.82 |
| 45 | -25.67 | -26.11 | -25.96 | -27.32 | -26.80 | -26.14 | -27.36 | -26.91 |
| 49 | -25.97 | -25.67 | -26.21 | -25.58 | -26.28 | -27.45 | -26.47 | -26.25 |
| 53 | -25.98 | -25.74 | -26.27 | -25.34 | -26.54 | -26.50 | -26.58 | -26.32 |
| 57 | -25.84 | -25.78 | -26.66 | -25.97 | -26.29 | -26.73 | -26.68 | -25.72 |
| 61 | -26.10 | -27.38 | -26.03 | -25.29 | -25.91 | -27.59 | -26.53 | -25.78 |
| 65 | -26.19 | -26.32 | -25.77 | -25.49 | -26.19 | -26.66 | -26.56 | -25.98 |
| 69 | -26.07 | -26.13 | -25.91 | -25.81 | -27.95 | -26.14 | -26.18 | -26.26 |
| 73 | -25.67 | -26.40 | -26.00 | -24.82 | -26.57 | -26.38 | -26.68 | -26.22 |
| 77 | -25.03 | -26.36 | -25.89 | -24.47 | -27.16 | -25.94 | -26.42 | -26.39 |
| 81 | -25.91 | -25.83 | -25.58 | -26.25 | -26.58 | -26.16 | -26.83 | -25.96 |

**Table B3:** *membrane fatty acid quantities for all investigated Peatlands in 2013 and 2017; DN: undrained site Degerö Stormyr, DR: Rewetted site Degerö Stormyr; LU: undrained site Lakkasuo, LD: drained site Lakkasuo; acidobacterial marker: i-C15:0, C16:1ω7c ; general bacterial marker: C14:0, C17:0; fungal marker: C18:2ω6c*

| | Degerö Stormyr | | | | | Undrained Lakkasuo | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **normD [cm]** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** |
| 4-6 | 2..0 | 0.3 | 13.9 | 1.3 | 6.5 | 2..0 | 0.3 | 13.9 | 1.3 | 13.3 |
| 14-16 | 2.3 | 1.5 | 6.2 | 0.9 | 4.4 | 4.1 | 1.4 | 4.1 | 1.0 | 10.1 |
| 22-24 | 3.3 | 3.2 | 4.3 | 1.1 | 2.6 | 3.0 | 0.9 | 3.4 | 0.7 | 2.2 |
| 36-38 | 4.1 | 1.4 | 2.8 | 3,4 | 2.4 | 3.9 | 0.8 | 5.3 | 1.8 | 1.2 |
| 44-46 | 4.5 | 5.3 | 5.3 | 1.7 | 0.3 | 2.9 | 0.1 | 8.2 | 2.3 | 0.1 |
| 60-62 | 1.7 | 1.1 | 5.5 | 0.1 | 0.5 | 2.0 | 0.2 | 6.4 | 1.1 | 0.3 |
| | **Rewetted Degerö Stormyr 1** | | | | | **Drained Lakkasuo 1** | | | | |
| **Depth [cm]** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** |
| 2-4 | 4.5 | 5.4 | 6.1 | 4.3 | 4.6 | 4.5 | 6.1 | 5.4 | 4.3 | 4.5 |
| 4-6 | 9.8 | 3.6 | 0.0 | 0.7 | 2.7 | 3.9 | 0.1 | 4.4 | 6.6 | 13.8 |
| 8-10 | 11.7 | 7.9 | 3.5 | 3.8 | 23.4 | 3.2 | 12.7 | 3.4 | 15.5 | 17.4 |
| 12-14 | 12.8 | 8.3 | 4.1 | 4.2 | 30.8 | 22.5 | 14.7 | 20.7 | 0.1 | 17.9 |
| 16-18 | 15.8 | 12.9 | 6.9 | 7.8 | 60.8 | 28.7 | 9.4 | 27.9 | 1.1 | 12.8 |
| 20-22 | 12.5 | 7.2 | 4.7 | 13.6 | 22.7 | 31.5 | 7.7 | 23.4 | 2.1 | 7.7 |
| 24-26 | 22.7 | 13.4 | 16.6 | 1.9 | 7.9 | 5.0 | 2.0 | 16.7 | 1.4 | 3.0 |
| 28-30 | 11.2 | 8.4 | 7.7 | 2.1 | 7.7 | 6.6 | 5.8 | 11.2 | 1.9 | 4.3 |
| 32-34 | 5.0 | 3.5 | 2.0 | 1.4 | 3.0 | 4.3 | 2.3 | 10.3 | 1.5 | 3.0 |
| 36-38 | 9.6 | 4.0 | 5.8 | 1.9 | 4.3 | 1.0 | 0.8 | 2.1 | 0.3 | 0.8 |
| 44-46 | 4.3 | 2.2 | 2.3 | 1.5 | 3.0 | 0.4 | 0.6 | 0.5 | 0.1 | 0.3 |
| 52 -54 | | | | | | 0.4 | 0.2 | 1.2 | 0.1 | 0.4 |
| 60-62 | 6.3 | 3.2 | 3.4 | 1.6 | 3.4 | 3.3 | 1.4 | 1.8 | 1.2 | 1.1 |
| | **Degerö Stormyr 2** | | | | | **Lakkasuo 2** | | | | |
| **Depth [cm]** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** |
| 2-4 | 2.6 | 2.7 | 3.4 | 2.5 | 2.3 | 2.1 | 0.4 | 2.5 | 0.4 | 10.1 |
| 4-6 | 5.4 | 1.9 | 0.8 | 0.5 | 1.4 | 0.5 | 0.8 | 3.5 | 0.2 | 8.4 |
| 8-10 | 7.2 | 4.6 | 3.1 | 2.5 | 37.6 | 8.0 | 6.7 | 34.6 | 2.3 | 16.1 |
| 12-14 | 14.3 | 11.0 | 11.4 | 5.5 | 42.2 | 10.2 | 9.3 | 32.9 | 2.1 | 12.8 |
| 16-18 | 12.4 | 7.4 | 6.6 | 8.7 | 22.3 | 12.4 | 11.8 | 31.1 | 1.9 | 9.5 |
| 20-22 | 19.4 | 13.8 | 15.0 | 3.8 | 9.9 | 0.5 | 1.0 | 2.1 | 0.2 | 0.8 |
| 24-26 | 6.6 | 4.8 | 4.3 | 1.2 | 4.7 | 4.4 | 4.5 | 12.4 | 1.1 | 5.3 |
| 28-30 | 3.3 | 2.2 | 1.6 | 0.8 | 2.3 | 2.6 | 2.6 | 6.9 | 0.6 | 3.0 |
| 32-34 | 5.5 | 2.3 | 3.6 | 1.1 | 2.8 | 0.7 | 0.7 | 1.3 | 0.1 | 0.7 |
| 36-38 | 2.5 | 1.3 | 1.6 | 0.8 | 1.8 | 0.5 | 0.6 | 1.0 | 0.1 | 0.5 |
| 44-46 | 0.4 | 0.2 | 0.2 | 0.1 | 0.4 | 0.3 | 0.5 | 0.6 | 0.1 | 0.3 |
| 52 -54 | 7.5 | 3.2 | 3.4 | 1.9 | 14.1 | 4.3 | 1.7 | 1.8 | 1.1 | 1.2 |
| 60-62 | 2.6 | 2.7 | 3.4 | 2.5 | 2.3 | 2.1 | 0.4 | 2.5 | 0.4 | 10.1 |
| | **Degerö Stormyr 3** | | | | | **Lakkasuo 3** | | | | |
| **Depth [cm]** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** | **iC15** | **C16:1** | **C14** | **C17** | **C18:2** |
| 2-4 | 3.3 | 3.3 | 4.0 | 2.4 | 7.3 | 4.1 | 19.0 | 48.9 | 0.1 | 36.3 |
| 4-6 | 2.2 | 0.5 | 4.0 | 3.4 | 11.1 | 10.9 | 9.0 | 41.0 | 1.5 | 32.4 |
| 8-10 | 5.6 | 9.7 | 19.0 | 8.9 | 16.8 | 9.3 | 5.8 | 8.7 | 2.2 | 16.1 |
| 12-14 | 16.4 | 12.0 | 26.8 | 1.1 | 15.4 | 11.1 | 8.8 | 10.5 | 4.0 | 8.9 |
| 16-18 | 20.6 | 13.6 | 22.5 | 1.5 | 11.2 | 12.7 | 7.9 | 20.0 | 5.1 | 5.2 |
| 20-22 | 16.0 | 4.4 | 12.8 | 1.2 | 4.3 | 10.5 | 5.0 | 10.8 | 3.7 | 3.0 |
| 24-26 | 4.7 | 3.3 | 14.6 | 1.3 | 4.2 | 8.2 | 5.4 | 11.6 | 4.1 | 3.3 |
| 28-30 | 2.6 | 4.2 | 9.0 | 1.3 | 3.7 | 6.7 | 5.9 | 8.5 | 1.9 | 2.6 |
| 32-34 | 2.5 | 1.5 | 5.8 | 0.8 | 1.9 | 4.9 | 2.5 | 7.1 | 1.2 | 3.0 |
| 36-38 | 1.4 | 1.0 | 3.2 | 0.5 | 1.1 | 5.2 | 2.3 | 7.0 | 1.8 | 3.3 |
| 44-46 | 0.4 | 0.6 | 0.3 | 0.1 | 0.3 | 3.6 | 1.5 | 6.1 | 1.4 | 2.0 |
| 52 -54 | 0.4 | 0.2 | 1.2 | 0.1 | 0.4 | 3.2 | 1.2 | 8.3 | 1.0 | 2.0 |
| 60-62 | 3.3 | 3.3 | 4.0 | 2.4 | 7.3 | 4.1 | 19.0 | 48.9 | 0.1 | 36.3 |

# C

# Supplemental Material: Drainage history of European fens in reflected by stable isotopes ($\delta^{13}C$, $\delta^{15}N$) and membrane fatty acids of microbial communities

**Table C1:** *Vegetation and hydrological regime (HR) of all investigated sites (Emsens et al., 2020; Krüger et al., 2016)*

| Site | HR | Site characterization | Vegetation |
|---|---|---|---|
| Arlon | Undrained | Fen | *Carex appropinquata, Comarum palustre, Calliergonella cuspidata* |
| | Drained | Fen | *Fillipendula, Juncus acutiflorus, Persicaria bistorta, Calliergonella cuspidate, Brachythecium* |
| | Rewetted | Fen | *Carex acutiformis, Sphagnum subnitens* |
| Zwarte Beek | Undrained | Fen | *Carex rostrata, Equisetum fluviatile, Juncus acutiflorus, Lotus uliginosus, Calliergonella cuspidata, Calliergon cordifolium, Eriophorum angustifolia* |
| | Drained | Wet grassland | *Anthoxanthum odoratum, Carex nigra, Holcus lanatus, Brachythecium rutabulum* |
| | Rewetted | Fen | *Caltha palustris, Carex rostrata, Juncus acutiflorus* |
| Binnenveld | Undrained | Fen | *Calliergonella cuspidata, Plagiomnium species, Sphagnum subnitens* |
| | Drained | Wet grassland | *Carex acuta, Holcus lanatus, Phalaris arundinacea, Poa pratensis, Poa trivialis* |
| | Rewetted | Fen | *Carex rostrata, Camarum palustre* |
| Drentse Aa | Undrained | Fen | *Menyanthes trifoliata, Calliergonella cuspidata* |
| | Drained | Wet grassland | *Agrostis stolonifera, Poa trivialis, Ranunculus repens* |
| | Rewetted | Fen | *Carex rostrata, Calliergonella cuspidata, Fontinalis spec.* |
| Gützkow | Undrained | Fen | *Carex appropinquata, Carex nigra, Carex panicea, Juncus subnodulosus, Calliergonella cuspidata* |
| | Drained | Wet grassland | *Carex nigra, Holcus lanatus, Phalaris arundinacea, Poa pratensis, Rhinanthus angustifolius* |
| | Rewetted | Fen | *Carex acuta, Juncus subnodulosus* |
| Peene mouth | Undrained | Fen | *Agrostis stolonifera, Carex appropinquata, Carex nigra, Juncus subnodulosus, Calliergonella cuspidata, Drepanocladus aduncus* |
| | Drained | Wet grassland | *Carex acutiformis, Juncus effusus, Scirpus sylvaticus* |
| | Rewetted | Fen | *Caltha palustris, Carex acuta, Carex disticha, Carex nigra* |
| Kiel | Undrained | Fen | *Filipendula ulmaria, Calliergonella cuspidata, Rhytidiadelphus squarrosus* |
| | Drained | Wet grassland | *Agrostis stolonifera, Alopecurus geniculatus, Poa trivialis, Ranunculus repens* |
| | Rewetted | Wet grassland | *Ranunculus repens, Rhinanthus angustifolius, Calliergonella cuspidata, Rhytidiadelphus squarrosus* |
| Recknitz | Undrained | Fen, little part bog | *Carex nigra, Equisetum fluviatile, Lysimachia thyrsiflora, Menyanthes trifoliata, Comarum palustre* |
| | Drained | Wet grassland | *Poa pratensis, Ranunculus repens* |
| | Rewetted | Fen | *Carex acutiformis* |
| Cuxhaven | Undrained | Fen | *Erica tetralix, Sphagnum fallax, Eriophorum angustifolium Honck, Carex acutifolium* |
| | Drained | Fen | *Erica tetralix, Eriophorum angustifolium Honck* |
| Biebrza | Undrained | Fen | *Carex diandra, Menyanthes trifoliata, Hamatocaulis vernicosus* |
| | Drained | Wet grassland | *Festuca rubra, Poa trivialis, Ranunculus repens, Rumex acetosa, Brachythecium* |

| | | | |
|---|---|---|---|
| | | | *rutabulum* |
| | Rewetted | Fen | *Carex acuta, Carex nigra, Drepanocladus aduncus* |
| Rospuda | Undrained | Fen | *Carex rostrata, Festuca rubra, Menyanthes trifoliata, Aulacomnium palustre, Hamatocaulis vernicosus, Tomentypnum nitens* |
| | Drained | Wet grassland | *Carex cespitosa, Filipendula ulmaria, Holcus lanatus* |
| | Rewetted | Fen | *Carex paniculata, Carex rostrata, Equisetum fluviatile, Calliergonella cuspidata* |
| Suwalszczyzna | Undrained | Fen | *Carex rostrata, Eriophorum angustifolium, Aulacomnium palustre, Calliergonella cuspidata, Drepanocladus aduncus, Helodium blandowii, Marchantia polymorpha, Plagiomnium ellipticum* |
| | Drained | Wet grassland | *Anthoxanthum odorarum, Helictotrichon pubescens, Carex cespitosa, Cirsium rivulare, Filipendula ulmaria, Geum rivale, Geum rivale, Climacium dendroides* |
| | Rewetted | Wet grassland | *Carex acutiformis, Cirsium rivulare, Deschampsia cespitosa, Festuca rubra, Filipendula ulmaria, Galium rivale, Geum rivale, Ranunculus repens* |
| Mazury | Undrained | Fen | *Menyanthes trifoliata, Calliergon giganteum, Calliergonella cuspidata, Hamatocaulis vernicosus, Plagiomnium spec.* |
| | Drained | Wet grassland | *Anthoxanthum odoratum, Festuca rubra, Geum rivale, Poa trivialis, Ranunculus repens* |
| | Rewetted | Fen | *Carex appropinquata, Carex rostrata, Epilobium palustre, Calliergonella cuspidata, Drepanocladus aduncus* |
| Anglesey | Undrained | Fen | *Menyanthes trifoliata, Calliergon giganteum, Calliergonella cuspidata* |
| | Drained | Wet grassland | *Carex acuta, Holcus lanatus, Juncus acutiflorus, Calliergonella cuspidata* |
| | Rewetted | Fen | *Juncus subnodulosus, Molinia caerula, Myrica gale* |

**Table C2:** *Stable isotope bulk values (nitrogen, carbon), clustered for the hydrological regime (undrained: U, drained: D, rewetted: R) and time of rewetting (<10 years (n=6), 10-25 years(n=4), >25 years (n=3))*

| Time [years] | Depth [cm] | $\delta^{15}N$ | | | $\delta^{13}C$ | | |
|---|---|---|---|---|---|---|---|
| | | U | D | R | U | D | R |
| average | | | | | | | |
| | 5 | -1.2, +/-0.8 | 2.8, +/- 0.8 | 2.2, +/- 1.0 | -29.6, +/- 0.5 | -28.8, +/- 0.8 | -29.1, +/- 0.5 |
| | 15 | -0.5, +/- 0.8 | 2.6, +/- 0.6 | 1.9, +/- 1.1 | -28.6, +/- 0.7 | -28.1, +/- 0.8 | -28.5, +/- 0.9 |
| | 45 | 1.3, +/- 1.2 | 1.0, +/- 1.2 | 1.3, +/- 0.3 | -28.4, +/- 0.8 | -28.2, +/- 0.4 | -28.3, +/- 0.5 |
| <10 | | | | | | | |
| | 5 | -0.6, +/- 1.2 | 3.4, +/- 0.7 | 2.6, +/- 1.3 | -29.1, +/- 0.4 | -28.7, +/- 1.2 | -28.9, +/- 0.8 |
| | 15 | 0.2, +/- 1.0 | 2.7, +/- 1.1 | 2.2, +/- 0.7 | -28.3, +/- 0.6 | -27.8, +/- 0.4 | -28.0, +/- 0.5 |
| | 45 | 0.9, +/- 0.8 | 1.4, +/- 1.3 | 0.8, +/- 0.1 | -28.5, +/- 0.6 | -27.9, +/- 0.4 | -28.3, +/- 0.5 |
| 10 - 25 | | | | | | | |
| | 5 | -1.8, +/- 0.5 | 2.3, +/- 0.9 | 0.9, +/- 0.5 | -29.3, +/- 0.7 | -29.0, +/- 0.9 | -29.1, +/- 0.3 |
| | 15 | -0.6, +/- 0.4 | 2.4, +/- 0.5 | 0.8, +/- 1.4 | -28.4, +/- 0.9 | -28.0, +/- 1.1 | -28.6, +/- 0.7 |
| | 45 | 1.0, +/- 1.5 | 0.4, +/- 1.2 | 1.2, +/- 0.5 | -27.9, +1.1 | -28.3, +/- 0.2 | -28.3, +/- 0.5 |
| >25 | | | | | | | |
| | 5 | -1.3, +/- 0.5 | 2.8, +/- 0.7 | -0.3, +/- 1.4 | -29.5, +/- 0.3 | -28.7, +/- 0.3 | -29.5, +/- 0.5 |
| | 15 | -1.1, +/- 0.9 | 2.7, +/- 0.2 | 2.7, +/- 1.1 | -29.1, +/- 1.0 | -28.6, +/- 0.8 | -28.9, +/- 1.4 |
| | 45 | 1.9, +/- 1.2 | 1.9, +/- 1.0 | 2.1, +/- 0.4 | -28.8, +/-0.9 | -28.3, +/- 0.7 | -28.3, +/- 0.6 |

**Table C3:** *Comparison of microbial-derived fatty acid quantities of "Zwarte Beek" for all depth, measured with both methods; black = Ceske Budejovice Lab, grey = Basel Lab*

| Depth [cm] | undrained | | | drained | | | rewetted | | |
|---|---|---|---|---|---|---|---|---|---|
| | Bacteria | Fungi | Total microbes | Bacteria | Fungi | Total microbes | Bacteria | Fungi | Total microbes |
| 5 | 34.48/ 30.27 | 29.64/ 25.44 | 54.02/ 55.09 | 22.68/ 17.56 | 6.86/ 4.89 | 29.54/ 22.45 | 16.98/ 18.32 | 8.63/ 7.56 | 25.61/ 24.88 |
| 15 | 19.42/ 15.75 | 3.66/ 4.57 | 23.08/ 20.32 | 4.94/ 3.25 | 0.24/ 0.87 | 5.18/ 4.12 | 9.13/ 7.89 | 1.53/ 1.67 | 10.66/ 9.56 |
| 45 | 1.93/ 5.42 | 0.32/ 0.02 | 2.25/ 4.44 | 3.65/ 2.34 | 0.27/ 0.16 | 3.91/ 2.50 | 1.35/ 4.73 | 0.02/ 0.04 | 1.37/ 4.77 |

**Table C4:** *Comparison of fungi to bacteria ratio [%] in Zwarte Beek for all depth, measured with both methods; black = Ceske Budejovice Lab, grey = Basel Lab*

| Depth [cm] | F/B | | |
|---|---|---|---|
| | Undrained | Drained | Rewetted |
| 5 | 46.2/ 44.6 | 23.2/ 21.8 | 33.7/ 29.2 |
| 15 | 15.9/ 22.4 | 4.7/ 21.1 | 14.3/ 17.5 |
| 45 | 14.4/ 10.5 | 6.6/ 6.4 | 1.3/ 0.8 |

**Table C5:** *Average carbon:nitrogen ratio (CN) and standard deviation (STDEV), separated for time since rewetting (<10 years (n=6), 10-25 years(n=4), >25 years (n=3))*

| Time [years] | undrained | | drained | | rewetted | |
|---|---|---|---|---|---|---|
| | CN | STDEV | CN | STDEV | CN | STDEV |
| average | | | | | | |
| | 21 | 5 | 13 | 2 | 17 | 4 |
| | 18 | 7 | 13 | 3 | 16 | 3 |
| | 17 | 3 | 17 | 2 | 17 | 4 |
| <10 | | | | | | |
| | 21 | 4 | 12 | 2 | 14 | 3 |
| | 16 | 4 | 12 | 1 | 14 | 1 |
| | 16 | 3 | 17 | 2 | 16 | 1 |
| 10 - 25 | | | | | | |
| | 20 | 2 | 13 | 2 | 19 | 3 |
| | 18 | 3 | 13 | 4 | 16 | 1 |
| | 18 | 4 | 16 | 3 | 19 | 1 |
| >25 | | | | | | |
| | 23 | 4 | 15 | 3 | 22 | 2 |
| | 20 | 2 | 13 | 5 | 19 | 2 |
| | 20 | 4 | 18 | 3 | 18 | 4 |

**Table C6:** *Average microbial-derived membrane fatty acid quantities (µg/g dry weight$^{-1}$), separated for bacteria, fungi and total microbes,*

| Depth [cm] | Average Bacteria | Fungi | Total microbes |
|---|---|---|---|
| 5 | 19.35, +/- 7.20 | 11.62, +/−10.15 | 30.97, +/- 8.67 |
| 15 | 10.22, +/- 4.84 | 2.54, +/- 6.09 | 12.76, +/- 5.47 |
| 45 | 3.36, +/- 2.94 | 0.55, +/- 1.65 | 3.91, +/- 2.30 |

**Table S7:** *Microbial-derived membrane fatty acid quantities (µg/g dry weight$^{-1}$), separated for bacteria, fungi and total microbes, clustered for the hydrological regime (undrained, drained, rewetted) and time of rewetting (<10 years (n=6), 10-25 years(n=4), >25 years (n=3))*

| Time [years] | Depth [cm] | Undrained Bacteria | Fungi | Total microbes | Drained Bacteria | Fungi | Total microbes | Rewetted Bacteria | Fungi | Total microbes |
|---|---|---|---|---|---|---|---|---|---|---|
| all | 5 | 21.06, +/- 6.49 | 20.27, +/−11.49 | 41.33, +/- 8.99 | 16.43, +/- 7.24 | 5.28, +/- 4.01 | 21.71, +/- 5.62 | 20.54, +/- 6.71 | 9.32, +/- 7.04 | 29.86, +/- 6.87 |
| | 15 | 13.21, +/- 5.29 | 5.90, +/- 7.75 | 19.11, +/- 6.52 | 8.31, +/- 4.44 | 0.48, +/- 0.44 | 8.78, +/- 2.44 | 9.14, +/- 4.56 | 1.25, +/- 1.43 | 10.39, +/- 2.99 |
| | 45 | 3.91, +/- 2.71 | 1.26, +/- 1.94 | 5.17, +/- 2.33 | 3.54, +/- 1.93 | 0.17, +/- 0.13 | 3.17, +/- 1.03 | 2.63, +/- 1.39 | 0.23, +/- 0.75 | 2.86, +/- 10.07 |
| <10 | 5 | 20.20, +/- 10.22 | 15.83, +/- 14.42 | 36.03, +/- 12.32 | 13.71, +/- 9.96 | 4.96, +/- 6.76 | 20.06, +/- 8.36 | 22.23, +/- 7.77 | 6.70, +/- 4.98 | 28.93, +/- 6.38 |
| | 15 | 13.29, +/- 7.69 | 7.71, +/- 13.26 | 20.99, +/- 10.47 | 6.62, +/- 1.59 | 0.16, +/- 0.08 | 9.44, +/- 0.83 | 7.60, +/- 3.24 | 0.33, +/- 0.19 | 7.93, +/- 1.72 |
| | 45 | 4.36, +/- 4.04 | 1.83, +/- 3.78 | 6.19, +/- 3.91 | 3.40, +/- 1.23 | 0.9, +/- 0.06 | 4.01, +/- 0.65 | 2.30, +/- 0.45 | 0.26, +/- 0.33 | 2.56, +/- 0.39 |
| 10-25 | 5 | 20.34, +/- 3.16 | 19.37, +/- 8.75 | 39.70, +/- 5.96 | 15.86, +/- 5.71 | 5.20, +/- 2.41 | 20.06, +/- 4.06 | 23.04, +/- 8.26 | 9.17, +/- 6.80 | 33.21, +/- 7.53 |
| | 15 | 11.70, +/- 5.06 | 2.31, +/- 1.14 | 14.01, +/- 3.10 | 8.84, +/- 7.39 | 0.60, +/- 0.75 | 9.44, +/- 4.07 | 10.40, +/- 5.12 | 1.92, +/- 3.39 | 12.32, +/- 4.26 |
| | 45 | 3.64, +/- 1.03 | 0.50, +/- 0.29 | 4.15, +/- 0.66 | 3.76, +/- 1.89 | 0.25, +/- 0.23 | 4.01, +/- 1.06 | 2.39, +/- 1.50 | 0.26, +/- 1.75 | 2.65, +/- 1.63 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| >25 | 5 | 22.64, +/- 6.09 | 25.61, +/- 11.30 | 48.25, +/- 8.70 | 19.73, +/- 6.06 | 6.67, +/- 2.85 | 26.40, +/- 4.45 | 18.37; +/- 4.10 | 11.08, +/- 9.33 | 43.24, +/- 6.71 |
| | 15 | 14.63, +/- 3.13 | 7.69; +/- 8.85 | 22.31; +/- 5.99 | 9.46; +/- 4.34 | 0.67; +/- 0.48 | 10.12, +/- 2.41 | 9.41, +/- 5.33 | 1.50, +/- 0.69 | 10.91, +/- 3.01 |
| | 45 | 3.73, +/- 3.05 | 1.45, +/- 1.76 | 5.18; +/- 2.41 | 3.46, +/- 2.65 | 0.17; +/- 0.09 | 3.63; +/- 1.37 | 3.21, +/- 2.21 | 0.16, +/- 0.16 | 3.37, +/- 1.19 |

**Table C8:** *Fungi to bacterial-derived mFA – ratio, clustered for the hydrological regime (undrained, drained, natural) and time of rewetting (<10 years (n=6), 10-25 years(n=4), >25 years (n=3))*

| Time [years] | Depth [cm] | Undrained | Drained | Rewetted |
|---|---|---|---|---|
| all | 5 | 49.0 | 25.5 | 30.4 |
| | 15 | 30.9 | 5.4 | 12.0 |
| | 45 | 24.4 | 4.6 | 7.9 |
| <10 | 5 | 43.9 | 26.6 | 23.2 |
| | 15 | 36.7 | 2.4 | 4.2 |
| | 45 | 29.6 | 2.7 | 10.2 |
| 10-25 | 5 | 48.8 | 24.7 | 28.5 |
| | 15 | 16.5 | 6.3 | 15.6 |
| | 45 | 12.1 | 6.2 | 9.8 |
| >25 | 5 | 53.1 | 25.3 | 40.4 |
| | 15 | 34.4 | 6.6 | 13.7 |
| | 45 | 27.9 | 4.7 | 4.6 |

**Table C9:** *p-values of all investigated sites for mFA amounts (bacteria, fungi, microbes), separated by time of rewetting and hydrological regime (U = undrained, D = drained, R = rewetted) bold = significance (p ≤0.05)*

| Time [years] | bacteria | | fungi | | microbes | |
|---|---|---|---|---|---|---|
| | D:R | R:U | D:R | R:U | D:R | R:U |
| all | **0.05** | 0.60 | **0.01** | 0.21 | 0.56 | **0.01** |
| | 1.00 | **0.01** | 0.09 | 0.09 | 0.23 | 1.00 |
| | 0.10 | 0.06 | 0.25 | 0.20 | 0.66 | 0.33 |
| <10 | 0.24 | 0.73 | 0.63 | 0.13 | 0.98 | **0.06** |
| | 0.58 | **0.01** | 0.06 | 0.20 | 0.10 | 0.27 |
| | 0.07 | 0.13 | 0.27 | 0.34 | 0.14 | 0.20 |
| 10 - 25 | 0.06 | 0.58 | **0.03** | 0.13 | 0.55 | **0.04** |
| | 0.64 | 0.73 | 0.16 | 0.70 | 0.09 | 0.22 |
| | 0.30 | 0.22 | 0.42 | 0.95 | 0.50 | 0.62 |
| >25 | **0.03** | 0.27 | **0.02** | 0.21 | 0.15 | 0.20 |
| | **0.05** | 0.11 | 0.16 | 0.32 | 0.07 | 0.56 |
| | 0.25 | 0.82 | 0.42 | 0.30 | 0.65 | 0.89 |

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# Curriculum Vitae

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