

1 *Reply to reviewers' comments concerning the manuscript:*

2 ***“C/N ratio, stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ), and n-alkane patterns of bryophytes***  
3 ***along hydrological gradients of low-centred polygons of the Siberian Arctic”***

4 by R. Zibulski et al.

5

6 ***Anonymous Referee #1***

7 *Received 11<sup>th</sup> September 2016*

8

9 We thank reviewer #1 for the valuable comments which have contributed to the improvement of the  
10 article.

11

12 **general comments:**

13 ***Title. why not use brown mosses or equivalent instead of bryophytes?***

14

15 Our response: We changed the title as follows:

16 *"C/N ratio, stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ), and n-alkane patterns of brown mosses along hydrological*  
17 *gradients of low-centred polygons of the Siberian Arctic"*

18

19

20 ***The Title and Abstract suggest that you investigate the effects of a hydrological gradient on  $^{13}\text{C}$ ,***  
21  ***$^{15}\text{N}$ , C/N and n-alkane distribution, but from the paper it remains unclear to me if this really has***  
22 ***been done, i.e., it seems that certain species are labelled meso-hygrophilic/xero-mesophylic, and***  
23 ***compared as such, but the same species may occur in different habitats (water levels) and compared***  
24 ***according to habitat (as is suggested by the title). I would recommend to make this explicitly clear,***  
25 ***already in the Abstract but also throughout the ms. So, make clear how you define meso-hygrophilic***  
26 ***mosses, are these well-known dry habitat mosses OR are you looking at the difference between***  
27 ***individuals in a certain habitat?***

28

29 Our response: We accept the reviewer's comment and have refined the Methods section 'Sampling and  
30 studied moss species'. The parameter h is not the absolute plant position in relation to water-level, it is  
31 the mean plant position calculated from the plot position in relation to water-level of all individuals for  
32 each studied species as an approximation. The classification of habitat types is based on our findings  
33 during the field expedition.

34

35 **comments in the text**

<b>line</b>	<b>reviewer comment</b>
	our response
	adjustments in the text

20ff ***Number of samples: In line 20 you speak about 400 samples from 10 species, and in***  
***line 22 ‘six of these taxa’, it not clear how many samples (from those 400) were***

*investigated for n-alkanes.*

We add the sample number of *n*-alkane measurements in the sentence.

*Additionally, n-alkane patterns of six of these species (n = 16) were investigated.*

**Table A2** *why is there so much variation in the number of samples analysed (n)? n for 15N is lacking*

As we mentioned in the Methods, the C/N ratio of mosses has a wide range. Thus, the high weight needed for the sample replicates for the  $\delta^{15}\text{N}$  measurements meant that in some cases there was not enough material to make this measurement. Furthermore, *n* for  $\delta^{15}\text{N}$  is not lacking, but it seems that the table format was not optimal, so we 'left aligned' the headings and shaded the columns.

The sentence of the isotope methods was added as follows:

*Due to the relatively wide range of C/N ratios of mosses, we used 1.5 mg for each carbon stable isotope measurement and a replicate of 3.0 mg for each nitrogen stable isotope measurement and the analysis of elemental composition. The high weight needed for the nitrogen sample replicates prevented the measurement of  $\delta^{15}\text{N}$  and the C/N analysis for some samples.*

**35** *is '... as a function of microbial symbiosis' also an assumption? If not from which data is this concluded?*

It is an assumption. We refine the sentences as follows:

*We find differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures between both habitat types. For some species of the meso-hygrophilic group, we suggest that a relationship between the individual habitat water-level and isotopic signature can be inferred as a function of microbial symbiosis.*

**37** *... and intermediate (C25) chain length, respectively.'*

We accept the reviewers comment and added the intermediate chain length:

*[...]of n-alkanes with long (*n*-C<sub>29</sub>, *n*-C<sub>31</sub>) and intermediate (*n*-C<sub>25</sub>) chain lengths, respectively.*

**37 - 39** *Be more specific. 'Isotopic and biochemical signals' are mentioned, I recommend using C/N and n-alkanes instead of biochemical. Also 'certain moss taxa' could you mention them?*

*I would be more careful in extrapolating the results to be useful in paleoenvironmental studies, this is not the subject of the ms, [...]*

We accept the comments and changed the sentence as follows:

*Overall, our results reveal that  $C/N_{(wt)}$  ratios, isotopic signals and n-alkanes of studied brown moss taxa from polygonal wetlands are characteristic of their habitat.*

**49** *Do you mean mosses in general with 'their'? the abundance of mosses in peat and permafrost is probably more related to ecology (cold wet conditions), instead of to its intrinsic low decomposition rate.*

Yes we agree with the reviewer, but we mention the advantages for mosses and the 'surface' ecology in the sentence before. For example, we show in Zibulski et al. 2016 the recent vegetation composition on the surface and the dominance of mosses. The commented sentence focused on the buried organic material, which shows, in contrast

to recent vegetation composition, a dominance of mosses. Products of their second metabolic path protect moss material from degradation by fungi and microbial organisms for example.

**51 - 52** *I don't think that little is known about stable isotopes and 'biochemical characteristics' of mosses, the effect of this study (habitat) is very interesting and indeed not much of it is known. In the next sentence (line 56-58) you say that these are the most commonly used parameters, isn't that contradicting?*

*I recommend to use 'n-alkane and C/N ratio' instead of 'biochemical characteristics' throughout the paper. Because the term biochemical characteristics is much broader*

In comparison with vascular plants, little is known. We accept the reviewers comment and refined the sentence to dispel misunderstandings with 'the most commonly used parameters'.

*Despite the significance of mosses in high-latitude biodiversity and matter cycles only little is known about their C/N ratio, stable isotopes and n-alkane characteristics in comparison to vascular plants.*

**60** *microbial material instead of activity?*

We used the reference of Chanway et al. (2014) and they used 'microbial activity'. Furthermore, the microbial activity in such regions depends on a lot of processes and is an important parameter of decomposition.

**75** *Explicitly mention this point earlier (already in the Abstract), because mosses and peatlands are often associated with Sphagnum. Indeed this study is more novel especially of the focus on non-sphagnum mosses, but this is not clear from the beginning and may also solve the other problem mentioned above.*

We accept and changed the term 'mosses' to 'brown mosses' from the beginning.

**104** *This is a very good idea, I would mention this already in the Abstract, see earlier comments. But then I see the Methodology in lines 124-131 and the question arises if this really has been studied because mean values are used to determine its hydrological habitat, thereby losing important information on the effect of water level. Relevant information is missing on how many plants were studied for each of these means and how is the variation within each group?? It is again not clear to me how the two groups (xero-meso and meso-hygro) are defined, on the basis of species or hydrological habitat?*

Due to the unknown 'real plant position in relation to water-level', we think the effects of water-level are expressed in the single representations of results for each individual species with their specific habitat requirements.

**135** *abbreviations have already been used*

We have therefore corrected the sentence as follows:

*The total content of carbon and nitrogen and the ratio of stable isotopes were measured with a DELTAplusXL isotope ratio mass spectrometer [...]*

**178** *perhaps individual instead of single?*

We have changed the sentence as follows:

*The medians of the individual species in the xero-mesophilic group [...]*

- 188 **Fig. 3b?**  
Thank you for this comment, we added the Figure reference.  
*[...] exhibit a positive relationship between  $\delta^{15}N$  values and position relative to the water-level (Fig. 3b).*
- 190 ***If the alkanes are meant to use as a proxy for species or water level, then the data of absolute abundance must be presented as well, as this is highly variable like you indicate here. In a mixture of species like in peat and soil, a certain distribution can only be related to the species (or water level) if differences in absolute abundance is taken into account.***  
We agree with the reviewer's comment and have added the absolute abundances of *n*-alkanes (Table 2). Furthermore, we calculated the ACL<sub>21-33</sub> and the P<sub>aq</sub> for comparison to other data and complete the Discussion section '4.4 *n*-alkane patterns'.
- 195 ***I don't understand this. According to the figure there is not really a species- preferred position all a-d have a -3 and 10 for example. If you look at the highly variable water levels within each species in Fig. 4, then I would not say that the species can be separated into those groups of xero and mesophilic. It must be more explicitly mentioned how these groups are defined, based on what.***  
Due to the added Table 1 and our explanations how we determine the mean plant position in relation to water-level in the Methods section 'Sampling and studied moss species', we think this misunderstanding is dispelled.  
We refined the caption of Fig. 4 as follows: *The relative amounts [%] of n-alkanes with an odd number of carbon atoms in selected brown mosses grouped by species and ordered by their preferences with respect to their mean plant position relative to water-level for xero-mesophilic (a, b) and meso-hygrophilic (c, d) mosses.*
- 196/197 ***I would delete the enter between lines***  
We deleted the line return between both lines.
- 225-226 ***Now I understand it better. This is a pity. It would be very interesting do such a study, correlate the water level to the plant chemistry, at the plant detail, not the plot. It should be made very clear in the Method Section, now I had the impression that it was done on the individual plant level.***  
We are very sorry for the misunderstanding; we have refined the method part to clarify the explanation for the calculation of the mean plant position in relation to water-level.
- 228-229 ***this must be mentioned must earlier.***  
Yes, we now use 'brown mosses' throughout to make it clearer.
- 297 ***but there is a large variability. See line 195***  
Correct, but we do not think it is relevant here.
- 329 ***I do not understand the word choice 'individuals' in the context of the sampling design, see earlier comments***  
We agree with the reviewers comment and changed the word.  
*We also find that n-alkane patterns of recent brown mosses are species' specific characteristics, with only minor modifications imposed by the hydrological conditions.*

333

*no fossil material was studied, so this conclusion cannot be made*

We accept the comment and deleted this conclusion.

*Overall, our study indicates that C/N, isotopic and n-alkane analyses of brown moss material has a high environmental indicator potential [...]*

36 **C/N ratio, stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ), and *n*-alkane patterns of**  
37 **bryophytes brown mosses along hydrological gradients of low-**  
38 **centred polygons of the Siberian Arctic**

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54

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56 **Abstract**

57 Mosses are a major component of the arctic vegetation, particularly ~~of~~in wetlands. We present C/N  
58 ~~ratio; ratios (by weight)~~,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data of 400 brown moss samples belonging to 10 species that  
59 were collected along hydrological gradients within polygonal mires located on the southern Taymyr  
60 Peninsula and the Lena River delta in northern Siberia. Additionally, *n*-alkane patterns of six of these  
61 ~~taxa~~species (n = 16) were investigated. The aim of the study is to see whether the inter- and ~~intra-~~  
62 ~~specific~~intraspecific differences in ~~biochemical and C/N~~, isotopic signatures and n-alkanes are  
63 indicative of habitat with particular respect to water-level. Overall, we find high variability in all  
64 investigated parameters. The  $C/N_{(wt)}$  ratios range between 15.4 and 70.4 (median: 42.943) and show  
65 large variations at ~~intra-specific~~intraspecific level. However, species preferring a dry habitat (xero-

66 mesophilic mosses) show higher  $C/N_{(wt)}$  ratios than those preferring a wet habitat (meso-hygrophilic  
67 mosses). We assume that this mainly originates from the association of mosses from wet habitats with  
68 microorganisms which supply them with nitrogen. Furthermore, because of the stability provided by  
69 water, they do not need to invest in a sturdy stem-structure and accordingly have lower C contents in  
70 their biomass. The  $\delta^{13}C$  values range between -37.0 and -22.5‰ (median = -27.8‰). The  $\delta^{15}N$  values  
71 range between -6.596 and +1.697‰ (median = -2.172‰). We find differences in  $\delta^{13}C$  and  $\delta^{15}N$   
72 signatures between both habitat types ~~and, for. For~~ some species of the meso-hygrophilic group, ~~a~~  
73 ~~significant relation~~ we suggest that a relationship between the individual habitat water-level and  
74 isotopic signature ~~was can be~~ inferred as a function of microbial symbiosis. The *n*-alkane distribution  
75 also shows differences primarily between xero-mesophilic and meso-hygrophilic mosses, i.e. having a  
76 dominance of *n*-alkanes with long (*n*-C<sub>29</sub>, *n*-C<sub>31</sub>) and intermediate (*n*-C<sub>25</sub>) chain lengths ~~(*n*-C<sub>25</sub>)<sub>7,2</sub>~~  
77 respectively. Overall, our results reveal that ~~biochemical and~~  $C/N_{(wt)}$  ratios, isotopic signals and  
78 *n*-alkanes of ~~certain~~ studied brown moss taxa from polygonal wetlands are characteristic of their habitat  
79 ~~and can thus be used in (palaeo-)environmental studies.~~

## 80 1. Introduction

81 Specific physiological and morphological traits enable mosses to attain extensive surface coverage in  
82 low-temperature ecosystems such as arctic tundra (Turetsky et al., 2012; Wasley et al., 2006). Mosses  
83 are a major component of the biomass in arctic wetlands and contribute strongly to the biodiversity. In  
84 particular, the vegetation of the widely distributed polygonal tundra is rich in moss taxa, which partly  
85 originates from the strong compositional turnover along a small-scale hydrologic gradient (Zibulski et  
86 al. 2016). As an intermediate layer between air and the permafrost soil, mosses control the water cycle,  
87 greenhouse gas and energy exchange (Blok et al., 2011; McFadden et al., 2003), and the structure of  
88 the habitats of vascular plant communities in arctic landscapes (Beringer et al., 2001; Gornall et al.,  
89 2011; Malmer et al., 1994). Because of their low decomposition rates (Aerts et al., 1999; Turetsky,  
90 2003), they contribute strongly to the peat and permafrost carbon pool (Tarnocai et al., 2009).

91 Despite the significance of mosses in high-latitude biodiversity and matter cycles only little is  
92 known about their C/N ratio, stable isotope and ~~biochemical~~n-alkane characteristics in comparison to  
93 vascular plants. Such information is not only necessary to improve our understanding of the  
94 physiological adaptation or plasticity of mosses to certain environmental characteristics, but can also  
95 be used when similar measurements of fossil plant material are interpreted as proxies of former  
96 ecological or environmental conditions (e.g. Birks, 1982).

97 Carbon-to-nitrogen ratios (C/N), stable carbon and nitrogen isotope values ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) and the *n*-  
98 -alkane fingerprints of bulk organic matter are among the most commonly measured parameters of  
99 plant matter (Chambers and Charman, 2004). The C/N ratios of mosses are generally in the range of  
100 those of higher terrestrial plants (Prahl et al., 1980) but are known to depend on the available nitrogen,  
101 which originates in pristine regions from decomposition of organic matter, microbial activity or  
102 atmosphere deposits (e.g. Chanway et al., 2014; Lee et al., 2009). We provide C/N ratios by weight of  
103 arctic brown mosses, in anticipation that they will be useful for comparative palaeo-environmental  
104 reconstructions (Andersson et al. 2011, ) and in the evaluation of organic matter sources in Russian  
105 permafrost soils with regard to species and habitat-specific patterns. Furthermore, C/N ratios may be  
106 related to growth form, i.e. higher ratios can be expected for mosses which compete with vascular  
107 plants for light and thus need to invest in a high stem-stability (Sveinbjörnsson and Oechel, 1992).

108 As well as the C/N ratio, the  $\delta^{13}\text{C}$  signature is barely altered by decomposition processes in the  
109 soil and also suitable for palaeo-environmental reconstructions. The  $\delta^{13}\text{C}$  signatures of an individual  
110 plant are a mixed signal of the physiological traits of the species and the individual's direct  
111 environment. Mosses use the  $\text{C}_3$  pathway for carbon assimilation (O'Leary, 1988, Farquhar et al.,  
112 1989) and despite a lack of stomata in the photosynthetic active parts, they have a similar range in  
113 their  $\delta^{13}\text{C}$  values of between -24 and -32 ‰ (Ménot and Burns, 2001; Rundel et al., 1979; Smith and  
114 Epstein, 1971) as vascular  $\text{C}_3$  plants. Differences in  $\delta^{13}\text{C}$  values among several species can be  
115 explained by individual plant physiology and biochemistry (Galimov, 2000). Differences within a  
116 single species have been linked with environmental conditions such as temperature (Skrzypek et al.,  
117 2007; Waite and Sack, 2011), ~~the~~ growing depth below water-level (Raghoebarsing et al., 2005), ~~the~~



118 | position within a cushion or hummock (Price et al., 1997), ~~the~~ lipid content (Rundel et al., 1979) or the  
119 | influence of microbial symbioses (Liebner et al., 2011; Vile et al., 2014). Furthermore, even  
120 | differences among branches and stems of single individuals ~~are~~have been reported (Loader et al.,  
121 | 2007). However, almost all of these studies were made on Sphagnaceae, which are not representative  
122 | of all mosses because of their specific morphology (i.e. the occurrence of a photosynthetic active cell  
123 | type and a dead cell type, which is responsible for water storage and often an additional coating of the  
124 | photosynthetic active cell) and their specific habitat preferences (i.e. preferring acidic wetlands).  
125 | Hence, this information cannot simply be transferred to brown mosses – which form the major  
126 | component in northern Siberian lowlands – due to their different morphology.

127 | Most studies on  $\delta^{15}\text{N}$  values of moss material have focused on the anthropogenic impact on the  
128 | nitrogen cycle (Harmens et al., 2011; Liu et al., 2008; Poikolainen et al., 2009), whereas reports on the  
129 |  $\delta^{15}\text{N}$  signatures of mosses from relatively pristine ecosystems such as the Arctic are rare or have been  
130 | investigated in relation to the study of bird colonies (e.g. Lee et al., 2009). Potentially, such  
131 | information can indicate pathways and sources of the nutrient supply in these N-limited ecosystems  
132 | (Kielland, 1997; Michelsen et al., 1996, 1998).

133 | Compared with vascular plants and *Sphagnum* species, relatively few investigations of *n*-alkane  
134 | patterns of brown mosses are available. ~~*Sphagnum* species, for example, show a dominance of *n*-C<sub>23</sub>~~  
135 | ~~and *n*-Palaeoenvironmental reconstructions use the potential of *n*-alkanes to distinguish between~~  
136 | ~~different plant groups (Ficken et al., 1998, moisture conditions (Pancost et al., 2000, Nichols et al~~  
137 | ~~2006, Zhou et al. 2010), whether organic material is to decomposed and changes in temperature~~  
138 | ~~(Feakins et al., 2016, Sachse et al., 2006) along distinct gradients. *Sphagnum* species, for example,~~  
139 | ~~show a dominance of *n*-C<sub>23</sub> and *n*-C<sub>25</sub> homologues (Baas et al., 2000) that are comparable to the~~  
140 | ~~pattern of vascular submerged plants (Ficken et al., 2000-), and ratios are used as a proxy for wet~~  
141 | ~~moisture conditions.~~ Other studies discuss the suitability of *n*-alkane patterns in moss species for  
142 | chemotaxonomical studies on recent and fossil material (Bush and McInerney, 2013; Nott et al., 2000;  
143 | Schellekens and Buurman, 2011). A ~~higher~~greater protection potential of waxes with a higher content  
144 | of long-chain *n*-alkanes against solar irradiation or alternatively an enhanced loss of short-chain *n*-  
145 | alkanes by evaporation have been suggested as possible mechanisms to cause different *n*-alkane

146 patterns in leaf waxes of trees (Sachse et al., 2006). However, with respect to mosses the pattern and  
147 mechanisms are even less understood.

148 This study presents  $C/N_{(wt)}$  isotopic ( $\delta^{13}C$ ,  $\delta^{15}N$ ) and ~~biochemical~~  $(C/N, n\text{-alkanes})$  alkane  
149 characteristics of mosses from low-centred polygons in northern Siberia. Low-centred polygons are  
150 geomorphological forms in arctic landscapes originating from frost-heave processes in the soil. They  
151 are characterized by elevated dry rims and a water-saturated or water-filled centre. This centimetre-  
152 scale hydrological gradient is well reflected by a strong turnover in the vascular plant and moss  
153 composition (Zibulski et al., 2016). We investigate the relationship between the  $C/N_{(wt)}$  isotopic and  
154 ~~biochemical~~  $n$ -alkane signatures and the hydrological conditions within low-centred polygons. In  
155 particular, we aim to reveal whether fingerprints are habitat-specific or rather species-specific.

## 156 2. Material and methods

### 157 2.1 Sites

158 The plant material was collected from eight low-centred polygons located along a zonal vegetation  
159 gradient ranging from open forest via the forest-tundra intersection to subarctic tundra (Matveev,  
160 1989) to obtain a representative sample set of northern Siberian lowlands (Fig. 1). Six of the polygons  
161 (06/P, 17/P, P3/I, P3/II, P3/III, 12/P), sampled in 2011, are located in the Khatanga River region (70–  
162 72° N, 97–102° E, southern Taymyr Peninsula) and a further two polygons (LP1 and LP2), sampled in  
163 2012, are located on Samoylov Island in the Lena River Delta (72.4° N, 126.5° E). The climate is  
164 cold-humid (Khatanga climate station annual mean temperature and precipitation: -13.2°C and  
165 272 mm, Rivas-Martinez and Rivas-Saenz, 2009; Samoylov climate station annual mean temperature  
166 and precipitation: -12.5°C and 232.7 mm, Boike et al., 2013)).

### 167 2.2 Sampling and studied moss species

168 A representative continuous transect of adjacent one square-metre plots (from rim to rim) was selected  
169 for sampling in each polygon. The surface height in relation to water-level (~~collected~~ measured at the  
170 centre of each plot) and vegetation (abundance information) were recorded. Individual characteristics  
171 of each low-centred polygon are presented in Table A1. Moss plants were hand-picked, dried in the  
172 field and transported to the Alfred Wegener Institute in Potsdam. Taxa identification is based on the

173 relevant literature (Frahm and Frey, 2004; Lobin et al., 1995; Smith, 1978) and the Bryophyte Flora of  
 174 North America internet source (<http://www.efloras.org>).

175 In total, eight species that were observed to have different water-regime preferences were included in  
 176 the analyses. ~~The species were divided into xero-mesophilic and meso-hygrophilic habitat type groups.~~  
 177 ~~Generally the xero-mesophilic group represented by *Hylocomium splendens* (16 cm), *Tomentypnum*  
 178 *nitens* (13 cm), *Aulacomnium turgidum* (13 cm) and *Aulacomnium palustre* (13 cm) can be separated  
 179 from meso-hygrophilic taxa represented by *Hamatocaulis lapponicus* (3 cm), *Warnstorfia exannulata*  
 180 (swimming mat), *Meesia triquetra* (-1 cm), *Drepanocladus revolvens* (-5 cm), *Scorpidium scorpioides*  
 181 (-13 cm), and *Calliergon giganteum* (-30 cm). (Numbers in brackets denote the observed mean plant-  
 182 position relative to the water level.) To approximate water-regime preferences of each species, we  
 183 calculated the mean plant-position in relation to water-level (h) from the recorded plot surface height.  
 184 *Warnstorfia exannulata* was observed to grow as part of a swinging mat at water-level, it was assigned  
 185 a preference for water-level. Using this information the species were classified as either as of xero-  
 186 mesophilic mosses (mean plant-position between 13 and 16 cm in relation to water-level) or to the  
 187 group of meso-hygrophilic mosses (mean plant-position between 3 and -30 cm in relation to water-  
 188 level) to ease the presentation of results.~~

189 **Table 1:** *Calculated mean plant-position relative to the water-level and the classification of the sampled brown moss species.*  
 190 *(\* Samples of *Warnstorfia exannulata* were growing on a swinging mat at water-level and mean plant position was thus set to*  
 191 *zero.)*

<u>species</u>	<u>abbreviation</u>	<u>h (mean plant-position in relation to water-level in cm)</u>	<u>classification</u>
<i>Hylocomium splendens</i>	Hyl_spl	16	xero-mesophilic
<i>Tomentypnum nitens</i>	Tom_nit	13	xero-mesophilic
<i>Aulacomnium turgidum</i>	Aul_tur	13	xero-mesophilic
<i>Aulacomnium palustre</i>	Aul_pal	13	xero-mesophilic
<i>Hamatocaulis lapponi</i>	Ham_lap	3	meso-hygrophilic
<i>Warnstorfia exannulata</i>	War_exa	0 *	meso-hygrophilic
<i>Meesia triquetra</i>	Mee_tri	-1	meso-hygrophilic
<i>Drepanocladus revolvens</i>	Dre_rev	-5	meso-hygrophilic
<i>Scorpidium scorpioides</i>	Sco_sco	-13	meso-hygrophilic
<i>Calliergon giganteum</i>	Cal_gig	-30	meso-hygrophilic

192

## 193 **2.4 Measurements of C/N<sub>(wt)</sub> ratios, stable carbon and nitrogen isotope values and** 194 **n-alkane distributions**

195 Selected plant material (i.e. apical parts of a specimen) ~~were~~was rinsed with de-ionised water and  
 196 mechanically cleaned from organic particulate material. The total content of carbon and nitrogen ( $C_{total}$   
 197 ~~and  $N_{total}$ )~~ and the ratio of stable isotopes ( $\delta^{13}C$ ,  $\delta^{15}N$ ) were measured with a DELTAplusXL isotope  
 198 ratio mass spectrometer (Thermo Fischer Scientific) coupled to an elemental analyser (NC2500 Carlo

199 Erba) via a CONFLOW III Interface. Due to the relatively wide range of C/N-ratios of mosses, we  
200 used about 1.5 mg for each carbon stable isotope measurement and a replicate of 3.0 mg for each  
201 nitrogen stable isotope measurement and the analysis of elemental composition. The high weight  
202 needed for the nitrogen sample replicates prevented the measurement of  $\delta^{15}\text{N}$  and thus the C/N<sub>(wt)</sub> for  
203 some samples. The calibration for carbon was performed using ~~a certified elemental~~ an urea standard  
204 ~~(urea)~~ and a  $\delta^{13}\text{C}$  isotopic standard (IAEA CH-7). The nitrogen contents were calibrated against an  
205 acetanilide standard and the nitrogen isotopic composition with ammonium sulphate standard (IAEA  
206 N-1). The reliability of the method was checked with the NIST plant standard SRM 1547. The isotopic  
207 ratios are given in delta notation relative to VPDB for  $\delta^{13}\text{C}$  values and relative to air for  $\delta^{15}\text{N}$  values,  
208 respectively. The reproducibility for replicate analyses is 0.2% for carbon and nitrogen and 0.2‰ for  
209  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.

210 *n*-Alkane analyses were performed on a subset of samples. We took material from the polygon  
211 complex P3 from the Khatanga region (72.149° N, 102.693° E), which comprises three successive  
212 low-centred polygons (Table A1) to exclude effects of environmental conditions at different locations.  
213 The moss samples were washed, identified and air-dried. They were weighed (150–1000 mg dry  
214 weight) and samples extracted with an accelerated solvent extractor (ASE) (Dionex, Sunnyvale; USA)  
215 using  $\text{Cl}_2\text{Me}:\text{MeOH}$  (10:1) at 5 bar and 75°C. The extract was separated into aliphatic hydrocarbon,  
216 aromatic hydrocarbon and nitrogen, sulphur and oxygen compound fractions using medium pressure  
217 liquid chromatography ~~according to~~ following Radke et al. (1980). Considering the low *n*-alkane  
218 concentrations of our samples, 5  $\mu\text{g}$  of quantification standard (5 $\alpha$ -androstane, 1-ethylpyrene, 5  $\alpha$ -  
219 androstan-17-one and erucic acid) were added. Gas chromatography (GC) of aliphatic hydrocarbon  
220 fractions was performed using a GC Agilent 6890 equipped with an Ultra-1 fused silica capillary  
221 column (Model Agilent 19091A-105, length 50 m, inner diameter 200  $\mu\text{m}$ , film thickness 0.33  $\mu\text{m}$ ).  
222 Helium was used as a carrier gas at a constant flow rate of 1  $\text{ml min}^{-1}$ . The GC oven was heated from  
223 40 °C (2 min hold time) to 300 °C (65 min hold time) at a rate of 5 °C per minute. The samples were  
224 injected by means of splitless injection. Quantitative evaluation of data was done with ChemStation  
225 software. Additionally, we calculate the average chain length (ACL<sub>21-33</sub>) assumed to represent a proxy  
226 for moisture (Andersson et al, 2011) and temperature (Bush and McInerney, 2015) with a

227 comprehensible extended range from  $n\text{-C}_{21}$  to  $n\text{-C}_{33}$  and the proxy ratio  $P_{aq}$ , which was developed as a  
228 proxy ratio to distinguish submerged or floating aquatic macrophytes from emergent and terrestrial  
229 plants (Ficken et al., 2000):

$$ACL_n = \frac{\sum(n \times C_n)}{\sum C_n}, n = 21 - 33$$

$$P_{aq} = \frac{(C_{23} + C_{25})}{(C_{23} + C_{25} + C_{29} + C_{31})}$$

230

## 231 **2.5 Statistical Tests**

232 We calculated the range, .25, .5, and .75 quantiles of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and the  $C/N_{(wt)}$  ratios for all  
233 species (Table A2). Significant differences in the  $C/N_{(wt)}$  ratios and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among  
234 different groups were ~~tested~~assessed with a t-test. In addition, we performed linear regression between  
235 the obtained values for each singleindividual species and surface height. All analyses were  
236 implemented in R version 3.2.0 (R Core Team, 2015). Furthermore, we performed a PCA with the  
237 percentage of  $n$ -alkane homologues (square-root transformed) in R ~~with~~using the vegan package  
238 version 2.0-10 (Oksanen et al., 2013).

## 239 **3. Results**

240 The overall ranges in  $C/N_{(wt)}$  ratios of both groups have a broad overlap (xero-mesophilic: 22.5–67.9;  
241 meso-hygrophilic: 15.4–70.4). However, the medians of the  $C/N_{(wt)}$  values of the xero-mesophilic  
242 species ranging from 47.6 to 52.9 (Fig. 2) are significantly higher than those of the meso-hygrophilic  
243 group, which range from 37.1 to 46.5 ( $t = 8.17$ ,  $p \ll 0.001$ ). The  $C/N_{(wt)}$  ratios among individual  
244 species are not significantly correlated with the water-level (Fig. 3a), except for *Tomentypnum nitens*  
245 ( $r^2 = 0.11$ ,  $p < 0.05$ ).

246 The  $\delta^{13}\text{C}$  values of the meso-hygrophilic group (-34.9 to -22.5‰) cover the range of the xero-  
247 mesophilic group (-32.1 to -24.2‰), which have a noticeably lower variance in  $\delta^{13}\text{C}$  values (Fig. 2).  
248 The medians of the singleindividual species in the xero-mesophilic group (range: -29.4 to -27.1‰) are  
249 not significantly different ( $t = -1.69$ ,  $p = 0.09$ ) from those of the meso-hygrophilic group (range: -29.2

250 to -24.8‰).  $\delta^{13}\text{C}$  values of *Meesia triquetra*, *Drepanocladus revolvens*, and *Scorpidium scorpioides*  
251 (all belonging to the meso-hydrophilic group) are significantly positively correlated with the position  
252 of the water-level (Fig. 3b), while no member of the xero-mesophilic group revealed such relationship  
253 (Fig. 3a).

254 The ranges of  $\delta^{15}\text{N}$  values of both groups are rather similar (Fig. 2). However, individual species  
255 medians of both groups are significantly different ( $t = -6.96$ ,  $p \ll 0.001$ ; xero-mesophilic group; -3.2  
256 to -2.7‰, meso-hydrophilic group: -2.9 to -0.1). *Drepanocladus revolvens*, *Scorpidium scorpioides*,  
257 and *Calliergon giganteum*, all belonging to the meso-hydrophilic group, exhibit a positive  
258 ~~relationship~~ relationship between the  $\delta^{15}\text{N}$  values and position relative to ~~the~~ water-level. (Fig. 3b).

259 *n*-Alkane distributions show the expected ~~odd over even~~ predominance of the odd chain length.  
260 (Table 2). The absolute *n*-alkane concentrations (*n*-C<sub>19</sub> to *n*-C<sub>33</sub>) range from 34 to 238  $\mu\text{g g}^{-1}$  of dry  
261 weight. The individual taxa show significant differences with respect to carbon number of the most  
262 abundant *n*-alkane: (*n*-C<sub>max</sub>) forming unimodal distribution patterns. It is *n*-C<sub>31</sub> for *Tomentypnum*  
263 *nitens*, which is also the only species containing *n*-C<sub>33</sub> in detectable amounts, *n*-C<sub>29</sub> for *Aulacomnium*  
264 *turgidum*, *n*-C<sub>27</sub> for *Aulacomnium palustre*, *n*-C<sub>27</sub> and *n*-C<sub>25</sub> for the *Drepanocladus* taxa, and ~~*n*-C<sub>25</sub>~~ C<sub>max</sub>  
265 = 25 for *Scorpidium scorpioides*. These differences in the *n*-alkane composition largely correlate with  
266 the species-preferred mean plant-position relative to water-level (Fig. 4).

267 ~~The described~~ Evaluations of the *n*-alkane biomarker proxies, ACL<sub>21-33</sub> and P<sub>aq</sub>, also show a clear  
268 division between the xero-mesophilic and the meso-hydrophilic species groups (Table 2), whereas  
269 intraspecific variations are rather small (with the exception of *Drepanocladus*). The xero-mesophilic  
270 group is notable for high averages of ACL<sub>21-33</sub> (28.41) and P<sub>aq</sub> (-0.06) compared to low averages of  
271 ACL<sub>21-33</sub> (25.61) and P<sub>aq</sub> (-0.7) for the meso-hydrophilic group. There are no intersections, with the  
272 exception of *Drepanocladus*.

273 The general trends are also visible in the biplot of the first two PCA axes which together explain  
274 only 16.9% of the variance in the dataset (Fig. 5). The first axis separates xero-mesophilic from meso-  
275 hydrophilic taxa. *Aulacomnium* taxa are located in the upper range and *Tomentypnum nitens* in the

276 lower range of the second PCA axis, while no trend is observed within the meso-hygrophilic group  
 277 along the second axes.

278 **Table 2:** *The concentration ( $\mu\text{g/g}$  dry weight) and  $ACL_{21-33}$  and  $P_{aq}$  (after Ficken et al., 2000) of n-alkanes in*  
 279 *brown moss samples. (Numbers in brackets relates to the sample number.)*

<u>species</u>	<u>n-C<sub>19</sub></u>	<u>n-C<sub>21</sub></u>	<u>n-C<sub>23</sub></u>	<u>n-C<sub>25</sub></u>	<u>n-C<sub>27</sub></u>	<u>n-C<sub>29</sub></u>	<u>n-C<sub>31</sub></u>	<u>n-C<sub>33</sub></u>	<u>ACL<sub>21-33</sub></u>	<u>P<sub>aq</sub></u>
<b>Xero-mesophilic habitat group</b>										
Tom_nit (1)	0	2.0689	2.6374	6.0816	10.7454	17.7273	34.0742	0	28.86	0.13
Tom_nit (2)	0.5571	1.041	1.4493	2.6964	9.1008	8.4867	20.2818	7.2312	29.47	0.11
Tom_nit (3)	0.9936	1.456	2.175	2.8712	9.6118	7.2721	21.2309	4.9717	29.14	0.14
Aul_tur (1)	0	0.968	1.126	2.2001	8.9548	23.5267	3.5595	0	28.15	0.1
Aul_tur (2)	1.028	1.3468	1.2794	4.8797	18.7427	50.9291	5.5645	0	28.22	0.16
Aul_pal (1)	0	1.9298	2.5459	4.7646	20.5085	7.5826	7.979	0	27.35	0.25
Aul_pal (2)	0.7341	1.0767	1.5183	2.9728	12.3293	11.0909	4.9109	0	27.69	0.07
<b>Meso-hygrophilic habitat group</b>										
Dre_rev (1)	0.7868	1.5426	2.3659	43.833	19.0836	5.1551	3.5637	0	25.92	0.58
Dre_rev(2)	0.981	1.5227	2.7605	22.5638	14.5103	6.5356	7.5623	0	26.6	0.34
Dre_sp.	1.4696	1.9968	5.0986	29.6729	30.4582	9.9108	5.1317	0	26.38	0.18
Sco_Sco (1)	0	3.7612	11.7002	133.4207	29.0024	6.2023	1.9425	0	25.3	0.56
Sco_Sco (2)	0	3.8911	10.4693	93.7009	21.4601	5.8531	1.7706	0	25.29	0.40
Sco_Sco (3)	0.8856	2.7949	11.8988	134.378	24.2348	5.4035	2.4969	0	25.28	0.55
Sco_Sco (4)	1.6217	5.5813	11.705	101.7602	21.3126	6.9161	2.4522	0	25.26	0.44
Sco_Sco (5)	1.4083	3.8857	11.8966	121.5701	23.3167	4.315	1.7261	0	25.21	0.41
Sco_Sco (6)	1.345	2.6672	19.4796	170.3015	34.3255	6.8599	3.1732	0	25.28	0.95

## 280 4. Discussion

### 281 4.1 C/N<sub>(wt)</sub> ratios

282 The C/N ratios of mosses from polygonal tundra in Northern Siberia are relatively low—when  
 283 compared with those obtained for mosses from Antarctic bogs that range between 80 and 100 (Björck  
 284 et al., 1991) or from western Canada that range between 55 and 76 (Kuhry and Vitt, 1996). However,  
 285 neither the taxa nor the habitats sampled were fully comparable to those of our analyses, i.e. many  
 286 more taxa typical of xeric and mesic growing conditions were sampled in Antarctica and Canada. All  
 287 investigated species are considered as ectohydric mosses, which receive nitrogen mostly from  
 288 precipitation deposits (Ayres et al., 2006). Our results reveal that C/N<sub>(wt)</sub> ratios for the xero-mesophilic  
 289 moss group are higher than for the meso-hygrophilic group, probably ~~portraying~~ reflecting the known  
 290 difference between terrestrial and aquatic plants (Meyers and Ishiwatari, 1993). Competition with  
 291 vascular plants (1) and accessibility of nitrogen pools (2) may be the main reasons for this finding. (1)



292 If moss plants invest in a high stem-to-leaf biomass ratio, which ~~is reflected by results in~~ a high  $C/N_{(wt)}$   
293 ratio, they will increase their height and stability, ~~resulting in better competition with and thus their~~  
294 ~~competitive ability against~~ vascular plants for light (Sveinbjörnsson and Oechel, 1992). Furthermore,  
295 ~~the low N input by precipitation and~~ a low N content of moss litter slows down the fungal and  
296 bacterial N mineralisation which increases the thickness of moss litter mats (Gornall et al., 2007;  
297 Turetsky, 2003). This in turn will increase the isolating function of moss mats, thus negatively  
298 affecting seed germination of vascular plants (Gornall et al., 2007). (2) ~~Higher~~  $C/N_{(wt)}$  ratios of  
299 ~~meso-hygrophilic mosses may originate from higher~~ amounts of dissolved nitrogen in ~~water due~~  
300 ~~to polygon waters as a result of high net primary productivity, the presence of  $N_2$ -fixation of~~  
301 ~~algae, fixers such as~~ cyanobacteria, and ~~other microorganisms may lead to a lower C/N ratio. the~~  
302 ~~exudations of zooplankton.~~ Frahm (2001) assumes that loose ~~epi-~~epiphytic and endophytic symbiotic  
303 relationships between mosses and cyanobacteria are probably restricted to wetland taxa. Lindo et al.  
304 (2013) report such associations between brown mosses and cyanobacteria. Thus, the N supply is better  
305 for brown mosses preferring ~~wet~~ meso-hygrophilic than ~~dry~~ xero-mesophilic habitats, and the  
306 respective taxa accordingly have lower  $C/N_{(wt)}$  ratios: ~~indicating habitat-specific variation in  $C/N_{(wt)}$~~   
307 ~~ratios.~~ We expected to also find ~~a relationship in~~ intraspecific variations between  $C/N_{(wt)}$  ratios and  
308 water-level. However, the signal-to-noise ratio is probably too low to give a meaningful result because  
309 only the average water level of each plot but not of each individual plant was recorded.

## 310 **4.2 $\delta^{13}C$ values**

311 With respect to bryophytes, most isotopic studies have hitherto been performed on *Sphagnum* (Markel  
312 et al., 2010, Ménot and Burns, 2001) while our study focuses on brown mosses – a major component  
313 in Siberian wetlands. ~~For~~ The intraspecific variability for some meso-hygrophilic species (i.e. *Meesia*  
314 *triquetra*, *Drepanocladus revolvens*, *Scorpidium scorpioides*) ~~we find~~ show that the  $\delta^{13}C$  signals are  
315 significantly related to the hydrological conditions at the growing site of each individual, i.e.  
316 individuals growing at dry sites showed higher  $\delta^{13}C$  values than those growing at wet sites. No  
317 significant difference among the two habitat-groups is observed; rather they partly contradict the  
318 intraspecific findings in that some of the xero-mesophilic species known to prefer dry rims such as



319 | *Hylocomium splendens* and *Tomentypnum nitens* ~~known to prefer dry rims~~ have particularly low  $\delta^{13}\text{C}$   
320 | medians.

321 | Differences in moss  $\delta^{13}\text{C}$  values either reflect a source signal depending on water level or a  
322 | physiological reaction of the plant related to water-level (Bramley-Alves et al., 2014; Proctor et al.,  
323 | 1992). Mosses are typical  $\text{C}_3$  plants (Farquhar et al., 1989, Rundel et al., 1979) characterized by a high  
324 |  $\text{CO}_2$  compensation point (Bain and Proctor, 1980; Dilks and Proctor, 1975; Salvucci and Bowes,  
325 | 1981). The high availability of atmospheric  $\text{CO}_2$  and elevated diffusion rates of  $\text{CO}_2$  in air compared to  
326 | water (O'Leary) result in typical terrestrial  $\text{C}_3$  land plant  $\delta^{13}\text{C}$  characteristics, because of a decreasing  
327 | cell water pressure in dry habitats which entails a strong discrimination rate against  $^{13}\text{CO}_2$  induced by  
328 | RuBisCO (Rice and Giles, 1996). ~~With respect to the xero-mesophilic group, we observe an increase~~  
329 | ~~in discrimination against  $^{13}\text{C}$  from taxa preferring a low position relative to the water-level (e.g.~~  
330 | ~~*Aulacomnium* taxa) than those preferring high positions (e.g. *Hylocomium splendens*). In contrast, if~~  
331 | ~~plant tissue is coated by a water film, the cell water pressure ~~reaches~~ should reach an optimum, which~~  
332 | ~~is expected to~~ results in a weaker discrimination rate against  $^{13}\text{C}$  by RuBisCO (Rice and Giles, 1996),  
333 | because of a source restriction by the slower diffusion rate of  $\text{CO}_2$  in water (Lloyd and Farquhar,  
334 | 1994). ~~This A lower carbon isotope discrimination related to water saturation is observed for only~~  
335 | ~~three species out of six meso-hygrophilic mosses. However, this~~ basic signal may be masked by  
336 | variations in  $\delta^{13}\text{C}$  values of different carbon sources, which are expected to be more influential ~~in~~  
337 | ~~water saturated habitats. As  $\text{CO}_2$  uptake in mosses occurs exclusively by the above soil organs, the  $^{13}\text{C}$~~   
338 | ~~enriched sources of deeper soil sections, originating from simple kinetic fraction by weight within the~~  
339 | ~~vertical soil profile, should not be accessible.~~

340 | ~~for meso-hygrophilic mosses in water-saturated conditions. Ménot and Burns (2001) studied~~  
341 | ~~intraspecific variations for three *Sphagnum* species, which prefer three different habitat types (dry,~~  
342 | ~~meso, wet) along an elevational gradient, which was positively correlated with precipitation. They find~~  
343 | ~~a decline in discrimination against  $^{13}\text{C}$  with increasing wetness, and similar to our results no~~  
344 | ~~relationship for species with a strong wet –preference. This is attributed to the variation in  $\delta^{13}\text{C}$  from~~  
345 | ~~highly varying dissolved inorganic carbon (Proctor et al., 1992). The studies of Ruttner (1947) and~~

346 ~~Bain and Proctor (1980) show that, in general, moss taxa are incapable of bicarbonate uptake. Hence,~~  
347 ~~bicarbonate, known to be a carbon source for submerged vascular plants and algae (Herzschuh et al.,~~  
348 ~~2010; Merz, 1992), can most probably be excluded as a carbon source for moss and thus as a factor~~  
349 ~~influencing the  $\delta^{13}\text{C}$  value. Moreover, the bicarbonate content in pond waters in northern Siberian~~  
350 ~~landscapes is very low (Wetterich et al., 2008).~~ Mosses potentially access  $^{13}\text{C}$ -depleted  $\text{CO}_2$  that  
351 originates from oxidation of typically strongly  $^{13}\text{C}$ -depleted biogenic methane by methanotrophic  
352 microorganisms (Kip et al., 2010; Liebner et al., 2011; Raghoebarsing et al., 2005). Studies by Nichols  
353 et al. (2009) show that a higher water level at the peat surface is crucial for an increasing high  
354 methane-derived  $\text{CO}_2$  release. Furthermore, symbiosis with methanotrophs enhances the moisture-  
355 related effect on the  $\delta^{13}\text{C}$  signal of bryophytes. Endophytic microorganisms in hyalocytes of  
356 submerged *Sphagnum* (Raghoebarsing et al., 2005) or epiphytic microorganisms on submerged brown  
357 mosses (Liebner et al., 2011) are presumed to provide ~~directly~~ $^{13}\text{C}$ -depleted  $\text{CO}_2$  directly to the lamina  
358 cells of mosses. The studies of Ruttner (1947) and Bain and Proctor (1980) show that, in general, moss  
359 taxa are incapable of bicarbonate uptake. Hence, bicarbonate, known to be a carbon source for  
360 submerged vascular plants and algae (Herzschuh et al., 2010; Merz, 1992), can most probably be  
361 excluded as a carbon source for moss and thus as a factor influencing the  $\delta^{13}\text{C}$  value. Moreover, the  
362 bicarbonate content in pond waters in northern Siberian landscapes is very low (Wetterich et al.,  
363 2008). Other sources of  $^{13}\text{C}$ -depleted  $\text{CO}_2$  are surface run-off during spring flooding, rain events ~~or~~and  
364 decomposition processes in the pond (Leng and Marshall, 2004; Maberly et al., 2013). Yet we cannot  
365 fully eliminate the possibility that the measured bulk material was contaminated in parts with ~~epi-~~  
366 epiphytic or ~~endo-phytic~~endophytic microorganisms. The overall signature would, however, likely be  
367 unaffected, as Ménot and Burns (2001) ~~could show~~have shown that the  $\delta^{13}\text{C}$  values of bulk organic  
368 material and alpha-cellulose of *Sphagnum* are very similar. Finally, considering the relationship of  
369 selected brown mosses to mean plant position, the complex origin of plant-available carbon makes it  
370 difficult to interpret the  $\delta^{13}\text{C}$  record, especially for meso-hygrophilic brown mosses as well as  
371 *Sphagnum* (Prince et al., 1997, Ménot and Burns, 2001).

#### 372 4.3 $\delta^{15}\text{N}$ isotopes

373 Like  $\delta^{13}\text{C}$ , the interpretation of stable nitrogen isotope signatures of mosses is challenging because,  
374 again, source signals need to be separated from those originating from physiological isotopic  
375 discrimination processes. Our results yield relatively  $^{15}\text{N}$ -depleted  $\delta^{15}\text{N}$  values for xero-mesophilic  
376 mosses growing preferentially on rims compared to meso-hygrophilic mosses.

377 The terrestrial arctic systems are generally thought to be nitrogen limited (Gordon et al., 2001;  
378 Kielland, 1997). On the rim sites, atmospheric deposition can be considered to be the most important  
379 source for nitrogen (Jonasson and Shaver, 1999) originating from fog, dew, precipitation and surface  
380 run-off (Sveinbjörnsson and Oechel, 1992). However, most of the nitrogen available to rim mosses  
381 originates from recycling of already  $^{15}\text{N}$ -depleted higher plant and moss litter (Turetsky, 2003). The  
382 ectohydric morphology enables an efficient nutrient uptake across the entire moss plant surface via  
383 trapped water. In fact, the meso-hygrophilic group has a higher N content than the xero-mesophilic  
384 group (see section on C/N ratio). Inorganic nitrogen, but especially the high amounts of organic  
385 nitrogen provided by N-mineralization in tundra soils (Kielland, 1995) are important for mosses  
386 growing on the rather dry sites such as the polygonal rims (Atkin, 1996).

387 Three of the investigated submerged or floating moss species show a significant positive  
388 relationship between water-level and  $\delta^{15}\text{N}$  values. These results are similar to those of Asada et al.  
389 (2005) who tested a relationship between  $\delta^{15}\text{N}$  values of different *Sphagnum* species and their position  
390 relative to the groundwater level, which they assumed to originate from different nitrogen sources and  
391 different internal fractionating processes. We assume that the often heavier nitrogen isotope signature  
392 of meso-hygrophilic brown moss individuals originates from the high degree of symbiotic associations  
393 with aquatic atmospheric nitrogen-fixing autotrophic microorganisms such as *Nostoc* or *Anabena*  
394 (Lindo et al., 2013) or methanotrophs (Vile et al., 2014). The high spatial degree with endo- or  
395 ectosymbiotic  $\text{N}_2$ -fixing microorganisms enables the direct uptake of their nitrogen products, which is  
396 similar to that of  $\text{N}_2$  in air.

#### 397 **4.4 *n*-alkane patterns**

398 Compared to vascular plants that are characterized by a thick leaf-wax layer, mosses produce only a  
399 small amount of *n*-alkanes (Baas et al., 2000; Ficken et al., 1998). Like previous studies on vascular

400 plants (Aichner et al., 2010; Ficken et al., 2000; Meyers and Ishiwatari, 1993), our results generally  
401 reveal a differentiation between terrestrial taxa (i.e. xero-mesophilic group) characterized mainly by *n*-  
402 *n*-alkanes maximizing at *n*-C<sub>29</sub> and *n*-C<sub>31</sub> and submerged living taxa (i.e. the meso-hygrophilic group)  
403 maximizing at *n*-C<sub>25</sub> and *n*-C<sub>27</sub>. ~~Our results thus confirm earlier~~ Earlier investigations of Nott et al.  
404 (2000), Baas et al. (2000) and Bingham et al. (2010), who compared the *n*-alkane fingerprints of  
405 *Sphagnum* taxa growing along a hydrological gradient, agree with our results.

406 ~~We furthermore found that individual specimens of a single xero-mesophilic moss species show~~  
407 ~~high variability in their *n*-alkane patterns, potentially originating from significant small scale~~  
408 ~~environmental variability on polygon rims. In contrast, the *n*-alkane patterns of wet habitat taxa cover~~  
409 ~~a small range only, potentially reflecting the buffering function of water, and thus these patterns are~~  
410 ~~promising for chemotaxonomic identification of their remains in peat sequences (Bush and~~  
411 ~~McInerney, 2013; Nott et al., 2000). However, these initial results of our study need to be corroborated~~  
412 ~~with a larger data set.~~

413 Huang et al. (2012a) and Ficken et al. (1998) used proxy ratios (ACL, P<sub>aq</sub>) to divide moss taxa roughly  
414 by their moisture preferences. They calculate the ACL<sub>23-33</sub> for samples of lichens and *Racomitrum*  
415 *lanuginosum*, which have similar hydrological requirements to our xero-mesophilic mosses. Despite  
416 the slightly narrower ACL<sub>23-33</sub> range, their results show similarities to our xero-mesophilic group. A  
417 comparison between ACL<sub>21-33</sub> ratios of *Sphagnum* (plant position nearly at water-level) of Huang et al.  
418 (2012b) and our brown mosses shows that the ACL<sub>21-33</sub> ratios of *Sphagnum* species are rather lower.  
419 The intraspecific conclusion of Huang et al. (2012b) (wetter moisture conditions entail lower ACL<sub>21-</sub>  
420 33) for *Sphagnum* is reflected by our measurements for *Drepanocladus* and *Scorpidium*, i.e. they show  
421 a dependence with water level. As we observed a clear difference in the ACL<sub>21-33</sub> between the xero-  
422 mesophilic and the meso-hygrophilic group, we suggest that the inclusion of mid-chain *n*-alkanes (*n*-  
423 C<sub>21</sub> to *n*-C<sub>25</sub>) in the equation of ACL improves its value as a proxy for moisture conditions. Andersson  
424 et al. (2011) inferred ACL<sub>27-31</sub> values of 29 for brown-moss peat from western Russian during wet  
425 phases, which is however, poorly comparable to our results because they investigated total peat  
426 organic matter instead of pure moss material.

427 Ficken et al. (2000) proposed  $P_{aq}$  as a semi-quantitative proxy ratio for the differentiation of  
428 terrestrial and aquatic plants (<0.1 terrestrial plants, 0.1–0.4 emergent macrophytes, 0.4–1  
429 submerged/floating macrophytes). Our inferred  $P_{aq}$  results for the individual species fit well with these  
430 assumptions. For example, submerged/floating *Scorpidium* ( $P_{aq}$  median: 0.56) has a higher median  $P_{aq}$   
431 value than floating/mesic *Drepanocladus* ( $P_{aq}$  median: 0.34), which is again higher than that of the  
432 xero-mesophilic mosses *Tomentypnum* ( $P_{aq}$  median: 0.13) and *Aulacomnium* ( $P_{aq}$  median: 0.13).  
433 Ficken et al. (2000) also measured a *Drepanocladus* sample ( $P_{aq} = 0.30$ ). Overall, our results do not  
434 support the inference of Nichols et al. (2006) that a hydrological classification is possible between  
435 *Sphagnum* and non-*Sphagnum* formed peat as the latter show wide variations between different  
436 habitats. The inferred broad  $P_{aq}$  range of *Drepanocladus* and *Aulacomnium* probably indicates that  
437 intraspecific variation is related to the individual's growing condition, which could provide the basis  
438 to develop  $P_{aq}$  as a proxy for water-level when measured on taxonomically identified fossil plant  
439 material.

440 As with  $P_{aq}$ , *n*-alkanes seem to be species-specific given stable environmental parameters and are  
441 related to the species-specific moisture requirements, which are adapted to changing environmental  
442 conditions. Thus, our results confirm the conclusions of Bingham et al. (2010), Bush and McNerney  
443 (2015) and Nott et al. (2000) that the pattern of *n*-alkanes has the potential to become a valuable proxy  
444 for chemotaxonomic identification and moisture conditions. *Scorpidium scorpioides*, a species with a  
445 rather narrow preference range (i.e. it is limited to open water conditions), shows low intraspecific  
446 variations. This matches the results for *Sphagnum* compiled by Bingham et al. (2010), which also  
447 show minor intraspecific variations. *Aulacomnium* in contrast, which grows in a rather wide range of  
448 moisture conditions, shows strong variations in its *n*-alkane spectra: whether this is a function of the  
449 individual's growing conditions, however, needs to be investigated in a more extensive study.

## 450 **5. Conclusions**

451 The habitat and intraspecific isotopic and chemical patterns of 10 brown-moss species detected along  
452 small-scale hydrological gradients in Siberian polygonal tundra ~~was~~were studied.

453 The observed higher C/N<sub>(wt)</sub> ratios of xero-mesophilic mosses compared to those of the meso-  
454 hygrophilic mosses originate from the different ~~trait~~environmental requirements when living emergent  
455 (i.e. investment in a higher stability resulting in high C/N ratios) as opposed to submerged.  
456 Furthermore, the latter group may also gain a better nitrogen supply through microbial symbioses.

457 With respect to the isotopic source pools, the meso-hygrophilic species have greater access than  
458 xero-mesophilic species, probably through symbioses with microorganisms- and dissolved carbon. The  
459 approximate habitat-specific division of  $\delta^{13}\text{C}$  values resulting from discrimination by RuBisCO under  
460 different hydrological regimes, is overturned by the influence of microbial symbioses and makes a  
461 clear distinction between both habitat types impossible. For species, growing near the water level, no  
462 intraspecific relationship with water level was observed probably as a result of the parallel impact of  
463 processes causing opposing  $\delta^{13}\text{C}$  trends.

464 Our analyses reveal that, compared with xero-mesophilic mosses, meso-hygrophilic mosses are  
465 characterized by enriched  $\delta^{15}\text{N}$  values probably originating from microbial symbioses. Both carbon  
466 and nitrogen isotopic ratios seem to be valuable proxies to differentiate between taxa preferring the  
467 polygon rim or pond. Moreover, with respect to meso-hygrophilic mosses, the detected positive  
468 relations between intraspecific variations and the individuals' relative growing position could allow  
469 even more semi-quantitative information about water-level changes to be inferred. The *n*-alkane  
470 patterns of brown mosses (limited 16 individuals belonging to five species) indicate that they are  
471 species-specific and have thus the potential to be developed as a chemotaxonomic proxy.

472 ~~We also find that *n* alkane patterns of brown mosses are characteristic for single species as well~~  
473 ~~as for the individuals' specific hydrological growing conditions. However, the potential~~  
474 ~~chemotaxonomic and proxy value of *n* alkane analyses needs to be further explored in a more~~  
475 ~~extensive study.~~

476 Overall, our study indicates that C/N, isotopic and ~~biochemical~~*n*-alkane analyses of ~~recent or~~  
477 ~~fossil~~brown moss material has a high environmental indicator potential, particularly if species-specific  
478 material, ~~because of the physiological characteristics of mosses~~, instead of bulk material is analysed.

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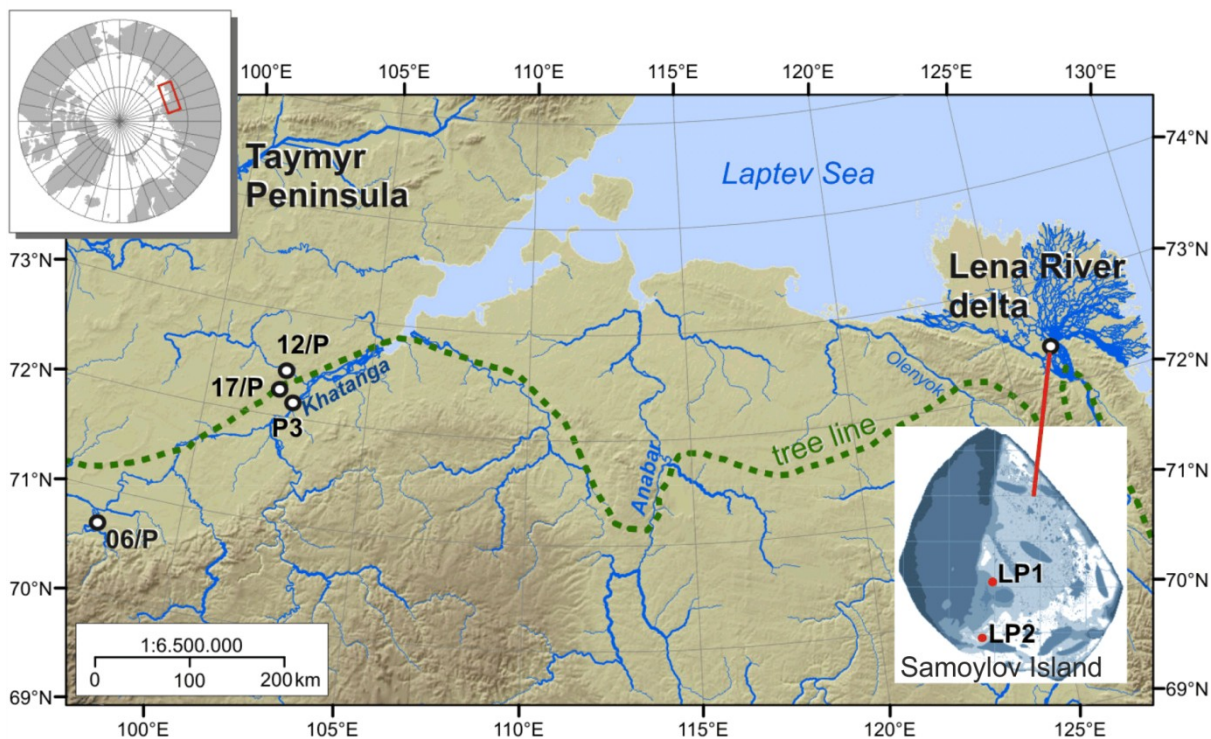
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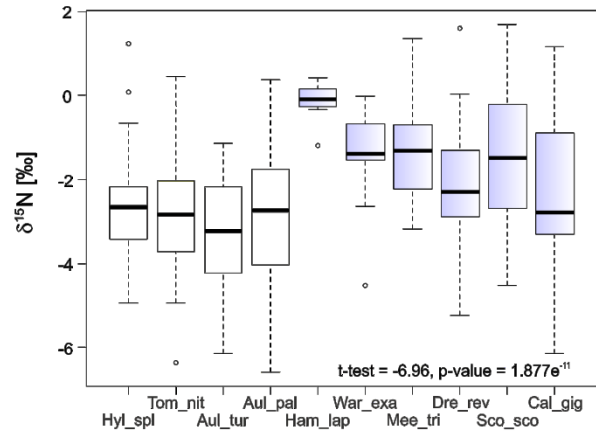
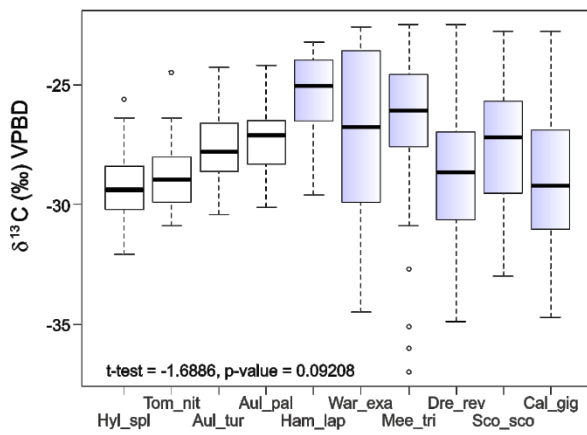
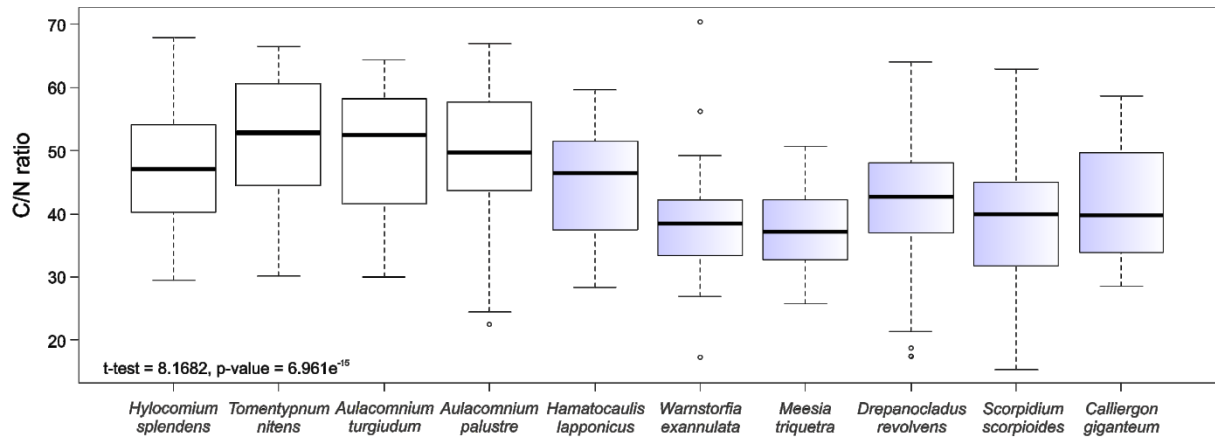
718 **Figures**



719

720 *Fig. 1: The Khatanga study sites are located in the south-east of the Taymyr Peninsula and both the sites on*  
721 *Samoylov Island are in the southern Lena River delta (Map by Th. Böhmer).*

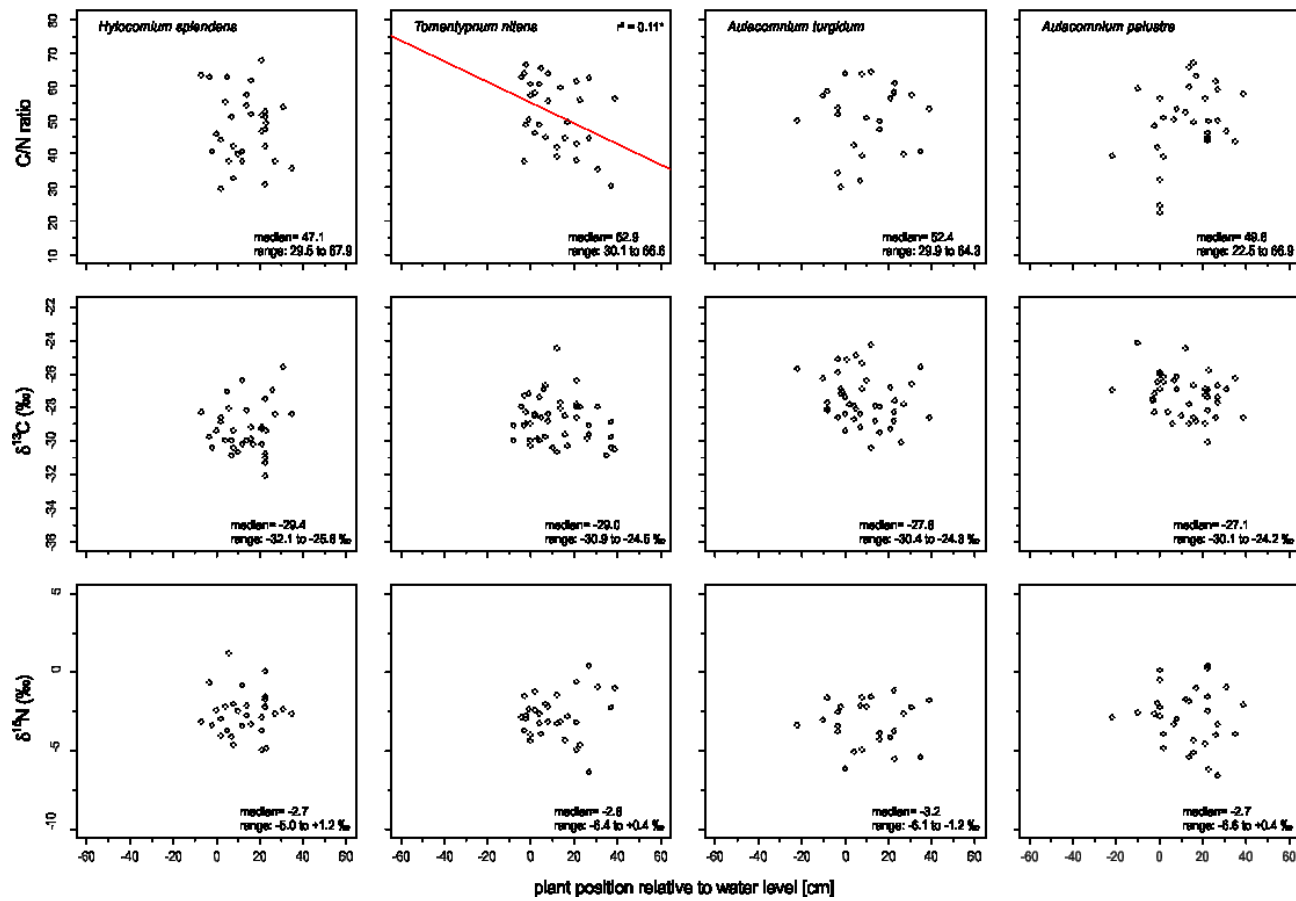
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724 **Fig. 2:** *C/N ratios by weight,  $\delta^{13}C$  and  $\delta^{15}N$  values of the 10 moss taxa studied. White boxplots are the xero-*  
 725 *mesophilic group and boxplots shaded in blue are the meso-hygrophilic group ~~which prefers mesic to wet~~*  
 726 *moisture conditions. A t-test was done to distinguish the signals between both the two habitat groups.*

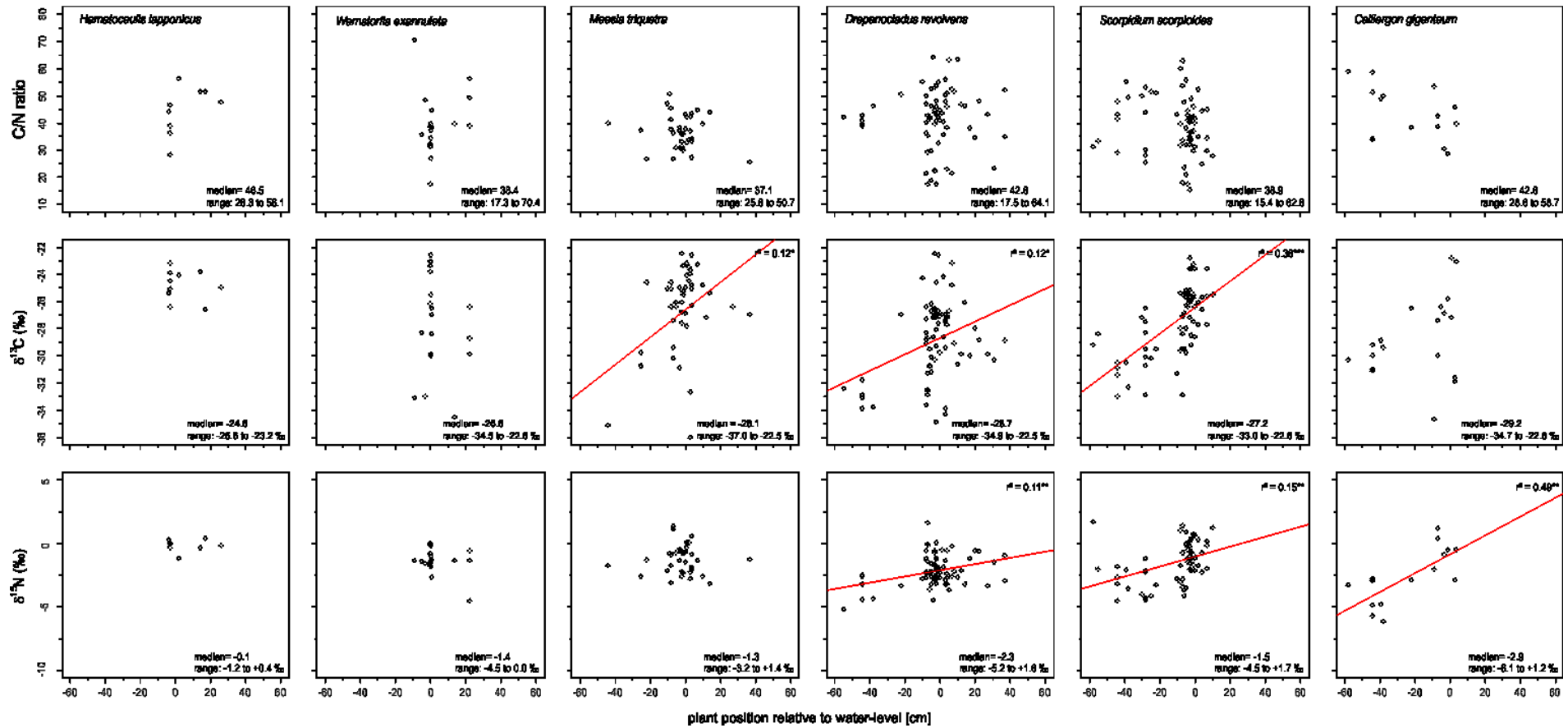
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729 | **Fig. 3a:** Intraspecific relationships of the  $C/N_{(w)}$  ratio and the stable isotope values of carbon and nitrogen related to the water-level of the xero-mesophilic moss group.  
 730 Regression lines (red) are only plotted for significant data sets.

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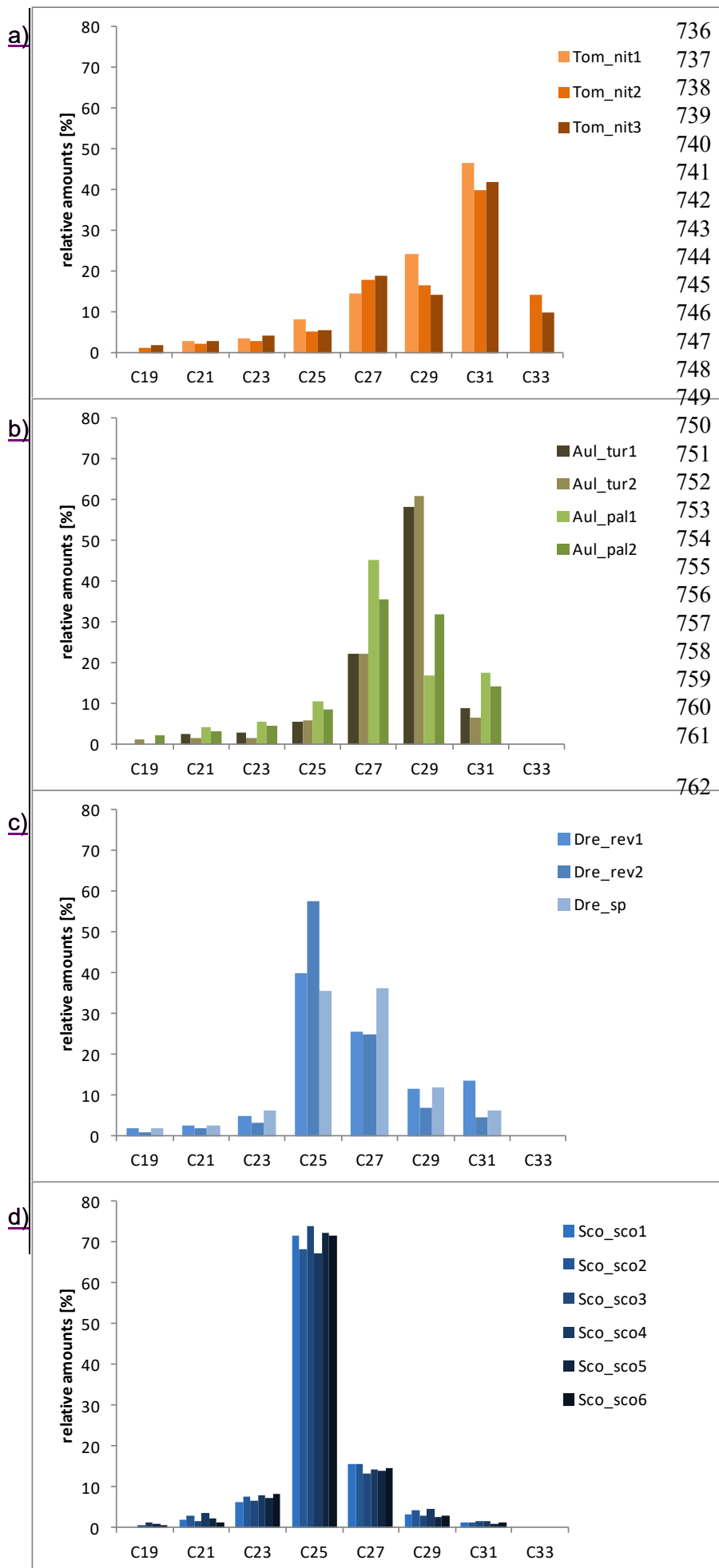


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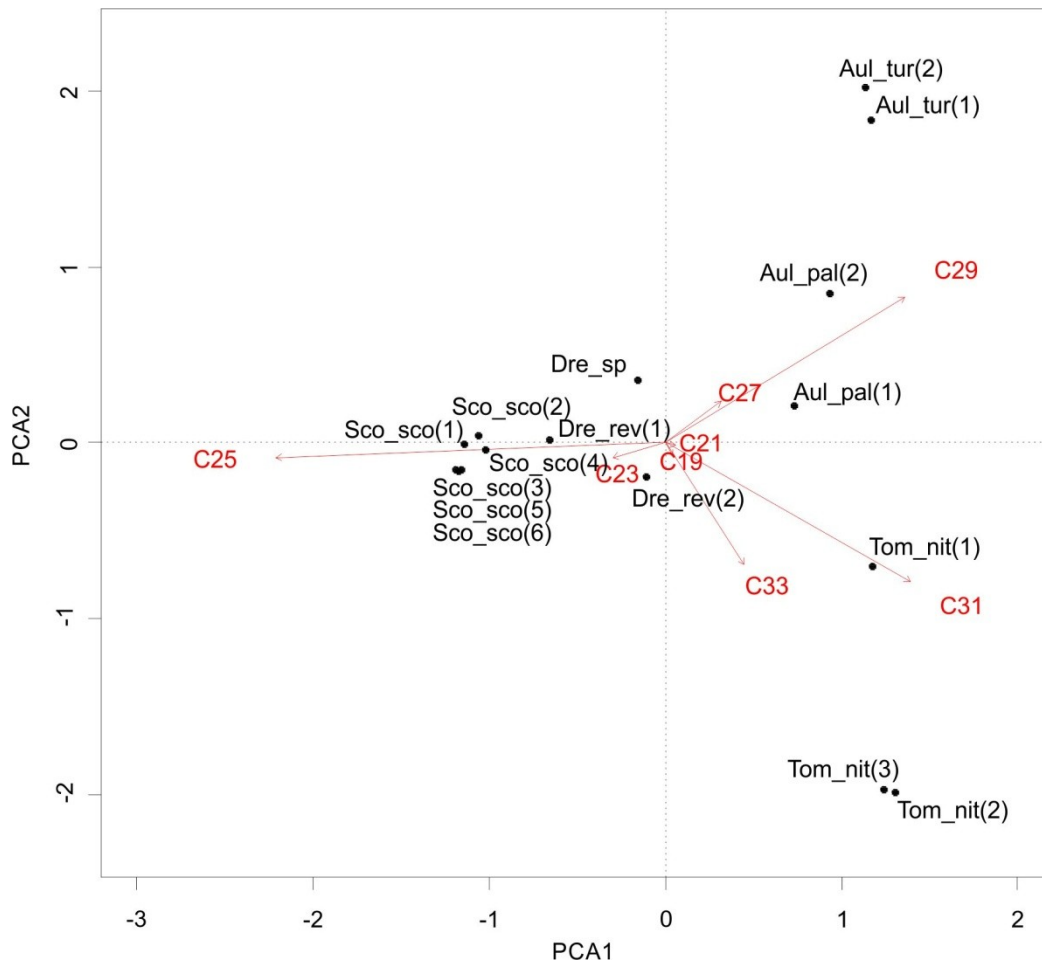
733 | **Fig 3b:** Intraspecific ~~relations~~relationships of the  $C/N_{(wt)}$ -ratio and the stable isotope values of carbon and nitrogen related to the water-level of the meso-hygrophilic moss  
 734 group. Regression lines (red) are only plotted for significant data sets.

735





**Fig. 4:** The relative amounts [%] of n-alkanes with an odd number of carbon atoms in selected moss species along the P3 polygon complex (species code plus position in metres at P3) brown mosses grouped by species and ordered by their preferences with respect to their mean plant-position relative to water-level from dry for xero-mesophilic (a) to wet (, b) and meso-hygrophilic (c, d). Additionally, the sample-specific water level in cm is given after the species code in square brackets) mosses. Tom-nit: Tomentypnum nitens; Aul\_tur: Aulacomnium turgidum; Aul\_pal: Aulacomnium palustre; Dre\_rev: Drepanocladus revolvens; Dre\_sp: Drepanocladus sp.; Sco\_sco: Scorpidium scorpioides


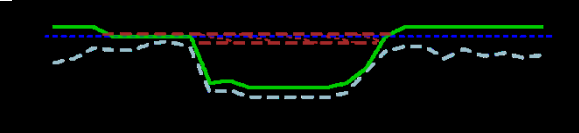
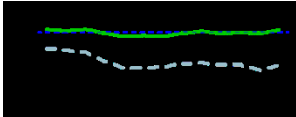
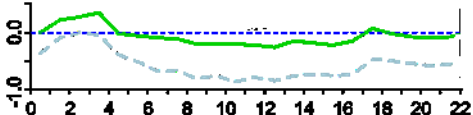
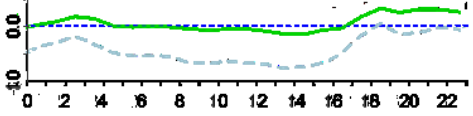
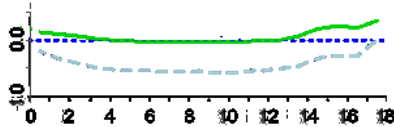
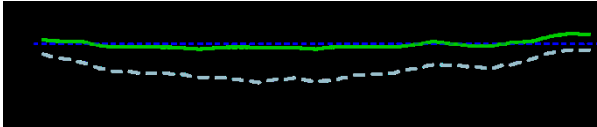
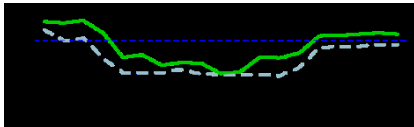
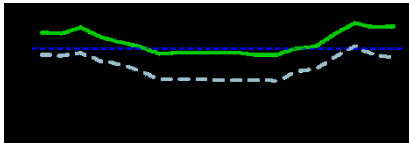


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764 **Fig 5:** PCA of n-alkanes separates the meso-hygrophilic group on the left side of axis 1 from the xero-mesophilic  
 765 group on the right side. Along the second axis the Aulacomniaceae are distinguished from Tomentypnum nitens  
 766 according to the distribution of long-chain n-alkanes with more or less than 30 carbon atoms.

767

769 **Table A1:** Brief description of studied polygons. (For further information see Zibulski et al., 2016)

polygon cross section, (length of transect = polygon size)		coordinates	short description vegetation type; additional information
		70.666° N, 97.708° E	open forest; swinging bog (mat of mosses)
		72.243° N, 102.233° E	forest-tundra intersection; shallow and sparsely vegetated
		P3/I	forest-tundra intersection; a complex of three individual polygons:
		P3/II	P3/I - deep, open water body
		P3/III	P3/II - shallow, open water body
		72.431° N, 102.373° E	tundra; shallow and vegetated
		72.375° N, 126.483° E	tundra; deep polygon without thaw depth below the water body
		72.370° N, 126.481° E	tundra; shallow and vegetated

771 | **Table A2:** C/N ratio *by weight*,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data of individual mosses depending on their position relative to the water-level (cm).

Species	C/N <sub>(wt)</sub> ratio		$\delta^{13}\text{C}$ [‰]			$\delta^{15}\text{N}$ [‰]		
	median	range	n	median	range	n	median	range
<i>H. splendens</i> (Hyl_spl)	47.1	29.5 to 67.9	34	-29.4	-32.1 to -25.6	31	-2.7	-5.0 to +1.2
<i>T. nitens</i> (Tom_nit)	52.9	30.1 to 66.6*	46	-29.0	-30.9 to -24.5	30	-2.8	-6.4 to +0.4
<i>A. turgidum</i> (Aul_tur)	52.4	29.9 to 64.3	41	-27.8	-30.4 to 24.3	24	-3.2	-6.1 to -1.2
<i>A. palustre</i> (Aul_pal)	49.6	22.5 to 66.9	40	-27.1	-30.1 to -24.2	30	-2.7	-6.6 to +0.4
<i>H. lapponicus</i> (Ham_lap)	46.5	28.3 to 56.1	10	-24.8	-26.6 to -23.2	9	-0.1	-1.2 to +0.4
<i>W. exannulata</i> (War_exa)	38.4	17.3 to 70.4	20	-26.8	-34.5 to -22.6	19	-1.4	-4.5 to 0.0
<i>M. triquetra</i> (Mee_tri)	37.1	25.8 to 50.7	45	-26.1	-37.0 to -22.5*	34	-1.3	-3.2 to +1.4
<i>D. revolvens</i> (Dre_rev)	42.6	17.5 to 64.1	72	-28.7	-34.9 to -22.5*	67	-2.3	-5.2 to +1.6**
<i>S. scorpioides</i> (Sco_sco)	38.9	15.4 to 62.8	69	-27.2	-33.0 to -22.8***	65	-1.5	-4.5 to +1.7**
<i>C. giganteum</i> (Cal_gig)	42.6	28.6 to 58.7	21	-29.2	-34.7 to -22.8	17	-2.9	-6.1 to +1.2**

772 Stars designate significant linear regressions between parameter and the plant position relative to water-level (\* p≤0.01, \*\* p≤0.05,  
773 \*\*\* p≤0.001).  
774  
775