Reply to editors' comments concerning the manuscript:

"C/N ratio, stable isotope ($\delta^{13}C$, $\delta^{15}N$), and n-alkane patterns of bryophytes along hydrological gradients of low-centred polygons of the Siberian Arctic"
by R. Zibulski et al.

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We thank editor for the valuable comments which have contributed to the improvement of the article.

General comments and comments in the text

line	*reviewer comment*
	our response
	adjustments in the text

1. Regarding ratio C to N. The reviewer did not mean necessarily that you added the word "by weight". I would rather change it to molar ratio to make it comparable con literature. For instance (Meyers and Ishiwatari 1993, used (as it was described originally) molar ratio.

We calculated the molar ratios, and we changed the text and figures 2, 3a, and 3b.

2. Abstract. Sentence "…ratios (by weight), δ13C and δ15N data of 400 brown …⸮⸮"" is misleading since there is data for less than 20 samples not 400. Please change accordingly.

We describe it correctly. There were 400 samples for isotopic and elementary measurements (as we described in the information about individual *n* for each species in table A2) and only 16 samples for the *n*-alkane study.

We added the sample counts for each measurement and changed the method part as follows:

Due to the relatively wide range of C/N ratios of mosses, we used about 1.5 mg for each carbon stable isotope measurement (n = 400) and a replicate of 3 mg for each nitrogen stable isotope measurement (n = 326) and the analysis of elemental composition.
n-Alkane analyses were performed on a subset of 16 samples.

120   *3. Regarding word "preferred". Is it proven that there is preference? Or just they are there? Please change accordingly.*

Plant distribution depends on water-level and the importance of micro relief for bryophyte species distribution was demonstrated in the paper "Vegetation patterns along micro-relief and vegetation type transects in polygonal landscapes of the Siberian Arctic" (Zibulski et al., 2016). The studied species show an azonal distribution depending on water-level gradient (micro relief) within low-centred polygons. Furthermore, we calculated the mean plant height for this dataset, which matches with our field observations and the descriptions in the relevant literature for these well-known species and thus we consider the use of "preferred" acceptable in this instance.

123-124   *4. "Furthermore, because of the stability provided by water, they do not need to invest in a sturdy stem-structure and accordingly have lower C contents in their biomass." In an abstract, you convey the message of your results; you did not study sturdiness of mosses,*

Did you?

That is correct, we have now deleted this assumption and the relevant sentences.

5. I understand the term "signature" for d13C, and d15N, but you really mean isotopic composition. I don′t see why not use proper terms.

We accept the editor's comment and changed the term from signature to composition in the whole manuscript.

6. Abstract, Line 119. Your statistic results in significant differences, but it appears that there are large standard deviations (Fig. 3) and not much differences are evidence in C/N. Are you sure that all requirements for a t-test are fulfilled? Normality, homoscedasticity, etc. C/N of Hylocomium splendens (xero-mesophyloic) and of Hamatocaulis lapponicus (meso hygrophylic) in Fig. 3 are essentially the same but different according to the statistics. What is the value of this information to make it to the abstract ("main findings")? Please change accordingly.

The value of this information is the difference between moisture conditions. Some of the species with large standard deviations show an expected intraspecific variability between the measured parameter and water-level.

We have checked the $C/N_{(m)}$ data against normality giving the following result:
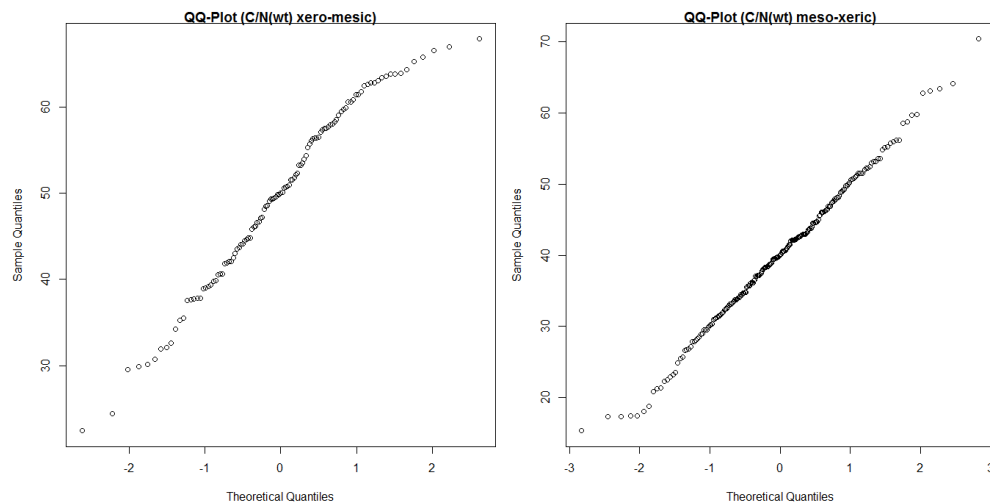
The xero qq-plot looks weak for normality, and the sharp Shapiro-test for this group (`W = 0.97474, p-value = 0.02839`) failed the t-test for normality, but the t-test is robust against infringement of the requirements for data with n>30 ($n_{(xm)}$ = 152).

Additionally, we tested the homoscedasticity of the data with the following results:
```
Levene's Test
      Df F value Pr(>F)
group  1  0.6606 0.4169

Two Sample t-test
t = 8.1707, p-value = 6.841e-15
```
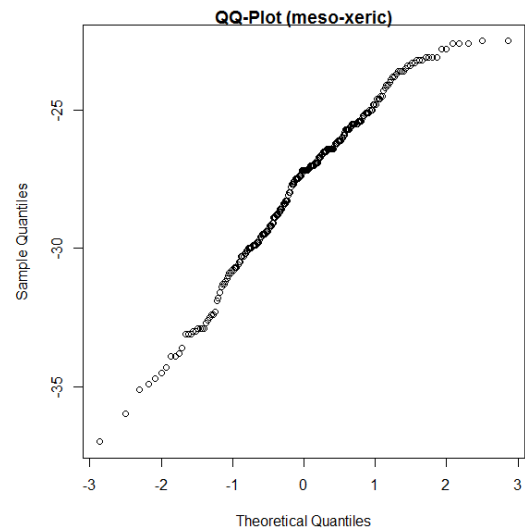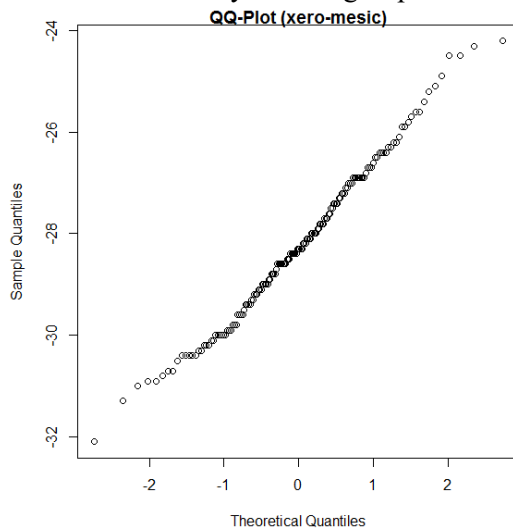
Also a Mann-Whitney-U test, to ascertain the differentiation of both groups, gave a significant result for the C/N ratio:
```
W = 18280, p-value = 1.83e-13
```

We can conclude that both groups are non-identical (`α=0.05`).

2

#+++++++++++++ $d^{13}C$

Check for normality of both groups:


```
Shapiro-Wilk normality test
W = 0.97466, p-value = 0.0002813 → failed
```

Homoscedasticity for $d^{13}C$ is also not evidenced:

```
Levene's Test
      Df F value  Pr(>F)
group  1   52.03 2.78e-12 ***  → failed
```
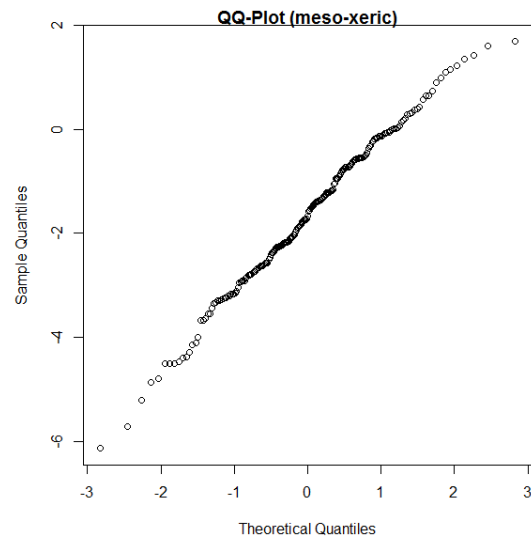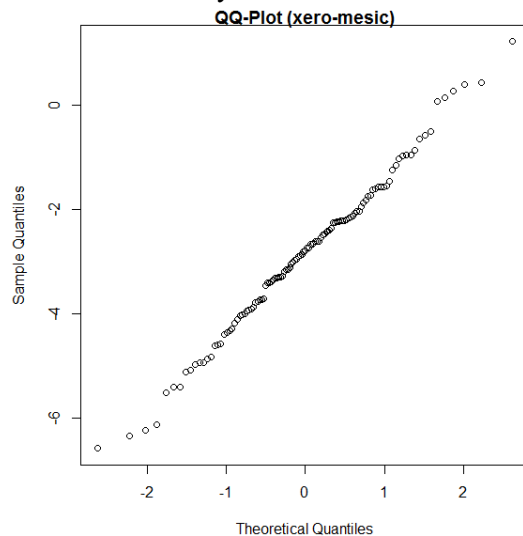
Due to the heteroscedasticity of $d^{13}C$ data and the failed normality, we used the Mann-Whitney-U test

```
W = 16232, p-value = 0.007988   → new result
```

We can conclude that both groups are non-identical ($\alpha=0.05$).

#+++++++++++++ $d^{15}N$

Tests of Normality:


```
Shapiro-Wilk normality test
W(xm) = 0.99295, p-value = 0.8285
W(mh) = 0.99304, p-value = 0.4156
```

Homoscedasticity

```
Levene's Test
      Df F value Pr(>F)
group  1  0.0135 0.9076

Two Sample t-test
t = -6.9599p-value = 1.878e-11
mean in group 1 mean in group 2
    -2.869826       -1.664576
```

We can conclude that both groups are non-identical (α=0.05) in their d[15]N values.

We refined our statements and changed the figures and the different parts as follows:

<u>Abstract:</u> *Overall, we find high variability in all investigated parameters for two different moisture-related groups of moss species.[...] The C/N$_{(m)}$ ratios range between 11 and 53 (median: 32) and show large variations at the intraspecific level.*

<u>Results:</u> *However, the medians of the C/N$_{(m)}$ values of the xero-mesophilic species ranging from 47.6 to 52.9 (Fig. 2) are significantly higher than those of the meso-hygrophilic group, which range from 37.1 to 46.5 (W = 18280, p << 0.001). The C/N$_{(m)}$ ratios show no intraspecific relations among individual species and water-level (Fig. 3a), except for Tomentypnum nitens (r² = 0.11, p < 0.05).*

The medians of the individual species in the xero-mesophilic group (range: -29.4 to -27.1‰) are significantly different (W = 16232, p = 0.008) from those of the meso-hygrophilic group (range: -29.2 to -24.8‰).

<u>Discussion:</u> *Our results reveal that averaged C/N$_{(m)}$ ratios for the xero-mesophilic moss group are higher than for the meso-hygrophilic group, probably reflecting the known difference between terrestrial and aquatic plants (Meyers and Ishiwatari, 1993). There are two possible impacts, which can influence the C/N ratio of these groups: (1) competition with vascular plants and (2) accessibility of nitrogen pools . [...]. The large variability in the C/N data may be a result of atmospheric conditions and organic matter degradation being the principal sources at xeric sites, whereas in mesic and wet sites microbial symbionts play an important role in the C/N ratio. However, the signal-to-noise ratio is probably too low to give a meaningful result because only the average water level of each plot but not of each individual plant was recorded.*

[...] individuals growing at dry sites showed higher medial $\delta^{13}C$ values than those growing at wet sites. A difference among the two habitat groups is observed; they partly contradict the intraspecific findings in that some of the xero-mesophilic species known to prefer dry rims such as Hylocomium splendens and Tomentypnum nitens have particularly low $\delta^{13}C$ medians. [...]The detected differences in moss $\delta^{13}C$ values, particularly of the meso-hygrophilic group, either reflect a source signal depending on water-level or a physiological reaction of the plant related to water-level [...]

Thus, the large ranges within several species of meso-hgryophilic habitats in arctic regions suggest that the existence of open water leads to more depleted $\delta^{13}C$ values and measurements of the isotopic composition of methane when present and microbial groups in the water and terrestrial litter should be possible.

<u>Conclusions:</u> *With respect to the isotopic source pools, the meso-hygrophilic species have greater access than xero-mesophilic species, which is seen in their large ranges. The approximate habitat-specific division of $\delta^{13}C$ values as a result of discrimination by RuBisCO under different hydrological regimes is overturned by the influence of different*

sources and cannot provide a clear distinction from a single measurement of either habitat type.

124-129

7. With the exception of two cases (Fig. 3b), most determination coefficients (regression) are lower than ca. 10% or non-existent; and you suggest "… that a relationship between the individual habitat water-level and ⌷isotopic signature wascan be inferred as a function of microbial symbiosis ". I do not see evidence for that. Please change accordingly.

Yes we agree with the editor and have deleted this assumption.

8. Was sampling in 2011 and 1012 during the same season? Should this source of variability be considered? Why?

We accept the editor's comment and describe the vegetation season in the methods (2.1 Sites) more precisely. We chose July and August for our expeditions to avoid the influence of different water sources during spring flooding and because of the low impact of environmental parameters such as absence of circadian rhythm cycle and small temperature variations during a day in the summer north of the polar circle.

We added the sentences as follows:

The plant material was collected during the vegetation season (July–August) from eight low-centred polygons located along a zonal vegetation gradient ranging from open forest via the forest-tundra intersection to subarctic tundra (Matveev, 1989) to obtain a representative sample set of northern Siberian lowlands (Fig. 1).

327-329

9. How can a general trend can be deduced if 17% of variance of first 2 axes?

We accept the editor's comment and refined the sentence:

The observed trend was also assumed in the biplot of the first two PCA axes, even though their declared variance is relatively low (16.9%) in the dataset.

10. Regarding Paq, ACL, and CPI. ⌷What is the conclusion of this comparison? Can they be graphically compared? Do they support your conclusions? Reviewer 2 specifically ask for inclusion of those indices since "n-alkane data are inadequately presented and interpreted"

The ratios of ACL_{21-33} and P_{aq} support the differentiation between both environmental groups. We created a figure of these data, but we think it is unnecessary and inflates the manuscript. We abstain from a mathematical evaluation and interpretation of ratios within both environmental groups due to the small *n* for most of the individual species. Thus, we still show the ratios in table form (Table 2) and supplement the text in the Results and Discussion sections with a refined presentation and interpretation.
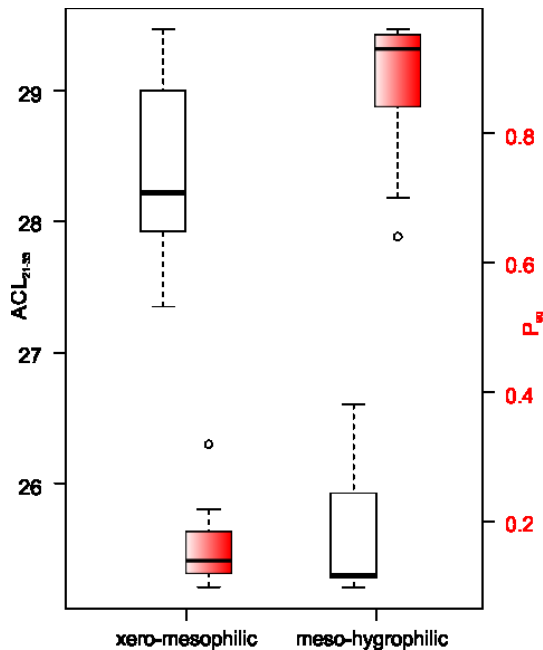
Discussion:
ACL21-33:

dry (ACL$_{21-33}$ = 29.1 – 27.5) **< moisture condition >** (ACL$_{21-33}$ = 26.4 – 25.2) **wet**
  Tom_nit < Aul_tur < Aul_pal < Dre_rev < Sco_sco

Paq: *Our inferred P$_{aq}$ results for the individual species agree with these assumptions. If we consider that the proxy ratio levels were created by vascular plants from a limited dataset of lakes in Kenya and as we focus on non-vascular plants of the arctic, we chose other level terms.*

terms by Ficken et al. (2000)	*emergent macrophytes*		*submerged/floa[...]* *macrophytes*
adapted terms for mosses	*xero-mesophilic mosses*		*meso-hygrophilic n[...]*
species sorted by P$_{aq}$	*Aul_tur* < *Tom_nit*	< *Aul_pal* < *Dre_rev* <	*[...]*

Conclusions: *The applicability of proxy ratios (ACL$_{21-33}$ and P$_{aq}$) could be attested for arctic mosses after adjustments of the levels.*

11. "The total content ⌷of carbon". Total is redundant since we hope you are measuring total and not part of it.
We accept the editor's comment and delete "total".
The content of carbon and nitrogen and the ratio of stable isotopes were measured [...]

271 **12. The argument "Considering the low n-alkane ⌷… " is not necessary since we always have to use quantification standard independent of low or high contents**
We have changed the sentence as follows:
Five µg of the quantification standard (5α-androstane, 1-ethylpyrene, 5 α-androstan-17-one and erucic acid) were added.

279 **13. Replace calculate with calculated**
Done.

6

Additionally, we calculated the average chain length [...]

298   **14. R2 is regression, not correlation. What do you want to detect? 2 dependent variables or one dependent and one independent?**

We calculated the regression because plant position in relation to water-table is an independent variable and the C/N ratio, $d^{13}C$ and $d^{15}N$ are dependent variables. We replace "correlated" with "related" in the text.

257   **15. -some samples. Specify how many? Same with line 264. Does it change your**
264   **conclusions?**

There were 74 samples from which we could only measure $C/d^{13}C$. Due to the addition of n in the previous sentence, it does not change our conclusion, because there were still more than 300 samples for N and from both groups (xero/meso).

We added in the sentence before: *Due to the relatively wide range of C/N ratios of mosses, we used about 1.5 mg for each carbon stable isotope measurement (**n = 400**) and a replicate of 3 mg for each nitrogen stable isotope measurement (**n = 326**) and the analysis of elemental composition.*

340   **16. Xeric and mesic [|] are adjectives and need a noun such as environments, or soils**

We choose as noun 'growing conditions'. "xeric and mesic" refer to "conditions".

334-   **17. See comment # 6**
363

We changed the sections see comment #6

475   **18. " clear differences in ACL" are not so clear in the text. Please change accordingly.**

We present our data in Table 2 and support the clear difference with this little series in the discussion.

dry (ACL_{21-33} = 29.1 – 27.5)   **< moisture condition >**   (ACL_{21-33} = 26.4 – 25.2) **wet**

Tom_nit   <   Aul_tur   <   Aul_pal   <   Dre_rev   <   Sco_sco

530-   **19. See previous comments on C/N and d13C**
532

We do not follow you, because lines 530-532 are citations, which were added in our previous reply to the reviewer comments. Despite searching for other possibilities, we could not see what problem your comment referred to.

20. Reviewer 1. # 35, about symbiosis. See my comment # 4

Yes, this is right, but as this is the Discussion section we treat it is a point of interest that should be considered for following measurements.

We deleted this assumption from the Abstract and Conclusions.

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

Romy Zibulski[1,2], Felix Wesener[4], Heinz Wilkes[3,5], Birgit Plessen[3,], Luidmila A. Pestryakova[6], Ulrike Herzschuh[1,2,7]

[1] {Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, 14473 Potsdam, Germany}

[2] {University of Potsdam, Institute of Earth and Environmental Sciences, 14476 Potsdam-Golm, Germany}

[3] {Helmholtz Centre Potsdam GFZ German Research Centre for Geosciences, 14473 Potsdam, Germany}

[4] {Humboldt University of Berlin, Institute of Biology, 10115 Berlin, Germany}

[5] {Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl von Ossietzky University, 26111 Oldenburg, Germany}

[6] {Northeast Federal University, Department for Geography and Biology, 677000 Yakutsk, Russia}

[7] {University of Potsdam, Institute of Biochemistry and Biology, 14476 Potsdam-Golm, Germany}

Correspondence to: Romy Zibulski (R. Zibulski@awi.de)

Abstract

Mosses are a major component of the arctic vegetation, particularly in wetlands. We present C/N ratios (by weightmolar), δ^{13}C and δ^{15}N data of 400 brown moss samples belonging to 10 species that were collected along hydrological gradients within polygonal mires located on the southern Taymyr Peninsula and the Lena River delta in northern Siberia. Additionally, *n*-alkane patterns of six of these species (16 samples) were investigated. The aim of the study is to see whether the inter- and intraspecific differences in C/N, isotopic signaturecompositions and *n*-alkanes are indicative of habitat with particular respect to water-level. Overall, we find high variability in all investigated parameters for two different moisture-related groups of moss species. The C/N$_{(mwt)}$ ratios range between 151 and 5370 (median: 432) and show large variations at the intraspecific level. However, species preferring a

dry habitat (xero-mesophilic mosses) show higher $C/N_{(wtm)}$ ratios than those preferring a wet habitat (meso-hygrophilic mosses). ~~We assume that this mainly originates from the association of mosses from wet habitats with microorganisms which supply them with nitrogen. Furthermore, because of the stability provided by water, they do not need to invest in a sturdy stem structure and accordingly have lower C contents in their biomass.~~ The $\delta^{13}C$ values range between -37.0 and $-22.5‰$ (median = -27.8‰). The $\delta^{15}N$ values range between -6.6 and $+1.7‰$ (median = -2.2‰). We find differences in $\delta^{13}C$ and $\delta^{15}N$ ~~signature~~compositions 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~~composition can be inferred as a function of microbial symbiosis. The *n*-alkane distribution also shows differences primarily between xero-mesophilic and meso-hygrophilic mosses, i.e. having a dominance of *n*-alkanes with long (*n*-C$_{29}$, *n*-C$_{31}$) and intermediate (*n*-C$_{25}$) chain lengths, respectively. Overall, our results reveal that $C/N_{(wtm)}$ ratios, isotopic signals and *n*-alkanes of studied brown moss taxa from polygonal wetlands are characteristic of their habitat.

1. Introduction

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

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

57 plants. Such information is not only necessary to improve our understanding of the physiological

58 adaptation or plasticity of mosses to certain environmental characteristics, but can also be used when

59 similar measurements of fossil plant material are interpreted as proxies of former ecological or

60 environmental conditions (e.g. Birks, 1982).

61 Carbon-to-nitrogen ratios (C/N), stable carbon and nitrogen isotope values ($\delta^{13}C$, $\delta^{15}N$) and the

62 *n*-alkane fingerprints of bulk organic matter are among the most commonly measured parameters of

63 plant matter (Chambers and Charman, 2004). The C/N ratios of mosses are generally in the range of

64 those of higher terrestrial plants (Prahl et al., 1980) but are known to depend on the available nitrogen,

65 which originates in pristine regions from decomposition of organic matter, microbial activity or

66 atmosphere deposits (e.g. Chanway et al., 2014; Lee et al., 2009). We provide C/N ratios by weight of

67 arctic brown mosses, in anticipation that they will be useful for comparative palaeo-environmental

68 reconstructions (Andersson et al. 2011,) and in the evaluation of organic matter sources in Russian

69 permafrost soils with regard to species and habitat-specific patterns. Furthermore, C/N ratios may be

70 related to growth form, i.e. higher ratios can be expected for mosses which compete with vascular

71 plants for light and thus need to invest in a high stem-stability (Sveinbjörnsson and Oechel, 1992).

72   As well as the C/N ratio, the $\delta^{13}C$ ~~signature~~composition is barely altered by decomposition

73 processes in the soil and also suitable for palaeo-environmental reconstructions. The $\delta^{13}C$ ~~signatures~~

74 ratio of an individual plant are a mixed signal of the physiological traits of the species and the

75 individual's direct environment. Mosses use the C$_3$ pathway for carbon assimilation (O'Leary, 1988,

76 Farquhar et al., 1989) and despite a lack of stomata in the photosynthetic active parts, they have a

77 similar range in their $\delta^{13}C$ values of between -24 and -32 ‰ (Ménot and Burns, 2001; Rundel et al.,

78 1979; Smith and Epstein, 1971) as vascular C$_3$ plants. Differences in $\delta^{13}C$ values among several

79 species can be explained by individual plant physiology and biochemistry (Galimov, 2000).

80 Differences within a single species have been linked with environmental conditions such as

81 temperature (Skrzypek et al., 2007; Waite and Sack, 2011), growing depth below water-level

82 (Raghoebarsing et al., 2005), position within a cushion or hummock (Price et al., 1997), lipid content

83 (Rundel et al., 1979) or the influence of microbial symbioses (Liebner et al., 2011; Vile et al., 2014).

84   Furthermore, even differences among branches and stems of single individuals have been reported

85   (Loader et al., 2007). However, almost all of these studies were made on Sphagnaceae, which are not

86   representative of all mosses because of their specific morphology (i.e. the occurrence of a

87   photosynthetic active cell type and a dead cell type, which is responsible for water storage and often

88   an additional coating of the photosynthetic active cell) and their specific habitat preferences (i.e.

89   preferring acidic wetlands). Hence, this information cannot simply be transferred to brown mosses –

90   which form the major component in northern Siberian lowlands – due to their different morphology.

91   Most studies on δ^{15}N values of moss material have focused on the anthropogenic impact on the

92   nitrogen cycle (Harmens et al., 2011; Liu et al., 2008; Poikolainen et al., 2009), whereas reports on the

93   δ^{15}N ~~signature~~compositions of mosses from relatively pristine ecosystems such as the Arctic are rare

94   or have been investigated in relation to the study of bird colonies (e.g. Lee et al., 2009). Potentially,

95   such information can indicate pathways and sources of the nutrient supply in these N-limited

96   ecosystems (Kielland, 1997; Michelsen et al., 1996, 1998).

97   Compared with vascular plants and *Sphagnum* species, relatively few investigations of *n*-alkane

98   patterns of brown mosses are available. Palaeoenvironmental reconstructions use the potential of

99   *n*-alkanes to distinguish between different plant groups (Ficken et al., 1998, moisture conditions

100   (Pancost et al., 2000, Nichols et al 2006, Zhou et al. 2010), whether organic material is to decomposed

101   and changes in temperature (Feakins et al., 2016, Sachse et al., 2006) along distinct gradients.

102   *Sphagnum* species, for example, show a dominance of *n*-C_{23} and *n*-C_{25} homologues (Baas et al., 2000)

103   that are comparable to the pattern of vascular submerged plants (Ficken et al., 2000), and ratios are

104   used as a proxy for wet moisture conditions. Other studies discuss the suitability of *n*-alkane patterns

105   in moss species for chemotaxonomical studies on recent and fossil material (Bush and McInerney,

106   2013; Nott et al., 2000; Schellekens and Buurman, 2011). A greater protection potential of waxes with

107   a higher content of long-chain *n*-alkanes against solar irradiation or alternatively an enhanced loss of

108   short-chain *n*-alkanes by evaporation have been suggested as possible mechanisms to cause different

109   *n*-alkane patterns in leaf waxes of trees (Sachse et al., 2006). However, with respect to mosses the

110   pattern and mechanisms are even less understood.

111   This study presents C/N$_{(wtm)}$, isotopic (δ^{13}C, δ^{15}N) and *n*-alkane characteristics of mosses from

112   low-centred polygons in northern Siberia. Low-centred polygons are geomorphological forms in arctic

113   landscapes originating from frost-heave processes in the soil. They are characterized by elevated dry

114   rims and a water-saturated or water-filled centre. This centimetre-scale hydrological gradient is well

115   reflected by a strong turnover in the vascular plant and moss composition (Zibulski et al., 2016). We

116   investigate the relationship between the C/N$_{(wtm)}$, isotopic and *n*-alkane ~~signature~~compositions and the

117   hydrological conditions within low-centred polygons. In particular, we aim to reveal whether

118   fingerprints are habitat-specific or rather species-specific.

2. Material and methods

2.1 Sites

121   The plant material was collected during the vegetation season (July-August) from eight low-centred

122   polygons located along a zonal vegetation gradient ranging from open forest via the forest-tundra

123   intersection to subarctic tundra (Matveev, 1989) to obtain a representative sample set of northern

124   Siberian lowlands (Fig. 1). Six of the polygons (06/P, 17/P, P3/I, P3/II, P3/III, 12/P), sampled in 2011,

125   are located in the Khatanga River region (70–72° N, 97–102° E, southern Taymyr Peninsula) and a

126   further two polygons (LP1 and LP2), sampled in 2012, are located on Samoylov Island in the Lena

127   River Delta (72.4° N, 126.5° E). The climate is cold-humid (Khatanga climate station annual mean

128   temperature and precipitation: -13.2°C and 272 mm, Rivas-Martinez and Rivas-Saenz, 2009;

129   Samoylov climate station annual mean temperature and precipitation: -12.5°C and 232.7 mm, Boike et

130   al., 2013)).

2.2 Sampling and studied moss species

132   A representative continuous transect of adjacent one square-metre plots (from rim to rim) was selected

133   for sampling in each polygon. The surface height in relation to water-level (measured at the centre of

134   each plot) and vegetation (abundance information) were recorded. Individual characteristics of each

135   low-centred polygon are presented in Table A1. Moss plants were hand-picked, dried in the field and

136   transported to the Alfred Wegener Institute in Potsdam. Taxa identification is based on the relevant

137   literature (Frahm and Frey, 2004; Lobin et al., 1995; Smith, 1978) and the Bryophyte Flora of North

138   America internet source (http://www.efloras.org).

139   In total, eight species that were observed to have different water-regime preferences were included in

140   the analyses. To approximate water-regime preferences of each species, we calculated the mean plant-

141   position in relation to water-level (h) from the recorded plot surface height. *Warnstorfia exannulata*

142   was observed to grow as part of a swinging mat at water-level, it was assigned a preference for water-

143   level. Using this information the species were classified as either as of xero-mesophilic mosses (mean

144   plant-position between 13 and 16 cm in relation to water-level) or to the group of meso-hygrophilic

145   mosses (mean plant-position between 3 and -30 cm in relation to water-level) to ease the presentation

146   of results.

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

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

150

151 2.4 Measurements of C/N$_{(wtm)}$ ratios, stable carbon and nitrogen isotope values
152 and *n*-alkane distributions

153   Selected plant material (i.e. apical parts of a specimen) was rinsed with de-ionised water and

154   mechanically cleaned from organic particulate material. The ~~total~~ content of carbon and nitrogen and

155   the ratio of stable isotopes were measured with a DELTAplusXL isotope ratio mass spectrometer

156   (Thermo Fischer Scientific) coupled to an elemental analyser (NC2500 Carlo Erba) via a CONFLOW

157   III Interface. Due to the relatively wide range of C/N ratios of mosses, we used about 1.5 mg for each

158   carbon stable isotope measurement (*n* = 400) and a replicate of 3 mg for each nitrogen stable isotope

159   measurement (*n* = 326) and the analysis of elemental composition. The high weight needed for the

160   nitrogen sample replicates prevented the measurement of δ^{15}N and thus the C/N$_{(wtm)}$ for some samples.

161   The calibration for carbon was performed using an urea standard and a δ^{13}C isotopic standard (IAEA

162   CH-7). The nitrogen contents were calibrated against an acetanilide standard and the nitrogen isotopic

163   composition with ammonium sulphate standard (IAEA N-1). The reliability of the method was

164   checked with the NIST plant standard SRM 1547. The isotopic ratios are given in delta notation

165   relative to VPDB for $\delta^{13}C$ values and relative to air for $\delta^{15}N$ values, respectively. The reproducibility

166   for replicate analyses is 0.2% for carbon and nitrogen and 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ values.

167   *n*-Alkane analyses were performed on a subset of 16 samples. We took material from the polygon

168   complex P3 from the Khatanga region (72.149° N, 102.693° E), which comprises three successive

169   low-centred polygons (Table A1) to exclude effects of environmental conditions at different locations.

170   The moss samples were washed, identified and air-dried. They were weighed (150–1000 mg dry

171   weight) and samples extracted with an accelerated solvent extractor (ASE) (Dionex, Sunnyvale; USA)

172   using Cl_2Me:MeOH (10:1) at 5 bar and 75°C. The extract was separated in to aliphatic hydrocarbon,

173   aromatic hydrocarbon and nitrogen, sulphur and oxygen compound fractions using medium pressure

174   liquid chromatography following Radke et al. (1980). ~~Considering the low *n*-alkane concentrations of~~

175   ~~our samples,~~ Five µg of ~~5 µg of~~the quantification standard (5α-androstane, 1-ethylpyrene, 5 α-

176   androstan-17-one and erucic acid) were added . Gas chromatography (GC) of aliphatic hydrocarbon

177   fractions was performed using a GC Agilent 6890 equipped with an Ultra-1 fused silica capillary

178   column (Model Agilent 19091A-105, length 50 m, inner diameter 200 µm, film thickness 0.33 µm).

179   Helium was used as a carrier gas at a constant flow rate of 1 ml min^{-1}. The GC oven was heated from

180   40 °C (2 min hold time) to 300 °C (65 min hold time) at a rate of 5°C per minute. The samples were

181   injected by means of splitless injection. Quantitative evaluation of data was done with ChemStation

182   software. Additionally, we calculated the average chain length (ACL_{21-33}) assumed to represent a

183   proxy for moisture (Andersson et al, 2011) and temperature (Bush and McInerney, 2015) with a

184   comprehensible extended range from *n*-C_{21} to *n*-C_{33} and the proxy ratio P_{aq}, which was developed as a

185   proxy ratio to distinguish submerged or floating aquatic macrophytes from emergent and terrestrial

186   plants (Ficken et al., 2000):

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

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

187

2.5 Statistical Tests

189 We calculated the range, .25, .5, and .75 quantiles of $\delta^{13}C$ and $\delta^{15}N$ values and the C/N$_{(wtm)}$ ratios for

190 all species (Table A2). Significant differences in the C/N$_{(wtm)}$ ratios and $\delta^{13}C$ and $\delta^{15}N$ values among

191 different groups were assessed with a t-test. In addition, we performed linear regression between the

192 obtained values for each individual species and surface height. All analyses were implemented in R

193 version 3.2.0 (R Core Team, 2015). Furthermore, we performed a PCA with the percentage of

194 *n*-alkane homologues (square-root transformed) in R using the vegan package version 2.0-10

195 (Oksanen et al., 2013).

3. Results

197 The overall ranges in C/N$_{(wtm)}$ ratios of both groups have a broad overlap (xero-mesophilic: 22.5–67.9;

198 meso-hygrophilic: 15.4–70.4). However, the medians of the C/N$_{(wtm)}$ values of the xero-mesophilic

199 species ranging from 47.6 to 52.9 (Fig. 2) are significantly higher than those of the meso-hygrophilic

200 group, which range from 37.1 to 46.5 (~~t~~ W = ~~8.17~~18280, *p* << 0.001). The C/N$_{(wtm)}$ ratios show no

201 intraspecific relations among individual species ~~are not significantly correlated with~~and ~~the~~ water-level

202 (Fig. 3a), except for *Tomentypnum nitens* (r² = 0.11, *p* < 0.05).

203 The $\delta^{13}C$ values of the meso-hygrophilic group (-34.9 to -22.5‰) cover the range of the xero-

204 mesophilic group (-32.1 to -24.2‰), which have a noticeably lower variance in $\delta^{13}C$ values (Fig. 2).

205 The medians of the individual species in the xero-mesophilic group (range: -29.4 to -27.1‰) are ~~not~~

206 significantly different (~~t~~ W = ~~-1.69~~16232, *p* = 0.~~09~~008) from those of the meso-hygrophilic group

207 (range: -29.2 to -24.8‰). $\delta^{13}C$ values of *Meesia triquetra, Drepanocladus revolvens,* and *Scorpidium*

208 *scorpioides* (all belonging to the meso-hydrophilic group) are significantly positively ~~correlat~~related

209 with the position of the water-level (Fig. 3b), while no member of the xero-mesophilic group revealed

210 such relationship (Fig. 3a).

211 The ranges of $\delta^{15}N$ values of both groups are rather similar (Fig. 2). However, individual species

212 medians of both groups are significantly different (t = -6.96, $p \ll 0.001$; xero-mesophilic group; -3.2

213 to -2.7‰, meso-hygrophilic group: -2.9 to -0.1). *Drepanocladus revolvens, Scorpidium scorpioides,*

214 and *Calliergon giganteum*, all belonging to the meso-hygrophilic group, exhibit a positive relationship

215 between the $\delta^{15}N$ values and position relative to water-level (Fig. 3b~~)~~.

216 *n*-Alkane distributions show the expected predominance of the odd chain length (Table 2). The

217 absolute *n*-alkane concentrations (*n*-C_{19} to *n*-C_{33}) range from 34 to 238 µg g^{-1} of dry weight. The

218 individual taxa show significant differences with respect to carbon number of the most abundant

219 *n*-alkane (*n*-C_{max}) forming unimodal distribution patterns. It is *n*-C_{31} for *Tomentypnum nitens*, which is

220 also the only species containing *n*-C_{33} in detectable amounts, *n*-C_{29} for *Aulacomnium turgidum*, *n*-C_{27}

221 for *Aulacomnium palustre*, *n*-C_{27} and *n*-C_{25} for the *Drepanocladus* taxa, and *n*-C_{max} = 25 for

222 *Scorpidium scorpioides*. These differences in the *n*-alkane composition largely ~~correlat~~relate with the

223 species-preferred mean plant-position relative to water-level (Fig. 4).

224 Evaluations of the *n*-alkane biomarker proxies, ACL_{21-33} and P_{aq}, also show a clear division

225 between the xero-mesophilic and the meso-hygrophilic species groups (Table 2), whereas intraspecific

226 variations are rather small (with the exception of *Drepanocladus*). The xero-mesophilic group is

227 notable for high averages of ACL_{21-33} (28.41) and P_{aq} (0.17) compared to low averages of ACL_{21-33}

228 (25.61) and P_{aq} (0.87) for the meso-hygrophilic group. ~~There are no intersections, with the exception~~

229 ~~of Drepanocladus.~~

230 The ~~general~~ observed trend~~s~~ is ~~are~~ also assumed ~~visible~~ in the biplot of the first two PCA axes,

231 even though their explained variance is relatively low ~~which together explain only~~ (16.9%~~-~~) ~~of the~~

232 ~~variance in~~in the dataset (Fig. 5). The first axis separates xero-mesophilic from meso-hygrophilic taxa.

233 *Aulacomnium* taxa are located in the upper range and *Tomentypnum nitens* in the lower range of the

234 second PCA axis, while no trend is observed within the meso-hygrophilic group along the second

235 axes.

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

species	*n*-C_{19}	*n*-C_{21}	*n*-C_{23}	*n*-C_{25}	*n*-C_{27}	*n*-C_{29}	*n*-C_{31}	*n*-C_{33}	ACL_{21-33}	P_{aq}

Xero-mesophilic habitat group									
Tom_nit (1)	0	2.0689	2.6374	6.0816	10.7454	17.7273	34.0742	0	28.86	0.14
Tom_nit (2)	0.5571	1.041	1.4493	2.6964	9.1008	8.4867	20.2818	7.2312	29.47	0.13
Tom_nit (3)	0.9936	1.456	2.175	2.8712	9.6118	7.2721	21.2309	4.9717	29.14	0.15
Aul_tur (1)	0	0.968	1.126	2.2001	8.9548	23.5267	3.5595	0	28.15	0.11
Aul_tur (2)	1.028	1.3468	1.2794	4.8797	18.7427	50.9291	5.5645	0	28.22	0.10
Aul_pal (1)	0	1.9298	2.5459	4.7646	20.5085	7.5826	7.979	0	27.35	0.32
Aul_pal (2)	0.7341	1.0767	1.5183	2.9728	12.3293	11.0909	4.9109	0	27.69	0.22
Meso-hygrophilic habitat group									
Dre_rev (1)	0.7868	1.5426	2.3659	43.833	19.0836	5.1551	3.5637	0	25.92	0.84
Dre_rev(2)	0.981	1.5227	2.7605	22.5638	14.5103	6.5356	7.5623	0	26.6	0.640
Dre_sp.	1.4696	1.9968	5.0986	29.6729	30.4582	9.9108	5.1317	0	26.38	0.70
Sco_Sco (1)	0	3.7612	11.7002	133.4207	29.0024	6.2023	1.9425	0	25.3	0.95
Sco_Sco (2)	0	3.8911	10.4693	93.7009	21.4601	5.8531	1.7706	0	25.29	0.93
Sco_Sco (3)	0.8856	2.7949	11.8988	134.378	24.2348	5.4035	2.4969	0	25.28	0.95
Sco_Sco (4)	1.6217	5.5813	11.705	101.7602	21.3126	6.9161	2.4522	0	25.26	0.92
Sco_Sco (5)	1.4083	3.8857	11.8966	121.5701	23.3167	4.315	1.7261	0	25.21	0.96
Sco_Sco (6)	1.345	2.6672	19.4796	170.3015	34.3255	6.8599	3.1732	0	25.28	0.95

4. Discussion

4.1 C/N$_{(wtm)}$ ratios

The C/N ratios of mosses from polygonal tundra in Northern Siberia are relatively low compared with those obtained for mosses from Antarctic bogs that range between 80 and 100 (Björck et al., 1991) or from western Canada that range between 55 and 76 (Kuhry and Vitt, 1996). However, neither the taxa nor the habitats sampled were fully comparable to those of our analyses, i.e. many more taxa typical of xeric and mesic growing conditions were sampled in Antarctica and Canada. All investigated species are considered as ectohydric mosses, which receive nitrogen mostly from precipitation deposits (Ayres et al., 2006). Our results reveal that averaged C/N$_{(wtm)}$ ratios for the xero-mesophilic moss group are higher than for the meso-hygrophilic group, probably reflecting the known difference between terrestrial and aquatic plants (Meyers and Ishiwatari, 1993). There are two possible impacts, which can influence the C/N ratio of these groups: (1) Competition with vascular plants (1) and (2) accessibility of nitrogen pools (2) may be the main reasons for this finding. (1) If moss plants invest in a high stem-to-leaf biomass ratio, which results in a high C/N$_{(wtm)}$ ratio, they will increase their height and stability, and thus their competitive ability against vascular plants for light (Sveinbjörnsson and Oechel, 1992). Furthermore, the low N input by precipitation and a low N content of moss litter slows

254   down the fungal and bacterial N mineralisation which increases the thickness of moss litter mats

255   (Gornall et al., 2007; Turetsky, 2003). This in turn will increase the isolating function of moss mats,

256   thus negatively affecting seed germination of vascular plants (Gornall et al., 2007). (2) Lower C/N$_{(wtm)}$

257   ratios of meso-hygrophilic mosses may originate from higher amounts of dissolved nitrogen in

258   polygon waters as a result of high net primary productivity, the presence of N$_2$-fixers such as

259   cyanobacteria, and the exudations of zooplankton. Frahm (2001) assumes that loose epiphytic and

260   endophytic symbiotic relationships between mosses and cyanobacteria are probably restricted to

261   wetland taxa. Lindo et al. (2013) report such associations between brown mosses and cyanobacteria.

262   Thus, the N supply is better for brown mosses preferring meso-hygrophilic than xero-mesophilic

263   habitats, and the respective taxa accordingly have lower C/N$_{(wtm)}$ ratios indicating habitat-specific

264   variation in C/N$_{(wtm)}$ ratios. We expected to also find intraspecific variations between C/N$_{(wtm)}$ ratios

265   and water-level. The large variability in the C/N data may be a result of atmospheric conditions and

266   organic matter degradation being the principal sources at xeric sites, whereas in mesic and wet sites

267   microbial symbionts play an important role in the C/N ratio. However, the signal-to-noise ratio is

268   probably too low to give a meaningful result because only the average water level of each plot but not

269   of each individual plant was recorded.

270 4.2 δ^{13}C values

271 With respect to bryophytes, most isotopic studies have hitherto been performed on *Sphagnum* (Markel

272 et al., 2010, Ménot and Burns, 2001) while our study focuses on brown mosses – a major component

273 in Siberian wetlands. The intraspecific variability for some meso-hygrophilic species (i.e. *Meesia*

274 *triquetra, Drepanocladus revolvens, Scorpidium scorpioides*) show that the δ^{13}C signals are related to

275 the hydrological conditions at the growing site of each individual, i.e. individuals growing at dry sites

276 showed higher medial δ^{13}C values than those growing at wet sites. No significantA difference among

277 the two habitat- groups is observed; rather they partly contradict the intraspecific findings in that some

278 of the xero-mesophilic species known to prefer dry rims such as *Hylocomium splendens* and

279 *Tomentypnum nitens* have particularly low δ^{13}C medians.

280   DThe detected differences in moss δ^{13}C values, particularly of the meso-hygrophilic group, either

281   reflect a source signal depending on water–level or a physiological reaction of the plant related to

18

282   water-level (Bramley-Alves et al., 2014; Proctor et al., 1992). Mosses are typical C_3 plants (Farquhar

283   et al., 1989, Rundel et al., 1979) characterized by a high CO_2 compensation point (Bain and Proctor,

284   1980; Dilks and Proctor, 1975; Salvucci and Bowes, 1981). The high availability of atmospheric CO_2

285   and elevated diffusion rates of CO_2 in air compared to water (O'Leary) result in typical terrestrial C_3

286   land plant $\delta^{13}C$ characteristics, because of a decreasing cell water pressure in dry habitats which entails

287   a strong discrimination rate against $^{13}CO_2$ induced by RuBisCO (Rice and Giles, 1996). With respect

288   to the xero-mesophilic group, we observe an increase in discrimination against ^{13}C from taxa

289   preferring a low position relative to the water-level (e.g. *Aulacomnium* taxa) than those preferring high

290   positions (e.g. *Hylocomium splendens*). In contrast, if plant tissue is coated by a water film, the cell

291   water pressure should reach an optimum, which is expected to results in a weaker discrimination rate

292   against ^{13}C by RuBisCO (Rice and Giles, 1996), because of a source restriction by the slower diffusion

293   rate of CO_2 in water (Lloyd and Farquhar, 1994). A lower carbon isotope discrimination related to

294   water saturation is observed for only three species out of six meso-hygrophilic mosses. However, this

295   basic signal may be masked by variations in $\delta^{13}C$ values of different carbon sources, which are

296   expected to be more influential for meso-hygrophilic mosses in water-saturated conditions. Ménot and

297   Burns (2001) studied intraspecific variations for three *Sphagnum* species, which prefer three different

298   habitat types (dry, meso, wet) along an elevational gradient, which was positively correlat~~relat~~ed with

299   precipitation. They find a decline in discrimination against ^{13}C with increasing wetness, and similar to

300   our results no relationship for species with a strong wet –preference. This is attributed to the variation

301   in $\delta^{13}C$ from highly varying dissolved inorganic carbon (Proctor et al., 1992). Mosses potentially

302   access ^{13}C-depleted CO_2 that originates from oxidation of typically strongly ^{13}C-depleted biogenic

303   methane by methanotrophic microorganisms (Kip et al., 2010; Liebner et al., 2011; Raghoebarsing et

304   al., 2005). Studies by Nichols et al. (2009) show that a higher water level at the peat surface is crucial

305   for high methane-derived CO_2 release. Furthermore, symbiosis with methanotrophs enhances the

306   moisture-related effect on the $\delta^{13}C$ signal of bryophytes. Endophytic microorganisms in hyalocytes of

307   submerged *Sphagnum* (Raghoebarsing et al., 2005) or epiphytic microorganisms on submerged brown

308   mosses (Liebner et al., 2011) are presumed to provide ^{13}C-depleted CO_2 directly to the lamina cells of

309   mosses. The studies of Ruttner (1947) and Bain and Proctor (1980) show that, in general, moss taxa

are incapable of bicarbonate uptake. Hence, bicarbonate, known to be a carbon source for submerged vascular plants and algae (Herzschuh et al., 2010; Merz, 1992), can most probably be excluded as a carbon source for moss and thus as a factor influencing the δ^{13}C value. Moreover, the bicarbonate content in pond waters in northern Siberian landscapes is very low (Wetterich et al., 2008). Other sources of ^{13}C-depleted CO_2 are surface run-off during spring flooding, rain events and decomposition processes in the pond (Leng and Marshall, 2004; Maberly et al., 2013). Yet we cannot fully eliminate the possibility that the measured bulk material was contaminated in parts with epiphytic or endophytic microorganisms. The overall ~~signature~~ isotopic composition would, however, likely be unaffected, as Ménot and Burns (2001) have shown that the δ^{13}C values of bulk organic material and alpha-cellulose of *Sphagnum* are very similar. Thus, the large ranges within several species of meso-hgryophilic habitats in arctic regions suggest that the existence of open water leads to more depleted δ^{13}C values and measurements of the isotopic composition of methane when present and microbial groups in the water and terrestrial litter should be possible. Finally, considering the relationship of selected brown mosses to mean plant position, the complex origin of plant-available carbon makes it difficult to interpret the δ^{13}C record, especially for meso-hygrophilic brown mosses as well as *Sphagnum* (Prince et al., 1997, Ménot and Burns, 2001).

4.3 δ^{15}N isotopes

Like δ^{13}C, the interpretation of stable nitrogen isotope ~~signature~~compositions of mosses is challenging because, again, source signals need to be separated from those originating from physiological isotopic discrimination processes. Our results yield relatively ^{15}N-depleted δ^{15}N values for xero-mesophilic mosses growing preferentially on rims compared to meso-hygrophilic mosses.

The terrestrial arctic systems are generally thought to be nitrogen limited (Gordon et al., 2001; Kielland, 1997). On the rim sites, atmospheric deposition can be considered to be the most important source for nitrogen (Jonasson and Shaver, 1999) originating from fog, dew, precipitation and surface run-off (Sveinbjörnsson and Oechel, 1992). However, most of the nitrogen available to rim mosses originates from recycling of already ^{15}N-depleted higher plant and moss litter (Turetsky, 2003). The ectohydric morphology enables an efficient nutrient uptake across the entire moss plant surface via trapped water. In fact, the meso-hygrophilic group has a higher N content than the xero-mesophilic

338 group (see section on C/N ratio). Inorganic nitrogen, but especially the high amounts of organic

339 nitrogen provided by N-mineralization in tundra soils (Kielland, 1995) are important for mosses

340 growing on the rather dry sites such as the polygonal rims (Atkin, 1996).

341   Three of the investigated submerged or floating moss species show a significant positive

342 relationship between water-level and δ^{15}N values. These results are similar to those of Asada et al.

343 (2005) who tested a relationship between δ^{15}N values of different *Sphagnum* species and their position

344 relative to the groundwater level, which they assumed to originate from different nitrogen sources and

345 different internal fractionating processes. We assume that the often heavier nitrogen isotope

346 ~~signature~~composition of meso-hygrophilic brown moss individuals originates from the high degree of

347 symbiotic associations with aquatic atmospheric nitrogen-fixing autotrophic microorganisms such as

348 *Nostoc* or *Anabena* (Lindo et al., 2013) or methanotrophs (Vile et al., 2014). The high spatial degree

349 with endo- or ectosymbiotic N_2-fixing microorganisms enables the direct uptake of their nitrogen

350 products, which is similar to that of N_2 in air.

351 **4.4 *n*-alkane patterns**

352 Compared to vascular plants that are characterized by a thick leaf-wax layer, mosses produce only a

353 small amount of *n*-alkanes (Baas et al., 2000; Ficken et al., 1998). Like previous studies on vascular

354 plants (Aichner et al., 2010; Ficken et al., 2000; Meyers and Ishiwatari, 1993), our results generally

355 reveal a differentiation between terrestrial taxa (i.e. xero-mesophilic group) characterized mainly by

356 *n*-alkanes maximizing at *n*-C_{29} and *n*-C_{31} and submerged living taxa (i.e. the meso-hygrophilic group)

357 maximizing at *n*-C_{25} and *n*-C_{27}. Earlier investigations of Nott et al. (2000), Baas et al. (2000) and

358 Bingham et al. (2010), who compared the *n*-alkane fingerprints of *Sphagnum* taxa growing along a

359 hydrological gradient, agree with our results.

360 Huang et al. (2012a) and Ficken et al. (1998) used proxy ratios (ACL, P_{aq}) to divide moss taxa roughly

361 by their moisture preferences. They calculate the ACL_{23-33} for samples of lichens and *Racomitrum*

362 *lanuginosum*, which have rather similar hydrological requirements to our xero-mesophilic mosses.

363 Despite the slightly narrower ACL_{23-33} range, their results show similarities to our xero-mesophilic

364 group. A comparison between ACL_{21-33}, ratios of *Sphagnum* (plant position nearly at water-level) of

365 Huang et al. (2012b) and our brown mosses shows that the ACL_{21-33} ratios of *Sphagnum* species are

366 rather lower. The intraspecific conclusion of Huang et al. (2012b) (wetter moisture conditions entail

367 lower ACL_{21-33}) for *Sphagnum* is reflected by our measurements.

dry (ACL_{21-33} = 29.1 – 27.5)   **< moisture condition >**   (ACL_{21-33} = 26.4 – 25.2) **wet**

 Tom_nit   ≤   Aul_tur   ≤   Aul_pal   ≤   Dre_rev   ≤   Sco_sco

368 for *Drepanocladus* and *Scorpidium*, i.e. they show a dependence with water level.

369   As we observed a clear difference in the ACL_{21-33} between the xero-mesophilic and the meso-

370 hygrophilic group, we suggest that the inclusion of mid-chain *n*-alkanes (*n*-C_{21} to *n*-C_{25}) in the

371 equation of ACL improves its value as a proxy for moisture conditions. Andersson et al. (2011)

372 inferred ACL_{27-31} values of 29 for brown-moss peat from western Russian during wet phases, which is

373 however, poorly comparable to our results because they investigated total peat organic matter instead

374 of pure moss material.

375   Ficken et al. (2000) proposed P_{aq} as a semi-quantitative proxy ratio for the differentiation of

376 terrestrial and aquatic plants (<0.1 terrestrial plants, 0.1–0.4 emergent macrophytes, 0.4-1

377 submerged/floating macrophytes). Our inferred P_{aq} results for the individual species fit agree well with

378 these assumptions. If we consider that the proxy ratio levels were created by vascular plants from a

379 limited dataset of lakes in Kenya and as we focus on non-vascular plants of the arctic, we chose other

380 level terms.

terms by Ficken et al. (2000)	emergent macrophytes		submerged/floating macrophytes	
adapted terms for mosses	xero-mesophilic mosses		meso-hygrophilic mosses	
species sorted by P_{aq}	Aul_tur ≤ Tom_nit	≤ Aul_pal	≤ Dre_rev	≤ Sco_sco

382   For example, submerged/floating *Scorpidium* (P_{aq} median: 0.95) has a higher median P_{aq} value

383 than floating/mesic *Drepanocladus* (P_{aq} median: 0.7), which is again higher than that of the xero-

384 mesophilic mosses *Tomentypnum* (P_{aq} median: 0.14) and *Aulacomnium* (P_{aq} mean: 0.13). Ficken et al.

385 (2000) also measured a *Drepanocladus* sample (P_{aq} = 0.30). Overall, our results do not support the

386 inference of Nichols et al. (2006) that a hydrological classification is possible between *Sphagnum* and

387 non-*Sphagnum* formed peat as the latter show wide variations between different habitats. The inferred

388 broad P_{aq} range of *Drepanocladus* and between both *Aulacomnium* probably indicates that

389 intraspecific variation is related to the individual´s growing condition, which could provide the basis

390 to develop P_{aq} as a proxy for water-level when measured on taxonomically identified fossil plant

391 material.

392   As with P_{aq}, *n*-alkanes seem to be species-specific given stable environmental parameters and are

393 related to the species-specific moisture requirements, which are adapted to changing environmental

394 conditions. Thus, our results confirm the conclusions of Bingham et al. (2010), Bush and McInerney

395 (2015) and Nott et al. (2000) that the pattern of *n*-alkanes has the potential to become a valuable proxy

396 for chemotaxonomic identification and moisture conditions. *Scorpidium scorpioides,* a species with a

397 rather narrow preference range (i.e. it is limited to open water conditions), shows low intraspecific

398 variations. This matches the results for *Sphagnum* compiled by Bingham et al. (2010), which also

399 show minor intraspecific variations. *Aulacomnium* in contrast, which grows in a rather wide range of

400 moisture conditions, shows strong variations in its *n*-alkane spectra: whether this is a function of the

401 individual's growing conditions, however, needs to be investigated in a more extensive study.

5. Conclusions

403 The habitat and intraspecific isotopic and chemical patterns of 10 brown-moss species detected along

404 small-scale hydrological gradients in Siberian polygonal tundra were studied.

405   The observed higher C/N$_{(\text{~~wt~~}\underline{m})}$ ratios of xero-mesophilic mosses compared to those of the meso-

406 hygrophilic mosses originate from the different environmental requirements when living emergent (i.e.

407 investment in a higher stability resulting in high C/N ratios) as opposed to submerged. Furthermore,

408 the latter group may also gain a better nitrogen supply through microbial symbioses.

409   With respect to the isotopic source pools, the meso-hygrophilic species have greater access than

410 xero-mesophilic species_, which is seen in their large ranges_, ~~probably through symbioses with~~

411 ~~microorganisms and dissolved carbon~~. The approximate habitat-specific division of δ^{13}C values _as a_

412 result~~ing from~~ _of_ discrimination by RuBisCO under different hydrological regimes~~,~~ is overturned by

413 the influence of ~~microbial symbioses~~_different sources_ and _cannot provide_ ~~makes~~ a clear distinction

414 _from a single measurement_ ~~between both~~_of either_ habitat type~~s~~ ~~impossible~~. For species, growing near

415   the water level, no intraspecific relationship with water level was observed probably as a result of the

416   parallel impact of processes causing opposing $\delta^{13}C$ trends.

417   Our analyses reveal that, compared with xero-mesophilic mosses, meso-hygrophilic mosses are

418   characterized by enriched $\delta^{15}N$ values probably originating from microbial symbioses. Both carbon

419   and nitrogen isotopic ratios seem to be valuable proxies to differentiate between taxa preferring the

420   polygon rim or pond. Moreover, with respect to meso-hygrophilic mosses, the detected positive

421   relations between intraspecific variations and the individuals' relative growing position could allow

422   even more semi-quantitative information about water-level changes to be inferred.

423   The *n*-alkane patterns of brown mosses (limited 16 individuals belonging to five species) indicate

424   that they are species-specific and have thus the potential to be developed as a chemotaxonomic proxy.

425   The applicability of proxy ratios (ACL and Paq) could be attested for arctic mosses after adjustments

426   of the levels.

427   Overall, our study indicates that C/N, isotopic and *n*-alkane analyses of brown moss material has

428   a high environmental indicator potential, particularly if species-specific material instead of bulk

429   material is analysed.

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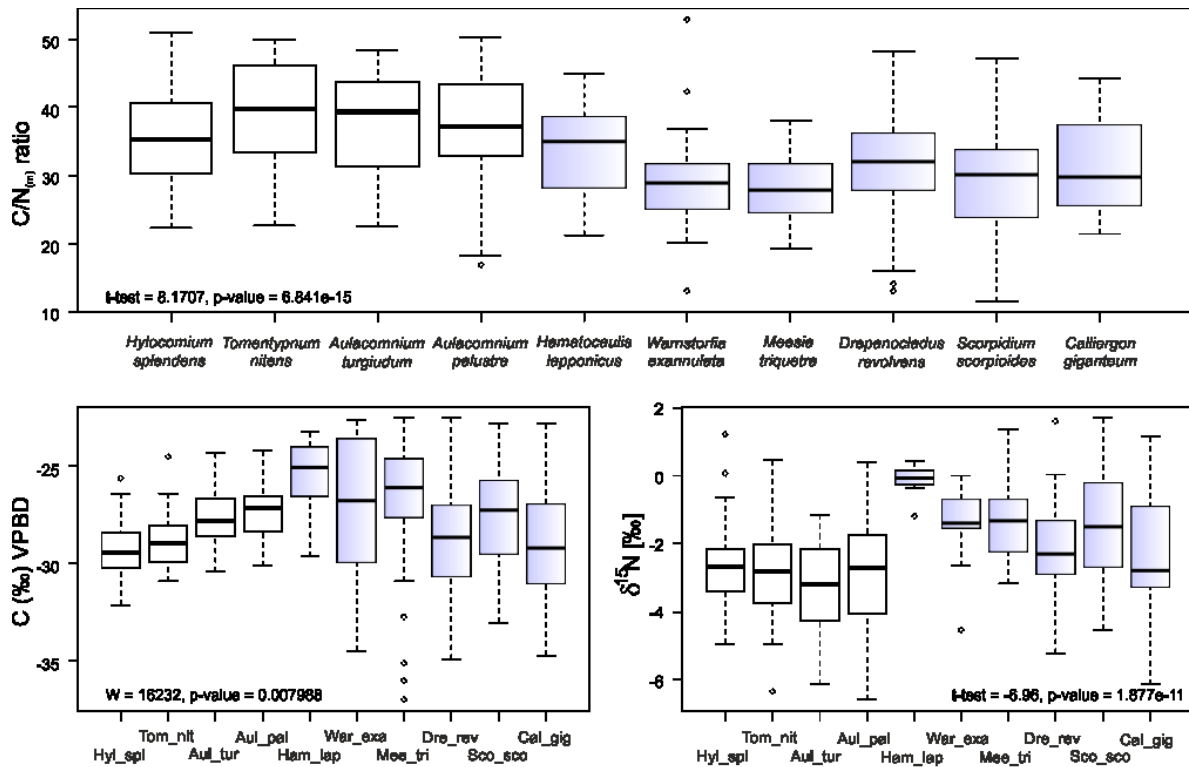668   doi:10.1111/jvs.12356, 2016.

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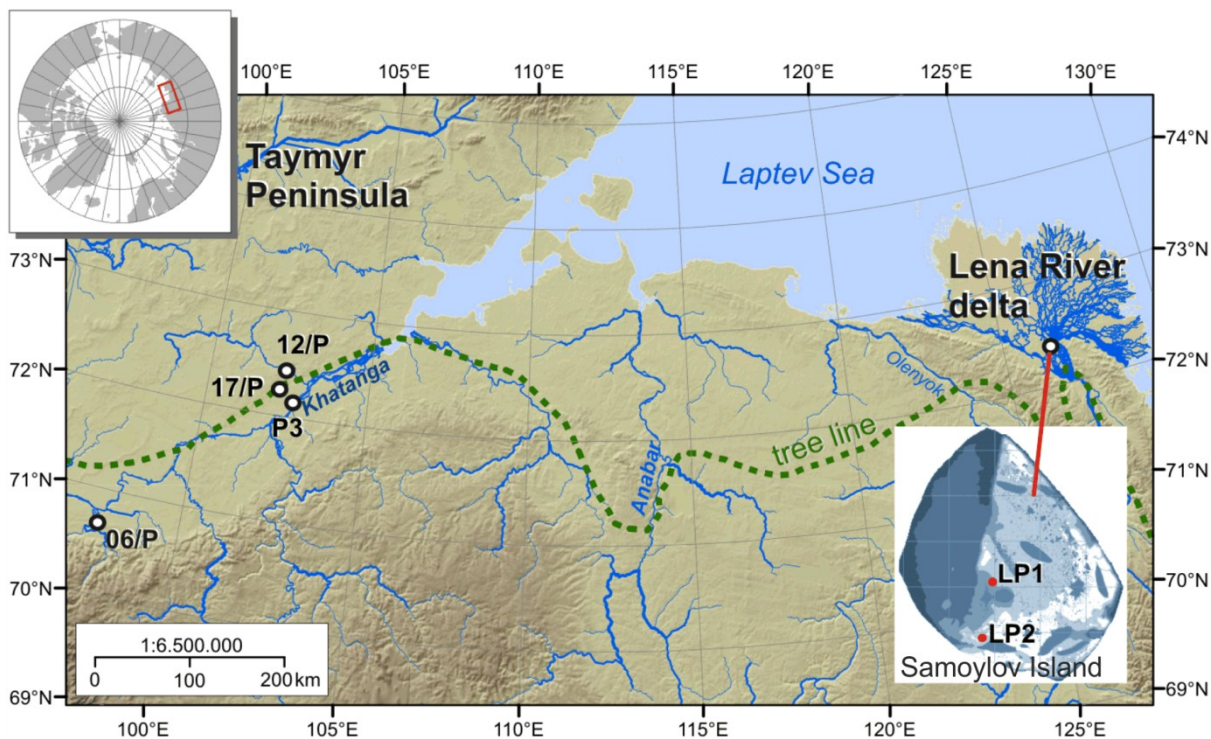
Fig. 1: The Khatanga study sites are located in the south-east of the Taymyr Peninsula and both the sites on Samoylov Island are in the southern Lena River delta (Map by Th. Böhmer).

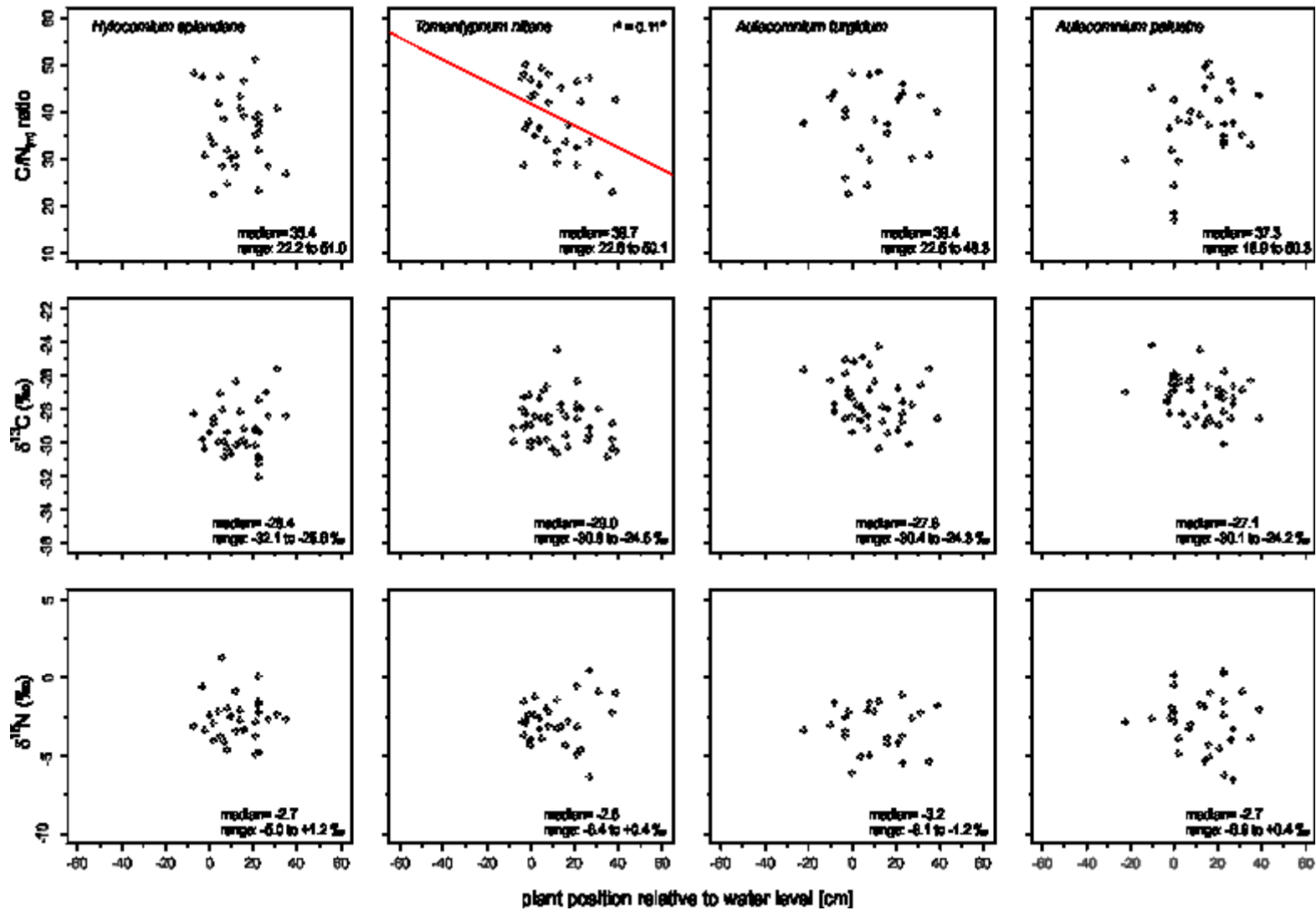*Fig. 2:* *C/N (m) ratios* ~~by weight~~*, $\delta^{13}C$ and $\delta^{15}N$ values of the 10 moss taxa studied. White boxplots are the xero-mesophilic group and boxplots shaded in blue are the meso-hygrophilic group. A t-test was done to distinguish the signals between the two habitat groups.*
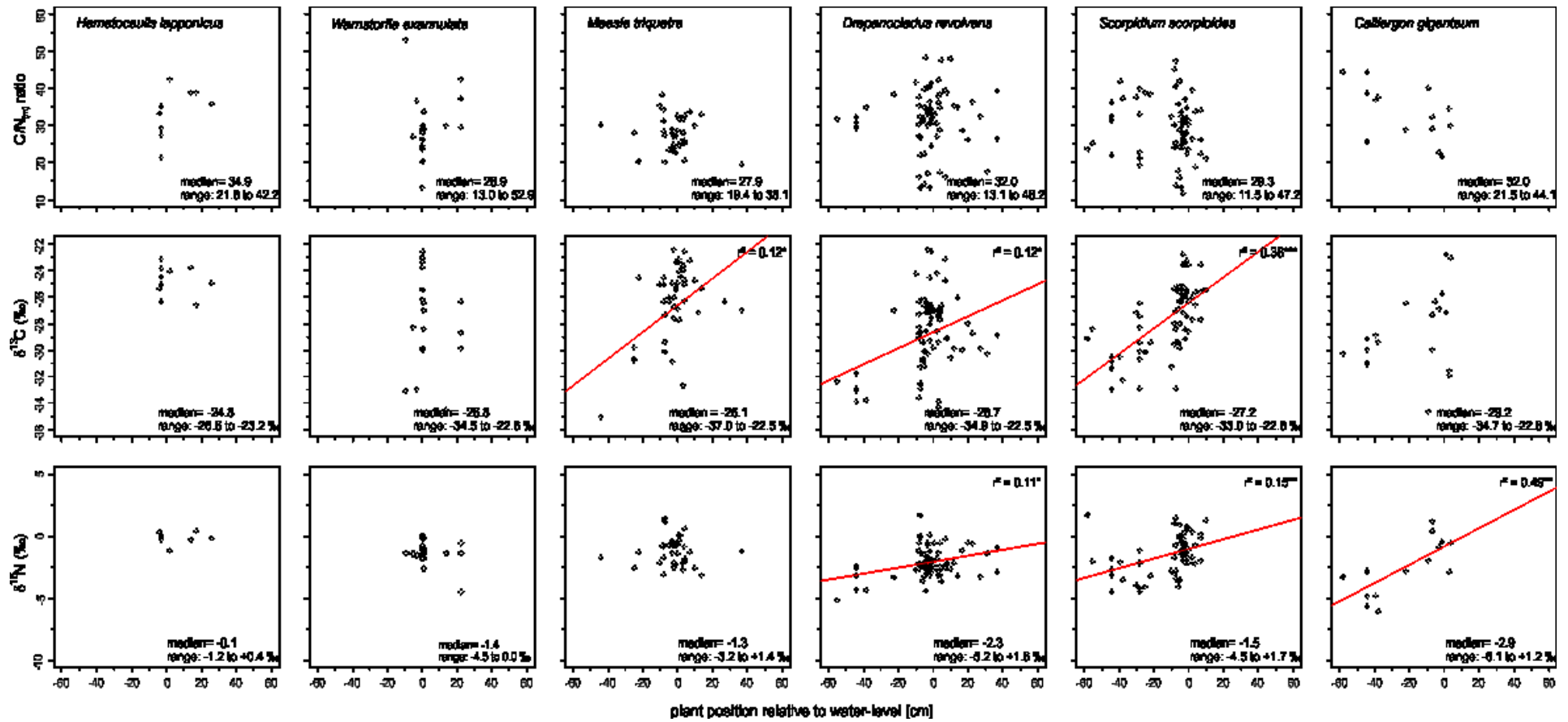
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Fig. 3a: *Intraspecific relationships of the C/N$_{(m)}$ ratio and the stable isotope values of carbon and nitrogen related to the water-level of the xero-mesophilic moss group.*
Regression lines (red) are only plotted for significant data sets.

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

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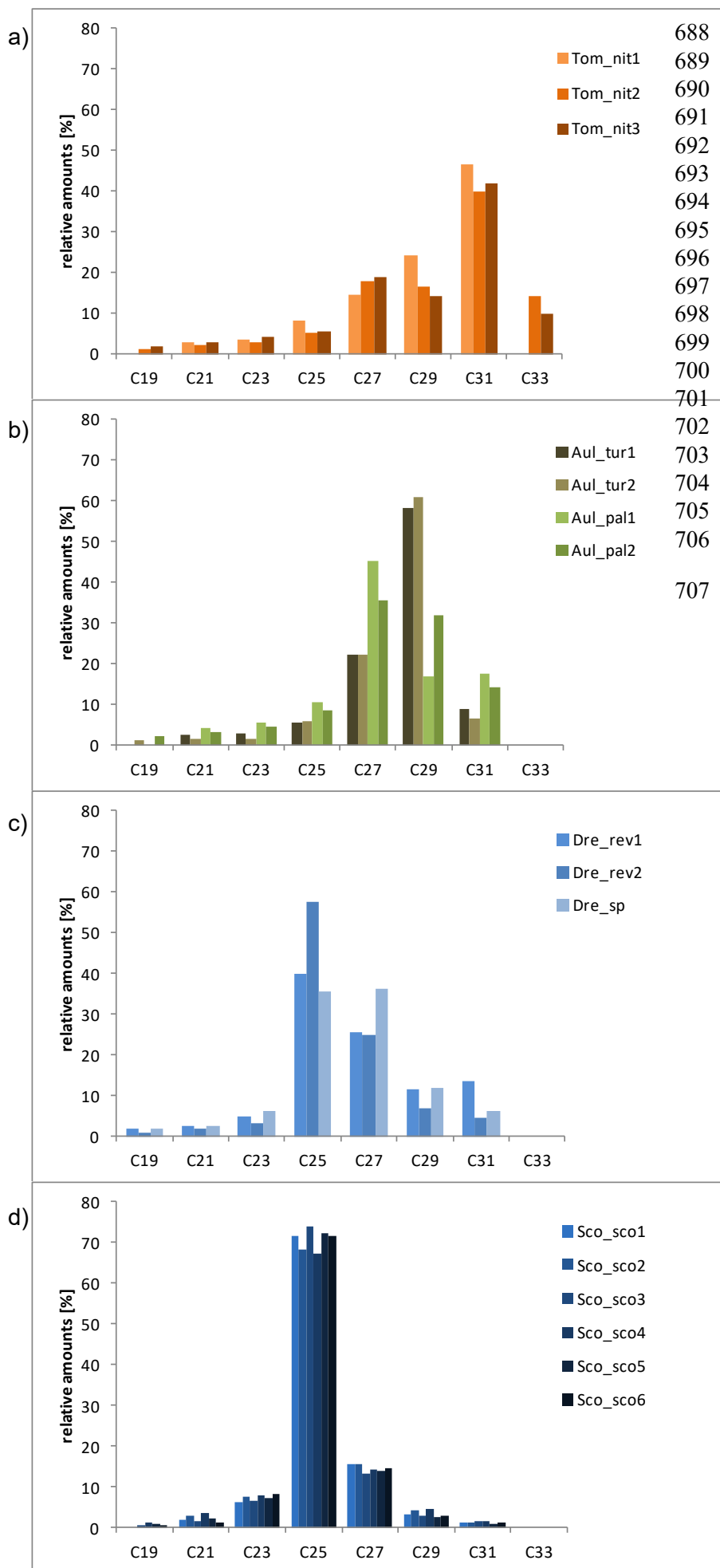
Fig. 4: *The relative amounts [%] of* n-*alkanes with an odd number of carbon atoms in selected brown mosses grouped by species and ordered by their preferences with respect to their mean plant-position relative to water-level for xero-mesophilic (a, b) and meso-hygrophilic (c, d) mosses. Tom-nit: Tomentypnum nitens; Aul_tur: Aulacomnium turgidum; Aul_pal: Aulacomnium palustre; Dre_rev: Drepanocladus revolvens; Dre_sp: Drepanocladus sp.; Sco_sco: Scorpidium scorpioides*
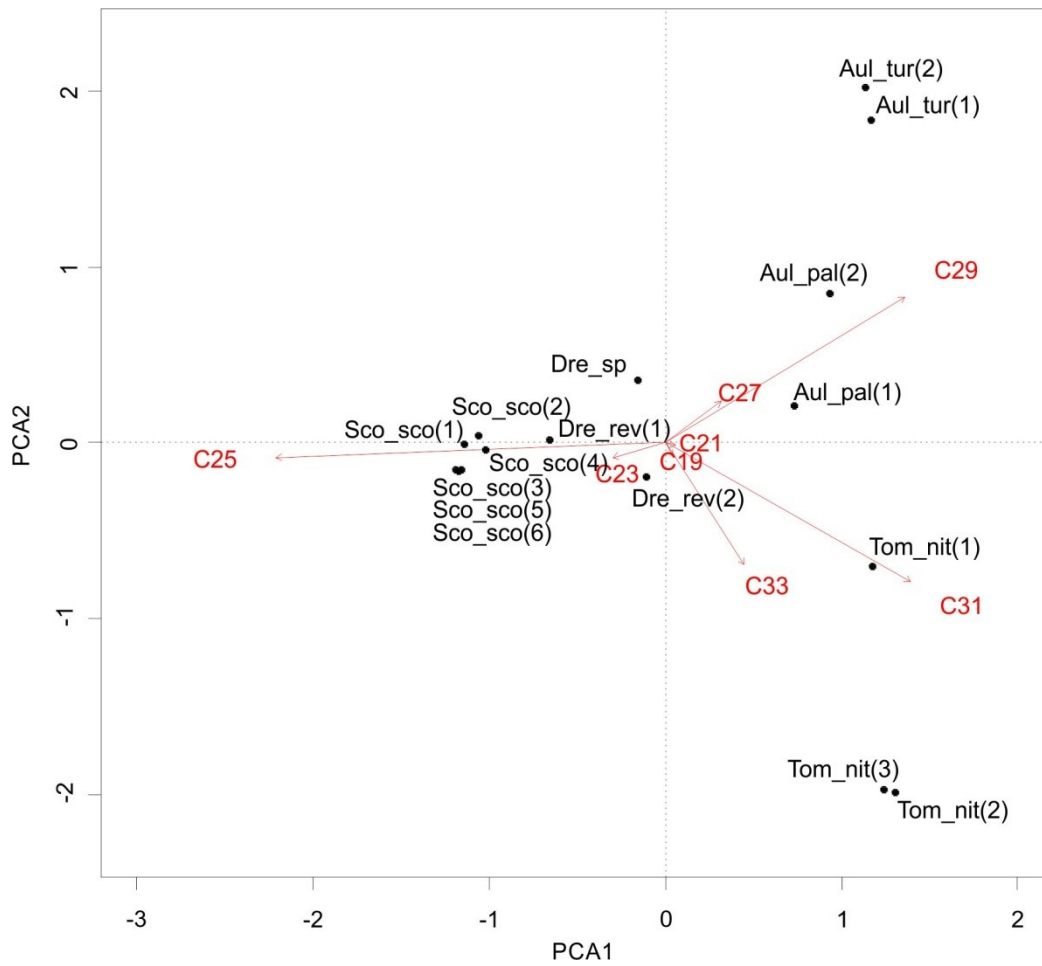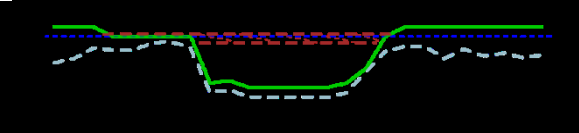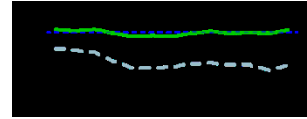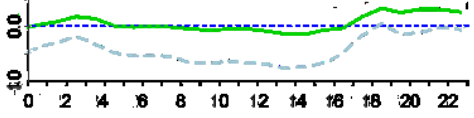
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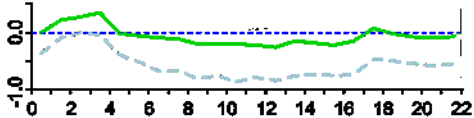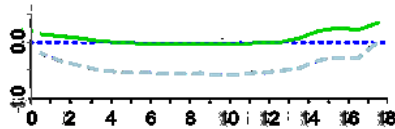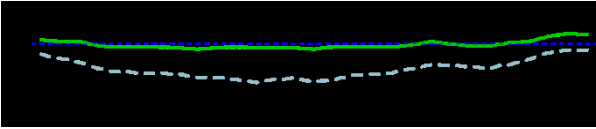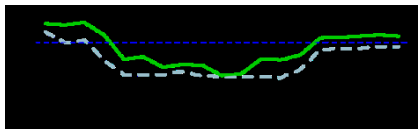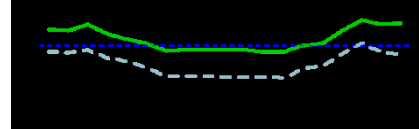709 ***Fig 5:*** *PCA of* n-*alkanes separates the meso-hygrophilic group on the left side of axis 1 from the xero-mesophilic*
710 *group on the right side. Along the second axis the* Aulacomniaceae *are distinguished from* Tomentypnum nitens
711 *according to the distribution of long-chain* n-*alkanes with more or less than 30 carbon atoms.*

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713   **Appendix**

714   ***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
	06/P	70.666° N, 97.708° E	open forest; swinging bog (mat of mosses)
	17/P	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/I - deep, open water body
	P3/II	72.149° N, 102.693° E	P3/II - shallow, open water body
	P3/III		P3/III - shallow completely vegetated
	12/P	72.431° N, 102.373° E	tundra; shallow and vegetated
	LP1	72.375° N, 126.483° E	tundra; deep polygon without thaw depth below the water body
	LP2	72.370° N, 126.481° E	tundra; shallow and vegetated

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Table A2: *C/N~~(m)~~ ratio* ~~*by weight*~~*, δ^{13}C and δ^{15}N data of individual mosses depending on their position relative to the water-level (cm).*

Species	C/N~~(w+m)~~ ratio		δ^{13}C [‰]			δ^{15}N [‰]		
	median	range	n	median	range	n	median	range
H. splendens (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
T. nitens (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
A. turgidum (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
A. palustre (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
H. lapponicus (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
W. exannulata (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
M. triquetra (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
D. revolvens (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**
S. scorpioides (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**
C. giganteum (Cal_gig)	42.6	28.6 to 58.7	23	-29.2	-34.7 to -22.8	17	-2.9	-6.1 to +1.2**

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718 Stars designate significant linear regressions between parameter and the plant position relative to water-level (* p≤0.01, ** p≤0.05, *** p≤0.001).
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	C/N~~(w+m)~~ ratio		δ^{13}C [‰]			δ^{15}N [‰]		
	median	range	n	median	range	n	median	range