

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

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21 **Abstract**

22 Mosses are a major component of the arctic vegetation, particularly in wetlands. We present C/N
23 ratios molar, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data of 400 brown moss samples belonging to 10 species that were
24 collected along hydrological gradients within polygonal mires located on the southern Taymyr
25 Peninsula and the Lena River delta in northern Siberia. Additionally, *n*-alkane patterns of six of these
26 species (16 samples) were investigated. The aim of the study is to see whether the inter- and
27 intraspecific differences in C/N, isotopic compositions and *n*-alkanes are indicative of habitat with
28 particular respect to water-level. Overall, we find high variability in all investigated parameters for
29 two different moisture-related groups of moss species. The $C/N_{(m)}$ ratios range between 11 and 53
30 (median: 32) and show large variations at the intraspecific level. However, species preferring a dry

31 habitat (xero-mesophilic mosses) show higher $C/N_{(m)}$ ratios than those preferring a wet habitat (meso-
32 hygrophilic mosses). The $\delta^{13}C$ values range between -37.0 and -22.5‰ (median = -27.8‰). The $\delta^{15}N$
33 values range between -6.6 and +1.7‰ (median = -2.2‰). We find differences in $\delta^{13}C$ and $\delta^{15}N$
34 compositions between both habitat types. For some species of the meso-hygrophilic group, we suggest
35 that a relationship between the individual habitat water-level and isotopic composition can be inferred
36 as a function of microbial symbiosis. The *n*-alkane distribution also shows differences primarily
37 between xero-mesophilic and meso-hygrophilic mosses, i.e. having a dominance of *n*-alkanes with
38 long (*n*-C₂₉, *n*-C₃₁) and intermediate (*n*-C₂₅) chain lengths, respectively. Overall, our results reveal that
39 $C/N_{(m)}$ ratios, isotopic signals and *n*-alkanes of studied brown moss taxa from polygonal wetlands are
40 characteristic of their habitat.

41 **1. Introduction**

42 Specific physiological and morphological traits enable mosses to attain extensive surface coverage in
43 low-temperature ecosystems such as arctic tundra (Turetsky et al., 2012; Wasley et al., 2006). Mosses
44 are a major component of the biomass in arctic wetlands and contribute strongly to the biodiversity. In
45 particular, the vegetation of the widely distributed polygonal tundra is rich in moss taxa, which partly
46 originates from the strong compositional turnover along a small-scale hydrologic gradient (Zibulski et
47 al. 2016). As an intermediate layer between air and the permafrost soil, mosses control the water cycle,
48 greenhouse gas and energy exchange (Blok et al., 2011; McFadden et al., 2003), and the structure of
49 the habitats of vascular plant communities in arctic landscapes (Beringer et al., 2001; Gornall et al.,
50 2011; Malmer et al., 1994). Because of their low decomposition rates (Aerts et al., 1999; Turetsky,
51 2003), they contribute strongly to the peat and permafrost carbon pool (Tarnocai et al., 2009).

52 Despite the significance of mosses in high-latitude biodiversity and matter cycles only little is
53 known about their C/N ratio, stable isotope and *n*-alkane characteristics in comparison to vascular
54 plants. Such information is not only necessary to improve our understanding of the physiological
55 adaptation or plasticity of mosses to certain environmental characteristics, but can also be used when

56 similar measurements of fossil plant material are interpreted as proxies of former ecological or
57 environmental conditions (e.g. Birks, 1982).

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

69 As well as the C/N ratio, the $\delta^{13}\text{C}$ composition is barely altered by decomposition processes in the
70 soil and also suitable for palaeo-environmental reconstructions. The $\delta^{13}\text{C}$ ratio of an individual plant
71 are a mixed signal of the physiological traits of the species and the individual's direct environment.
72 Mosses use the C_3 pathway for carbon assimilation (O'Leary, 1988, Farquhar et al., 1989) and despite
73 a lack of stomata in the photosynthetic active parts, they have a similar range in their $\delta^{13}\text{C}$ values of
74 between -24 and -32 ‰ (Ménot and Burns, 2001; Rundel et al., 1979; Smith and Epstein, 1971) as
75 vascular C_3 plants. Differences in $\delta^{13}\text{C}$ values among several species can be explained by individual
76 plant physiology and biochemistry (Galimov, 2000). Differences within a single species have been
77 linked with environmental conditions such as temperature (Skrzypek et al., 2007; Waite and Sack,
78 2011), growing depth below water-level (Raghoebarsing et al., 2005), position within a cushion or
79 hummock (Price et al., 1997), lipid content (Rundel et al., 1979) or the influence of microbial
80 symbioses (Liebner et al., 2011; Vile et al., 2014). Furthermore, even differences among branches and
81 stems of single individuals have been reported (Loader et al., 2007). However, almost all of these
82 studies were made on Sphagnaceae, which are not representative of all mosses because of their

83 specific morphology (i.e. the occurrence of a photosynthetic active cell type and a dead cell type,
84 which is responsible for water storage and often an additional coating of the photosynthetic active cell)
85 and their specific habitat preferences (i.e. preferring acidic wetlands). Hence, this information cannot
86 simply be transferred to brown mosses – which form the major component in northern Siberian
87 lowlands – due to their different morphology.

88 Most studies on $\delta^{15}\text{N}$ values of moss material have focused on the anthropogenic impact on the
89 nitrogen cycle (Harmens et al., 2011; Liu et al., 2008; Poikolainen et al., 2009), whereas reports on the
90 $\delta^{15}\text{N}$ compositions of mosses from relatively pristine ecosystems such as the Arctic are rare or have
91 been investigated in relation to the study of bird colonies (e.g. Lee et al., 2009). Potentially, such
92 information can indicate pathways and sources of the nutrient supply in these N-limited ecosystems
93 (Kielland, 1997; Michelsen et al., 1996, 1998).

94 Compared with vascular plants and *Sphagnum* species, relatively few investigations of *n*-alkane
95 patterns of brown mosses are available. Palaeoenvironmental reconstructions use the potential of
96 *n*-alkanes to distinguish between different plant groups (Ficken et al., 1998, moisture conditions
97 (Pancost et al., 2000, Nichols et al 2006, Zhou et al. 2010), whether organic material is to decomposed
98 and changes in temperature (Feakins et al., 2016, Sachse et al., 2006) along distinct gradients.
99 *Sphagnum* species, for example, show a dominance of *n*-C₂₃ and *n*-C₂₅ homologues (Baas et al., 2000)
100 that are comparable to the pattern of vascular submerged plants (Ficken et al., 2000), and ratios are
101 used as a proxy for wet moisture conditions. Other studies discuss the suitability of *n*-alkane patterns
102 in moss species for chemotaxonomical studies on recent and fossil material (Bush and McInerney,
103 2013; Nott et al., 2000; Schellekens and Buurman, 2011). A greater protection potential of waxes with
104 a higher content of long-chain *n*-alkanes against solar irradiation or alternatively an enhanced loss of
105 short-chain *n*-alkanes by evaporation have been suggested as possible mechanisms to cause different
106 *n*-alkane patterns in leaf waxes of trees (Sachse et al., 2006). However, with respect to mosses the
107 pattern and mechanisms are even less understood.

108 This study presents $C/N_{(m)}$, isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and *n*-alkane characteristics of mosses from low-
109 centred polygons in northern Siberia. Low-centred polygons are geomorphological forms in arctic

110 landscapes originating from frost-heave processes in the soil. They are characterized by elevated dry
111 rims and a water-saturated or water-filled centre. This centimetre-scale hydrological gradient is well
112 reflected by a strong turnover in the vascular plant and moss composition (Zibulski et al., 2016). We
113 investigate the relationship between the $C/N_{(m)}$, isotopic and *n*-alkane compositions and the
114 hydrological conditions within low-centred polygons. In particular, we aim to reveal whether
115 fingerprints are habitat-specific or rather species-specific.

116 **2. Material and methods**

117 **2.1 Sites**

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

128 **2.2 Sampling and studied moss species**

129 A representative continuous transect of adjacent one square-metre plots (from rim to rim) was selected
130 for sampling in each polygon. The surface height in relation to water-level (measured at the centre of
131 each plot) and vegetation (abundance information) were recorded. Individual characteristics of each
132 low-centred polygon are presented in Table A1. Moss plants were hand-picked, dried in the field and
133 transported to the Alfred Wegener Institute in Potsdam. Taxa identification is based on the relevant
134 literature (Frahm and Frey, 2004; Lobin et al., 1995; Smith, 1978) and the Bryophyte Flora of North
135 America internet source (<http://www.efloras.org>).

136 In total, eight species that were observed to have different water-regime preferences were included in
 137 the analyses. To approximate water-regime preferences of each species, we calculated the mean plant-
 138 position in relation to water-level (h) from the recorded plot surface height. *Warnstorfia exannulata*
 139 was observed to grow as part of a swinging mat at water-level, it was assigned a preference for water-
 140 level. Using this information the species were classified as either as of xero-mesophilic mosses (mean
 141 plant-position between 13 and 16 cm in relation to water-level) or to the group of meso-hygrophilic
 142 mosses (mean plant-position between 3 and -30 cm in relation to water-level) to ease the presentation
 143 of results.

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

species	abbreviation	h (mean plant-position in relation to water-level in cm)	classification
<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

147

148 **2.4 Measurements of C/N_(m) ratios, stable carbon and nitrogen isotope values and** 149 **n-alkane distributions**

150 Selected plant material (i.e. apical parts of a specimen) was rinsed with de-ionised water and
 151 mechanically cleaned from organic particulate material. The content of carbon and nitrogen and the
 152 ratio of stable isotopes were measured with a DELTAplusXL isotope ratio mass spectrometer (Thermo
 153 Fischer Scientific) coupled to an elemental analyser (NC2500 Carlo Erba) via a CONFLOW III
 154 Interface. Due to the relatively wide range of C/N ratios of mosses, we used about 1.5 mg for each
 155 carbon stable isotope measurement ($n = 400$) and a replicate of 3 mg for each nitrogen stable isotope
 156 measurement ($n = 326$) and the analysis of elemental composition. The high weight needed for the
 157 nitrogen sample replicates prevented the measurement of $\delta^{15}\text{N}$ and thus the C/N_(m) for some samples.
 158 The calibration for carbon was performed using an urea standard and a $\delta^{13}\text{C}$ isotopic standard (IAEA
 159 CH-7). The nitrogen contents were calibrated against an acetanilide standard and the nitrogen isotopic
 160 composition with ammonium sulphate standard (IAEA N-1). The reliability of the method was
 161 checked with the NIST plant standard SRM 1547. The isotopic ratios are given in delta notation

162 relative to VPDB for $\delta^{13}\text{C}$ values and relative to air for $\delta^{15}\text{N}$ values, respectively. The reproducibility
163 for replicate analyses is 0.2% for carbon and nitrogen and 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

164 *n*-Alkane analyses were performed on a subset of 16 samples. We took material from the polygon
165 complex P3 from the Khatanga region (72.149° N, 102.693° E), which comprises three successive
166 low-centred polygons (Table A1) to exclude effects of environmental conditions at different locations.
167 The moss samples were washed, identified and air-dried. They were weighed (150–1000 mg dry
168 weight) and samples extracted with an accelerated solvent extractor (ASE) (Dionex, Sunnyvale; USA)
169 using $\text{Cl}_2\text{Me}:\text{MeOH}$ (10:1) at 5 bar and 75°C. The extract was separated into aliphatic hydrocarbon,
170 aromatic hydrocarbon and nitrogen, sulphur and oxygen compound fractions using medium pressure
171 liquid chromatography following Radke et al. (1980). Five μg of the quantification standard (5 α -
172 androstane, 1-ethylpyrene, 5 α -androstane-17-one and erucic acid) were added. Gas chromatography
173 (GC) of aliphatic hydrocarbon fractions was performed using a GC Agilent 6890 equipped with an
174 Ultra-1 fused silica capillary column (Model Agilent 19091A-105, length 50 m, inner diameter
175 200 μm , film thickness 0.33 μm). Helium was used as a carrier gas at a constant flow rate of 1 ml
176 min^{-1} . The GC oven was heated from 40 °C (2 min hold time) to 300 °C (65 min hold time) at a rate of
177 5°C per minute. The samples were injected by means of splitless injection. Quantitative evaluation of
178 data was done with ChemStation software. Additionally, we calculated the average chain length
179 (ACL_{21-33}) assumed to represent a proxy for moisture (Andersson et al, 2011) and temperature (Bush
180 and McInerney, 2015) with a comprehensible extended range from *n*-C₂₁ to *n*-C₃₃ and the proxy ratio
181 P_{aq} , which was developed as a proxy ratio to distinguish submerged or floating aquatic macrophytes
182 from emergent and terrestrial plants (Ficken et al., 2000):

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

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

183

184 2.5 Statistical Tests

185 We calculated the range, .25, .5, and .75 quantiles of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and the $\text{C}/\text{N}_{(\text{m})}$ ratios for all
186 species (Table A2). Significant differences in the $\text{C}/\text{N}_{(\text{m})}$ ratios and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among
187 different groups were assessed with a t-test. In addition, we performed linear regression between the
188 obtained values for each individual species and surface height. All analyses were implemented in R
189 version 3.2.0 (R Core Team, 2015). Furthermore, we performed a PCA with the percentage of
190 *n*-alkane homologues (square-root transformed) in R using the vegan package version 2.0-10
191 (Oksanen et al., 2013).

192 3. Results

193 The overall ranges in $\text{C}/\text{N}_{(\text{m})}$ ratios of both groups have a broad overlap (xero-mesophilic: 22.5–67.9;
194 meso-hygrophilic: 15.4–70.4). However, the medians of the $\text{C}/\text{N}_{(\text{m})}$ values of the xero-mesophilic
195 species ranging from 47.6 to 52.9 (Fig. 2) are significantly higher than those of the meso-hygrophilic
196 group, which range from 37.1 to 46.5 ($W = 18280$, $p \ll 0.001$). The $\text{C}/\text{N}_{(\text{m})}$ ratios show no
197 intraspecific relations among individual species and water-level (Fig. 3a), except for *Tomentypnum*
198 *nitens* ($r^2 = 0.11$, $p < 0.05$).

199 The $\delta^{13}\text{C}$ values of the meso-hygrophilic group (-34.9 to -22.5‰) cover the range of the xero-
200 mesophilic group (-32.1 to -24.2‰), which have a noticeably lower variance in $\delta^{13}\text{C}$ values (Fig. 2).
201 The medians of the individual species in the xero-mesophilic group (range: -29.4 to -27.1‰) are
202 significantly different ($W = 16232$, $p = 0.008$) from those of the meso-hygrophilic group (range: -29.2
203 to -24.8‰). $\delta^{13}\text{C}$ values of *Meesia triquetra*, *Drepanocladus revolvens*, and *Scorpidium scorpioides*
204 (all belonging to the meso-hydrophilic group) are significantly positively related with the position of
205 the water-level (Fig. 3b), while no member of the xero-mesophilic group revealed such relationship
206 (Fig. 3a).

207 The ranges of $\delta^{15}\text{N}$ values of both groups are rather similar (Fig. 2). However, individual species
208 medians of both groups are significantly different ($t = -6.96$, $p \ll 0.001$; xero-mesophilic group; -3.2
209 to -2.7‰, meso-hygrophilic group: -2.9 to -0.1). *Drepanocladus revolvens*, *Scorpidium scorpioides*,

210 and *Calliergon giganteum*, all belonging to the meso-hygrophilic group, exhibit a positive relationship
 211 between the $\delta^{15}\text{N}$ values and position relative to water-level (Fig. 3b).

212 *n*-Alkane distributions show the expected predominance of the odd chain length (Table 2). The
 213 absolute *n*-alkane concentrations (*n*-C₁₉ to *n*-C₃₃) range from 34 to 238 $\mu\text{g g}^{-1}$ of dry weight. The
 214 individual taxa show significant differences with respect to carbon number of the most abundant
 215 *n*-alkane (*n*-C_{max}) forming unimodal distribution patterns. It is *n*-C₃₁ for *Tomentypnum nitens*, which is
 216 also the only species containing *n*-C₃₃ in detectable amounts, *n*-C₂₉ for *Aulacomnium turgidum*, *n*-C₂₇
 217 for *Aulacomnium palustre*, *n*-C₂₇ and *n*-C₂₅ for the *Drepanocladus* taxa, and *n*-C_{max} = 25 for
 218 *Scorpidium scorpioides*. These differences in the *n*-alkane composition largely relate with the species-
 219 preferred mean plant-position relative to water-level (Fig. 4).

220 Evaluations of the *n*-alkane biomarker proxies, ACL₂₁₋₃₃ and P_{aq}, also show a clear division
 221 between the xero-mesophilic and the meso-hygrophilic species groups (Table 2), whereas intraspecific
 222 variations are rather small (with the exception of *Drepanocladus*). The xero-mesophilic group is
 223 notable for high averages of ACL₂₁₋₃₃ (28.41) and P_{aq} (0.17) compared to low averages of ACL₂₁₋₃₃
 224 (25.61) and P_{aq} (0.87) for the meso-hygrophilic group.

225 The observed trend is also assumed in the biplot of the first two PCA axes, even though their
 226 explained variance is relatively low (16.9%) in the dataset (Fig. 5). The first axis separates xero-
 227 mesophilic from meso-hygrophilic taxa. *Aulacomnium* taxa are located in the upper range and
 228 *Tomentypnum nitens* in the lower range of the second PCA axis, while no trend is observed within the
 229 meso-hygrophilic group along the second axes.

230 **Table 2:** The concentration ($\mu\text{g/g}$ dry weight) and ACL₂₁₋₃₃ and P_{aq} (after Ficken et al., 2000) of *n*-alkanes in
 231 brown moss samples. (Numbers in brackets relates to the sample number.)

species	<i>n</i> -C ₁₉	<i>n</i> -C ₂₁	<i>n</i> -C ₂₃	<i>n</i> -C ₂₅	<i>n</i> -C ₂₇	<i>n</i> -C ₂₉	<i>n</i> -C ₃₁	<i>n</i> -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

232 4. Discussion

233 4.1 C/N_(m) ratios

234 The C/N ratios of mosses from polygonal tundra in Northern Siberia are relatively low compared with
235 those obtained for mosses from Antarctic bogs that range between 80 and 100 (Björck et al., 1991) or
236 from western Canada that range between 55 and 76 (Kuhry and Vitt, 1996). However, neither the taxa
237 xeric and mesic growing conditions were sampled in Antarctica and Canada. All investigated species
238 are considered as ectohydric mosses, which receive nitrogen mostly from precipitation deposits (Ayres
239 et al., 2006). Our results reveal that averaged C/N_(m) ratios for the xero-mesophilic moss group are
240 higher than for the meso-hygrophilic group, probably reflecting the known difference between
241 terrestrial and aquatic plants (Meyers and Ishiwatari, 1993). There are two possible impacts, which can
242 influence the C/N ratio of these groups: (1) competition with vascular plants and (2) accessibility of
243 nitrogen pools (2)g. (1) If moss plants invest in a high stem-to-leaf biomass ratio, which results in a
244 high C/N_(m) ratio, they will increase their height and stability, and thus their competitive ability
245 against vascular plants for light (Sveinbjörnsson and Oechel, 1992). Furthermore, the low N input by
246 precipitation and a low N content of moss litter slows down the fungal and bacterial N mineralisation
247 which increases the thickness of moss litter mats (Gornall et al., 2007; Turetsky, 2003). This in turn
248 will increase the isolating function of moss mats, thus negatively affecting seed germination of
249 vascular plants (Gornall et al., 2007). (2) Lower C/N_(m) ratios of meso-hygrophilic mosses may
250 originate from higher amounts of dissolved nitrogen in polygon waters as a result of high net primary
251 productivity, the presence of N₂-fixers such as cyanobacteria, and the exudations of zooplankton.
252 Frahm (2001) assumes that loose epiphytic and endophytic symbiotic relationships between mosses

253 and cyanobacteria are probably restricted to wetland taxa. Lindo et al. (2013) report such associations
254 between brown mosses and cyanobacteria. Thus, the N supply is better for brown mosses preferring
255 meso-hygrophilic than xero-mesophilic habitats, and the respective taxa accordingly have lower
256 $C/N_{(m)}$ ratios indicating habitat-specific variation in $C/N_{(m)}$ ratios. We expected to also find
257 intraspecific variations between $C/N_{(m)}$ ratios and water-level. The large variability in the C/N data
258 may be a result of atmospheric conditions and organic matter degradation being the principal sources
259 at xeric sites, whereas in mesic and wet sites microbial symbionts play an important role in the C/N
260 ratio. However, the signal-to-noise ratio is probably too low to give a meaningful result because only
261 the average water level of each plot but not of each individual plant was recorded.

262 **4.2 $\delta^{13}C$ values**

263 With respect to bryophytes, most isotopic studies have hitherto been performed on *Sphagnum* (Markel
264 et al., 2010, Ménot and Burns, 2001) while our study focuses on brown mosses – a major component
265 in Siberian wetlands. The intraspecific variability for some meso-hygrophilic species (i.e. *Meesia*
266 *triquetra*, *Drepanocladus revolvens*, *Scorpidium scorpioides*) show that the $\delta^{13}C$ signals are related to
267 the hydrological conditions at the growing site of each individual, i.e. individuals growing at dry sites
268 showed higher medial $\delta^{13}C$ values than those growing at wet sites. A difference among the two habitat
269 groups is observed; they partly contradict the intraspecific findings in that some of the xero-mesophilic
270 species known to prefer dry rims such as *Hylocomium splendens* and *Tomentypnum nitens* have
271 particularly low $\delta^{13}C$ medians.

272 The detected differences in moss $\delta^{13}C$ values, particularly of the meso-hygrophilic group, either
273 reflect a source signal depending on water-level or a physiological reaction of the plant related to
274 water-level (Bramley-Alves et al., 2014; Proctor et al., 1992). Mosses are typical C_3 plants (Farquhar
275 et al., 1989, Rundel et al., 1979) characterized by a high CO_2 compensation point (Bain and Proctor,
276 1980; Dilks and Proctor, 1975; Salvucci and Bowes, 1981). The high availability of atmospheric CO_2
277 and elevated diffusion rates of CO_2 in air compared to water (O’Leary) result in typical terrestrial C_3
278 land plant $\delta^{13}C$ characteristics, because of a decreasing cell water pressure in dry habitats which entails
279 a strong discrimination rate against $^{13}CO_2$ induced by RuBisCO (Rice and Giles, 1996). With respect
280 to the xero-mesophilic group, we observe an increase in discrimination against ^{13}C from taxa

281 preferring a low position relative to the water-level (e.g. *Aulacomnium* taxa) than those preferring high
282 positions (e.g. *Hylocomium splendens*). In contrast, if plant tissue is coated by a water film, the cell
283 water pressure should reach an optimum, which is expected to result in a weaker discrimination rate
284 against ^{13}C by RuBisCO (Rice and Giles, 1996), because of a source restriction by the slower diffusion
285 rate of CO_2 in water (Lloyd and Farquhar, 1994). A lower carbon isotope discrimination related to
286 water saturation is observed for only three species out of six meso-hygrophilic mosses. However, this
287 basic signal may be masked by variations in $\delta^{13}\text{C}$ values of different carbon sources, which are
288 expected to be more influential for meso-hygrophilic mosses in water-saturated conditions. Ménot and
289 Burns (2001) studied intraspecific variations for three *Sphagnum* species, which prefer three different
290 habitat types (dry, meso, wet) along an elevational gradient, which was positively correlated with
291 precipitation. They find a decline in discrimination against ^{13}C with increasing wetness, and similar to
292 our results no relationship for species with a strong wet –preference. This is attributed to the variation
293 in $\delta^{13}\text{C}$ from highly varying dissolved inorganic carbon (Proctor et al., 1992). Mosses potentially
294 access ^{13}C -depleted CO_2 that originates from oxidation of typically strongly ^{13}C -depleted biogenic
295 methane by methanotrophic microorganisms (Kip et al., 2010; Liebner et al., 2011; Raghoebarsing et
296 al., 2005). Studies by Nichols et al. (2009) show that a higher water level at the peat surface is crucial
297 for high methane-derived CO_2 release. Furthermore, symbiosis with methanotrophs enhances the
298 moisture-related effect on the $\delta^{13}\text{C}$ signal of bryophytes. Endophytic microorganisms in hyalocytes of
299 submerged *Sphagnum* (Raghoebarsing et al., 2005) or epiphytic microorganisms on submerged brown
300 mosses (Liebner et al., 2011) are presumed to provide ^{13}C -depleted CO_2 directly to the lamina cells of
301 mosses. The studies of Ruttner (1947) and Bain and Proctor (1980) show that, in general, moss taxa
302 are incapable of bicarbonate uptake. Hence, bicarbonate, known to be a carbon source for submerged
303 vascular plants and algae (Herzschuh et al., 2010; Merz, 1992), can most probably be excluded as a
304 carbon source for moss and thus as a factor influencing the $\delta^{13}\text{C}$ value. Moreover, the bicarbonate
305 content in pond waters in northern Siberian landscapes is very low (Wetterich et al., 2008). Other
306 sources of ^{13}C -depleted CO_2 are surface run-off during spring flooding, rain events and decomposition
307 processes in the pond (Leng and Marshall, 2004; Maberly et al., 2013). Yet we cannot fully eliminate
308 the possibility that the measured bulk material was contaminated in parts with epiphytic or endophytic

309 microorganisms. The overall isotopic composition would, however, likely be unaffected, as Ménot and
310 Burns (2001) have shown that the $\delta^{13}\text{C}$ values of bulk organic material and alpha-cellulose of
311 *Sphagnum* are very similar. Thus, the large ranges within several species of meso-hygrophilic habitats
312 in arctic regions suggest that the existence of open water leads to more depleted $\delta^{13}\text{C}$ values and
313 measurements of the isotopic composition of methane when present and microbial groups in the water
314 and terrestrial litter should be possible. Finally, considering the relationship of selected brown mosses
315 to mean plant position, the complex origin of plant-available carbon makes it difficult to interpret the
316 $\delta^{13}\text{C}$ record, especially for meso-hygrophilic brown mosses as well as *Sphagnum* (Prince et al., 1997,
317 Ménot and Burns, 2001).

318 **4.3 $\delta^{15}\text{N}$ isotopes**

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

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

333 Three of the investigated submerged or floating moss species show a significant positive
334 relationship between water-level and $\delta^{15}\text{N}$ values. These results are similar to those of Asada et al.
335 (2005) who tested a relationship between $\delta^{15}\text{N}$ values of different *Sphagnum* species and their position

336 relative to the groundwater level, which they assumed to originate from different nitrogen sources and
 337 different internal fractionating processes. We assume that the often heavier nitrogen isotope
 338 composition of meso-hygrophilic brown moss individuals originates from the high degree of symbiotic
 339 associations with aquatic atmospheric nitrogen-fixing autotrophic microorganisms such as *Nostoc* or
 340 *Anabena* (Lindo et al., 2013) or methanotrophs (Vile et al., 2014). The high spatial degree with endo-
 341 or ectosymbiotic N₂-fixing microorganisms enables the direct uptake of their nitrogen products, which
 342 is similar to that of N₂ in air.

343 **4.4 *n*-alkane patterns**

344 Compared to vascular plants that are characterized by a thick leaf-wax layer, mosses produce only a
 345 small amount of *n*-alkanes (Baas et al., 2000; Ficken et al., 1998). Like previous studies on vascular
 346 plants (Aichner et al., 2010; Ficken et al., 2000; Meyers and Ishiwatari, 1993), our results generally
 347 reveal a differentiation between terrestrial taxa (i.e. xero-mesophilic group) characterized mainly by
 348 *n*-alkanes maximizing at *n*-C₂₉ and *n*-C₃₁ and submerged living taxa (i.e. the meso-hygrophilic group)
 349 maximizing at *n*-C₂₅ and *n*-C₂₇. Earlier investigations of Nott et al. (2000), Baas et al. (2000) and
 350 Bingham et al. (2010), who compared the *n*-alkane fingerprints of *Sphagnum* taxa growing along a
 351 hydrological gradient, agree with our results.

352 Huang et al. (2012a) and Ficken et al. (1998) used proxy ratios (ACL, P_{aq}) to divide moss taxa roughly
 353 by their moisture preferences. They calculate the ACL₂₃₋₃₃ for samples of lichens and *Racomitrum*
 354 *lanuginosum*, which have rather similar hydrological requirements to our xero-mesophilic mosses.
 355 Despite the slightly narrower ACL₂₃₋₃₃ range, their results show similarities to our xero-mesophilic
 356 group. A comparison between ACL₂₁₋₃₃ ratios of *Sphagnum* (plant position nearly at water-level) of
 357 Huang et al. (2012b) and our brown mosses shows that the ACL₂₁₋₃₃ ratios of *Sphagnum* species are
 358 rather lower. The intraspecific conclusion of Huang et al. (2012b) (wetter moisture conditions entail
 359 lower ACL₂₁₋₃₃) for *Sphagnum* is reflected by our measurements.

dry (ACL₂₁₋₃₃ = 29.1 – 27.5) < **moisture condition** > (ACL₂₁₋₃₃ = 26.4 – 25.2) **wet**
 Tom_nit < Aul_tur < Aul_pal < Dre_rev < Sco_sco

360 .

361 As we observed a clear difference in the ACL_{21-33} between the xero-mesophilic and the meso-
 362 hygrophilic group, we suggest that the inclusion of mid-chain *n*-alkanes (*n*-C₂₁ to *n*-C₂₅) in the
 363 equation of ACL improves its value as a proxy for moisture conditions. Andersson et al. (2011)
 364 inferred ACL_{27-31} values of 29 for brown-moss peat from western Russian during wet phases, which is
 365 however, poorly comparable to our results because they investigated total peat organic matter instead
 366 of pure moss material.

367 Ficken et al. (2000) proposed P_{aq} as a semi-quantitative proxy ratio for the differentiation of
 368 terrestrial and aquatic plants (<0.1 terrestrial plants, 0.1–0.4 emergent macrophytes, 0.4-1
 369 submerged/floating macrophytes). Our inferred P_{aq} results for the individual species agree with these
 370 assumptions. If we consider that the proxy ratio levels were created by vascular plants from a limited
 371 dataset of lakes in Kenya and as we focus on non-vascular plants of the arctic, we chose other level
 372 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

373

374 Overall, our results do not support the inference of Nichols et al. (2006) that a hydrological
 375 classification is possible between *Sphagnum* and non-*Sphagnum* formed peat as the latter show wide
 376 variations between different habitats. The inferred broad P_{aq} range of *Drepanocladus* and between
 377 both *Aulacomnium* probably indicates that intraspecific variation is related to the individual's growing
 378 condition, which could provide the basis to develop P_{aq} as a proxy for water-level when measured on
 379 taxonomically identified fossil plant material.

380 As with P_{aq} , *n*-alkanes seem to be species-specific given stable environmental parameters and are
 381 related to the species-specific moisture requirements, which are adapted to changing environmental
 382 conditions. Thus, our results confirm the conclusions of Bingham et al. (2010), Bush and McInerney
 383 (2015) and Nott et al. (2000) that the pattern of *n*-alkanes has the potential to become a valuable proxy
 384 for chemotaxonomic identification and moisture conditions. *Scorpidium scorpioides*, a species with a

385 rather narrow preference range (i.e. it is limited to open water conditions), shows low intraspecific
386 variations. This matches the results for *Sphagnum* compiled by Bingham et al. (2010), which also
387 show minor intraspecific variations. *Aulacomnium* in contrast, which grows in a rather wide range of
388 moisture conditions, shows strong variations in its *n*-alkane spectra: whether this is a function of the
389 individual's growing conditions, however, needs to be investigated in a more extensive study.

390 **5. Conclusions**

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

393 The observed higher $C/N_{(m)}$ ratios of xero-mesophilic mosses compared to those of the meso-
394 hygrophilic mosses originate from the different environmental requirements when living emergent (i.e.
395 investment in a higher stability resulting in high C/N ratios) as opposed to submerged. Furthermore,
396 the latter group may also gain a better nitrogen supply through microbial symbioses.

397 With respect to the isotopic source pools, the meso-hygrophilic species have greater access than
398 xero-mesophilic species, which is seen in their large ranges. The approximate habitat-specific division
399 of $\delta^{13}C$ values as a result of discrimination by RuBisCO under different hydrological regimes is
400 overturned by the influence of different sources and cannot provide a clear distinction from a single
401 measurement of either habitat type. For species, growing near the water level, no intraspecific
402 relationship with water level was observed probably as a result of the parallel impact of processes
403 causing opposing $\delta^{13}C$ trends.

404 Our analyses reveal that, compared with xero-mesophilic mosses, meso-hygrophilic mosses are
405 characterized by enriched $\delta^{15}N$ values probably originating from microbial symbioses. Both carbon
406 and nitrogen isotopic ratios seem to be valuable proxies to differentiate between taxa preferring the
407 polygon rim or pond. Moreover, with respect to meso-hygrophilic mosses, the detected positive
408 relations between intraspecific variations and the individuals' relative growing position could allow
409 even more semi-quantitative information about water-level changes to be inferred.

410 The *n*-alkane patterns of brown mosses (limited 16 individuals belonging to five species) indicate
411 that they are species-specific and have thus the potential to be developed as a chemotaxonomic proxy.
412 The applicability of proxy ratios (ACL and Paq) could be attested for arctic mosses after adjustments
413 of the levels.

414 Overall, our study indicates that C/N, isotopic and *n*-alkane analyses of brown moss material has
415 a high environmental indicator potential, particularly if species-specific material instead of bulk
416 material is analysed.

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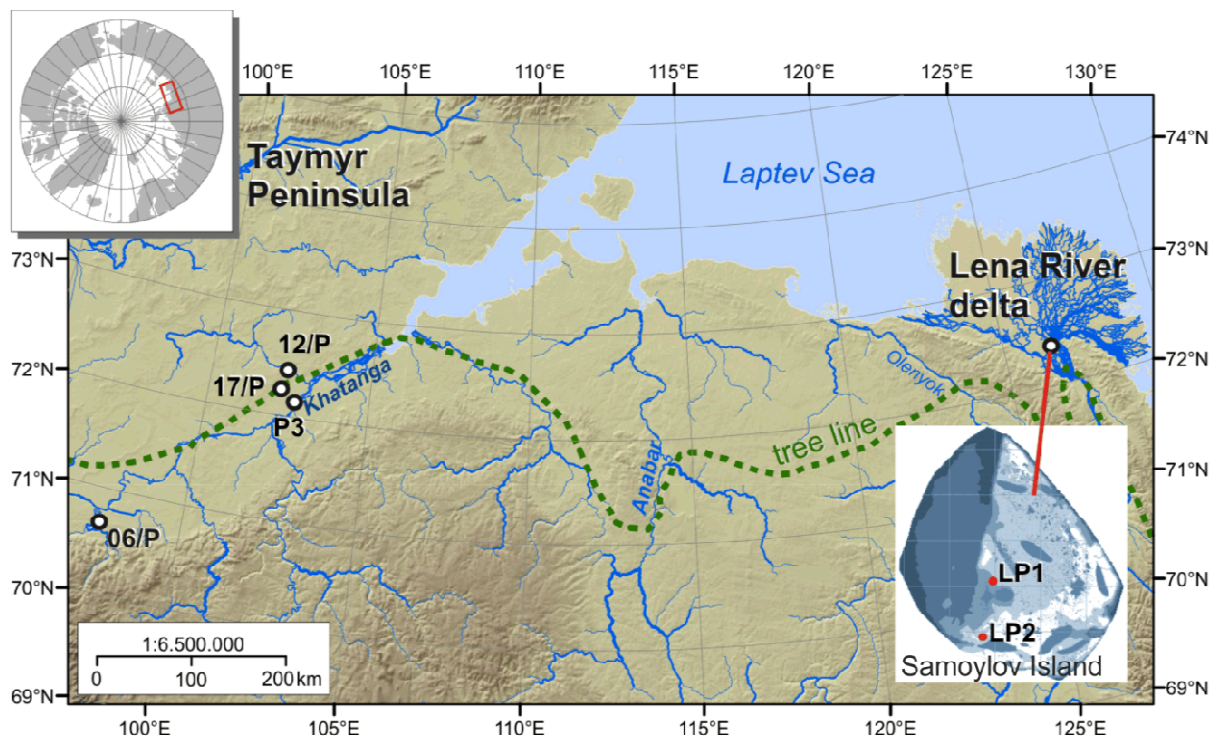
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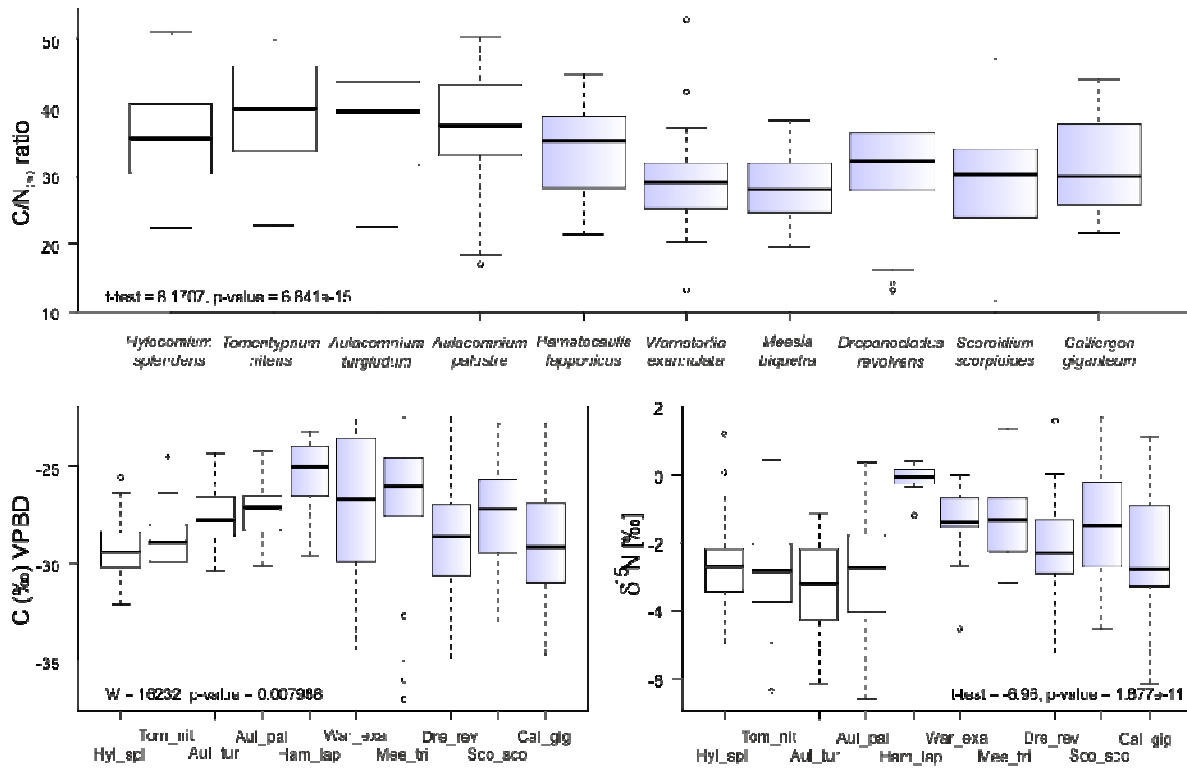
658 **Figures**



659

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

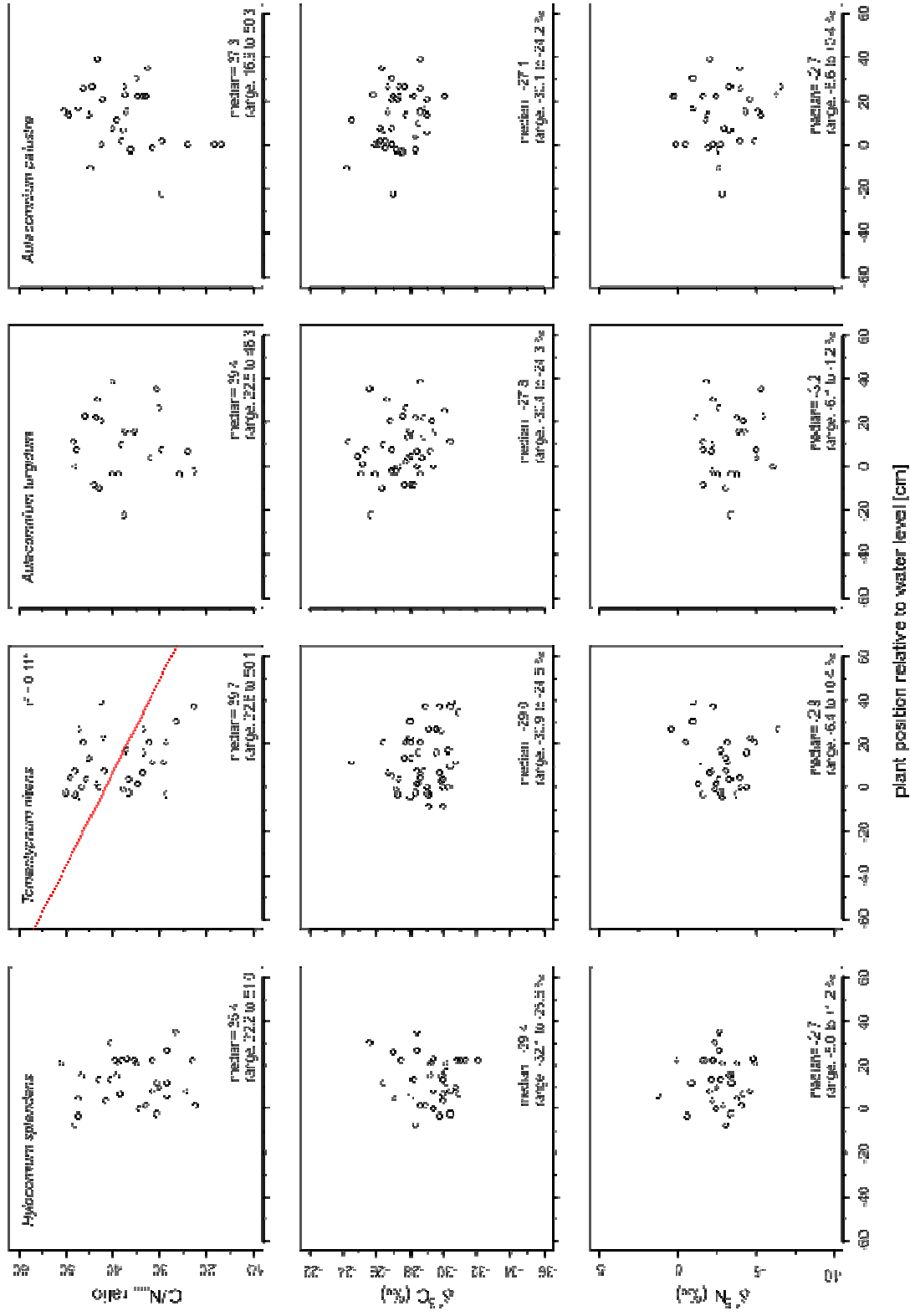
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664 **Fig. 2:** $C/N(m)$ ratios, $\delta^{13}C$ and $\delta^{15}N$ values of the 10 moss taxa studied. White boxplots are the xero-mesophilic
 665 group and boxplots shaded in blue are the meso-hygrophilic group. A t -test was done to distinguish the signals
 666 between the two habitat groups.

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668

669 **Fig. 3a:** Intraspecific relationships of the $\text{CN}_{(m)}$ ratio and the stable isotope values of carbon and nitrogen related to the water-level of the xero-mesophilic moss group.
 670 Regression lines (red) are only plotted for significant data sets.

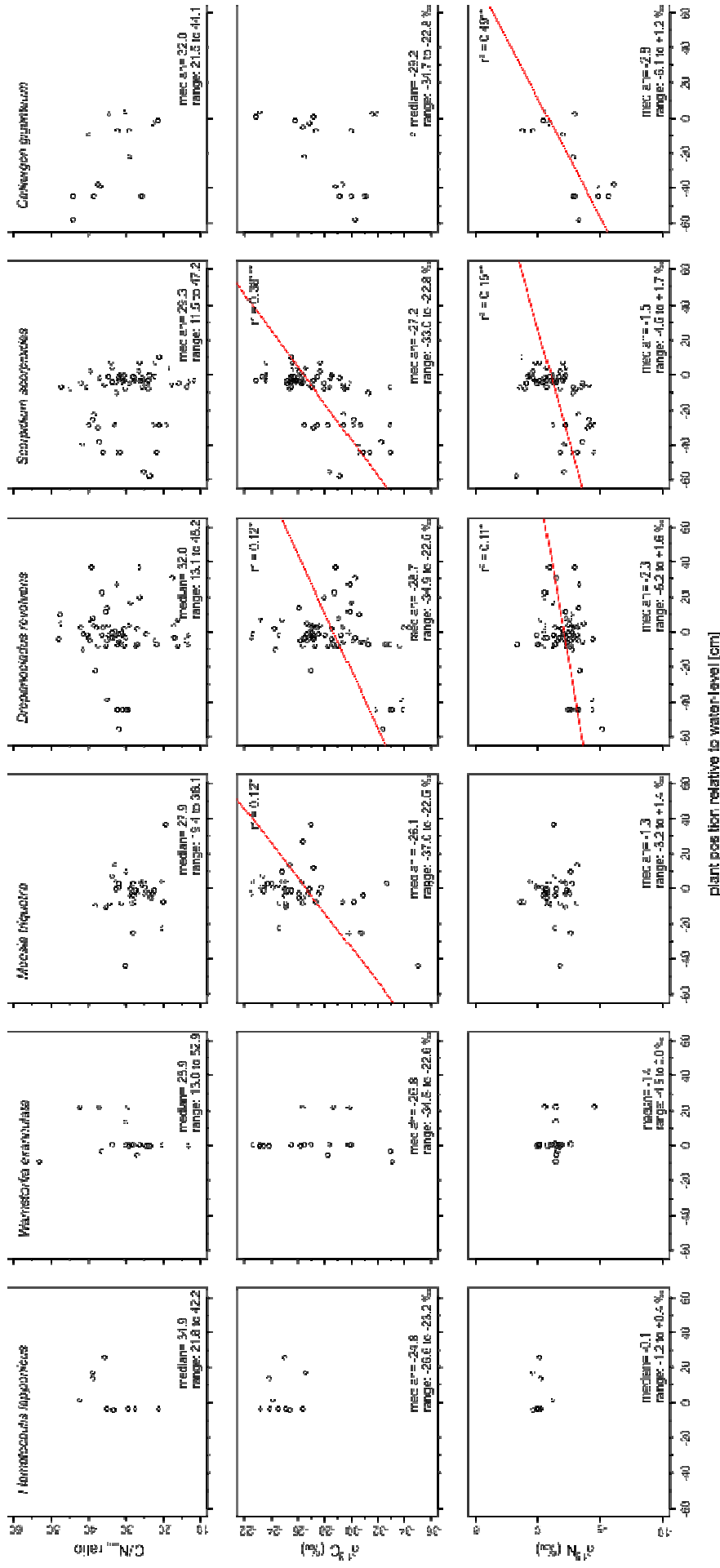
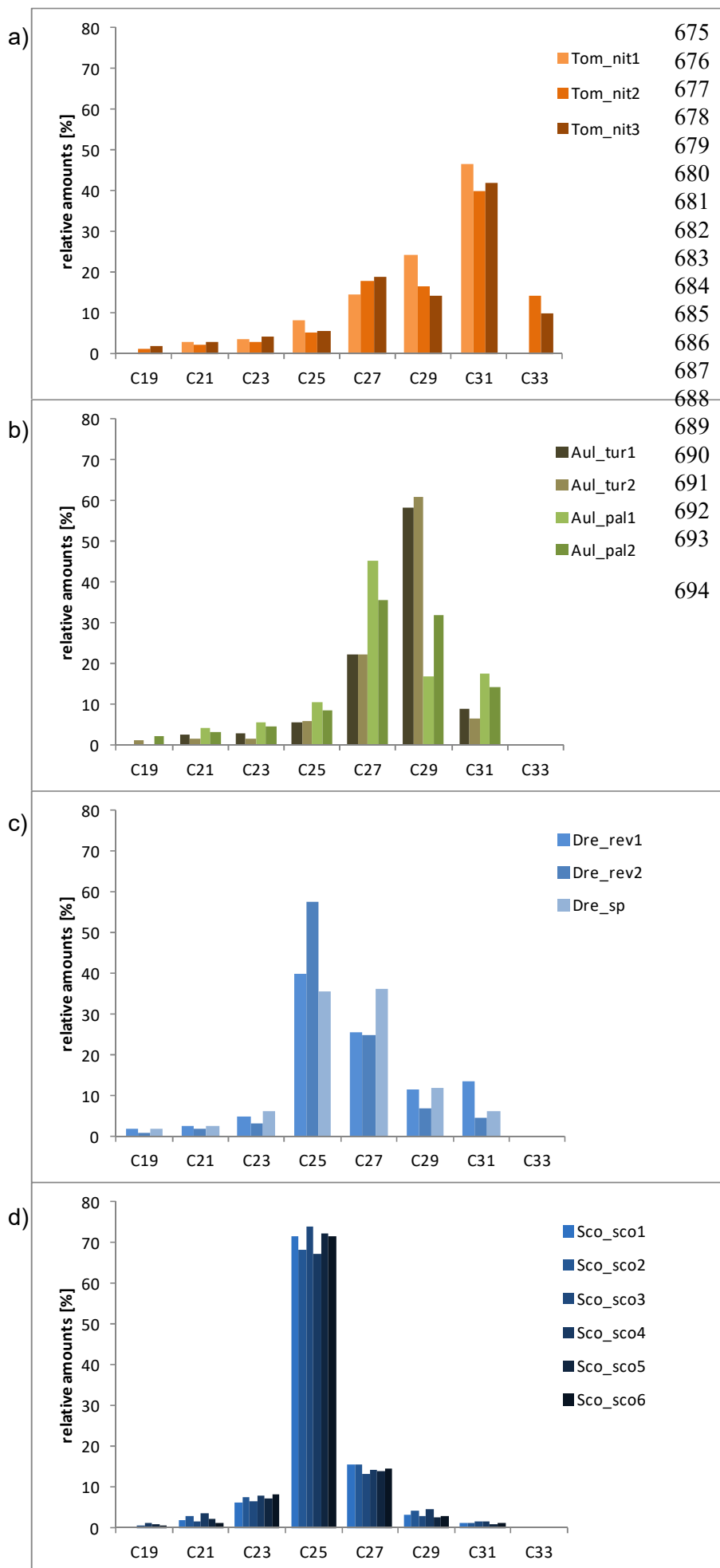
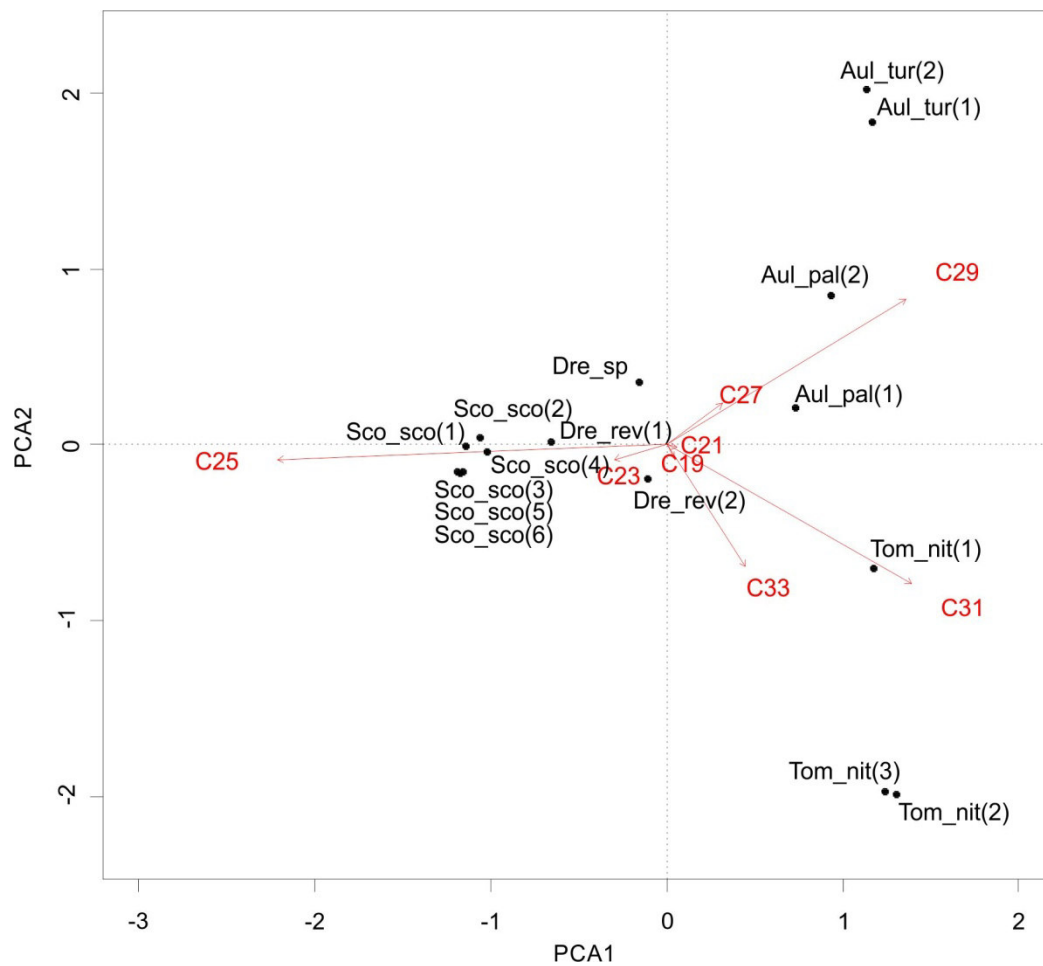


Fig 3b: Intraspecific relationships of the C/N_m ratio and the stable isotope values of carbon and nitrogen related to the water-level of the meso-hygrophilic moss group. Regression lines (red) are only plotted for significant data sets.



675 **Fig. 4:** The relative amounts
 676 [%] of n-alkanes with an odd
 677 number of carbon atoms in
 678 selected brown mosses
 679 grouped by species and
 680 ordered by their preferences
 681 with respect to their mean
 682 plant-position relative to
 683 water-level for xero-
 684 mesophilic (a, b) and meso-
 685 hygrophilic (c, d) mosses.
 686 Tom-nit: *Tomentypnum nitens*;
 687 Aul_tur: *Aulacomnium*
 688 *turgidum*; Aul_pal:
 689 *Aulacomnium palustre*;
 690 Dre_rev: *Drepanocladus*
 691 *revolvans*; Dre_sp:
 692 *Drepanocladus sp.*; Sco_sco:
 693 *Scorpidium scorpioides*
 694



695

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

699

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

polygon cross section, (length of transect = polygon size)	- - - moss layer — surface height - - - permafrost table — water level	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 P3/III - shallow completely vegetated
		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

703

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

Species	$C/N_{(m)}$ ratio		$\delta^{13}C$ [‰]			$\delta^{15}N$ [‰]		
	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	23	-29.2	-34.7 to -22.8	17	-2.9	-6.1 to +1.2**

Stars designate significant linear regressions between parameter and the plant position relative to water-level (* $p \leq 0.01$, ** $p \leq 0.05$, *** $p \leq 0.001$).

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