

1 **Vegetation patterns along micro-relief and tree-line** 2 **transects in polygonal landscapes of the Siberian Arctic**

3 **Journal of Vegetation Science**

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13 **Abstract**

14 **Question:** How do absolute cover, alpha-diversity, and the compositional turnover of vascular plants
15 and bryophytes change along micro-relief levels (rim to pond) within polygons in northern Siberia
16 located along a vegetation gradient from open larch forests to subarctic tundra?

17 **Methods:** In total, 152 one square-metre vegetation plots were investigated in eight low-centred
18 polygons located south of the Taymyr Peninsula and on Samoylov Island in the Lena River delta in
19 northern Siberia.

20 **Results:** The cover of vascular plants displays no significant differences between the rim and rim-
21 pond transition but is significantly lower in the pond. Their alpha-diversity decreases strongly from
22 rim to pond in the polygons. We found no trend in vascular plant cover from open forest to tundra
23 vegetation and only a slightly decreasing trend for alpha-diversity. Bryophyte cover and alpha-
24 diversity are highest on the rim and significantly distinct from the pond, but not from the rim-pond
25 transition. There is no clear trend in cover or alpha-diversity along the tree-line transect. Separate

26 ordinations of the vascular plant and bryophyte composition data indicate that both the micro-scale
27 relief gradient (within each polygon) as well as the regional-scale vegetation gradient (across the tree
28 line) is reflected by the vegetation composition. The micro-relief gradient explains a slightly higher
29 variance of vegetation composition as revealed by a series of partial redundancy analyses than the
30 vegetation type over the subarctic tundra, in particular with respect to bryophytes.

31 The applied indicator species analysis identified characteristic taxa of certain environmental
32 conditions and combinations of them. We found that 26 vascular plant and 22 bryophyte taxa are
33 characteristic for the three individual micro-relief levels, and 28 vascular plant and 24 bryophyte taxa
34 are characteristic for single vegetation types.

35 **Conclusions:** The observed gradual pattern in alpha-diversity and composition of polygonal
36 vegetation suggests that the local water regime is the main driver of changes in vegetation composition
37 while regional temperature and related forest-cover change is of subordinate importance for polygonal
38 vegetation-type patterns.

39 **Keywords:**

40 vascular plants; bryophytes; indicator species; low-centred polygon; NMDS; arctic vegetation; tree
41 line; tundra; Siberia; Russia

42 **Nomenclature:**

43 USDA, NRCS. 2014. The PLANTS Database (<http://plants.usda.gov>)
44

45 **Introduction**

46 Euarctic or hyperarctic vegetation is assumed to be particularly vulnerable to climate change (Sturm et
47 al. 2001; Callaghan et al. 2004) i.e. it is expected that the northern boreal forest zone will become
48 more dense and spread northward into the arctic tundra (MacDonald et al. 2000; Kharuk et al. 2006).
49 Such changes would entail strong effects not only on a regional, but also on a global scale due to
50 complex vegetation-climate feedbacks (Bonan et al. 1992; Foley et al. 1994). For example, along with
51 shrub and forest establishment the albedo decreases, which affects the energy budgets of permafrost

52 soils leading to changes in microbial decomposition and methane release (Oechel et al. 1993; Betts
53 2000; Smith et al. 2004). Accordingly, vegetation transect studies across the tree line help to
54 approximate better the ongoing and future changes. However, such investigations are lacking for the
55 vast polygonal landscapes of northern Siberia, even though vegetation-change related effects on
56 methane release in these regions would be of particular relevance for global climate because of the
57 tremendous fossil carbon storage in the ice-rich deposits underlying most of these areas (Grosse et al.
58 2006).

59 The Siberian Lowlands are characterized by low-centred polygons resulting from the interaction
60 between the sub-continental climate and permafrost conditions. Here, very low and rapidly falling
61 winter temperatures in combination with only a thin snow cover leads to tensions in the soil generating
62 a regular crack pattern. Filling of the cracks by melt-water in spring and summer and recurring
63 freezing during the following winter leads to the formation of ice-veins that grow, over time, to ice-
64 wedges (Minke et al. 2007; French 2007). Frost-heave forces the overlying soil layer up to form
65 polygon rims. Hence the centre of the polygon has a lower elevation and is often filled by water. The
66 slow decomposition of organic matter due to water-logged conditions with a permanent exclusion of
67 oxygen leads to the long-term deposition of organic matter in such landscapes. Palaeoecological
68 studies using these sediments show that the position of polygonal centres and rims are stable on
69 decadal to millennial time-scales (Minke et al. 2009; Zibulski et al. 2013).

70 Bryophytes are important components of polygonal vegetation both in terms of modern diversity
71 and vegetation cover. Their remains dominate peaty deposits (de Klerk et al. 2011; Zibulski et al.
72 2013) and because of their climate-relevant carbon sink/release function, they are of significance for
73 high-latitude vegetation-climate feedback mechanisms. However, the taxonomic composition of arctic
74 bryophytes and their relationship with environmental gradients have seldom been taken into account in
75 environmental investigations of modern and fossil material.

76 The guiding questions of this vegetation study from northern Siberia are: 1) how do absolute
77 cover, alpha-diversity, and the composition of vascular plants and bryophytes change along a micro-
78 relief transect within low-centred polygons, 2) how do total vascular plant and bryophyte cover, alpha-

79 diversity and composition change along a regional scale (tree line) transect, and 3) is the information
 80 gained useful for environmental reconstructions and predictions?

81 **Material and methods**

82 **Regional setting**

83 Two areas in North Siberia were investigated: a tree-line transect (Fig. 1) across different vegetation
 84 types in the lower Khatanga River region (70–72° N, 97–102° E) and on Samoylov Island in the Lena
 85 River delta (72.4° N, 126.5° E). In total, six polygons in the Khatanga region were studied and two on
 86 Samoylov Island. The Khatanga study area extends along the Khatanga River south of the Taymyr
 87 Peninsula in the northern Siberian lowlands. Samoylov Island is situated in the southern part of the
 88 Lena River delta on a terrace that was formed during the late Holocene (Boike et al. 2013). Both
 89 regions are characterized by polygonal wet tundra and thermokarst lakes (Botch et al. 1995;
 90 Schwamborn et al. 2002; Boike et al. 2013). The lower elevated western part of Samoylov becomes
 91 flooded each spring whereas the higher terraces of the island are affected only during extreme flooding
 92 events (Kutzbach et al. 2004) and during these rare events, allochthonous material may be washed in.

93 *Table 1: Short description of studied polygons.*

Polygon	coordinates	short description site; vegetation type; distance to nearby water features; transect length; additional information
06/P	70.666° N, 97.708° E	Khatanga; open forest; 240 m to nameless lake; 26 m; swinging bog on an aggradation plain of a lake at the edge of an elevated larch forest (tallest trees: 12 m)
17/P	72.243° N, 102.233° E	Khatanga; forest-tundra intersection; 110 m to nameless lake; 13 m; shallow polygon; located on aggradation plain of a lake at the edge of an elevated larch forest with low cover
P3	72.149° N, 102.693° E	Khatanga; forest-tundra intersection; P3/I: 630 m, P3/II: 610 m, P3/III: 590 m to Khatanga River; 63 m (a complex of three polygons along a transect with P3/I: 1 - 22 m (deep centre, open water body without vegetation), P3/II: 23 - 45 m (shallow polygon, open water body without vegetation), P3/III: 46 - 63 m (shallow and completely vegetated polygon)); in a polygon field within an old meander belt
12/P	72.431° N, 102.373° E	Khatanga; tundra; 70 m to nameless thermokarst lake; 29 m; shallow; southwards of the Novaya River, a northern tributary of the Khatanga River in a broad thermokarst depression connecting several lakes, infrequent isolated groups of larch krummholz in the surrounding area
LP1	72.375° N, 126.483° E	Samoylov Island (Lena River delta); tundra; 50 m to 'fish lake' (unofficial name) and 820 m to Lena River; 19 m; deep polygon centre with an open water area; on a late-

		Holocene terrace, at the margin of the thermokarst depression around the ‘fish lake’
LP2	72.370° N, 126.481° E	Samoylov Island (Lena River delta); tundra; 140 m to ‘Banja lake’ (unofficial name) and 250 m to Lena River; 19 m; shallow; on a late-Holocene terrace, without an open water area

94

95 The climate of the study area is characterized by strong seasonal contrasts despite its proximate
96 location to the Laptev Sea. Both regions are humid with a precipitation peak in July (annual
97 precipitation of Khatanga: 272 mm (Rivas-Martinez & Rivas-Saenz 2007); annual precipitation of
98 Samoylov: 232.7 mm (Boike et al. 2013)) though the water availability for plants is limited by
99 temperatures below 0°C for approximately 8.5 to 9 months each year. The average annual temperature
100 of Khatanga is -13.2°C (Rivas-Martinez & Rivas-Saenz 2007) and of Samoylov it is -12.5 °C (Boike
101 et al. 2013).

102 Study site locations extend along a vegetation gradient (Matveev, 1989; Mutke & Barthlott 2005) from
103 open larch forests (<70.5°N) to subarctic tundra (>72.3°N) connected by a forest-tundra intersection
104 zone. Samoylov is treeless subarctic tundra. The longitudinal vegetation compositional turnover
105 between these areas is low according to Matveyeva & Chernov (2000).

106 **Field methods and environmental data collection**

107 Field work in the Khatanga area lasted from mid-July to mid-August in 2011 and on Samoylov it was
108 completed in July 2012. For all polygons representative transects (from rim to rim), divided into 1
109 square metre plots, were selected by visual inspection. The plot size chosen is a balance for vegetation
110 surveys of both plant groups (vascular plants and bryophytes).

111 Environmental information (surface elevation, thaw depth, water depth) was measured at the
112 centre of each plot relative to a reference line and calibrated to the water level (Fig. 2). (It was
113 impossible to recognize the water-sediment transition at 06/P because of a dense bryophyte swinging
114 mat. Therefore, we estimated an average height for the three micro-relief levels by applying the
115 height/thaw depth relations gained from roughly comparable polygon types: LP1 and LP2.) All plots
116 that were located ≥ 6 cm over the water level were classified as rim, all plots with water depth ≥ 7 cm

117 as pond and all sites in-between as rim-pond transition. The distance to the nearest water-body (lake or
118 river) was calculated from the middle of the polygon to the bank of the water-body.

119 Vegetation cover of trees, shrubs/herbs and bryophyte layer were recorded for each plot
120 according to the Braun-Blanquet floristic approach (Braun-Blanquet 1964). The plot size necessitated
121 a finer modification to the abundance scale (Reichelt and Wilmanns 1973) to capture the quantitative
122 presence of small bryophytes. Identification of vascular plant taxa and bryophytes in the field was
123 verified by investigation of herbarium material from the sites after the expedition. Vascular plants were
124 identified using Jäger (2005). For bryophytes, the identification keys of Lobin et al. (1995), Frahm and
125 Frey (2004) and the online “Bryophyte Flora of North America”
126 (<http://www.mobot.org/plantscience/bfna/bfnamenu.htm>) were used.

127 **Data analysis**

128 Data on the Braun-Blanquet scale were transformed to percentages by using the average cover of
129 classes for each of the 152 plots prior to further computations. Occasionally that produced an
130 artificially high cover of slightly >100%. The cover of trees and the shrub/herb layer were combined
131 to one vascular plant layer. The Shannon Index was calculated in R version 3.1.1 (R Core Team 2014)
132 separately for the recorded vascular plants and bryophytes for the micro relief and vegetation type.
133 Results were analysed by Kruskal-Wallis tests with alpha-adjustment (Benjamini and Hochberg, 1995)
134 for multiple comparisons using the ‘agricolae’ package (de Mendiburu 2014).

135 Non-metric multidimensional scaling (NMDS) was applied separately to vascular plant and
136 bryophyte taxa to extract the major patterns in the vegetation with respect to both inter-taxa
137 relationships and relationships among sites. The Bray-Curtis dissimilarity was used to avoid the
138 double-zero problem with regard to the high proportion of rare taxa. All taxa that appear at least 3
139 times and sum up to at least 10% cover in the whole data set are included. Non-vegetated plots were
140 removed from the data set prior to analyses (LP1: I09 and I10 and 06/P: 05 and 06). Nominal data
141 such as micro-relief level (rim, rim-pond transition, pond) and vegetation type (open forest, forest-

142 tundra intersection, tundra) were included as dummy variables. NMDS was performed in R version
143 3.1.1 (R Core Team 2014) using the ‘vegan’ package (Oksanen 2011; Oksanen et al. 2013).

144 Relationships between plant taxa and environmental characteristics (micro-relief level, vegetation
145 type) were investigated by variance partitioning (Borcard et al. 1992, Legendre 2008) using
146 Redundancy Analysis (RDA) of Hellinger transformed species data (Legendre & Gallagher 2001)
147 performed in the ‘vegan’ R package.

148 Indicator species for certain micro-relief levels and combinations of them as well as for certain
149 vegetation types and combinations of them were identified using the IndVal.g correlation coefficient
150 in the indicator species approach according to De Cáceres & Legendre (2009) implemented in the
151 ‘indicspecies’ R package version 1.6.7 (De Cáceres et al. 2013).

152

153 Results

154 Characteristics of polygonal vegetation

155 The thaw depth of the southernmost studied polygon 06/P ranges between 13 and 83 cm (Fig. 2f). The
156 rim vegetation is mainly composed of vascular plants such as *Betula nana* (37.5%), various Ericaceae
157 (*Vaccinium uliginosum*, *V. vitis-idaea*, *Ledum palustre*) and bryophytes such as *Hylocomium*
158 *splendens* (62.5%), *Pleurozium schreberi* (20%), *Sphagnum rubellum*, and *S. angustifolium*
159 (Sphagnopsida add up to 87.5%). *Eriophorum* spp. and *Aulacomnium palustre* obtain the highest cover
160 (37.5%) in the rim-pond transition. The polygon centre is completely covered by a 20 cm thick
161 swinging mat formed by Amblystegiaceae (*Warnstorfia exannulata* with some *W. pseudostraminea*
162 and *Menyanthes trifoliata* (each up to 37.5%)).

163 Despite the minor micro-relief difference of only 13 cm in polygon 17/P (Fig. 2e), there occur
164 marked differences in thaw depth (pond: 55 cm rim-pond transition: 35 cm to 65 cm) and vegetation
165 composition. The rim-pond transition plots are vegetated by *Betula nana* (20%), *Carex* spp. (37.5%),
166 and *Eriophorum* spp. (37.5%). *Aulacomnium palustre* (10%), *Calliergon richardsonii* (37.5%), and
167 *Drepanocladus revolvens* (62.5%) represent the most common bryophytes. Additionally *Dicranum* sp.
168 (20%) and *Sphagnopsida* (*Sphagnum rubellum* (10%) and *S. angustifolium* (10%)) occur in rather dry
169 plots. Pond and wet rim-pond transition plots are characterized by sedges and tussocks rising above
170 the water level which supports *Drepanocladus revolvens* (10%).

171 Only a few *Larix* individuals grow on the rims between the individual polygons at site P3. The
172 three polygons are characterized by differences in surface height and vegetation (Fig. 2d). The crown
173 of a *Larix gmelinii* tree in P3/I covers much of the rim-pond transition and rim (~62.5%). The
174 dominant rim taxa are *Betula nana*, *Alnus viridis* ssp. *fruticosa*, *Vaccinium uliginosum*, *Carex* spp.
175 (each up to 37.5%), and *Dryas punctata* (20%). For bryophytes we recognize a gradient of dominant
176 species from P3/I with *Aulacomnium turgidum* and *A. palustre* (each 62.5%) and a liverwort cover up
177 to 37.5%. *Hylocomium splendens* and *Tomentypnum nitens* (each 62.5%) characterize the rim in P3/II,
178 whereas the rim of P3/III is of low height and is dominated by *Drepanocladus revolvens* (20%),
179 *Scorpidium scorpioides* (up to 87.5% in the lowest rim plots) and *Tomentypnum nitens* (37.5%). *Carex*

180 spp. characterize the rim-pond transition with 37.5% as well as various deciduous shrubs (*Betula*
181 *nana*, *Alnus viridis* ssp. *fruticosa*, *Vaccinium uliginosum*) whose cover sums to 10%. The dominant
182 bryophytes are *Scorpidium scorpioides* (up to 87.5% in P3/III), *Drepanocladus revolvens* (37.5%), and
183 *Aulacomnium turgidum* (62.5%). The few vegetated pond plots of P3/I and P3/II are dominated by
184 *Scorpidium scorpioides* (P3/I: 10%; P3/II: 37.5%) and *Drepanocladus revolvens* (37.5%).

185 The northernmost polygon of the Khatanga region 12/P has a gentle micro-relief (Fig. 2c) with a
186 maximum surface height difference of 27 cm between rim and pond. The thaw depth ranges between
187 25 cm on the rim and 61 cm in the pond. Only *Dryas punctata* (obtaining cover up to 20%) is
188 restricted to the rim. *Betula nana* (20%), *Salix* spp. (20%), *Tomentypnum nitens* (62.5%), and
189 *Sphagnum* spp. (20%) occur on the rim and partially in the rim-pond transition together with
190 *Eriophorum* species (20%), *Carex* spp. (62.5%), and the bryophytes *Scorpidium scorpioides* (up to
191 62.5%), *Drepanocladus revolvens* (up to 87.5%), and *Aulacomnium turgidum* (20%). Pond plots are
192 dominated by *Carex* spp. and *Scorpidium scorpioides* (each 37.5%).

193 The polygons LP1 (Fig. 2b) and LP2 (72.370° N, 126.481° E; Fig. 2a) are completely different in
194 their micro-relief characteristics. LP1 has a large open water area (maximum water depth at transect:
195 58 cm) with small thaw depths (only 2 to 5 cm) in the centre of the polygon, which increase towards
196 marginal pond plots (12 to 31 cm) and the rim (15 to 45 cm). Various vascular plant taxa were
197 recorded although they do not obtain a high cover (mostly <5% per plot). *Dryas punctata* (10%) is
198 common together with *Hylocomium splendens* (87.5%) on the rim. *Comarum palustre* (10%) occurs in
199 marginal pond plots, whereas the pond is colonized mainly by *Calliergon giganteum* (87.5%) and
200 *Scorpidium scorpioides* (87.5%). *Carex* species are common in all vegetated plots. LP2 is a shallow
201 low-centred polygon with a completely vegetated water area (maximum water depth: 11 cm). The
202 thaw depth varies only slightly (range: 37 to 53 cm) having both the maximum and the minimum on
203 the rim. *Carex* species reach a cover of up to 37.5% in rim plots and *Hylocomium splendens* (87.5%)
204 is the prevailing bryophyte. The rim-pond transition is characterized by patches of *Sphagnum* sp.
205 (10%) and tussocks composed of *Aulacomnium palustre* (37.5%), *A. turgidum* (10%) or *Meesia*
206 *triquetra* (10%). The pond is sparsely vegetated by *Carex aquatilis* (20%), *Scorpidium scorpioides*
207 (10%), and *Calliergon giganteum* (10%).

208 **Vegetation cover and its relationships with micro-relief level and vegetation type**

209 *Larix gmelinii*, the only tree occurring in the study area, was recorded at 17/P and P3 where it grew
210 only on the rims and covered <1% (17/P), 37.1% (P3/I), and 0.4% (P3/II and P3/III) of the plots.
211 Additionally, open larch forest occurred in the vicinity of 06/P and 17/P on elevated slopes, but it
212 rarely occurred in the areas directly surrounding the investigated polygons.

213 The absolute cover of vascular plants is highest on the rims ranging from 25% to 97% with a
214 maximum in the forest-tundra intersection P3/I (Fig. 3). Rim vascular plant vegetation in the open
215 forest and forest-tundra intersection polygons is characterized by a high percentage of deciduous
216 shrubs (mostly between 30% and 50%) but evergreen shrubs also occur. Cover of Poales varied
217 throughout the tree-line transect between 4% and 40%. The vascular plant cover is mostly lower in the
218 rim-pond transition plots, but there is no significant difference between rim and rim-pond transition
219 (Kruskal Wallis test: $p > 0.1$). The cover ranges below 30% in the pond plots where only Poales occur.
220 The cover of pond plots significantly differs from rim plots (Kruskal Wallis with post-hoc test:
221 $p < 0.001$) and from rim-pond-transitions (Kruskal Wallis with post-hoc test: $p < 0.01$). There are no
222 significant differences in vascular plant cover between the vegetation types (Kruskal Wallis test:
223 $p > 0.1$).

224 The bryophyte layer obtains a cover of 100% in most rim and rim-pond transition plots (no
225 significant differences between either micro-relief levels, Kruskal Wallis with post-hoc test: $p > 0.1$)
226 across the whole tree-line transect while the cover in the ponds is lower (0% to 73%) and differs
227 significantly from that of the rim and rim-pond transitions, $p < 0.01$). The bryophyte layer is strongly
228 dominated by Bryopsida while Sphagnopsida only occurs in a few plots, mainly on the rim and in the
229 rim-pond transition at <5%. Only on the rim of the open forest site (06/P) is average Sphagnopsida
230 cover as high as 35%. Liverworts occur in most rim and rim-pond transition plots of the forest-tundra
231 intersection but at low cover. There is no significant difference in bryophyte cover between the
232 vegetation types (Kruskal Wallis with post-hoc test: $p > 0.1$).

233 **Vegetation alpha-diversity and its relationship with micro-relief level and vegetation**
 234 **type**

235 In total, we found 67 vascular plant taxa and 96 bryophyte taxa. Both alpha-diversity analyses (species
 236 richness (Table 2) and Shannon Index (Fig. 3a)) of vascular plants for each polygon are highest for the
 237 two polygons of Samoylov, whereas the maxima of bryophyte diversity (Fig. 3b) are equally
 238 distributed along the tree-line transect. There are no significant differences in species richness or
 239 Shannon Index among the vegetation types, either with respect to vascular plants or with respect to
 240 bryophytes (Kruskal Wallis with post-hoc test: $p > 0.1$).

241 *Table 2: Species richness of both plant groups by micro-relief level.*

Plant type Polygon	Vascular plants				Bryophytes			
	complete	rim	rp- transition	pond	complete	rim	rp- transition	pond
LP2	30	29	10	3	39	36	15	5
LP1	21	20	-	7	25	20	-	12
12/P	10	7	8	3	38	13	34	2
P3/III	11	11	2	-	31	29	11	-
P3/II	14	14	12	7	40	29	31	15
P3/I	12	12	12	10	25	19	20	16
17/P	15	-	15	2	30	-	30	4
06/P	10	9	4	2	24	24	8	7

242 Within the individual polygons, Shannon index and species richness of vascular plants are often
 243 highest on the rims and differ significantly from the rim-pond transitions (Kruskal Wallis with post-
 244 hoc test: $p < 0.1$) and especially from the ponds ($p < 0.001$), where diversity is almost zero. For
 245 example, the Samoylov polygon LP2 has the highest Shannon Index value for vascular plants on the
 246 rim with 2.39, and in the transition it is 1.45, but only 0.03 in the pond plots where *Carex* species are
 247 the only common vascular plants.

248 In contrast, the Shannon Index of bryophytes is greatest in the rim-pond transition (2.1 in P3/I) and is
 249 still high in the pond (0.91 in LP2) compared with the vascular plant layer, but the multiple
 250 comparisons of alpha-diversity between the several micro-relief levels show no difference between the
 251 rim and the rim-pond transition. Species diversity between the rim-pond and the rim-pond transition to
 252 pond, however, are highly significantly different (Kruskal Wallis with post-hoc test: $p > 0.001$) from
 253 each other.

254 **Vegetation composition and its relationship with micro-relief and vegetation type**

255 The arrangement of individual plots along the first NMDS axis generally traces the micro-relief both
256 for vascular plants (see Fig. 4a, stress = 0.13) and bryophytes (Fig. 4b, stress = 0.15). Likewise the
257 second NMDS axis separates the vegetation types. The included dummy variables for micro-relief
258 level (rim, rim-pond transition, pond) and vegetation type (open forest, forest-tundra intersection,
259 tundra) mostly yield a significant relationship with the NMDS axes.

260 The vascular plant species are not evenly distributed in the NMDS plot (Fig. 4a). While most taxa are
261 located in the left part of the plot, i.e. related to the rim (among them shrubs such as *Vaccinium vitis-*
262 *idaea*, *V. uliginosum*, *Ledum palustre*, *Salix* spp. and herbs such as *Saxifraga tenuis*, *Poa* spp.,
263 Caryophyllaceae and Fabaceae), only few taxa (among them *Comarum palustre*, *Carex* spp.,
264 *Eriophorum* spp., *Menyanthes trifoliata*, and *Epilobium* sp.) are characteristic of rim-pond transition
265 plots and pond plots. Shrub taxa such as *Vaccinium oxycoccus*, *V. vitis-idaea*, *Ledum palustre* and
266 *Rubus chamaemorus* are located in the lower section of the ordination plot reflecting their high
267 abundance in open forests. Generally the separation among the three vegetation types is more obvious
268 for vascular plant ordination, whereas it is less well-defined (and for the tree line not significant) in the
269 bryophyte ordination. Results from variance partitioning generally support the NMDS results.
270 Variables for micro-relief level and vegetation type significantly explain the vascular plant and
271 bryophyte composition of polygons without having overlapping effects (residuals: 0.75); however,
272 explained variance for distance to the nearest water-body calculated by variance partitioning in RDA
273 does not exceed 7.8% for vascular plants and 5.7% for bryophytes. Vegetation type explains the
274 compositional turnover better than micro-relief for vascular plants (micro-relief: 7.8%, vegetation
275 type: 13.2%), whereas bryophytes show a reversed result (micro-relief: 15.2%, vegetation type: 8.6%).

276 In contrast to vascular plants, bryophytes are more evenly distributed in the NMDS plot although
277 more taxa are characteristic of rim vegetation (*Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium*
278 *crista-castrensis*, and *Climacium dendroides*) than pond vegetation (mainly *Scorpidium* and
279 *Calliergon* taxa). *Meesia triquetra* has an intermediate position. Bryophyte taxa such as *Calliergon*

280 *giganteum*, *Meesia triquetra*, and *Climacium dendroides* are found mainly in the tundra sites, whereas
281 *Calliergon stramineum* and *Drepanocladus* spp. are restricted to the open forest sites.

282 Indicator taxa analyses (Table A1; Table A2) of vascular plants suggest that many taxa are
283 indicative of tundra (Fig. 5). In contrast, many bryophyte taxa are indicative of the forest-tundra
284 intersection. Typical micro-relief indicators (Fig. 6) for the pond sites are *Calliergon giganteum* and
285 *Menyanthes trifoliata*. Three bryophyte species (*Aneura pinguis*, *Calliergon trifarium*,
286 *Sarmenthypnum sarmentosum*) are indicative of the rim-pond transition. No vascular plant is
287 indicative of the rim-pond transition. The majority of indicator species of rims are vascular plants (20
288 species), in contrast to only six bryophyte species.

289 Discussion

290 **Patterns of cover, alpha-diversity and compositional turnover of vascular plants and** 291 **bryophytes along the micro-relief transect (local scale)**

292 Our investigations demonstrate that vegetation cover, alpha-diversity, and composition change
293 significantly at the micro-relief level within polygons, while changes along the regional vegetation
294 transect are not as clear. Additionally, compositional turnover is stronger between the pond and rim-
295 pond transition compared to the rim-pond-transition. The low correlation between polygonal
296 vegetation and regional vegetation might originate from the low number of sampled polygons and the
297 overall strong heterogeneity.

298 Generally only few individuals of *Larix gmelinii* trees inhabit the polygon rims. Their rare occurrence
299 may be due to inhibition of their vertical and lateral root system development (Kajimoto et al. 2007)
300 and the low probability of survival due to the permanently water-logged soils (Nikolov and Helmisaari
301 (1992) cited by Kullman (1998)). Compared to the tree layer pattern the shrub and herb layer is better
302 able to indicate the individual micro-relief levels within the polygons. Shrub cover is highest on the
303 rims mostly and shrubs rarely occur in the ponds. This supports the conclusions of Aleksandrova
304 (1980) that dwarf shrubs in tundra grow better on well-drained sites than in water-logged depressions.

305 The Poales recorded include *Carex* spp., *Eriophorum* spp., and *Poa* spp., which span a wide range of
306 moisture preferences (Jäger 2005). Poales cover varies strongly among plots but does not show a clear
307 trend at micro-relief level, which corresponds with the general preferences of Cyperaceae for wet
308 habitats. Herbs are rare; only *Comarum palustre* occurs frequently and prefers the rim-pond transition
309 sites, as was observed by de Klerk et al. (2009) in polygons in the Chersky area near the lower
310 Kolyma River. The inference of *Menyanthes trifoliata* as an indicator for ponds needs to be treated
311 with caution, for although it was recorded in the centre of a polygon, it was, however, growing on a
312 bryophyte mat. Its occurrence on swamp mats was also noted by Walters et al. (1998).

313 The characteristics of bryophytes (poikilohydric and drought tolerant) makes them rather
314 indifferent to frost and heat damage, and thus tolerable of arctic environmental conditions
315 (Wielgolaski et al. 1981). At drier sites like the rims it may be of advantage that they have a short lag-

316 time when changing from desiccation to a productive state when moistened (Proctor 1982; Frahm
317 2001). Furthermore, they can start photosynthesising under low temperature and light conditions,
318 partially even under a thin layer of snow or ice. Soil moisture is not considered to be an important
319 variable for bryophyte presence, because the rhizoids are merely used for ground fixation (Schofield
320 1985). Their high cover in comparison to vascular plants, particularly in the rim-pond transition and
321 pond plots, illustrates this advantage (Matveyeva, 1994; Minke et al., 2007). The slightly lower cover
322 and diversity of bryophytes on some rims in comparison to the rim-pond transition may result from
323 their low competitive ability for space and light in comparison to vascular plants (Frahm 2001).

324 Bryophyte diversity is particularly high at the rim-pond transition. Here, typical rim taxa and
325 typical taxa of wet locations are intermixed. The ponds of polygons are dominated by one to three
326 floating or submerged species of Amblystegiaceae. The dominance of Amblystegiaceae agrees with
327 other studies in the Russian Arctic (de Klerk et al., 2009, Minke et al., 2009). They are characteristic
328 species of rich fens with a slightly acidic to alkaline pH (>5.5) and abundant in arctic regions (Nebel
329 and Philippi, 2000). Like vascular plants, bryophytes show a complete turnover from rim to pond sites.
330 Liverworts often grow among other species on the rim, but in exclusive patches in rim-pond transition
331 plots.

332 **Patterns of cover, alpha-diversity and compositional turnover of vascular plants and** 333 **bryophytes along the regional-scale tree-line transect**

334 A marked compositional turnover of vascular plant and bryophyte abundances across the investigated
335 tree-line transect is indicated by the arrangement of sites in the NMDS that corresponds fairly well
336 with the sequence of vegetation type (Aleksandrova 1980). However, the cover of the local vegetation
337 along the tree-line transect shows no clear pattern. Local vegetation, in accordance with the vegetation
338 type (Matveyeva & Chernov 2000), shows a decline in the vertical structure of vegetation, i.e. a
339 northward thinning out of tree cover.

340 Our investigations do not yield a clear trend in shrub cover along the vegetation transect. For example,
341 the highest rim cover of deciduous shrubs is found at P3 in the forest-tundra intersection. P3 is situated
342 near to the Khatanga River that may provide nutrient enrichment as a result of flooding and thus allow

343 a more northerly extend for those deciduous shrubs that are known for their low nutrient-use
344 efficiency (Chapin & Shaver 1989). Chernov and Matveyeva (1997) point out that vascular plant
345 cover decreases from 50–80% in the forest-tundra intersection to 5–50% in the northern subarctic
346 tundra, which fits with our finding that all rims in the forest and forest-tundra intersection have
347 vascular plant cover >50% and all tundra sites <50%. Herbs maintain relatively low cover at rim sites
348 in the open forest polygon, which may reflect their low competitiveness for light and nutrients
349 compared to the taller and deeper rooting shrubs (Swank & Oechel 1991).

350 All shrubs that we recorded on polygonal rims represent common elements in the prevailing
351 vegetation type of the respective polygon location (Matveyeva 1994; Matveyeva & Chernov 2000). In
352 particular, Ericaceae and *Rubus chamaemorus* are common taxa of subarctic tundra vegetation of the
353 Taymyr peninsula (Matveyeva 1994; Matveyeva & Chernov 2000). Generally our investigation shows
354 that the vegetation composition of shrubs and herbs of polygonal rims reflects well the regional
355 vegetation composition.

356 Vascular plant alpha-diversity (species richness and Shannon Index) of the individual polygon
357 plots shows no trends along the tree-line transect, which contradicts the known global trend of
358 decreasing diversity with increasing latitude (Rosenzweig 1995) and also does not match alpha-
359 diversity trends described from zonal vegetation studies across the boreal tree line in Siberia (Chernov
360 & Matveyeva 1997; Matveyeva & Chernov 2000). Highest herb alpha-diversity is found at Samoylov
361 Island in the Lena River delta and in the polygons (P3) near the Khatanga River. This likely originates
362 from the corridor function of large rivers for southern taxa (Matveyeva & Chernov 2000), which
363 additionally causes a more temperate climate. Furthermore, the high herb diversity at our tundra sites
364 may portray the regional diversity centre of Saxifragaceae and Brassicaceae that has previously been
365 described for the northern subarctic tundra, comparable to taxa of Rosaceae and Fabaceae for the
366 typical tundra (Matveyeva & Chernov 2000). All families are represented by several species in the
367 polygon plots.

368 Bryophyte cover is high at all sites and seems not to be affected by latitude, which fits with the
369 findings of Matveyeva and Chernov (2000) who describe a reduction of bryophyte cover along a
370 transect across the Taymyr Peninsula only at the transition from northern tundra to polar desert. The

371 high number of bryophyte taxa in the polygon plots illustrates the high diversity that even exceeds
372 vascular plant diversity. Our findings are in line with the high bryophyte taxa numbers documented by
373 the floristic studies of Fedosov and Ignatova (2005) who found 233 species at Ledyanaya Bay
374 (Taymyr Peninsula), of Fedosov (2008) who counted 130 species on the Longdoko Massif, and of
375 Fedosov et al. (2011) who described 520 taxa for the Anabar Plateau. Furthermore, bryophytes of the
376 arctic are highly diverse at the species level often due to a fixation of ecotype adaption as genetic
377 heterogeneity (McGraw 1995). We do not observe an alpha-diversity trend along the tree-line transect,
378 and no study exists that show a trend in moss diversity across the Russian boreal tree line (Mutke &
379 Barthlott 2005), plus Shaw et al. (2005) show that the latitudinal gradient in bryophyte diversity is
380 weak. In our plots, we do find a marked taxa turnover as indicated by NMDS. *Drepanocladus* spp.
381 (including *Warnstorfia* spp.), for example, is common in the pond of the forest site while *Scorpidium*
382 *scorpioides* and *Calliergon giganteum* communities dominate the ponds from the tree line to more
383 northerly sites. Furthermore, *Meesia triquetra* was first observed in the forest-tundra intersection and
384 its cover increases farther north which aligns with its identification as a glacial relict (Nebel & Philippi
385 2005).

386 **Indicator potential of vascular plant and bryophyte remains from polygonal peats for** 387 **the reconstruction of local hydrological and regional vegetation changes**

388 Polygonal sediments are frequently used for the reconstruction of past arctic environments and
389 climates. Commonly pollen (de Klerk et al. 2009; Minke et al. 2009) and vascular plant macrofossil
390 analyses (Birks 2001, Kienast et al. 2001) are applied but identified moss remains are also used for
391 reconstruction (Zibulski et al. 2013). Investigations of sub-fossil assemblages reveal that preserved
392 remains mainly originate from the local vegetation (Birks 2001) even for pollen in polygonal
393 structures (de Klerk et al. 2011).

394 The high vegetation turnover at the local scale, and thus changes in the polygon morphology over
395 time, will result in a marked vegetation change that does not necessarily reflect changes in the
396 vegetation type or climate but rather traces variations in the local hydrological conditions. The
397 separate interpretation of qualitative changes of preserved rim taxa, in particular of leaves of shrubs

398 (for example *Dryas*, *Vaccinium*, and *Ledum*) and herbs, will allow the reconstruction of vegetation-
399 type changes. Our results indicate that the absence of *Larix* macrofossils in polygonal sediments does
400 not reliably indicate a position beyond the tree-line. Generally, the deposition of allochthonous
401 material from sites further south need to be taken into account in palaeoecological studies using
402 sediments from polygons located near to rivers due to frequent flooding (Zibulski et al., 2013).

403 Among the bryophyte taxa, *Hylocomium splendens*, *Climacium dendroides* and *Pleurozium schreberi*
404 are of potential use for the indication of dry rim sites. The high number of inferred moss indicators for
405 tracing micro-relief conditions indicates that bryophyte remains from polygonal sediments—in
406 particular from the rim-pond transition—are useful for tracing changes of the water-level. Useful
407 indicators of the water-level are *Sarmenthyphnum sarmentosum* and *Calliergon trifarium* that are easy
408 to determine and are thus suitable for palaeo-investigations (Jakab & Sümegi 2011). Liverworts such
409 as *Aneura pinguis* are not commonly usable for palaeo-investigations, because they are poorly
410 preserved in sediments (Janssens 1988). Remains of *Calliergon richardsonii* are sometimes difficult to
411 separate from *Calliergon giganteum*. Easily identifiable bryophytes are *Tomentypnum nitens*,
412 *Aulacomnium turgidum* and *A. palustre* for drier rim-pond transition sites. In addition, a high
413 abundance of *Meesia triquetra* is a reliable distinguishing feature to separate wet rim-pond transition
414 from pond sites. Our study reveals no vascular plant taxon as a suitable indicator for the rim-pond
415 transition.

416 Using deep-pond sediments for environmental reconstructions has the advantage that
417 sedimentation rates are mostly higher than at the rim or rim-pond transition and preservation
418 conditions are better. However, there are several risks. First, the fossil record has low diversity or is
419 even absent and thus not responsive to slight environmental changes. Second, some submersed living
420 Amblystegiaceae can have very long shoots which complicates the stratigraphical interpretation. For
421 example, *Calliergon giganteum* plants in LP1 had a length of around 60 cm, suggesting a high annual
422 growth rate of 10 mm year⁻¹, as also inferred for Canadian lakes (Sand-Jensen et al. 1999).
423 Accordingly, even though bryophyte remains are autochthonous, they are not necessarily in the correct
424 stratigraphical context (Birks 1982). Third, the close association between submerged brown mosses
425 and methanotrophic bacteria leads to an uptake of old carbon from bacterial methane oxidation

426 products into the biomass of mosses (Liebner et al. 2011), which affects dating results. It is
427 recommended to date terrestrial mosses rather than submerged species.

428 **Implications of vegetation changes for future Arctic warming and conclusions**

429 Taking the spatial patterns of cover, diversity, and composition as a guideline, the following
430 implications can be drawn for future changes in the Siberian lowlands characterized by polygonal
431 landscapes.

432 Vascular plant cover decreases from the southern open forest to the northern subarctic tundra,
433 whereas the cover of bryophytes is less affected by the latitudinal gradient. Cover of both plant groups
434 decreases from the rim to pond, but bryophytes still occur at reasonably high abundance in shallow
435 ponds. Bryophytes at northern sites in particular, strongly contribute or even dominate plant cover
436 (and probably also standing biomass) and, because of low decomposition rates in the ponds, also
437 dominate buried organic material in arctic regions and thus contribute to carbon storage. The low
438 nitrogen and phosphorus content of bryophyte remains (Aerts et al. 1999) and the high content of
439 phenolic and non-polar cell compounds slows decomposition by micro-organisms and fungi (Turetsky
440 2003), which leads to high organic matter accumulation in arctic landscapes. Furthermore, thick mats
441 of bryophytes isolate the soil against thermal radiation resulting in a high permafrost table and water
442 saturation of the soil (Woo & Young 2006). The low soil temperatures inhibit the germination of seeds
443 or shorten the development phase for vascular plants.

444 The alpha-diversity patterns differ between vascular plants and bryophytes. The increasing
445 Shannon Index of vascular plants from the open forest to the tundra suggest the known dispersal along
446 river corridors, while the unclear trend for bryophytes show that the tree line is not the threshold for
447 directional patterns in bryophyte composition (Matveyeva & Chernov 2000). A strong decrease in
448 alpha-diversity is revealed for vascular plants from rim to pond while bryophytes show highest
449 diversity at the rim-pond transition mostly. Higher temperatures in the future will probably cause
450 greater cover of vascular plants on the rims, in particularly for shrubs (Pajunen et al. 2011; Myers-
451 Smith et al. 2011). This increasing competitive pressure associated with lower water-levels could leads
452 to a decreasing carbon sink and permafrost-isolation function of bryophytes (Billings et al. 1982).

453 However, the negative effect of shrub expansion in tundra ecosystems, which leads to a decrease in the
454 cover and diversity of bryophytes (Pajunen et al. 2011), cannot be underpinned by the calculated
455 bryophyte cover and diversity parameter, whereas the cover of herbs is lower, if shrubs are abundant
456 on the rim.

457 Our analyses reveal a turnover in community composition along the vegetation-type gradient
458 from open forest to tundra. However, this latitudinal gradient is less pronounced in the bryophyte
459 composition. In contrast, bryophytes show a strong taxa turnover along the micro-relief gradient
460 within each polygon, while vascular plants are almost absent from the rim-pond transition and pond
461 sites. Accordingly, future compositional changes of polygonal vegetation will strongly depend on the
462 regional (increase of soil wetness by thawing permafrost) and local (change in drainage conditions)
463 climatic expression of global warming. On the landscape scale new taxa-combinations and taxa-
464 reshuffling will probably appear because vascular plants and bryophytes on the rim and in the pond
465 react in different ways. For example, future changes of a polygon may rather depend on changes in
466 local water conditions than on changes in air temperature, although these can affect the local water
467 conditions.

468 **Acknowledgements**

469 We thank M. Wieczorek and J. Klemm for assistance in the field and Dierk Michaelis for the
470 confirmation of *Sphagnum rubellum*.

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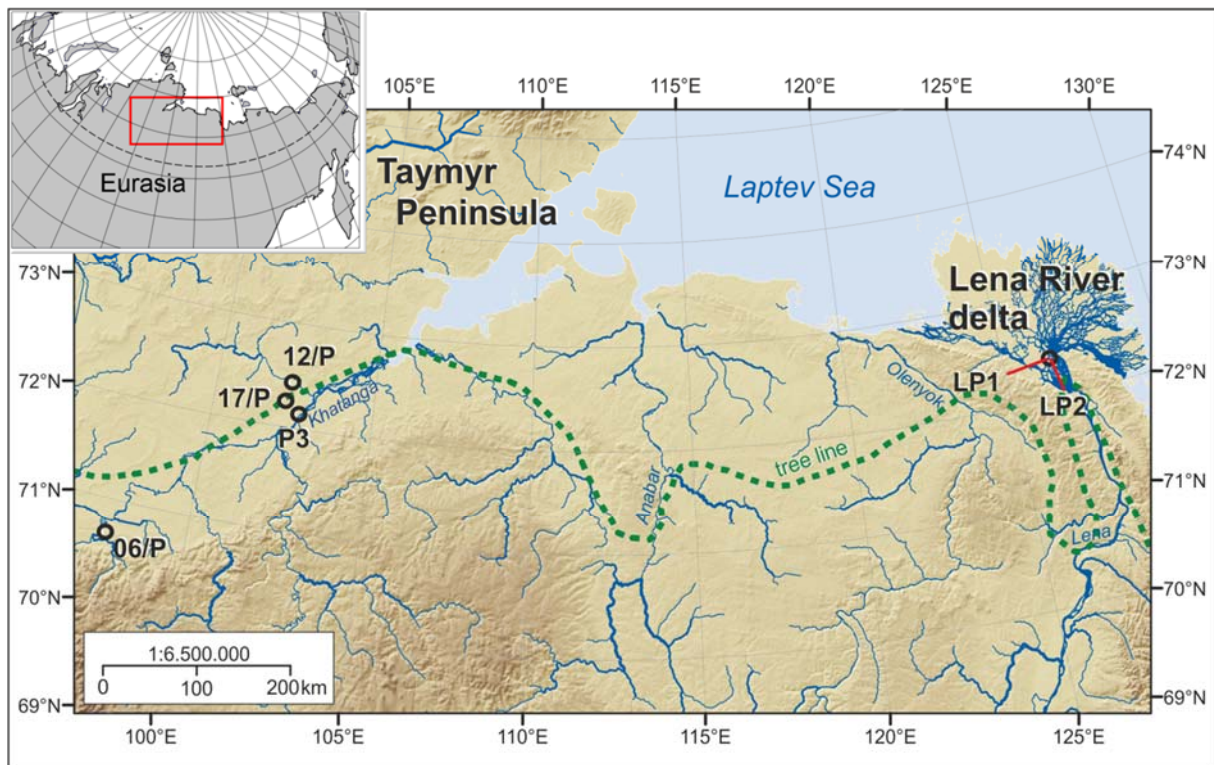
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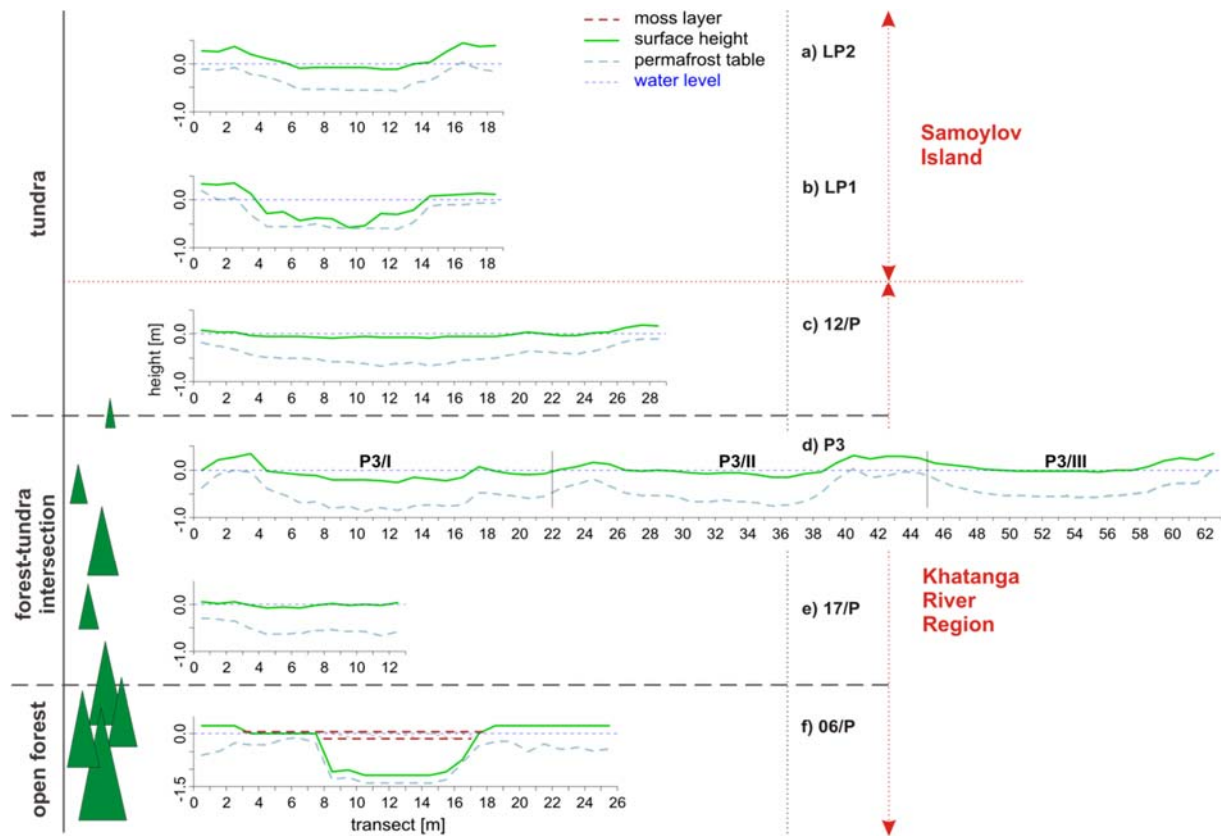
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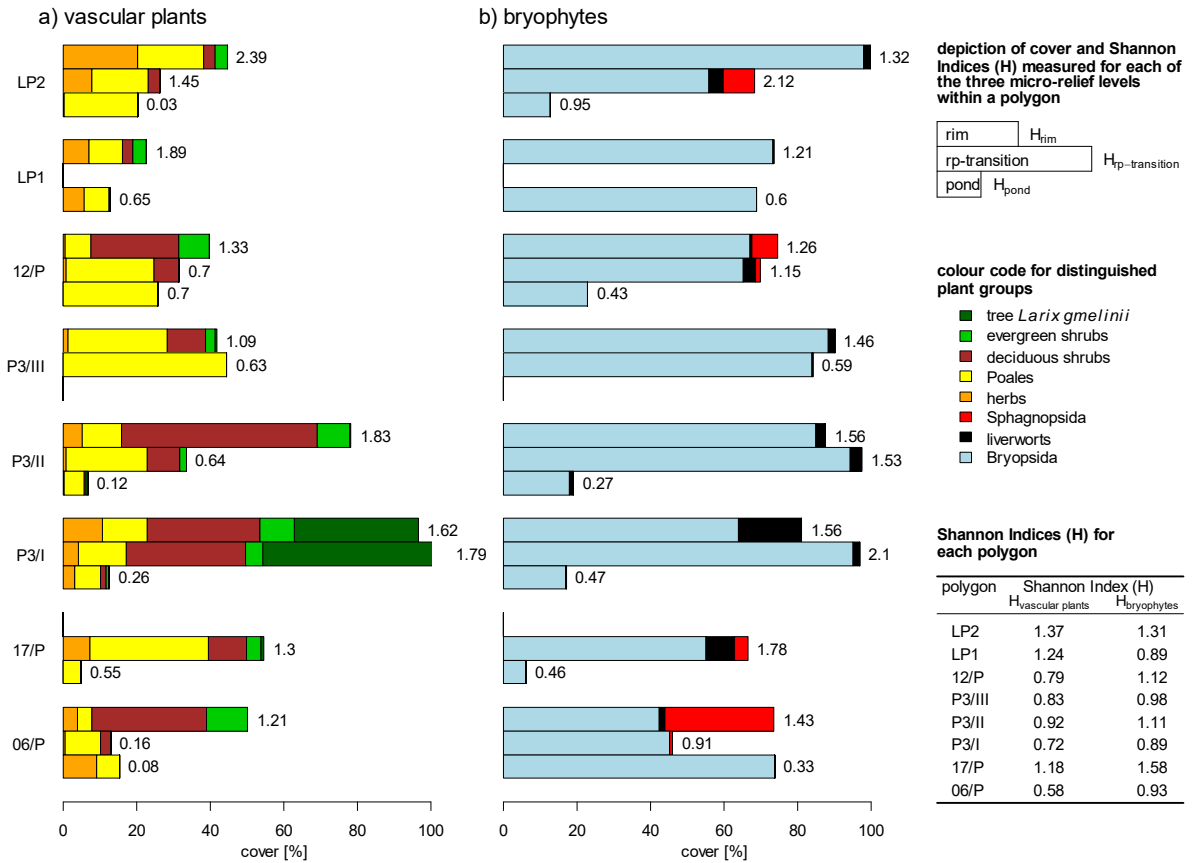
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653 **Fig. 1:** Map of the two study areas: Khatanga in the south-east of the Taymyr Peninsula and Samoylov Island in the Lena
 654 River delta, with the six polygon sites sampled and the current tree line marked (MAP by Th. Böhmer).

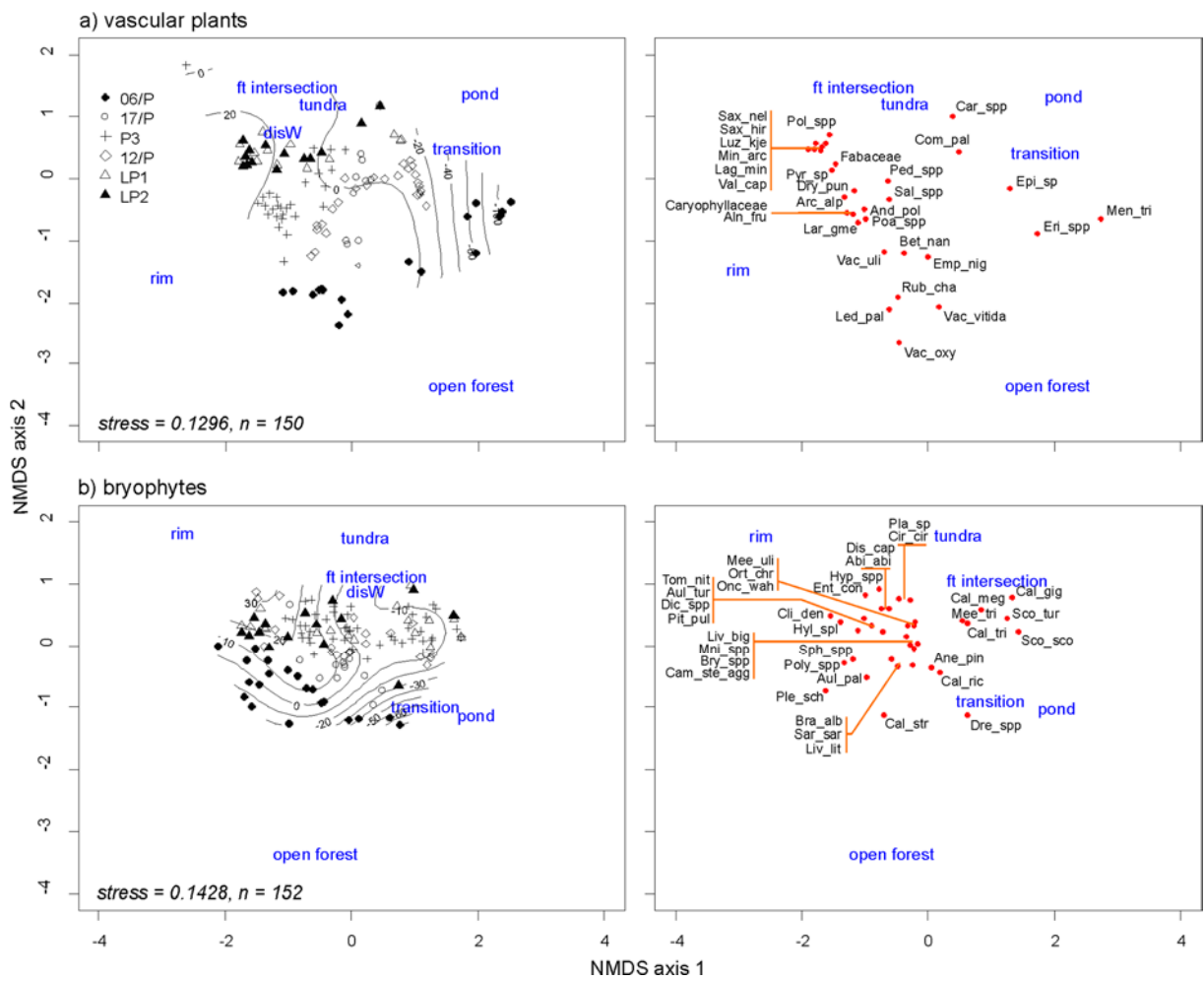


656 Fig. 2: Cross sections of the eight polygons, arranged according to their geographical position from north to south. Two low-
 657 centred polygons (a+b) were studied on Samoylov Island in the Lena River Delta in the northern subarctic tundra. A further
 658 six sites were investigated in the Khatanga Region (c-f). Polygon 12/P (c) is located in a treeless subarctic tundra part. A
 659 sequence of three adjacent polygons P3 (d), is situated in a polygon field in the vicinity of the Khatanga River. Polygon 17/P
 660 (e) is situated close to the tree line (forest-tundra intersection – forest site). The southernmost Khatanga site 06/P is an open
 661 forest site. The length of the cross section transects in metres corresponds to the number of plots.



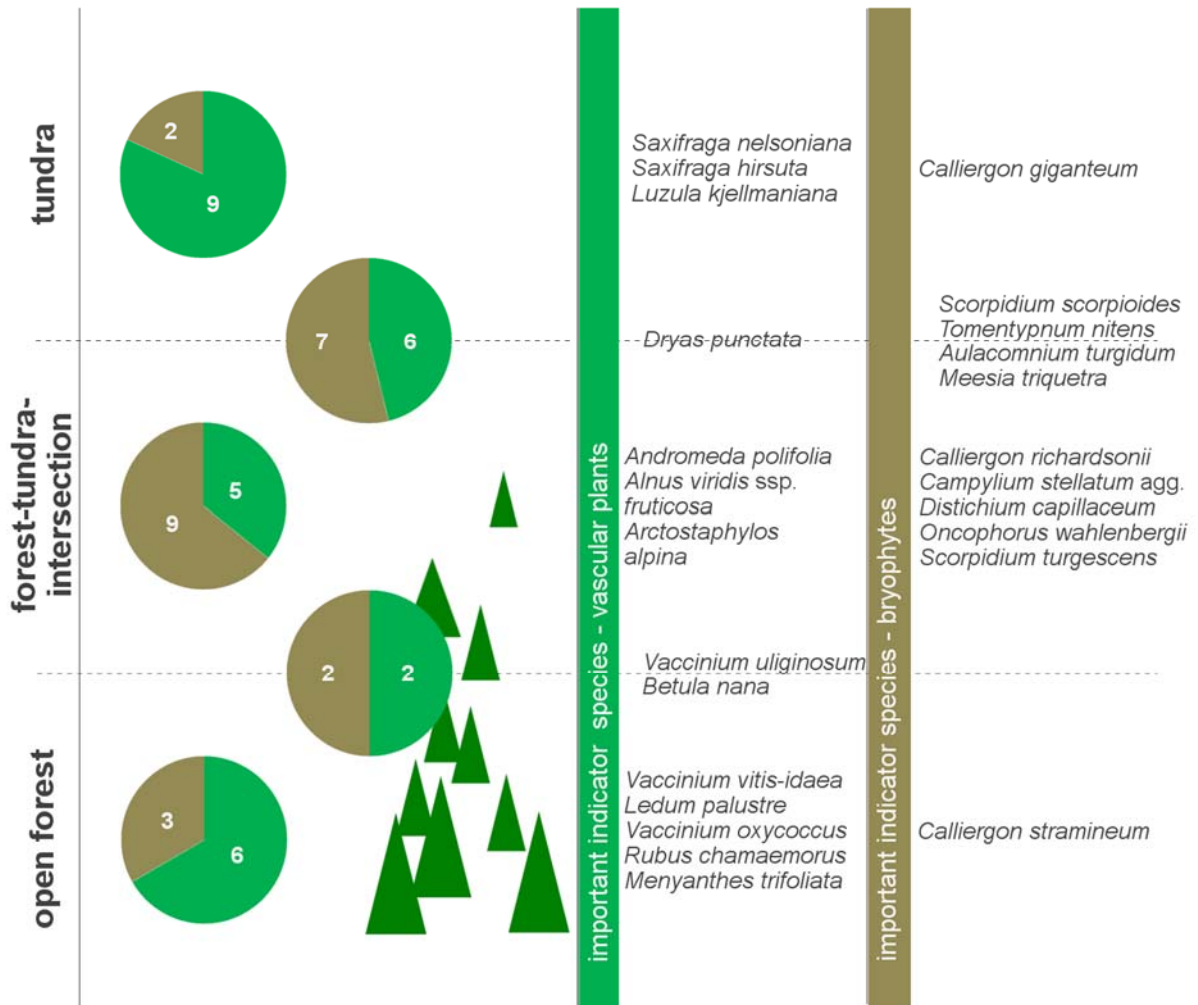
662 **Fig. 3:** Vegetation cover of all polygons separated into vascular plant layer (a), and bryophyte layer (b). The Shannon Index
 663 for the polygon micro-relief levels (rim, rim-pond transition, and pond) is shown beside the columns. The Shannon Index of
 664 each layer in the complete polygon is shown at the bottom right.

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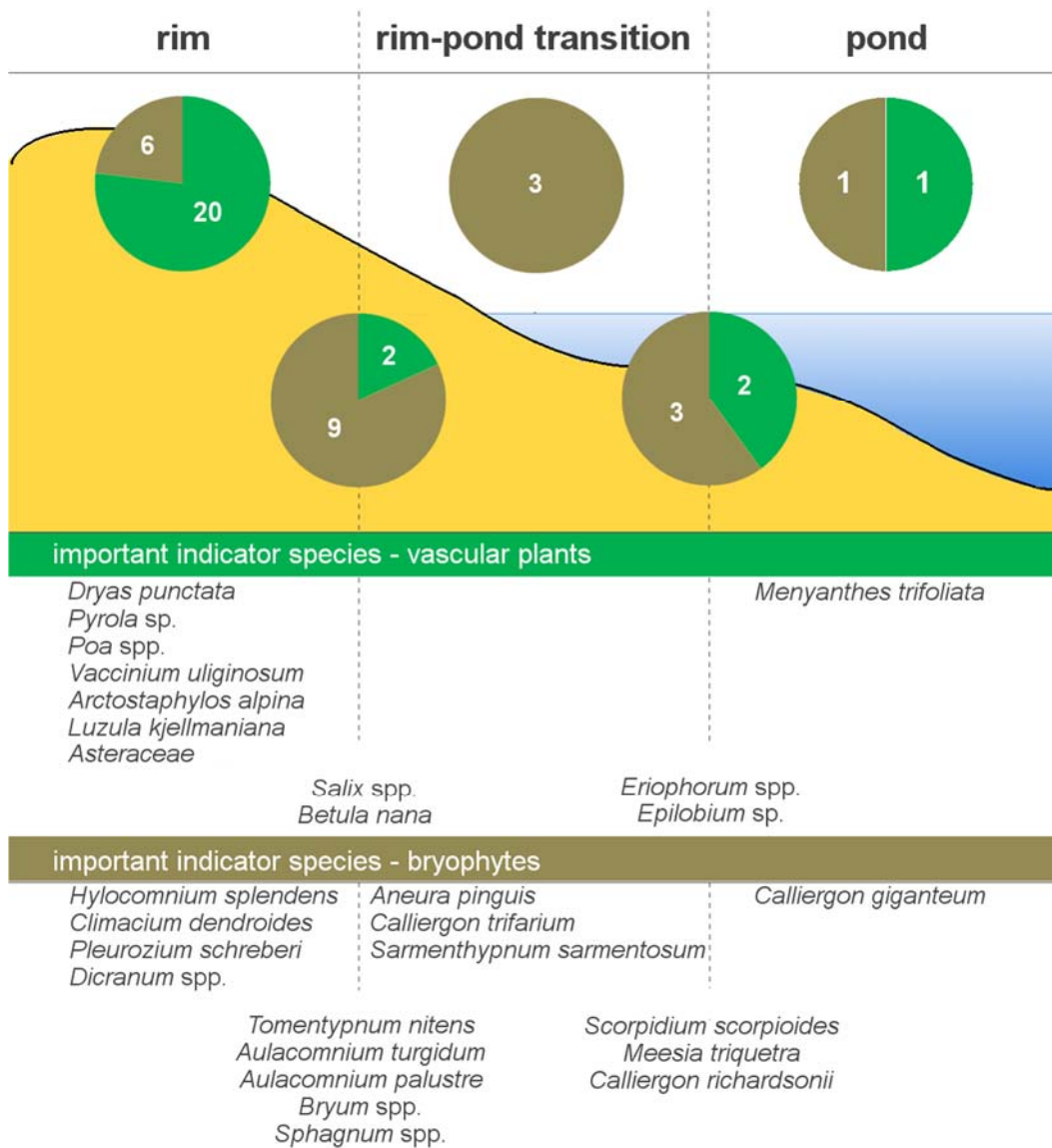


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667 **Fig. 4:** NMDS plots on the left side showing the distribution of sample sites based on a) the vascular plant community and b)
 668 the bryophyte community (underlain by plant position at surface height in centimetres) and on the right side the species
 669 distribution for both plant groups. The micro-relief level and vegetations types are included as dummy variables.



670 **Fig. 5:** Important indicator species for the latitudinal vegetation gradient (pie charts show the proportion of indicator species
 671 for vascular plants (green) and bryophytes (brown)).



672 **Fig. 6:** Important indicator species for the different micro-relief levels. Pie charts show the total number of indicator species
 673 for vascular plants (green) and bryophytes (brown).

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Table A1: All plant species of the vegetation survey with their suitability as an indicator (significances are marked with asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and their cover for the micro-relief levels of a polygon.

species	abbr.	indicator micro-relief	cover [%]								
			rim			rim-pond transition			pond		
			max	min	median	max	min	median	max	min	median
vascular plants											
<i>Alnus viridis</i> spp. <i>fruticosa</i>	Aln_fru	rim**	37.5	0	0	10	0	0	4	0	0
<i>Andromeda polifolia</i>	And_pol	rim**	4	0	0	4	0	0	4	0	0
<i>Arctostaphylos alpina</i>	Arc_alp	rim***	10	0	0	3	0	0	3	0	0
Asteraceae	Asteraceae	rim***	3	0	0	0	0	0	0	0	0
<i>Betula nana</i>	Bet_nan	rim/rp-transition***	37.5	0	0.5	20	0	0	4	0	0
<i>Caltha palustris</i>	Cal_pal	-	0	0	0	0.5	0	0	0.5	0	0
<i>Carex</i> spp.	Car_spp	-	37.5	0	4	20	0	0	4	0	0
Caryophyllaceae	Caryo- phyllaceae	rim***	3	0	0	3	0	0	0	0	0
<i>Chrysosplenium alternifolium</i>	Chr_alt	-	3	0	0	0	0	0	0	0	0
<i>Comarum palustre</i>	Com_pal	-	10	0	0	10	0	0	10	0	0
<i>Draba alpina</i>	Dra_alp	rim*	3	0	0	0	0	0	0	0	0
<i>Dryas punctata</i>	Dry_pun	rim***	20	0	3	3	0	0	0	0	0
<i>Empetrum nigrum</i>	Emp_nig	-	0	0	0	10	0	0	0	0	0
<i>Epilobium</i> sp.	Epi_sp	pond/rp- transition***	0	0	0	20	0	0	4	0	0
<i>Eriophorum</i> spp.	Eri_spp	pond/rp- transition***	10	0	0	37.5	0	0	20	0	0
Fabaceae	Fabaceae	rim**	10	0	0	3	0	0	3	0	0
<i>Gentiana plebeja</i>	Gen_ple	-	3	0	0	0	0	0	0	0	0
<i>Lagotis minor</i>	Lag_min	rim***	4	0	0	0	0	0	0	0	0
<i>Larix gmelinii</i>	Lar_gme	-	62.5	0	0	87.5	0	0	0	0	0
<i>Ledum palustre</i>	Led_pal	rim*	37.5	0	0	10	0	0	0	0	0
<i>Luzula kjellmaniana</i>	Luz_kje	rim***	4	0	0	0	0	0	0	0	0

<i>Menyanthes trifoliata</i>	Men_tri	pond**	0	0	0	0	0	0	37.5	0	0
<i>Micranthes hieracifolia</i>	Mic_hie	-	4	0	0	0	0	0	0	0	0
<i>Minuartia arctica</i>	Min_arc	rim**	3	0	0	0	0	0	0	0	0
<i>Oxycoccus palustris</i>	Oxy_pal	-	4	0	0	3	0	0	0	0	0
<i>Pedicularis</i> spp.	Ped_spp	-	4	0	0	3	0	0	3	0	0
<i>Poa</i> spp.	Poa_spp	(rim***)	20	0	0	0	0	0	0	0	0
<i>Polygonum</i> spp.	Pol_spp	(pond/rim**)	20	0	0	10	0	0	20	0	0
<i>Pyrola</i> sp.	Pyr_sp	rim***	4	0	0	3	0	0	0	0	0
<i>Rubus chamaemorus</i>	Rub_cha	rim*	20	0	0	0	0	0	0	0	0
<i>Salix</i> spp.	Sal_spp	(rim/rp-transition***)	20	0	0.5	20	0	0	10	0	0
<i>Saxifraga foliolosa</i>	Sax_fol	-	0	0	0	0	0	0	0.5	0	0
<i>Saxifraga hirculus</i>	Sax_hir	rim**	4	0	0	3	0	0	0	0	0
<i>Saxifraga nelsoniana</i>	Sax_nel	rim***	4	0	0	0	0	0	0	0	0
<i>Saxifraga tenuis</i>	Sax_ten	-	3	0	0	3	0	0	0	0	0
<i>Tofieldia coccinea</i>	Tof_coc	-	0	0	0	0.5	0	0	0	0	0
<i>Vaccinium uliginosum</i>	Vac_uli	rim***	37.5	0	0	20	0	0	0.5	0	0
<i>Vaccinium vitis-idaea</i>	Vac_vitida	rim***	20	0	0	3	0	0	0	0	0
<i>Valeriana capitata</i>	Val_cap	rim***	4	0	0	0.5	0	0	0	0	0
non-vascular plants											
<i>Equisetum</i> spp.	Equ_spp		4	0	0	3	0	0	0	0	0
lichens	lichens		4	0	0	10	0	0	0	0	0
bryophytes											
<i>Abietinella abietina</i>	Abi_abi	-	4	0	0	4	0	0	0	0	0
<i>Aneura pinguis</i>	Ane_pin	rp-transition***	3	0	0	4	0	0	3	0	0
<i>Aulacomnium palustre</i>	Aul_pal	rim/rp-transition***	62.5	0	4	37.5	0	0	37.5	0	0
<i>Aulacomnium turgidum</i>	Aul_tur	rim/rp-transition***	62.5	0	3	62.5	0	0	10	0	0
<i>Brachythecium albicans</i>	Bra_alb	rim*	4	0	0	3	0	0	0	0	0
<i>Bryum</i> spp.	Bry_spp	rim/rp-transition**	4	0	0	10	0	0	4	0	0
<i>Calliergon giganteum</i>	Cal_gig	pond***	0	0	0	10	0	0	87.5	0	0
<i>Calliergon megalophyllum</i>	Cal_meg	-	20	0	0	20	0	0	20	0	0

<i>Calliergon richardsonii</i>	Cal_ric	pond/rp-transition*	10	0	0	37.5	0	0	20	0	0
<i>Calliergon stramineum</i>	Cal_str	-	4	0	0	4	0	0	0	0	0
<i>Calliergon trifarium</i>	Cal_tri	rp-transition**	4	0	0	4	0	0	4	0	0
<i>Campylium stellatum</i> agg.	Cam_ste_agg	-	20	0	0	4	0	0	20	0	0
<i>Cirriphyllum cirrosum</i>	Cir_cir	-	4	0	0	4	0	0	0	0	0
<i>Climacium dendroides</i>	Cli_den	rim***	4	0	0	0	0	0	0	0	0
<i>Dicranum</i> spp.	Dic_spp	rim**	20	0	4	20	0	0	10	0	0
<i>Distichium capillaceum</i>	Dis_cap	-	4	0	0	4	0	0	3	0	0
<i>Drepanocladus</i> spp.	Dre_spp	-	20	0	0.5	87.5	0	10	87.5	0	0.5
<i>Entodon concinnus</i>	Ent_con	rim***	4	0	0	0	0	0	0	0	0
<i>Fissidens adianthoides</i>	Fis_adi	-	4	0	0	0	0	0	0	0	0
<i>Herzogiella seligeri</i>	Her_sel	-	4	0	0	0	0	0	0	0	0
<i>Herzogiella turfacea</i>	Her_tur	-	3	0	0	0	0	0	0	0	0
<i>Hylocomium splendens</i>	Hyl_spl	rim***	87.5	0	20	20	0	0	0	0	0
<i>Hypnum</i> spp.	Hyp_spp	-	4	0	0	4	0	0	0	0	0
Liverwort (big)	Liv_big	rim/rp-transition**	37.5	0	0	10	0	0	4	0	0
Liverwort (little)	Liv_lit	rim/rp-transition**	4	0	0	10	0	0	0.5	0	0
<i>Meesia triquetra</i>	Mee_tri	pond/rp-transition*	10	0	0	10	0	0	10	0	0
<i>Meesia uliginosa</i>	Mee_uli	-	4	0	0	4	0	0	4	0	0
<i>Mnium spinosum</i>	Mni_spi	-	3	0	0	0	0	0	0	0	0
<i>Mnium</i> spp.	Mni_spp	-	4	0	0	10	0	0	4	0	0
<i>Myurella sibirica</i>	Myu_sib	-	4	0	0	0	0	0	0	0	0
<i>Oncophorus wahlenbergii</i>	Onc_wah	-	4	0	0	10	0	0	4	0	0
<i>Orthothecium chryseum</i>	Ort_chr	-	4	0	0	20	0	0	4	0	0
<i>Philonotis fontana</i>	Phi_fon	-	4	0	0	0	0	0	0	0	0
<i>Ptilidium pulcherrimum</i>	Pit_pul	-	4	0	0	4	0	0	0	0	0
<i>Pleurozium schreberi</i>	Ple_sch	rim***	20	0	0	10	0	0	0	0	0
<i>Polytrichum</i> spp.	Poly_spp	rim/rp-transition**	10	0	0	4	0	0	3	0	0
<i>Ptilium crista-castrensis</i>	Pti_cri_cas	-	3	0	0	0	0	0	0	0	0
<i>Racomitrium canescens</i>	Rac_can	-	0	0	0	3	0	0	0	0	0

<i>Sarmenthypnum sarmentosum</i>	Sar_sar	rp-transition*	3	0	0	10	0	0	0	0	0
<i>Scorpidium scorpioides</i>	Sco_sco	pond/rp-transition***	87.5	0	0	87.5	0	15	87.5	0	10
<i>Scorpidium turgescens</i>	Sco_tur	rim/rp-transition*	4	0	0	4	0	0	0	0	0
<i>Sphagnum</i> spp.	Sph_spp	rim/rp-transition**	87.5	0	0	20	0	0	0	0	0
<i>Timmia norvegica</i>	Tim_nor	-	4	0	0	0	0	0	0	0	0
<i>Tomentypnum nitens</i>	Tom_nit	rim/rp-transition***	62.5	0	4	62.5	0	0	20	0	0
<i>Tortella fragilis</i>	Tor_fra	-	4	0	0	0	0	0	0	0	0
<i>Tortula ruralis</i>	Tor_rur	-	3	0	0	0	0	0	0	0	0

677 **Table A2:** All plant species of the vegetation survey with their suitability as an indicator (significances: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; vegetation type in brackets means that the species is
678 potentially not feasible or is part of a species group with a large range of local preferences) and their cover for the vegetation types along the tree-line transect.

species	abbr.	indicator zonal vegetation type	cover [%]								
			open forest			forest-tundra intersection			tundra		
			max	min	median	max	min	median	max	min	median
vascular plants											
<i>Alnus viridis</i> spp. <i>fruticosa</i>	Aln_fru	ft-intersection***	0	0	0	37.5	0	0	0	0	0
<i>Andromeda polifolia</i>	And_pol	ft-intersection***	4	0	0	4	0	0	0	0	0
<i>Arctostaphylos alpina</i>	Arc_alp	ft-intersection***	0	0	0	10	0	0	3	0	0
Asteraceae	Asteraceae	(tundra**)	0	0	0	0	0	0	3	0	0
<i>Betula nana</i>	Bet_nan	ft-intersection/ open forest*	37.5	0	0	37.5	0	0	20	0	0
<i>Caltha palustris</i>	Cal_pal	-	0	0	0	0	0	0	0.5	0	0
<i>Carex</i> spp.	Car_spp	(ft-intersection/ tundra***)	0	0	0	62.5	0	10	62.5	0	10
Caryophyllaceae	Caryo-phyllaceae	(ft-intersection*)	0	0	0	3	0	0	3	0	0
<i>Chrysosplenium alternifolium</i>	Chr_alt	-	0	0	0	0	0	0	3	0	0
<i>Comarum palustre</i>	Com_pal	-	0	0	0	10	0	0	10	0	0
<i>Draba alpina</i>	Dra_alp	-	0	0	0	0	0	0	3	0	0

<i>Dryas punctata</i>	Dry_pun	ft-intersection/ tundra**	0	0	0	20	0	0	20	0	0
<i>Empetrum nigrum</i>	Emp_nig	-	0	0	0	10	0	0	0	0	0
<i>Epilobium</i> sp.	Epi_sp	(tundra***)	3	0	0	0	0	0	20	0	0
<i>Eriophorum</i> spp.	Eri_spp	(open forest***)	37.5	0	3	37.5	0	0	20	0	0
Fabaceae	Fabaceae	tundra*	0	0	0	0.5	0	0	10	0	0
<i>Gentiana plebeja</i>	Gen_ple	-	0	0	0	0	0	0	3	0	0
<i>Lagotis minor</i>	Lag_min	(tundra*)	0	0	0	0	0	0	4	0	0
<i>Larix gmelinii</i>	Lar_gme	(ft-intersection*)	0	0	0	87.5	0	0	0	0	0
<i>Ledum palustre</i>	Led_pal	open forest***)	37.5	0	0	10	0	0	0	0	0
<i>Luzula kjellmaniana</i>	Luz_kje	tundra***)	0	0	0	0	0	0	4	0	0
<i>Menyanthes trifoliata</i>	Men_tri	open forest***)	37.5	0	0	0	0	0	0	0	0
<i>Micranthes hieracifolia</i>	Mic_hie	-	0	0	0	0	0	0	4	4	0
<i>Minuartia arctica</i>	Min_arc	tundra*	0	0	0	0	0	0	3	0	0
<i>Oxycoccus palustris</i>	Oxy_pal	open forest***)	4	0	0	0	0	0	0	0	0
<i>Pedicularis</i> spp.	Ped_spp	ft-intersection/ tundra**	0	0	0	4	0	0	3	0	0
<i>Poa</i> spp.	Poa_spp	-	3	0	0	20	0	0	4	0	0
<i>Polygonum</i> spp.	Pol_spp	(ft-intersection/ tundra**)	0	0	0	20	0	0	4	0	0
<i>Pyrola</i> sp.	Pyr_sp	(ft-intersection/ tundra*)	0	0	0	4	0	0	3	0	0
<i>Rubus chamaemorus</i>	Rub_cha	open forest**	20	0	0	10	0	0	0	0	0
<i>Salix</i> spp.	Sal_spp	(ft-intersection/ tundra***)	0	0	0	20	0	0	20	0	0
<i>Saxifraga foliolosa</i>	Sax_fol	-	0	0	0	0	0	0	0.5	0	0
<i>Saxifraga hirculus</i>	Sax_hir	tundra**	0	0	0	0	0	0	4	0	0
<i>Saxifraga nelsoniana</i>	Sax_nel	tundra**	0	0	0	0	0	0	4	0	0
<i>Saxifraga tenuis</i>	Sax_ten	-	0	0	0	0	0	0	3	0	0
<i>Tofieldia coccinea</i>	Tof_coc	-	0	0	0	0	0	0	0.5	0	0
<i>Vaccinium uliginosum</i>	Vac_uli	ft-intersection/ open forest***)	10	0	0	37.5	0	0	0	0	0

<i>Vaccinium vitis-idaea</i>	Vac_vitida	open forest***	20	0	0	3	0	0	0	0	0
<i>Valeriana capitata</i>	Val_cap	tundra**	0	0	0	0	0	0	4	0	0
non-vascular plants											
<i>Equisetum</i> spp.	Equ_spp	-	4	0	0	0	0	0	3	0	0
lichens	lichens	-	0	0	0	10	0	0	4	0	0
bryophytes											
<i>Abietinella abietina</i>	Abi_abi	-	0	0	0	4	0	0	3	0	0
<i>Aneura pinguis</i>	Ane_pin	ft-intersection/ tundra*	0	0	0	4	0	0	4	0	0
<i>Aulacomnium palustre</i>	Aul_pal	-	37.5	0	4	62.5	0	0	37.5	0	0
<i>Aulacomnium turgidum</i>	Aul_tur	ft-intersection/ tundra***	4	0	0	62.5	0	0	20	0	0.5
<i>Brachythecium albicans</i>	Bra_alb	-	4	0	0	4	0	0	0	0	0
<i>Bryum</i> spp.	Bry_spp	-	4	0	0	10	0	3	4	0	0
<i>Calliergon giganteum</i>	Cal_gig	tundra***	0	0	0	3	0	0	87.5	0	0
<i>Calliergon megalophyllum</i>	Cal_meg	(ft-intersection**)	0	0	0	20	0	0	0	0	0
<i>Calliergon richardsonii</i>	Cal_ric	ft-intersection***	10	0	0	37.5	0	0	0	0	0
<i>Calliergon stramineum</i>	Cal_str	open forest***	4	0	0	3	0	0	0	0	0
<i>Calliergon trifarium</i>	Cal_tri	ft-intersection/ tundra*	0	0	0	4	0	0	4	0	0
<i>Campylium stellatum</i> agg.	Cam_ste_agg	ft-intersection***	0	0	0	20	0	0	4	0	0
<i>Cirriphyllum cirrosum</i>	Cir_cir	-	0	0	0	4	0	0	3	0	0
<i>Climacium dendroides</i>	Cli_den	(tundra**)	0	0	0	4	0	0	4	0	0
<i>Dicranum</i> spp.	Dic_spp	(ft-intersection/ open forest***)	20	0	0	20	0	0	10	0	0
<i>Distichium capillaceum</i>	Dis_cap	(ft-intersection***)	0	0	0	4	0	0	3	0	0
<i>Drepanocladus</i> spp.	Dre_spp	(ft-intersection/ open forest***)	87.5	0	4	62.5	0	10	87.5	0	0
<i>Entodon concinnus</i>	Ent_con	-	0	0	0	4	0	0	4	0	0
<i>Fissidens adianthoides</i>	Fis_adi	-	0	0	0	4	0	0	4	0	0
<i>Herzogiella seligeri</i>	Her_sel	-	0	0	0	4	0	0	0	0	0
<i>Herzogiella turfacea</i>	Her_tur	-	0	0	0	0	0	0	3	0	0

<i>Hylocomium splendens</i>	Hyl_spl	-	62.5	0	0	62.5	0	0	87.5	0	0
<i>Hypnum</i> spp.	Hyp_spp	(ft-intersection*)	0	0	0	4	0	0	0	0	0
Liverwort (big)	Liv_big	(ft-intersection***)	0	0	0	37.5	0	0	0	0	0
Liverwort (little)	Liv_lit	-	4	0	0	10	0	0	4	0	0
<i>Meesia triquetra</i>	Mee_tri	ft-intersection/ tundra***	0	0	0	10	0	0	10	0	0
<i>Meesia uliginosa</i>	Mee_uli	-	0	0	0	4	0	0	4	0	0
<i>Mnium spinosum</i>	Mni_spi	-	0	0	0	0	0	0	3	0	0
<i>Mnium</i> spp.	Mni_spp	ft-intersection/ tundra*	4	0	0	10	0	0	10	0	0
<i>Myurella sibirica</i>	Myu_sib	-	0	0	0	4	0	0	0	0	0
<i>Oncophorus wahlenbergii</i>	Onc_wah	ft-intersection**	0	0	0	10	0	0	3	0	0
<i>Orthothecium chryseum</i>	Ort_chr	ft-intersection**	0	0	0	20	0	0	0	0	0
<i>Philonotis fontana</i>	Phi_fon	-	0	0	0	0	0	0	4	0	0
<i>Ptilidium pulcherrimum</i>	Pit_pul	-	4	0	0	4	0	0	3	0	0
<i>Pleurozium schreberi</i>	Ple_sch	open forest***	20	0	0	0	0	0	10	0	0
<i>Polytrichum</i> spp.	Poly_spp	open forest/tundra***	10	0	0	3	0	0	10	0	0
<i>Ptilium crista-castrensis</i>	Pti_cri_cas	-	3	0	0	0	0	0	0	0	0
<i>Racomitrium canescens</i>	Rac_can	-	0	0	0	0	0	0	3	0	0
<i>Sarmenthyllum sarmentosum</i>	Sar_sar	-	3	0	0	3	0	0	10	0	0
<i>Scorpidium scorpioides</i>	Sco_sco	ft-intersection/ tundra***	0	0	0	87.5	0	4	87.5	0	4
<i>Scorpidium turgescens</i>	Sco_tur	ft-intersection***	0	0	0	4	0	0	0	0	0
<i>Sphagnum</i> spp.	Sph_spp	open forest***	87.5	0	0	10	0	0	37.5	0	0
<i>Timmia norvegica</i>	Tim_nor	-	0	0	0	0	0	0	4	0	0
<i>Tomentypnum nitens</i>	Tom_nit	ft-intersection/ tundra***	3	0	0	62.5	0	0.5	62.5	0	0
<i>Tortella fragilis</i>	Tor_fra	-	0	0	0	0	0	0	4	0	0
<i>Tortula ruralis</i>	Tor_rur	-	0	0	0	0	0	0	3	0	0