1 # Vegetation patterns along micro-relief and tree-line

2 # transects in polygonal landscapes of the Siberian Arctic

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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 follwoing 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?

Material and methods

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

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

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

Field methods and environmental data collection

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

Environmental information (surface elevation, thaw depth, water depth) was measured at the centre of each plot relative to a reference line and calibrated to the water level (Fig. 2). (It was impossible to recognize the water-sediment transition at 06/P because of a dense bryophyte swinging mat. Therefore, we estimated an average height for the three micro-relief levels by applying the height/thaw depth relations gained from roughly comparable polygon types: LP1 and LP2.) All plots 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   verifed 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

Results

Characteristics of polygonal vegetation

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

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

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

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

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

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

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

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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 Additonally, 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: $p > 0.1$).

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

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

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

Plant type	Vascular plants				Bryophytes			
Polygon	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

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

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

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

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

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

In contrast to vascular plants, bryophytes are more evenly distributed in the NMDS plot although more taxa are characteristic of rim vegetation (*Hylocomium splendens*, *Pleurozium schreberi, Ptilium crista-castrensis,* and *Climacium dendroides*) than pond vegetation (mainly *Scorpidium* and *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.

Discussion

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

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

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

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

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

14

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

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

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

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

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

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

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

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

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

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

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

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

The high vegetation turnover at the local scale, and thus changes in the polygon morphology over time, will result in a marked vegetation change that does not necessarily reflect changes in the vegetation type or climate but rather traces variations in the local hydrological conditions. The 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 *Sarmenthypnum 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.

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651

Figures
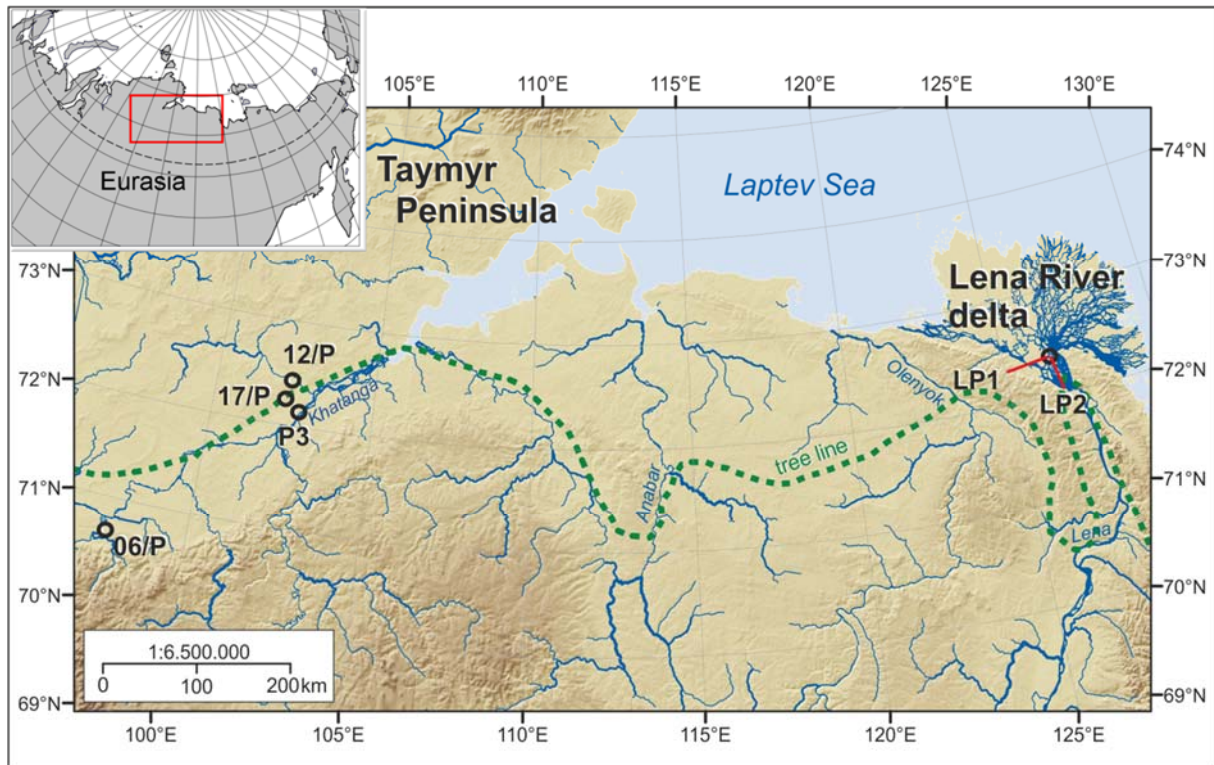
653   **Fig. 1**: Map of the two study areas: Khatanga in the south-east of the Taymyr Peninsula and Samoylov Island in the Lena

654   River delta, with the six polygon sites sampled and the current tree line marked (MAP by Th. Böhmer).

655
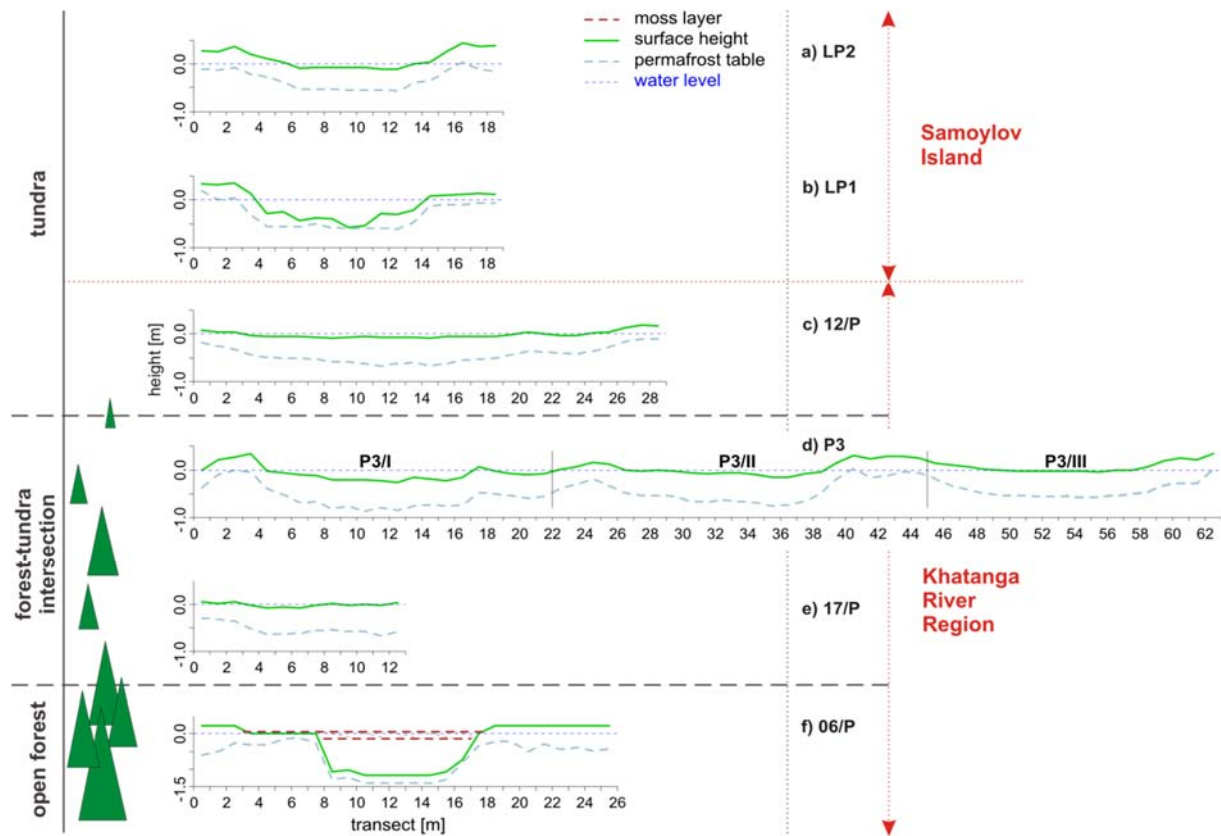
Fig. 2: Cross sections of the eight polygons, arranged according to their geographical position from north to south. Two low-centred polygons (a+b) were studied on Samoylov Island in the Lena River Delta in the northern subarctic tundra. A further six sites were investigated in the Khatanga Region (c-f). Polygon 12/P (c) is located in a treeless subarctic tundra part. A sequence of three adjacent polygons P3 (d), is situated in a polygon field in the vicinity of the Khatanga River. Polygon 17/P (e) is situated close to the tree line (forest-tundra intersection – forest site). The southernmost Khatanga site 06/P is an open forest site. The length of the cross section transects in metres corresponds to the number of plots.
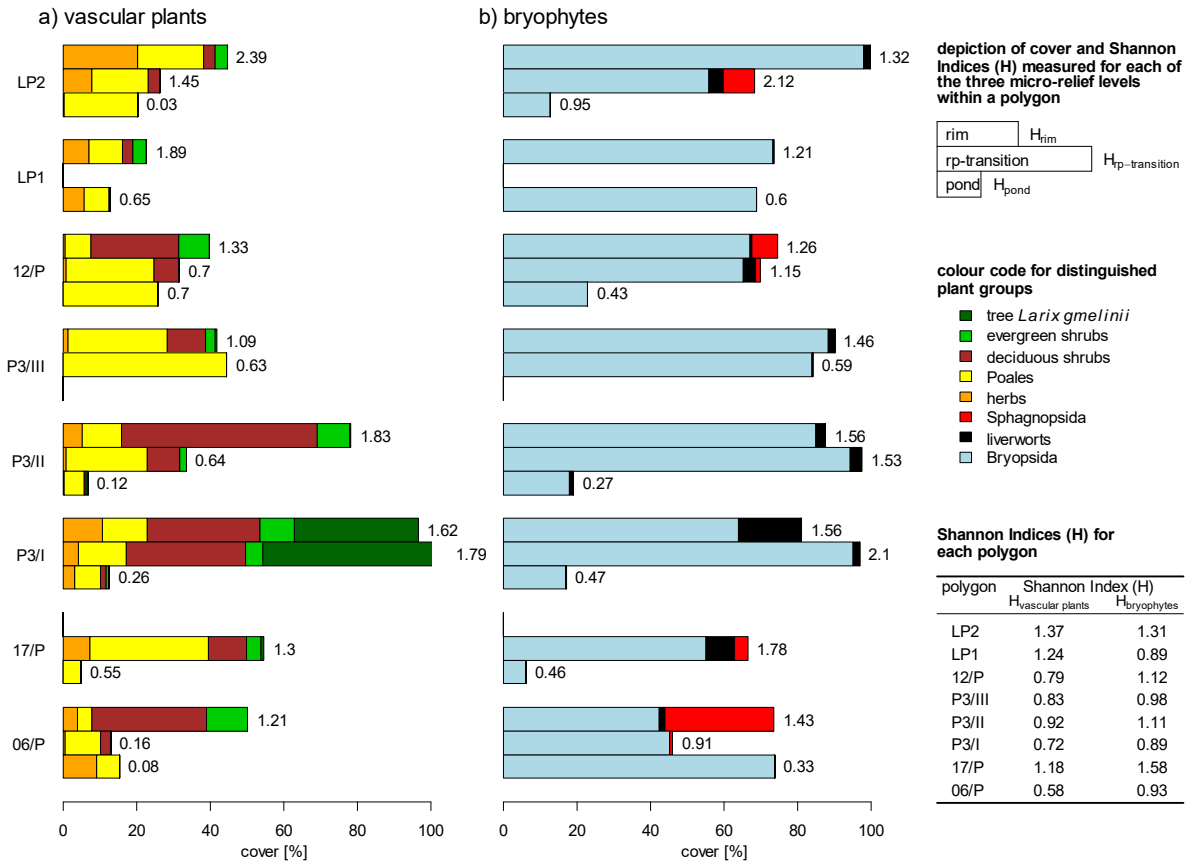
Fig. 3: Vegetation cover of all polygons separated into vascular plant layer (a), and bryophyte layer (b). The Shannon Index for the polygon micro-relief levels (rim, rim-pond transition, and pond) is shown beside the columns. The Shannon Index of each layer in the complete polygon is shown at the bottom right.

666
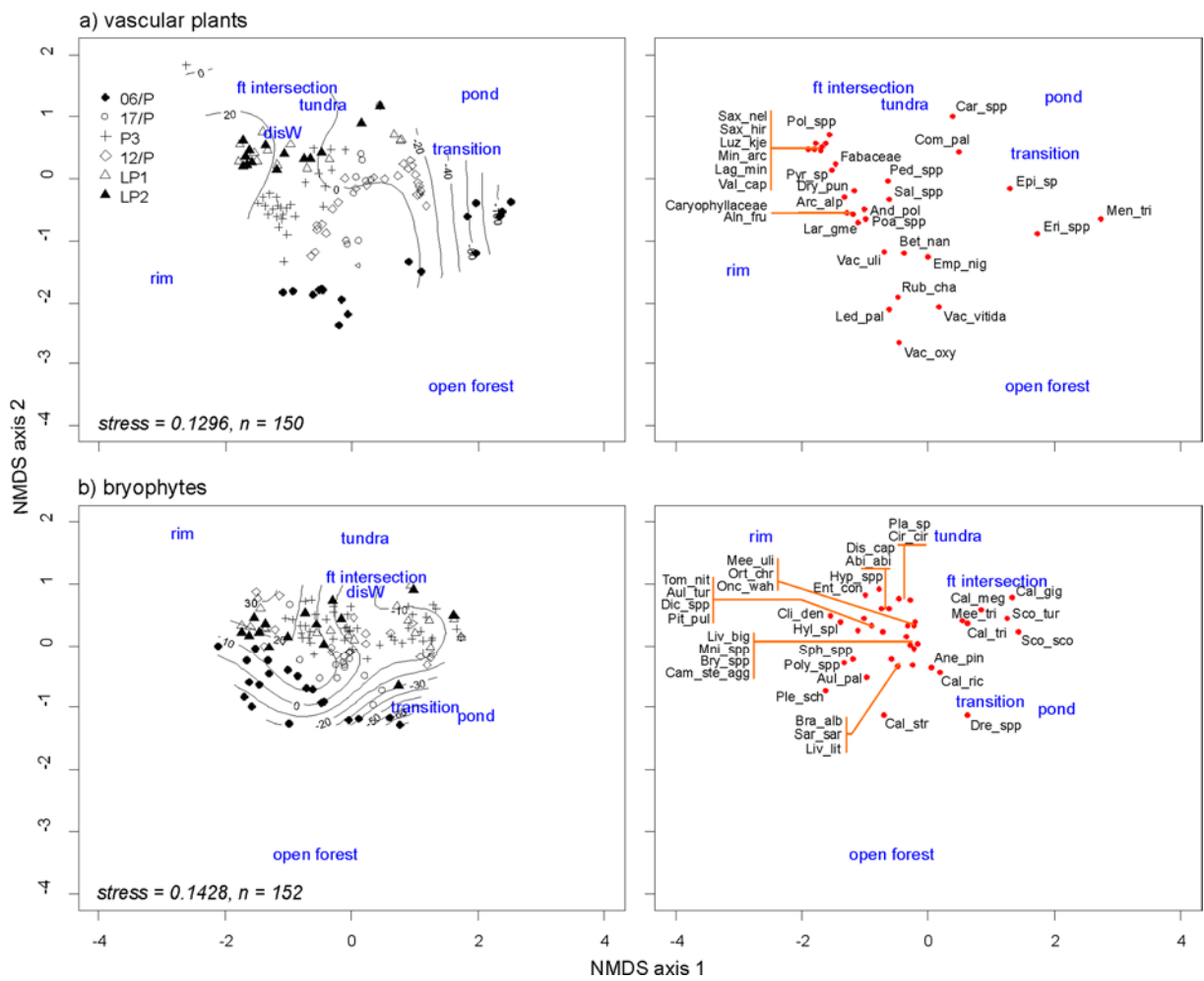
Fig. 4: NMDS plots on the left side showing the distribution of sample sites based on a) the vascular plant community and b) the bryophyte community (underlain by plant position at surface height in centimetres) and on the right side the species distribution for both plant groups. The micro-relief level and vegetations types are included as dummy variables.
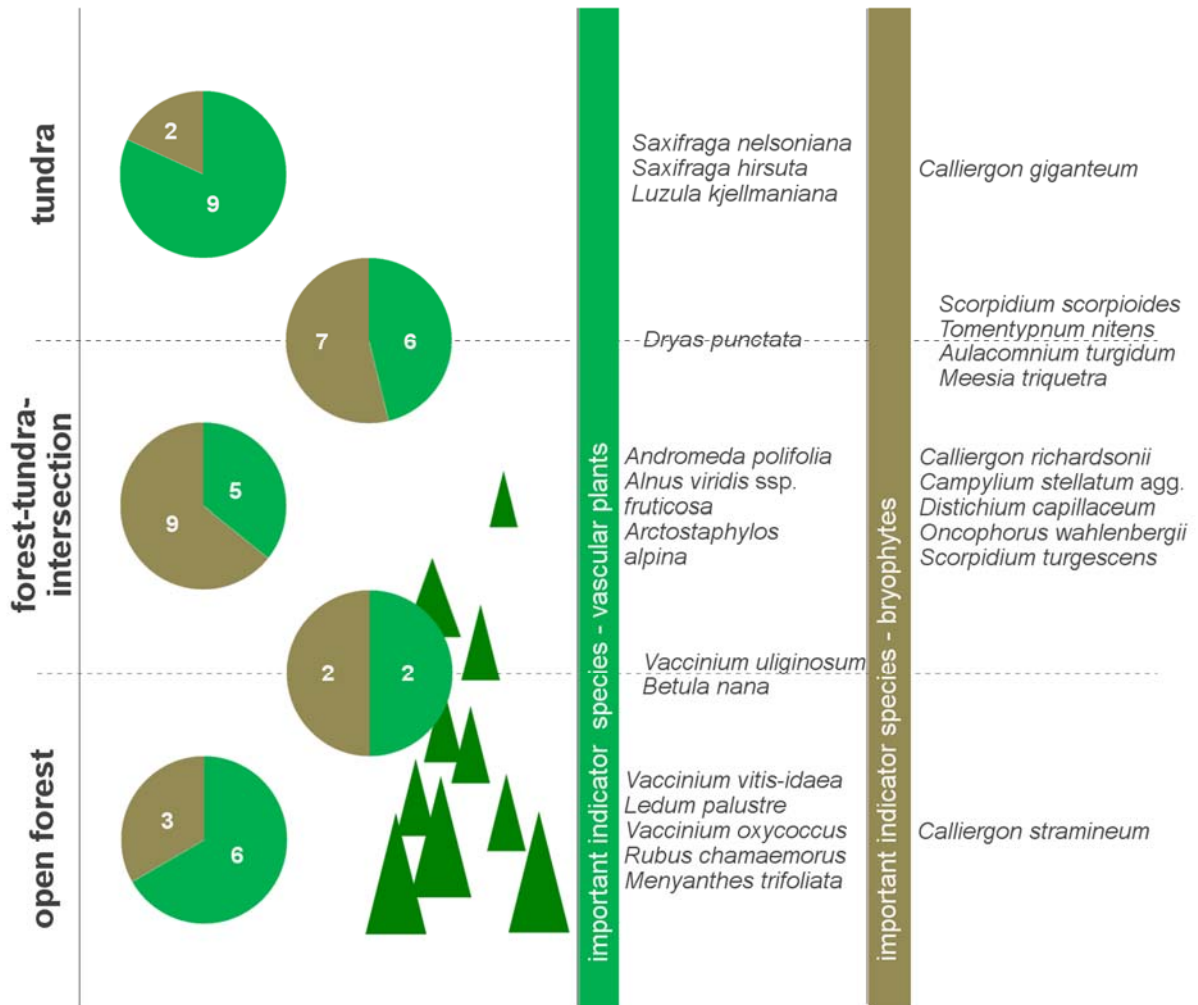
Fig. 5: Important indicator species for the latitudinal vegetation gradient (pie charts show the proportion of indicator species for vascular plants (green) and bryophytes (brown)).
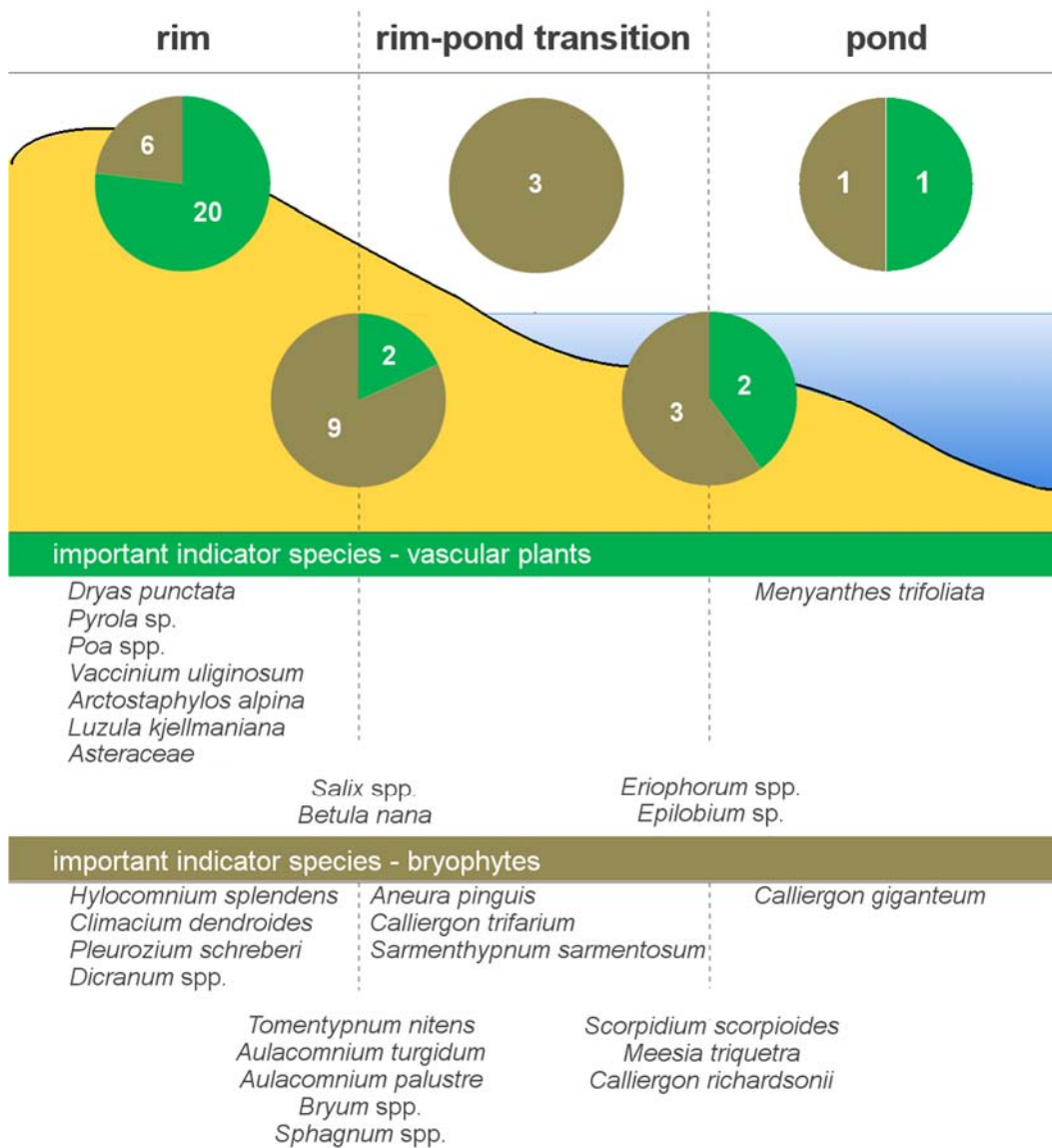
Fig. 6: Important indicator species for the different micro-relief levels. Pie charts show the total number of indicator species for vascular plants (green) and bryophytes (brown).

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											
Alnus viridis spp. *fruticosa*	Aln_fru	rim**	37.5	0	0	10	0	0	4	0	0
Andromeda polifolia	And_pol	rim**	4	0	0	4	0	0	4	0	0
Arctostaphylos alpina	Arc_alp	rim***	10	0	0	3	0	0	3	0	0
Asteraceae	Asteraceae	rim***	3	0	0	0	0	0	0	0	0
Betula nana	Bet_nan	rim/rp-transition***	37.5	0	0.5	20	0	0	4	0	0
Caltha palustris	Cal_pal	-	0	0	0	0.5	0	0	0.5	0	0
Carex 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
Chrysosplenium alternifolium	Chr_alt	-	3	0	0	0	0	0	0	0	0
Comarum palustre	Com_pal	-	10	0	0	10	0	0	10	0	0
Draba alpina	Dra_alp	rim*	3	0	0	0	0	0	0	0	0
Dryas punctata	Dry_pun	rim***	20	0	3	3	0	0	0	0	0
Empetrum nigrum	Emp_nig	-	0	0	0	10	0	0	0	0	0
Epilobium sp.	Epi_sp	pond/rp-transition***	0	0	0	20	0	0	4	0	0
Eriophorum 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
Gentiana plebeja	Gen_ple	-	3	0	0	0	0	0	0	0	0
Lagotis minor	Lag_min	rim***	4	0	0	0	0	0	0	0	0
Larix gmelinii	Lar_gme	-	62.5	0	0	87.5	0	0	0	0	0
Ledum palustre	Led_pal	rim*	37.5	0	0	10	0	0	0	0	0
Luzula kjellmaniana	Luz_kje	rim***	4	0	0	0	0	0	0	0	0

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

33

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

species	abbr.	indicator zonal vegetation type	max	min	median	max	min	median	max	min	median
Sarmenthypnum sarmentosum	Sar_sar	rp-transition*	3	0	0	10	0	0	0	0	0
Scorpidium scorpioides	Sco_sco	pond/rp-transition***	87.5	0	0	87.5	0	15	87.5	0	10
Scorpidium turgescens	Sco_tur	rim/rp-transition*	4	0	0	4	0	0	0	0	0
Sphagnum spp.	Sph_spp	rim/rp-transition**	87.5	0	0	20	0	0	0	0	0
Timmia norvegica	Tim_nor	-	4	0	0	0	0	0	0	0	0
Tomentypnum nitens	Tom_nit	rim/rp-transition***	62.5	0	4	62.5	0	0	20	0	0
Tortella fragilis	Tor_fra	-	4	0	0	0	0	0	0	0	0
Tortula ruralis	Tor_rur	-	3	0	0	0	0	0	0	0	0

677
678 **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 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											
Alnus viridis spp. *fruticosa*	Aln_fru	ft-intersection***	0	0	0	37.5	0	0	0	0	0
Andromeda polifolia	And_pol	ft-intersection***	4	0	0	4	0	0	0	0	0
Arctostaphylos alpina	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
Betula nana	Bet_nan	ft-intersection/ open forest*	37.5	0	0	37.5	0	0	20	0	0
Caltha palustris	Cal_pal	-	0	0	0	0	0	0	0.5	0	0
Carex 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
Chrysosplenium alternifolium	Chr_alt	-	0	0	0	0	0	0	3	0	0
Comarum palustre	Com_pal	-	0	0	0	10	0	0	10	0	0
Draba alpina	Dra_alp	-	0	0	0	0	0	0	3	0	0

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

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

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

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