



Title	Tundra fire alters vegetation patterns more than the resultant thermokarst
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1 ORIGINAL PAPER

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3 **Tundra fire alters vegetation patterns more than the resultant thermokarst**

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22

23 **Abstract**

24 Tundra fires are increasing their frequencies and intensities due to global warming and alter  
25 revegetation patterns through various pathways. To understand the effects of tundra fire and the  
26 resultant thermokarst on revegetation, vegetation and related environmental factors were compared  
27 between burned and unburned areas of Seward Peninsula, Alaska, using 140 50 cm × 50 cm plots.  
28 The area was burned in 2002 and surveyed in 2013. Seven vegetation types were classified by a  
29 cluster analysis and were categorized along a fire severity gradient from none to severe fire intensity.  
30 The species richness and diversity were higher in intermediately disturbed plots. Severe fire  
31 allowed the immigration of fire-favored species (e.g., *Epilobium angustifolium*, *Ceratodon*  
32 *purpureus*) and decreased or did not change the species diversity, indicating that species replacement  
33 occurred within the severely burned site. Although thermokarsts (ground subsidence) broadly  
34 occurred on burned sites, due to thawing, the subsidence weakly influenced vegetation patterns.  
35 These results suggest that the fire directly altered the species composition at a landscape scale  
36 between the burned and unburned sites and it indirectly altered the plant cover and diversity through  
37 the differential modification, such as thermokarst, at a small scale within the burned site.

38

39 **Key words** Polygonal ground · Landscape patterns · Thawing · Thermokarst · Tundra fire

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## 42 Introduction

43  
44 Climate change at high latitudes is inducing ecosystem changes, particularly, in the Arctic tundra  
45 region, which is the most sensitive (Jones et al. 2015). The frequency and extent of tundra fires are  
46 increasing due to global warming (Hu et al. 2015), although the effects of severe tundra fires on  
47 revegetation have not been well studied because of their low frequency and intensity (Racine et al.  
48 2004). Tundra fire in the Arctic is accelerating global warming, because a large amount of organic  
49 carbon in the soil and permafrost is released into the atmosphere (Mack et al. 2011). Vegetation, in  
50 particular, *Sphagnum* moss cover, maintains the underground soil and ice structures by the  
51 adiabatic effects (Raynolds et al. 2008). Therefore, more focus should be given to the patterns and  
52 paces of vegetation recovery after tundra fire.

53 Interactions among topographical, physical and biological processes after disturbances,  
54 including tundra fire, occur at different times and have different responses and durations (Grosse et  
55 al. 2011). Tundra fires alter thermokarsts (ground subsidence) (Jones et al. 2015) that may change  
56 the vegetation patterns. The alteration occurs through various pathways (Kokelj and Jorgenson  
57 2013). Fire removes plants from the ground surface, and creates low albedo that increases the  
58 active layer (Beringer et al. 2001, Tsuyuzaki et al. 2009). Ground subsidence occurred in a  
59 polygonal network on thawing after the 2002 tundra fire at Kougarok in the Seward Peninsula  
60 (Iwahana et al. 2016). Ice wedge degradation occurs over a decadal time scale in both continuous  
61 and discontinuous permafrost zones (Tsuyuzaki et al. 1999, Jorgenson et al. 2006). Plant  
62 establishment is affected greatly by land modifications, including thermokarst (Lloyd et al. 2003,  
63 Grosse et al. 2011). These reports suggest that fire affects vegetation structures at various  
64 spatio-temporal scales. Satellite imagery confirms that thermokarsts occur frequently in the  
65 burned areas of Kougarok where polygonal networks of high-centered polygon derived by melting  
66 ice wedges are well developed (Iwahana et al. 2016). However, no subsidence was observed in  
67 adjacent unburned sites. Therefore, we compared the vegetation development patterns between  
68 burned and unburned areas and investigated the effects of thermokarsts on vegetation within the  
69 burned area. We hypothesized that: (1) the fire had altered the vegetation (as indicated by the  
70 presence of fire-adapted species even 11 years after the last fire), (2) the effects of thermokarsts

71 (ground subsidence) on vegetation cover and species diversity were weaker or slower than the effects  
72 of fire, because the environmental changes induced by topographic changes were not drastic as  
73 compared with the changes by fire, and (3) the fire affected the vegetation structures at landscape and  
74 habitat scales through the alterations of topography and its related factors.

## 75 **Study area and methods**

76

### 77 **Study area and field methods**

78 The study site is located in Kougarok, Seward Peninsula (65°26''N, 164°39'W, 90 m elevation) in  
79 northwestern Alaska (Fig. 1). The region is located in a transitional area between discontinuous and  
80 continuous permafrost zones, and it is underlain locally by a thin (15-50 m) continuous permafrost (>  
81 90% areal cover) (Brown et al. 1997). The characteristics of climate in this region are as follows  
82 (Liljedahl et al. 2007): The annual mean air temperature during 2000 and 2006 was between -2.7°C  
83 and -5.9°C. Summer rainfall from June to August averaged 94 mm during the seven years. Winter  
84 precipitation for the seven years averaged 80 mm, as estimated by the snow water equivalent in early  
85 May. The study site suffered from a tundra fire during 4 August and 10 October 10 2002. In an  
86 area close to our study site, the fire intensity was moderate to severe and consumed 50% of organic  
87 layer (Liljedahl et al. 2007). Thermokarsts were observed firstly on the burned area in 2006  
88 (Iwahana et al. 2016). The soil profiles had peat sediments or mixed layers of peat and silty mineral  
89 soils. Peaty soil profiles contained few or thin ice lenses, while mineral soil particles did thick  
90 ones.

91 The present surveys were conducted during 7 to 12 August 2013, 11 years after the 2002 fire.  
92 The study area is distributed in a zone of nearly continuous permafrost of which active layer  
93 averaged 56 cm, because of the continental climate near the center of Seward Peninsula (Hinzman et  
94 al. 2003). On a southwest facing slope, seven transects were set up randomly within a 250 m × 100  
95 m area (Fig. 1). The field investigations confirmed that the landscape was broadly homogenous in  
96 any slope direction (Iwahana et al. 2016) if fires did not occur for long term (Narita et al. 2015).  
97 Three transects were set up in the burned site, and the other three transects were set up in the  
98 unburned site. All the transects in the burned site were established on areas where thermokarsts  
99 were observed. The distance from subsidence was recorded on each plot. On each transect, 50 cm

100 × 50 cm plots were set up at 1-m intervals. The lengths of the transects were between 11 m and 19  
101 m. A total number of plots was 140.

102 Plant cover was visually estimated by overlying a 50 cm × 50 cm frame, which was subdivided  
103 into 25 10 cm × 10 cm cells by strings on each plot. The total number of cells occupied by each  
104 plant species was counted when the plant cover was higher than 4% (= 1 cell). When the cover was  
105 less than 4%, the cover intervals became narrowed. The litter cover was estimated, as well as plant  
106 cover, and litter thickness was measured using a ruler. The litter amount was evaluated as the cover  
107 multiplied by the average thickness. The relative longitudes, latitudes and elevations of the four  
108 corners of each plot were determined by an RTK differential GPS system with a base station (GS15  
109 VIVA, Leica Geosystems, Norcross, GA) and a rover (GS14 GNSS Receiver, Leica). The  
110 horizontal and vertical measurement errors were less than 10 mm and 20 mm, respectively. In  
111 addition, the maximum and minimum elevations were measured in each plot. Therefore, a total of  
112 six geographical positions were measured on each plot. At the six points, the thaw depth and peat  
113 moisture were measured. The peat moisture (% v/v) was measured by a time domain reflectometry  
114 (TDR) (Hydrosense, Campbell Scientific, Logan) with 12-cm probes. Based on the positioning  
115 data, the slope gradient and aspect were calculated. The standard deviation of the elevations of the  
116 six positions measured in each plot were calculated and used as a surrogate for ground surface  
117 roughness (Tsuyuzaki et al. 1999).

118

### 119 **Statistical analysis**

120 The total plant cover, species richness, species diversity ( $H'$ ) and evenness ( $J'$ ) were calculated on  
121 each 50 cm × 50 cm plot. Based on the cover of each species in each plot, a two-way indicator  
122 species analysis (TWINSpan) was performed to recognize vegetation types. A feature of  
123 TWINSpan is that vegetation is classified based on considering the balance between frequency and  
124 abundance of species. Pseudo-species is used to retain the quantitative information (Jongman et al.  
125 1995). Steel-Dwass test, a non-parametric multiple comparison procedure, was used for *post-hoc*  
126 multiple comparisons to compare differences in the species composition characteristics and measured  
127 environmental factors between the cluster groups when the non-parametric Kruskal-Wallis one-way  
128 analysis of variance (ANOVA) was significant (Underwood 1997). For all the analyses, the number

129 of samples ( $n$ ) was the 140 plots.

130 Non-metric multidimensional scaling (NMDS) was conducted to investigate the relationships  
131 between environmental factors and vegetation types and between environmental factors and species  
132 (McCune and Grace 2002). The stress was referred to decide the effectiveness of the non-metric of  
133 NMDS. The biplots of NMDS were made for plot-environment and species-environment  
134 relationships. All statistical analyses except for TWINSpan were conducted with the statistical  
135 package *vegan* on the program R (version 3.4.0) (R Core Team 2017). TWINSpan was conducted  
136 with the software CANOCO version 4.5 (ter Braak & Smilauer 2002).

137

## 138 **Results**

139

### 140 **Vegetation patterns**

141 In total, 30 species were recorded in the 140 plots. Seven cluster groups (hereafter, groups A to G)  
142 were recognized by the TWINSpan cluster analysis (Fig. 2). At the first cluster division, the plant  
143 communities were divided into two groups by the dominance of *Betula nana*, *Vaccinium vitis-idaea*  
144 and *Vaccinium uliginosum* (A to D) and by the dominance of *Polytrichum commune* and  
145 *Calamagrostis canadensis* (E to G). Group D (*Eriophorum* vegetation type) was separated from  
146 groups A to C by the dominance of *C. canadensis*, *Eriophorum vaginatum* and *Polytrichum*  
147 *commune*. Group A (*Vaccinium*) was separated from groups B and C by the establishment of  
148 *Sphagnum fuscum*. The presence of *Cladonia* sp. separated group B from group C (*Carex*). Group  
149 B (*Ledum*) also showed high cover of *Ledum groenlandicum*. Among groups E through G, group G  
150 (*Calamagrostis-Ceratodon*) was separated by the presence of *Ceratodon purpureus*. Groups E and  
151 G showed high frequency and cover of *C. canadensis* and *P. commune*. Group E  
152 (*Calamagrostis-Polytrichum*) was separated from group F (*Polytrichum-Calamagrostis*) by the  
153 presence of *Carex bigelowii*, *Epilobium angustifolium* and *Rubus chamaemorus*. Few seedlings  
154 were observed in all the plots.

155 The highest cover and frequency were obtained by a tussock-forming cottongrass, *E. vaginatum*  
156 whose mean cover and occurrence frequency were 21% and 89%, respectively. *L. groenlandicum*  
157 occurred with the second highest frequency (82%) in the plots (Table 1), followed by *R.*

158 *chamaemorus* (63%), *V. vitis-idaea* (61%) and *V. uliginosum* (61%), all of which showed more than  
 159 10% in cover. Because all of these four species, except for *R. chamaemorus* (perennial herb), were  
 160 shrubs, the plant communities were categorized as tussock-shrub tundra.

161 There were significant differences in the total plant cover (Kruskal-Wallis test,  $\chi^2 = 20.098$ ,  $P =$   
 162  $0.003$ ), species richness ( $\chi^2 = 13.79$ ,  $P = 0.032$ ) and diversity ( $\chi^2 = 16.197$ ,  $P = 0.013$ ) among the  
 163 vegetation groups. Evenness did not show differences among the groups ( $\chi^2 = 11.700$ ,  $P = 0.069$ ).  
 164 The average total plant cover exceeded 100% in all the vegetation groups (Table 1). Plot cover was  
 165 20-40% higher in groups C and E than in group B (Steel-Dwass test,  $t > 2.82$ ,  $P < 0.05$ ). The  
 166 species richness in each plot ranged from 4 to 10, and it was higher in groups C and D than in group  
 167 G ( $t > 2.24$ ,  $P < 0.05$ ). The species diversity was higher in groups C than in groups E through G ( $t$   
 168  $> 2.79$ ,  $P < 0.05$ ). Thus, species richness and diversity tended to be higher in groups C and D, and  
 169 it was low in group G. The evenness did not differ among the seven groups ( $t < 2.19$ ,  $P > 0.05$ ).

170

### 171 **Environmental characteristics**

172 The ratio of plots measured in the burned sites increased from groups A to G (Table 2). None of the  
 173 plots in group A (*Vaccinium* type) received fire damage in the last fire, and they were therefore used  
 174 as a benchmark. Group A was characterized by high shrub covers, represented by *Vaccinium*  
 175 species, and *S. fuscum* establishment (Table 1). Groups B to D were established on both unburned  
 176 and burned sites (Table 2). Groups E to G were established only on burned sites and they were the  
 177 first to separate from the other groups on TWINSPAN (Fig. 2), demonstrating that groups E to G  
 178 possessed specific vegetation. The trace of charcoal still remained in the plots on the burned sites.  
 179 These three groups were characterized by the fire-favored species, *P. commune* and *C. canadensis*.  
 180 Therefore, the seven vegetation types varied along a fire-severity gradient.

181 On burned sites in groups D and E, *S. fuscum* survived vegetatively in a few plots possessing  
 182 ground subsidence and surface water flow (Table 1). The distance from subsidence was the longest  
 183 in groups A and B, which received the least fire (Table 2), demonstrating that thawing occurred least  
 184 on the unburned sites. Since the subsidence did not occur on the unburned sites, the distance from  
 185 subsidence was significantly different between the burned and unburned sites (Kruskal-Wallis test,  $\chi^2$   
 186  $= 63.175$ ,  $P < 0.001$ ; Steel-Dwass test,  $t > 3.319$ ,  $P < 0.05$ ). On the burned sites, however, the



187 vegetation patterns were not related to ground subsidence, i.e., the distance from ground subsidence  
 188 was not different among the cluster groups C to G. The thaw depth ranged from 23 cm to 61 cm  
 189 and did not differ among the vegetation groups or between the burned and unburned sites  
 190 (Kruskal-Wallis test,  $\chi^2 = 7.322$ ,  $P = 0.292$ ).

191 The litter amount was higher in groups E and G than in group B (Kruskal-Wallis test,  $\chi^2 =$   
 192 18.704,  $P = 0.005$ , Steel-Dwass test,  $t > 2.928$ ,  $P < 0.05$ ) (Table 2). Group B was distributed mostly  
 193 in unburned sites, and groups E and G were distributed among burned sites, demonstrating that the  
 194 litter amount tended to be the highest on burned sites. The litter was mostly composed of  
 195 tussock-forming monocotyledons (e.g., *C. canadensis*, *C. bigelowii* and *E. vaginatum*). The plots  
 196 where *C. canadensis* had high cover (i.e., in groups E and G; Table 1) possessed a great amount of  
 197 litter, indicating that litter accumulation was promoted by the dominance of this species in the area.

198 The ground-surface roughness was the highest in groups B and D, and it was the lowest in  
 199 groups A and G (Kruskal-Wallis test,  $\chi^2 = 21.279$ ,  $P = 0.001$ ; Steel-Dwass test,  $t > 2.63$ ,  $P < 0.05$ )  
 200 (Table 2). The high roughness was derived from induced thermokarsts, tussock development and/or  
 201 different burning of organic layer. The mean peat moisture ranged from 52 in group F to 77 in  
 202 group C, and it was higher in groups A and G than in group F (Kruskal-Wallis test,  $\chi^2 = 18.569$ ,  $P =$   
 203 0.005; Steel-Dwass test,  $t > 2.932$ ,  $P < 0.05$ ). Group A was located in an unburned site, and group  
 204 G was located in a burned site, implying that peat moisture was distributed heterogeneously at a  
 205 small scale, irrespective of fire.

206 The slope gradient ranged from 0° to 29°, and it did not differ among the vegetation types  
 207 (Kruskal-Wallis test,  $\chi^2 = 11.311$ ,  $P = 0.079$ ). The steep gradient was mostly derived from  
 208 thermokarsts. Aspect showed a wide range and did not differ among groups (Kruskal-Wallis test,  
 209  $\chi^2 = 5.080$ ,  $P = 0.534$ ). Because the slope gradient and aspect were mostly determined by  
 210 thermokarsts, these two topographical characteristics had little effect on the differentiation of  
 211 vegetation types.

212

### 213 **Relationships between plant community and topography**

214 Coefficients of determination on NMDS indicated that the distance from subsidence and litter  
 215 amount significantly explained the ordination patterns (test of random data permutations,  $r^2 > 0.071$ ,

216  $P < 0.01$ ) and peat moisture and ground-surface roughness ( $P < 0.05$ ). Thaw depth, slope and  
217 aspect were not significantly related to the first two axes ( $r^2 < 0.037$ ,  $P > 0.075$ ). The stress was  
218 0.258 and the non-metric fit was significant ( $r^2 = 0.934$ ).

219 The vegetation groups A to G were ordered from the highest to the lowest scores along the axis I  
220 of NMDS (Fig. 3). The scores of groups E to G, which were all burned plots, did not overlap the  
221 scores of groups A to D, and group G was separated clearly from groups E and F. This trend was  
222 supported by TWINSpan (Fig. 2) and the ratio of burned plots (Table 2). Because the unburned  
223 site did not develop thermokarsts, the distance from subsidence was a surrogate for the damages  
224 caused by the 2002 tundra fire. Therefore, the vegetation groups that were established along axis I  
225 represented a fire severity gradient.

226 Axis II was significantly related to peat moisture and surface roughness (Fig. 3). These two  
227 factors were significantly different among the cluster groups (Table 2). On axis II, group C showed  
228 lower scores than groups F and G. Group F tended to show higher scores than group G (Fig. 3).  
229 These results indicated that peat moisture and surface roughness differentiated the vegetation types  
230 within the burned site.

231 With respect to species scores on NMDS (Fig. 4), *C. purpureus* and *E. angustifolium*, *P.*  
232 *commune* and *C. canadensis* showed the lowest scores along axis I. *C. purpureus* and *E.*  
233 *angustifolium* established only on burned plots, and *P. commune* and *C. canadensis* established less  
234 often on unburned plots, indicating that these four species preferred to establish after the tundra fire.  
235 In addition, these species established mostly on the burned site, but species richness did not differ  
236 between groups A and B and groups E and F (Table 1), indicating that species replacement occurred  
237 in groups E and F after the tundra fire. *E. vaginatum* and *V. uliginosum* showed high scores along  
238 axis II, and *C. bigelowii* and *E. angustifolium* showed low scores. Because axis II reflected peat  
239 moisture and surface roughness, the former two species established more frequently on wet and/or  
240 rough-surface sites and the latter two were more prevalent on dry and/or smooth-surface sites.

241

## 242 Discussion

243

### 244 Effects of tundra fire on vegetation

245 Because shrubs, represented by *L. groenlandicum*, *V. vitis-idaea* and *V. uliginosum*, were dominant,  
246 the overall plant communities were categorized as tussock-shrub tundra (Viereck et al. 1992). The  
247 tundra fire affected the overall vegetation patterns. The revegetation patterns suggested that the  
248 2002 tundra fire burned the ground surface in a heterogeneous and patchy manner. The recovery of  
249 ecosystems occurs slowly after a severe disturbance, and more rapidly after a mild disturbance  
250 (Tsuyuzaki et al. 2013). The plant cover and albedo returned to the original status by the third  
251 plant-growing season after the 2007 Anaktuvuk River fire in tundra (Rocha and Shaver 2011). The  
252 net primary productivity returned to the pre-fire status but the biomass was still reduced four years  
253 after the 2007 fire (Bret-Harte et al. 2013).

254 Species richness and/or diversity were relatively high in moderately-burned plots (groups C and  
255 D). The species composition changed with the establishment of fire-favored species on burned  
256 plots. Intermediate disturbance hypothesis could explain that (Wilson and Tilman 2002).  
257 Although fire-favored plants, such as *E. angustifolium* and *C. purpureus*, establish soon after tundra  
258 fires (Racine et al. 2004), these fire-favored plants did not become dominant in Kougarak (Narita et  
259 al. 2015). These patterns showed that these fire-favored species persisted with low cover for a long  
260 time. Therefore, the effects of tundra fire long-lived.

261

### 262 **Effects of fire on plant life forms**

263 Lichens were less frequent on burned sites than on unburned sites, although the lichen cover was low  
264 even on unburned sites. The recovery of lichens takes longer than vascular plant recovery after  
265 wildfires (Jandt et al. 2008).

266 Shrubs except for *L. groenlandicum* showed lower cover on burned sites, particularly, in groups E  
267 to G. Since seedlings were few in the plots, vegetative reproduction had an important role on the  
268 persistence and revegetation. However, most shrubs did not increase their cover. In contrast,  
269 shrubs, including *L. groenlandicum* and *Vaccinium* species, recover quickly by vegetative  
270 reproduction (as sprouters) when they survive a fire on post-burned forest floor, which is dominated  
271 by *Sphagnum* mosses, in a *Picea mariana* forest (Tsuyuzaki et al. 2013). These recovery paces  
272 should be related to their climates, i.e., the climate is more stressful in tundra. In addition, the  
273 tundra fire in 2002 was more severe than usual and had prolonged effects on the vegetation, although

274 the effects were spatially heterogeneous. In Arctic tundra that does not experience disturbances  
275 (such as fires), global warming typically shifts the vascular plant biomass from  
276 monocotyledon-dominated tundra to shrub-dominated tundra (Walker et al. 2006; Shuur et al. 2007).  
277 The persistence of sprouters and the limited availability of soil nitrogen seem to promote the  
278 development of mixed shrub/sedge tussock tundra after severe fire along the Anaktuvuk River,  
279 Alaska, unless the permafrost thaws (Bret-Harte *et al.* 2013). The vegetation structures were still  
280 different between the burned and unburned sites even 11 years after the tundra fire. To understand  
281 the revegetation mechanisms, the behaviors of sprouters, e.g., *Vaccinium*, *Ledum* and *Calamagrostis*,  
282 should be mentioned more.

283

#### 284 **Microtopography derived by thermokarst**

285 Thermokarst was observed only on the burned area. The development of thermokarst after the fire  
286 is confirmed by the temporal changes in satellite imagery (Iwahana et al. 2016). However, the  
287 thermokarst development did not affect significantly the vegetation patterns in the study sites.  
288 These results showed that the fire primarily induced the ground subsidence. Various  
289 microenvironments are changed with the development of thermokarsts (Rocha and Shaver 2011;  
290 Kokelj and Jorgenson 2013). The post-fire ecosystem increased its thaw depth in non-polygonal  
291 areas for 11 years after the tundra fire in the Seward Peninsula, where a deep thaw depth was  
292 associated with the monocotyledon-rich areas and a shallow thaw depth was associated with  
293 shrub-rich areas (Narita et al. 2015). In contrast, no clear changes in thaw depth were observed  
294 within thermokarsts in the polygonal network. One cause should be that the subsidence occurred  
295 behind the tundra fire and therefore affected the vegetation patterns later than the fire. In addition,  
296 the species composition consisted mostly of perennial shrubs and herbs. The responses of these  
297 plants to the gradual environmental changes are often slow due to the vegetative habits (Cotto et al.  
298 2017). However, tall shrub thickets develop rapidly on retrogressive thaw slumps and following  
299 tundra fires in ice-rich tundra (Lantz et al. 2010, Jones et al. 2013). The responses of vegetation to  
300 tundra fire may be site-or region-specific.

301 The peat moisture did not differ greatly between the burned and unburned sites for 11 years after  
302 the tundra fire, while the peat moisture increased in the burned tussock site in the Seward Peninsula

303 soon after the 2002 fire (Liljedahl et al. 2007). These suggested that the peat moisture recovered  
304 rapidly in the burned sites. In addition, the peat moisture was related to the vegetation  
305 differentiation in the burned sites. Groups F (*Polytricum-Calamagrostis* type) and G  
306 (*Calamagrostis-Ceratodon*) experienced severe fire within burned sites showed high and low levels  
307 of peat moisture, respectively. The peat moisture was affected more by topographical  
308 characteristics, such as thermokarsts, than by fire-driven effects after a severe tundra fire, and such  
309 topographical characteristics differentiated groups F and G independent of the fire.

310 The ground surface roughness was higher in group D (*Eriophorum*) and lower in group G on the  
311 burned site, and it was higher in group B (*Ledum*) and lower in group A (*Vaccinium*) on the unburned  
312 site. The 2002 tundra fire in Kougarok left tussocks and increased surface roughness for a short  
313 period of time until 2006 (Liljedahl et al. 2007). *E. vaginatum* was widespread in both the burned  
314 and the unburned sites, and it formed tussocks well in Group D where the species richness was high.  
315 *E. vaginatum* increases the cover soon after a tundra fire by vegetative reproduction (Narita et al.  
316 2015). *E. vagiantum* seemed to survive through the fire and had facilitative effects in the tundra, as  
317 well as in the *Sphagnum* peatland. The tussocks formed by *E. vaginatum* provided litter that  
318 facilitated the establishment of cohabitants by ameliorating harsh environments of the *Sphagnum*  
319 peatland, except for instances of extreme weather (Koyama and Tsuyuzaki 2013).

320 Tundra fire reduced soil organic layer, including peat. The trace of charcoal still remained  
321 patchily on the ground surface. This reduction has both positive and negative roles on seedling  
322 emergence. For example, the reduction assists the seedling emergence of broad-leaved trees and  
323 disturbs that of black spruce after a wildfire in a boreal forest (Tsuyuzaki et al. 2014). Since there  
324 were few seedlings even on the unburned surface, the effects of organic layer on seedlings seemed to  
325 be weak for 11 years after the fire.

326

### 327 **Spatio-temporal vegetation patterns**

328 The tundra fire altered the vegetation and topography for a decade at various spatial scales. The  
329 vegetation patterns were explained by scale-dependent environmental factors (Tsuyuzaki et al. 2004;  
330 Turner et al. 2003). Fire firstly determined the vegetation structure at large scale and then  
331 differentiated the vegetation within the burned area through the manipulation of microenvironments.

332 Remote sensing combined with field monitoring will provide insights into the dynamics of Arctic  
333 landscapes, where plant cover varies over short distances due to microtopographic effects (Panda et  
334 al. 2010, Gamon et al. 2012). The present study provided evidence that diverse vegetation  
335 developed due to a tundra fire because the fire intensity was spatially heterogeneous, such that areas  
336 that were affected by severe and moderate fire developed different vegetation patterns.

337

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Table 1. Vegetation patterns classified by TWINSpan in 140 plots on burned and unburned sites, Seward Peninsula, Alaska. The species used as pseudo-species, shown in Fig. 2, are shown. Pseudo-species classified by TWINSpan are enclosed by frames. Diversity variables and plot cover are shown as the mean and standard deviation. Multiple comparisons in richness, diversity, evenness and cover were performed by the Steel-Dwass test when the ANOVA was significant at  $P < 0.05$ . The significance of ANOVA is indicated by asterisks on the names of parameters. \*\*: significant at  $P < 0.01$ . \*: significant at  $P < 0.05$ . NS: not significant. The different letters indicate that the medians are significantly different at  $P < 0.05$  using the Steel-Dwass test. Mean cover of each species is shown with frequency in parentheses. +: less than 1%. .: not observed.

Cluster group	A	B	C	D	E	F	G	Total
Number of plots	12	32	14	49	15	10	8	140
Species richness *	6.5 ± 1.4	6.9 ± 1.2	7.5 ± 1.5 a	7.0 ± 1.2 a	6.5 ± 0.9	6.2 ± 1.0	5.6 ± 1.4 b	6.7 ± 1.3
Species diversity *	1.47 ± 0.37	1.53 ± 0.21	1.64 ± 0.16 a	1.47 ± 0.25	1.45 ± 0.18 b	1.42 ± 0.11 b	1.19 ± 0.46 b	1.48 ± 1.28
Evenness <sup>NS</sup>	0.79 ± 0.17	0.80 ± 0.08	0.83 ± 0.05	0.76 ± 0.10	0.78 ± 0.09	0.79 ± 0.09	0.68 ± 0.22	0.77 ± 0.11
Species								
<i>Betula nana</i> L.	9 (75)	17 (91)	12 (57)	15 (63)	4 (33)	.	2 (25)	12 (60)
<i>Vaccinium vitis-idaea</i> L.	15 (92)	8 (94)	10 (86)	4 (49)	1 (20)	5 (40)	+ (12)	6 (61)
<i>Vaccinium uliginosum</i> L.	26 (100)	13 (59)	28 (79)	15 (65)	7 (27)	8 (50)	1 (38)	15 (61)
<i>Polytrichum commune</i> Hedw.	+ (8)	.	2 (43)	8 (55)	36 (100)	30 (100)	38 (88)	11 (47)
<i>Calamaglostis canadensis</i> (Michx.) Beauv.	.	+ (6)	4 (29)	3 (63)	38 (100)	27 (100)	44 (100)	10 (50)
<i>Carex bigelowii</i> Torr.	6 (67)	7 (78)	17 (100)	1 (12)	15 (73)	1 (10)	2 (12)	6 (47)
<i>Eriophorum vaginatum</i> L.	22 (75)	15 (97)	9 (93)	32 (98)	11 (80)	32 (90)	4 (38)	21 (89)
<i>Ceratodon purpureus</i> (Hedw.) Brid.	.	.	1 (14)	+ (2)	.	+ (10)	14 (100)	1 (9)
<i>Rubus chamaemorus</i> L.	1 (25)	8 (75)	17 (86)	6 (65)	3 (60)	1 (30)	2 (62)	6 (63)
<i>Ledum groenlandicum</i> Oeder	8 (67)	33 (97)	25 (86)	22 (88)	14 (67)	8 (80)	6 (38)	21 (82)
<i>Sphagnum fuscum</i> (Schimp.) Klinger	9 (58)	+ (3)	.	+ (6)	.	.	.	1 (8)
<i>Epilobium angustifolium</i> L.	.	.	.	+ (8)	5 (60)	+ (10)	.	1 (10)
<i>Cladonia</i> spp.	.	1 (31)	.	+ (2)	.	+ (10)	.	+ (9)
Total plant cover (%) **	110 ± 21	103 ± 18 a	128 ± 28 b	115 ± 25	139 ± 33 b	119 ± 11	115 ± 29	116 ± 26

Other species recorded from the plots: *Hylocomium splendens* (Hedw.) Schimp., *Poaceae* sp., *Sphagnum* spp., *Polytrichum formosum* Hedw., *Empetrum*

*nigrum* L. ssp. *hermaphroditum* (Lange ex Hagerup) Bocher, Bryophytes spp. (three species), *Marchantia polymorpha* L., *Umbilicaria* sp., *Peltigera leucophlebia* (Nyl.) Gyelnik, *Betula nana* L., *Calamagrostis canadensis* (Michx.) Beauv., *Polemonium acutiflorum* Willd., *Petasites frigidus* (L.) Franch., *Salix lanata* L., *Salix pulchra* Cham., *Salix* sp., *Cetraria* spp.

Table 2. The characteristics of environmental factors examined in seven vegetation types, A to G, classified by TWINSpan on burned and unburned sites in Seward Peninsula, Alaska. Each numeral indicates the mean and standard deviation. Multiple comparisons were conducted by the Steel-Dwass test when the Kruskal-Wallis ANOVA was significant. The significance of ANOVA is indicated by asterisks on the names of parameters. \*\*: significant at  $P < 0.01$ . NS: non-significant. The different letters indicate that the medians are significantly different at  $P < 0.05$  using the Steel-Dwass test. Number of plots, see Table 1.

Cluster group	A	B	C	D	E	F	G	Total
Burned plots (%)	0.0	15.6	85.7	98.0	100.0	100.0	100.0	70.0
Distance from subsidence (m) **	14.9 ± 0.7 a	12.4 ± 5.1 a	2.7 ± 5.7 b	3.3 ± 4.0 b	1.7 ± 1.0 b	2.9 ± 2.1 b	3.0 ± 1.8 b	6.1 ± 6.1
Litter amount **	0.73 ± 0.51	0.50 ± 0.38 a	0.69 ± 0.38	0.67 ± 0.56	1.01 ± 0.50 b	0.85 ± 0.47	1.20 ± 0.72 b	0.72 ± 0.52
Thaw depth (cm) <sup>NS</sup>	38.8 ± 8.8	38.2 ± 7.7	34.7 ± 7.7	37.0 ± 5.4	36.1 ± 3.7	37.8 ± 2.8	39.1 ± 3.6	37.3 ± 6.3
Ground surface roughness **	6.1 ± 2.4 a	8.8 ± 2.2 b	8.6 ± 3.0	8.7 ± 3.3 b	7.3 ± 3.1	7.2 ± 3.2	5.0 ± 1.4 a	8.0 ± 3.0
Peat moisture (%) **	72 ± 17 a	60 ± 14	77 ± 21	68 ± 18	62 ± 8	69 ± 9 a	52 ± 9 b	66 ± 17
Slope gradient (°) <sup>NS</sup>	8.3 ± 4.2	11.2 ± 5.7	10.2 ± 5.9	9.9 ± 6.8	8.2 ± 6.4	9.5 ± 6.5	4.2 ± 2.1	9.6 ± 6.1
Aspect (°) <sup>NS</sup>	18 ± 44	16 ± 57	0 ± 58	22 ± 55	41 ± 50	32 ± 55	19 ± 73	21 ± 55

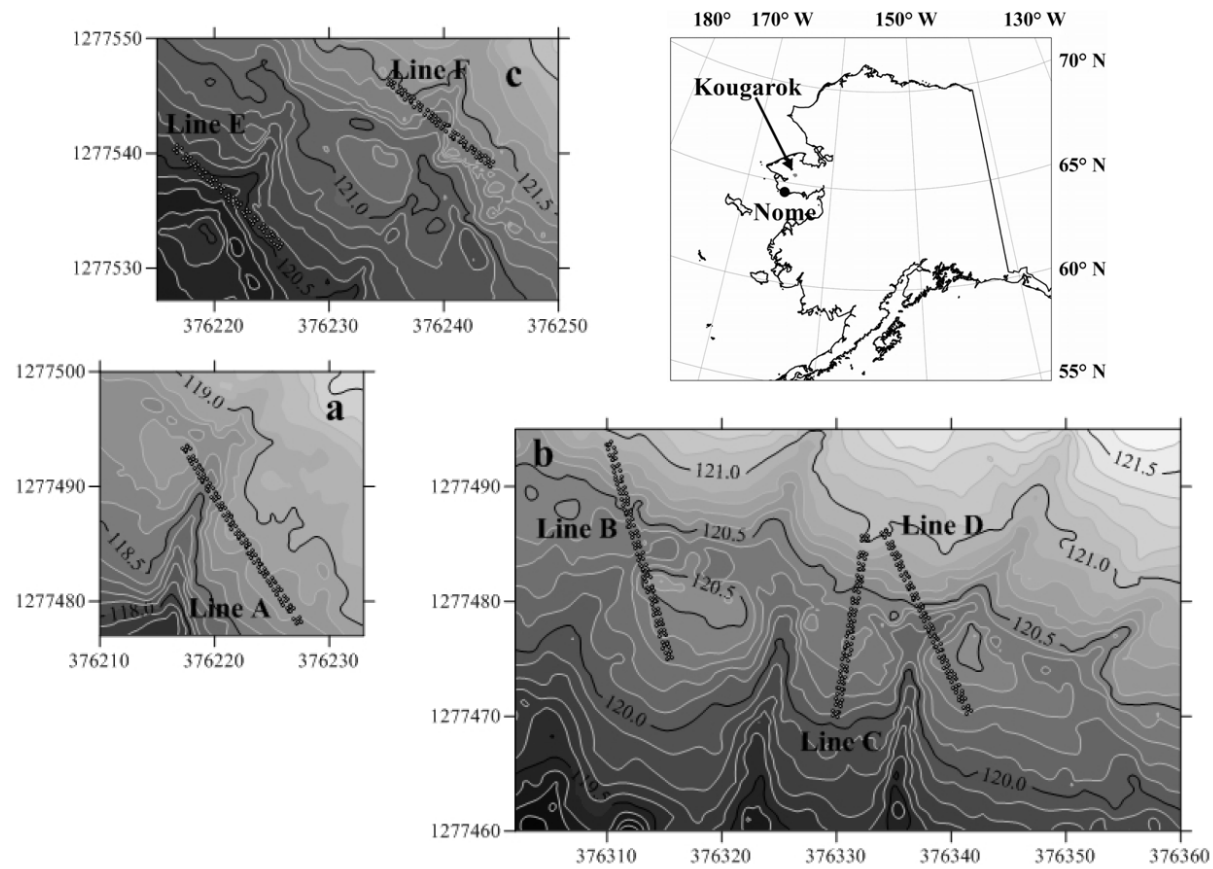


Fig. 1. Topological maps (a-c) shown with the locations of transects A-F, determined by differential GPS survey. Major contour lines are 0.5 m intervals. The coordinate system is given in meters. The right-top map indicates the location of study area (Kougarak) in Alaska.

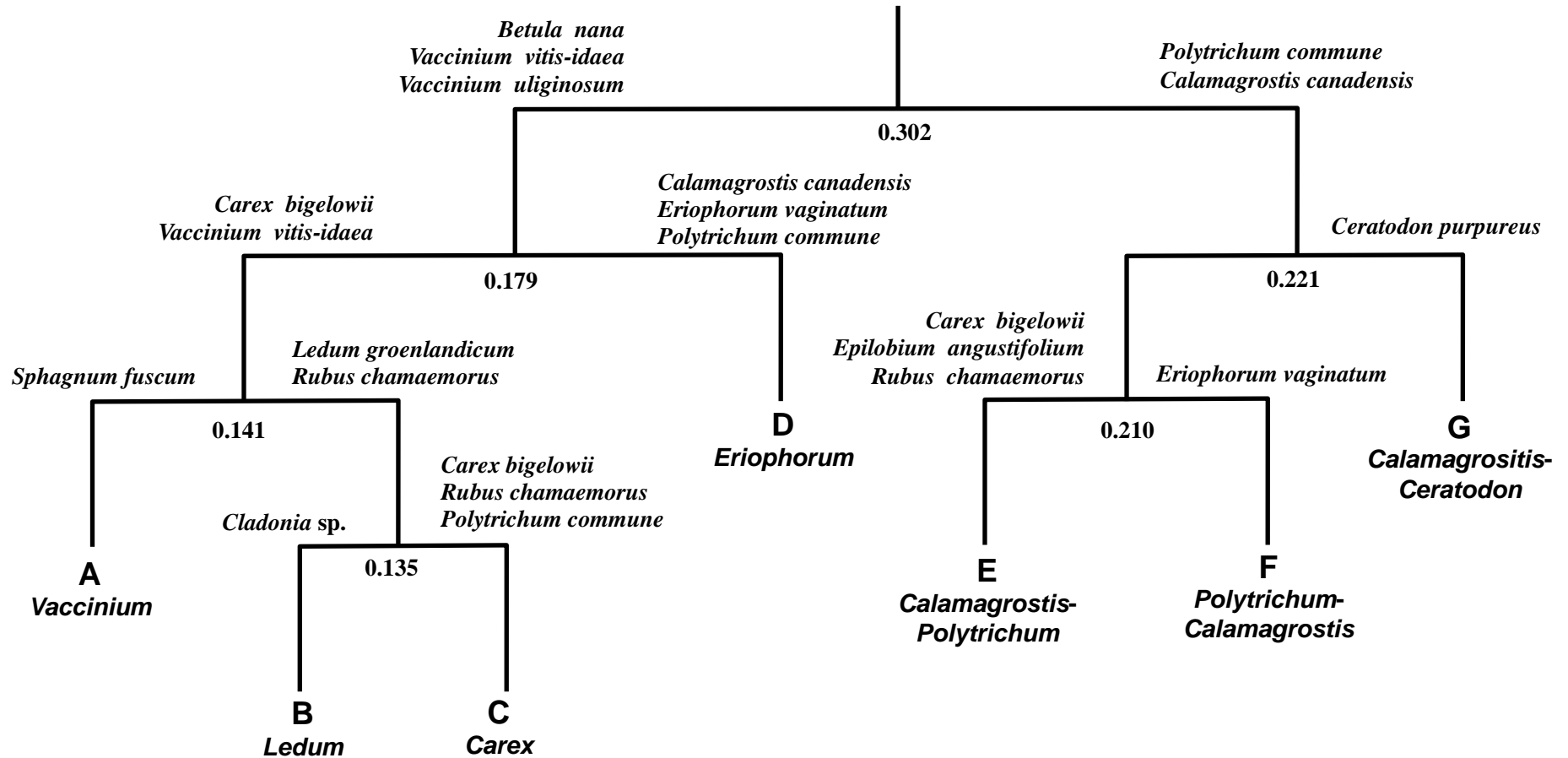


Fig. 2. Vegetation development patterns examined by TWINSpan using 140 plots in burned and unburned sites, Seward Peninsula, Alaska. Each number indicates an eigenvalue at the division point. The group names, shown below codes A-G, are labelled by the genera of frequently-occurring species. The indicator species that were used for the divisions are shown on the left and right sides of the cluster branches. Refer to Table 1.

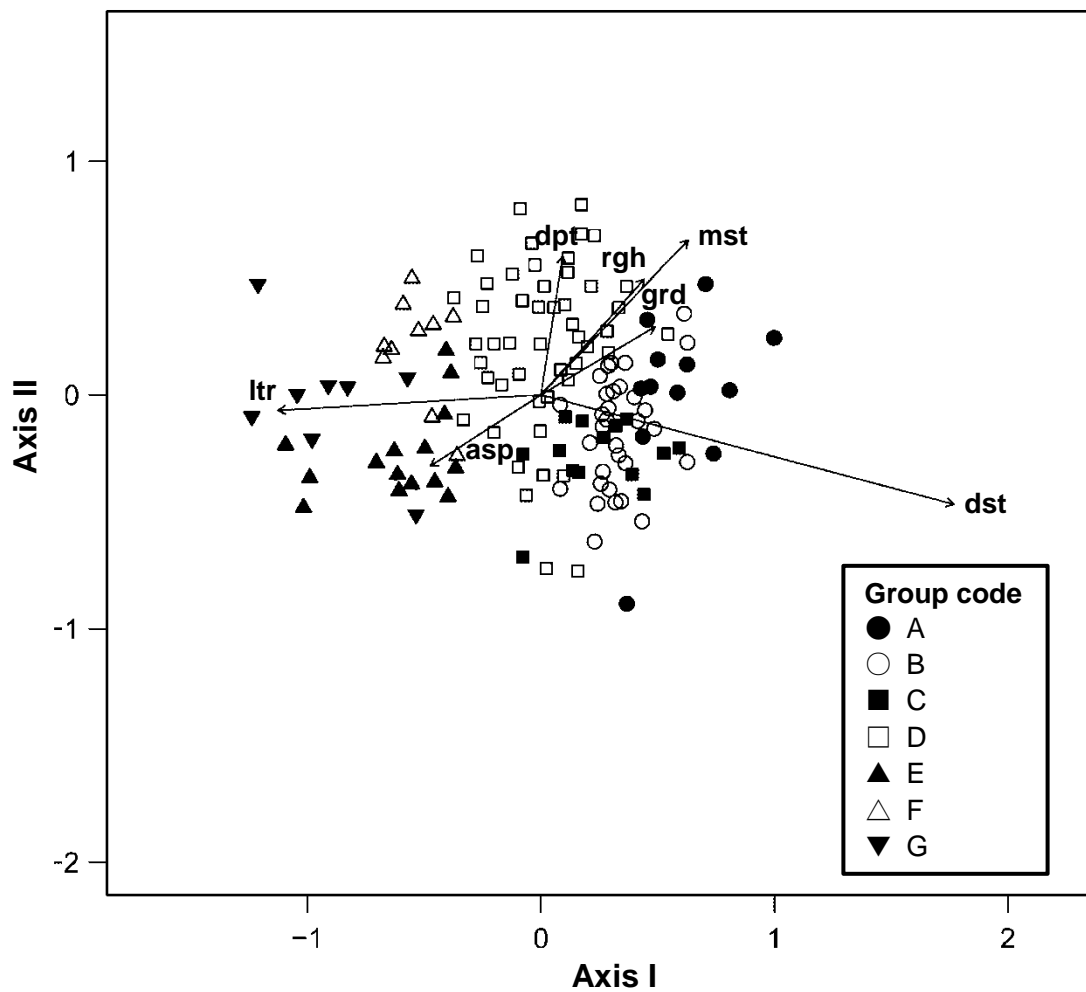


Fig. 3. NMDS ordination diagram on plot scores in 140 50 cm  $\times$  50 cm plots surveyed in Seward Peninsula after the 2002 tundra fire. Environmental factors: dst = distance from subsidence, mst = peat moisture, grd = slope gradient, rgh = surface roughness, dpt = thaw depth, ltr = litter amount. See also, Table 1.

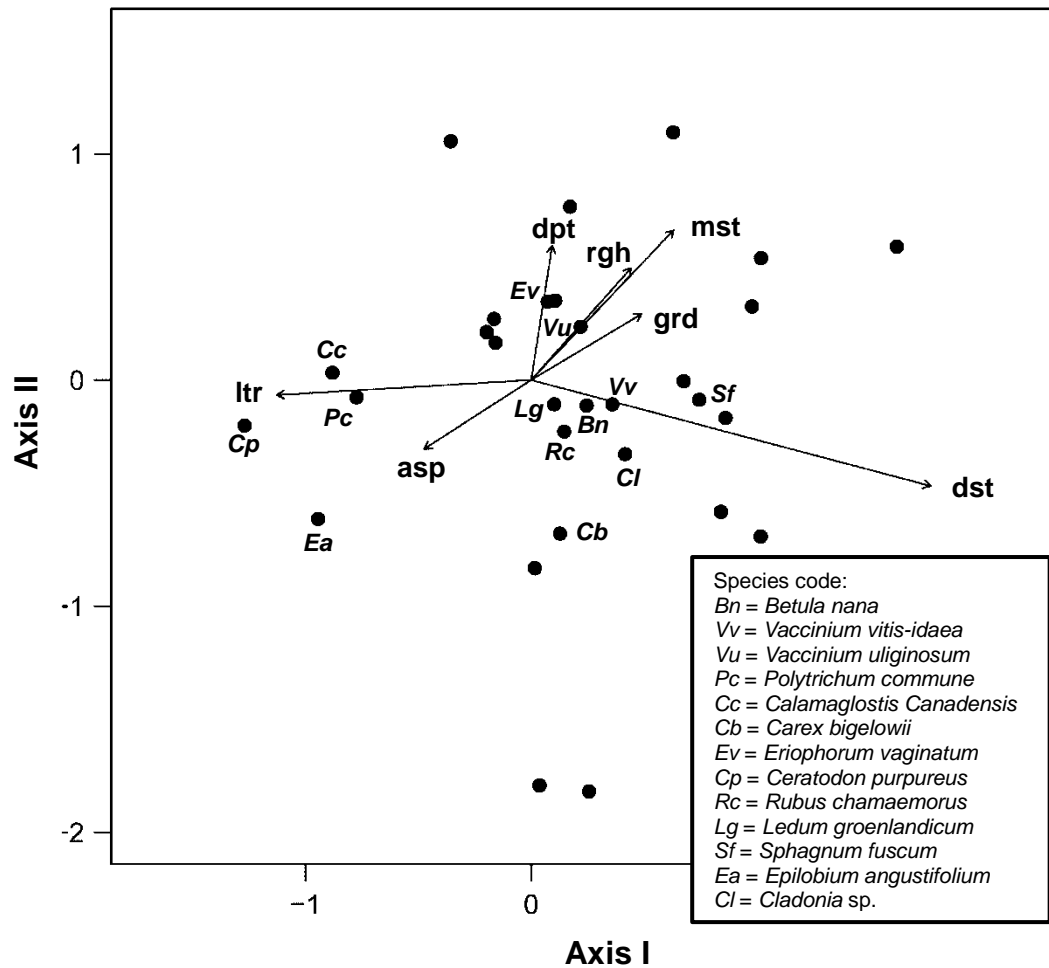


Fig. 4. NMDS ordination diagram on species scores in 140 50 cm × 50 cm plots surveyed in Seward Peninsula after the 2002 tundra fire. The codes of environmental factors, see the same as in Fig. 3.