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Instructions for use

1 **Habitat-specific responses of shoot growth and distribution of alpine dwarf-pine (*Pinus***

2 ***pumila*) to climate variation**

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17 **Abstract**

18 Alpine dwarf-pine (*Pinus pumila*) in dominant in the alpine regions of Japan, and often forms

19 the krummholz zone of stunted alpine forest. The distribution of *P. pumila* is strongly related

20 to the distribution of snow, and shoot growth is also sensitive to weather conditions. Changes

21 in temperature and snowmelt regimes may well affect the distribution patterns of the

22 krummholz zone. *P. pumila* usually occupies the habitat between the fellfield and snowbed

23 communities, and responses to climate change may differ depending on whether plants are

24 close to the fellfield or the snowbed. We compared the distribution and shoot growth patterns

25 of *P. pumila* close to both surrounding ecosystems in the Taisetsu Mountains, northern Japan.

26 *P. pumila* has expanded its distribution area by 14 % toward both edges over the last 32 years.

27 Annual shoot growth was positively affected by summer temperature and sunshine duration,

28 but negatively related to spring temperature toward the fellfield side. Shoot growth was

29 greater at the southeastern edge of patches, where snowdrifts were formed. The results

30 indicated that shoot growth and distribution area increased in warm summers. However, warm

31 springs might have a negative influence on shoot growth, probably because the earlier

32 reduction in cold-resistance enhances the risk of frost damage in spring close to the fellfield

33 side. This study suggests the importance of understanding the site-specific responses of

34 shrubs to predict the impacts of climate change on alpine ecosystems.

35

36 **Keywords** Alpine, climate warming, *Pinus pumila*, shoot growth, GIS

37

Introduction

Rapid vegetation changes with global warming are thought to cause the extinction of many species, especially in the arctic and high mountain regions (Grabherr et al. 1994; IPCC 2007). Increases in shrub biomass, cover, and abundance have been observed in multiple arctic, high-latitude and alpine tundra ecosystems over the past century (Myers-Smith et al. 2011). Upward shifts of tree lines are reported in several montane and sub-alpine regions (Kullman 2002; Wang et al. 2006; Danby and Hik 2007; Peñuelas et al. 2007). The invasion and expansion of woody plants with large biomass and tall canopy structures may have serious impacts on tundra and alpine vegetation (Wilson and Nilsson 2009; Pajunen et al. 2011), because most tundra plants are sensitive to shading stress (Chapin et al. 1995). Furthermore, the reduction in abiotic stress because of global warming may change the biological interactions among plant species from facilitative to competitive relationships (Choler et al. 2001). This may cause a decrease in species diversity through intensive interspecific competition. Therefore, the dynamics of shoot growth and the canopy expansion of shrubs are important issues in assessing global change impacts on alpine ecosystems.

The zonal distribution of *Pinus pumila* (Pallas) Regel, an alpine dwarf-pine, is a characteristic physiognomy of alpine vegetation in Japan (Tatewaki 1958). Biomass accumulation of *P. pumila* at the krummholz zone (Tranquillini 1979) is extremely large in alpine ecosystems (Kajimoto 1989), and its productivity is estimated as being 10 times larger than other alpine plant communities (Okitsu 1985). Therefore, changes in the growth and distribution of *P. pumila* may cause serious impacts to the structure and diversity of alpine ecosystems. Previous studies have reported that the net photosynthetic rates of current needles were high in temperatures of 10–15 °C (Kajimoto 1990), and that the current shoot elongation was positively related to the previous summer temperature (Sano et al. 1977; Takahashi 2003;

63 Wada et al. 2005). Annual shoot elongation has tended to increase in the mountain regions of

64 the main island of Japan, probably in response to recent climate warming (Wada et al. 2005;

65 Ozeki et al. 2011). In contrast to the field reports, a vegetation dynamics model based on

66 climate change scenarios predicts that the potential distribution area of *P. pumila* will

67 decrease to 14.7–25.0 % of the current suitable area and that *P. pumila* will disappear from

68 many mountain regions in Japan, except for the high mountains in central Japan and

69 Hokkaido (Horikawa et al. 2009). Therefore, it is crucial to understand the relationship

70 between the shoot growth and distribution responses to climatic variation   to appreciate the

71 dynamics of *P. pumila* in alpine ecosystems.

72   Typical alpine vegetation in Japan is classified into fellfield plant communities, snowbed

73 plant communities, and *P. pumila*-dominated communities (Koizumi 1974). In fellfield

74 habitat, the soil surface is exposed throughout the year due to strong winds, and the soil is

75 frozen in the winter and dry in the summer. Thus, plants inhabiting fellfield habitat are

76 required to have high cold and drought tolerance. In the snowbed habitat however, a large

77 accumulation of snow protects plants from freezing temperatures during winter, and snowmelt

78 water maintains moist soil conditions in the summer. However, the length of the growing

79 period is strongly limited due to late snowmelt (Körner 2003). *P. pumila* inhabits the

80 intermediate habitat between the fellfield and snowbed, especially on gentle rocky slopes with

81 moderate snow depth in winter (30–300 cm deep, Okitsu and Ito 1984). The density and plant

82 height of *P. pumila* declines with increasing wind exposure and its growth form changes from

83 zonal to patchy toward the fellfield habitat. Density and plant height tended to be remain

84 stable toward the snowbed but the plant abruptly disappears in typical snowbed habitat

85 probably due to photosynthetic periods that are too short (Okitsu and Ito 1984). Therefore,

86 factors affecting *P. pumila* growth may differ between the fellfield side and snowbed side of

87 the *P. pumila* zone.

88   The distribution and phenology of alpine plants are strongly affected by snow conditions

89   (Billings and Bliss 1959; Kudo and Ito 1992; Choler 2005; Kudo and Hirao 2006). The effects

90   of global warming on alpine ecosystems include not only increases in plant growth but also an

91   increased risk of frost damage early in the season (Inouye 2008; Wheeler et al. 2014). So far,

92   there has been little attention paid to the significance of frost damage in Japanese mountains,

93   but it needs to be taken into account in the growth and survival of *P. pumila* (Maruta et al.

94   1996; Ishida et al. 2001; Nakamoto et al. 2012). Frost damage tends to occur more frequently

95   in the fellfield habitat, so climate change may result in different impacts on alpine vegetation

96   depending on their proximity to fellfield and snowbed communities (e.g. Kudo et al. 2010).

97   The aim of this study is to clarify the growth responses and distribution changes in *P.*

98   *pumila* during the last 20–30 years in relation to the fellfield and snowbed edges of the *P.*

99   *pumila* zone, with reference to climate variations. Our specific questions are as follows:

100   1) How has the extent of the distribution area of *P. pumila* been changed in recent years?

101   2) Are environmental factors affecting shoot growth differently depending on proximity to

102   the fellfield or the snowbed edge of the *P. pumila* zone?

103   3) Is there any trend in the direction of the distribution shift? If so, does it reflect the shoot

104   growth pattern between the fellfield side and snowbed side?

105

106   **Materials and Methods**

107

108   Study site

109

110   This study was conducted in the Taisetsu Mountains (Daisetsuzan National Park) in the

111   central part of Hokkaido, northern Japan (Fig.1). We selected two habitats as research sites,

112   one on the fellfield side and one on the snowbed side of the *P. pumila* zone. The fellfield

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113 tends to not retain snow cover during the winter due to strong winds, whereas the snowbed is

114 covered with thick snow until the middle of summer. The fellfield side habitat (hereafter the

115 HF site) is located on a plateau of 1670–1690 m in elevation close to Lake Hisago, 2 km

116 south of Mt. Kaun-dake (N 43°32′, E 142°52′). The snowbed side habitat (hereafter the GS

117 site) is located on a gentle east-facing slope of 1700–1850 m in elevation in the

118 Goshikigahara (N 43°33′, E 142°54′; Fig. 1).

119   The HF site has typical fellfield vegetation composed of dwarf shrubs (*Arctous alpinus*

120 (L.) Niedenzu var. japonicus (Nakai) Ohwi, *Loiseleuria procumbens* (L.) Desv., *Diapensia*

121 *lapponica* (L.) var. *obovata* Fr. Schm. and *Vaccinium uliginosum* (L.)), and lichens (*Cladonia*

122 spp.). In the GS site, snow-meadow vegetation was commonly composed of herbaceous

123 species, such as *Anemone narcissiflora* (L.) var. *sachalinensis* Miyabe et Miyake, *Trollius*

124 *riederianus* Fisch. Et Mey., and *Saussurea riederi* Herder var. yezoensis Maxim. Over recent

125 years, the time of snow melt has become earlier (Kudo and Hirao 2006) and populations of

126 typical snow-meadow species have decreased rapidly since the 1990s in this area, while dwarf

127 bamboos (*Sasa kurilensis* (Rupr.) Makino et Shibata) have increased their distribution area

128 (Kudo et al. 2011). In both sites, *P. pumila* commonly grows as isolated patches of various

129 sizes. The nomenclature follows Ohwi and Kitagawa (1983).

130   The annual mean air temperature of the HF site was −2.0 °C. Mean temperatures during

131 the summer season were 2.9 °C in May, 8.5 °C in June, 11.6 °C in July, 12.5 °C in August,

132 and 7.8 °C in September (mean values from 2002–2010; Kudo et al. 2011).

133

134 GIS analysis

135

136   Using aerial photographs provided by the Geospatial Information Authority of Japan (on

137 25 Sept 1977) and Photec Co. Ltd., Sapporo, Japan (on 3 Sept 2009), changes in the

138 distribution of *P. pumila* in the HF and GS sites were quantified. Vegetation on these

139 photographs was digitized after orthogonal projection transformation at a ground resolution of

140 25 cm. For orthogonal projection, we selected large rocks located within the area and used

141 them as ground control points. Clear color photographs taken in September enabled us to

142 discriminate *P. pumila* from other vegetation. All works were conducted using the GIS

143 software ArcMap10.0 (ESRI Inc., Redlands, CA, USA) using the Plane Rectangular XII

144 projection system of the Japanese Geodetic Datum 2000.

145   The distribution of *P. pumila* was observed within a 25-ha area in the HF site (Fig. 2). *P.*

146 *pumila* canopies were easily discernible in this site and they were extracted as polygons using

147 non-hierarchical clustering with an ISODATA clustering algorithm,which automatically

148 groups pixels based on the reflectance level of each wavelength (Japan Association on

149 Remote Sensing 2001). Each photograph was classified into 20 groups, and the group

150 categorized as a specific color type was taken to represent *P. pumila*. According to our

151 preliminary analysis for testing the accuracy of the vegetation classification, the Kappa

152 coefficient was 0.96 and 0.82 in 1977 and 2009, respectively. The distribution of *P. pumila* in

153 the GS site was observed within a 50 ha (500 × 1000 m) area (Fig. 2). The canopies of other

154 shrubs and dwarf bamboos were sometimes difficult to distinguish from *P. pumila* canopies

155 using non-hierarchical clustering. Therefore, *P. pumila* canopies were extracted as polygons

156 from each photograph by visual observation in which the difference in vegetation height

157 (using a stereoscope), canopy architecture, and leaf color were evaluated. The area of *P.*

158 *pumila* was calculated. Extracted polygons were verified by field observations to ensure the

159 accuracy of classifications based on the 2009 photographs. The difference in observation area

160 between the HF (25 ha) and GS (50 ha) sites reflected the topographic features of fellfield and

161 snowbed habitats in this region.

162

163   Measurements in the field

164

165   The stems and branches of *P. pumila* retain the annual scars of dormant buds over the last

166   20 years on average. Thus, annual shoot elongation can be obtained by measuring the

167   internodal length between bud-scar marks (Sano 1977, Okitsu 1988, Takahashi 2003). Taking

168   advantage of this characteristic, annual shoot growth over the last 20 years was measured

169   using a digital caliper at the accuracy of 0.1 mm. We randomly selected 24 patches within the

170   25 ha area in the HF site, and 20 patches within the 50-ha area in the GS site. In each patch,

171   we selected four trunks without physical damage and measured branches facing north, south,

172   east, and west.

173   Measurements in the GS site were conducted in July 2011 and annual shoot elongation

174   was recorded from 1991 to 2010 because the current shoot growth (in 2011) had not been

175   completed yet. Measurement in the HF site was conducted in September 2012 and shoot

176   elongation from 1993 to 2012 was recorded.

177

178   Shoot growth analysis

179

180   First, the temporal sequences in annual shoot growth in each habitat over the last 20 years

181   were examined using linear regression, following the standardization of annual shoot

182   elongations within stems (Fig. 3 a). Then, factors affecting shoot elongation were analyzed

183   using generalized linear mixed-effect models (GLMMs) without data standardization.

184   In the first model, environmental and internal factors related to shoot growth were tested in

185   each habitat. Environmental factors in the GLMM included: (1) summer temperature (mean

186   air temperature from June to August) of the current and previous years; (2) sunshine duration

187   during the summer season of the current and previous years; (3) snowmelt time of the current

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188   year; (4) spring temperature (mean air temperature during April and May) of the current year;

189   and (5) distance from the closest *P. pumila* zone to the specific patches. Shoot growth of *P.*

190   *pumila* may indicate size-dependency (Takahashi and Yoshida 2009). A previous study

191   reported that the relationship between tree-ring width and shoot elongation of *P. pumila*

192   varied among trees depending on the competitive situation (Yasuda and Okitsu 2012). To

193   eliminate these endogenous factors, therefore, we included (6) patch size; and (7) the length

194   of the stem over the last 20 years (hereafter stem size) as explanatory factors in the GLMM.

195   Patch size, expressed as the canopy projection area, represented total plant size, while stem

196   size represented the ontogenetic and/or growth situation of individual stems. In the GLMM,

197   assigned the number to each patch which we investigated (hereafter patch ID) was included as

198   a random factor, and a Gamma error distribution was assumed with log-link function. To

199   detect the site-specific factors affecting shoot growth in each habitat, the GLMM was

200   performed for each habitat, and factors were selected in each model based on the Akaike

201   information criterion (AIC) in which we adopted the set of factors with the lowest AIC values.

202   There is no long-term meteorological data in the Taisetsu Mountains, so we estimated the

203   previous climatic conditions using the data observed in Nukabira Town (N 43°22.0′, E

204   143°11.5′, 540 m elevation; Japan Meteorological Agency 2012) which was the nearest

205   weather station to the HF and GS sites. A comparison of the available temperature records

206   between the HF site and Nukabira Gensenkyo revealed that the temperature lapse rate was −

207   0.5 °C/100 m elevation. Previous temperatures in the HF and GS sites were calculated using

208   this value. The snowmelt day has been recorded since 1988 at a site with similar snow

209   conditions to the GS site, located approximately 3 km away from Goshikigahara (G. Kudo,

210   unpublished data). We used this record for the analysis of the GS site. Snowmelt time was not

211   included in the GLMM for the HF site because the fellfield-side habitat received only a small

212   amount of snow accumulation during the winter because of exposure to strong winds.

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213   In the second model, we compared the sensitivity of shoot growth to the direction within

214   patches between the HF and GS sites. Direction influences the microenvironment for shoots,

215   such as solar radiation and snow condition, and it may determine the direction of patch

216   expansion. Analysis was performed using a GLMM with a postulated Gamma error

217   distribution with log-link function, in which site (HF, GS) and direction within a patch (N, S,

218   W, E) were set as fixed factors, and patch ID as a random factor. We used the R statistical

219   software version 2.15.2 (R Core Team 2012) for all data analyses. The GLMMs were

220   performed using the function glmer included in the R package lme4 (Bates et al. 2013).

221

222   **Results**

223

224   Changes in distribution over the past 32 years

225

226   Projection images of *P. pumila* canopies in 1997 and 2009 are shown in Figure 2. In the HF

227   site (25 ha), the area occupied by *P. pumila* was 13.1 ha (52 %) in 1977, and 15.0 ha (60 %)

228   in 2009. In the GS site (50 ha), the area occupied by *P. pumila* was 8.8 ha (18 %) in 1977, and

229   10.1 ha (20 %) in 2009. These results indicate that *P. pumila* has increased its distribution by

230   almost the same proportion (14 %) toward the fellfield side and snowbed side over the last 32

231   years (Table 1).

232

233   Comparisons of shoot growth between the fellfield side and snowbed side

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235   Annual mean shoot elongation was 41.1 ± 5.9 (SD) mm (ranging from 29.8 to 50.9 mm) in

236   the HF site and 52.2 ± 4.0 mm (ranging from 47.1 to 58.9 mm) in the GS site. Patch size was

237   16.4 ± 3.3 (SE) m^2 (ranging from 2.9 to 70.7 m^2) in the HF site and 235.6 ± 86.4 m^2 (ranging

238 from 6.0 to 1400.0 m^2) in the GS site. Simple linear regressions based on the standardized

239 shoot elongation in each site revealed that annual shoot growth tended to increase from year

240 to year in both the HF ($r = 0.54$, $P = 0.013$ by Pearson's correlation test) and GS sites ($r =$

241 0.46, $P = 0.041$; Fig. 3 a). Annual shoot growth had increased on average by 11 mm in the HF

242 site and 6 mm in the GS site over the last 20 years.

243   The results of the GLMMs with the smallest AIC are described in Table 2. In the HF site,

244 stem size, previous summer temperature and sunshine duration were positively related to

245 shoot growth, whereas spring temperature of the current year was negatively related (Table 2

246 a). In the GS site, stem size, previous summer temperature and sunshine duration were

247 positively related to shoot growth (Table 2 b). In both sites, distance from the *P. pumila* zone

248 and patch size were excluded by AIC. These results indicated that (1) warm and sunny

249 summers enhanced the shoot growth in the following season at both sites, and (2) warm

250 spring temperatures negatively affected plants only at the fellfield side.

251   The responses of shoot growth to direction within patches were apparent in both sites (Fig.

252 3 b, c, Table 3 and Table 4). Annual shoot elongations (mean ± SD) were 38.8 ± 5.7 mm

253 (north), 52.7 ± 8.3 mm (east), 44.2 ± 8.5 mm (south) and 29.3 ± 3.5 mm (west) in the HF site,

254 and 50.5 ± 4.0 mm (north), 55.0 ± 5.4 mm (east), 54.0 ± 6.5 mm (south) and 49.3 ± 4.7 mm

255 (west) in the GS site. The annual shoot growth tended to increase at the east edges ($r = 0.72$, P

256 < 0.001 in the HF site; $r = 0.58$, $P = 0.008$ in the GS site by Pearson's correlation test) and

257 south edges ($r = 0.57$, $P = 0.009$ in the HF site; $r = 0.48$, $P = 0.032$ in the GS site) and to

258 decrease at north edges ($r = 0.17$, $P = 0.483$ in the HF site; $r = -0.17$, $P = 0.476$ in the GS

259 site) and west edges ($r = 0.14$, $P = 0.546$ in the HF site; $r = 0.11$, $P = 0.648$ in the GS site) in

260 both sites. Shoot growth was larger in the eastern and southern sides of patches. Shoot growth

261 in the GS site was larger than in the HF site, and significant site–direction interactions were

262 detected.

263

Discussion

265

266 The present study revealed that *P. pumila* in the Taisetsu Mountains has increased its

267 distribution area toward both the fellfield and snowbed edges in the same proportion (14 %)

268 over the last three decades. Our previous study (Kudo et al. 2011) reported that dwarf-bamboo

269 (*Sasa kurilensis*), an evergreen shrubby bamboo forming dense clonal patches, had increased

270 its distribution area by 26 % (1.4 ha) during the same time period in the GS site. Therefore,

271 about 33 % of this area is occupied by *P. pumila* (20 %) and dwarf bamboo (13 %), and the

272 shrubby area has increased by 5 %, corresponding to a 2.6 ha decrease in snow-meadow

273 vegetation. The invasion of dwarf bamboo was prominent in places with low soil moisture

274 (Hoshino et al. 2009; Kudo et al. 2011). The invasion of *P. pumila* and dwarf bamboo toward

275 late-snowmelt habitat was reported also in the alpine moors of central Japan (Yasuda and

276 Okitsu 2001). They speculated that the ongoing soil aridification might be a driving force of

277 the vegetation change on alpine moors. Expansion of shrubs in tundra ecosystems is a

278 worldwide vegetation pattern owing to the extension of the snow-free period and the increase

279 in temperature resulting from climate change (Sturm et al. 2001, 2005; Dullinger et al. 2003;

280 Tape et al. 2006). In Japanese mountain regions, dwarf bamboo and *P. pumila* are thought to

281 be key species causing rapid vegetation change under warming climate, because they can

282 expand their canopies by vigorous vegetation growth of shoots.

283 In accordance with the increase in distribution, shoot growth of *P. pumila* has been

284 accelerated at both habitat edges. The GLMM analysis indicated that the temperature and

285 sunshine duration of the previous summer were positively related to the annual growth at both

286 sides. Several studies have reported the positive effects of temperature and/or sunshine

287 duration of previous summer on current shoot growth of *P. pumila* (Sano et al. 1977;

11

288 Takahashi 2003, 2006; Wada et al. 2005; Yasuda and Okitsu 2007; Ozeki et al. 2011). It

289 indicates that the resources stored in needles and stems during the last growing period may be

290 used for shoot growth in the current season. Shoot growth of *P. pumila* commonly starts in

291 early June and terminates in late July (Kajimoto 1993). Photosynthetic activity of *P. pumila* is

292 generally low in the early season (May and June), then it increases to its maximum level in

293 August (Kajimoto 1990; Ishida et al. 2001). Kibe and Masuzawa (1992) demonstrated that

294 photosynthetic carbohydrate fixed during the summer was transformed into sugar in the late

295 growing period, and reserved in branches and needles during the winter. Therefore, old

296 needles and branches of *P. pumila* act as storage organs, and shoot growth from June to July

297 may strongly depend on stored resources.

298   Spring temperatures negatively affected shoot growth at the fellfield side (HF site). The

299 freezing resistance of dwarf shrubs rapidly decreases under the exposure to warm conditions

300 (Sakai and Larcher 1987). The early phenological responses to the increase in daytime

301 temperature may also enhance the risk of exposure to freezing temperatures at night

302 (Bokhorst et al 2008, 2011; Inouye 2008). The increase in spring temperatures then enhances

303 the risk of frost damage in the fellfield-side habitat. Needle damage of *P. pumila* was reported

304 in warm and/or early-snowmelt springs on Mt. Tateyama (Maruta et al. 1996) and Mt.

305 Norikura (Nakamoto et al. 2012) in central Japan. A negative effect of spring temperatures at

306 the fellfield side might be related to physiological damage through freezing temperature in

307 warm springs. Indeed, we confirmed that one third of days during April and May showed

308 above-zero degree temperatures for daily minimums and the remaining two thirds of days had

309 freezing temperatures. However, spring temperature was excluded by AIC at the snowbed

310 side (GS site). In these sites, *P. pumila* is completely protected by snow cover during April

311 and May when frost damage may happen, so the effect of spring temperatures is negligible in

312 the GS site.

313 The harsh climate conditions in the fellfield-side habitat and the restricted growing period

314 in the snowbed-side habitat are major limiting factors to the establishment of the *P. pumila*

315 zone (Okitsu and Ito 1984). Shoot growth generally decreases at wind-exposed places with

316 little snow cover (Okitsu and Ito 1984). Large patches can trap more snow resulting in more

317 protection from the harsh winter climate (Essery and Pomeroy 2004), so significant effects of

318 distance from *P. pumila* zone and patch size were expected at the fellfield side. In contrast,

319 early snowmelt may be beneficial for growth in the snowbed-side habitat. Thus, significant

320 effects of snowmelt time and distance from the *P. pumila* zone were expected at the snowbed

321 side. Nevertheless, all of these factors were excluded by AIC in both habitats. One reason for

322 this is that microtopography might affect the duration of snow cover more strongly than the

323 simple distance effect for local snow conditions (Holtmeier and Broll 2005).

324 The larger shoot growth at the snowbed side in comparison with the fellfield side indicates

325 that the snow-covered habitat is more suitable for the growth of *P. pumila* than the exposed

326 habitat. Furthermore, annual shoot growth was accelerated at the east- and south-facing edges

327 within patches, especially in the HF site. Protection by snow cover from low temperature,

328 desiccation, and mechanical damage by strong winds during winter and early spring is

329 beneficial for *P. pumila* (Okitsu and Ito 1984; Hadley and Smith 1987). The northwest wind

330 is predominant during the winter in Japanese mountain regions, so snowdrifts are formed in a

331 southeastern direction, accelerating shoot growth on the east- and south-facing sides within

332 patches. This indicates the great importance of protection by snowdrifts at the fellfield side.

333 In conclusion, recent climate conditions obviously enhanced the shoot growth and distribution

334 of *P. pumila* in the Taisetsu Mountains toward both fellfield and snowbed habitats. However,

335 the relationship between shoot growth and distribution area is not clear in the present study.

336 Further studies on the population dynamics of *P. pumila* are necessary. As mentioned before,

337 the vegetation dynamics model predicts a large reduction in the distribution of *P. pumila* in

338   the Japanese mountains with climate warming (Horikawa et al. 2009). The discrepancy

339   between the model prediction at a geographic scale and the actual trend at a regional scale

340   suggests that responses of *P. pumila* to climate change may be strongly specific to the region

341   and habitat. The dynamics of shrubs may cause great impacts on the biodiversity of alpine

342   ecosystems, so monitoring of key species at the regional scale is important for precise

343   prediction, conservation and management of alpine ecosystems under a warming climate.

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514 Figure legends

515

516 Fig.1. Location of the fellfield-side habitat (HF site) and the snowbed-side habitat (GS site) in

517 the Taisetsu Mountains, Hokkaido, northern Japan.

518

519 Fig.2. Projections of *Pinus pumila* canopies in the fellfield-side habitat (25 ha) on 25 Sept

520 1977 (a) and 3 Sept 2009 (b), extracted using the unsupervised classification of the

521 ISODATA clustering algorithm, and in the snowbed-side habitat (50 ha) in 1977 (c) and 2009

522 (d) extracted using visual observation. The fellfield-side habitat is located close to Lake

523 Hisago and the snowbed-side habitat is located in Goshikigahara, Taisetsu Mountains,

524 Hokkaido, northern Japan. Patches of *P. pumila* are enclosed by yellow lines.

525

526 Fig.3. Year-to-year trends of annual shoot growth of *Pinus pumila* in the fellfield-side habitat

527 (HF site) and the snowbed-side habitat (GS site) over the last 20 years. (a) Results of simple

528 linear regression for standardized values and Pearson's correlation test are shown. The solid

529 line and broken line indicate the HF site and the GS site, respectively. Comparison of the

530 effects of direction on annual shoot growth (vertical bars standard error) in HF site (b) and GS

531 site (c). Results of simple linear regression are shown as significant in the east and south sides

532 of patches.

533

534 Table 1. Area occupied by *Pinus pumila* in 1977 and 2009 in the fellfield-side habitat (HF

535 site) and the snowbed-side habitat (GS site), and the percentage of expansion over the past 32

536 years.

537

Site	Plot area (ha)	Canopy cover area of *P. pumila* (ha)		
		1977	2009	△area (%)
HF	25	13.08 (52.3%)	14.96 (59.8%)	14.4
GS	50	8.80 (17.6%)	10.07 (20.1%)	14.4

538

539   Table 2. Results of generalized linear mixed-effect model (GLMM) for environmental factors

540   related to annual shoot growth in (a) the fellfield-side habitat (HF site), and (b) the snowbed-

541   side habitat (GS site).

542

Variables	Coefficient	SE	t	P
(a) HF site				
Intercept	1.687	0.109	15.46	< 0.0001
Stem size	0.001	< 0.001	38.39	< 0.0001
Current summer temperature	−0.017	0.009	−1.86	0.0632
Previous summer temperature	0.038	0.009	4.18	< 0.0001
Spring temperature	−0.089	0.009	−9.89	< 0.0001
Current summer sunshine	0.001	0.001	1.88	0.0599
Previous summer sunshine	0.004	0.001	6.82	< 0.0001
(b) GS site				
Intercept	2.273	0.106	21.54	< 0.0001
Stem size	0.001	< 0.001	29.43	< 0.0001
Current summer temperature	0.012	0.007	1.77	0.0773
Previous summer temperature	0.042	0.009	4.78	< 0.0001
Previous summer sunshine	0.001	< 0.001	2.29	0.0222

543

544   Variables were selected based on the smallest Akaike information criterion (AIC).

545

546 Table 3. Annual mean shoot elongation and shoot growth increasing rate of *Pinus pumila* in

547 the four compass directions in the fellfield-side habitat (HF site) and the snowbed-side habitat

548 (GS site).

549

	HF site		GS site	
Direction	Shoot elongation Mean ± SD (mm)	Increasing rate (mm year^{-1})	Shoot elongation Mean ± SD (mm)	Increasing rate (mm year^{-1})
North	38.8 ± 5.7	0.16	50.5 ± 4.0	−0.12
East	52.7 ± 8.3	1.02 ***	55.0 ± 5.4	0.53 **
South	44.2 ± 8.5	0.81 **	54.0 ± 6.5	0.53 *
West	29.3 ± 3.5	0.09	49.3 ± 4.7	0.09

550 *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ (by Pearson's correlation test)

551

552 Table 4. Results of the generalized linear mixed-effect models (GLMM) for the analysis of

553 direction within patches related to annual shoot growth between the fellfield-side habitat (HF

554 site) and the snowbed-side habitat (GS site).

555

Variables	Coefficient	SE	t	P
Intercept (North, HF)	3.643	0.027	134.88	< 0.0001
East	0.305	0.025	12.23	< 0.0001
South	0.135	0.025	5.46	< 0.0001
West	−0.300	−0.025	−12.23	< 0.0001
Site, GS	0.262	0.040	6.58	< 0.0001
East × GS	−0.217	0.036	−5.94	< 0.0001
South × GS	−0.061	0.036	−1.67	0.0954
West × GS	0.271	0.037	7.41	< 0.0001

556