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1 **Habitat-specific responses of shoot growth and distribution of alpine dwarf-pine (*Pinus***
2 ***pumila*) to climate variation**

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16

17 **Abstract**

18 Alpine dwarf-pine (*Pinus pumila*) is 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

38 **Introduction**

39

40 Rapid vegetation changes with global warming are thought to cause the extinction of many
41 species, especially in the arctic and high mountain regions (Grabherr et al. 1994; IPCC 2007).
42 Increases in shrub biomass, cover, and abundance have been observed in multiple arctic, high-
43 latitude and alpine tundra ecosystems over the past century (Myers-Smith et al. 2011).
44 Upward shifts of tree lines are reported in several montane and sub-alpine regions (Kullman
45 2002; Wang et al. 2006; Danby and Hik 2007; Peñuelas et al. 2007). The invasion and
46 expansion of woody plants with large biomass and tall canopy structures may have serious
47 impacts on tundra and alpine vegetation (Wilson and Nilsson 2009; Pajunen et al. 2011),
48 because most tundra plants are sensitive to shading stress (Chapin et al. 1995). Furthermore,
49 the reduction in abiotic stress because of global warming may change the biological
50 interactions among plant species from facilitative to competitive relationships (Choler et al.
51 2001). This may cause a decrease in species diversity through intensive interspecific
52 competition. Therefore, the dynamics of shoot growth and the canopy expansion of shrubs are
53 important issues in assessing global change impacts on alpine ecosystems.

54 The zonal distribution of *Pinus pumila* (Pallas) Regel, an alpine dwarf-pine, is a
55 characteristic physiognomy of alpine vegetation in Japan (Tatewaki 1958). Biomass
56 accumulation of *P. pumila* at the krummholz zone (Tranquillini 1979) is extremely large in
57 alpine ecosystems (Kajimoto 1989), and its productivity is estimated as being 10 times larger
58 than other alpine plant communities (Okitsu 1985). Therefore, changes in the growth and
59 distribution of *P. pumila* may cause serious impacts to the structure and diversity of alpine
60 ecosystems. Previous studies have reported that the net photosynthetic rates of current needles
61 were high in temperatures of 10–15 °C (Kajimoto 1990), and that the current shoot elongation
62 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

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

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.

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

234

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) m² (ranging from 2.9 to 70.7 m²) in the HF site and 235.6 ± 86.4 m² (ranging

238 from 6.0 to 1400.0 m²) 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 \pm 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

264 **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;

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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345

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351

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513 varies with the positional environment in *Pinus pumila*. *HortResearch* 66: 49–54

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 <i>P. pumila</i> (ha)		
		1977	2009	Δ 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	<i>t</i>	<i>P</i>
(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

Direction	HF site		GS site	
	Shoot elongation Mean \pm SD (mm)	Increasing rate (mm year ⁻¹)	Shoot elongation Mean \pm SD (mm)	Increasing rate (mm year ⁻¹)
North	38.8 \pm 5.7	0.16	50.5 \pm 4.0	-0.12
East	52.7 \pm 8.3	1.02 ***	55.0 \pm 5.4	0.53 **
South	44.2 \pm 8.5	0.81 **	54.0 \pm 6.5	0.53 *
West	29.3 \pm 3.5	0.09	49.3 \pm 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	<i>t</i>	<i>P</i>
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