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Title	Role of Salix reinii patches in spatio-temporal patterns of cohabitants on a Japanese volcano
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Citation	Journal of Plant Ecology, 15(1), 71-84 https://doi.org/10.1093/jpe/rtab072
Issue Date	2022-02
Doc URL	http://hdl.handle.net/2115/87813
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Type	article (author version)
Additional Information	There are other files related to this item in HUSCAP. Check the above URL.
File Information	plant_inside_vs_outside.pdf

Research article

Role of *Salix reinii* patches in spatio-temporal patterns of cohabitants on a Japanese volcano

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Running head: Shrub patch felicitation on a volcano

17 **Abstract**

18 Shrub patches often support the colonizers particularly under stressful and/or disturbed

19 environments. The intensities of stresses and disturbances on mountains are often related to

20 an elevation gradient and are decreased by shrub patches (canopy and litter). We aim to

21 clarify these relationships by using shrub patches at different elevations on a volcano. We

22 monitored all shoots in plots established inside and outside of patches of *Salix reinii*

23 (Salicaceae) and their related environments, such as temperature, light, moisture and

24 chemistry, at three elevations on Mount Koma (1131 m elevation), northern Japan, from

25 early spring in 2005 to summer in 2006. The patch structures were evaluated by area, branch

26 density and litter thickness. The structures of shrub patches did not differ among the

27 elevations. The patches increased the diversity of rare species, by an overall increase in plant

28 species richness. The moisture, nitrogen and phosphate contents in the patches were higher

29 than outside of patches. The effects of shrub patches on the cohabitants were overall positive,

30 although the effects were negative on seedling abundance, shoot survival and flowering.

31 These results suggest that the growth patterns of shrub patches determine the plant

32 community structures and facilitate plant diversity.

33

34 *Keywords:* elevational difference, interspecific interaction, litter accumulation,

35 microenvironment, shrub patch

36

37 # INTRODUCTION

38 Inter-specific interactions are one of the most important determinants of plant community

39 structures and functions (Callaway 2007). The interactions are primarily divided into two

40 types, inhibition (negative interaction) and facilitation (positive interaction) (Losapio et al.

41 2021). Facilitation often accelerates succession after catastrophic disturbances, such as

42 volcanic eruptions (del Moral and Wood 1993, Titus and Tsuyuzaki 2003). The 1929

43 catastrophic eruptions on Mount Koma, northern Japan, denuded the mountainous regions.

44 Nowadays, a willow shrub patch formed by *Salix reinii* Franch. et Savat. ex Seemen

45 provides safe sites for a few specific species (Uesaka and Tsuyuzaki 2004). Shrub patches

46 ameliorate the soils in arid and semiarid regions through nutrient supply by litter (Sthultz et

47 al. 2007, Zhou et al. 2020). The effects of shrub patches are considered to be different with

48 litter thickness since litter accumulation promotes seedbank development (Egawa and

49 Tsuyuzaki 2013). In addition, inter-specific interactions may differ between the elevations,

50 because of microclimatic differences (Körner 2007). Although shrub patches alter the

51 microclimate, such as light, temperature, water content and nutrient, the intensity of patch

52 effects is likely to be different among the elevations (Tsuyuzaki et al. 2011).

53   In addition, interspecific interactions are changing with global warming, in particular, at

54 high elevations (Anthelme et al. 2014, Urza et al. 2019) and occasionally promote the

55 establishment of biologically invasive species (Lucero et al. 2019). For example, an invasive

56 tree, *Larix kaempferi*, establishes in the *Salix reinii* shrubs with different ways at different

57 elevations on Mount Koma (Akasaka and Tsuyuzaki 2005). *Larix kaempferi* changes flexibly

58 the pathways of nitrogen uptake directly form the volcanic deposits and indirectly from

59 mycorrhizal fungi while *S. reinii* does not change the nitrogen dependence on them (Kwon

60 and Tsuyuzaki 2016). Therefore, the effects of shrub patches on the cohabitants should be

61 evaluated with different elevations (Schöb et al. 2013).

62   Another paradigm is that facilitation intensity is changed with the structure and size of

63 facilitators (Bruno and Kennedy 2000). For example, large and unfragmented vegetation

64 patches maintain high diversity in Mediterranean alpine grasslands (Pescador et al. 2020).

65 Although not only shrub patch size but also branch density and litter accumulation affect the

66 interspecific interactions (Loydi et al. 2013), the interactive effects of these shrub

67 characteristics should be clarified. The interannual variations of facilitation intensity are

68 expected if the variations are large, because the effects of facilitation are collapsed when

69 strong disturbances and/or stresses occur (Koyama and Tsuyuzaki 2013). Furthermore, the

70 patch effects act differently on the life-history stages, such as seedling emergence, flowering

71   and mortality, of cohabitants (Koyama and Tsuyuzaki 2010, Urza et al. 2019).

72   We hypothesized that: (i) the effects of shrubs were facilitative at community level

73   expressed by species richness, (ii) size-dependent effects of patches on the life-history stages

74   differ between the cohabitant species at different elevations and years and (iii) the overall

75   effects of shrub patches on the cohabitants were positive, although the effects of patches

76   were sometimes negative for a few life-history stages of cohabitants. To clarify these, the

77   recruitment, survival, growth of plants in the inside and outside of *S. reinii* patches were

78   compared on Mount Koma with three elevations for two summer seasons.

79

80   **MATERIALS AND METHODS**

81   **Study sites**

82   Mount Koma is located in southern Hokkaido, northern Japan (42º03'48''N, 140º40'38''E,

83   1131 m a.s.l.). The south-western slope was used for this study. The recent major eruption

84   occurred in 1929 producing 0.38 km^3 of ash and 0.14 km^3 of volcanic ejecta (Kondo and

85   Tsuyuzaki 1999), of which thickness was more than 100 m near the crater and decreased

86   with increasing distance from the crater (Yoshimoto et al. 2007). The vegetation recovery

87   has slowly progressed from the bottom of the mountain. Nowadays, the vegetation cover

88   makes a gradient along elevation, and treeline is ragged (Nishi and Tsuyuzaki 2004). The

89   canopy mostly consists of a deciduous, needle-leaved, exotic tree *Larix kaempferi* above 450

90   m in elevation, due to intensive artificial plantations on the foot after 1953 (Kondo and

91   Tsuyuzaki 1999). A broad-leaved forest develops below 400 m in elevation. On the ground

92   surface, plant cover also decreases with increasing elevation (Tsuyuzaki et al. 2011). Near

93   the summit area, a deciduous dwarf shrub *Salix reinii* forms patch that facilitate the

94   establishment of cohabitants (Uesaka and Tsuyuzaki 2004). A few small-scale eruptions

95   recently occurred on the summit from 1996 to 2000, but the impacts were least on the study

96   area.

97   The climate zone is classified as a warm-cool temperate, with the temperature ranging

98   from -6.9°C in January to 24.6°C in August on average (data obtained from Japan

99   Meteorological Agency (JMA) 2019). The snow-free period usually occurs from May to

100 October. Monthly precipitation data for 2005 and 2006 were obtained from O-numa

101 Meteorological Station (131 m elevation), which is approximately 8 km from the study area

102 and managed by JMA. Summer precipitation (May to September) averages 564.7 mm and

103 winter precipitation (October to April) does 559.4 mm for the last 30 years (JMA 2019). The

104 annual precipitation did not differ between 2005 and 2006, i.e., it was 1,093.0 mm in 2005

105 and 1058.5 mm in 2006 but precipitation during the summer (from July to September)

106 differed greatly between the two years, i.e., it was 424.0 mm in 2005 and 224.5 mm in 2006

107 (Fig. S1). The summer precipitation in 2006 was lower than usual, although the annual

108 precipitation was not different greatly between the surveyed and averaged years.

109

110 **Measurements of environmental factors**

111 The measurements were conducted at low (550-588 m a.s.l.), middle (677-718 m) and high

112 (759-781 m) elevations (Fig. 1). The forest canopy, dominated by *Larix kaempferi* (larch),

113 was more developed at lower elevations (Kondo and Tsuyuzaki 1999).

114   The microclimate was measured at 10 min intervals by weather stations (Hobo Weather

115 Station, Onset, Bourne) at the three elevations (Tsuyuzaki et al. 2011). Wind speed was

116 measured by a wind gauge (S-WCA-M003) at 50 cm above the ground surface on the

117 bareground at each elevation. Temperature and photosynthetic active radiation (PAR) were

118 measured by a thermometer (S-TMA-M017) and a PAR sensor (S-LIA-M003) at ground

119 level on bareground and in the center of *Salix reinii* shrub patch at each elevation.

120 Precipitation at the middle elevation was measured by a rain gauge (S-RGB-M006) on

121 bareground. The measurements were conducted from 1 July 2005 to 31 October 2005 and

122 from 1 June 2006 to 30 June 2006 at 10-min intervals.

123   The volcanic deposits were collected by a steel soil tin (20 cm^2 in surface area, 5 cm in

124 depth) to measure water content, pH, total nitrogen (N) and phosphorus (P). The samples

125   were collected from the three elevations in a pair of bareground and patch at each elevation

126   at 1-month intervals from June to October in 2005. Therefore, the total number of samples

127   was 90. To avoid the disturbances on the ground surface, the patches monitored shoot

128   dynamics were not selected for the chemical measurements. The samples were kept in plastic

129   bags, carried to the laboratory soon after the sampling, and the fresh weight was measured.

130   To measure pH, 10 g of the volcanic deposits was saturated with 25-mL distilled water and

131   agitated well. The mixture was left for 1 hour, and then pH was measured by a glass

132   electrode (MP120, Mettler-Toledo, GmbH, Schwerzenbach). Then, the samples were dried at

133   110°C in an oven for three days and the dry weight was measured. Soil moisture was

134   calculated as: (fresh weight - dry weight)/(dry weight) $\times$ 100 (Marshall et al. 1996). N was

135   measured by particles passed through a sieve of which mesh was 2 mm in diameter, and P

136   was measured by particles less than 0.05 mm in diameter. N was measured by a C/N coder

137   (Elementar Vario EL, GmbH Japan Siberhegner), and P was measured by a Truog method

138   (Patnaik 1997).

139

140   ### *Salix reinii* shrub patches

141   At each of the three elevations, 20 patches, of which area ranging from 0.46 m^2 to 1.16 m^2

142   were marked in early May 2005. Close to each patch, 1 m $\times$ 1m plots were established on the

143   bareground used for control. The patch and bareground were separated at more than 50 cm to

144   avoid the effects of patches on bareground. Shrub area, height and branch density were

145   measured on each patch by the following procedure. First, each plot or shrub was divided

146   into 10 cm $\times$ 10 cm cells. At each lattice point of the cells, the height was measured. Also,

147   the number of leaves and branches touched at a slim rod was counted at each lattice point.

148   Litter thickness was also measured by a ruler at each lattice point. Thereafter, the averages of

149   branch density (number of hits) and litter thickness were calculated on each patch.

150

151   ### Monitoring shoot dynamics

152   The shoot dynamics was monitored at every month from June to October in 2005 and from

153   May to September in 2006. The height, area (cover) and number of leaves were recorded on

154   each shoot at every monitoring. The cover was calculated by measuring lengths of major and

155   minor axes, as an assumption of oval shape. At the last monitoring in 2006, all the marked

156   shoots were harvested to measure the biomass, expect for shoots consisting of *S. reinii*

157   patches. The samples were dried at 70ºC in an oven for 48 hours soon after the sampling and

158   weighed.

159

160   **Statistical analysis**

161   The plant cover in each plot or patch was calculated by the sum of shoot areas on each

162   species. All the statistical analyses were conducted by R (ver. 3.6.1) (R Core Team 2019). To

163   investigate relationships between patch characteristics, i.e., area, height, branch density

164   (number of hits) and litter thickness, correlation coefficients were used. Shrub characteristics,

165   i.e., area, height, patch density and litter thickness were compared between the three

166   elevations with random effects of plot code and year by generalized linear mixed-effects

167   models (GLMMs). Moisture, pH, total nitrogen and phosphate were compared between the

168   habitats and between the elevations with their interactions by two-way repeated-measures

169   analysis of variance (ANOVA) after Shapiro-Wilk test of normality that indicated all the

170   examined variables followed normal distribution ($P < 0.05$), because the data were not

171   analyzed by GLMMs due to the sampling design. The patch height was excluded for the

172   analyses shown below, because of the small variation.

173   Species richness, diversity and evenness were calculated based on the plant cover by a

174   package vegan (Oksanen et al. 2019). Since cover diversity is affected more by disturbances

175   and stresses than the shoot density diversity (Tsuyuzaki and del Moral 1994, Tsuyuzaki

176   1996), cover was used to investigate the effects of disturbances on the community diversity.

177   Differences in these three parameters between the inside and outside of patches in 2006 were

178   investigated with elevation by a generalized linear model (GLM) with the assumptions of

179 Poisson, gamma and binomial distribution, since these three parameters did not differ

180 between 2005 and 2006 (GLM, $P > 0.05$). As well, determinants on these three parameters in

181 the inside of patches were investigated with elevation, branch density and litter thickness by

182 GLM. The interactions between these explanatory variables are included. The best models

183 were selected by Akaike's Information Criteria with a stepwise procedure.

184   Based on the records of shoots, the shoots were separated into two life-history stages,

185 seedling and non-seedlings. When new shoot was firstly recorded, the shoot was recorded as

186 (annual) seedlings. Since few seedlings were observed in May, all the shoots recorded in

187 May were regarded as non-seedling. The relative growth rate (RGR) of each shoot was

188 calculated by: log(maximum height in 2006) – log(maximum height in 2005) for shoots

189 recorded for the 2 years.

190   Zero-inflated Poisson (ZIP) model was applied for investigating the determinants on

191 numbers of seedlings and non-seedlings, because of excess zero, using a package pscl

192 (Jackman 2017). Determinants on shoot mortality during the surveyed period were

193 investigated by Cox regression model by a package survival. The determinants on flower

194 production were investigated by a GLMM with a Poisson distribution. On these two models,

195 the response variables are mortality and flowering. For all these analyses, differences

196 between the inside and outside of patches were examined firstly and then the inside of

197 patches were examined with the explanatory variables (patch area, patch density, litter

198 thickness and elevation). In the case of flowering, year was also used as an explanatory

199 variable.

200

201 **RESULTS**

202 **Shrub patch structures and the environments**

203 Wind speed decreased with decreasing elevations, i.e., 3.6 m/s (in average, maximum gust =

204 14.8), 2.6 (11.0) and 1.0 (9.5) at high, middle and low elevations, respectively, mostly due to

205 the shelter effects of the larch canopy. Total precipitation during July and September, when

206 most plants grew, was 536 mm in 2005 and 317 mm in 2006, respectively. The PAR was

207 approximately 30 times higher on the bareground than in the shrub patch (Table S2) with the

208 seasonal changes, suggesting that shading by the patch was the main factor determining the

209 PAR in the patches. Associated with low PAR in the patches, the temperature was also lower

210 in the patches. The mean temperature was more than 1°C lower in the shrub patches than on

211 the bareground throughout the snow-free period, showing that not only leaves but also

212 branches reduced the temperature (Table S2). These results showed that the shrubs affected

213 the aboveground environments.

214 The water content ranged from 9% to 25% in the bareground and from 9% to 48% in

215 the patches (Fig. 2). The water content was higher in the patches (two-way ANOVA, $P <$

216 0.001) and differed among the elevations ($P < 0.001$). The pH in the volcanic deposits was

217 less than 6.5 and did not differ between habitats and among elevations ($P > 0.50$). The total

218 nitrogen was lower in the baregrounds than in the patches ($P = 0.004$) and did not differ

219 among the elevations ($P = 0.14$). Phosphate in the volcanic deposits ranged from 1.0 μm/g to

220 14.7 μm/g in the baregrounds and from 2.9 μg/g to 25.2 μg/g in the shrub patches. The

221 phosphate concentrations were higher in the patches ($P < 0.001$) and did not differ among

222 the elevations ($P = 0.09$). Overall, therefore, the nutrients and moisture in the volcanic

223 deposits were increased by the *Salix* patches. Since the interactions between elevation and

224 habitat were not detected except for water content ($P > 0.05$), the effects of patches on the

225 properties in the volcanic deposits were affected by the elevation.

226 The shrub heights were less than 46 cm, 33 and 34 cm at the low, middle and high

227 elevations, respectively (Table S1). The branch densities were less than 6.2 (hits averaged

228 per 10 cm long). The litter thickness varied greatly in the inside of shrub patches, ranging

229 from 0.0 mm, i.e., no litter, to 6.5 mm, and was 0 cm in the outside. The litter consisted

230 mostly of *S. reinii* leaves. Shrub structure, i.e., the height, area, density and litter thickness,

231 did not differ among the three elevations (GLMM, $P > 0.05$). Shrub structure did not change

232 for the two surveyed years ($P > 0.05$), indicating that the unexpected events, such as

233 herbivore damage, occurred least for the two years. Correlations between the branch density

234 and litter thickness were not significant (r = -0.115 and -0.149 in 2005 and 2006, n = 60, P >

235 0.26), and those between the patch area and litter thickness were also not significant (r =

236 +0.219 in 2005 and +0.203 in 2006, P > 0.09). These results indicated that the litter

237 thickness was not determined by the shrub area and branch density.

238

239 **Vegetation patterns**

240 In total, 1881 shoots were recorded from 28 vascular plant species, including an

241 un-identified shoot (Table S3). The common species were *Carex oxyandra*, *Luzula capitata*,

242 *Calamagrositis hakonensis*, *Larix kaempferi*, *Salix reinii* and *Gaultheria miqueliana* (Fig. 3).

243 Of these, *C. oxyandra*, *L. capitate* and *C. hakonensis* were perennial herbs, *S. reinii* and *G.*

244 *miqueliana* were shrubs and *L. kaempferi* was an exotic tree. These six species comprised

245 1487 shoots (79.1% to total) for the 2 years.

246   On the six common species, 357 and 327 shoots originated from seedlings in 2005 and

247 2006, respectively. Most seedlings emerged in June and July for both years (Fig. 3).

248 *Calamagrostis hakonensis* and *S. reinii* increased their shoots with increasing the elevations,

249 while the other species decreased their shoots with the elevations. The numbers of seedlings

250 for all the species except for *L. kaempferi* were different between 2005 and 2006 (Table 1),

251 probably because of the climate differences. The seedling emergence of *C. oxyandra* and *C.*

252 *hakonensis* was negatively and positively related to the elevation increase, respectively. The

253 year was correlated significantly to the seedlings of all the species at binomial and/or

254 Poisson part. The numbers of non-seedlings were 683 and 1345 in 2005 and 2006,

255 respectively, showing that the most of seedlings emerged in 2005 survived until 2006. As

256 well as the annual seedlings, the elevation and year affected the numbers of non-seedlings.

257 These results showed that the interannual variations of seedling emergence were large,

258 depending on the species characteristics, and survived once established.

259   The mortality was size-dependent, i.e., negatively correlated to the plant height for all

260   the species (Cox regression model, $P < 0.01$, Table 3), showing that small plants died more.

261   When the differences between inside and outside patches were not considered, the mortality

262   increased with increasing elevation for *C. hakonensis*, *L. kaempferi*, *S. reinii* and *G.*

263   *miqueliana*. The elevation did not affect the mortality of the other two common species, *C.*

264   *oxyandra* and *L. capitata*. As well as the mortality, flowering was related to the shoot heights,

265   i.e., taller shoots produced more flowers for all the examined species ($P < 0.01$) (Table 3).

266   Therefore, the elevation did not affect the flowering for all the species.

267

268   **Differences between inside vs outside of patches**

269   Over the whole elevation gradient, species richness in 2006 averaged 2.87 ± 2.38 outside

270   patches and was 3.05 ± 2.20 inside. The species richness was higher in the patches than on

271   the bareground (slope = + 2.003, GLM, $P = 0.028$) and was higher at higher elevation

272   ($+0.003$, $P = 0.002$) in 2006. Interactions between the elevation and habitat was significant

273   (-0.003, $P = 0.033$). Six species establishing only in the patches: *Pyrola incarnata*

274   (frequency = 7), *Agrostis flaccida* (3), *Platanthera metabifolia* (2), *Agrostis scabra* (1),

275   *Chimaphila umbellata* (1) and *Solidago virgaurea* (1). There were four species established

276   only outside: *Populus sieboldii* (2), *Drosera rotundifolia* (1), *Pinus densifolia* (1) and *Salix*

277   *bakko* (1). Diversity increased with elevation ($+0.002$, $P = 0.007$) and did not differ between

278   the patches and bareground ($P = 0.508$). The evenness was affected by neither the elevation

279   ($P = 0.357$) and patches ($P = 0.956$). In total, therefore, the effects of patches were

280   facilitative to the establishment of rare species and were more intensive at higher elevation

281   where the environments were more severe.

282   Seedlings emerged more within the patches (517) than on the baregrounds (429) and

283   more in 2005 (805) than in 2006 (141) (Fig. 3). *C. oxyandra*, *C. hakonensis*, *S. reinii* and *G.*

284   *miqueliana* emerged more seedlings in the patches, while *L. capitata* and *L. kaempferi* did

285   more on the bareground (Table 1). The maxima of numbers of non-seedlings were 27 and 42

286   in the outside and inside of the patches, respectively, in 2005 and 27 and 44 outside and

287 inside patches in 2006. On the zero-inflated Poisson model, *C. oxyandra*, *L. capitata* and *C.*

288 *hakonensis* showed more non-annual seedlings inside the patches than outside when number

289 of seedlings was examined by the Poisson part. *Salxi reinii* showed the positive effect of

290 patches on the non-seedlings when the presence or absence of seedlings was examined by

291 the binomial part. The patch effect was negative for *L. capitata* at the binomial part. The

292 patch effects on non-seedlings were positive for four of the six common species.

293 The mortality was higher inside patches than outside for *L. capitata* (Cox regression

294 model, $P = 0.0001$) and *S. reinii* ($P = 0.044$). However, these two species favored to establish

295 on the bareground, as shown by annual seedlings. The other four examined species did not

296 differ their mortalities between the inside and outside ($P > 0.05$). The flowering was less for

297 *C. hakonensis* within the patches (GLMM, $P < 0.01$) and was not different for *C. oxyandra*,

298 *L. capitata* and *G. miqueliana* between the inside and outside of the patches. The flowering

299 of other species was not examined due to the sample sizes. In total, the patches weakly

300 affected mortality and flowering for most species.

301

302 **Effects of patch structures on cohabitants**

303 The species richness investigated only within the patches was affected negatively by the

304 three parameters of patch structures, area, branch density and litter thickness, with their

305 interactions (Table S4), although the richness was higher in the patches as compared with the

306 bareground. The species diversity was not different among the three elevations and was

307 affected negatively by the patch area and branch density negatively with their interaction.

308 The evenness was not related to any examined parameters. Considering with higher species

309 richness within the patches than on the bareground, the optimal size of patches should be

310 presented.

311 Seedling emergence within the shrub patches was not tightly related to the area, branch

312 density and litter thickness of patches with a few exceptions (Table 2). Elevation affected the

313 seedlings of *C. oxyandra*, *C. hakonensis* and *L. kaempferi* when the number of seedlings was

314 examined. Seedling emergence differed between 2005 and 2006 for four of the six common

315 species. Non-seedling *C. oxyandra* decreased the number with increasing the shrub patch

316 area and branch density. Branch density also reduced the non-seedlings of *S. reinii* and *G.*

317 *miqueliana*. In contrast, *L. kaempferi* increased the non-seedlings with increasing the branch

318 density. The non-seedlings of *G. miqueliana* established less in the large patches. Litter

319 thickness negatively affected the number of non-seedlings for *L. capitata*, *S. reinii* and *G.*

320 *miqueliana*. Since the patches were larger than 1 m^2 in this study, these results considering

321 with the richness suggested that the optimal size of patches for facilitation was smaller than

322 1 m^2.

323 The area, branch density and litter thickness of patches, affected the shoot mortalities on

324 *L. capitata* and *S. reinii* (Table 3). *Luzula capitata* shoots died more in denser patches at low

325 elevation. The mortality of *S. reinii*, itself, was positively related to the patch area and

326 negatively to the branch density, suggesting that the area functioned differently from the

327 branch density.

328 Flowering was investigated for three well-flowered species (Table 3), because of the

329 sample sizes. *Calamagrostis hakonensis* decreased the flowering when the litter was thick.

330 The interannual variation of flowering was detected only for *C. hakonensis*. The patch

331 characteristics did not affect the RGRs of shoot volume for all the species (Fig. S2). RGR on

332 four species, *C. oxyandra*, *L. capitata*, *C. hakonensis* and *G. miqueliana*, increased with

333 increasing elevation, independent of shrub patches, but did not affect *L. kaempferi* and *S.*

334 *reinii*. Therefore, the shrub patches affected the shoot density more than the shoot growth.

335

336 ## DISCUSSION

337 ### The effects of patches on vegetation development

338 The rare species established in the patches more than on the bareground, showing that the

339 shrub contributed to increase the community and landscape diversities. Shrub facilitation

340 increases species richness and diversity by allowing the establishment of stress-intolerant

341 species into harsh environments in an arid scrubland, despite increasing shrub-seedling

342 competition (van Zonneveld et al. 2012). Furthermore, the annual and non-annual shoots

343 tended to be more in the patches for the common species. These indicated that the overall

344 effect of patches was facilitative.

345   The *Salix reinii* patches ameliorated the microclimates, i.e., moisture, nitrogen and

346 phosphate, in the volcanic deposits. Shrub patches of *Caragana microphylla* and *Salix*

347 *gordejevii* increase nutrient (N and P) and moisture in the soils and act as seed traps in

348 Mongolian sand dunes (Zhao et al. 2007), although ecosystem changes are determined by

349 multiple mechanisms of shrub facilitation through seedbank development, etc. in drylands

350 (Filazzola et al. 2019). The baregrounds on Mount Koma showed higher temperature and

351 light during the plant growing seasons and the patches moderate these climatic conditions

352 (Tsuyuzaki et al. 2011).

353   However, the growth (RGR) did not differ between the patches and baregrounds for all

354 the common species and the mortality was higher for the two species, *L. capitata* and *S.*

355 *reinii*. The flowering was different along the elevations for four of the six common species.

356 These indicated that the patch effects were negative at a few life-history stages, although the

357 establishment of shoots was higher in the patches. Facilitators decrease the survival and

358 increase competition for young plants, such as seedlings, in Brazilian coastal dunes, although

359 the overall facilitation of facilitator works positive (Beduschi and Castellani 2013).

360

Effects of shrub patch structures on cohabitants

362 The structural characteristics of shrub patches, i.e., area, height, branch density and litter,

363 were not strongly correlated to each other, indicating that the shrub patches acted variously

364 to the cohabitants. Of these shrub characteristics, litter accumulation within shrub patches is

365 often the key to determine the patch effects. Moderate litter accumulation assists the seedling

366 establishment by improving the microenvironments, including the reduction of strong

367 sunshine and drought (Egawa and Tsuyuzaki 2013). Optimal litter thickness seems to be

368   present for seed trap effect and seed germination as well as patch size and is different

369   between the cohabitant species (Zhang et al. 2017). Since the litter accumulation was not

370   determined by the aboveground structures of shrubs on Mount Koma, the litter accumulation

371   should be determined by microtopography such as soil texture and small rill-ridge pattern

372   (Otaki et al. 2016).

373   The overall effects of patches on the cohabitants were positive when the patches were

374   compared with the bareground. However, the effects of patch structures, i.e., patch area,

375   branch density and litter thickness, were often negative to the cohabitants only when the

376   inside of patches was investigated. These results suggested all these patch structure

377   characteristics had the optimal sizes for the facilitation, which were smaller than the

378   surveyed patches, i.e., 1 m^2. Since the overall effects of patches, of which size is larger than

379   approximately 0.1 m^2, are facilitative (Uesaka and Tsuyuzaki 2004), the optimal size for

380   facilitation should range from 0.1 to 1.0 m^2. However, larger patches increase the seed

381   germination of *Polygonum sachalinense* and *Miscanthus sinensis* up to 4 m^2 in area (Holle

382   and Tsuyuzaki 2018). Since shrubs formed by *Artemisia tridentata* changed the

383   morphological forms with size, the facilitative function is changed with the shrub size (Urza

384   et al. 2019). These indicate that the optimal patch sizes differ among the species. Litter has

385   the optimal thickness as well as patch area. Litter has a positive effect on seedling

386   establishment under dry conditions and/or with low to medium litter amounts, although

387   excess litter negatively affects the establishment (Loydi et al. 2013).

388

389   **Variations in shoot dynamics**

390   The interactions between *Salix reinii* shrub patches and the cohabitants, examined by number

391   of shoots, in particular, for non-seedling shoots, differed among the elevations. RGR

392   increased with increasing elevation for *C. oxyandra*, *L. capitata* and *G. miqueliana*,

393   irrespective of the shrub patches. These results indicated that the effects of shrub patches

394   were weak to the vegetative growth of these species. As *L. kaempferi* became larger and

395 denser at lower elevations on Mount Koma (Tsuyuzaki et al. 2011), the effects of *L.*

396 *kaempferi* should be higher than the effects of *S. reinii* with decreasing the elevations. An

397 exotic tree, *Larix kaempferi*, accelerates the succession for non-tree species (Titus and

398 Tsuyuzaki 2003). Two facilitators have more beneficial effects on the cohabitants than single

399 facilitator in an arid shrub-herbaceous community (Zhang et al. 2011). Further research is

400 required to clarify if the positive effects of *S. reinii* are reduced by *L. kaempferi* trees. The

401 belowground strategy of plants is also important for the establishments of these species, in

402 particular, at the high elevations where light resource is high without shade (Tsuyuzaki and

403 Hase 2005). The belowground traits of plants should be focused more for understanding

404 facilitation (Rohhauser and Pucheta 2016).

405   The seedling emergence for most species differed between the two surveyed years. The

406 precipitation was lower in 2006. Although the moisture in the volcanic deposits was

407 measured only in 2005, the moisture should be lower in the summer from July to September

408 in 2006 than in 2005, because the moisture fluctuation followed precipitation in summer

409 (Tsuyuzaki et al. 2011). Germination phenology or timing is tightly related to a tradeoff

410 between facilitation and competition (Leverett 2017). In such years as seen in 2006, the

411 effects of drought precluded the facilitative effects of patches. The facilitation intensity is

412 increased with increasing stresses and disturbances until these factors are not beyond the

413 thresholds of resilience (Koyama and Tsuyuzaki 2013, Hotes et al. 2010). The shift from

414 facilitation to competition was triggered by low rainfall on a shrubland in southeast Spain

415 (O'Brien et al. 2017). Therefore, interannual variations were conspicuous and hindered the

416 effects of patches.

417   In conclusion, the *S. reinii* patches facilitated the establishment of cohabitants and

418 increased the species richness, showing that the facilitation is beneficial not only for

419 common species but also for rare species. The interspecific interactions changed with

420 climatic variations along elevational gradients. For example, the seedling establishment of *C.*

421 *oxyandra* and *L. kaempferi* decreased with increasing elevation and that of *C. hakonensis*

increased. Also, the shrub patches affected differently to each species with the optimal sizes of facilitation. Therefore, the distributions and growth patterns of shrub patches determined the plant community structures at mountain scale.

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539

Table 1: The numbers of annual seedlings and non-seedlings in the inside and outside of *S. reinii* patches, examined by zero-inflated Poisson model. Binomial and Poisson mean negative binomial and Poisson parts in the model. **: significant at $P < 0.01$. *: $P < 0.05$. -: not determined, due to small sample size. Total number of shoots on each species is shown in parentheses.

	Carex oxyandra		*Luzula capitata*		*Calamagrostis hakonensis*		*Larix kaempferi*		*Salix reinii*		*Gaultheria miqueliana*	
	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson
Seedling	(200)		(185)		(207)		(70)		(220)		(64)	
Intercept	+5.279**	+4.134**	+3.788*	+2.025**	+3.763	-7.602**	-0.268	+5.205	+4.200*	+0.244	+0.155	+1.735
Patch	+0.039	+0.376*	-1.371**	+0.294	-0.433	+0.418**	-1.237*	-0.447**	+1.077**	+0.135	+2.252**	-0.414
Elevation	-0.007*	-0.004**	-0.004	-0.001	-0.005	+0.012**	+0.004	-0.007	-0.006*	+0.002*	+0.002	-0.001
Year	-0.180	-3.756**	+1.178*	-1.477**	+1.099*	-1.703**	-0.783	+0.346	+1.637**	-0.059	+1.310*	-0.753
Non-seedling	(156)		(143)		(89)		(38)		(84)		(31)	
Intercept	+3.563**	+4.148**	+4.518**	+2.453**	+10.538**	-5.652**	-3.858	+5.396	+7.293**	-1.126	+1.481	+6.512**
Patch	-0.336	+0.514**	-1.395**	+0.398**	+0.560	+0.008**	-0.846	+0.301	+1.510**	-0.151	+0.001	-0.612
Elevation	-0.004	-0.004**	-0.005*	-0.002**	-0.016**	+0.729**	+0.007	-0.008	-0.001**	+0.004**	+1.801**	-0.008**
Year	-1.245**	+0.131	+0.293**	+0.244*	-1.400**	+0.586**	-0.028	-0.393	-0.961**	+0.177	-0.964*	+0.035

Table 2: Determinants on the numbers of annual seedlings and non-seedlings within the *S. reinii* patches, examined by zero-inflated Poisson model. Binomial and Poisson mean negative binomial and Poisson parts in the model. **: significant at $P < 0.01$. *: $P < 0.05$. -: not determined, due to small sample size. Total number of shoots on each species is shown in parentheses.

Species	*Carex oxyandra*		*Luzula capitata*		*Calamagrostis hakonensis*		*Larix kaempferi*		*Salix reinii*		*Gaultheria miqueliana*	
	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson	Binomial	Poisson
Seedling	(113)		(90)		(127)		(44)		(147)		(33)	
Intercept	+7.420	+11.466**	-0.213	+3.123	+3.652	-6.184**	+9.010	+4.157	-0.337	+1.990	-10.360	-87.293
Patch												
Area	-0.555	-2.820	+3.603	-0.694	+0.448	-0.031	+8.880	+6.612**	-2.077	-16.465**	-34.700	+48.541
Density	-0.050	-0.487*	+0.203	-0.138	-0.381	+0.214	-1.295	+0.232	+1.474	+0.639	+15.592	+9.954
Litter	-1.585	+0.534	-1.581	+0.646	+1.983	-0.163	-3.390	-2.444	-1.729	+1.361	-163.087	-127.768
Elevation	-0.008	-0.009**	-0.003	-0.002	-0.005	+0.010**	-0.009	-0.014**	-0.004	+0.009	+0.031	+0.078
Year	-0.511	-3.950**	-10.951	-3.379**	+0.851	-1.481**	-3.872	-0.190	+2.263*	+1.520	+56.581	+44.550
Non-seedling	(243)		(238)		(169)		(64)		(157)		(62)	
Intercept	+4.132	+8.106**	+2.324	+3.441**	+13.083**	-3.996*	+52.288	+3.431*	+4.596	+6.017**	-1.669	+1.820
Patch												
Area	-4.492*	-2.554**	+1.197	-0.506	+1.357	-0.438	-138.835	+3.203**	+4.609	-2.390	-120.296**	+1.213
Density	+0.061	-0.281**	+0.022	+0.084	-0.048	+0.118	+35.058	+0.726**	+0.616	-0.631**	-104.884	-2.865*
Litter	-0.428	+0.541	-2.073*	+0.289	-0.141	-0.215	+129.140	-0.158	-2.684*	-0.091	-21.085	-10.182*
Elevation	-0.000	-0.006**	-0.003	-0.003**	-0.019**	+0.007**	-0.407	-0.014**	-0.010*	-0.001	+0.863	+0.024**
Year	-1.197**	+0.035	-1.023*	+0.379**	-1.622**	+0.532**	+10310	-0.327	-0.466	+0.069	-186.105	-5797**

Table 3: Effects of elevation, patch area, branch density and litter thickness on the shoot mortality and flowering (number of inflorescences) of the six common species in the inside of patches on Mount Koma, examined by a Cox regression model and a generalized linear mixed-effects model with a Poisson distribution, respectively. Shoot height is the maximum height during the surveys on each shoot. On the characteristics of *S. reinii* patches, area, branch density and litter thickness are examined. **: significant at $P < 0.01$. *: $P < 0.05$. -: not examined because of no flowers.

| Species	*Carex oxyandra*	*Luzula capitata*	*Calamagrostis hakonensis*	*Larix kaempferi*	*Salix reinii*	*Gaultheria miqueliana*
Mortality						
Shoot height	-0.401**	-0.368**	-0.086**	-0.212**	-0.465**	-0.564**
Patch size						
Area	-0.734 ^{NS}	-1.766 ^{NS}	+1.387 ^{NS}	-2.067 ^{NS}	+12.314**	+0.012 ^{NS}
Density	+0.010 ^{NS}	+0.601**	-0.161 ^{NS}	+0.088 ^{NS}	-1.562**	+13.462 ^{NS}
Litter	+0.636 ^{NS}	-0.682 ^{NS}	+0.365 ^{NS}	+1.122 ^{NS}	-1.247 ^{NS}	+0.201 ^{NS}
Elevation	-0.004*	-0.003*	-0.001 ^{NS}	-0.002 ^{NS}	-0.002 ^{NS}	+0.005 ^{NS}
Flowering						
Intercept	+0.410	-3.386	-3.665*	-	-	-
Shoot height	+0.210**	+0.363**	+0.140**	-	-	-
Patch size				-	-	-
Area	-2.564	-1.504	+2.352	-	-	-
Density	-0.098	-0.205	-0.0115	-	-	-
Litter	-0.580	-0.584	-1.862**	-	-	-
Elevation	-0.002	+0.002	-0.000	-	-	-
Year	+0.096	-0.094	+0.207*	-	-	-
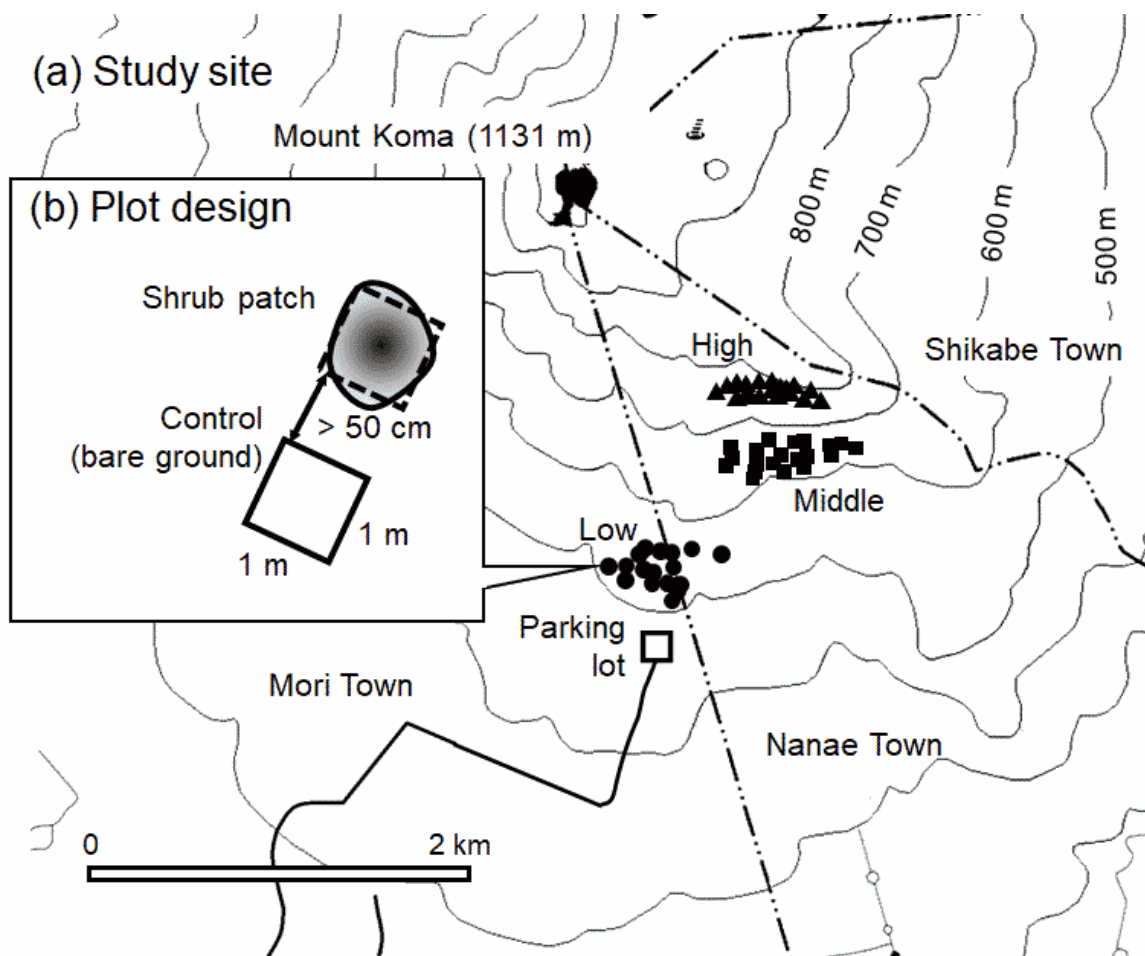
Figure 1: (a) Study site. The locations of plots at high, middle and low elevations are shown by closed triangles, squares and circles. Phantom lines indicate administrative boundaries. The top of graph is faced to north. (b) Plot design. Shrubs of which areas were approximately 1 m² were selected. On a patch and the bareground (control), climatological data were obtained by a weather station. In details, see also in the text.
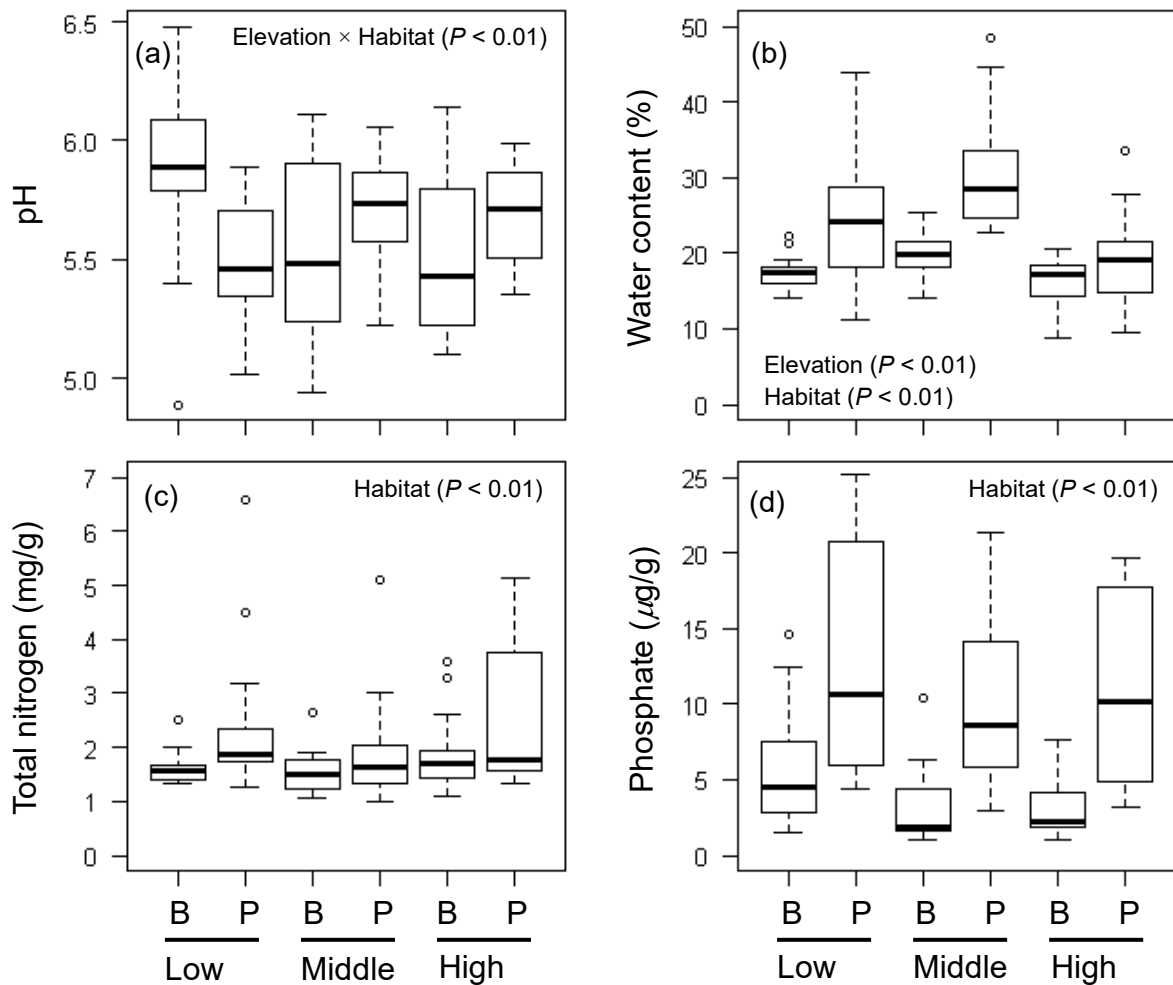
Figure 2: Chemical properties, pH (a), water content (b), nitrogen (b) and phosphate (d), of the volcanic ash in 2005 on Mount Koma, shown by box-whisker plots. Habitat: B = bareground, and P = *Salix reinii* patch. The differences in chemical properties are compared between elevation, and between the habitats with interactions between them, by two-way repeated-measures ANOVA. Sampling date is used as a random effect. The factors are shown in the figures when they are statistically significant at $P < 0.01$. Cross symbol means the interaction.
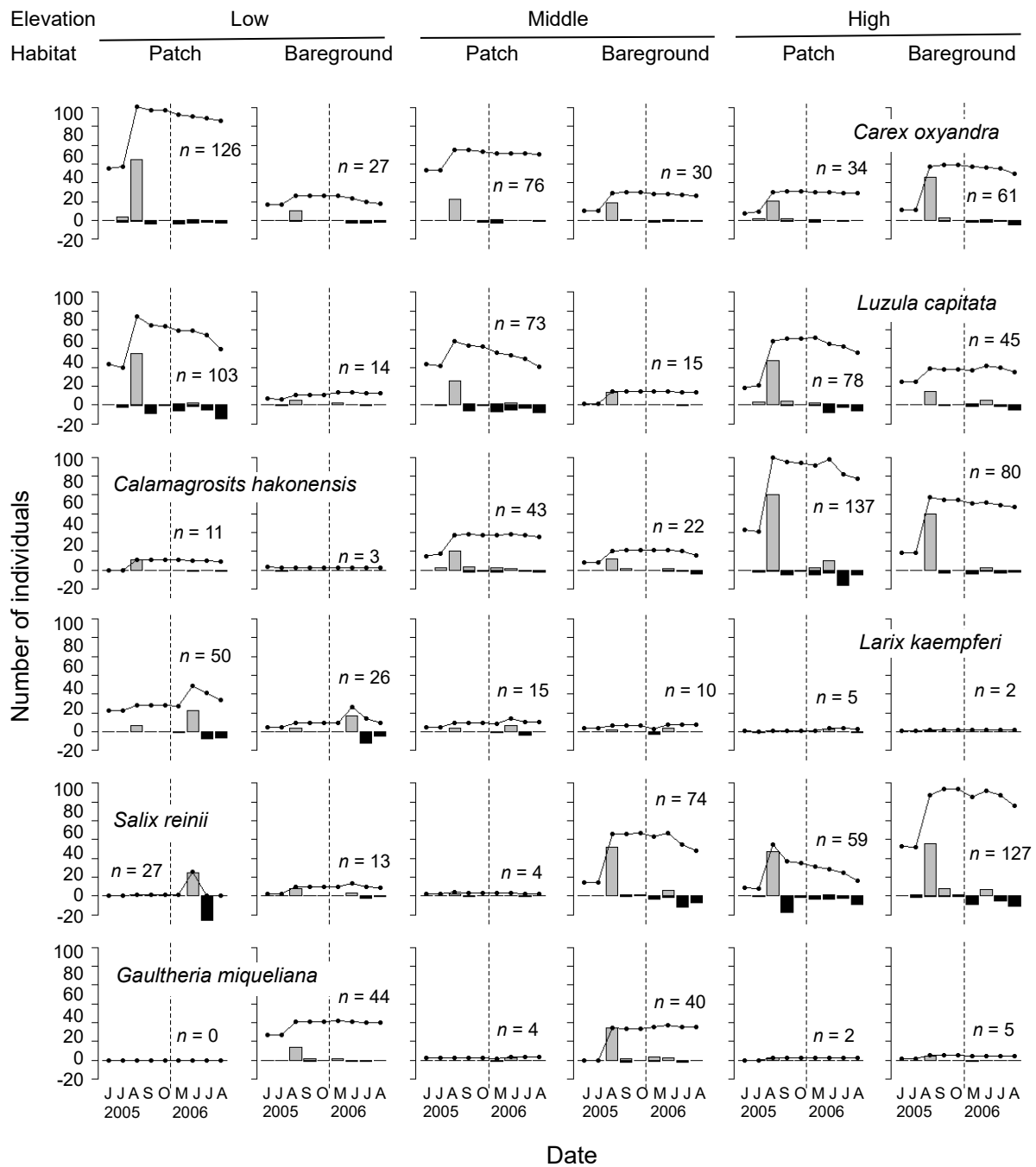
Figure 3: The fluctuations of number of shoots during snow-free periods from 2005 to August 2006 at low, middle and high elevations on six common species. Broken lines indicate the number of shoots observed. Positive and negative bars indicate number of emerged seedlings and number of shoots died, respectively. On the *S. reinii*, the shoots consisting of the shrub patches are excluded. *n* = total number of shoots.