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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

Abstract

Shrub patches often support the colonizers particularly under stressful and/or disturbed environments. The intensities of stresses and disturbances on mountains are often related to an elevation gradient and are decreased by shrub patches (canopy and litter). We aim to clarify these relationships by using shrub patches at different elevations on a volcano. We monitored all shoots in plots established inside and outside of patches of *Salix reinii* (Salicaceae) and their related environments, such as temperature, light, moisture and chemistry, at three elevations on Mount Koma (1131 m elevation), northern Japan, from early spring in 2005 to summer in 2006. The patch structures were evaluated by area, branch density and litter thickness. The structures of shrub patches did not differ among the elevations. The patches increased the diversity of rare species, by an overall increase in plant species richness. The moisture, nitrogen and phosphate contents in the patches were higher than outside of patches. The effects of shrub patches on the cohabitants were overall positive, although the effects were negative on seedling abundance, shoot survival and flowering. These results suggest that the growth patterns of shrub patches determine the plant community structures and facilitate plant diversity.

Keywords: elevational difference, interspecific interaction, litter accumulation, microenvironment, shrub patch

INTRODUCTION

Inter-specific interactions are one of the most important determinants of plant community structures and functions (Callaway 2007). The interactions are primarily divided into two types, inhibition (negative interaction) and facilitation (positive interaction) (Losapio et al. 2021). Facilitation often accelerates succession after catastrophic disturbances, such as volcanic eruptions (del Moral and Wood 1993, Titus and Tsuyuzaki 2003). The 1929 catastrophic eruptions on Mount Koma, northern Japan, denuded the mountainous regions.

Nowadays, a willow shrub patch formed by *Salix reinii* Franch. et Savat. ex Seemen provides safe sites for a few specific species (Uesaka and Tsuyuzaki 2004). Shrub patches ameliorate the soils in arid and semiarid regions through nutrient supply by litter (Sthultz et al. 2007, Zhou et al. 2020). The effects of shrub patches are considered to be different with litter thickness since litter accumulation promotes seedbank development (Egawa and Tsuyuzaki 2013). In addition, inter-specific interactions may differ between the elevations, because of microclimatic differences (Körner 2007). Although shrub patches alter the microclimate, such as light, temperature, water content and nutrient, the intensity of patch effects is likely to be different among the elevations (Tsuyuzaki et al. 2011).

In addition, interspecific interactions are changing with global warming, in particular, at high elevations (Anthelme et al. 2014, Urza et al. 2019) and occasionally promote the establishment of biologically invasive species (Lucero et al. 2019). For example, an invasive tree, *Larix kaempferi*, establishes in the *Salix reinii* shrubs with different ways at different elevations on Mount Koma (Akasaka and Tsuyuzaki 2005). *Larix kaempferi* changes flexibly the pathways of nitrogen uptake directly from the volcanic deposits and indirectly from mycorrhizal fungi while *S. reinii* does not change the nitrogen dependence on them (Kwon and Tsuyuzaki 2016). Therefore, the effects of shrub patches on the cohabitants should be evaluated with different elevations (Schöb et al. 2013).

Another paradigm is that facilitation intensity is changed with the structure and size of facilitators (Bruno and Kennedy 2000). For example, large and unfragmented vegetation patches maintain high diversity in Mediterranean alpine grasslands (Pescador et al. 2020). Although not only shrub patch size but also branch density and litter accumulation affect the interspecific interactions (Loydi et al. 2013), the interactive effects of these shrub characteristics should be clarified. The interannual variations of facilitation intensity are expected if the variations are large, because the effects of facilitation are collapsed when strong disturbances and/or stresses occur (Koyama and Tsuyuzaki 2013). Furthermore, the patch effects act differently on the life-history stages, such as seedling emergence, flowering

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

We hypothesized that: (i) the effects of shrubs were facilitative at community level expressed by species richness, (ii) size-dependent effects of patches on the life-history stages differ between the cohabitant species at different elevations and years and (iii) the overall effects of shrub patches on the cohabitants were positive, although the effects of patches were sometimes negative for a few life-history stages of cohabitants. To clarify these, the recruitment, survival, growth of plants in the inside and outside of *S. reinii* patches were compared on Mount Koma with three elevations for two summer seasons.

MATERIALS AND METHODS

Study sites

Mount Koma is located in southern Hokkaido, northern Japan (42°03'48"N, 140°40'38"E, 1131 m a.s.l.). The south-western slope was used for this study. The recent major eruption occurred in 1929 producing 0.38 km³ of ash and 0.14 km³ of volcanic ejecta (Kondo and Tsuyuzaki 1999), of which thickness was more than 100 m near the crater and decreased with increasing distance from the crater (Yoshimoto et al. 2007). The vegetation recovery has slowly progressed from the bottom of the mountain. Nowadays, the vegetation cover makes a gradient along elevation, and treeline is ragged (Nishi and Tsuyuzaki 2004). The canopy mostly consists of a deciduous, needle-leaved, exotic tree *Larix kaempferi* above 450 m in elevation, due to intensive artificial plantations on the foot after 1953 (Kondo and Tsuyuzaki 1999). A broad-leaved forest develops below 400 m in elevation. On the ground surface, plant cover also decreases with increasing elevation (Tsuyuzaki et al. 2011). Near the summit area, a deciduous dwarf shrub *Salix reinii* forms patch that facilitate the establishment of cohabitants (Uesaka and Tsuyuzaki 2004). A few small-scale eruptions recently occurred on the summit from 1996 to 2000, but the impacts were least on the study area.

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

from -6.9°C in January to 24.6°C in August on average (data obtained from Japan Meteorological Agency (JMA) 2019). The snow-free period usually occurs from May to October. Monthly precipitation data for 2005 and 2006 were obtained from O-numa Meteorological Station (131 m elevation), which is approximately 8 km from the study area and managed by JMA. Summer precipitation (May to September) averages 564.7 mm and winter precipitation (October to April) does 559.4 mm for the last 30 years (JMA 2019). The annual precipitation did not differ between 2005 and 2006, i.e., it was 1,093.0 mm in 2005 and 1058.5 mm in 2006 but precipitation during the summer (from July to September) differed greatly between the two years, i.e., it was 424.0 mm in 2005 and 224.5 mm in 2006 (Fig. S1). The summer precipitation in 2006 was lower than usual, although the annual precipitation was not different greatly between the surveyed and averaged years.

Measurements of environmental factors

The measurements were conducted at low (550-588 m a.s.l.), middle (677-718 m) and high (759-781 m) elevations (Fig. 1). The forest canopy, dominated by *Larix kaempferi* (larch), was more developed at lower elevations (Kondo and Tsuyuzaki 1999).

The microclimate was measured at 10 min intervals by weather stations (Hobo Weather Station, Onset, Bourne) at the three elevations (Tsuyuzaki et al. 2011). Wind speed was measured by a wind gauge (S-WCA-M003) at 50 cm above the ground surface on the bareground at each elevation. Temperature and photosynthetic active radiation (PAR) were measured by a thermometer (S-TMA-M017) and a PAR sensor (S-LIA-M003) at ground level on bareground and in the center of *Salix reinii* shrub patch at each elevation. Precipitation at the middle elevation was measured by a rain gauge (S-RGB-M006) on bareground. The measurements were conducted from 1 July 2005 to 31 October 2005 and from 1 June 2006 to 30 June 2006 at 10-min intervals.

The volcanic deposits were collected by a steel soil tin (20 cm² in surface area, 5 cm in depth) to measure water content, pH, total nitrogen (N) and phosphorus (P). The samples

were collected from the three elevations in a pair of bareground and patch at each elevation at 1-month intervals from June to October in 2005. Therefore, the total number of samples was 90. To avoid the disturbances on the ground surface, the patches monitored shoot dynamics were not selected for the chemical measurements. The samples were kept in plastic bags, carried to the laboratory soon after the sampling, and the fresh weight was measured. To measure pH, 10 g of the volcanic deposits was saturated with 25-mL distilled water and agitated well. The mixture was left for 1 hour, and then pH was measured by a glass electrode (MP120, Mettler-Toledo, GmbH, Schwerzenbach). Then, the samples were dried at 110°C in an oven for three days and the dry weight was measured. Soil moisture was calculated as: $(\text{fresh weight} - \text{dry weight}) / (\text{dry weight}) \times 100$ (Marshall et al. 1996). N was measured by particles passed through a sieve of which mesh was 2 mm in diameter, and P was measured by particles less than 0.05 mm in diameter. N was measured by a C/N coder (Elementar Vario EL, GmbH Japan Siberhegner), and P was measured by a Truog method (Patnaik 1997).

***Salix reinii* shrub patches**

At each of the three elevations, 20 patches, of which area ranging from 0.46 m² to 1.16 m² were marked in early May 2005. Close to each patch, 1 m × 1m plots were established on the bareground used for control. The patch and bareground were separated at more than 50 cm to avoid the effects of patches on bareground. Shrub area, height and branch density were measured on each patch by the following procedure. First, each plot or shrub was divided into 10 cm × 10 cm cells. At each lattice point of the cells, the height was measured. Also, the number of leaves and branches touched at a slim rod was counted at each lattice point. Litter thickness was also measured by a ruler at each lattice point. Thereafter, the averages of branch density (number of hits) and litter thickness were calculated on each patch.

Monitoring shoot dynamics

The shoot dynamics was monitored at every month from June to October in 2005 and from May to September in 2006. The height, area (cover) and number of leaves were recorded on each shoot at every monitoring. The cover was calculated by measuring lengths of major and minor axes, as an assumption of oval shape. At the last monitoring in 2006, all the marked shoots were harvested to measure the biomass, except for shoots consisting of *S. reinii* patches. The samples were dried at 70°C in an oven for 48 hours soon after the sampling and weighed.

Statistical analysis

The plant cover in each plot or patch was calculated by the sum of shoot areas on each species. All the statistical analyses were conducted by R (ver. 3.6.1) (R Core Team 2019). To investigate relationships between patch characteristics, i.e., area, height, branch density (number of hits) and litter thickness, correlation coefficients were used. Shrub characteristics, i.e., area, height, patch density and litter thickness were compared between the three elevations with random effects of plot code and year by generalized linear mixed-effects models (GLMMs). Moisture, pH, total nitrogen and phosphate were compared between the habitats and between the elevations with their interactions by two-way repeated-measures analysis of variance (ANOVA) after Shapiro-Wilk test of normality that indicated all the examined variables followed normal distribution ($P < 0.05$), because the data were not analyzed by GLMMs due to the sampling design. The patch height was excluded for the analyses shown below, because of the small variation.

Species richness, diversity and evenness were calculated based on the plant cover by a package vegan (Oksanen et al. 2019). Since cover diversity is affected more by disturbances and stresses than the shoot density diversity (Tsuyuzaki and del Moral 1994, Tsuyuzaki 1996), cover was used to investigate the effects of disturbances on the community diversity. Differences in these three parameters between the inside and outside of patches in 2006 were investigated with elevation by a generalized linear model (GLM) with the assumptions of

Poisson, gamma and binomial distribution, since these three parameters did not differ between 2005 and 2006 (GLM, $P > 0.05$). As well, determinants on these three parameters in the inside of patches were investigated with elevation, branch density and litter thickness by GLM. The interactions between these explanatory variables are included. The best models were selected by Akaike's Information Criteria with a stepwise procedure.

Based on the records of shoots, the shoots were separated into two life-history stages, seedling and non-seedlings. When new shoot was firstly recorded, the shoot was recorded as (annual) seedlings. Since few seedlings were observed in May, all the shoots recorded in May were regarded as non-seedling. The relative growth rate (RGR) of each shoot was calculated by: $\log(\text{maximum height in 2006}) - \log(\text{maximum height in 2005})$ for shoots recorded for the 2 years.

Zero-inflated Poisson (ZIP) model was applied for investigating the determinants on numbers of seedlings and non-seedlings, because of excess zero, using a package *pscl* (Jackman 2017). Determinants on shoot mortality during the surveyed period were investigated by Cox regression model by a package *survival*. The determinants on flower production were investigated by a GLMM with a Poisson distribution. On these two models, the response variables are mortality and flowering. For all these analyses, differences between the inside and outside of patches were examined firstly and then the inside of patches were examined with the explanatory variables (patch area, patch density, litter thickness and elevation). In the case of flowering, year was also used as an explanatory variable.

RESULTS

Shrub patch structures and the environments

Wind speed decreased with decreasing elevations, i.e., 3.6 m/s (in average, maximum gust = 14.8), 2.6 (11.0) and 1.0 (9.5) at high, middle and low elevations, respectively, mostly due to the shelter effects of the larch canopy. Total precipitation during July and September, when

most plants grew, was 536 mm in 2005 and 317 mm in 2006, respectively. The PAR was approximately 30 times higher on the bareground than in the shrub patch (Table S2) with the seasonal changes, suggesting that shading by the patch was the main factor determining the PAR in the patches. Associated with low PAR in the patches, the temperature was also lower in the patches. The mean temperature was more than 1°C lower in the shrub patches than on the bareground throughout the snow-free period, showing that not only leaves but also branches reduced the temperature (Table S2). These results showed that the shrubs affected the aboveground environments.

The water content ranged from 9% to 25% in the bareground and from 9% to 48% in the patches (Fig. 2). The water content was higher in the patches (two-way ANOVA, $P < 0.001$) and differed among the elevations ($P < 0.001$). The pH in the volcanic deposits was less than 6.5 and did not differ between habitats and among elevations ($P > 0.50$). The total nitrogen was lower in the baregrounds than in the patches ($P = 0.004$) and did not differ among the elevations ($P = 0.14$). Phosphate in the volcanic deposits ranged from 1.0 $\mu\text{m/g}$ to 14.7 $\mu\text{m/g}$ in the baregrounds and from 2.9 $\mu\text{g/g}$ to 25.2 $\mu\text{g/g}$ in the shrub patches. The phosphate concentrations were higher in the patches ($P < 0.001$) and did not differ among the elevations ($P = 0.09$). Overall, therefore, the nutrients and moisture in the volcanic deposits were increased by the *Salix* patches. Since the interactions between elevation and habitat were not detected except for water content ($P > 0.05$), the effects of patches on the properties in the volcanic deposits were affected by the elevation.

The shrub heights were less than 46 cm, 33 and 34 cm at the low, middle and high elevations, respectively (Table S1). The branch densities were less than 6.2 (hits averaged per 10 cm long). The litter thickness varied greatly in the inside of shrub patches, ranging from 0.0 mm, i.e., no litter, to 6.5 mm, and was 0 cm in the outside. The litter consisted mostly of *S. reinii* leaves. Shrub structure, i.e., the height, area, density and litter thickness, did not differ among the three elevations (GLMM, $P > 0.05$). Shrub structure did not change for the two surveyed years ($P > 0.05$), indicating that the unexpected events, such as

herbivore damage, occurred least for the two years. Correlations between the branch density and litter thickness were not significant ($r = -0.115$ and -0.149 in 2005 and 2006, $n = 60$, $P > 0.26$), and those between the patch area and litter thickness were also not significant ($r = +0.219$ in 2005 and $+0.203$ in 2006, $P > 0.09$). These results indicated that the litter thickness was not determined by the shrub area and branch density.

Vegetation patterns

In total, 1881 shoots were recorded from 28 vascular plant species, including an un-identified shoot (Table S3). The common species were *Carex oxyandra*, *Luzula capitata*, *Calamagrostis hakonensis*, *Larix kaempferi*, *Salix reinii* and *Gaultheria miqueliana* (Fig. 3). Of these, *C. oxyandra*, *L. capitata* and *C. hakonensis* were perennial herbs, *S. reinii* and *G. miqueliana* were shrubs and *L. kaempferi* was an exotic tree. These six species comprised 1487 shoots (79.1% to total) for the 2 years.

On the six common species, 357 and 327 shoots originated from seedlings in 2005 and 2006, respectively. Most seedlings emerged in June and July for both years (Fig. 3). *Calamagrostis hakonensis* and *S. reinii* increased their shoots with increasing the elevations, while the other species decreased their shoots with the elevations. The numbers of seedlings for all the species except for *L. kaempferi* were different between 2005 and 2006 (Table 1), probably because of the climate differences. The seedling emergence of *C. oxyandra* and *C. hakonensis* was negatively and positively related to the elevation increase, respectively. The year was correlated significantly to the seedlings of all the species at binomial and/or Poisson part. The numbers of non-seedlings were 683 and 1345 in 2005 and 2006, respectively, showing that the most of seedlings emerged in 2005 survived until 2006. As well as the annual seedlings, the elevation and year affected the numbers of non-seedlings. These results showed that the interannual variations of seedling emergence were large, depending on the species characteristics, and survived once established.

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

the species (Cox regression model, $P < 0.01$, Table 3), showing that small plants died more. When the differences between inside and outside patches were not considered, the mortality increased with increasing elevation for *C. hakonensis*, *L. kaempferi*, *S. reinii* and *G. miqueliana*. The elevation did not affect the mortality of the other two common species, *C. oxyandra* and *L. capitata*. As well as the mortality, flowering was related to the shoot heights, i.e., taller shoots produced more flowers for all the examined species ($P < 0.01$) (Table 3). Therefore, the elevation did not affect the flowering for all the species.

Differences between inside vs outside of patches

Over the whole elevation gradient, species richness in 2006 averaged 2.87 ± 2.38 outside patches and was 3.05 ± 2.20 inside. The species richness was higher in the patches than on the bareground (slope = + 2.003, GLM, $P = 0.028$) and was higher at higher elevation (+0.003, $P = 0.002$) in 2006. Interactions between the elevation and habitat was significant (-0.003, $P = 0.033$). Six species establishing only in the patches: *Pyrola incarnata* (frequency = 7), *Agrostis flaccida* (3), *Platanthera metabifolia* (2), *Agrostis scabra* (1), *Chimaphila umbellata* (1) and *Solidago virgaurea* (1). There were four species established only outside: *Populus sieboldii* (2), *Drosera rotundifolia* (1), *Pinus densifolia* (1) and *Salix bakko* (1). Diversity increased with elevation (+0.002, $P = 0.007$) and did not differ between the patches and bareground ($P = 0.508$). The evenness was affected by neither the elevation ($P = 0.357$) and patches ($P = 0.956$). In total, therefore, the effects of patches were facilitative to the establishment of rare species and were more intensive at higher elevation where the environments were more severe.

Seedlings emerged more within the patches (517) than on the baregrounds (429) and more in 2005 (805) than in 2006 (141) (Fig. 3). *C. oxyandra*, *C. hakonensis*, *S. reinii* and *G. miqueliana* emerged more seedlings in the patches, while *L. capitata* and *L. kaempferi* did more on the bareground (Table 1). The maxima of numbers of non-seedlings were 27 and 42 in the outside and inside of the patches, respectively, in 2005 and 27 and 44 outside and

inside patches in 2006. On the zero-inflated Poisson model, *C. oxyandra*, *L. capitata* and *C. hakonensis* showed more non-annual seedlings inside the patches than outside when number of seedlings was examined by the Poisson part. *Salix reinii* showed the positive effect of patches on the non-seedlings when the presence or absence of seedlings was examined by the binomial part. The patch effect was negative for *L. capitata* at the binomial part. The patch effects on non-seedlings were positive for four of the six common species.

The mortality was higher inside patches than outside for *L. capitata* (Cox regression model, $P = 0.0001$) and *S. reinii* ($P = 0.044$). However, these two species favored to establish on the bareground, as shown by annual seedlings. The other four examined species did not differ their mortalities between the inside and outside ($P > 0.05$). The flowering was less for *C. hakonensis* within the patches (GLMM, $P < 0.01$) and was not different for *C. oxyandra*, *L. capitata* and *G. miqueliana* between the inside and outside of the patches. The flowering of other species was not examined due to the sample sizes. In total, the patches weakly affected mortality and flowering for most species.

Effects of patch structures on cohabitants

The species richness investigated only within the patches was affected negatively by the three parameters of patch structures, area, branch density and litter thickness, with their interactions (Table S4), although the richness was higher in the patches as compared with the bareground. The species diversity was not different among the three elevations and was affected negatively by the patch area and branch density negatively with their interaction. The evenness was not related to any examined parameters. Considering with higher species richness within the patches than on the bareground, the optimal size of patches should be presented.

Seedling emergence within the shrub patches was not tightly related to the area, branch density and litter thickness of patches with a few exceptions (Table 2). Elevation affected the seedlings of *C. oxyandra*, *C. hakonensis* and *L. kaempferi* when the number of seedlings was

examined. Seedling emergence differed between 2005 and 2006 for four of the six common species. Non-seedling *C. oxyandra* decreased the number with increasing the shrub patch area and branch density. Branch density also reduced the non-seedlings of *S. reinii* and *G. miqueliana*. In contrast, *L. kaempferi* increased the non-seedlings with increasing the branch density. The non-seedlings of *G. miqueliana* established less in the large patches. Litter thickness negatively affected the number of non-seedlings for *L. capitata*, *S. reinii* and *G. miqueliana*. Since the patches were larger than 1 m² in this study, these results considering with the richness suggested that the optimal size of patches for facilitation was smaller than 1 m².

The area, branch density and litter thickness of patches, affected the shoot mortalities on *L. capitata* and *S. reinii* (Table 3). *Luzula capitata* shoots died more in denser patches at low elevation. The mortality of *S. reinii*, itself, was positively related to the patch area and negatively to the branch density, suggesting that the area functioned differently from the branch density.

Flowering was investigated for three well-flowered species (Table 3), because of the sample sizes. *Calamagrostis hakonensis* decreased the flowering when the litter was thick. The interannual variation of flowering was detected only for *C. hakonensis*. The patch characteristics did not affect the RGRs of shoot volume for all the species (Fig. S2). RGR on four species, *C. oxyandra*, *L. capitata*, *C. hakonensis* and *G. miqueliana*, increased with increasing elevation, independent of shrub patches, but did not affect *L. kaempferi* and *S. reinii*. Therefore, the shrub patches affected the shoot density more than the shoot growth.

DISCUSSION

The effects of patches on vegetation development

The rare species established in the patches more than on the bareground, showing that the shrub contributed to increase the community and landscape diversities. Shrub facilitation increases species richness and diversity by allowing the establishment of stress-intolerant

species into harsh environments in an arid scrubland, despite increasing shrub-seedling competition (van Zonneveld et al. 2012). Furthermore, the annual and non-annual shoots tended to be more in the patches for the common species. These indicated that the overall effect of patches was facilitative.

The *Salix reinii* patches ameliorated the microclimates, i.e., moisture, nitrogen and phosphate, in the volcanic deposits. Shrub patches of *Caragana microphylla* and *Salix gordejewii* increase nutrient (N and P) and moisture in the soils and act as seed traps in Mongolian sand dunes (Zhao et al. 2007), although ecosystem changes are determined by multiple mechanisms of shrub facilitation through seedbank development, etc. in drylands (Filazzola et al. 2019). The baregrounds on Mount Koma showed higher temperature and light during the plant growing seasons and the patches moderate these climatic conditions (Tsuyuzaki et al. 2011).

However, the growth (RGR) did not differ between the patches and baregrounds for all the common species and the mortality was higher for the two species, *L. capitata* and *S. reinii*. The flowering was different along the elevations for four of the six common species. These indicated that the patch effects were negative at a few life-history stages, although the establishment of shoots was higher in the patches. Facilitators decrease the survival and increase competition for young plants, such as seedlings, in Brazilian coastal dunes, although the overall facilitation of facilitator works positive (Beduschi and Castellani 2013).

Effects of shrub patch structures on cohabitants

The structural characteristics of shrub patches, i.e., area, height, branch density and litter, were not strongly correlated to each other, indicating that the shrub patches acted variously to the cohabitants. Of these shrub characteristics, litter accumulation within shrub patches is often the key to determine the patch effects. Moderate litter accumulation assists the seedling establishment by improving the microenvironments, including the reduction of strong sunshine and drought (Egawa and Tsuyuzaki 2013). Optimal litter thickness seems to be

present for seed trap effect and seed germination as well as patch size and is different between the cohabitant species (Zhang et al. 2017). Since the litter accumulation was not determined by the aboveground structures of shrubs on Mount Koma, the litter accumulation should be determined by microtopography such as soil texture and small rill-ridge pattern (Otaki et al. 2016).

The overall effects of patches on the cohabitants were positive when the patches were compared with the bareground. However, the effects of patch structures, i.e., patch area, branch density and litter thickness, were often negative to the cohabitants only when the inside of patches was investigated. These results suggested all these patch structure characteristics had the optimal sizes for the facilitation, which were smaller than the surveyed patches, i.e., 1 m². Since the overall effects of patches, of which size is larger than approximately 0.1 m², are facilitative (Uesaka and Tsuyuzaki 2004), the optimal size for facilitation should range from 0.1 to 1.0 m². However, larger patches increase the seed germination of *Polygonum sachalinense* and *Miscanthus sinensis* up to 4 m² in area (Holle and Tsuyuzaki 2018). Since shrubs formed by *Artemisia tridentata* changed the morphological forms with size, the facilitative function is changed with the shrub size (Urza et al. 2019). These indicate that the optimal patch sizes differ among the species. Litter has the optimal thickness as well as patch area. Litter has a positive effect on seedling establishment under dry conditions and/or with low to medium litter amounts, although excess litter negatively affects the establishment (Loydi et al. 2013).

Variations in shoot dynamics

The interactions between *Salix reinii* shrub patches and the cohabitants, examined by number of shoots, in particular, for non-seedling shoots, differed among the elevations. RGR increased with increasing elevation for *C. oxyandra*, *L. capitata* and *G. miqueliana*, irrespective of the shrub patches. These results indicated that the effects of shrub patches were weak to the vegetative growth of these species. As *L. kaempferi* became larger and

denser at lower elevations on Mount Koma (Tsuyuzaki et al. 2011), the effects of *L. kaempferi* should be higher than the effects of *S. reinii* with decreasing the elevations. An exotic tree, *Larix kaempferi*, accelerates the succession for non-tree species (Titus and Tsuyuzaki 2003). Two facilitators have more beneficial effects on the cohabitants than single facilitator in an arid shrub-herbaceous community (Zhang et al. 2011). Further research is required to clarify if the positive effects of *S. reinii* are reduced by *L. kaempferi* trees. The belowground strategy of plants is also important for the establishments of these species, in particular, at the high elevations where light resource is high without shade (Tsuyuzaki and Hase 2005). The belowground traits of plants should be focused more for understanding facilitation (Rohhauser and Pucheta 2016).

The seedling emergence for most species differed between the two surveyed years. The precipitation was lower in 2006. Although the moisture in the volcanic deposits was measured only in 2005, the moisture should be lower in the summer from July to September in 2006 than in 2005, because the moisture fluctuation followed precipitation in summer (Tsuyuzaki et al. 2011). Germination phenology or timing is tightly related to a tradeoff between facilitation and competition (Leverett 2017). In such years as seen in 2006, the effects of drought precluded the facilitative effects of patches. The facilitation intensity is increased with increasing stresses and disturbances until these factors are not beyond the thresholds of resilience (Koyama and Tsuyuzaki 2013, Hotes et al. 2010). The shift from facilitation to competition was triggered by low rainfall on a shrubland in southeast Spain (O'Brien et al. 2017). Therefore, interannual variations were conspicuous and hindered the effects of patches.

In conclusion, the *S. reinii* patches facilitated the establishment of cohabitants and increased the species richness, showing that the facilitation is beneficial not only for common species but also for rare species. The interspecific interactions changed with climatic variations along elevational gradients. For example, the seedling establishment of *C. 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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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.

	<i>Carex oxyandra</i>		<i>Luzula capitata</i>		<i>Calamagrostis hakonensis</i>		<i>Larix kaempferi</i>		<i>Salix reinii</i>		<i>Gaultheria miqueliana</i>	
	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	<i>Carex oxyandra</i>		<i>Luzula capitata</i>		<i>Calamagrostis hakonensis</i>		<i>Larix kaempferi</i>		<i>Salix reinii</i>		<i>Gaultheria miqueliana</i>	
	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	<i>Carex</i> <i>oxyandra</i>	<i>Luzula</i> <i>capitata</i>	<i>Calamagrostis</i> <i>hakonensis</i>	<i>Larix</i> <i>kaempferi</i>	<i>Salix</i> <i>reinii</i>	<i>Gaultheria</i> <i>miqueliana</i>
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*	-	-	-

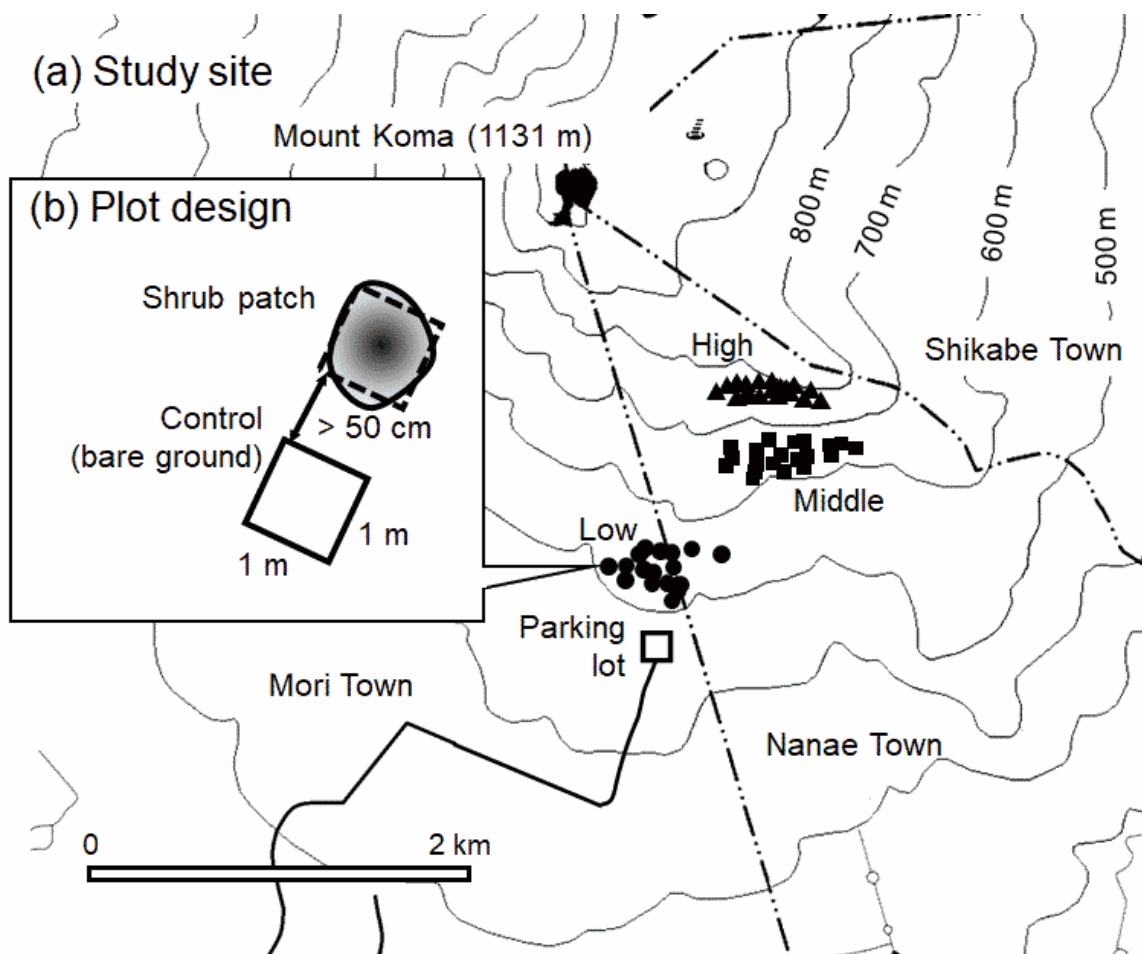


Figure 1: (a) Study site. The locations of plots at high, middle and low elevations are shown by closed triangles, squares and circles. Phantom lines indicate administrative boundaries. The top of graph is faced to north. (b) Plot design. Shrubs of which areas were approximately 1 m^2 were selected. On a patch and the bareground (control), climatological data were obtained by a weather station. In details, see also in the text.

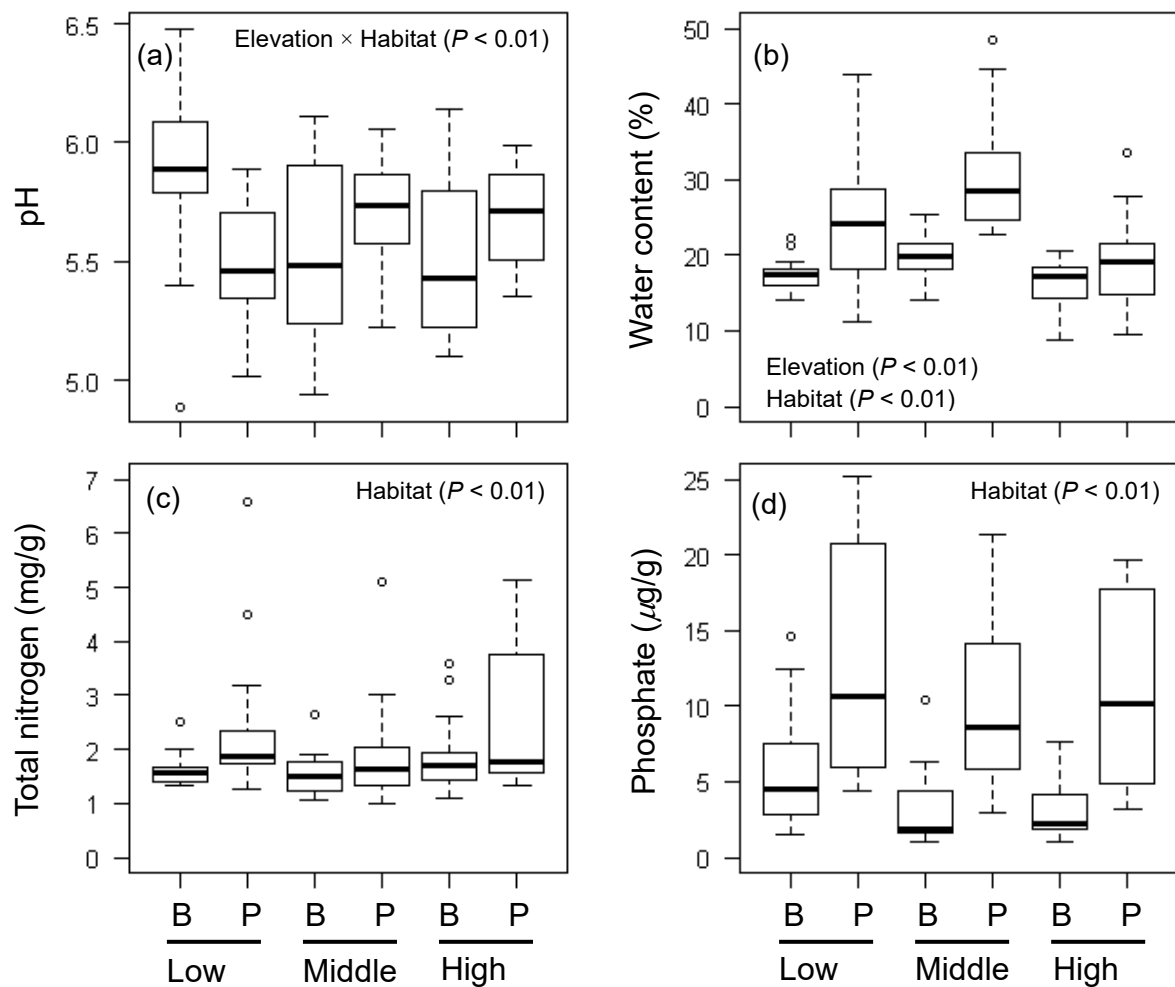


Figure 2: Chemical properties, pH (a), water content (b), nitrogen (b) and phosphate (d), of the volcanic ash in 2005 on Mount Koma, shown by box-whisker plots. Habitat: B = bareground, and P = *Salix reinii* patch. The differences in chemical properties are compared between elevation, and between the 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.

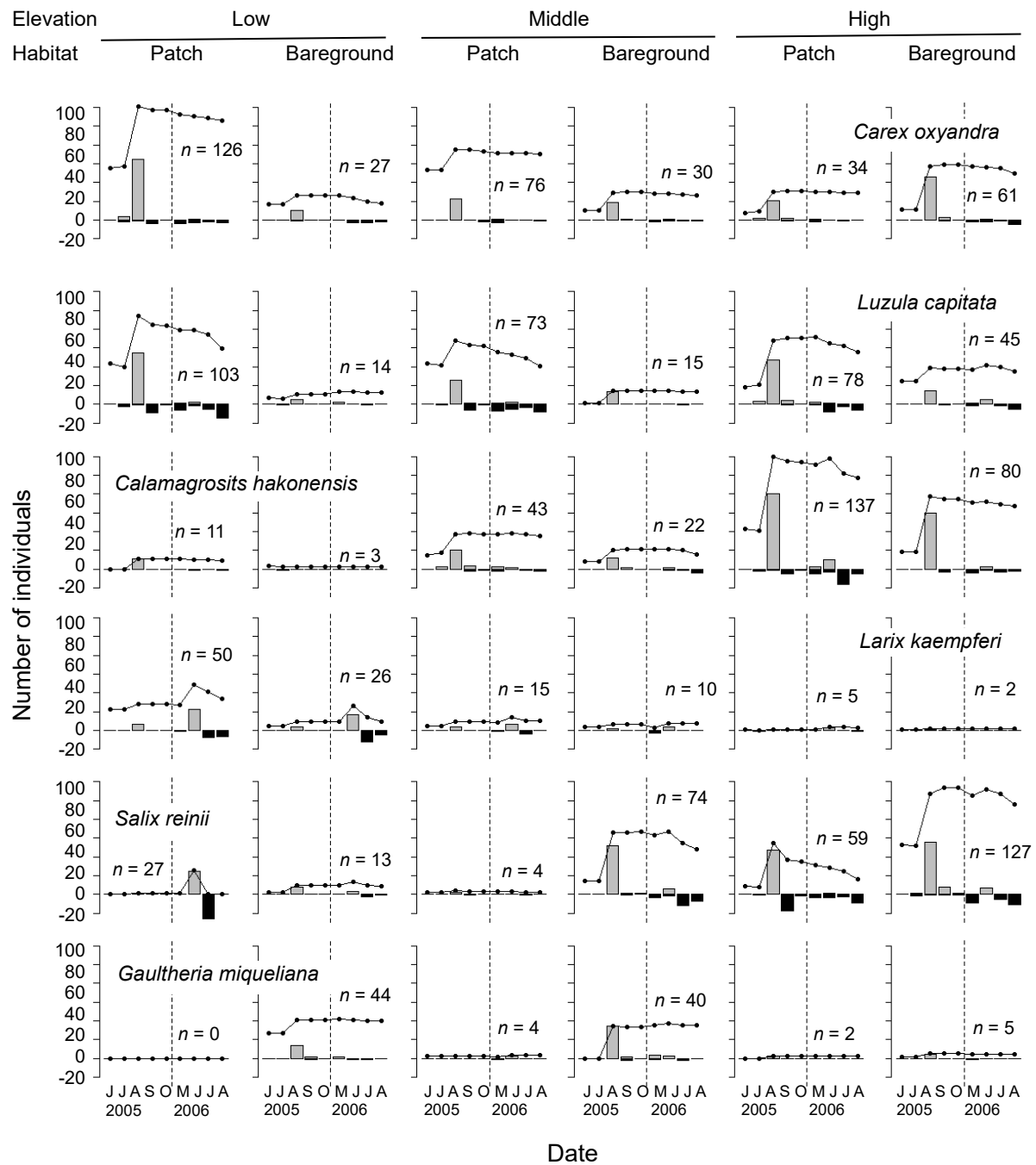


Figure 3: The fluctuations of number of shoots during snow-free periods from 2005 to August 2006 at low, middle and high elevations on six common species. Broken lines indicate the number of shoots observed. Positive and negative bars indicate number of emerged seedlings and number of shoots died, respectively. On the *S. reinii*, the shoots consisting of the shrub patches are excluded. n = total number of shoots.