Far Eastern Studies Vol.6 May 2007
Center for Far Eastern Studies, University of Toyama

Fine-scale species richness of alpine fellfield plant communities on a middle-latitude mountain of central Japan: Influences of alpine dwarf pine and substrate properties

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Abstract

I compared the vascular plant species richness of fellfield plant communities in the Northern Japan Alps, investigating fine-scale species-area relationships and comparing the number of species in different areas. I also investigated the relation of rate of species richness increase with area in different communities to substrate properties and cover of alpine dwarf pine *Pinus pumila*. Fellfield plant communities on fine gravel habitats had lower coverage and fewer species than communities on large gravel habitats. The plant community where *P. pumila* was distributed patchily had the lowest number of species per m^2 but the fastest rate of species richness increase with area. The plant community where *P. pumila* had developed continuous canopies was mostly composed of species usually found in the alpine-subalpine and lowland zones, whose seeds are dispersed by birds and mammals. The alpine dwarf pine appeared to exclude from habitats alpine specialists that are distributed only in the alpine life zone above the timberline.

Keywords: *Alpine community, Pinus pumila, species-area relationship, species diversity, species richness*

Introduction

With recent changes in the global environment, a great deal of concern has arisen about conserving biodiversity in various types of ecosystems (Baskin, 1997). To better understand biodiversity and its contribution to conservation on both regional and global scales, it is important to determine how many species are distributed in a given area. To this end, researchers have started to monitor biodiversity in the Western Pacific and Asia, with special focus on forest, freshwater, and coastal marine ecosystems (Stork and Nakashizuka, 2002). As compared to these ecosystems, little attention has been paid to the alpine life zone in Japan, which is at the southernmost limit of the geographical distributions of many circumpolar and alpine plants. This may increase their sensitivity to global warming (Gottfried et al., 2002; Spehn et al., 2002; Beniston, 2003).

Climates at high elevations are harsher for organisms, decreasing species richness in the alpine life zone. However, species richness at high elevations is greater than at low elevations when the smaller amount of available land area at high elevations is taken into account (Körner, 2002). This may be because alpine plants (plants above the timberline) reach only one tenth the size of their closest lowland relatives (Körner, 1999). A great number of such individuals and species can nest in

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any given space, including the many microhabitats highlands offer (Körner, 2002). Because of this, the alpine life zone has many small, highly species-rich microhabitats (Onipchenko and Semenova, 1995; Kammer and Möhl, 2002). Unfortunately, there is little information about spatial variations in species richness of alpine plant communities in the mountains of Japan. Information on species-area relationships is particularly lacking, which contrasts with a relative abundance of phytosociological studies (e.g., Tatewaki, 1963; Kobayashi, 1967; Ohba, 1974; Ito and Nishikawa, 1977). In this study, I report on fine-scale vascular plant species richness (alpha diversity; Whittaker, 1977) and heterogeneity of species richness within and between plant communities (beta diversity; Whittaker, 1977) located on wind-blown ridges or around the summits of Mt. Akaushi and Mt. Suisho, in the Northern Japan Alps, a middle-latitude mountain area of central Japan.

The uppermost zone (the alpine life zone above the timberline) of the high mountains in Japan has a landscape of vegetation unique in the world; a distinct zone (the so-called *Pinus pumila* zone) in the altitudinal series characterized by dominance of the alpine dwarf pine *Pinus pumila* (Pall.) Regal (Hamet-Ahti et al., 1974; Okitsu, 1985; Okitsu and Ito, 1989). This alpine evergreen scrub is highly efficient in energy fixation and net-production and maintains a large leaf biomass (Kajimoto, 1994) whose values are not very different from those of *Abies* trees in subalpine forests (Kajimoto, 1995). This suggests that *P. pumila* can greatly impact species richness of alpine plants by changing their habitat. It may do this by increasing shade cover with its dense evergreen foliage as it invades and establishes itself in open habitats (e.g., Watanabe, 2005).

The alpine ecosystem is generally composed of two contrasting habitats: fellfields and snowbeds (Körner, 1999). Snowbeds are located on leeward slops where a large amount of snow accumulates, while fellfields are located on ridges or around mountaintops where little snow accumulates, resulting in frozen soil in winter and cool air temperatures in spring (Shimono and Kudo, 2003; Wada and Nakai, 2004). The alpine dwarf pine frequently colonizes wind-blown fellfields (e.g., Kajimoto et al., 1998; Kajimoto, 2002) from its mature stands in intermediate habitats between fellfields and snowbeds, mostly by directional seed dispersal by a seed-hoarding nutcracker, *Nucifraga caryocatactes* (Hayashida, 1994). The dense foliage of *P. pumila*, prevents light from reaching other alpine plants even when the pine establishes its small patches in open habitats. This may considerably reduce species numbers if most alpine plants, which have adapted to full sun conditions, are not shade tolerant. The first aim of this study is to clarify the spatial associations between *P. pumila* and the other alpine plants in a fellfield plant community to reveal the effects of *P. pumila* on species richness of alpine plants.

In fellfield habitats, periglacial debris on the ground is moved around when the soil freezes in winter and thaws in spring (Koizumi, 1979, 1980; Chujo, 1983). This prevents many alpine plants from developing their roots and/or aboveground organs (Chujo, 1983) and from establishing seedlings (Shimono and Kudo, 2003). The magnitude of ground surface movements may vary with different substrate properties (Koizumi, 1979, 1980; Chujo, 1983), suggesting that variations in substrates strongly affect species richness of plant communities. The second aim of this study is to determine how substrate properties affect species richness of alpine fellfield.

Materials and methods

Study sites and vegetation survey

The study area is located at high elevations in the Hida Mountains in the Northern Japan Alps. In the summer of 2001, I established four study plots on fellfield communities on the ridges between Mt. Akaushi and Mt. Suisho. Plot Q1 (a 5 × 5 m quadrat) was located on an upper slope (a west-facing slope with a 15-degree incline) covered with fine gravel and reddish sand of granitic origin at 2550 m a.s.l. The particle size of the fine gravel was less than 1 cm. Plot Q2 (a 2 × 5 m quadrat) was located on a scree slope (a west-facing slope with a 5-degree incline) covered with large gravel of andesite origin at 2930 m a.s.l. The grain size of the dominant large gravel was more than 10 cm. There was no alpine dwarf pine *Pinus pumila* in these two plots. Plots Q3 (a 5 × 5 m quadrat on a gentle west-facing slope with a 2-degree incline at 2700 m a.s.l.) and B1 (a 1 × 20 m belt-transect on a west-facing slope with a 5-degree incline at 2850 m a.s.l.) were located on a crest and a mountain top of Mt. Akaushi, respectively, where the ground surface was made up of scattered stones, intermediate-sized gravel and reddish sand of granitic origin. *P. pumila* was patchily distributed in plot Q3 and covered most of B1. Each plot was divided into 1 × 1 m subquadrats, for which the number of vascular plant species and the coverage for each species were recorded.

Species-area relationships

Mean species richness, i.e., the number of vascular plant species per area, was calculated for each plot. In plots Q1 and Q3, mean species richness was calculated on five spatial scales by combining adjacent subquadrats on each spatial scale: 1 × 1 m (n = 25), 2 × 2 m (n = 16), 3 × 3 m (n = 9), 4 × 4 m (n = 4), and 5 × 5 m (n = 1). In plot Q2, mean species richness was calculated on five spatial scales: 1 × 1 m (n = 10), 1 × 2 m (n = 14), 2 × 2 m (n = 4), 1 × 9 m(n = 4), and 2 × 5 m (n = 1). In plot B1, mean species richness was calculated on five spatial scales: 1 × 1 m (n = 20), 1 × 4 m (n = 17), 1 × 9 m (n = 11), 1 × 16 m (n = 5), and 1 × 20 m (n = 1).

The species-area relationships were analyzed using the following formula (cf. Drakare et al., 2006):

$$S = c\,A^{z} \qquad (1),$$

where S is the number of species, A is the area under investigation and c and z are regression parameters. Parameter z represents the rate of increase in species richness within the area (i.e., beta diversity), and parameter c represents the number of species per m^2 (i.e., alpha diversity). These parameters were compared between the fellfield communities using analysis of covariance (ANCOVA).

Effect of Pinus pumila cover

To clarify the influence of *Pinus pumila* on spatial distribution and species richness of alpine plants, the spatial association between *P. pumila* and other species was analyzed by calculating the ω index as described by Iwao (1977) for the 1 × 1 m spatial scale (n = 25 subquadrats) in plot Q3, where the alpine dwarf pine was patchily distributed:

$$\omega = [(m^*_{XY}m^*_{YX} - m_X m_Y)/((m^*_x + 1)(m^*_Y + 1) - m_X m_Y)]^{1/2} \text{ (when } \omega \geq 0\text{) or}$$
$$\omega = [(m^*_{XY} / m_X)(m^*_{YX} / m_Y)]^{1/2} - 1 \text{ (when } \omega \leq 0\text{)},$$
$$m^*_{XY} = \sum x_{Xj}x_{Yj} / \sum x_{Xj},$$
$$m^*_{YX} = \sum x_{Xj}x_{Yj} / \sum x_{Yj},$$
$$m^*_X = \sum x_{Xj} (x_{Xj} - 1) / \sum x_{Xj},$$
$$m^*_Y = \sum x_{Yj} (x_{Yj} - 1) / \sum x_{Yj},$$

where x_{Xj} and x_{Yj} are coverage of species X and Y in the *j*th subquadrat and m_X and m_Y are the average coverage of species X and Y in subquadrats from $j = 1$ to $j = N$. The value of ω ranges from a maximum of +1, which corresponds to a complete overlap, to 0, which corresponds to independent occurrence, to a minimum of –1, which corresponds to complete exclusion (Iwao, 1977).

Results

Higher frequencies of perennial forbs and grasses and lower frequencies of shrubs (except for *Arctous alpinus* var. *japonicus* in Q2) were observed in both fine-gravel (Q1) and large-gravel (Q2) habitats (Table 1). However, lower species richness (m^{-2}) and sparser vegetation coverage were found in Q1, which was composed of *Potentilla matsumurae*, *Viola crassa*, and *Cardamine nipponica*, than in Q2, which was dominated by *A. alpinus* var. *japonicus*, *P. matsumurae*, and *Munuartia arctica* var. *hondoensis* (Table 1 and 2). In contrast, in habitats with canopies of alpine dwarf pine *Pinus pumila* on the intermediate-sized substrates (Q3 and B1), frequencies of perennial forbs were lower, and those of shrubs, mainly composed of evergreen species, were higher than in habitats without pine cover (Table 1). In Q3, where *P. pumila* was distributed patchily, *Vaccinium vitis-idaea*, *V. uliginosum*, and *Loiseleuria procumbens* were the predominant shrub species, and there were many species of sedges and grasses. In B1, where well-developed canopies of *P. pumila* were continuously distributed (Table 2), *Vaccinium ovalifolium*, *Empetrum nigrum* var. *japonicum*, and *Rubus pedatus* predominated, and there were relatively few grasses and sedges. Species richness (m^{-2}) and total coverage were lower in Q3 than in B1 (Table 1 and 2).

The relationships between species richness and area are shown in Fig. 1. The species-area relationship was statistically significant in each community (Table 3). Of the four alpine plant communities, Q2 showed the highest interception of the regression (parameter *c*), and the analysis of covariance (ANCOVA) indicated that Q2 had the highest species richness of these communities located on the large-gravel substrate (Table 4) by a significant margin, despite being the smallest survey area. The *z* value was also significantly higher in Q2 than in B1 (see C × A between Q2 and

B1 in Table 4), suggesting a higher beta-diversity of the community in the large gravel habitat than in the community with a well-developed canopy of *P. pumila*.

Table1. Frequency (%) of vascular plant species occurring in 1 × 1 m^2 subquadrats.

Plot No.	Q1	Q2	Q3	B1
Substrate	fine-gravel	large-gravel	intermadiate	intermadiate
	(unstable)	(stable)	(intermadiate)	(stable)
Plot size	5 x 5 m^2	2 x 5 m^2	5 x 5 m^2	1 x 20 m^2
Evergreen srcub				
Pinus pumila^{†2}			72	100
Evergreen shrub				
Empetrum nigrum var. *japonicum*^{†2}			20	50
Gaultheria pyroloides^{†2}				65
Loiseleuria procumbens^{*1}			48	
Phyllodoce aleutica^{*1}				30
Rododendron aureum^{*1}				20
Vaccinium vitis-idaea^{†2}			92	85
Deciduous shrub				
Arctous alpinus var. *japonicus*^{*2}	8	60	36	
Dryas octopetala var. *asiatica*^{*1}		20		
Sorbus sambucifolia^{†2}				45
Rubus pedatus^{†2}				100
Vaccinium ovalifolium^{†2}				75
Vaccinium smallii^{‡2}				25
Vaccinium uliginosum^{†2}			40	
Forb				
Bistora vivipara^{†1}		30		
Campanula chamissonis^{*1}	52	50	4	
Cardamine nipponica^{*1}	80			
Chamaepericlymenum canadense^{†2}				75
Coptis trifolia^{†1}				45
Euphrasia insignis^{*1}			20	
Gentiana algida^{*1}		30		
Munuartia arctica var. *hondoensis*^{*1}	44	100		
Pedicularis verticillata^{*1}		20		
Potentilla matsumurae^{*1}	100	100	60	
Rhodiola rosea^{†1}		60		
Schizocodon soldanelloides f. *alpinus*^{*1}				55
Stellaria nipponica^{*1}		10		
Viola crassa^{*1}	100	90		
Sedge				
Carex blepharicarpa^{‡1}			16	
Carex oxyandra^{‡1}			8	
Carex stenantha^{*1}	40		36	
Rush				
Luzula arcuata ssp. *Unalascensis*^{*1}	12	80		
Grass				
Agrostis flaccida^{‡1}	52	20	8	
Calamagrosis deschampsioides^{*1}			4	
Calamagrosis sesquiflora^{*1}		40		
Calamagrosis sp.		50		
Deschampsia caespitosa var. *festucaefolia*^{*1}			8	
Deschampsia flexuosa^{‡1}			28	1
Festuca ovina var. *alpina*^{*1}	56		4	
Festuca ovina var. *tateyamensis*^{*1}		100	12	
Number of species observed	10	16	18	14
Number of species (m^{-2})	5.4 ± 1.0	8.4 ± 1.8	5.2 ± 2.2	7.8 ± 2.4

*, alpine specialist; †, alpine-subalpine species; ‡, lowland species (cf. Shimizu (1982, 1983)).
^{1}, wind dispersal; ^{2}, animal dispersal (cf. Shimizu (1982, 1983)).

Table 2. Coverage (mean ± SD (%)) of vascular plant species in a 1 × 1 m^2 subquadrat.

Plot No.	Q1	Q2	Q3	B1
Substrate	fine-gravel (unstable)	large-gravel (stable)	intermediate (intermadiate)	intermediate (stable)
Evergreen srcub				
Pinus pumila			31.6 ± 39.2	80.8 ± 15.2
Evergreen shrub				
Empetrum nigrum var.*japonicum*			0.6 ± 1.5	9.2 ± 19.8
Gaultheria pyroloides				1.9 ± 3.1
Loiseleuria procumbens			4.2 ± 8.4	
Phyllodoce aleutica				0.9 ± 3.3
Rododendron aureum				0.5 ± 1.2
Vaccinium vitis-idaea			10.1 + 9.2	3.0 ± 2.9
Deciduous shrub				
Arctous alpinus var.*japonicus*	0.6 ± 0.1	3.3 ± 4.7	1.8 ± 4.5	
Dryas octopetala var.*asiatica*		0.3 ± 0.5		
Sorbus sambucifolia				1.1 ± 1.8
Rubus pedatus				4.1 ± 4.6
Vaccinium ovalifolium				14.6 ± 18.1
Vaccinium smallii				0.8 ± 2.0
Vaccinium uliginosum			4.2 ± 7.3	
Forb				
Bistora vivipara		0.1 ± 0.2		
Campanula chamissonis	0.3 ± 0.6	0.5 ± 0.5	0.1 ± 0.2	
Cardamine nipponica	0.2 ± 0.2			
Chamaepericlymenum canadense				0.4 ± 0.4
Coptis trifolia				0.2 ± 0.3
Euphrasia insignis			0.3 ± 0.7	
Gentiana algida		0.2 ± 0.3		
Munuartia arctica var.*hondoensis*	0.6 ± 1.0	2.1 ± 2.1		
Pedicularis verticillata		0.1 ± 0.2		
Potentilla matsumurae	3.0 ± 1.8	3.2 ± 1.8	1.0 ± 1.3	
Rhodiola rosea		0.7 ± 0.7		
Schizocodon soldanelloides f. *alpinus*				0.6 ± 0.9
Stellaria nipponica		0.1 ± 0.3		
Viola crassa	1.2 ± 0.8	0.7 ± 0.7		
Sedge				
Carex blepharicarpa			0.3 ± 0.8	
Carex oxyandra			0.2 ± 0.7	
Carex stenantha	0.4 ± 0.9		0.5 ± 1.6	
Rush				
Luzula arcuata ssp. *unalascensis*	0.1 ± 0.1	0.6 ± 0.4		
Grass				
Agrostis flaccida	0.1 ± 0.2	0.1 ± 0.2	0.1 ± 0.2	
Calamagrosis deschampsioides			0.1 ± 0.2	
Calamagrosis sesquiflora		0.5 ± 0.7		
Calamagrosis sp.		0.3 ± 0.4		
Deschampsia caespitosa var.*festucaefolia*			0.1 ± 0.3	
Deschampsia flexuosa			0.1 ± 0.3	0.1 ± 0.1
Festuca ovina var.*alpina*	0.1 ± 0.1		0.1 ± 0.1	
Festuca ovina var.*tateyamensis*		0.6 ± 0.3	0.1 ± 0.1	
Total coverage (%)	5.9	13.1	55.4	118.1

The value of *z* for Q3 was the highest of the fellfield plant communities, whereas the interception of the regression was the lowest (Table 3), and the species richness was significantly lower than in Q2 and B1 (Table 4). That is, the Q3 community, which has fragmented canopies of *P. pumila*, was characterized by low alpha-diversity and high beta-diversity: a higher turnover rate of species replacements even within a small spatial scale. The Q1 community located on the unstable fine-gravel substrate had low *c*- and *z*-values (Fig. 1 and Table 3), indicating the lowest species richness both in alpha- and beta-diversities among the fellfield communities (Table 4). When we focused on the fellfield communities with *P. pumila* (Q3 and B1), the pine-invaded community (Q3) had a lower alpha-diversity than the pine-developed community (B1) but a higher beta-diversity. Thus, both substrate properties and colonization by *P. pumila* had strong impacts on species richness and diversity within fellfield plant communities.

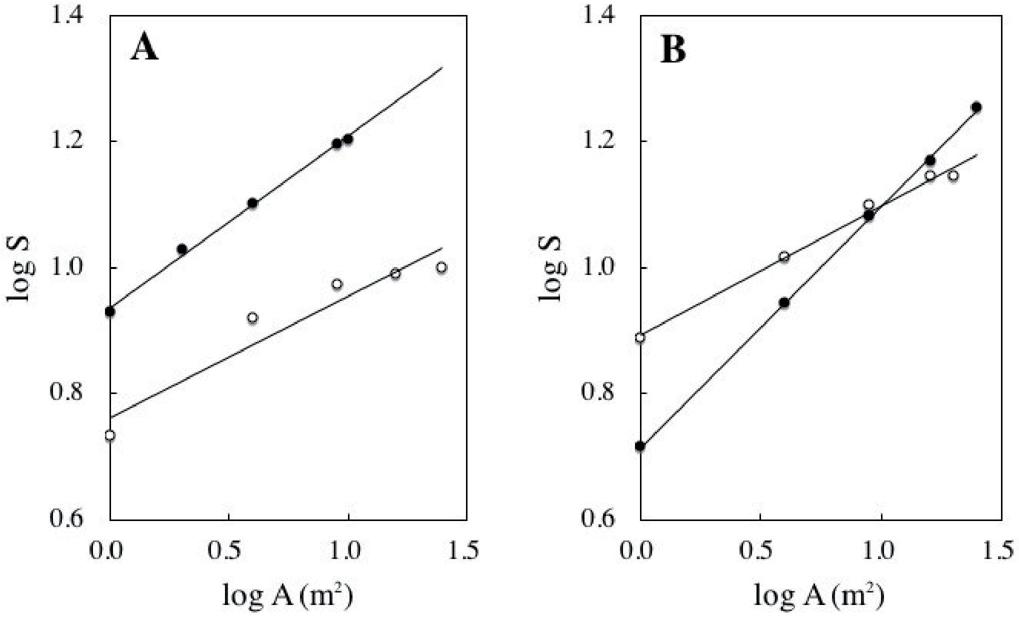

Figure 1. Species-area curves. A: communities without *P. pumila*, Q1 (open circles) and Q2 (solid circles). B: communities with *P. pumila*, Q3 (solid circles) and B1 (open circles). Log-transformed values of the number of species (S) and area (A) are shown here.

Table 3. Parameters (c and z) and statistical values of species-area relationships ($S = c\,A^z$).

Parameters	Q1	Q2	Q3	B1
n	5	5	5	5
c	5.8	8.6	5.2	7.8
z	0.193	0.272	0.383	0.205
r	0.956	0.998	0.999	0.996
F	31.487	848.107	7813.025	376.492
P	0.0112	< 0.0001	< 0.0001	0.0003

Table 4. Results of analysis of covariance (ANCOVA). In log-transformed relationships between species richness S and area A ($\log S = z \log A + \log 10^c$), differences in interceptions (community (C)) and slopes (C × A) between plots were analyzed.

		Q2		Q3		B1	
		F	*P*	*F*	*P*	*F*	*P*
Q1	Community (C)	28.496	0.0018	2.038	0.2033	13.960	0.0097
	Area (A)	131.381	< 0.0001	276.813	< 0.0001	118.140	< 0.0001
	C x A	3.818	0.0985	30.287	0.0015	0.118	0.7431
Q2	Community (C)			802.704	< 0.0001	13.992	0.0096
	Area (A)			4527.512	< 0.0001	1066.123	< 0.0001
	C x A			130.666	< 0.0001	20.791	0.0039
Q3	Community (C)					275.507	< 0.0001
	Area (A)					2729.451	< 0.0001
	C x A					249.526	< 0.0001

Further detailed observation and analysis were carried out in plot Q3 to assess the effects of *P. pumila* on species richness of the alpine communities. Figure 2 shows the spatial distributions of *P. pumila* and the other alpine species in terms of their coverage. The spatial associations of the dwarf pine with the other alpine species were analyzed on a 1 × 1 m scale using Iwao's ω index (Table 5). The results indicate that *Vaccinium vitis-idaea* had a strong positive spatial association only with *P. pumila*, while *Euphrasia insignis*, *Arctous alpinus* var. *japonicus*, *Potentilla matsumurae,* and *Carex stenantha*, which were frequently found either in Q1 or Q2 (except for *E. insignis*), had negative spatial associations with the pine. These four species were not found in the pine-developed community (B1). *Empetrum nigrum* var. *japonicum* and *Deschampsia flexuosa* had weakly positive associations, while *Loiseleuria procumbens* and *Vaccinium uliginosum* had weakly negative associations with *P. pumila* cover. *E. nigrum* var. *japonicum* and *D. flexuosa* were also found under higher coverage of *P. pumila* in B1. Within the Q3 community, moreover, *P. pumila* coverage was significantly negatively correlated with the number of other species found in 1 × 1 m subquadrats (Kendall's $\tau = -0.421$, $P = 0.0032$). Thus, it appears that *P. pumila* excludes from niches alpine specialists (*A. alpinus* var. *japonicus* and *P. matsumurae*) found only in the alpine life zone, strongly negatively impacting them and leading to reduced species richness. However, the fellfield community with a well-developed pine canopy (B1) showed higher species richness on a small spatial scale than Q3, the community with an immature pine canopy (see Fig. 1 and Table 4).

Table 6 shows floristic characteristics in each plant community. The most obvious features are lower proportions of alpine specialists and higher proportions of lowland species with increased *P. pumila* cover. Moreover, it is noteworthy that plant species that disperse their fruits and seeds via birds and mammals were more abundant in fellfield communities with *P. pumila* than in communities without the pine.

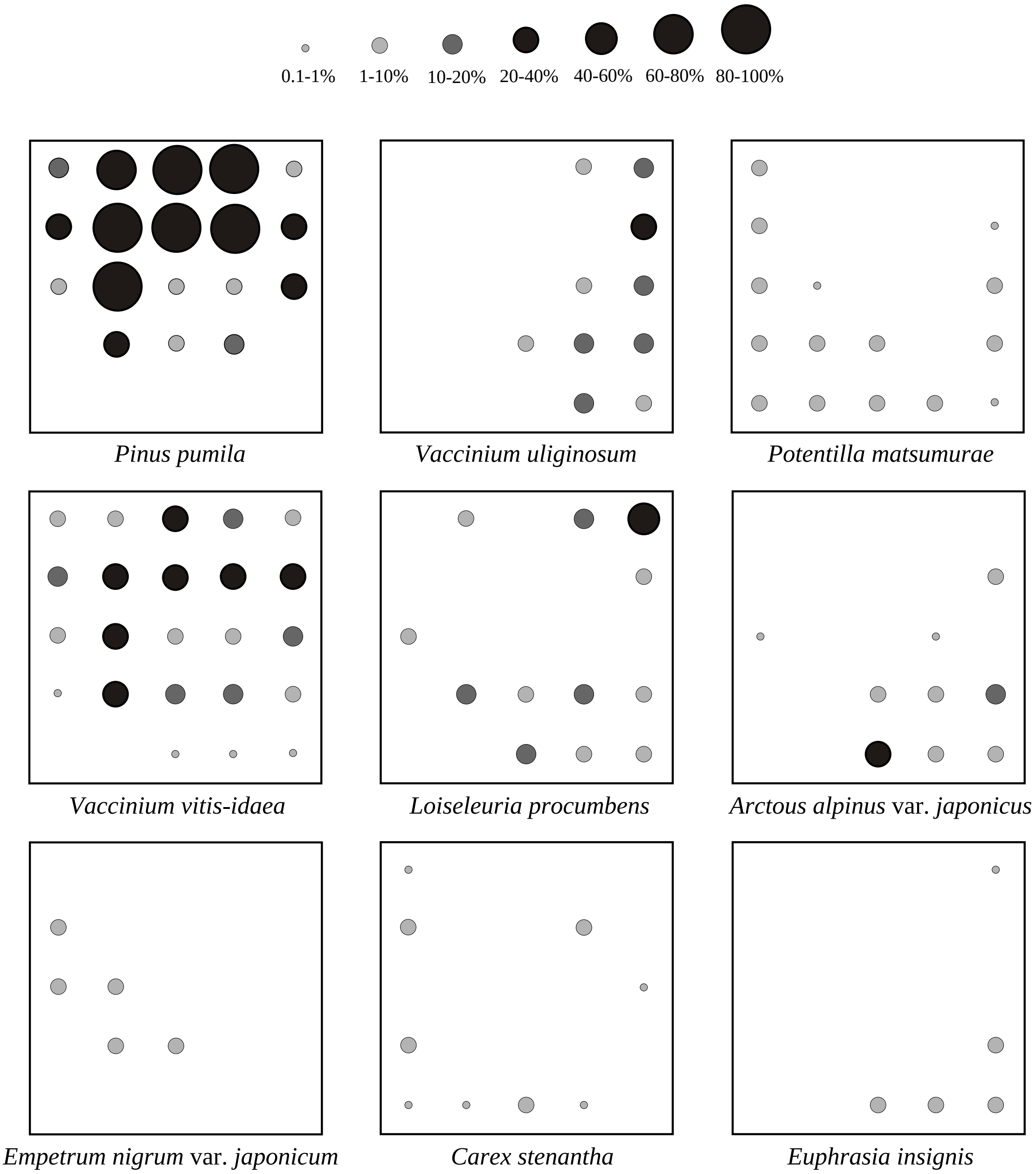

Figure 2. Spatial distributions of coverage of *Pinus pumila* and other representative species in plot Q3. Size of circles represents degree of coverage.

Table 5. Spatial associations between *Pinus pumila* and other representative plants in plot Q3. Iwao's ω indices (Iwao, 1977) were calculated in terms of their coverage at a 1 × 1 m^2 scale (n = 25 subquadrats).

Species	Positive association	Negative association
Vaccinium vitis-idaea	0.908	
Empetrum nigrum var.*japonicum*	0.257	
Deschampsia flexuosa	0.123	
Vaccinium uliginosum		-0.177
Loiseleuria procumbens		-0.188
Potentilla matsumurae		-0.477
Carex stenantha		-0.541
Arctous alpinus var.*japonicus*		-0.601
Euphrasia insignis		-0.982

Table 6. Floristic characteristics. Based on Shimizu (1982, 1983), all species found in each plot belonged to three categories: alpine specialist (species only found in alpine life zone above timberline), alpine-subalpine species (species distributed from subalpine zone to alpine zone), or lowland species (species distributed from lowland zone to alpine zone). Animal dispersal species are those bearing fresh fruits and nuts.

Floristic characteristics	Q1	Q2	Q3	B1
Alpine specialist (%)	90	75	55	21
Alpine-subalpine species (%)	10	25	28	58
Lowland species (%)	0	0	17	21
Animal dispersal species (%)	10	6	28	64

Discussion

In fellfield communities with fine-gravel substrates, sands on the ground surface tend to be easily moved by wind, gravity, and periglacial processes and substrates generally contain little water (Mizuno, 1989). This may prevent plants from establishing themselves in such habitats. The results of this study support this reasoning: the lowest coverage values (Table 2) and total number of species (Table 1) were found in plot Q1. In plot Q2, the large gravel may provide stable conditions for plants on the ground surface, resulting in the highest species richness (Table 3).

Alpine dwarf pine *Pinus pumila* had strong impact on species diversity in alpine fellfield plant communities. In plot Q3, where *P. pumila* colonized the fellfield patchily, alpha-diversity (parameter *c*) was the lowest, but beta-diversity (parameter *z*) was the highest among the four communities studied (Table 3). As shown in Figure 2 and Table 5, most species had negative spatial associations with *P. pumila*, suggesting that the alpine dwarf pine excludes other alpine plants from certain niches. However, *P. pumila* also provides suitable habitats for other species: *Vaccinium vitis-idaea* favored the floor and *Empetrum nigrum* var. *japonicum* appeared to be distributed at the edge of *P. pumila* cover. Thus, patchy *P. pumila* canopy may create heterogeneous environments for alpine plants, resulting in a high beta-diversity in such fellfield communities.

How does species diversity change in alpine fellfield communities that *P. pumila* colonized thoroughly? The results for plot B1 could give a partial answer. Whereas beta-diversity was lower, alpha-diversity was higher in B1 than in Q3. A well-developed canopy of *P. pumila* may provide homogeneous environments for alpine plants, resulting in lower beta-diversity as compared to plot Q3. The higher alpha-diversity in B1 may be attributable to increased occurrence of species normally found in lowland and subalpine zones, which are mainly dispersed by birds and mammals. This suggests that *P. pumila* provides habitats both for plants that usually grow at lower altitudes and for frugivorous animals. Although alpha-diversity was somewhat higher, the proportion of alpine specialist species was lower in B1 than in Q3. These results suggest that alpine dwarf pine strongly impacts species diversity in alpine fellfield communities by preventing establishment of habitats for alpine specialists and by aiding in the establishment of plants dispersed by birds and mammals that are generally found at lower altitudes.

Recently, a trend of increased temperatures has been observed even in the middle-latitude mountain area of central Japan (Wada et al., 2004). It is predicted that global warming may reduce species diversity in alpine plant communities by altering interspecific competition among alpine plants (Wada et al., 2002; Kudo and Suzuki, 2003). Wada et al. (2005) reported a significant increment in annual shoot elongation of *Pinus pumila* over the last 24 years in central Japan. If global warming aids the establishment and growth of *P. pumila* on fellfields, the pine could dramatically reduce species diversity in alpine plant communities by excluding alpine specialists. Therefore, the population dynamics of *P. pumila* should be investigated and monitored as global warming continues.

Acknowledgements

I sincerely thank Hiroto Motoki, Atsushi Makino, Junzo Masuda, Hideaki Nakajima, Junji Moribe, and members of the Tateyama Association for Nature Conservation (TANC) for their assistance and support of my fieldwork. I am grateful to Takuo Kitabatake and Yukio Nagai for their help in identifying plants. This study was supported by a grant from the Hokuriku branch of Yomiuri Shimbun to TANC, and by a grant from the Ministry of Education, Science, Sports, Culture and Technology of Japan to the author (No. 18570013).

References

Baskin, Y., 1997. *The Work of Nature: How the Diversity of Life Sustains Us,* Washinton, D. C.: Island Press.

Beniston, M., 2003. Climatic Change in Mountain Regions: A Review of Possible Impact. *Climatic Change*, 59, 5-31.

Chujo, H., 1983. Alpine Vegetation and Periglacial Movement of Slope Meterials on Mt. Ontake, Central Japan: Factors Controlling the *Cardamine nipponica* Community. . *Japanese Journal of Ecology*, 33, 461-472.

Drakare, S., Lennon, J. J. and Hillebrand, H., 2006. The Imprint of the Geographical, Evolutionary and Ecological Context on Species-Area Relationships. *Ecology Letters*, 9, 215-227.

Gottfried, M., Pauli, H., Reiter K. and Grabherr, G., 2002. Potential Effects of Climate Change on Alpine and Nival Plants in the Alps. In: Ch. Körner, E. M. Spehn, eds. *Mountain Biodiversity: A Global Assessment*, London: The Parthenon Publishing Group, 213-223.

Hamet-Ahti, L., Ahti, T., and Koponen, T., 1974. A Scheme of Vegetation Zones for Japan and Adjacent Regions. *Annales Botanici Fennici*, 11, 59-88.

Hayashida, M., 1994. Role of Nutcrackers on Seed Dispersal and Establishment of *Pinus pumila* and *P. pentaphylla*. In: W. C. Schmidt, F-K. Holtmeier, eds. *Subalpine Stone Pines and their Environment: The Status of our Knowledge. General Technical Report INT-GTR-309*, Ogden: USDA Forest Service, IRS, 159-162.

Ito, K. and Nishikawa, T., 1977. Alpine Communities of the Northern Taisetsu mountain (2). Syntaxonomy of Plant Communities. *Reports of the Taisetsuzan Institute of Science, Asahikawa College Hokkaido University of Education*, 12, 1-26.

Iwao, S., 1977. Analysis of Spatial Association between Two Species Based on the Interspecies Mean Crowding. *Researches on Population Ecology*, 18, 243-260.

Kajimoto, T., 1994. Aboveground Net Production and Dry Matter Allocation of *Pinus pumila* Forests in the Kiso Mountain Range, Central Japan. *Ecological Research*, 9, 193-204.

Kajimoto, T., 1995. Ecological Characteristics of *Pinus pumila* with Special Reference to Dry Matter Production and Regeneration. *Japanese Journal of Ecology*, 45, 57-72 (in Japanese with English abstract).

Kajimoto, T., 2002. Factors Affecting Seedling Recruitment and Survivorship of the Japanese Subalpine Stone Pine, *Pinus pumila*, after Seed Dispersal by Nutcrackers. *Ecological Research*, 17, 481-491.

Kajimoto, T., Onodera, H., Ikeda, S., Daimaru, H. and Seki, T., 1998. Seedling Establishment of Subalpine Stone Pine (*Pinus pumila*) by Nutcracker (*Nucifraga*) Seed Dispersal on Mt. Yumori, Northern Japan. *Arctic, Antarctic, and Alpine Research*, 30, 408-417.

Kammer, P. M. and Möhl, A., 2002. Factors Controlling Species Richness in Alpine Plant Communities: An Assessment of the Importance of Stress and Disturbance. *Arctic, Antarctic, and Alpine Research*, 34, 398-407.

Kobayashi, K., 1967. Phytosociological Studies on *Pinus pumila* Scrubs of the Daisetsu and the Hidaka Ranges in Hokkaido, Japan. *Japanese Journal of Ecology*, 17, 189-198.

Koizumi, T., 1979. Periglacial Processes and Alpine Plant Communities on the High Mountains in Japan, in Relation to Lithology. I. Alpine Stony Desert Vegetation on the Windward Slope of the Shirouma Mountain Region in the Northern Japan Alps. *Japanese Journal of Ecology*, 29, 71-81 (in Japanese with German abstract).

Koizumi, T., 1980. Periglacial Processes and Alpine Plant Communities on the High Mountains in Japan, in Relation to Lithology. III. Alpine Wind-Blown Heath and Meadow on the Areas Granoporphyry and Paleozoic Sandstone and Shale on Mt. Hachigatake, the Northern Japan Alps. *Japanese Journal of Ecology*, 30, 173-181 (in Japanese with English abstract).

Körner, Ch., 1999. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*, Berlin: Springer-Verlarg.

Körner, Ch., 2002. Mountain Biodiversity, its Causes and Function: an Overview. In: Ch. Körner, E. M. Spehn, eds. *Mountain Biodiversity: A Global Assessment*, London: The Parthenon Publishing Group, 3-20.

Kudo, G. and Suzuki, S., 2003. Warming Effects on Growth, Production, and Vegetation Structure of Alpine Shrubs: A Five-year Experiment in Northern Japan. *Oecologia*, 135, 280-287.

Mizuno, K., 1989. Distribution of Alpine Plant Communities in Relation to Surface Materials on Wind-Blown Slopes around Mt. Mitsu, the Northern Japan Alps. *Japanese Journal of Ecology*, 39, 97-105 (in Japanese with English abstract).

Ohba, T., 1974. Vergleichende Studien über die Alpine Vegetation Japans. 1. Carici rupestris-Kobresietea bellardii. *Phytocoenologia*, 1, 339-401.

Okitsu, S., 1985. Consideration on Vegetational Zonation Based on the Establishment Process of a *Pinus pumila* Zone in Hokkaido, Northern Japan. *Japanese Journal of Ecology*, 35, 113-121 (in Japanese with English abstract).

Okitsu, S. and Ito, K., 1989. Conditions for the Development of the *Pinus pumila* Zone of Hokkaido, Northern Japan. *Vegetatio*, 84, 127-132.

Onipchenko, V. G. and Semenova, G. V., 1995. Comparative analysis of the floristic richness of alpine communities in the Caucasus and the Central Alps. *Journal of Vegetation Science*, 6, 299-304.

Shimizu, H., 1982. The New Alpine Flora of Japan in Color. Vol. I, Osaka: Hoikusya Publishing Co.

Shimizu, H., 1983. The New Alpine Flora of Japan in Color. Vol. II, Osaka: Hoikusya Publishing Co.

Shimono, Y. and Kudo, G., 2003. Intraspecific Variations in Seedling Emergence and Survival of *Potentilla matsumurae* (Rosaceae) between Alpine Fellfield and Snowbed Habitats. *Annals of Botany*, 91, 21-29.

Spehn, E. M., Messerli, B. and Körner, Ch., 2002. A Global Assessment of Mountain Biodiversity: Synthesis. In: Ch. Körner, E. M. Spehn, eds. *Mountain Biodiversity: A Global Assessment*, London: The Parthenon Publishing Group, 325-330.

Stork, N. and Nakashizuka, T., 2002. What is IBOY. In: T. Nakashizuka, N. Stork, eds. *Biodiversity Research Methods: IBOY in Western Pacific and Asia*, Kyoto: Kyoto University Press, and Melbourne: Trans Pacific Press, 1-26.

Tatewaki, M., 1963. Alpine Plants in Hokkaido. *Science Reports of Tohoku University, Series 4, Biology*, 29, 165-188.

Wada, N., Shimono, M., Miyamoto, M. and Kojima, S., 2002. Warming Effects on Shoot Developmental Growth and Biomass Production in Sympatric Evergreen Alpine Dwarf Shrubs *Empetrum nigrum* and *Loiseleuria procumbens*. *Ecological Research*, 17, 125-132.

Wada, N. and Nakai, Y., 2004. Germinability of Seeds in a Glacial Relict *Dryas octopetala* var. *asiatica*: Comparison with a Snowbed Alpine Plant *Sieversia pentapetala* in a Middle-Latitude Mountain Area of Central Japan. *Far Eastern Studies***,** 3, 57-72.

Wada, N., Kawada, K., Kawamura, R., Aoki, K. and Kume, A., 2004. Increasing Winter Runoff in a Middle-Latitude Mountain Area of Central Japan. *Journal of the Meteorological Society of Japan*, 82, 1589-1597.

Wada, N., Watanuki, K., Narita, K., Suzuki, S., Kudo, G. and Kume, A., 2005. Climate Change and Shoot Elongation of Alpine Dwarf Pine (*Pinus pumila* Regel): Comparisons between Six Japanese Mountains. *Phyton – Annales Rei Botanicae*, 45, 253-260.

Watanabe, S., 2005. Decline of Ultrabasicosaxicolous Flora from 1954 to 2003 on Mt. Apoi, Hidaka Provience, Hokkaido, Japan. *Japanese Journal of Ecology*, 55, 105-110 (in Japanese with English abstract).

Whittaker, R. H., 1977. Evolution of Species Diversity in Land Communities. *Evolutionary Biology*, 10, 1-67.

Received 10 November 2006; accepted 23 January 2007