Ground beetle succession on Mount Fujisan

Katsuaki Jimbo[1*], Kôhei Kubota[2] and Zaal Kikvidze[3]

[1] The University of Tokyo, Graduate School of Frontier Science, Kashiwanoha 5-1-5,
Kashiwa-shi, Chiba 277-8563 Japan
[2] The University of Tokyo, Graduate School of Agricultural and Life Sciences, Yayoi 1-1-1,
Bunkyo-ku, Tokyo 113-8657 Japan
[3] Ilia State University, Institute of Ecology, 3/5 Cholokashvili Ave. Tbilisi 0162, Georgia

Abstract. We studied community structure of ground beetle species along vegetation succession gradient in a volcanic desert on Mt. Fujisan, with the aim to understand links between vegetation and ground beetle successions. We set sites representing three major succession stages: early primary patchy grassland on volcanic desert, seral forest, and a climax beech forest. In a volcanic desert, we sampled 20 patches of *Polygonum cuspidatum* of different sizes to analyze ground beetle assemblages at finer scale of vegetation succession. Overall, we captured 1853 beetle individuals and identified 13 species. Subfamily Opatrinae (in the family Tenebrionidae) predominated in herbaceous patches but were replaced by Carabinae (in the family Carabidae) in seral forest, whilst Pterostichinae (in the family Carabidae) dominated climax forest. Within vegetation patches, the following sub-stages of early succession could be discerned: (i) small patches dominated by *P. cuspidatum*, (ii) mid-size patches dominated by *P. cuspidatum* with a few dominant herb species, and (iii) large patches dominated by *P. cuspidatum* with tree seedlings and many species sharing dominance. Opatrinae beetles showed a clear pattern of species turnover across these sub-stages. Our results suggest consistent changes in species composition of ground beetle assemblages along primary vegetation succession.

Key words: Ground beetles, succession, Mt. Fujisan, *Gonocephalum sexuale*, *Gonocephalum japanum*

Introduction

Ecological successions have been intensively studied in plants and, to some extent, fungi (Nara *et al*., 2003ab), whilst the role of animals in these important and complex dynamic processes remains still poorly understood. For instant, there are very few studies analyzing plant-animal interactions during primary successions. Among animals, ground beetles are relatively often a target of studies on biological diversity in ecosystems such as forest and grasslands. Ground beetles are mostly flightless and the spatial range of their activity is small. They are abundant

and widespread group of animals that are very sensitive to changes in their environment (Thiele, 1977; Niemela *et al*., 1993). Therefore, ground beetles are tightly related to the local environmental conditions and can be used as ecological indicators. Indeed, many studies conducted in Europe (Irmler, 2003; Rainio and Niemela 2003; Niemela *et al*., 2007), North America (Scott and Anderson, 2003; Pearsall, 2007) and Japan (Ishitani, 1996; Ishitani *et al*., 2003; Shibuya *et al*., 2008, 2011) documented high sensitivity of ground beetle assemblages to environmental changes. Therefore, ground beetles potentially are also responsive to environmental changes associated with primary ecological successions such as accumulation and enrichment of soils, changing

temperature relations, turnover and increasing diversity of plant species. There were a few studies on the relationships between ground beetles and primary vegetation successions conducted on the slopes of volcanoes (Mt. Usu, Kuranishi *et al*., 1986; St. Helens, Parmenter *et al*., 2005). These authors sampled ground beetles along disturbance gradients and found that ground beetle communities changed along these gradients. Ground beetle communities also changed with time during 20 years of observation. However, these studies did not describe the stages of vegetation succession, nor linked the changing beetle community composition to vegetation successional changes. Unlike other ground beetle studies, we include Silphidae and Tenebrionidae in this study. Some Silphidae species have a good potential as a bioindicator (Shibuya *et al*., 2008) and some Tenebrionidae species are very important group on the primary succession process in Mt.Fujisan (Jimbo *et al*., 2011).

The aim of our study was to examine the links between vegetation and ground beetle successions. Such a study requires representing a wide range of succession stages starting from patches of plants that colonize bare ground. Appropriate sites can be found on Mt. *Fujisan*, where the last massive eruption happened a little more than 300 years ago. Here, habitats representing successions from early stage to climax forest can be found. Our specific purpose was to analyze the patterns of ground beetle species diversity along vegetation succession gradient in a southeastern slope on Mt. Fujisan. To achieve this goal, we set a chronosequence of sites from colonizing pioneer plants to climax beech forest. Particularly, we sampled patches of different size of *Polygonum cuspidatum*, a pioneer colonizer of this volcanic desert, in order to discern the early stages of successions in more detail. These were compared to the forest sites of different degree of succession. We used multivariate methods of analyses to find the relations between ground beetle assemblages and the chronosequence of vegetation succession.

Materials and Methods
Study site

Southeastern side of Mt. Fujisan, the highest mountain in Japan, is covered with scoria, since the last eruption that occurred in 1707. The biota existing on the southeast slope was completely destroyed, and is now recovering. While potential tree line is located at ca. 2500m above sea level on the other side of the mountain, there is no forest above ca.1300m on the southeastern side, although successions continue over 300yr after the eruption. Our research site was located between 1500m and 1600m on this southeastern side. Annual precipitation amounts to more than 2600mm, vegetation season is from June to November, and mean temperature is 6.6 ℃ (Fujimura, 1971). Vegetation in this area is scarce and patchy, characteristic for early stages of primary succession.

We set 30 plots in three different vegetation area, patch area, seral young forest and climax forest (Fig. 1). We set 20 plots haphazardly with 5m to 40m distances between them, in the area of patchy vegetation dominated by *Polygonum cuspidatum*. Two plots were destroyed during the study period and we analyzed the rest 18 plots. Beetle-sampling grids were overlaid on the vegetation patch so that the centers coincided. Five plots with 5m distances between them were set in a similar way in the young forest stand nearby (hereafter seral forest) with light and thin understory. The canopy was dominated by typical secondary forest species such as *Quercus crispula, Carpinus japonica, Acer micranthum*, and *Mongolia obovata*. Five more plots with 5m distances between them were set in a mature forest (hereafter climax forest) dominated by *Quercus crispula and Abies homolepis* with very dark understory built mainly by 2m tall bamboos.

Vegetation sampling

We sampled 18 patches as plots to reveal successional changes in them. We measured projective cover and maximum height of each identified species
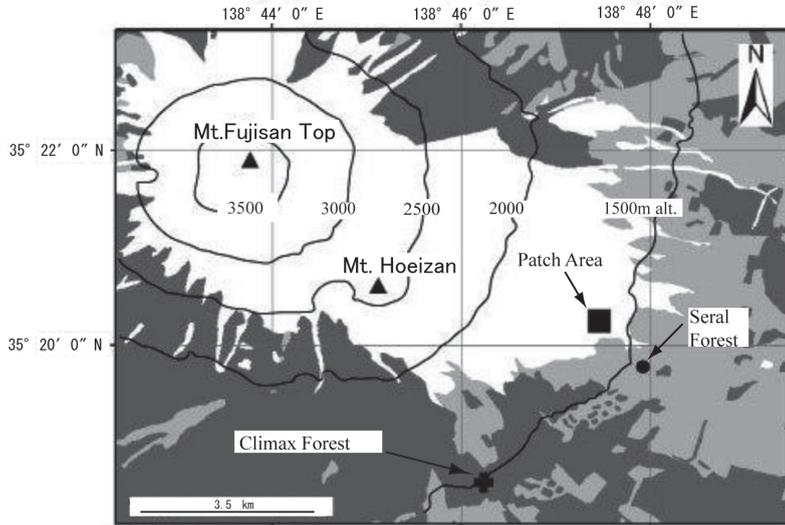
Fig. 1. Southeast slope of Mt. Fujisan and plots (modified from Jimbo *et al*. 2011). Black, gray and white colors show natural forest, secondary forest and volcanic desert with vegetation patches, respectively.

and used the product cover × height to calculate the "volume". We summed the volumes of all species to obtain the total value, from which we calculated relative dominance (RD) for each species. RD was then used as a measure of species abundance.

Environmental factors

To characterize the environment, we measured soil moisture content, litter depth and sky openness. Soil moisture content (%) was measured at five locations within each plot on 29th of September 2008, when it had been fine days for three days, by Time-Domain-Reflectometers (Hydrosense, Campbell Scientific Inc., QLD, Australia) with 12-cm probe rods. Sky openness was measured by analyzing hemispherical photographs taken 10 cm above ground at five points within each plot on 9th of September 2008 using software CanopOn Version 2.02 software (Takenaka, 2007). Litter depth was measured at 10 locations within each plot on 2nd of October by 1 cm order.

Ground beetle community

Dry pitfall traps without bait (plastic cups with 10cm top diameter and 12cm height) were used to sample ground beetles. At each plot size of 5m × 10m, fifteen traps were buried in a grid (3 × 5) with 2m distances between them. Traps were installed in August 2008 (peak of beetle activity in this year: Jimbo *et al*., 2011). The traps were left in place for two consecutive days, and then all trapped animals were collected, identified and counted.

Statistical analyses

The dominant plant species were determined by dominance analysis based on abundance distribution methods using Simpson's index of dominance (Ohsawa, 1984; Kikvidze and Ohsawa, 2002). The dominant ground beetles species were determined based on the numbers of individuals as abundance measure in the same way as for plants. Simpson's index was calculated in a usual way:

$$D = \Sigma \ p_i,$$

Where p_i is the proportion (relative abundance) of the ith species in the community matrix. The number of co-dominant species is simply the inverse value of

D rounded to integers.

Multivariate analyses (DCA and CCA) were performed using PC-ORD 5 (MjM Software). Similarity of species composition across the 18 *P. cuspidatum* patches was studied using Ward's cluster analysis, based on Euclidean distance calculated from RD values of plant species. Then we used Detrended Correspondence Analysis (DCA) based on RD values of plant species to ordinate the vegetation patches. In order to classify the 18 patches by ground beetle assemblages, we used cluster analysis (Euclidean distances, Ward's method) and then beetle species composition was analyzed by Canonical Correlation Analysis (CCA). The primary matrix was based on the composition and abundance (number of individuals) of ground beetles. The secondary matrix represented environmental factors, patch area, number of plant species per patch, number of tree species per patch, plant maximum height, and DCA axis 1 scores obtained from plant species analyses.

Ordinary statistical analyses were done using software JMP 9.0 (SAS Institute, Tokyo, Japan).

Results
Vegetation patches

We found 22 herbaceous, four shrub and three tree species inserted in the matrix of *Polygonum cuspidatum* pathces. Cluster analysis combined with DCA divided 18 patches in four groups (Fig. 2). Five patches of Group A were strongly dominated by *P.*

cuspidatum with only a minor presence of other herbaceous plants (Table 2). Three patches made group B, where *P. cuspidatum* shared dominance with *Miscanthus oligostachyus*. Group C represented three patches with *Salix reinii* as additional prominent species. Finally, group D were patches with many species sharing dominance including trees (Fig. 2). Patch area, number of plant species per patch, number of tree species per patch, plant maximum height and soil moisture increased, whilst sky openness decreased along DCA axis 1 (Table 1). Correlation
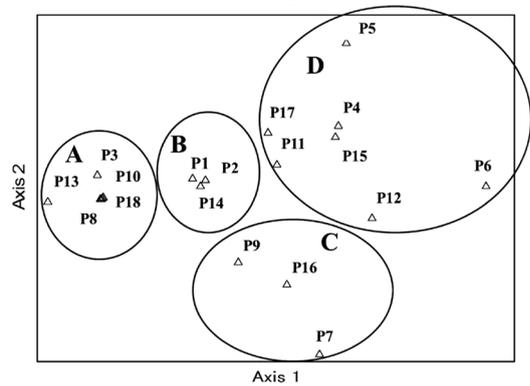

Fig. 2. DCA analysis of patch plot based on vegetation data. Four groups which is parted by cluster analysis are ordered A, B, C and D. Group A are patches with one dominant species of *Polygonum cuspidatum*, group B are patches with a few dominant species including *P. cuspidatum* and *Miscanthus oligostachyus*, group C are patches with a few dominant species including *P. cuspidatum* and *Salix reinii*. Group D are patches with many dominant species including trees.

Table 1. Area, cover, plant species number, tree species number, sky openness, soil moisture content and litter thickness in vegetation patches.
The order of patches is arranged according to increasing DCA axis 1 scores.

	P14	P3	P9	P11	P1	P15	P2	P10	P19	P12	P17	P8	P16	P4	P5	P13	P6
Patch Area (m²)	3.4	80	1	8.3	21	204	11	41	43	289	38	41	322	102	79	68	467
Number of Herb Species	6	10	6	6	15	17	13	12	15	15	14	9	17	11	12	19	12
Number of Tree Species	0	1	0	1	1	1	1	2	2	4	1	1	4	3	3	4	6
Plant max height (cm)	45	106	70	75	104	90	80	100	110	95	80	100	200	480	160	87	350
Sky Openess (%)	79	39	88	66	50	33	60	49	48	46	62	42	40	47	47	43	40
Soil moisture content (%)	4.4	9.1	5.1	5.8	6.8	7.9	5.8	6.8	6.7	7.6	6.5	7	7.4	8.8	9.6	7.3	11
Litter Depth (cm)	0.2	2.5	0	0.2	0.7	1.5	1.3	0.6	0.7	1.5	0.7	0.8	1	1.3	1.3	0.7	1.8
DCA1	0	29	33	36	88	96	97	120	139	144	150	171	183	185	192	206	280

The order of patches is arranged according to increasing DCA axis 1 scores.

Table 2. Correlation among analyzed environmental variables and DCA axis 1 scores in vegetation.

	Patch area	Number of plant species	Number of tree species	Plant max height (cm)	Sky openess (%)	Soil moisture content (%)	Litter depth (cm)
Patch Area (m²)	1.000						
Number of Plant Species	0.416	1.000					
Number of Tree Species	0.809 *	0.546 *	1.000				
Plant max height (cm)	0.502 *	0.082	0.593 *	1.000			
Sky Openess (%)	-0.563 *	-0.692 *	-0.602 *	-0.363	1.000		
Soil moisture content (%)	0.688 *	0.379	0.745 *	0.657 *	-0.748 *	1.000	
Litter Depth (cm)	0.549 *	0.375	0.457	0.376	-0.727 *	0.798 *	1.000
DCA1 axsis 1	0.628 *	0.582 *	0.861 *	0.597 *	-0.630 *	0.716 *	0.358

*: p<0.05

among these variables was mostly significant (Table 2) indicating that DCA axis 1 can reflect environmental and vegetation changes associated with successions. Consequently, we used DCA 1 axis scores and a composite proxy measure of succession chronosequence.

Ground beetles in patches and forests

The patches of *P. cuspidatum* represent an early stage of vegetation succession on our study site, where the final stage is expected to be a mixed beech forest (Ohsawa, 1984). We added plots for sampling ground beetles in a seral, young forest, and in a typical and stable (climax) beech forest, to extend the range of the chronosequence representing successions. When the beetles sampled in patches and for-

ests were compared, a pattern of strong taxonomic changes (at subfamily level) emerged (Fig. 3). These subfamilies were represented with various species, which were unevenly distributed among the sampled plots (Table 3). Opatrinae dominated patches, Carabinae dominated seral forest and Pterostichinae dominated climax forest.

Overall, we captured 1853 beetle individuals and identified 13 species. Dominant species in patches was *Gonocephalum sexuale*, whilst dominance was shared among *Carabus lewisianus, Leptocarabus procerulus, L. arboreus fujisanus*, and *Pterostichus rhanis angustistylis* in seral forest plots, and among *L. arboreus fujisanus* and *P. rhanis angustistylis* in climax forest plots (Table 3).

Beetle assemblages in *P. cuspidatum* patches of different sizes and those of seral and climax forest
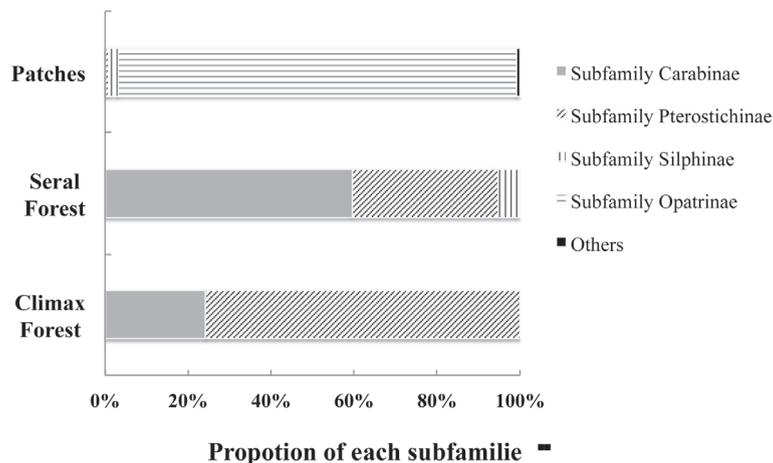

Fig. 3. Distribution of ground beetle subfamilies along successional gradient from vegetation patches through successional forest to climax forest.

plots clearly diverged when ordinated by DCA, occupying positions at different ends of DCA Axis 1 (Fig. 4).

Succession chronosequence in *Polygonum cuspidatum* patches

We focused on beetle assemblages of *P. cuspida-*

Table 3. Distribution of ground beetle species across plots.

Coleoptera	Family	Subfamily	Species	P13	P3	P8	P18	P10	P1	P14	P2	P9	P17	P11	P16	P7	P15	P4	P5	P12	P6	Patch total
	Carabidae	Carabinae	Carabus lewisianus Breuning																1			1
			Leptocarabus procerulus (Chaudoir)		1																	1
			Leptocarabus arboreus fujisanus (Bates)															1			2	3
		Pterostichinae	Pterostichus rhanis angustistylis Tanaka											1							1	2
			Pterostichus amagisanus Tanaka et Ishida																			
			Pterostichus macrogenys Bates																			
			Pterostichus samurai (Lutshnik)													3				5		8
			Synuchus cycloderus (Bates)																			
		Lebiinae	Apristus grandis Andrewes			3					2											5
	Silphidae	Silphinae	Silpha longicornis Portevin							1	2	1		1			7			3	1	16
			Eusilpha japonica (Motschulsky)											11			7					18
	Tenebrionidae	Opatrinae	Gonocephalum sexuale (Marseul)	7	4	3	167	86	142	18	100	333	62	20	112	139	24	2	25	87		1331
			Gonocephalum japanum Motschulsky	1	3	1	14	11	22	45	35	33	43	15	5	1	41	9	72	23	42	416
		Misolampinae	Misolampidius rugipennis Lewis							1					1							2
	Lagridae	Lagrinae	Lagriidae sp.													2						2
			Sum of ground beetle individuals	8	8	7	181	97	164	65	139	367	105	48	118	142	79	12	101	113	51	1805
			Number of species	2	3	3	2	2	2	4	4	3	2	5	3	3	4	3	4	3	5	12

Coleoptera	Family	Subfamily	Species	SF1	SF2	SF3	SF4	SF5	Seral Total	CL1	CL2	CL3	CL4	Cl5	Climax Total
	Carabidae	Carabinae	Carabus lewisianus Breuning	1	3	2	3	2	12				1		1
			Leptocarabus procerulus (Chaudoir)		1		1		2						
			Leptocarabus arboreus fujisanus (Bates)	1	3	2	1	1	8	1	2	2	2	1	8
		Pterostichinae	Pterostichus rhanis angustistylis Tanaka	2	4	2	3	1	12	2	7	3	4	2	18
			Pterostichus amagisanus Tanaka et Ishida							1	2	2		1	6
			Pterostichus macrogenys Bates				1		1						
			Pterostichus samurai (Lutshnik)												
			Synuchus cycloderus (Bates)								2		1	1	4
		Lebiinae	Apristus grandis Andrewes												
	Silphidae	Silphinae	Silpha longicornis Portevin	1					1						
			Eusilpha japonica (Motschulsky)				1		1						
	Tenebrionidae	Opatrinae	Gonocephalum sexuale (Marseul)												
			Gonocephalum japanum Motschulsky												
		Misolampinae	Misolampidius rugipennis Lewis												
	Lagridae	Lagrinae	Lagriidae sp.												
			Sum of ground beetle individuals	5	11	6	9	5	37	4	13	7	7	6	37
			Number of species	4	4	3	5	4	7	3	4	3	3	5	5

The order of plot is arranged According to DCA axis 1 scores. Number of individuals of each species caught at each plot is shown. Gray highlight indicates the dominant species.
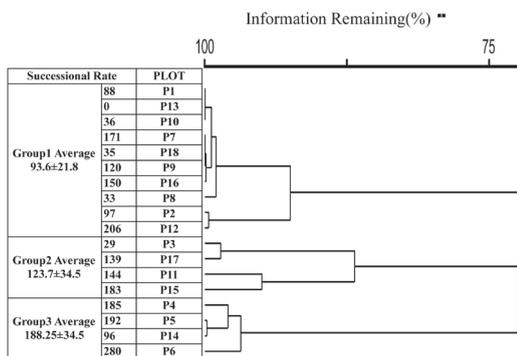

Fig. 4. Cluster analysis of plot in vegetation patches by ground beetle data. Successional rates were obtained from the score of DCA axis 1 obtained from vegetation analysis.
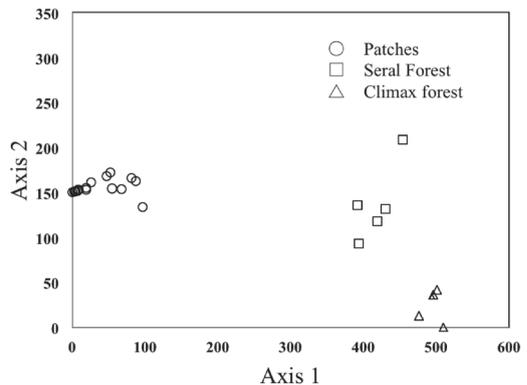

Fig. 5. DCA analysis of eighteen patches and two forest based on ground beetle data.

tum patches to analyze the early successional transitions. Cluster analysis distinguished three groups of patches based on <75% of dissimilarity among them (Fig. 5). The three groups are: the group with dominant species of *G. sexuale* only, the group with two dominant species of *G. sexuale* and *G. japanum* and the group with forest species. These plot groups differed considerably in mean values of DCA axis 1 scores obtained from plant species analyses, (Fig. 2), which indicates that ground beetle composition was related to vegetation succession. Consecutively performed CCA showed that the beetle assemblages were related to the variables characterizing patch environment (Fig. 6). Therefore, vegetation succession as measured by DCA axis 1 scores (based on plant species) was clearly related to growing patch area and height as well as to decreasing sky openness, increasing numbers of plant species and tree species

Fig. 7. CCA of major ground beetle species in patches. Primary matrix was constructed based on ground beetle species composition and abundance. DCA axis 1 obtained from vegetation analysis was used as an environmental variable.

Fig. 8. Trends of variation of dominant ground beetle species along successional gradient as measured by DCA axis 1 of vegetation analysis.
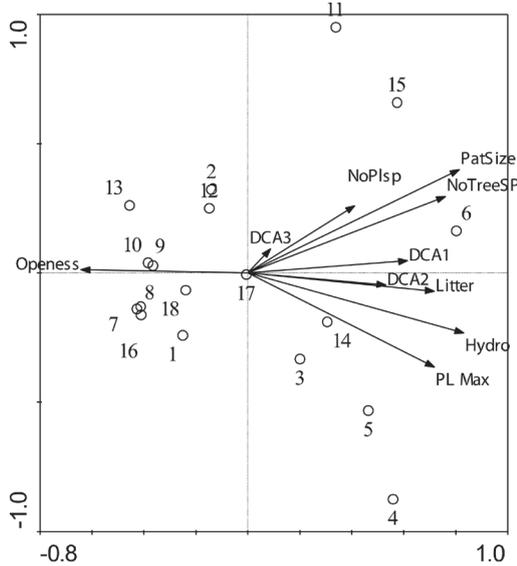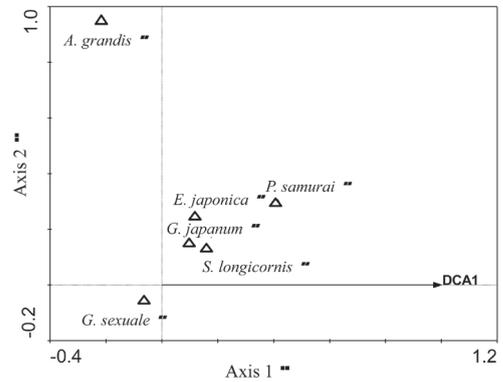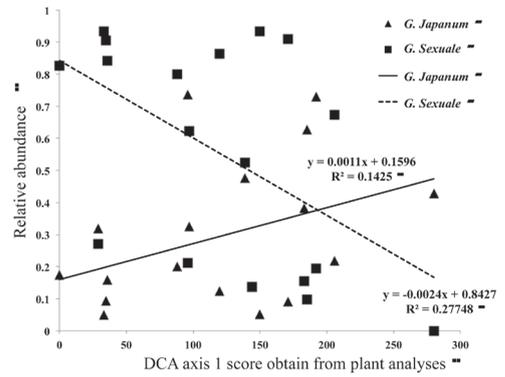
Fig. 6. CCA of plots based on beetle composition and abundance (primary matrix) and environmental factors (secondary matrix). Circles show plots and numbers show plot numbers. Environmental variables analyzed were: sky openness (Openness), number of plant species per patch (Noplsp), patch area (Patsize), number of tree species per patch (NoTreeSP), DCA axis 1 scores obtained from plant species analyses (DCA1), litter depth (Litter), soil moisture contents (Hydro) and plant maximum height (PL MAX).
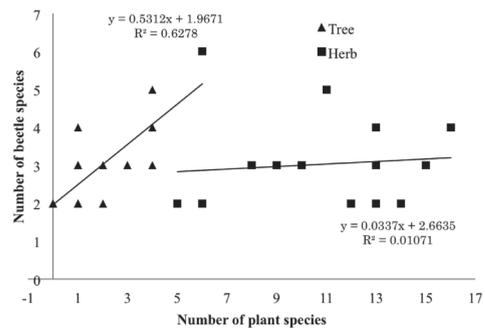
Fig. 9. Increasing trend of ground beetle relative dominance with the richness of herbaceous species and woody species.

invasions, litter accumulation, and improved water contents in the soils. Ordination of beetle species with CCA showed that *G. sexuale* was associated with successionally younger, smaller-sized *P. cuspidatum* patches, whilst other species – *G. japanum, E. japonica, S. longi* and *P. samurai* – associated with successionally more advanced, larger patches (Fig. 7). Indeed, *G. sexuale* showed significantly decreasing trend along succession gradient as measured by DCA 1 axis scores, correlation coefficient of -0.527 and p-value of 0.025, whilst its congeneric *G. japanum* increased, correlation coefficient of 0.378 and p-value of 0.1225 (Fig. 8). Overall, beetle species richness in the patches increased with increasing richness of plant species, especially clearly with significantly increasing number of tree species invading the patches, correlation coefficient of 0.792 and p-value <0.0001 (Fig. 9).

Discussion

Our results suggest a strong link between vegetation succession and changes in species composition of associated ground beetle community. Ground beetle assemblages clearly responded to the changes in vegetation structure and environment during succession. First, DCA analysis indicated to a clear successional sequence in vegetation patches. Indeed, ranking vegetation patches by DCA axis 1 scores coincided largely with increasing patch size: starting from small patches with only *P. cuspidatum*, patch size gradually increased along the DCA 1 axis and included increasing numbers of first herbaceous and then woody species. These stages of vegetation succession were already described in early studies (Ohsawa, 1984b; Adachi et el., 1996; Masuzawa, 1997). Tight correlation of DCA 1 axis with variables such as patch area, number of tree species and soil moisture contents also indicated that DCA 1 axis was a reasonable composite measure of ecological changes during vegetation succession at our study site. Second, these major successional vegetation transitions (primary-seral-climax) were strongly associated with changes in ground beetle assemblages that could be

seen at subfamily level. Opatrinae beetles dominated the primary stage – volcanic desert with patchy herbaceous vegetation. Carabinae beetles were dominant in seral forest, and Pterostichinae beetles overtook in climax forest. More detailed analysis, however, showed that changes were gradual and were strongly related with the invasion of woody species into the early successional patches - *G. sexuale*. dominating assemblages in small herbaceous patches was gradually replaced by *G. japanum* as woody plant species started to appear in larger patches.

In general, ground beetles are characterized with narrow ecological niches (Pearsall, 2007), hence the changes in niche structure associated with vegetation succession can be the major driver of ground beetle species composition. There is little literature on ecological requirements of Opatrinae beetles, however, *G. sexuale* was usually collected from open habitats such as riverbanks and beaches, whilst *G. japanum* was commonly collected from bright forests (Akita, personal communications). This may explain why *G. sexuale* were more common in small herbaceous patches whilst *G. japanum* preferred large patches with the presence of tree species as observed in our study.

Likewise, *C. lewisianus* was reported to prefer bright forest (Yamashita *et al.*, 2006), and correspondingly, this beetle dominated seral, relatively light forest in our study. The climax forest in our study was dark and with deep litter layer – the beetle species dominating this habitat probably are ecologically similar to species that prefer forests with thick litter layer elsewhere (Koivula *et al.*, 1999; Magura *et al.*, 2004).

Conclusion

Although ground beetles were studied intensively to show their sensitive responses to environmental changes in their habitats, there were no consistent studies along successsional chronosequences, particularly concerning primary successions. Here we presented such study documenting consistent changes in species composition of ground beetle assemblages

along primary succession chronosequence. In addition we show prominent representation of Opatrinae beetles at early stages of primary succession in a volcanic desert. Generally, insects have impacts on vegetation in volcanic desert (Edwards and Sugg, 1993; Fagan and Bishop, 2000). Yet, our findings are novel for entomological studies and call for reviewing the role of different groups of ground beetles at different stages of vegetation change and development, particularly of Opatrinae beetles.

Acknowledgments

References

Adachi, N., Terashima, I. & Takahashi, M., 1996. Central die-back of monoclonal stands of *Reynoutria japonica* in an early stage of primary succession on Mount Fuji. *Ann. Bot.*, **77**: 477-486.

Edwards, J. & Sugg, P., 1993. Arthropod fallout as a resource in the recolonization of Mount St. *Helens. Ecology*, **74**: 954-958.

Eyre, M.D., Lott, D.A. & Garside, A., 1996. Assessing the potential for environmental monitoring using ground beetles (Coleoptera: Carabidae) with riverside and Scottish data. *Ann. Zool. Fennici*, **33**: 157-163.

Fagan, W. & Bishop, J., 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. *Am. Nat.*, **155**: 238-251.

Fujimura, I., 1971. The climate and weather of Mt. Fuji. *Fujisan*: pp. 211-345. Fujikyuko Ltd. (In Japanese with English summary)

Ishitani, M., 1996. Ecological studies on ground beetles (Coloeptera: Carabidae, Brachinidae) as environmental indicators. *Miscellaneous Reports of the Hiwa Museum for Natural History*, **34**: 1-110. (In Japanese with English summary.)

Ishitani, M., Kotze, D. J. & Niemelä, J., 2003. Changes in carabid beetle assemblages across an urban-rural gradient in Japan. *Ecography*, **26**: 481-489.

Irmler, U., 2003. The spatial and temporal pattern of carabid beetles on arable fields in northern Germany (Schleswig-Holstein) and their value as ecological indicators. *Agric. Ecosyst. Environ.*, **98**: 141-151.

Jimbo, K., Kubota, K. & Kikvidze, Z., 2011. Ground beetle communities and their seasonal changes under the different environments on the primary succession process in Mt.Fujisan. *Bull. Biogeogr. Soc. Japan*, **66**: 7-16. (In Japanese with English summary.)

Kikvidze, Z. & Ohsawa, M., 2002. Measuring the number of co-dominants in ecological communities. *Ecol. Res.*, **17**: 519-525.

Koivula, M. & Vermeulen, H., 2005. Highways and forest fragmentation--effects on carabid beetles (Coleoptera, Carabidae). *Landsc. Ecol.*, **20**: 911-926.

Kuranishi, R., Higashi, S., Sato, H. & Fukuda, H., 1986. Ground Beetles on Mt. Usu Six Years after the 1977-78 Eruptions. *Envir. Sci.*, *Hokkaido.*, **9**:69–78.

Magura, T., Tothmeresz, B. & Elek, Z., 2004. Effects of leaf-litter addition on carabid beetles in a non-native Norway spruce plantation. *Acta Zool. Acad. Sci. Hung.*, **50**: 9-23.

Masuzawa, T., 1997. *Ecology of the alpine plants*. University of Tokyo Press, Tokyo. (In Japanese.)

Nara, K., Nakaya, H. & Hogetsu, T., 2003a. Ectomycorrhizal sporocarp succession and production during early primary succession Mount Fuji. *N. Phytol.*, **158**: 193-206.

Nara, K., Nakaya, H., Wu, B.Y., Zou, Z.H. & Hogetsu, T., 2003b. Underground primary succession of ectomycorrhizal fungi in a volcanic desert on Mount Fuji. *N. Phytol.*, **159**: 743-756.

Niemela, J., Langor, D. & Spence, J., 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conserv. Biol.*, **7**: 551-561.

Niemela, J., Koivula, M. & Kotze, D.J., 2007. The effects of forestry on carabid beetles (Coleoptera:Carabidae) in boreal forests. *J. Insect Consev.*, **11**: 5-18.

Ohsawa, M., 1984. Differentiation of vegetation zones and species strategies in the subalpine region of Mt. Fuji. *Vegetatio*, **57**: 15-52.

Parmenter, R., Crisafulli, C., Korbe, N., Parsons, G., Kreutzian, M. & MacMahon, J., 2005. Poster-uption arthropod succession on the Mount St. Helens volcano: the ground-dwelling beetle fauna (Coleoptera). In: Dale VH, Swanson FJ, Crisafulli, CM (eds) *Ecological responses to the 1980 eruption of Mount St. Helens*, pp. 139-150. Springer, New York.

Pearsall, I.A., 2007. Carabid beetles as ecological indicatores. Paper presented at the Monitoring the effectivness of biological conservation, 2-4 November 2004, Richmond, BC. [Cited 12 March 2012] Available from URL: http://www.forrex. org/events/mebc/papers.html

Rainio, J. & Niemela, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers. Conserv.*, **12**: 487-506.

Rykken, J., Capen, D. & Mahabir, S., 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conserv. Biol.*, **11**: 522-530.

Scott, W.A. & Anderson, R., 2003. Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. *Biol. Conserv.*, **110**: 197-210.

Shibuya, S., Kubota, K., Kikvidze, Z. & Osawa, M., 2008. Differential sensitivity of ground beetles, Eusilpha japonica and Carabidae, to vegetation disturbance in an abandoned coppice forest in central Japan. *Euras. J. For. Res.*, **11**: 61-72.

Shibuya, S., Kubota, K., Osawa, M. & Kikvidze, Z., 2011. Assembly rules in ground beetles: what decides comunity structure, environmental factors or competition? *Europ. J. Ent.*, **108**: 453-459.

Thiele, H. U., 1997. Carabid Beetles in Their Environment. A Study on Habitat Selection by adaptation in Physiology and Behaviour. 369pp. Springer Verlag, Berlin.

Yamashita, H., Kiritani, K., Togashi, K. & Kubota, K., 2006. Wing dimorphism in three carabid species living in the grasslands of Mt. Omuro, Shizuoka, Japan. *Appl. entomol. Zool.*, **41**: 463-470.