



Spatial and temporal effects of local climate change on the carabid beetle community in Baekdudaegan mountain of South Korea

Bak, Yonghyen

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Doctoral dissertation

**Spatial and temporal effects of local climate change on the carabid
beetle community in Baekdudaegan mountain of South Korea**

(韓国白頭大幹における局地気候変動がオサムシ群集に及ぼす
空間的・時間的な影響)

YONGHYEN BAK

朴容煥

Graduate school of Human Development and Environment

Kobe University

神戸大学大学院人間発達環境学研究科 人間環境学専攻

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Chapter 1.

General introduction

General introduction

Global climatic warming is suggested to be created by the enhanced greenhouse effect, and will precipitate other environmental changes in rainfall, winds, ocean currents, sealevel and storm patterns at a rate unprecedented in the least a century ago (Pearman 1988; Tangley 1988; Houghton & Woodall 1989; Pittock & Whetton 1990). Such climate-induced changes have the capacity to make dramatic alterations to floral and faunal composition, species dominance, and the structure, function and distribution of ecosystems, which may cause species extinction (Peters & Darling 1985; Busby 1988; Main 1988; Cohn 1989; Fajer 1989; Greenwood & Boardman 1989; Mansergh & Bennett 1989; Botkin *et al.* 1991; Dennis & Shreeve 1991; Woodward & Rochefort 1991). Thus, enhanced greenhouse climate change will present major problems for the survival of species. Understanding the effects of global warming has become an important issue in the preservation of the global environment and biodiversity.

Climate change poses major new challenges to biodiversity conservation. As atmospheric CO₂ increases over the next century, it is expected to become the first or second greatest driver of global biodiversity loss (Sala *et al.* 2000; Thomas *et al.* 2004). Global average temperatures have increased 0.2°C per decade since the 1970s, and global average precipitation increased 2% in the last 100 years (IPPC 2007). Moreover, climate changes are spatially heterogeneous. Some locations, while others, are exposed to secondary effects like sea level rise (IPPC 2007). Climate change may have already resulted in several recent species extinctions (McLaughlim *et al.* 2002; Pounds *et al.* 2006).

Conserving biodiversity in forests has become a key issue in national and international forest policy and management because forests support numerous species in

many taxonomic groups including invertebrate and microbes (Lindenmayer *et al.* 2006). In particular, rapid changes in landscapes due to urbanization, agriculture, and road construction have caused forest loss and fragmentation, threatening forest biodiversity worldwide (Brockerhoff *et al.* 2008).

Mountainous areas have very high biodiversity due to small environmental disturbance and habitat for many organisms, considered as a very important ecosystem for many local unique species and conserving biodiversity (Lomolino 2001). In Korea, forests are important for conserving and enhancing biodiversity because they cover approximately 64% of the nation (Lee 2012). During the Korean War and earlier, most primary forests in Korea were devastated, and growing stocks declined precipitously to 5.6 m³/ha in 1952 (Lee 2012). During reforestation periods, coniferous trees were planted in urbanized areas or agricultural landscapes, while deciduous trees were regenerating or planted in mountainous areas. Consequently, growing stocks of Korean forests have increased to 126 m³/ha in 2010 (Lee 2012).

Microclimate is a suite of climatic conditions measured in localized areas near the earth's surface (Geiger 1965). Environmental variables in microclimatic scale, which include temperature, light, wind speed, and moisture, have been critical for the ecology of organisms, providing meaningful indicators for their habitat selection and other activities. In seminal studies, Shirley (1929, 1945) emphasized microclimate as a determinant of ecological patterns in both plant and animal communities, and as a driver of such processes by influencing the growth and mortality of organisms. The effects of microclimate on ecological processes such as plant regeneration and growth, soil respiration, nutrient cycling and wildlife habitat selection has become an essential component of current ecological research (Perry 1994).

Relationships between microclimate and biological processes are complex and often nonlinear. For example, decomposition rates of organic material within pits, mounds, and the floor of a wetland are strongly related to soil temperature and moisture. However, microclimatic studies have traditionally focused on statistical summaries in relatively wide scales, and less attention has been paid to variability in microclimate or to the differences among microclimatic patterns across spatial and temporal scales. The microclimatic environment and its relative importance for driving biological processes can vary with spatial and temporal scales because ecosystem structure and function are scale dependent (Meentemeyer & Box 1987). Thus, relationships between microclimate and structural landscape features or ecosystem processes developed at any single scale of study may not be applicable at other scales (Levin 1992). However, most studies of global climate warming have paid less attention to spatial and temporal variation in microclimates.

Studies of insects have revealed strong declines of some groups, suggesting that biodiversity losses are disproportionately high for this class (Thomas & Clarke 2004). This is of concern because insects are important in ecosystem functions, and their declines are likely to cause serious disruptions of natural processes (Walpole *et al.* 2009). However, information on trends in population decline or persistence is lacking in many key insect groups with critical roles in ecosystems (Butchart *et al.* 2010). Beetles (order Coleoptera) are composed with 40% of total insects, which comprises approximately 0.8–1.2 million species. Coleoptera is diverse in size and feeding ecology, and plays an important role as primary and secondary consumers in the ecosystem. Of these, carabid beetles (family Carabidae) are a species-rich group and are ubiquitous in the majority of terrestrial ecosystems (Thiele 1977). In addition, carabid beetles are good environmental indicators due to the fact that they are likely to be affected by disturbance in local habitat because they are often flightless and have low dispersal ability (Thiele 1977; Ishitani *et al.* 1997; Rainio & Niemelä 2003; Pearce &

Venier 2006; Maleque *et al.* 2009). Carabid beetles are mainly carnivorous, with some omnivorous and plant-feeding species. Some carabid species live on the tree, but most species exercise food crawling on the ground surface. Thus, carabid beetles occupy an important position within the ecosystem as predators to prey on small terrestrial invertebrates (Pausch 1979; Sunderland 2002; Holland 2002; Kubota *et al.* 2001). These species mainly live in forest, grassland or wetland, and their inhabitations are affected by geographical and seasonal variation in environment, biological community, vegetation, and biomass of litter layer therein (Thiele 1977; Luff 1975; Luff *et al.* 1989).

The aim of this study is to provide insights into the impact of spatial and temporal environmental variations on the community of carabid beetle. I examined 1) how carabid beetle communities are distributed in Baekdudaegan Mountain Range; 2) which environmental parameters are responsible for variation in the carabid beetle communities; 3) how much variations are involved in spatial and temporal differences in communities and environmental variables. In the next chapter, Chapter 2, I conducted a basic survey for elucidating species composition and distribution of carabid ground beetles in Baekdudaegan Mountain Range, Korea. Field survey using pitfall traps were performed and collected beetles were identified. In Chapter 3, I examined whether and how carabid beetle communities change over time within sites, and how they differ between sites, on a local scale. In Chapter 4, I quantify spatial and temporal variations in carabid beetle community compositions and in background microclimatic variables, using a generalized linear modelling approach.

Chapter 2.

Community structure and distribution of carabid beetles (Coleoptera: Carabidae) in Baekdudaegan mountain of Gangwon-do, Korea

Introduction

Approximately 0.8 – 1.2 million species of insects are living all around the world, and 40% of which consist of beetles. The order Coleoptera is diverse in size, behavior, and feeding ecology, playing an important role as primary and secondary consumers in the ecosystem (Pausch 1979; Sunderland 2002; Holland 2002; Kubota *et al.* 2001). The family Carabidae is mainly carnivorous, but some species are omnivorous or herbivorous. Some species live on the tree, but most carabid beetles forage on the ground. They mainly live in forest, grassland or wetland, and their inhabitations are affected by geographical and seasonal environment, biological community, vegetation type, tree age, and biomass of litter layer therein (Thiele 1977; Luff 1975; Luff *et al.* 1989).

The ecological studies about distribution and population dynamics of carabid beetles have been conducted mainly in Europe (Thiele 1977; Luff 1975; Luff *et al.* 1989). It has been shown that carabid beetles occupy an important position within the ecosystem as predators of small invertebrates (Pausch 1979; Sunderland 2002; Holland 2002; Kubota *et al.* 2001). Since most of carabid beetles are flightless and have low dispersal ability, they are sensitive to habitat disturbance and thus suitable as environmental indicators (Thiele 1977; Ishitani *et al.* 1997; Rainio & Niemelä 2003; Pearce & Venier 2006; Maleque *et al.* 2009). However, knowledge about the ecology of Korean carabid beetles is relatively scarce. Elucidating distribution and abundance of species is of value for carabid beetle conservation and understanding relevant environmental factors.

I conducted a basic survey for elucidating species composition and distribution of carabid beetles in Baekdudaegan of Gangwon-do, Korea. Field survey using pitfall traps were performed at 11 study sites and then collected beetles were identified.

Material and Methods

Study area

Eleven study sites were selected in Baekdudaegan mountains, Gangwon-do, Korea: 3 sites in Mt. Jinburyung, 3 in Mt. Odaesan, 3 in Mt. Taebaeksan, and 2 in Mt. Dutasan. All study sites were dominated by *Quercus* trees. In some study sites, red pine tree occurred and *Pseudostellaria palibiniana* and *Dioscorea quinqueloba* were found as understory vegetation. Geographic coordinates, elevation, and vegetation of these sites were shown in Fig. 2-1 and Table 2-1.

In Mt. Jinburyung, the site 1 (J1) maintained developed litter layer and understory vegetation due to the restriction of civilian access for natural conservation and army operation. However, the sites 2 (J2) and 3 (J3) did not due to mountain trails and a valley topography.

In Mt. Odaesan, some *Sasamorpha purpurascens* was found in the forest floor of the site 1 (O1). The site 2 (O2) maintained developed litter layer and understory vegetation. In the site 3 (O3), Japanese red pine trees and *Quercus* trees occurred, and litter layer and understory vegetation was quite poor.

In Mt. Taebaeksan, the site 1 (T1) harbored broadleaf trees and a red pine trees. The site 2 (T2) maintained developed litter layer in its valley area which are dominated by broadleaf trees. The study site 3 (T3) was located in Manhangjae of Taebaeksan mountain area and had developed litter layer.

In Mt. Dutasan, the site 1 (D1) maintained developed litter layer and understory vegetation. The site 2 (D2) had high humidity and poor litter layer, and *Sasa borealis* was found in valley area.

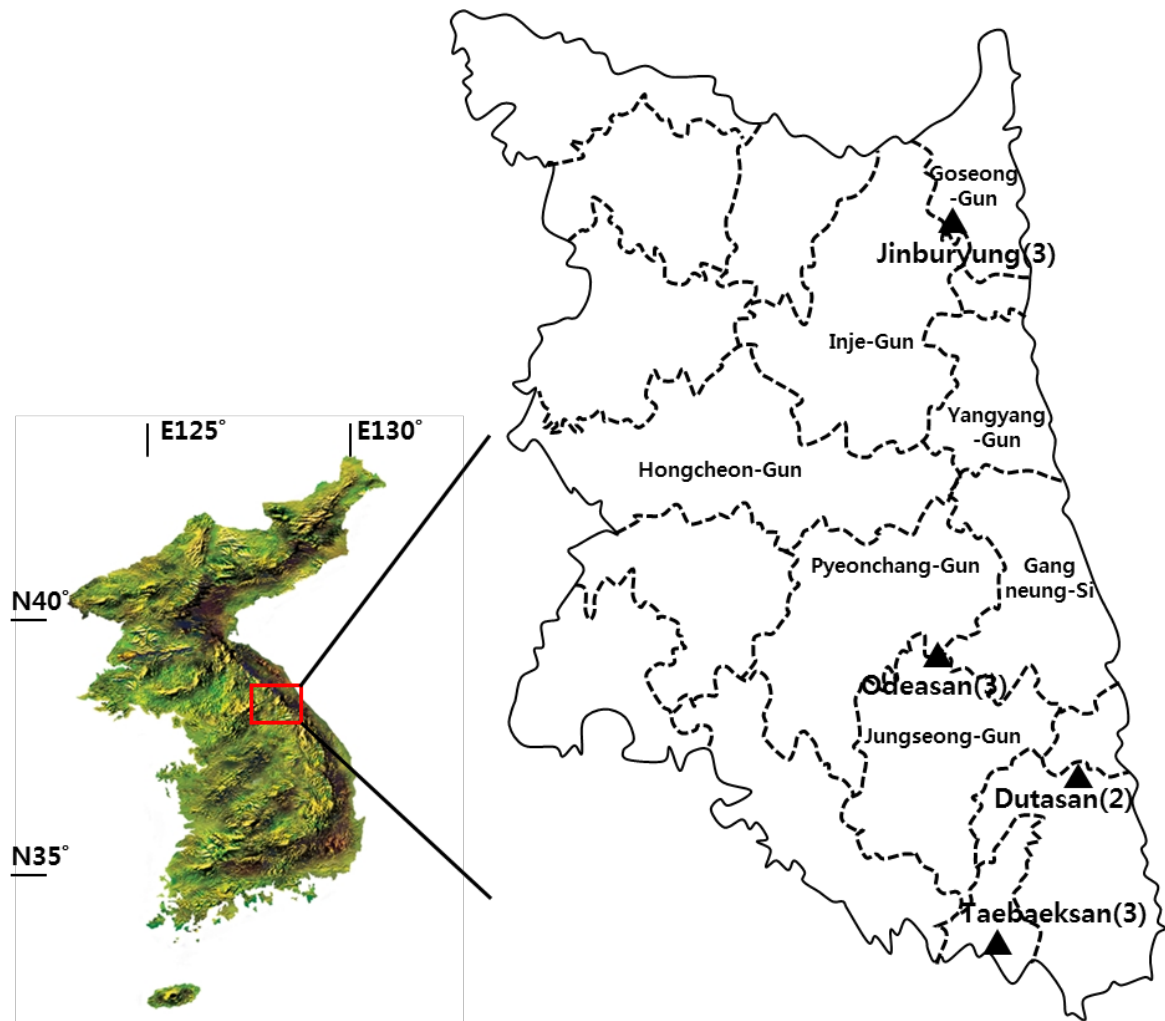


Figure 2-1. Locations of study mountains and sites in Baekdudaegan, Korea. Number of study sites was shown in parentheses attached to the name of mountains.

Table 2-1. Habitat environment of each survey site in Baekdudaegan.

Study sites		Latitude Longitude	Slope	Altitude (m)	Grad ient (°)	Doiminant tree species	Understory vegetation species
Jinbu- ryung	J1	N38°16'00.31" E128°23'07.14"	NW	694	20	<i>Quercus mongolica</i> , <i>Tilia mandshurica</i> , <i>Synplocos chinensis</i>	<i>Synurus deltoides</i> , <i>Impatiens textori</i> , <i>Isodon excisus</i> , <i>Oplismenus undulatifolius</i> etc.
	J2	N38°15'53.01" E128°20'01.94"	N	1,038	10	<i>Quercus mongolica</i> , <i>Acer pseudosieboldianum</i> , <i>Tilia mandshurica</i>	<i>Carex siderosticta</i> , <i>Hepatica asiatica</i> , <i>Adenophora remotiflora</i> , <i>Primula jesoana</i> etc.
	J3	N38°17'03.36" E128°21'40.76"	W	323	10	<i>Styrax obassia</i> , <i>Quercus mongolica</i> , <i>Pinus densiflora</i>	<i>Pseudostellaria palibiniana</i> , <i>Dioscorea quinqueloba</i> , <i>Isodon japonicus</i> , <i>Clematis heracleifolis</i> etc.
	O1	N38°44'31.86" E128°37'11.08"	W	741	25	<i>Quercus mongolica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , <i>Fraxinus rhynchophylla</i>	<i>Brachybotrys paridiformis</i> , <i>Pseudostellaria heterophylla</i> , <i>Carex siderosticta</i> , <i>Lespsdeza japonica</i> , <i>Rodgers iapodophylla</i> etc.
Odaesan	O2	N38°45'58.29" E128°36'20.22"	SW	1,062	32	<i>Quercus mongolica</i> , <i>Tilia mandshurica</i> , <i>Acer pseudosieboldianum</i>	<i>Sasa borealis</i> , <i>Ainsliaea acerifolia</i> , <i>Carex siderosticta</i> , <i>Tripterygium regelii</i> , <i>Viola albida</i> etc.
	O3	N38°47'10.76" E128°37'09.83"	N	668	20	<i>Fraxinus rhynchophylla</i> , <i>Pinus densiflora</i> , <i>Acer pseudosieboldianum</i>	<i>Disporums milacinum</i> , <i>Arisaema amurense</i> , <i>Pseudostellaria palibiniana</i> , <i>Pseudostellaria heterophylla</i> , <i>Isodon japonicas</i> etc.
Taebaeksan	T1	N37°06'36.02" E128°51'30.24"	SW	704	35	<i>Quercus mongolica</i> , <i>Fraxinus rhynchophylla</i> <i>Tilia mandshurica</i> ,	<i>Sasa borealis</i> , <i>Tripterygium regelii</i> , <i>Disporums milacinum</i> , <i>Carex siderosticta</i> etc.
	T2	N37°09'38.22" E128°53'10.35"	W	1,274	36	<i>Quercus mongolica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , <i>Fraxinus rhynchophylla</i>	<i>Astilbe koreana</i> , <i>Carex humilis</i> , <i>Athyrium niponicum</i> , <i>Viola albida</i> etc.
	T3	N37° 7'22.90" E128°57'32.88"	W	968	28	<i>Betula davurica</i> , <i>Pinus densiflora</i> , <i>Quercus mongolica</i>	<i>Athyrium niponicum</i> , <i>Syneilesis palmata</i> , <i>Disporums milacinum</i> , <i>Festuca ovina</i> etc.
Dutasan	D1	N37°20'43.00" E129°00'36.04"	N	1,024	26	<i>Quercus mongolica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , <i>Morus bombycis</i>	<i>Impatiens noli-tangere</i> , <i>Viola albida</i> , <i>Anemone reflexa</i> , <i>Impatiens textori</i> etc.
	D2	N37°23'26.00" E128°59'51.02"	EN	797	5	<i>Quercus mongolica</i> <i>Fraxinus rhynchophylla</i> <i>Rhus trichocarpa</i>	<i>Staphylea bumalda</i> , <i>Cimicifuga dahurica</i> , <i>Stephanandra incisa</i> , <i>Deutzia glabrata</i> etc.

Collection of ground beetles

Field survey was performed for two years (2011-2012) with two replications within a year (2011: Jul. 10-11 and Aug. 18-19 in Jinburyung, Jul. 11-12 and Aug. 19-20 in Odaesan, Jul. 13-14 and Aug. 20-21 in Taebaeksan, Jul. 14-15 and Aug. 21-22 in Dutasan; 2012: Jul. 19-20 and Aug. 18-19 in Jinburyung, Jul. 20-21 and Aug. 19-20 in Odaesan, Jul. 21-22 and Aug. 20-21 in Taebaeksan, Jul. 22-23 and Aug. 21-22 in Dutasan). Beetles were collected by pitfall traps (a plastic cup, 7.0 cm top diameter and 8.0 cm depth). Attractant (the powder of silkworm pupa) was put into the trap. Pitfall traps are devices for capturing small organisms living on the ground as they fall accidentally. The number of collected individuals were regarded as an indicator of the relative population density at the site, which reflects population density and biological activity (Briggs 1961; Erwin 1988; Heyborne *et al.* 2003). At each site, 200 traps were set in 2 or 3 lines with 2 m intervals. The traps were collected after 24 hours. All captured beetles were classified and counted. For the species belonging to the subfamily Carabinae, most of which belong to a single genus *Carabus*, subgenera were used for calculating genus-level diversity.

Analysis

Beetles belonging to the family Carabidae were used in the following analyses, and other taxonomic groups were used as an auxiliary data. All individuals were identified to species. Data from four samplings in each site were combined before analyses. Community diversity was compared with diversity index (Shannon-Wiener 1963) among sites.

To identify the similarity of beetle communities among study sites, Whittaker's percentage similarity (Whittaker 1975) was used to analyze similarity of community structure in sites, in which the number of individuals were transformed to $\log_{10}(N+1)$ before

calculation. The similarity matrix among sites was analyzed by a cluster analysis using unweighted pair-group method using average (UPGMA). Non-metric multi-dimensional scaling (NMDS) was also used to compare community structure. The NMDS is an iterative procedure, constructing the plot by successively refining the positions of points until satisfied (Clarke & Warwick 2001). In addition, first two dimensions often provide a reasonable starting point to the iterative computation for the 2-dimensional configuration (Clarke & Warwick 2001). The stress value obtained from the NMDS analysis is a measure of distortion between the positions of real data points and their graphical representation. Thus, a low stress value represents few distortions from the real position of the data points and is associated with a graph that more accurately represents the dissimilarities in species composition. These analyses were performed using SYSTAT version 5.2.

Results and Discussion

Distribution of species

Carabid beetles collected at 11 study sites in Baekdudaegan mountains were shown in Table 2-2. In total, 837 individuals were collected, which belonged to 32 species and 14 genera. Among them, 217, 303, 144, and 209 individuals were found in Mts. Jinburyung, Odaesan, Taebaeksan and Dutasan, respectively. The numbers of genera and species collected in these 4 mountains were summarized in Figures 2-2 and 2-3.

In Mt. Jinburyung, the carabid beetles were identified into 10 genera and 20 species, most of which were obtained from the site at the highest altitude (1,020 m). At genus level, *Leptocarabus* was most abundant, followed by *Synuchus*, and *Pterostichus* (Figure 2-3). At species level, *Leptocarabus seishinensis* (Lapoue, 1931) was most dominant, and *Synuchus nitidus* Motschulsky, 1861 and *Pterostichus audax* Tschitscherine, 1895 were the second and third dominant species. In particular, more *L. seishinensis* were collected in high altitudes than the lower site (316 m), and more *S. nitidus* were collected at the site of a medium altitude (702 m) than other altitudes.

In Mt. Odaesan, carabid beetles were identified into 12 genera and 29 species, most of which (18 species) were collected in O1 (altitude 742 m). At genus level, *Pterostichus* was most abundant, followed by *Synuchus* and *Eucarabus*. At species level, *Eucarabus sternbergi* (Roeschke, 1898) was most dominant, followed by *Synuchus* sp.1, *Pterostichus bellator* Csiki, 1930 and *Synuchus callitheres* Bates, 1873. *Eucarabus sternbergi* was collected in O3 twice as many as in O1 and O2. Two more species of Harpalinae were collected in O1.

In Mt. Taebaeksan, carabid beetles were identified into 9 genera and 18 species, most of which were collected in T2 at a high altitude (1,274 m). At genus level, *Synuchus* and

Pterostichus were the first and second dominant groups. At species level, *Synuchus* sp.1 was most dominant and *A. seishinensis*, *S. nitidus* and *E. sternbergi* were similarly dominant. *Synuchus* sp. was collected mostly in the high altitude (1,274 m).

In Mt. Dutasan, carabid beetles were identified into 11 genera and 21 species, which were collected evenly across the study sites. At genus level, *Anisodactylus* was most dominant, followed by *Pterostichus* and *Tomocarabus*. *Anisodactylus punctatipennis* Morawitz, 1862 was most dominant, and *Tomocarabus fraterculus* (Reitter, 1895) and *E. sternbergi* were the second and third dominant species.

In summary, the more carabid beetle species tended to be collected at the higher altitudes. In particular, an endangered species *Acoptolabrus mirabilissimus* (Ishikawa & Deuve, 1982) was collected at over 1,000 m altitude at the study sites in Mts. Jinburyung and Odaesan. This result suggest that carabid beetle diversity becomes high in sites with well-conserved vegetation, low levels of development of the organic material, which may be associated with altitude. It has been found that carabid beetle diversity increased according to altitude in the Amazon region (Gentry1998). Further investigation is needed to see why and how this species favors high altitudes, which may be important in determining the effect of climate change on distribution of this species. By contrast, *L. seishinensis* and *E. sternbergi* were collected in all study sites. These species may not favor particular altitudes, showing wide distributions across all study area. The genus *Synuchus* and *Pterostichus* were also distributed in all the study sites. Interestingly, a large number of *T. fraterculus* were collected in Mt. Dutasan. It may be related to the habitat conditions suitable for this species, and further investigation will be required.

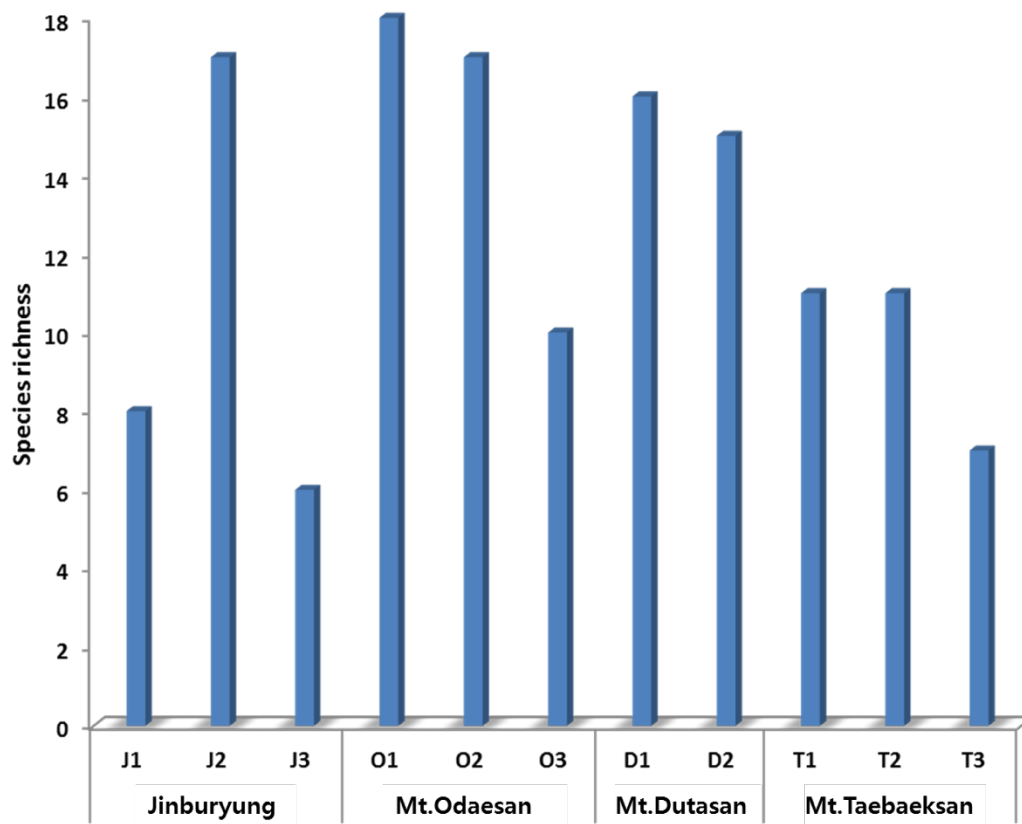


Figure 2-2. Species richness of carabid beetle communities in 11 study sites in Baekdudaegan.

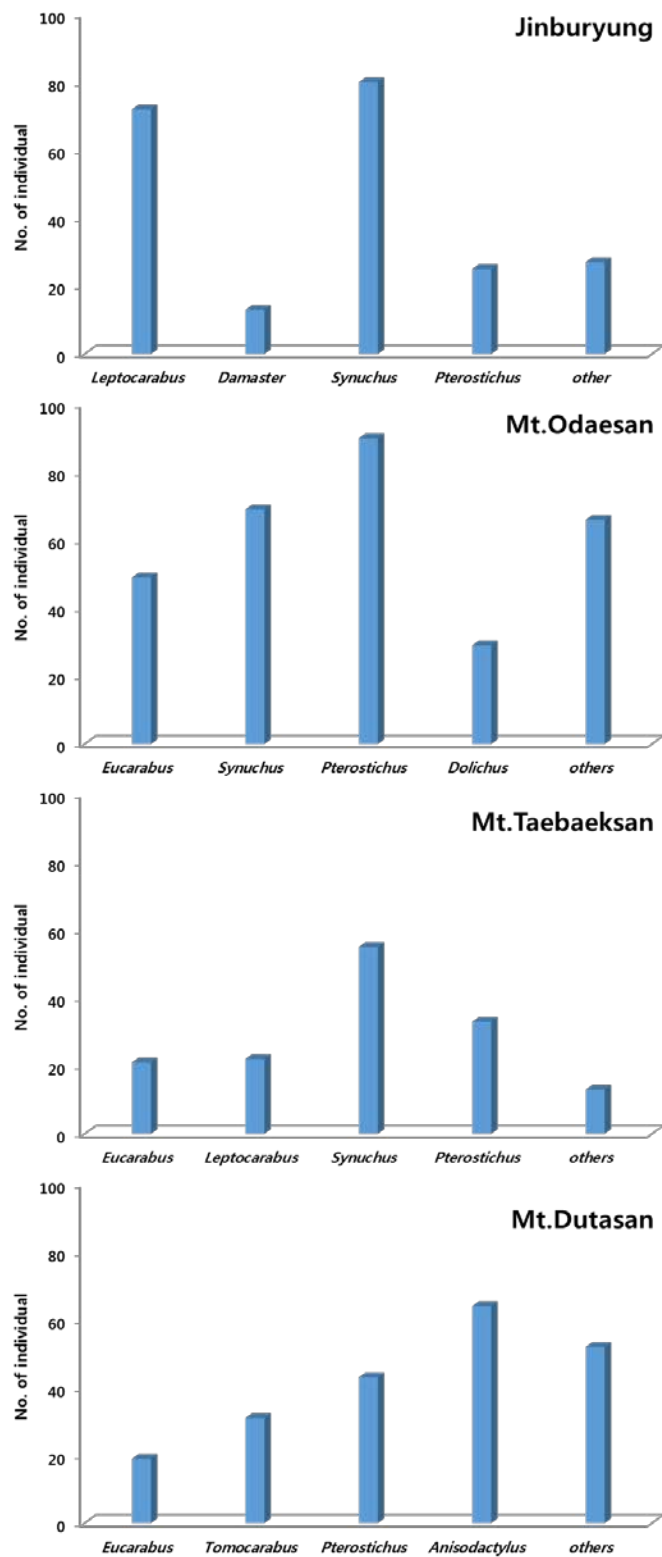


Figure 2-3. The individual abundances at genus level in carabid beetle communities in Baekdudaegan mountains.

Table 2-2. List of carabid beetles in Baekdudaegan, Gangwon do.

Genus	Species	Jinburyung				Odaesan				Taebaeksan				Dutasan		
		J1	J2	J3	Total	O1	O2	O3	Total	T1	T2	T3	Total	D1	D2	Total
<i>Eucarabus</i>	<i>Eucarabus sternbergi</i>	2	10		12	12	11	26	49		7	14	21	3	16	19
<i>Leptocarabus</i>	<i>Leptocarabus seishinensis</i>	14	51	4	69	4		16	20	10	2	10	22	1	12	13
	<i>Leptocarabus semiopacus</i>	1	2		3	1			1					2		2
<i>Morphocarabus</i>	<i>Morphocarabus venustus</i>		1		1		4		4						2	2
<i>Tomocarabus</i>	<i>Tomocarabus fraterculus</i>		2		2	5	1		6					11	20	31
<i>Coptolabrus</i>	<i>Coptolabrus smaragdinus</i>		3	2	5			6	6		3		3	3		3
	<i>Coptolabrus jankowskii</i>		1		1	3			3					13		13
<i>Acoptolabrus</i>	<i>Acoptolabrus mirabilissimus</i>		7		7		1		1							
<i>Synuchus</i>	<i>Synuchus callitheres</i>			4	4	11		13	24	2			2	5	6	11
	<i>Synuchus cycloides</i>					3	5	2	10							
	<i>Synuchus nitidus</i>	26	3		29		1	3	4	1	21		22			
	<i>Synuchus</i> sp.1	43	1		44	30	1		31	2	29		31	1	1	2
	<i>Synuchus</i> sp.2	2	1		3										2	2
<i>Platynus</i>	<i>Platynus assimilis</i>		4	3	7	8	3		11		2		2			
<i>Poecilus</i>	<i>Poecilus versicolor</i>		1	1	2		4	1	5	5	1	1	7	1		1
<i>Pterostichus</i>	<i>Pterostichus orientalis</i>		5		5		13		13					12	6	18
	<i>Pterostichus audax</i>	3		8	11	6		1	7	11	2		13	4	4	8
	<i>Pterostichus scurra</i>	6			6	4	15		19	1	1		2		2	2
	<i>Pterostichus compar</i>					3	2	3	8			4	4	1		1
	<i>Pterostichus bellator</i>		1		1	23	4		27	2	1		3	6	6	12
	<i>Pterostichus taebaegsanus</i>							1	1			1	1			
	<i>Pterostichus</i> sp.1					1			1	1			1		1	1
	<i>Pterostichus</i> sp.2					9			9	1	1		2			
	<i>Pterostichus coreicus</i>					18			18							
<i>Dolichus</i>	<i>Dolichus halensis</i>						1		1	4			4			
	<i>Dolichus</i> sp.					10			10							
<i>Pristosia</i>	<i>Pristosia vigil</i>		4		4		6		6					1		1
<i>Anisodactylus</i>	<i>Anisodactylus punctatipennis</i>					1			1			3	3	55	9	64
<i>Trigonognatha</i>	<i>Trigonognatha coreana</i>													1	1	2
<i>Harpalus</i>	<i>Harpalus griseus</i>		1		1		3		3							
	<i>Harpalus pseudophonoides</i>														1	1
<i>Chlaenius</i>	<i>Chlaenius pallipes</i>						4		4			1	1			
	Total	97	98	22	217	152	79	72	303	40	70	34	144	120	89	209

Species diversity

Diversity index was the highest at O1 and O2 in Mt. Odaesan (Fig. 2-4), probably due to the high species richness and no particular dominant species. The habitat of these two sites seemed stable with relatively infrequent environmental disturbance, where *Quercus* trees dominated and litter layer was developed at the forest floor.

By contrast, diversity index was low at J1 and J2 in Jinburyung, and T2 and T3 in Mt. Taebaeksan. Low diversity in J1 and J2 might be due to several reasons. In the case of the J1, the small number of species emergence may be resulted from extensive ecological disturbance due to the construction of ski resorts in its adjacent area. The abundance of a particular species (*Synuchus* sp.1) may also be a factor. The J2 was expected to show relatively high diversity because of genetic conservation area, but this site had a low diversity. This could be due to particular dominance of *L. seishinensis*.

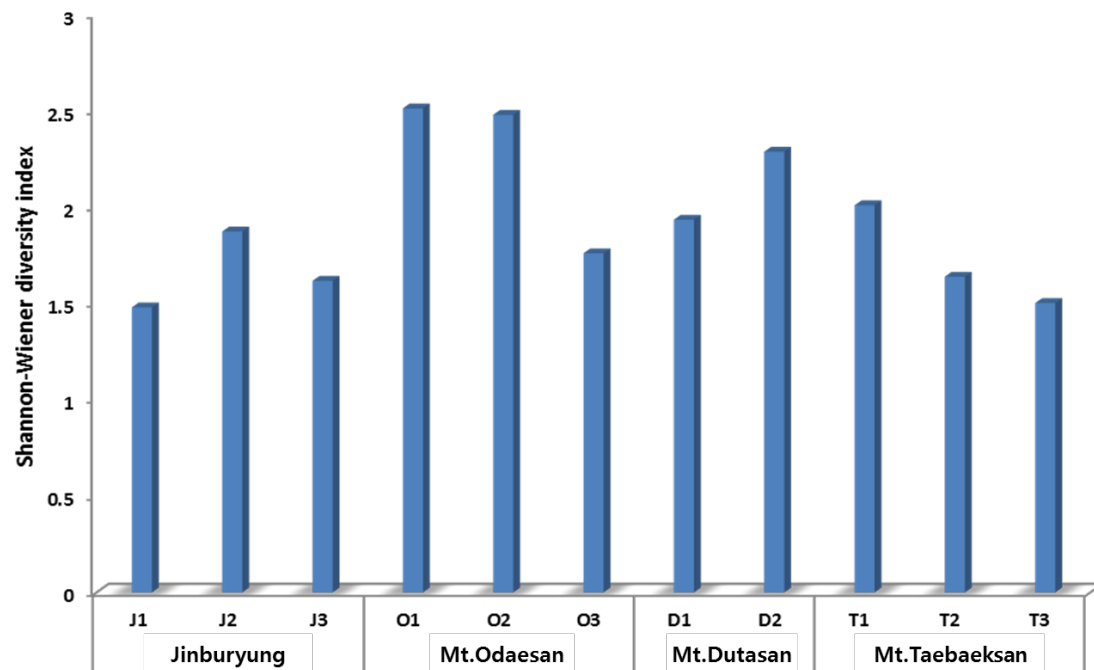


Figure 2-4. Shannon-Wiener diversity index of carabid beetle communities in 11 study sites in Baekdudaegan.

Similarity of community structure

Cluster analysis based on Whittaker's percentage similarity between communities showed that study sites were divided into two groups but not clustered with respect to geographical proximity (Fig. 2-5). The first group consisted of T1 and T3 in Mt. Taebaeksan, O3 in Mt. Odaesan, and J3 in Mt. Jinburyung. The second group included J1 in Mt. Jinburyung, T2 in Mt. Taebaeksan, and D1 and D2 in Mt. Dutasan. This result suggests that differences in community composition among sites may be associated with differences in dominant tree species. The sites in the second group, J1 in Mt. Jinburyung, T2 in Mt. Taebaeksan, and D1 and D2 in Mt. Dutasan were dominated by *Quercus mongolica*, while those in the first group, T1 and T3 in Mt. Taebaeksan, O3 in Mt. Odaesan, and J3 in Mt. Jinburyung harbored *Pinus densiflora* in relatively high densities.

Non-metric multidimensional scaling (NMDS) showed that the sites were arranged in relation to altitude (Fig. 2-6). The relatively higher sites (O2 in Mt. Odaesan, J2 in Mt. Jinburyung, D1 in Mt. Dutasan) exhibited larger scores in the dimension 2, but T2 in Mt. Taebaeksan was exceptional. By contrast, the relatively lower sites (O3 in Mt. Odaesan, J3 in Mt. Jinburyung, T1 in Mt. Taebaeksan) were located around the smaller scores of the dimension 2.

The present result suggests carabid beetle community compositions was primarily determined by altitude (Fig. 2-6). Some species were distributed in specific altitudinal ranges. By contrast, dominant species showed wide distributional ranges. In general, dominant species have a wide niche breadth (Suttiprapan *et al.* 2006), and thus likely affect the patterns of species richness, abundance, and diversity observed. In Korean mountains, any particular patterns had not been detected in carabid beetle communities along altitudinal gradient between 200 – 1400 m (Kim & Lee 1992b; Park *et al.* 1997; Park *et al.* 2003; Yeon *et al.*

2005). This study indicated that carabid beetles may respond to environmental factors such as altitude, slope, and vegetation. Long-term monitoring should be conducted to determine how the community changes along with various environmental factors.

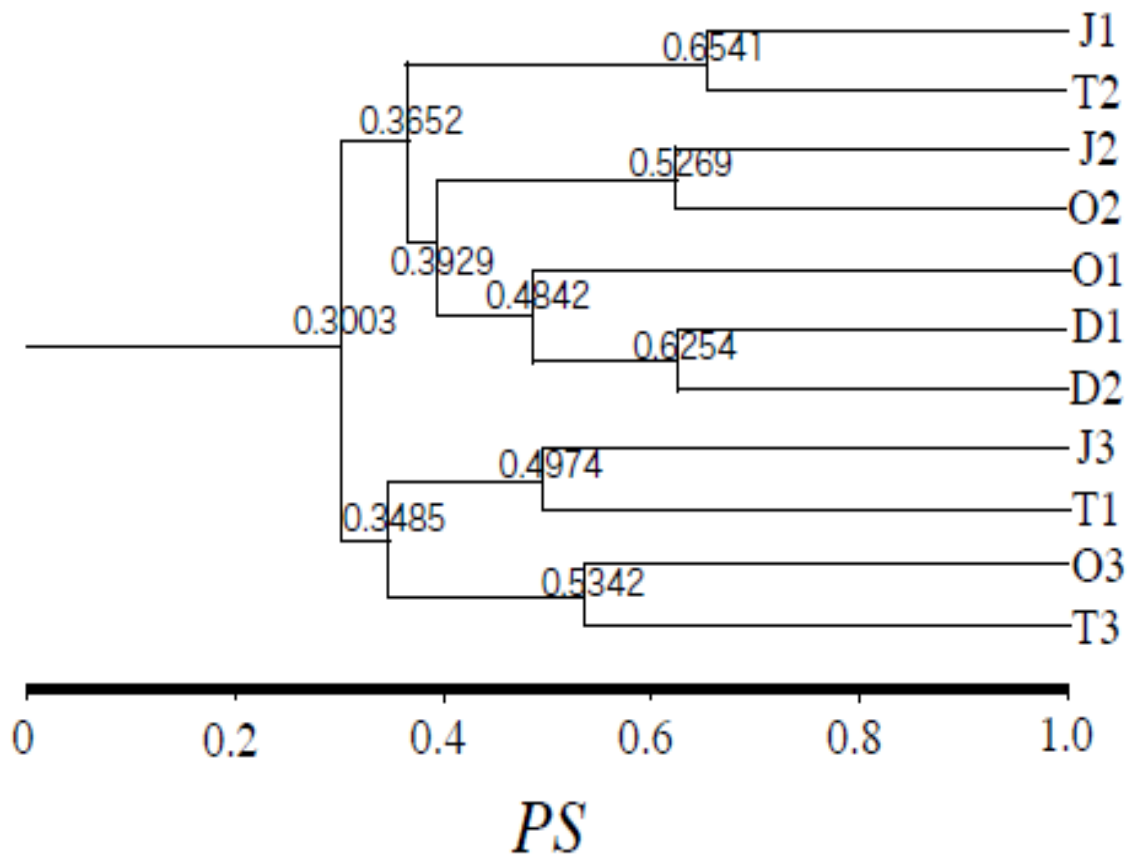


Figure 2-5. Cluster analysis using unweighted pair-group method using average (UPGMA) based on Whittaker's percentage similarity (PS) between 11 carabid beetle communities in Baekdudaegan mountains. PS was calculated based on $\log_{10}(N+1)$ transformed data.

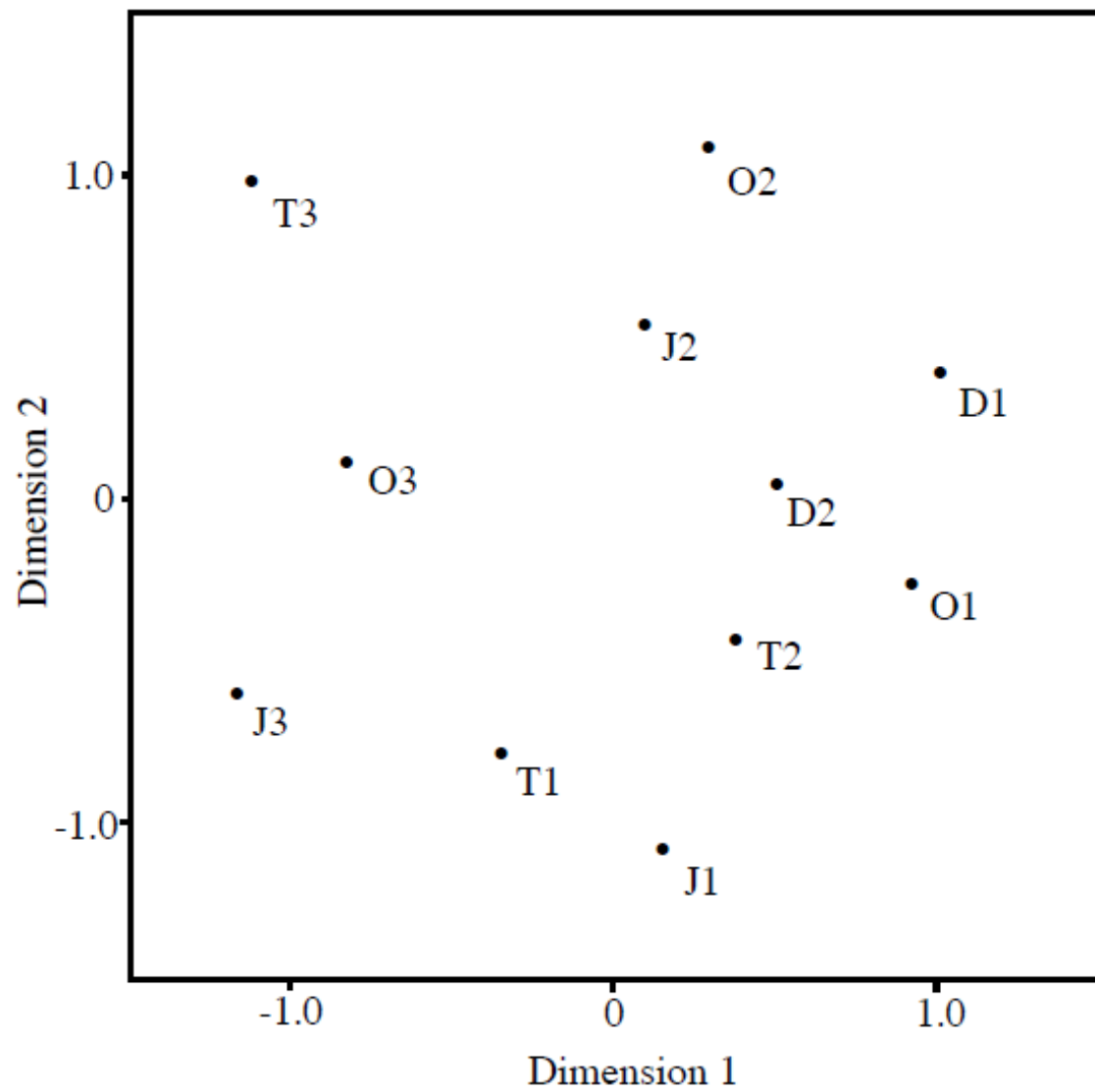


Figure 2-6. Non-metric multidimensional scaling (NMDS) ordination of 11 carabid beetle communities in Baekdudaegan mountains.

Chapter 3.

**Local climate mediates spatial and temporal
variation in carabid beetle communities in three
forests in Mount Odaesan, Korea**

Introduction

Global environmental changes may lead to dramatic alterations in floral and faunal composition, species dominance, and the structure, function and distribution of ecosystems, and via these processes may cause species extinctions (Peters 1985; Busby 1988; Main 1988; Cohn 1989; Fajer 1989; Greenwood & Boardman 1989; Mansergh & Bennett 1989; Botkin *et al.* 1991; Dennis & Shreeve 1991; Woodward & Rochefort 1991). Enhanced greenhouse effect climate change has presented major problems for the survival of species (Jackson *et al.* 2009; Loarie *et al.* 2009; Dawson *et al.* 2011; Bellard *et al.* 2012). Therefore, understanding the effects of global warming has become an important issue for the preservation of the global environment and biodiversity.

Studies of global climate change have mostly been based on statistical summaries of changes within relatively wide spatial and temporal scales (Gobbi *et al.* 2007), and less attention has been paid to variability in microclimates at narrower spatial and temporal scales. The microclimate is the suite of climatic conditions measured in a localised area (Geiger 1965; Bailey *et al.* 1997; Chen *et al.* 1999). Environmental variables that can be measured at the microclimatic scale include temperature, light, wind speed and moisture; these can be critical for the ecology of organisms and therefore may provide meaningful indicators for their habitat selection and other activities. In seminal studies, Shirley (1929, 1945) emphasised that microclimate can be a determinant of ecological patterns in both plant and animal communities, and a driver of ecological processes via its influence on the growth and mortality of organisms. Relationships between microclimate and biological processes are complex and often nonlinear (Chen *et al.* 1999; Eyre *et al.* 2005; Gillingham *et al.* 2012). The

microclimatic environment and its relative importance for driving biological processes can vary with spatial and temporal scales, because ecosystem structure and function are scale-dependent (Meentemeyer & Box 1987). Thus, relationships between microclimate and structural landscape features or ecosystem processes quantified at any single scale of study may not be applicable at other scales (Levin 1992). Additionally, global climatic change and its effects on global to local ecological processes are ongoing. Hence, continuous research is important to address this issue, although most researchers have examined only a snapshot of these processes based on data from one or a few years (Jung *et al.* 2012).

Examining the relative importance of environmental factors in determining faunal composition in adjacent sites or regions is a prerequisite for understanding the processes that shape communities. This understanding is vital for predicting interactions between regional species pools and local communities, delineating regions for environmental assessment and conservation, and predicting the effects of global change on species' distributions at large spatial scales. Here, I examine the effect of microclimate on carabid beetle communities and variation in the microclimate of adjacent sites. Carabid beetles (Coleoptera: Carabidae) are good environmental indicators: they are likely to be affected by disturbance in local habitats because they are often flightless and have low dispersal ability (Thiele 1977; den Boer *et al.* 1980; Ishitani *et al.* 1997; Rainio & Niemelä 2003; Pearce & Venier 2006; Maleque *et al.* 2009). In contrast to mobile species that can move to suitable environments, species with low mobility are expected to be influenced more directly by local environments. Beetles make up approximately 40% of the 0.8–1.2 million insect species. The Coleoptera are diverse in size and feeding ecology, and play important roles as primary and secondary consumers in many ecosystems. Carabid beetles are mainly carnivorous; some species are omnivorous or granivorous. Some carabid species live on trees, but most live and forage on the surface of the ground. Thus, carabid beetles occupy an important position within ecosystems as

predators of small terrestrial invertebrates (Pausch 1979; Sunderland 2002; Holland 2002; Kubota *et al.* 2001). The species mainly live in forest, grassland or wetland, and their habitats are affected by geographical and seasonal variation in the environment, biological communities, vegetation, and the biomass of the litter layer (Thiele 1977; Luff 1975; Luff *et al.* 1989).

The aim of this study was to examine 1) whether and how carabid beetle communities change over time within sites, and 2) how they differ between sites, on a local scale. The study sites were within one mountain area that exhibits variation in vegetation, slope direction and altitude. The within-site changes and between-site differences in communities are expected to be attributable to differing responses to local microclimates. Based on the results, we discuss the importance of understanding spatial and temporal variation in microclimates in studies of global environmental change.

Materials and methods

Study area and field survey

I conducted field surveys on Mount Odaesan, Korea, in 3 months of each year when adult carabid beetles are active (July, August and September) for 5 consecutive years (2011: 11–12. Jul, 19–20. Aug, 17–18. Sep, 2012: 20–21. Jul, 19–20. Aug, 20–21. Sep, 2013: 25–26. Jul, 18–19. Aug, 22–23. Sep, 2014: 27–28. Jul, 22–23. Aug, 23–24. Sep, 2015: 22–23. Jul, 12–13. Aug, 12–13. Sep). This sampling was arranged to capture both spring and autumn breeders in limited opportunities within the national park. Spring breeders are active in Korean mountains before July, but most of them continue their activities until autumn. Autumn breeders start their activities from June or July and end in September or October (e.g., Kim & Lee 1992a). The annual average temperature and precipitation in the study area were 6.4°C and 1,717 mm, respectively (Korea Meteorological Administration 2011). The three study sites were within the Odaesan National Park (Table 3-1, Fig. 3-1) and were used with permission from Baekdudaegan Mountain Range Ecological Monitoring (permit no. C1008923-01-01). The study sites were situated within primary (Site 2) and secondary (Sites 1 and 3) deciduous forests (Table 3-1) that were formed on a 4.8–11.5 cm deep litter layer on a 28–75 cm deep layer of stony soil. The soil mostly consisted of loam, sandy loam and silt loam (Kim 2006). Site 1 was on a west-facing slope near the bottom of a valley (steepness = 25°, 741 m above sea level), where trees were relatively tall and the forest canopy was mostly closed. Site 2, the highest elevation site, was on the ridge of a south-west-facing slope (32°, 1,062 m), where trees were relatively short and the forest canopy was thin and sporadically opened. Site 3 was on a continuous north-facing slope (20°, 668 m), where, as in Site 1, trees were relatively tall and the forest canopy was mostly closed.

Environmental measurements were obtained using HOBO data loggers (Onset Computer Corporation, Bourne, MA) to record air temperature, air humidity, light intensity and soil temperature hourly from June 2010 to September 2015. Each logger was attached to a tree trunk 120 cm above the ground. Soil temperature was measured 5 cm underground. The data were downloaded directly from each logger every month. This system cannot measure precipitation, and generally it is difficult to measure it hourly, although it is an important environmental parameter to predict carabid beetle communities. I expected that air humidity is closely related to the precipitation and can be a surrogate.

To capture community composition at each study site, I collected carabid beetles using pitfall traps (plastic cups 7.0 cm in diameter and 8.0 cm deep) containing an attractant (powder of silkworm pupa) (Lövei & Sunderland 1996; Holland 2002; Heyborne *et al.* 2003). Two hundred traps were set in two or three lines at 2 m intervals at each study site in each month and year, and beetles were collected 24 hours later. All the beetles caught in the 200 traps were combined to form the sample for that site, month and year. The exact position of the trap lines was changed arbitrarily within study sites each time to avoid any effects of previous captures. All carabid beetles that were captured were counted and identified to species, except for three *Pterostichus*, three *Synuchus* and one *Dolichus* species that were regarded only as morphospecies. My field survey resulted in 45 samples of carabid beetle communities: each of three sites was sampled in 3 months in each of 5 years.

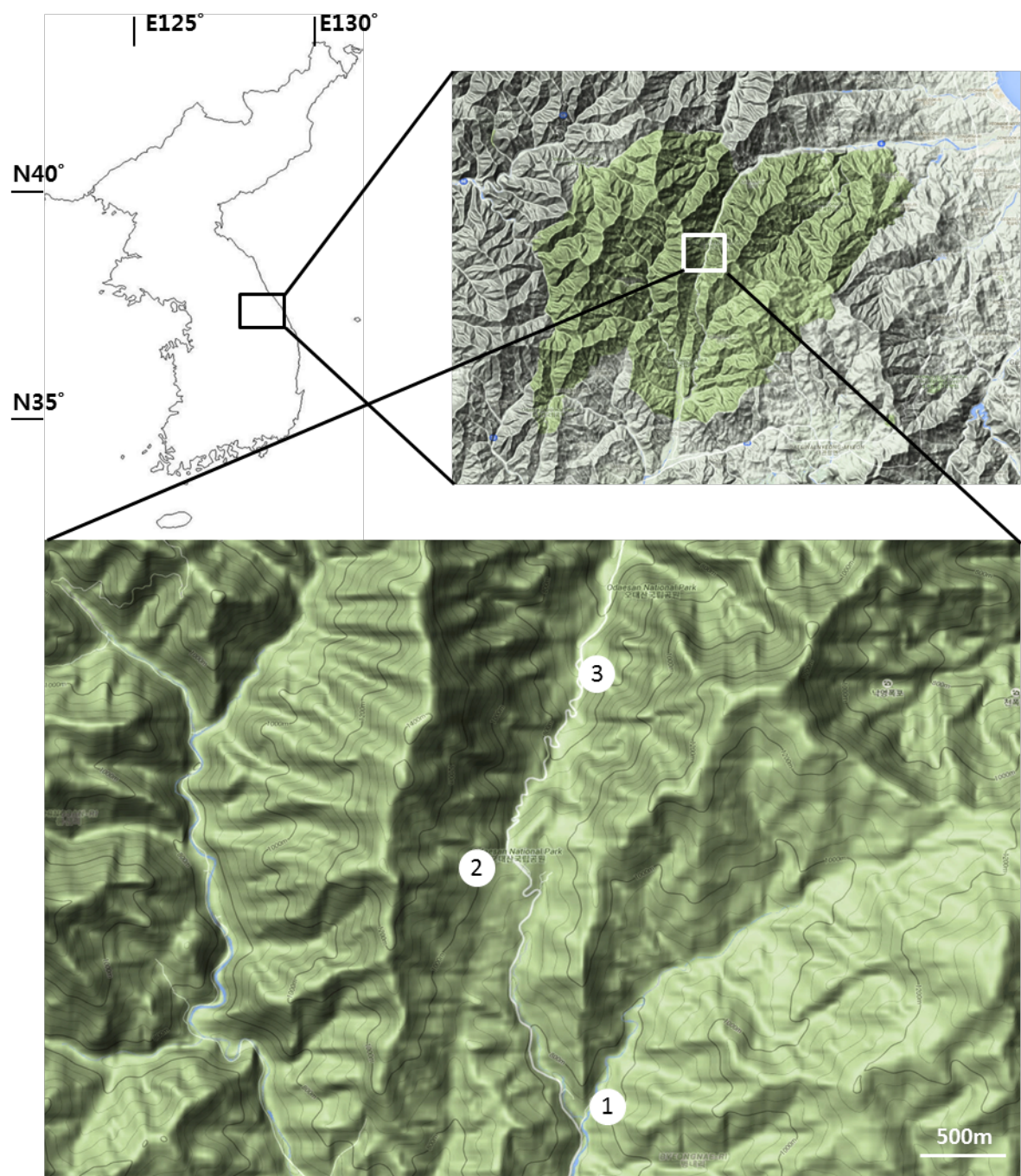


Figure 3-1. Locations of the three study sites on Mount Odaesan, Korea.

Table 3-1. Habitat and environmental information on the study sites on Mount Odaesan, Korea.

Site	Latitude Longitude	Slope	Gradient (%)	Altitude (m)	Dominant plants	Understorey vegetation species
1	N38°44'31.86" E128°37'11.08"	W	25	741	<i>Quercus mongolica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , <i>Fraxinus rhynchophylla</i>	<i>Brachybotrys paridiformis</i> , <i>Pseudostellaria heterophylla</i> , <i>Carex siderosticta</i> etc.
2	N38°45'58.29" E128°36'20.22"	SW	32	1,062	<i>Quercus mongolica</i> , <i>Tilia mandshurica</i> , <i>Acer pseudosieboldianum</i> <i>Fraxinus rhynchophylla</i> ,	<i>Sasa borealis</i> , <i>Ainsliaea acerifolia</i> , <i>Carex siderosticta</i> etc.
3	N38°47'10.76" E128°37'09.83"	N	20	668	<i>Pinus densiflora</i> , <i>Acer pseudosieboldianum</i>	<i>Disporum smilacinum</i> , <i>Arisaema amurense</i> , <i>Pseudostellaria palibiniana</i> etc.

Analysis of environmental factors

To summarise the microclimate data, I first calculated daily means from the data that had been collected at hourly intervals in each site. Then, 12 environmental variables were calculated for each year: summer mean air temperature (S.tem), winter mean air temperature (W.tem), summer highest mean air temperature (S.H.tem), winter highest mean air temperature (W.H.tem), summer lowest mean air temperature (S.L.tem), winter lowest mean air temperature (W.L.tem), summer mean air humidity (S.hum), winter mean air humidity (W.hum), summer mean illumination (S.illu), winter mean illumination (W.illu), summer mean soil temperature (S.Soil) and winter mean soil temperature (W.Soil). Winter variables were calculated from the data collected in the December to February period before the month of sampling. Summer variables were calculated from the data collected in the period from June to the date of sampling. I focused on summer and winter microclimates, because, for carabid beetles in this region, summer conditions may be important for reproduction and population growth, and winter conditions may be important for survival during hibernation (Kim & Lee 1992a, 1992b).

To examine directional trends in climate change (e.g., environmental warming) in our observation period, as well as local differences between study sites, I analysed each of the 12 climatic variables in turn using generalised linear models (GLMs). In this analysis, I used 1 of 12 climatic variables as the dependent variable, and site and year (as a continuous variable) as independent variables. Identity-link and normal distribution were assumed, and likelihood ratio tests were used to examine the statistical significance of parameters. A significant effect of year was expected if directional climate change occurred.

Analysis of beetle communities

Firstly, I examined relationships between variations in the carabid beetle community composition over the months and years of sampling and the 12 environmental variables by means of canonical correspondence analysis (CCA). Statistical significance of the effect of the environmental measures was examined by a randomisation test based on 999 pseudo-replications. I calculated the scores of the CCA axes (CCA1 and CCA2) for measures of community composition. This analysis was performed using the function `vegan` in the software package R 3.1.3 (R Development Core Team 2015).

Secondly, I examined whether temporal changes in carabid beetle communities differed between sites. To summarise the composition of communities, I calculated five measures characterising the community for each sample: species richness (the number of species), individual abundance (the total number of individuals), diversity index (Shannon-Wiener 1963), CCA1 and CCA2. I constructed GLMs with one of five measures of community composition as a dependent variable, and with site, year (as a categorical variable) and their interaction as independent variables. Log-link and Poisson distribution were used for count data (species richness and individual abundance); identity-link and normal distribution were used for metric data (diversity index and CCA scores). Statistical significance was based on likelihood ratio tests. Significant interactions were expected if the patterns of temporal change in communities differed between sites. In addition, to quantify spatial and temporal variations in communities, I calculated Sørensen's index among three sites based on the data pooled for five years and based on the data from each year (spatial β -diversity), and across five years within each site (temporal β -diversity). I also calculated

Shanon's diversity index for the data from each site and year and for pooled data across five years in each site (α -diversity).

Thirdly, to determine which environmental factors influenced temporal changes in communities in each site, and also to confirm the results of the CCA, I constructed generalised linear mixed models (GLMMs) for each site, with one of the five measures of community composition as the dependent variable, and the 12 environmental factors as independent variables. Since I sampled three times each year, year was included as a random term. Log-link and Poisson distribution were used for count data (species richness and individual abundance); identity-link and normal distribution were used for metric data (diversity index and CCA scores). I used the automated model selection procedure to run models for all possible combinations of the explanatory variables, and then selected the best-fitting models based on the Akaike Information Criterion (AIC), using $\Delta AIC < 4$ as a cut-off criterion to delineate a 'top model set' (Grueber *et al.* 2011). The relative importance of each predictor variable was calculated using the model average as a sum of the Akaike weights over all of the selected models in which the parameter of interest appeared. These analyses were performed using the function lme4 and MuMIn in R.

Results

Spatial and temporal variation in environmental factors

In all three study sites during the study period, the monthly means of air temperature, soil temperature and air humidity were highest in August and lowest in December or January (Fig. 3-2, 3-3, 3-4 and 3-5). Air temperature tended to be lowest in Site 1, followed by Sites 2 and 3 in winter. S.H.tem and W.H.tem were significantly higher in Site 2, and W.tem and S.L.tem were significantly higher in Site 3, than in Site 1 (Table 3-2). This tendency was slight in soil temperature, but W.Soil was significantly higher in Site 2 than in Site 1 (Table 3-2). Air humidity tended to be lowest at Site 3, significantly so for W.hum (Table 3-2). Illumination was highest in December or January and lowest in August (Fig. 3-5), and was significantly higher in Site 2 than in Site 1 (Table 3-2). I detected no significant directional trends in environmental changes in the 5 years of study (Table 3-2).

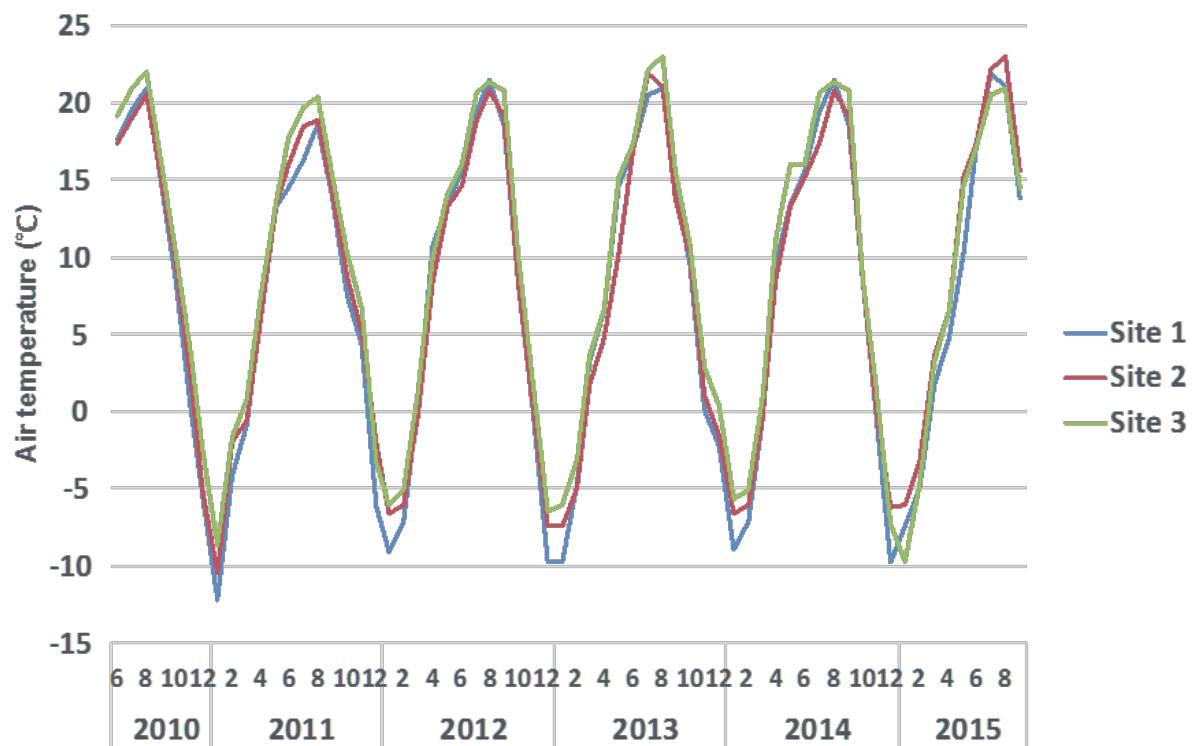


Figure 3-2. Temporal changes in monthly mean air temperature in the three study sites on Mount Odaesan, Korea

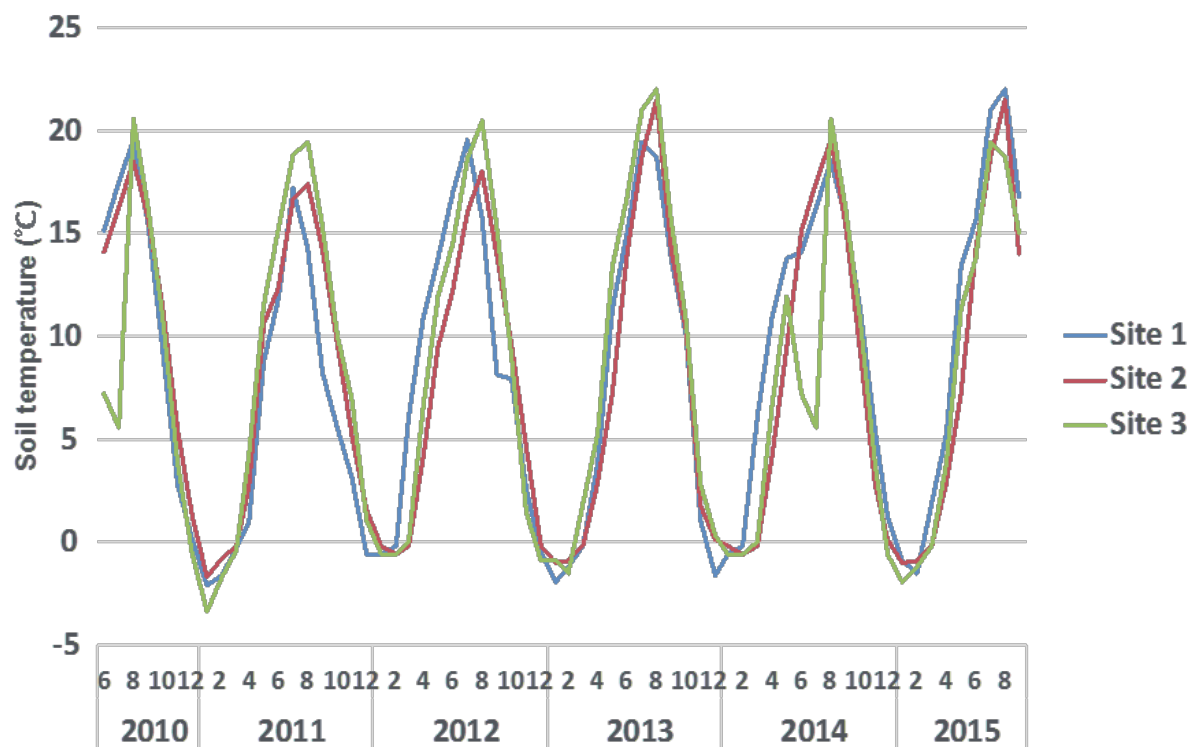


Figure 3-3. Temporal changes in monthly mean soil temperature in the three study sites on Mount Odaesan, Korea

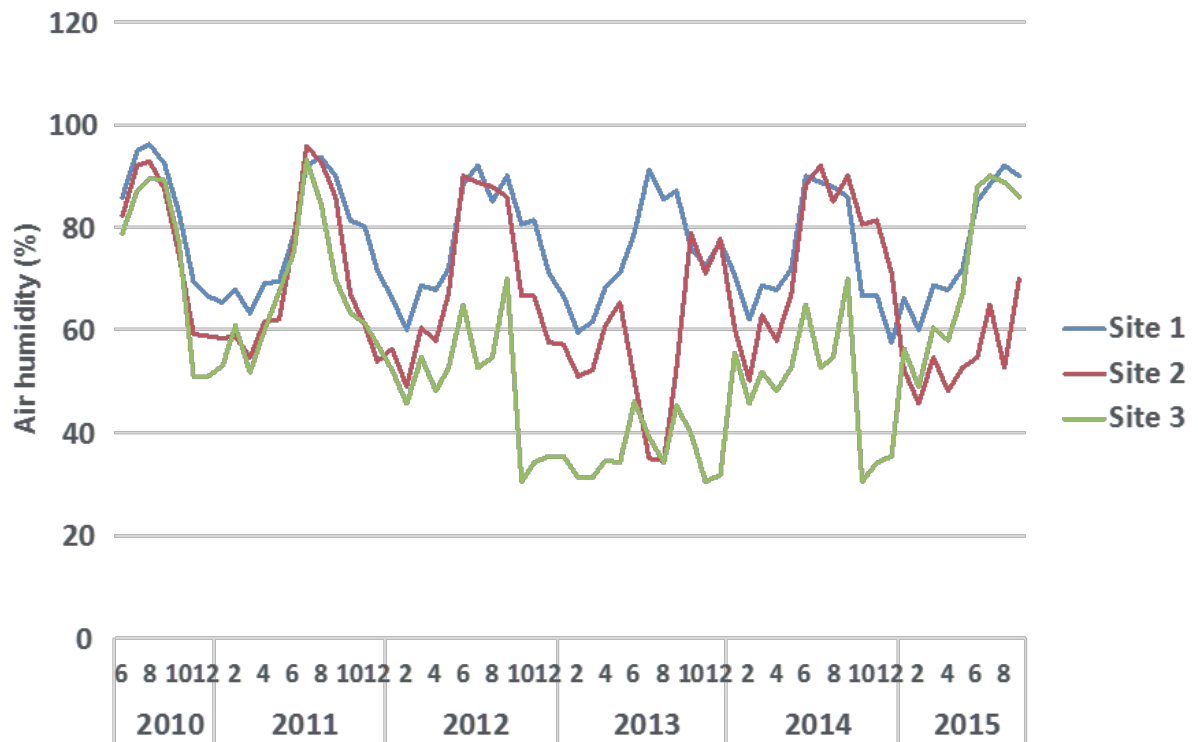


Figure 3-4. Temporal changes in monthly air humidity in the three study sites on Mount Odaesan, Korea

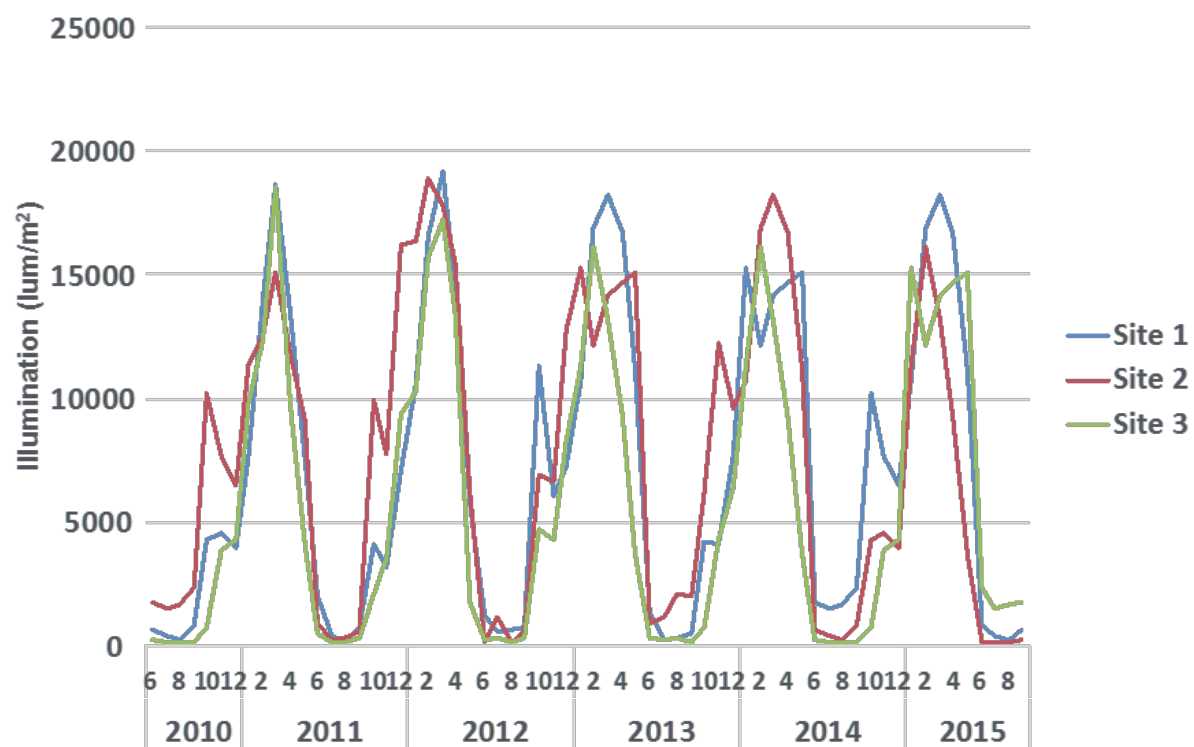


Figure 3-5. Temporal changes in monthly mean illumination in the three study sites on Mount Odaesan, Korea

Table 3-2. Generalised linear models explaining temporal and spatial variation in environmental measures.

	Estimate	SE	Pr (> t)
S.tem			
Year	0.232	0.170	0.200
Site 2	-0.154	0.590	0.799
Site 3	1.022	0.590	0.111
W.tem			
Year	0.303	0.232	0.218
Site 2	1.426	0.805	0.104
Site 3	2.412	0.805	0.012*
S.H.tem			
Year	-0.200	0.278	0.488
Site 2	2.498	0.964	0.025*
Site 3	0.33	0.964	0.739
W.H.tem			
Year	-0.261	0.294	0.393
Site 2	6.272	1.018	7.08e-05***
Site 3	2.594	1.018	0.027*
S.L.tem			
Year	0.142	0.148	0.358
Site 2	0.006	0.511	0.991
Site 3	1.852	0.511	0.004**
W.L.tem			
Year	0.433	0.546	0.444
Site 2	-0.174	1.890	0.928
Site 3	2.408	1.890	0.229
S.Soil			
Year	0.135	0.384	0.732
Site 2	0.576	1.330	0.673
Site 3	0.266	1.330	0.845
W.Soil			
Year	-0.165	0.135	0.248
Site 2	1.042	0.468	0.048*
Site 3	0.358	0.468	0.461
S.hum			
Year	-2.681	3.066	0.400
Site 2	-10.346	10.619	0.351
Site 3	-18.378	10.619	0.111
W.hum			
Year	-1.028	1.381	0.472
Site 2	-7.182	4.785	0.162
Site 3	-19.792	4.785	0.002**
S.illu			
Year	-0.787	0.818	0.357
Site 2	3.342	2.834	0.263
Site 3	-5.232	2.834	0.092
W.illu			
Year	-1.222	3.298	0.718
Site 2	34.320	11.426	0.012*
Site 3	0.996	11.426	0.932

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Spatial and temporal variation in beetle communities

This study collected 6,638 individual carabid beetles from three study sites. The beetles belonged to 31 species in 17 genera (Table 3-4). At the genus level, *Synuchus* (2,769 individuals), *Carabus* (1,409) and *Pterostichus* (1,076) were dominant, followed by *Pristosia* (779). The number of individuals captured tended to increase across years in the sites 2 and 3, whereas did not in Site 1 (Table 3-3).

The 45 community data-points (from three sites over 5 years, with repetitions in 3 months each year) were segregated along two CCA axes (Figs. 3-6, 3-7, 3-8, 3-9 and 3-10). Variation along the CCA1 axis was mainly determined by S.H.tem, W.H.tem, S.Soil and W.Soil. Variation along the CCA2 axis was by S.tem, S.L.tem, W.illu and W.Soil (Fig. 3-6). Total variation between communities was significantly influenced by variation in S.tem, S.illu, W.illu and W.Soil (Fig. 3-6). *Pterostichus* species showed large variation in their preferred environments along the CCA1 axis, and *Anisodactylus punctatipennis* Morawitz, 1862 and *Brachinus stenoderus* Bates, 1873 were positioned near the positive extreme of this axis (Fig. 3-7). By contrast, *Carabus* and *Synuchus* species showed large variation in their preferred environments along the CCA2 axis, and *Chlaenius pallipes* Geble, 1823 and *Pterostichus coreicus* Jedlička, 1962 were at the positive extreme of this axis (Fig. 3-7).

The patterns of temporal change in community composition differed between sites. Community compositions in Sites 1 and 2 varied mostly along the CCA2 axis, and tended to vary least in Site 1, with the exception of the sample from July 2011. By contrast, community composition in Site 3 varied mostly along the CCA1 axis (Figs. 3-8, 3-9 and 3-10). This variation could be attributed primarily to the communities observed in 2012. Variation between the three monthly replications in each site within each year was less than that

between years, indicating that this analysis mainly captured changes between years within each site.

Between-site differences in temporal community changes were confirmed by GLM analyses. Interaction terms between site and year were significant for individual abundance ($\chi^2_8 = 360, P < 0.00001$), diversity index ($F_{8,38} = 2.62, P = 0.026$) and CCA1 ($F_{8,38} = 7.97, P < 0.00001$), but not significant for species richness ($\chi^2_8 = 6.44, P = 0.598$) and CCA2 ($F_{8,38} = 1.40, P = 0.236$).

Temporal variation in communities among five years were as large as spatial variation among three sites: temporal β -diversity index ranged 0.41 to 0.53, while spatial β -diversity did 0.26 to 0.59 (Table 3-4). Spatial β -diversity decreased when based on the data pooled for five years (0.15). α -diversity ranged 0.62 to 1.25 in each site and year, and increased when pooled among five years (1.24-1.26). These results probably indicate that rare species dropped out from single year data were recovered when pooled.

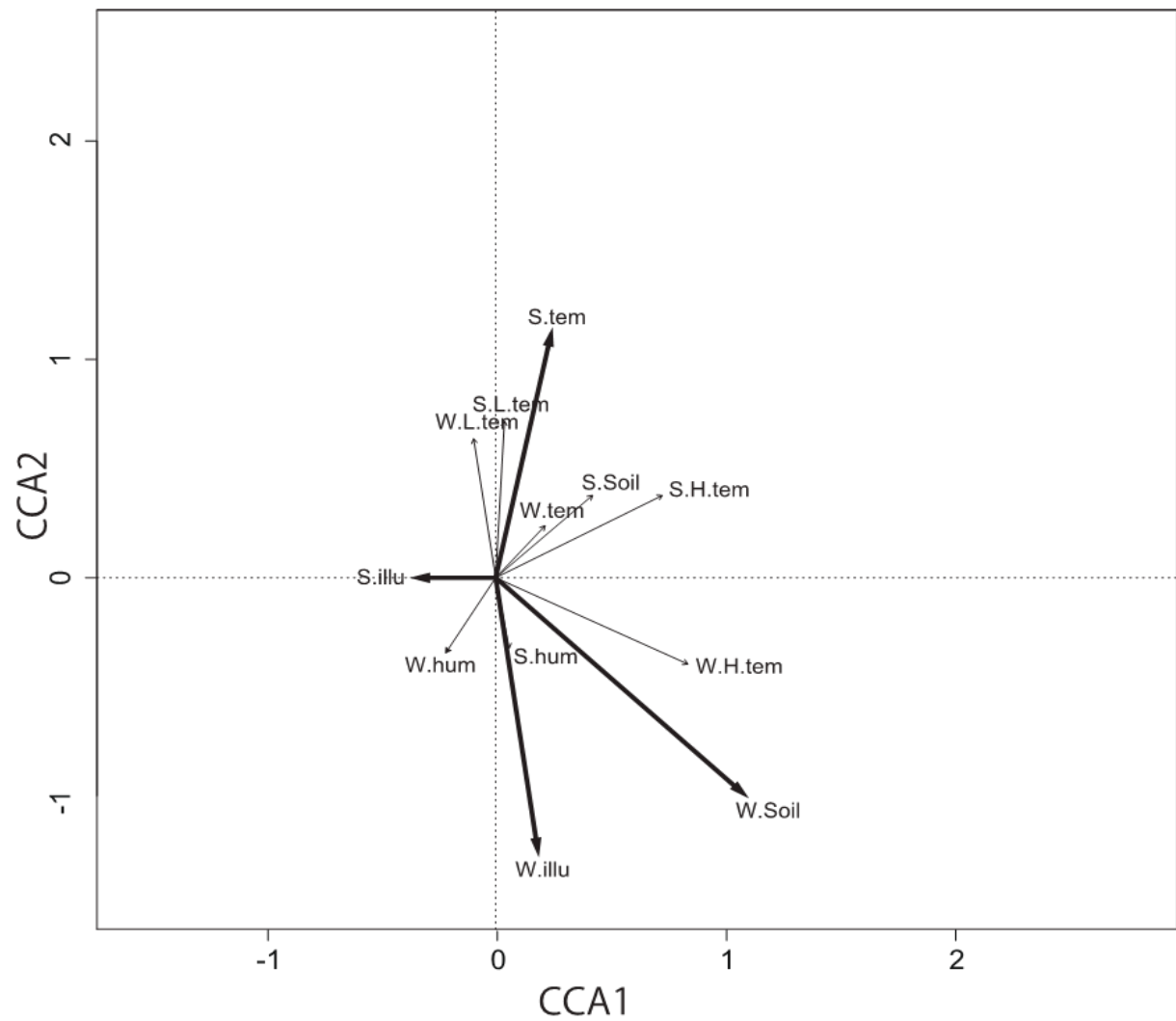


Figure 3-6. Canonical correspondence analysis (CCA) of associations between environmental conditions and carabid beetle community composition (Directions of environmental variation; significant factors are shown as bold vectors).

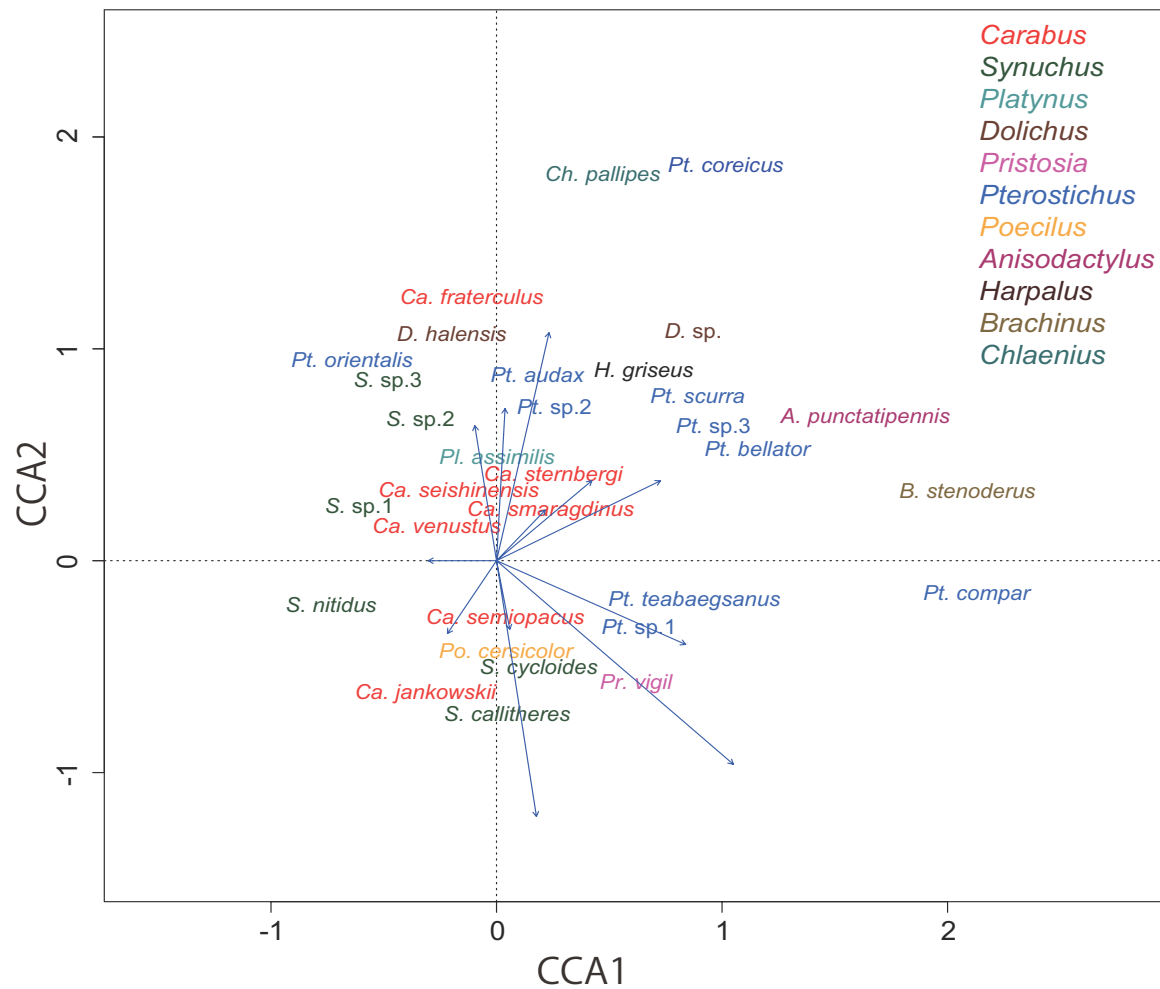


Figure 3-7. Canonical correspondence analysis (CCA) of associations between environmental conditions and carabid beetle community composition (Environmental preference of species; species with fewer than ten individuals are not shown).

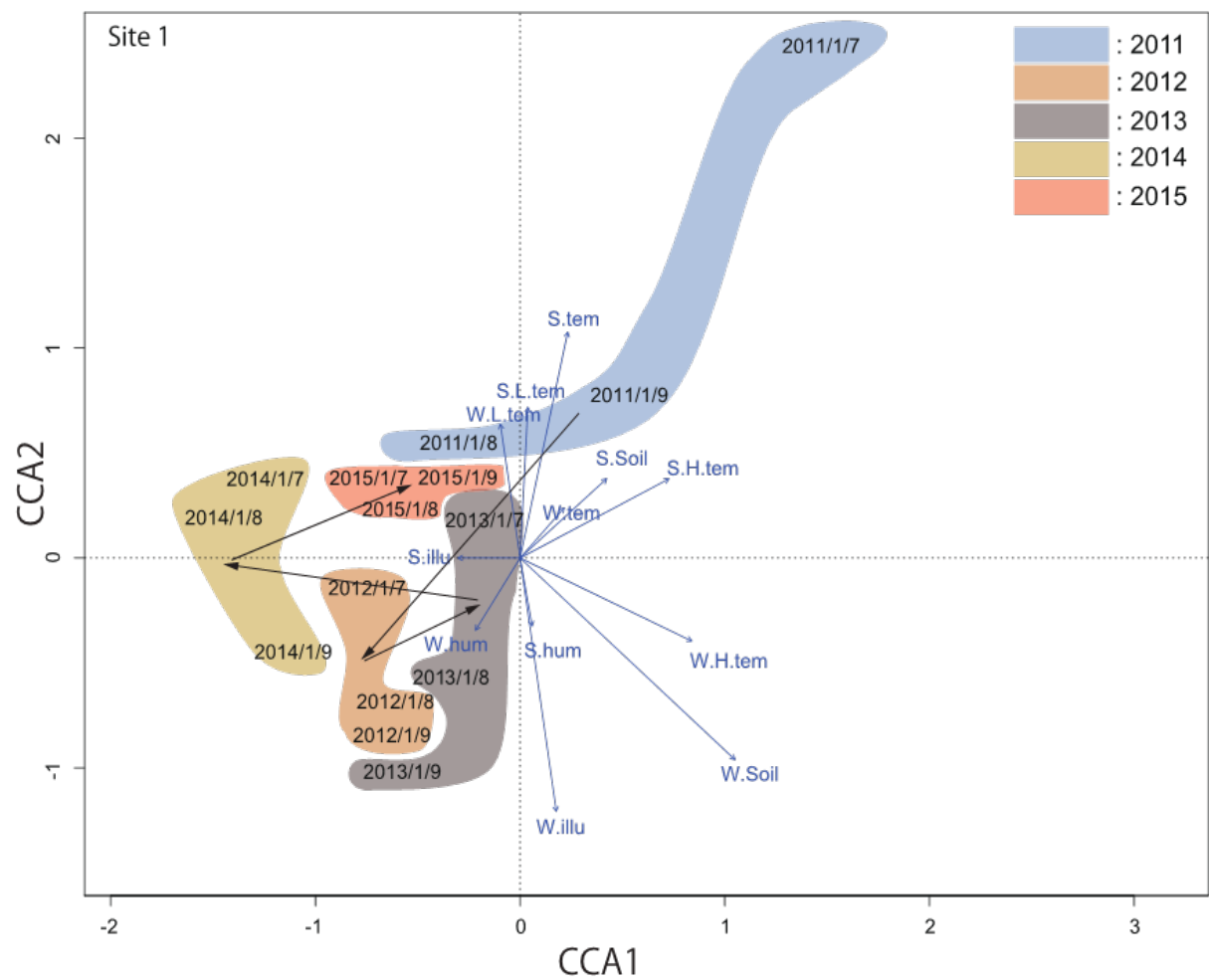


Figure 3-8. Canonical correspondence analysis (CCA) of temporal variations in communities in each study site. Black arrows are a rough indication of changes in carabid beetle community composition in each of the 5 years of sampling.

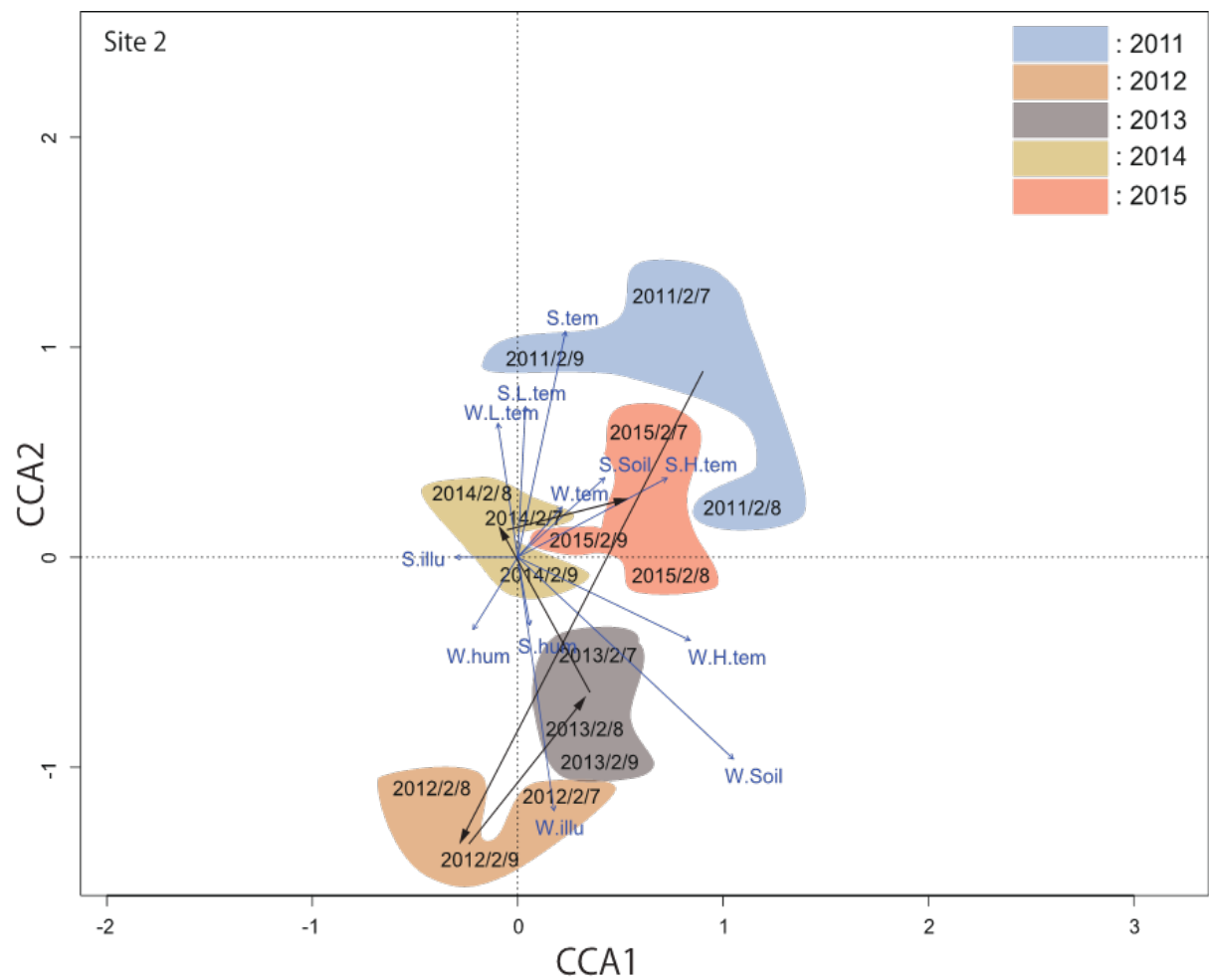


Figure 3-9. Canonical correspondence analysis (CCA) of temporal variations in communities in each study site. Black arrows are a rough indication of changes in carabid beetle community composition in each of the 5 years of sampling.

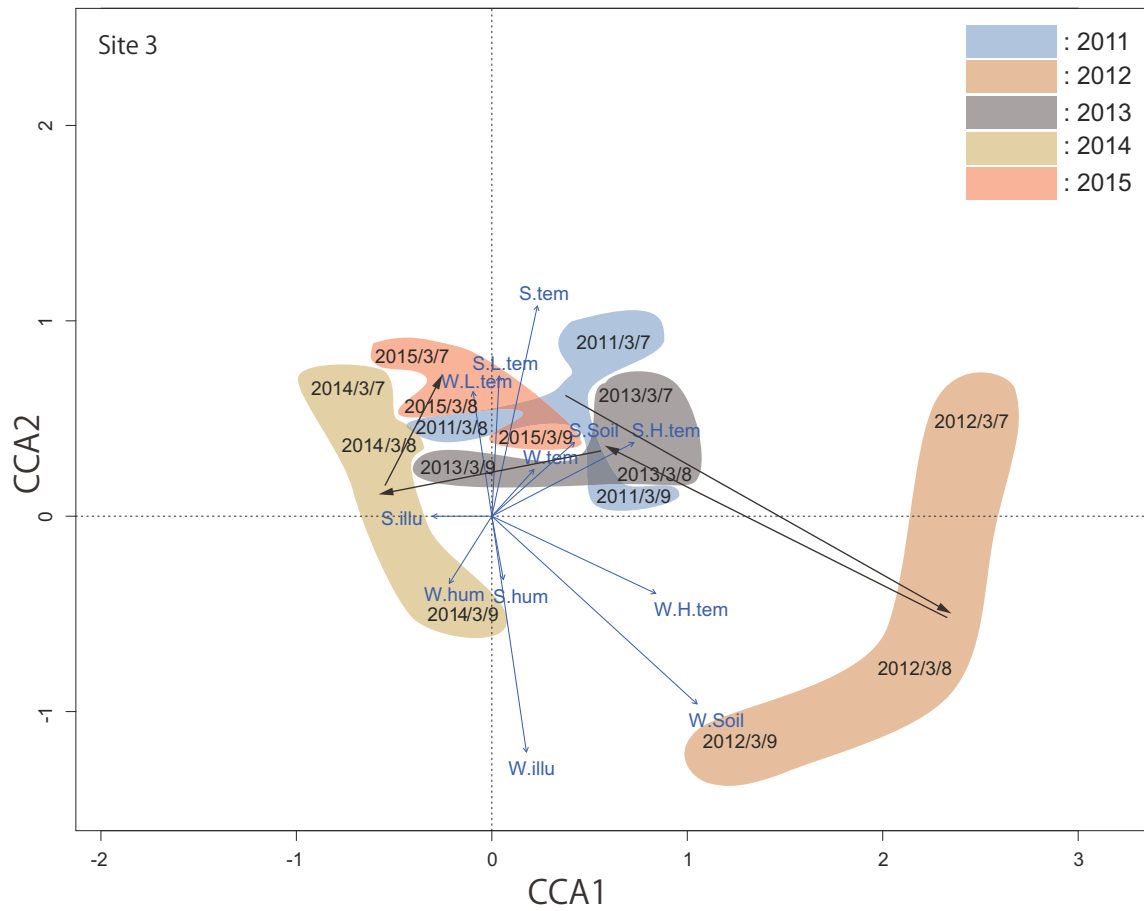


Figure 3-10. Canonical correspondence analysis (CCA) of temporal variations in communities in each study site. Black arrows are a rough indication of changes in carabid beetle community composition in each of the 5 years of sampling.

Table 3-3. List of numbers of ground beetles found on Mount Odaesan, Korea, at three study sites, each sampled in 3 months each year over 5 years.

Species	Site 1					Site 2					Site 3					Total
	2011	2012	2013	2014	2015	2011	2012	2013	2014	2015	2011	2012	2013	2014	2015	
<i>Carabus (Eucarabus) sternbergi</i>	92	67	39	11	21	43	18	25	133	43	86	28	26	114	50	796
<i>Carabus (Leptocarabus) seishinensis</i>	8	21	27	18	23		4	2	17	21	17	11	16	26	22	233
<i>Carabus (Leptocarabus) semiopacus</i>	4	19	15	22	11		17	26	2	2	4	18	15	2	52	209
<i>Carabus (Morphocarabus) venustus</i>				8	2	4		7		2			1		1	25
<i>Carabus (Tomocarabus) fraterculus</i>	10		2	2	5	7		1	5	1	4		3	21	12	73
<i>Carabus (Coptolabrus) smaragdinus</i>		3	2	0	1		1	1	6	7	7		2	5	6	41
<i>Carabus (Coptolabrus) jankowskii</i>	3	5	2	4	2		3	3		2		1			3	28
<i>Carabus (Acoptolabrus) mirabilissimus</i>						1	1							1		3
<i>Carabus (Acoptolabrus) leechi</i>										1						1
<i>Synuchus callitheres</i>	22	64	87	37	35		95	45	61	65	12	50	32	73	50	728
<i>Synuchus cycloides</i>	5	99	89	21	21	18	54	69	51	80	12	39	46	74	30	708
<i>Synuchus nitidus</i>		113	79	120	74	1	63	30	119	52	3		37	93	41	825
<i>Synuchus</i> sp.1	30	52	36	36	21	2		2	37	23			5	18	9	271
<i>Synuchus</i> sp.2			3	37	7			5	52	32			9	24	7	176
<i>Synuchus</i> sp.3				1	2				22	2				21	13	61
<i>Platynus assimilis</i>	8	39	9	2	32	9		10	40	37		5	23	20	24	258
<i>Poecilus versicolor</i>		47	1	7	8	13	7	9	34	23		8	1	2	7	167
<i>Pterostichus orientalis</i>			32	16	27	4		2	5	5	1		7	14	34	147
<i>Pterostichus audax</i>	6		10	8	23		2	2	30	46	1	1	23	15	33	200
<i>Pterostichus scurra</i>	4		7	13	9	15		2	10	49	5	19	35	27	13	208
<i>Pterostichus compar</i>	10		2	4	4	2		12	25	23	4	55	5	6	7	159
<i>Pterostichus bellator</i>	23		7	1	14	4		9	32	30		22	23	3	12	180
<i>Pterostichus teabaegsanus</i>			2					3			1		5			11
<i>Pterostichus coreicus</i>	18												3			21
<i>Pterostichus</i> sp.1	1	2	6	8	6		4	8	8	14		11	1	4	3	76
<i>Pterostichus</i> sp.2	9		2	4	11			3	13	9		2	2	1	6	62
<i>Pterostichus</i> sp.3					1				4	7						12
<i>Dolichus halensis</i>	10		1		1			2		2			3			19
<i>Dolichus</i> sp.		2	7	10	9	12	1	3	4	8		2	6	14	27	105
<i>Pristosia vigil</i>		71	59	24	37	16	66	57	107	90	16	104	39	55	38	779
<i>Anisodactylus punctatipennis</i>	1							1		13					1	16
<i>Harpalus griseus</i>			1		1	5	1	1					2			11
<i>Brachinus stenoderus</i>			1		1							5	4		3	14
<i>Lachnolebia cribricollis</i>										3						3
<i>Chlaenius pallipes</i>			1		1	4							3		3	12
Total	264	604	529	414	410	160	337	340	817	692	173	381	377	633	507	6,638

Table 3-4. Spatial and temporal variation in ground beetle communities. Plain and bold numbers indicate α - and β -diversity indices, respectively.

	5years	2011	2012	2013	2014	2015	Temporal β
Site 1	1.24	1.02	1.01	1.13	1.06	1.13	0.41
Site 2	1.26	1.07	0.92	1.11	1.18	1.25	0.53
Site 3	1.24	0.62	1.00	1.16	1.01	1.22	0.47
Spatial β	0.15	0.59	0.44	0.26	0.36	0.43	

Environmental factors influencing beetle community within sites

At Site 1, beetle species richness was significantly positively associated with S.L.tem. Individual abundance was significantly positively associated with S.tem and S.L.tem, and negatively associated with S.Soil. The diversity index was significantly positively associated with W.tem, S.L.tem, S.hum and W.Soil, and negatively associated with S.H.tem and S.Soil. The CCA1 score was significantly negatively associated with S.L.tem, and the CCA2 score was significantly negatively associated with S.tem and S.L.tem (Table 3-5).

At Site 2, species richness was significantly negatively associated with S.illu. Individual abundance was significantly positively associated with S.tem, S.L.tem, W.L.tem and W.Soil, and negatively associated with W.H.tem and S.illu. The diversity index was positively associated with W.tem, and negatively associated with S.illu. The CCA1 score was positively associated with S.illu (Table 3-5).

At Site 3, species richness was significantly negatively associated with S.H.tem. Individual abundance was significantly positively associated with W.tem and W.illu, and negatively associated with S.H.tem, W.H.tem, S.L.tem and W.L.tem. The diversity index was significantly negatively associated with W.illu. The CCA1 score was significantly positively associated with S.L.tem, W.tem, S.tem, W.L.tem and S.Soil, and negatively associated with W.H.tem, W.illu, W.Soil and S.H.tem (Table 3-5).

Table 3-5. Generalised linear mixed models (GLMMs) explaining temporal changes in carabid beetle communities in each of three study sites on Mount Odaesan, Korea, Bold values are statistically significant ($P < 0.05$).

	Species richness	Individual abundance	Diversity index	CCA 1	CCA 2
Site 1					
S.tem	0.220±0.125	0.125±0.032***	-	-0.178±0.262	-1.371±0.454**
W.tem	-0.048±0.142	1.205±2.164	0.123±0.034***	-0.245±0.233	-2.201±2.306
S.H.tem	-0.367±0.663	1.112±1.829	-0.118±0.046*	0.168±0.385	0.962±2.370
W.H.tem	0.511±0.635	0.506±0.329	-	-0.363±0.384	-2.597±3.858
S.L.tem	0.718±0.282*	0.382±0.171*	0.240±0.096*	-1.043±0.476*	-4.048±1.294**
W.L.tem	-0.052±0.247	-0.100±0.376	-	-0.124±0.099	0.124±0.958
S.Soil	-0.234±0.142	-0.287±0.132*	-0.071±0.034*	0.059±0.192	1.149±0.730
W.Soil	-1.432±1.725	-0.405±0.551	0.245±0.126*	1.025±0.750	6.230±8.518
S.hum	0.094±0.240	-0.014±0.102	0.040±0.019*	0.082±0.083	-0.764±1.474
W.hum	-0.018±0.141	0.632±0.701	-	0.092±0.064	-0.081±1.242
S.illu	0.299±0.336	0.003±0.354	-	-0.246±0.220	-1.480±2.679
W.illu	-0.011±0.062	0.014±0.031	-	-0.026±0.021	0.065±0.426
Site 2					
S.tem	1.127±0.674	1.931±0.132***	0.420±0.254	-4.451±8.659	0.423±0.532
W.tem	0.390±0.299	-	0.190±0.090*	-2.077±4.550	0.514±0.317
S.H.tem	0.130±0.083	-0.013±0.135	0.017±0.098	-0.533±3.454	-0.051±0.138
W.H.tem	-0.286±0.254	-3.647±0.222***	0.002±0.098	6.57±16.162	-0.167±0.186
S.L.tem	0.630±1.438	11.033±0.686***	0.257±0.512	-6.460±33.708	-0.407±0.646
W.L.tem	-0.121±0.357	1.451±0.097***	-0.002±0.356	-1.597±5.605	0.374±0.193
S.Soil	0.573±0.641	-0.186±1.948	0.523±0.333	3.653±42.822	0.663±0.692
W.Soil	-0.735±1.091	2.645±0.183***	0.067±0.298	-3.557±16.823	-0.317±0.503
S.hum	0.036±0.036	-0.025±0.013	0.004±0.013	-0.138±0.404	-0.017±0.022
W.hum	0.090±0.333	-	-0.107±0.231	0.480±5.504	0.116±0.165
S.illu	-0.055±0.019**	-0.094±0.012***	-0.017±0.005**	0.330±0.160*	-0.049±0.051
W.illu	-0.016±0.010	-	-0.002±0.014	0.086±2.559	0.002±0.013
Site 3					
S.tem	-0.436±0.446	-0.553±0.829	0.016±0.042	0.501±0.206*	-0.046±0.276
W.tem	-0.029±0.083	0.505±0.214*	-0.011±0.026	0.554±0.145***	-0.079±0.239
S.H.tem	-0.803±0.339*	-0.727±0.249**	-0.011±0.041	-0.592±0.242*	-0.472±0.344
W.H.tem	-0.928±1.865	-2.114±0.595***	-0.033±0.102	-1.361±0.497**	-0.606±1.197
S.L.tem	-0.020±0.103	-2.868±0.242***	0.008±0.029	0.343±0.138*	-0.082±0.224
W.L.tem	-0.002±0.089	-0.398±0.037***	0.012±0.024	0.417±0.090***	-0.168±0.117
S.Soil	0.132±0.150	0.061±0.506	-0.003±0.014	0.333±0.072***	-0.027±0.059
W.Soil	0.072±0.149	0.283±0.467	-0.018±0.031	-0.303±0.147*	-0.078±0.194
S.hum	-0.001±0.015	-0.042±0.065	-0.0001±0.001	-	0.004±0.008
W.hum	-0.028±0.029	0.0004±0.042	-0.001±0.003	-	0.003±0.015
S.illu	0.080±0.770	-0.141±1.021	-0.071±0.070	-	-0.275±0.331
W.illu	0.014±0.011	0.027±0.003***	-0.007±0.002***	-0.079±0.017***	0.008±0.024

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, - not included in final model.

Discussion

This study revealed temporal changes in carabid beetle communities, the patterns of which differed between sites (Figs. 3-8, 3-9 and 3-10) even within a relatively small area, i.e., a single mountain system (Fig. 3-1). This could be explained by neutral processes via stochastic changes in communities and/or by deterministic processes via ecological and environmental factors affecting communities. This study highlighted spatial and temporal variation in environmental factors that is important for understanding changes in carabid beetle communities. I found evidence that microclimatic factors could be used to predict changes in communities in all three of the study sites: the composition of the ground beetle communities was influenced by various combinations of environmental factors (Table 3-5). Additionally, these effects were not necessarily consistent between sites, and the directions of the effects (positive or negative) differed between sites. Thus, my results suggest that different modes of deterministic processes took place in each local community. My results also provide support for the notion that variation in the number of carabid beetle species and their abundance between years is to be expected, not only in temporary habitats, but also in permanent habitats (i.e., mountainous forest floors) (den Boer 1986; Luff 1990).

The present results indicate that microclimatic variables influencing carabid beetle communities differed between sites within a relatively small area (Table 3-5). This finding is concordant with the notion that large-scale features such as climate zonation determine the basic community structure of carabid beetles, while local-scale features such as habitat availability and landscape structure are more important in determining specific local species' distribution (Penev 1996). Additionally, this results revealed that communities can change in response to site-specific environmental change. For example, the carabid beetle community

in Site 3 changed drastically in 2012 (Fig. 3-10); those in other sites did not. In that year, an exceptionally large number of *Pterostichus compare* Tschitscherine, 1901 and *Pristosia vigil* Tschitscherine, 1895 were collected at Site 3 (Table 3-3), and this may have been responsible for the observed large change in the community. This site experienced relatively low air humidity in 2012 and thereafter (Fig. 3-10), and this could be a factor causing change in the community composition. Šustek (2007) suggested that the principal factor responsible for changes in carabid beetle communities was humidity, although we did not detect any effects of summer and winter humidities on measures of diversity and community composition in Site 3. The changes in communities that we observed were mostly related to variation in the relative abundance of individuals rather than to variation in species composition, and variation in individual abundance was more often explained by local environmental factors than variation in species richness (Table 3-5).

Why did responses to environmental factors differ between communities at the different sites? Firstly, the differences in the species composition of communities could play a role. Carabid beetle distribution depends on abiotic and biotic factors, involving temperature, humidity, food availability, presence of competitors and life history (Lövei & Sunderland 1996), and the relationships can differ between species (Ribera *et al.* 2001). Thus, communities with different species compositions may respond differently to similar environmental changes. Secondly, communities with similar species compositions may respond differently to local environmental conditions, if local environments *per se* vary between sites. This means that a species experiences different environmental conditions in different sites. For example, the temperature in one site may be optimal for one species, but in another site it may be lower and suboptimal for the species. If so, increased temperature in this area will affect the species inhabiting the first site negatively while simultaneously

affecting the species in the second site positively, resulting in different community responses at different sites. Although these two processes are not mutually exclusive, my results suggest that the second process played a major role in the study sites, because species compositions were similar at all three sites (Table 3-4). Additionally, interspecific interactions, especially competition, may affect carabid communities (Niemelä 1993), but this remains to be examined in my study sites.

Detailed examination of the data indicates that differences in environmental factors that determine the composition of carabid beetle communities may result from variation in environments *per se* between sites. For example, the effect of summer temperature was the opposite in Sites 1 and 3. Site 1 was relatively cold, so that even lower temperatures may have adversely affected the growth and activity of carabid beetles. The opposite may be true in Site 3, which had relatively high temperature. In addition, S.illu was negatively associated with species richness, individual abundance and diversity index in Site 2, while there was no relationship in the other sites. Site 2 is at higher elevation than the other two sites on a south-west-facing ridge, and vegetation height is relatively low there. In such an environment, excessive summer illumination may result in the desiccation of the forest floor, via increased temperature in the forest floor and/or increased transpiration by understorey plants. Carabid beetles reproduce in relatively humid seasons during which their prey is abundant. Thus, strong illumination in the summer may have an adverse effect on carabid beetle communities. Cardenas & Hidalgo (2000) suggested that the life-cycle of univoltine carabid beetles was primarily determined by annual fluctuations in environmental (climatic) conditions in temperate zones. My results are concordant with this suggestion.

The present data can involve some uncertainties, which remain to be clarified. The data may include variation in voltinism among species that can influence the results.

However I treated all the species samely irrespective of possible variation in voltinism, because of only a limited information about detailed life histories of carabids in Korea. Elucidation of life histories of individual species will benefit in further interpretation of my results. I also found that an increasing tendency of individuals across years in two of three sites. However, I cannot determine whether this is associated with global climate change or a result by chance. My ongoing survey in the wider geographical scales will provide further insights into this problem.

In conclusion, the present results suggest that local communities of carabid beetle are influenced by local variations in microclimate, and that these influences vary between sites. This indicates the importance of conducting temporal surveys of communities at local scales. Such investigations are expected to reveal an additional fraction of variation in communities, and to provide information on the underlying processes that have been overlooked, especially in studies of global community patterns and changes. Since the present data are relatively limited (5 years and three sites), increases in temporal and spatial scale sample sizes would be beneficial, and would allow more general conclusions to be drawn. Investigation of other environmental factors would also be beneficial; for instance, soil pH is of interest, as suggested by Elek *et al.* (2001). We did not find directional changes in microclimates over the 5 years of this study; therefore, my results cannot provide information on global climate change or on the effects of ongoing global warming.

Chapter 4.

**Quantifying spatial and temporal change of carabid
beetle communities and local environments in
Baekdudaegan mountains of Gangwon-do, Korea**

Introduction

Spatial and temporal variation in ecological environments is an important factor that can enhance the species pool within a given area, which is target for biodiversity conservation (Whittaker 1975; Huston 1979). Spatial variation in communities results from variation in the overlap of the geographical ranges of species (Arita & Rodriguez 2002). Similarly, temporal variation in communities results from variation in the overlap of phenological ranges of species. In particular, temporal studies of biodiversity are essential for forecasting future change in community structure and ecosystem function. Determining the mechanisms that drive temporal change in communities remains an important and interesting challenge in ecology (van der Putten *et al.* 2009). Spatial factors, such as landscape, determine the presence of potential colonizers (species pool), their population dynamics, and their ability to reach particular patches in the landscape. Local environmental conditions determine the suitability of the habitat or patch in question (Butaye *et al.* 2002; Eggleton *et al.* 2005; Summerville & Crist 2008). Although ecologists have focused on the causes of spatial variation in communities (Kaspari *et al.* 2000; Jetz & Rahbek 2001, 2002), temporal variation and their causes have received little attention (Morales *et al.* 2005). As the first step to understand the mechanisms shaping patterns of spatial and temporal community variations, it is necessary to quantify how much variations are involved in communities established in given spatial and temporal scales.

Carabid beetles are found almost everywhere on terrestrial habitats, but their distributions are often correlated with environmental variables (Butterfield *et al.* 1995; Allegro & Sciaky 2003). These beetles are often selective of or restricted to a particular

habitat, i.e. they show habitat specificity and fidelity (Thiele 1977; Lövei & Sunderland 1996; Rainio & Niemelä 2003; Pearce & Venier 2006; Botes *et al.* 2007). These ecological characteristics of ground beetles make them ideal organisms for study to assess biodiversity and habitat characteristics along environmental change. Thus, to understand spatial and temporal variations in carabid beetle communities, it is also vital to quantify how much variations are involved in environmental variables in given temporal and spatial scales.

In this study, I quantify the spatial and temporal variations in carabid beetle community compositions and in background microclimatic variables in Baekdudaegan Mountain Range, Korea, based on 5 years survey data. The 9 study sites were within three mountains, which exhibit variation in vegetation, slope direction and altitude. The within-site changes and between-site differences in communities and environmental variables are estimated using a generalized linear modelling approach.

Materials and methods

Study area and field survey

I conducted field surveys in 9 sites (3 sites each in 3 mountains: Mts. Jinburyung, Odaesan, Taebaeksan in Baekdudaegan Mountain Range, Korea). Baekdudaegan mountain range is a watershed-crest-line of around 1400-1500 km long, which runs through most of the length of the Korean Peninsula, from Mt. Paektusan in the north as far south as Mt. Jirisan (Fig. 4-1). All study sites were dominantly covered by *Quercus* trees and more or less with red pine trees. *Pseudostellaria palibiniana* and *Dioscorea quinqueloba* were found as understory vegetation. Jinburyung site 1 (J1) was on a north-west-facing slope (steepness = 20°, 694 m above sea level), where trees were relatively tall and the forest canopy was mostly closed. Jinburyung site 2 (J2) was of the highest site on a north-facing slope (10°, 1,038 m), where trees were relatively short and the forest canopy was thin and sporadically opened. Jinburyung site 3 (J3) was on a west-facing slope (10°, 323 m), where trees were relatively tall and the forest canopy was mostly closed. Odaesan site 1 (O1) was on a west-facing slope near the bottom of a valley (25°, 741 m), where trees were relatively tall and the forest canopy was mostly closed. Odaesan site 2 (O2) was the highest site on the ridge of a south-west-facing slope (32°, 1,062 m), where trees were relatively short and the forest canopy was thin and sporadically opened. Odaesan site 3 (O3) was on a continuous north-facing slope (20°, 668 m), where, as in O1, trees were relatively tall and the forest canopy was mostly closed. Taebaeksan site 1 (T1) was on a west-facing slope (28°, 968 m). Taebaeksan site 2 (T2) was the highest site was on a west-facing slope (36°, 1,274 m). Taebaeksan site 3 (T3) was on a south-west-facing slope (35°, 704 m). In all the sites in Mt. Taebaeksan, trees were relatively tall and the forest canopies were mostly closed (Table 4-1).

Environmental variables were obtained using HOBO data loggers (Onset Computer Corporation, Bourne, MA) to record air temperature, air humidity, light intensity and soil temperature hourly from June 2010 to September 2015. Each logger was attached to a tree trunk 120 cm above the ground. Soil temperature was measured 5 cm underground. The data were downloaded directly from each logger every month. This system cannot measure precipitation, and generally it is difficult to measure hourly, although it is an important environmental parameter to predict carabid beetle communities. I expected that air humidity is closely related to the precipitation and can be a surrogate.

To capture community composition at each study site, I collected carabid beetles twice a year (July and August) for 5 consecutive years (2011: Jul. 10-11 and Aug. 18-19 in Jinburyung, Jul. 11-12 and Aug. 19-20 in Odaesan, Jul. 13-14 and Aug. 20-21 in Taebaeksan; 2012: Jul. 19-20 and Aug. 18-19 in Jinburyung, Jul. 20-21 and Aug. 19-20 in Odaesan, Jul. 21-22 and Aug. 20-21 in Taebaeksan; 2013: Jul. 24-25 and Aug. 17-18 in Jinburyung, Jul. 25-26 and Aug. 18-19 in Odaesan, Jul. 26-27 and Aug. 19-20 in Taebaeksan; 2014: Jul. 26-27 and Aug. 21-22 in Jinburyung, Jul. 27-28 and Aug. 22-23 in Odaesan, Jul. 28-29 and Aug. 23-24 in Taebaeksan; 2015: Jul. 21-22 and Aug. 11-12 in Jinburyung, Jul. 22-23 and Aug. 12-13 in Odaesan, Jul. 23-24 and Aug. 13-14 in Taebaeksan) using pitfall traps (plastic cups 7.0 cm in diameter and 8.0 cm deep) containing an attractant (powder of silkworm pupa) (Lövei & Sunderland 1996; Holland 2002; Heyborne *et al.* 2003). This sampling season was chosen because adult carabid beetles are active. Two hundred traps were set in two or three lines at 2 m intervals at each study site in each month and year, and beetles were collected 24 hours later. All the beetles caught in the 200 traps constituted the sample for that site, month and year. The exact position of the trap lines was changed arbitrarily within study sites each time to avoid any effects of previous captures. All carabid beetles captured were counted and

identified to species, except for three *Pterostichus*, three *Synuchus* and one *Dolichus* species that were regarded only as morphospecies. Data from two repeated samplings within a year were combined before analysis, resulting in 45 community data points across 9 sites in 3 mountains and 5 years.

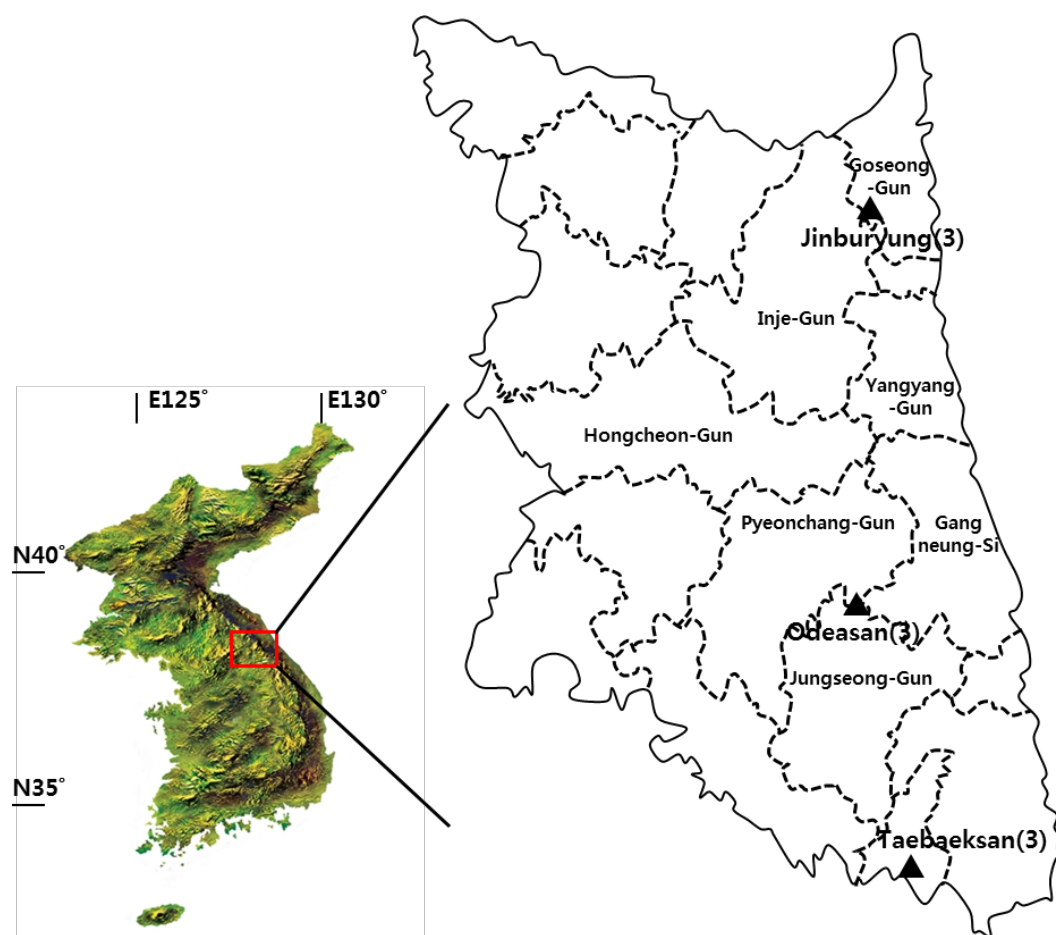


Figure 4-1. Locations of study sites on Baekdudaegan Mountain Range, Korea.

Table 4-1. Habitat and environmental information on the study sites on Baekdudaegan Mountain Range, Korea.

Site		Latitude Longitude	Slope	Altitude (m)	Gradi ent (°)	Dominant tree species	Understorey vegetation species
Jinbu- ryung	J1	N38°16'00.31" E128°23'07.14"	NW	694	20	<i>Quercus mongolica</i> , <i>Tilia mandshurica</i> , <i>Synplocos chinensis</i>	<i>Synurus deltooides</i> , <i>Impatiens textori</i> , <i>Isodon excisus</i> etc.
	J2	N38°15'53.01" E128°20'01.94"	N	1,038	10	<i>Quercus mongolica</i> , <i>Acer pseudosieboldianum</i> , <i>Tilia mandshurica</i>	<i>Carex siderosticta</i> , <i>Hepatica asiatica</i> , <i>Primula jesoana</i> etc.
	J3	N38°17'03.36" E128°21'40.76"	W	323	10	<i>Styrax obassia</i> , <i>Quercus mongolica</i> , <i>Pinus densiflora</i>	<i>Pseudostellaria palibiniana</i> , <i>Dioscorea quinqueloba</i> , <i>Isodon japonicus</i> etc.
Odae- san	O1	N38°44'31.86" E128°37'11.08"	W	741	25	<i>Quercus mongolica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , <i>Fraxinus rhynchophylla</i>	<i>Brachybotrys paridiformis</i> , <i>Carex siderosticta</i> , <i>Lespsdeza japonica</i> etc.
	O2	N38°45'58.29" E128°36'20.22"	SW	1,062	32	<i>Quercus mongolica</i> , <i>Tilia mandshurica</i> , <i>Acer pseudosieboldianum</i>	<i>Sasa borealis</i> , <i>Carex siderosticta</i> , <i>Viola albida</i> etc.
	O3	N38°47'10.76" E128°37'09.83"	N	668	20	<i>Fraxinus rhynchophylla</i> , <i>Pinus densiflora</i> , <i>Acer pseudosieboldianum</i>	<i>Disporums milacinum</i> , <i>Arisaema amurense</i> , <i>Isodon japonicus</i> etc.
Tae- baek- san	T1	N37° 7'22.90" E128°57'32.88"	W	968	28	<i>Betula davurica</i> , <i>Pinus densiflora</i> , <i>Quercus mongolica</i>	<i>Athyrium niponicum</i> , <i>Syneilesis palmata</i> , <i>Festuca ovina</i> etc.
	T2	N37°09'38.22" E128°53'10.35"	W	1,274	36	<i>Quercus mongolica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , <i>Fraxinus rhynchophylla</i>	<i>Astilbe koreana</i> , <i>Carex humilis</i> , <i>Viola albida</i> etc.
	T3	N37°06'36.02" E128°51'30.24"	SW	704	35	<i>Quercus mongolica</i> , <i>Fraxinus rhynchophylla</i> <i>Tilia mandshurica</i> ,	<i>Sasa borealis</i> , <i>Tripterygium regelii</i> , <i>Carex siderosticta</i> etc.

Analysis of environmental factors

To summarise the microclimate data, I first calculated daily means from the data that had been collected at hourly intervals in each site. Then, 12 environmental variables were calculated for each year: summer mean air temperature (S.tem), winter mean air temperature (W.tem), summer highest mean air temperature (S.H.tem), winter highest mean air temperature (W.H.tem), summer lowest mean air temperature (S.L.tem), winter lowest mean air temperature (W.L.tem), summer mean air humidity (S.hum), winter mean air humidity (W.hum), summer mean illumination (S.illu), winter mean illumination (W.illu), summer mean soil temperature (S.Soil) and winter mean soil temperature (W.Soil). Winter variables were calculated from the data collected in the December to February period before the month of sampling. Summer variables were calculated from the data collected in the period from June to the date of sampling. I focused on summer and winter microclimates, because, for carabid beetles in this region, summer conditions may be important for reproduction and population growth, and winter conditions may be important for survival during hibernation (Kim & Lee 1992a, 1992b). These climatic variables are associated with spatial and temporal variation in carabid beetle communities as indicated by my previous study (Chapter 3, Park *et al.* 2016).

To examine relative contributions of spatial and temporal variations to total variation in climates, I constructed generalised linear models (GLMs) with each of the 12 climatic variables as a dependent variable, and year, mountain, and site (nested within mountain) as independent variables. Identity link and normal distribution were assumed. Adjusted squared deviance, an equivalent to adjusted coefficient of variation, was calculated for year, mountain and site in each model of environmental variables (Peres-Neto *et al.* 2006).

Analysis of beetle communities

To summarize and visualize variation in community composition in relation to climatic variables, I performed canonical correspondence analysis (CCA) based on the 45 carabid beetle community composition data and the 12 environmental variables. Statistical significance of the effect of the environmental variables was examined by a randomisation test based on 999 pseudo-replications. This analysis was performed using the function `vegan` in the software package R 3.1.3 (R Development Core Team 2015).

I examined relative contributions of spatial and temporal variations to total variation in community composition. Firstly, I calculated Sørensen's indices among three sites within a mountain based on the data pooled for five years (spatial β -diversity among sites within mountain) and that among three mountains based on the data pooled for three sites and five years (spatial β -diversity among mountains). I also calculated Sørensen's indices across five years data within each site (temporal β -diversity within site) and within each mountain based on the data pooled for three sites (temporal β -diversity within mountain). In addition, I calculated Shannon's diversity indices (Shannon-Wiener 1963) for the data from each site and year (α -diversity within site and year), for pooled data across five years in each site (α -diversity within site), and for pooled data across three sites and five years in mountain (α -diversity within mountain).

Secondly, I partitioned total variation in community composition across all study sites and years into temporal and spatial variations. To summarise the composition of communities, I calculated five measures for community samples (i.e., data obtained from a site and a year): species richness (the number of species), individual abundance (the total number of individuals), diversity index (Shannon-Wiener 1963), and the scores of the CCA

axes (CCA1 and CCA2). I constructed GLMs with one of five measures of community composition as a dependent variable, and with year, mountain and site (nested within mountain). Log-link and Poisson distribution were used for count data (species richness and individual abundance); identity-link and normal distribution were used for metric data (diversity index and CCA scores). Variation partitioning was performed to determine how much the variation of the GLM was explained by the pure effect of each factor (year, mountain and site) and which proportion was attributable to their shared effect (Whittaker 1984; Legendre & Legendre 1998). Variation partitioning was carried out with the RsqGLM function in the R package modEVA. There are many different ways to calculate an R^2 for GLMs, and no consensus on which one is best. Therefore, I used 4 different measures. Cox & Snell's R^2 is based on the log likelihood for the model compared to the log likelihood for a baseline model (Cox 1970), whereas it has a theoretical maximum value of less than 1, even for a "perfect" model. Nagelkerke's R^2 is an adjusted version of the Cox & Snell R -square that adjusts the scale of the statistic to cover the full range from 0 to 1 (Nagelkerke 1991). McFadden's R^2 is another version, based on the log-likelihood kernels for the intercept-only model and the full estimated model (McFadden 1974). Pearson's R^2 is simplified method for solving a two variable simultaneous equation (Pearson 1895).

Results

Spatial and temporal variation in environmental factors

Environmental variables varied among mountains as well as sites within a mountain. In all study sites during the study period, the monthly means of air temperature, soil temperature and air humidity were highest in August and lowest in December or January. S.tem was highest in J3, followed by O3 and T3. W.tem was lowest in J2, followed by O1 and T2 (fig. 4-2). S.H.tem was highest in J3 and lowest in J2. W.H.tem was highest in O2 and lowest in T3 (fig. 4-3). S.L.tem was highest in J3 and lowest in O1. W.L.tem was highest in T3 and lowest in J2 (fig. 4-4). S.soil was highest in J3 and lowest in O1. W.soil was highest in J1 and lowest in T3 (fig. 4-5). S.hum was highest in O1 and lowest in T2. W.hum was highest in O1 and lowest in O3 (fig. 4-6). S.illu was highest in J2 and lowest in O3. W.illu was highest in J3 and lowest in T1 (fig. 4-7).

Site, mountain and year contributed variously to the variations in the environmental factors. All environmental factors except S.L.tem were significantly explained by site. S.Soil, S.illu and W.illu were significantly explained by mountain, and S.hum and W.L.tem were significantly explained by year. Variance partitioning revealed that site accounted for the largest proportion of explained variability in 10 of 12 environmental factors, while mountain accounted for the largest proportion of explained variabilities in S.Soil and S.illu. Year accounted for the second largest proportion of explained variability in all environmental factors (Table 4-2).

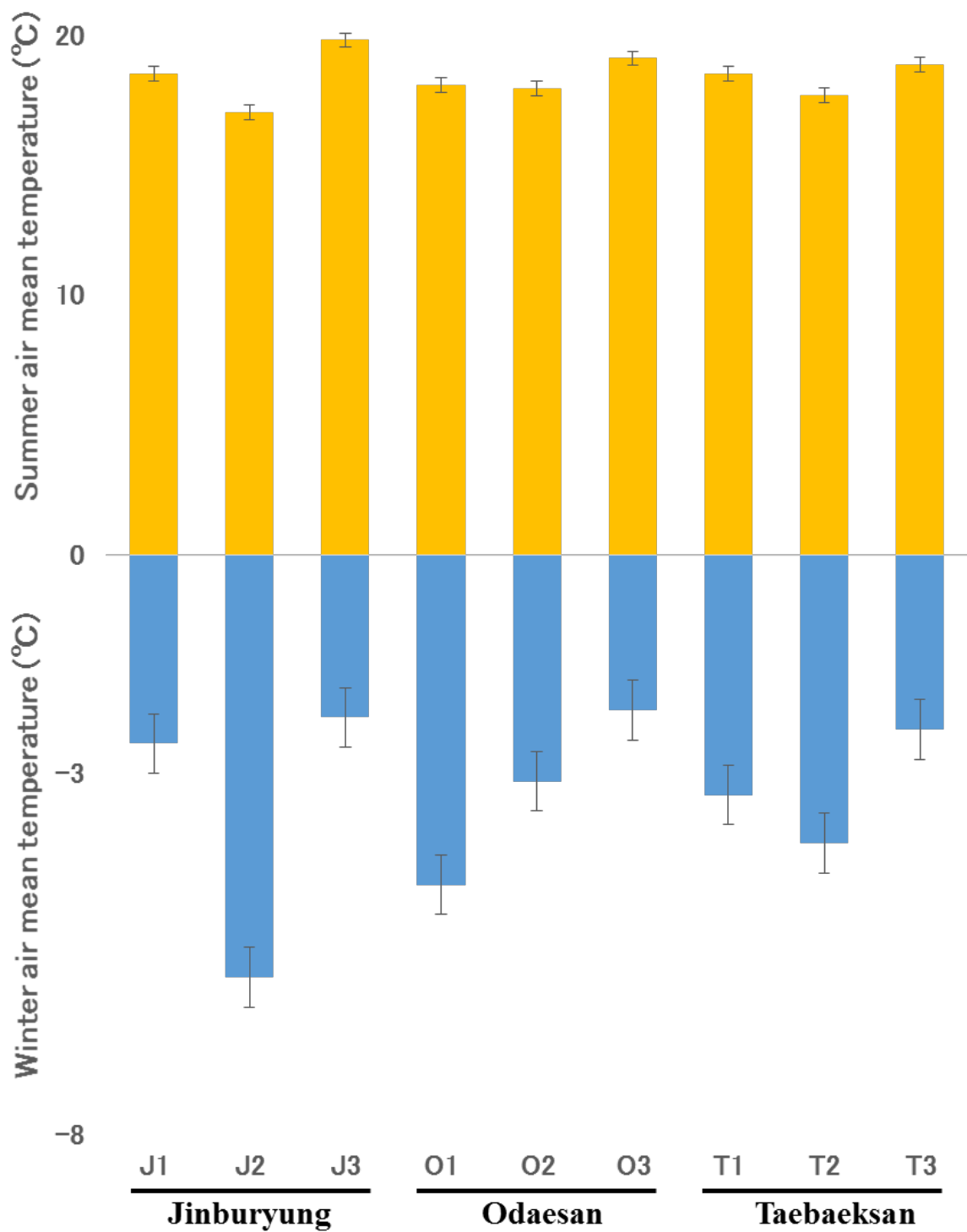


Figure 4-2. Mean of summer and winter mean air temperature in each study sites on Baekdudaegan Mountain Range, Korea

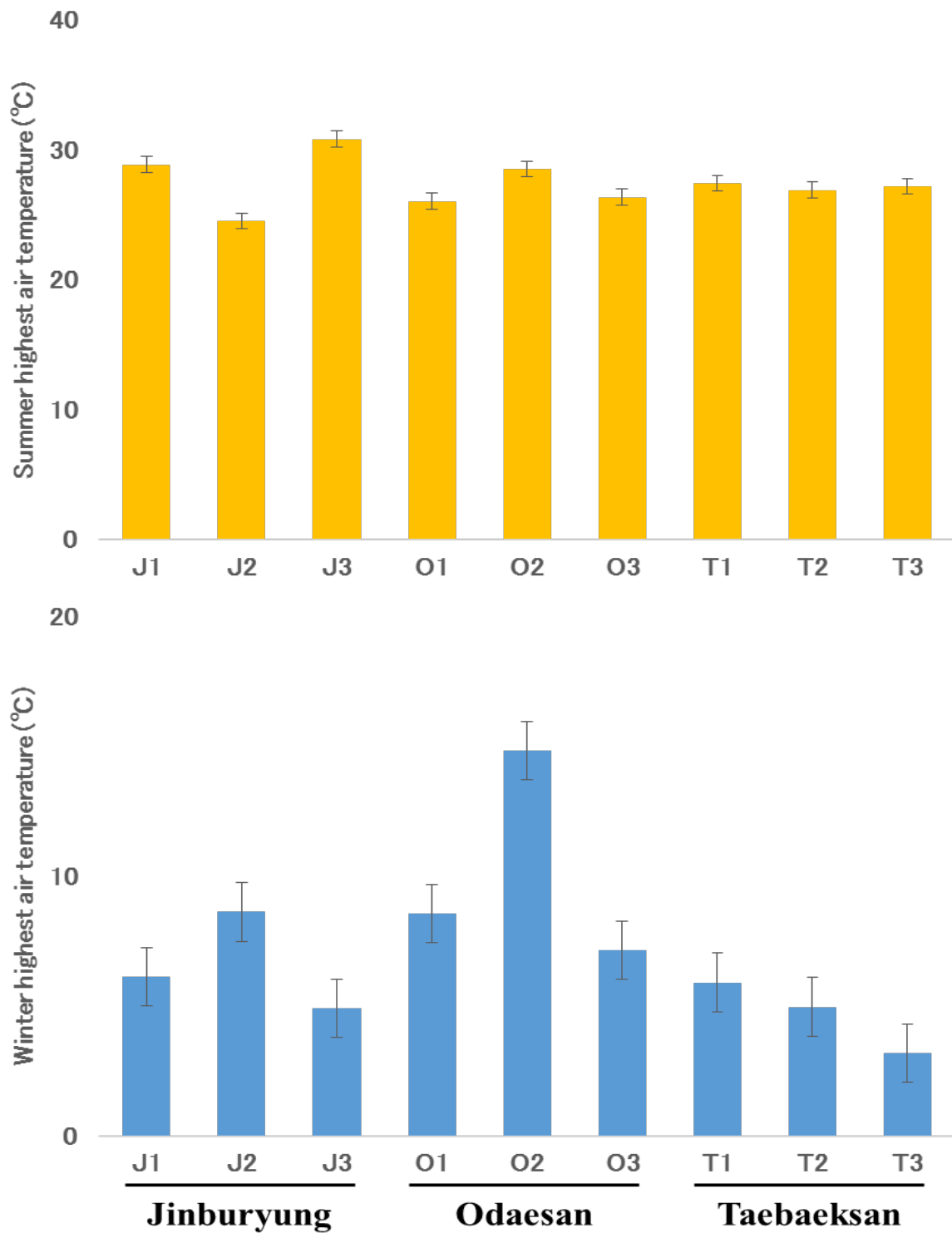


Figure 4-3. Mean of summer and winter highest air temperature in each study sites on Baekdudaegan Mountain Range, Korea

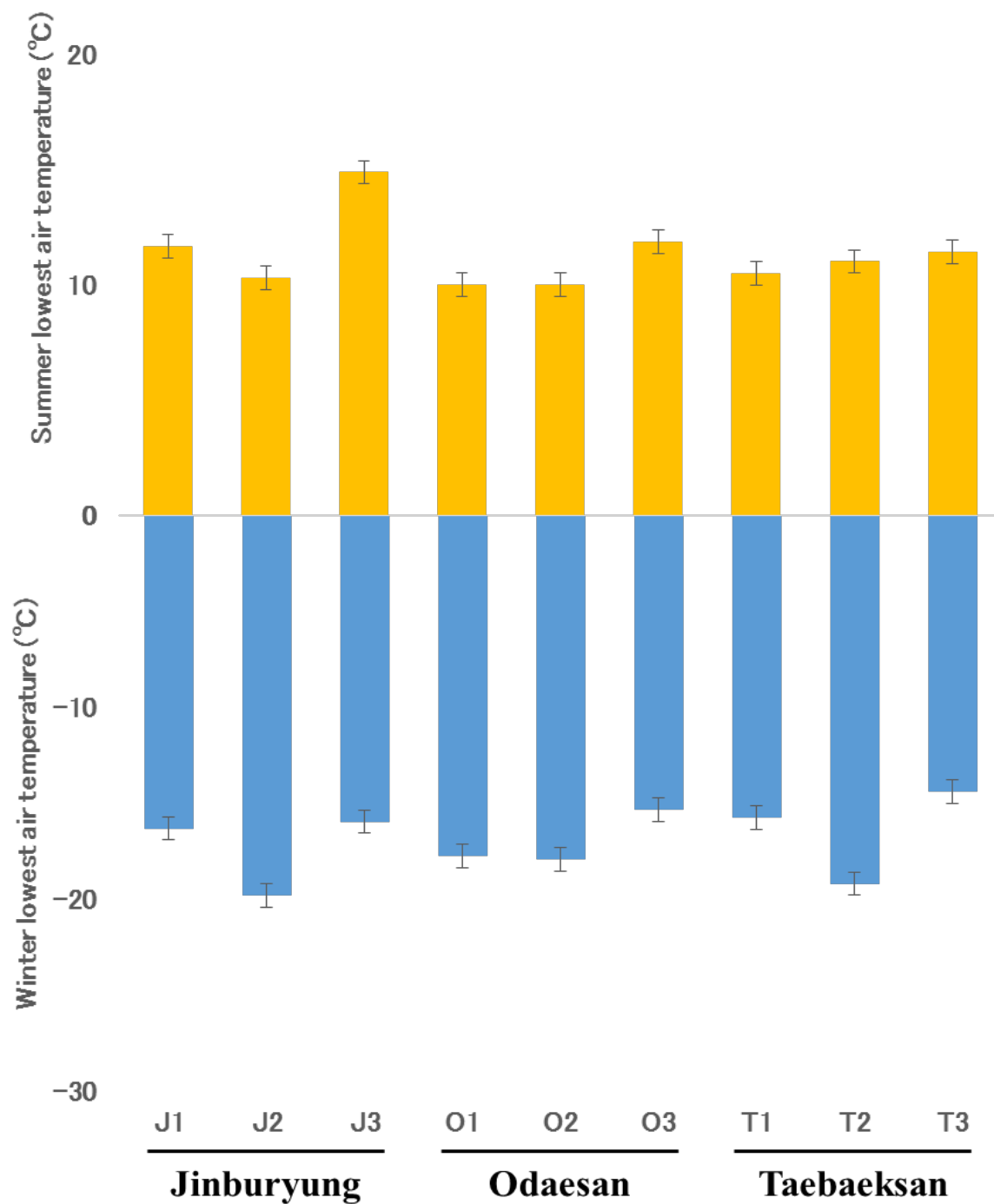


Figure 4-4. Mean of summer and winter lowest air temperature in each study sites on Baekdudaegan Mountain Range, Korea

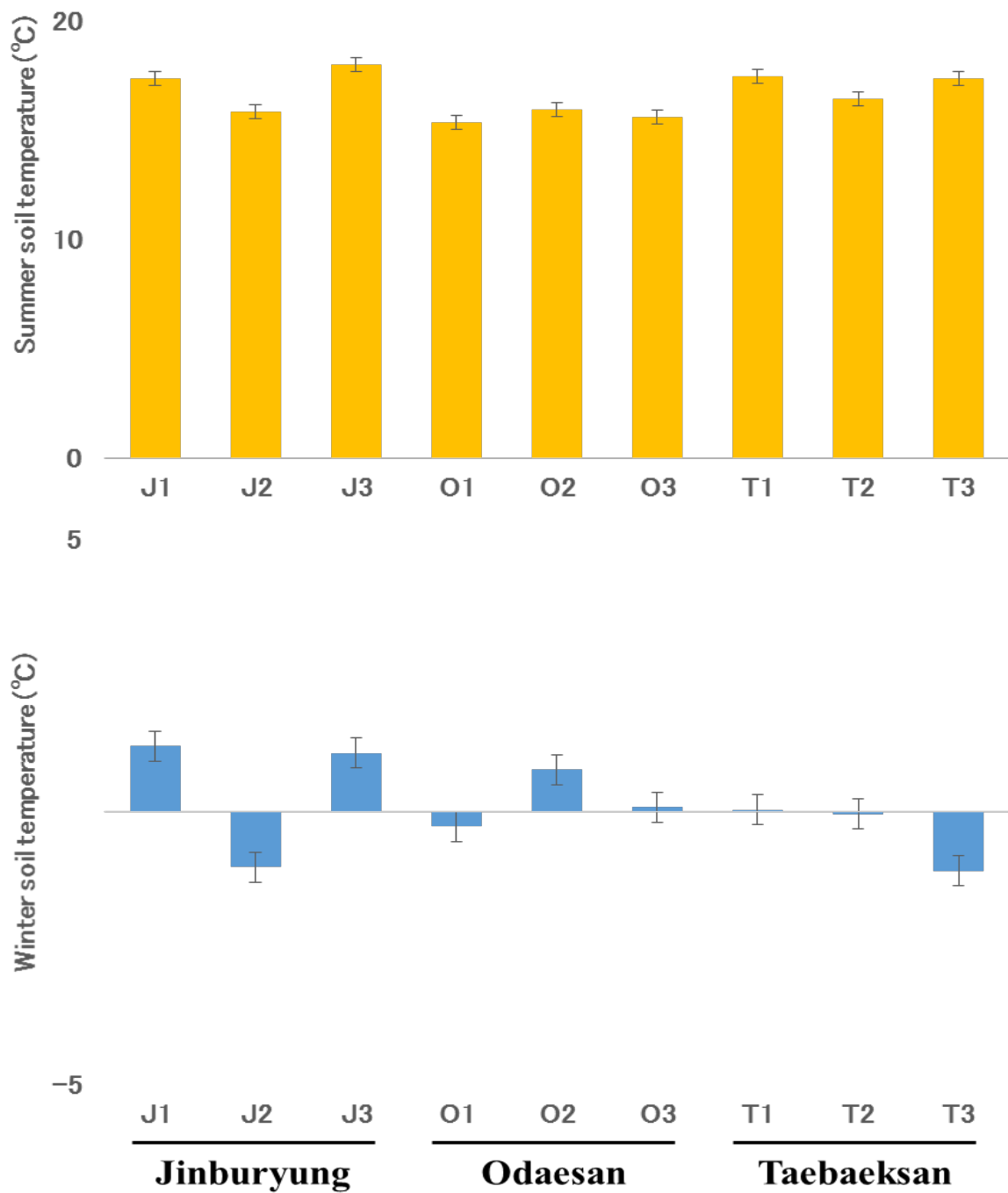


Figure 4-5. Mean of summer and winter soil temperature in each study sites on Baekdudaegan Mountain Range, Korea

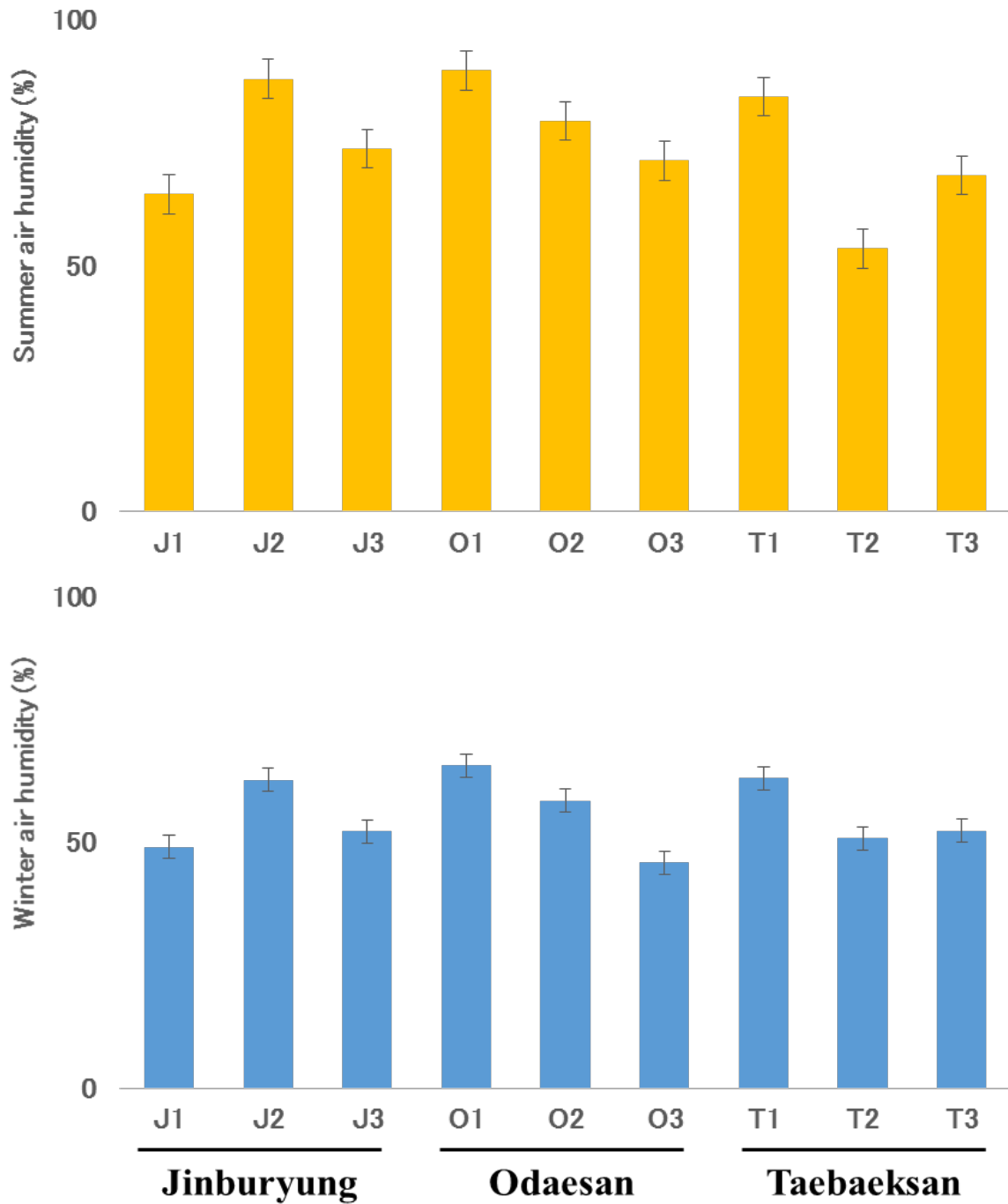


Figure 4-6. Mean of summer and winter air humidity in each study sites on Baekdudaegan Mountain Range, Korea

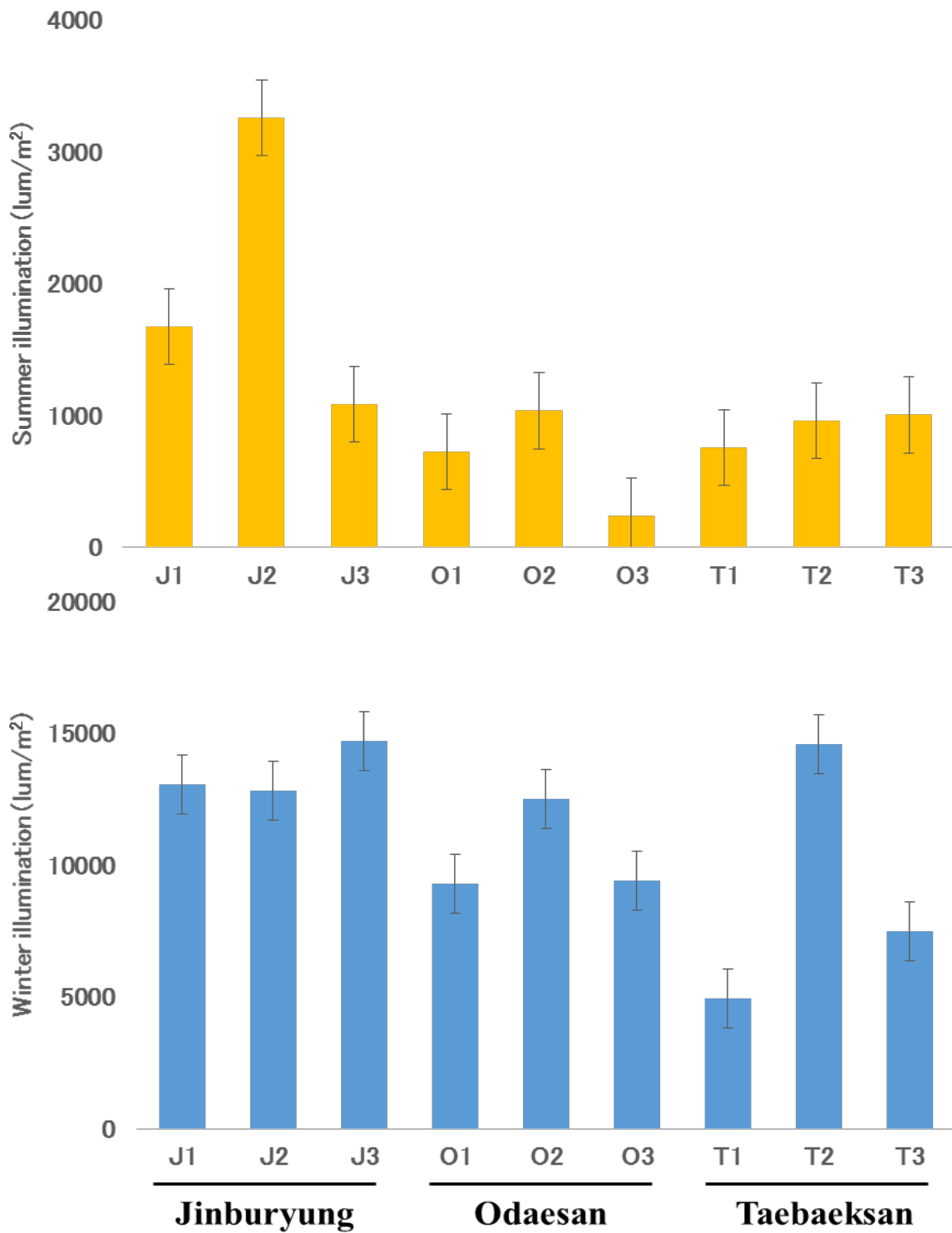


Figure 4-7. Mean of summer and winter illumination in each study sites on Baekdudaegan Mountain Range, Korea

Table 4-2. Variation partitioning of environmental factors among explanatory variables. The factors with the first and second largest effects were shown in boldfaces and italics, respectively.

	Year	Mountain	Site within mountain	Error
S.tem	<i>0.094</i>	0.002	0.512***	0.392
S.H.tem	0.022	<i>0.054</i>	0.644***	0.280
S.L.tem	<i>0.153</i>	0.078	0.235	0.534
S.Soil	<i>0.151</i>	0.188*	0.145*	0.516
S.hum	<i>0.219*</i>	0.084	0.395**	0.302
S.illu	<i>0.203</i>	0.216**	<i>0.203**</i>	0.549
W.tem	<i>0.274</i>	0.009	0.536***	0.182
W.H.tem	<i>0.089</i>	0.038	0.670***	0.203
W.L.tem	<i>0.288**</i>	0.017	0.347*	0.347
W.Soil	<i>0.188</i>	0.062	0.281*	0.469
W.hum	<i>0.114</i>	0.007	0.457**	0.422
W.illu	0.062	<i>0.264**</i>	0.480***	0.194

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Spatial and temporal variation in beetle communities

I collected 7,595 individuals of carabid beetles from the study sites which belonged to 33 species in 13 genera (Tables 4-3 and 4-4). At the genus level, *Synuchus* (2,405 individuals), *Carabus* (2,355) and *Pterostichus* (1,567) were dominant, followed by *Pristosia* (547).

The 45 community data-points were segregated along two CCA axes (Figs. 4-8, 4-9, 4-10, 4-11 and 4-12). Variation along the CCA1 axis explained 11.7% of total variation, and was mainly determined by S.tem, S.H.tem, W.illu and S.Soil. Variation along the CCA2 axis explained 7.5% of total variation, and was determined by S.L.tem, W.hum, S.illu and W.Soil (Fig. 4-8). However, these climatic variables were not statistically significant. *Pterostichus* species showed large variation in their preferred environments along the CCA1 axis (Fig. 4-9). By contrast, *Carabus* and *Synuchus* species showed large variation in their preferred environments along the CCA2 axis (Fig. 4-9). *Anisodactylus punctatipennis* Morawitz, 1862, *Lachnolebia cribricollis* Morawitz, 1862 and *Carabus (Acoptolabrus) leechi* Bates, 1888 were positioned near the positive extreme of the CCA1 axis, while *Trigonognatha coreana* Tschitscherine 1985 was at the positive extreme of the CCA2 axis (Fig. 4-9).

The patterns of temporal change in community composition differed between sites (Figs. 4-10, 4-11 and 4-12). Community compositions in Jinburyung and Odaesan varied mostly along the CCA2 axis. By contrast, community composition in Taebaeksan varied both along the CCA1 and CCA2 axes. Community compositions tended to vary least in Odaesan, with the exception of the sample from 2011 year. Variation between the five yearly replications in each site was larger than variation between sites, indicating that this analysis mainly captured changes between years within each site.

Temporal variation in communities among five years was as large as spatial variation among sites and among mountains: temporal β -diversity indices ranged 0.32 to 0.66, while spatial β -diversity did 0.35 to 0.59 (Table 4-4). α -diversity ranged 0.36 to 1.31 in each site and year, and increased when pooled among five years (1.04-1.28). Spatial β -diversity within mountain ranged 0.293 to 0.486 in each mountain and year, and decreased when pooled among five years (0.239-0.270). These suggest that rare species dropped out from single year data were recovered when pooled.

Site, mountain and year variously explained variations in the carabid communities. All measures of community compositions except CCA2 were significantly explained by year. In addition, species richness, individual abundance and CCA1 were significantly explained by mountain, and individual abundance and CCA1 were significantly explained by site. Variance partitioning revealed that year accounted for the largest proportion of explained variability in all the measures of community compositions. Mountain accounted for the second largest proportion of explained variability in 7 of 9 measures of community compositions, while site accounted for the second largest proportion of explained variabilities in CCA1 and CCA2 (Table 4-5).

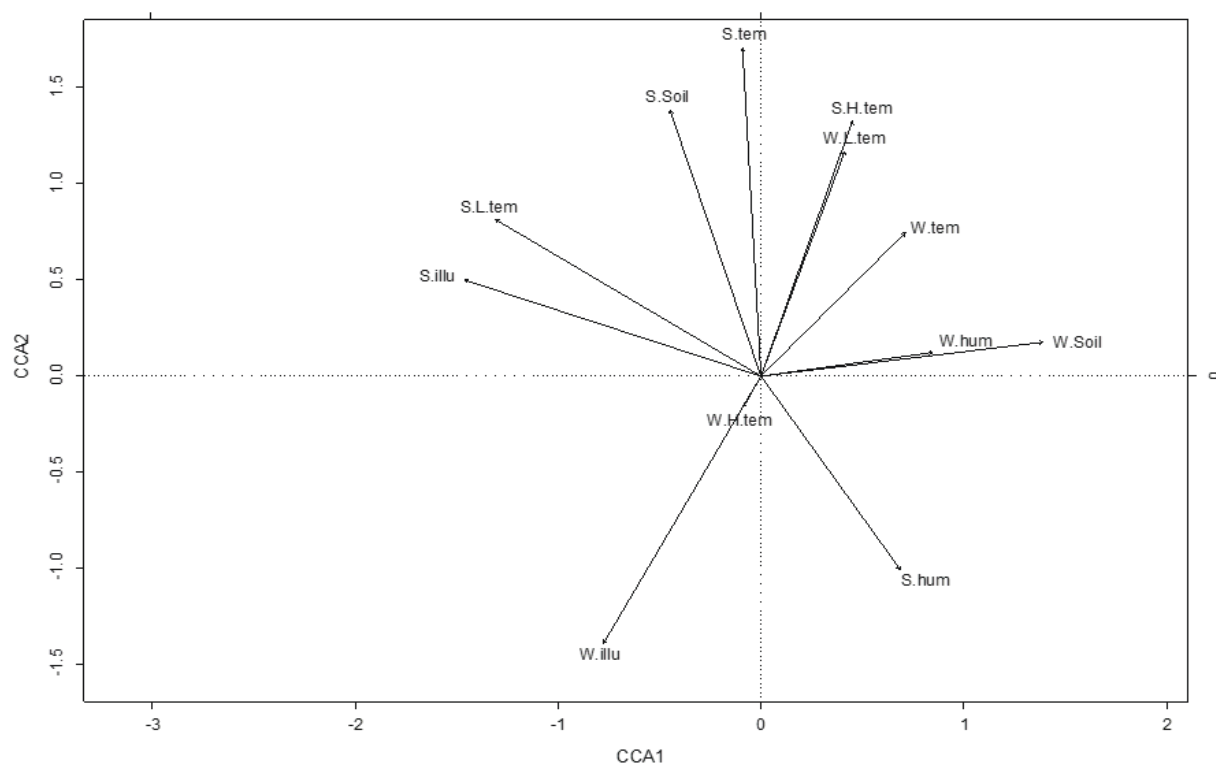


Figure 4-8. Canonical correspondence analysis (CCA) of associations between environmental conditions and carabid beetle community composition (Directions of environmental variation).

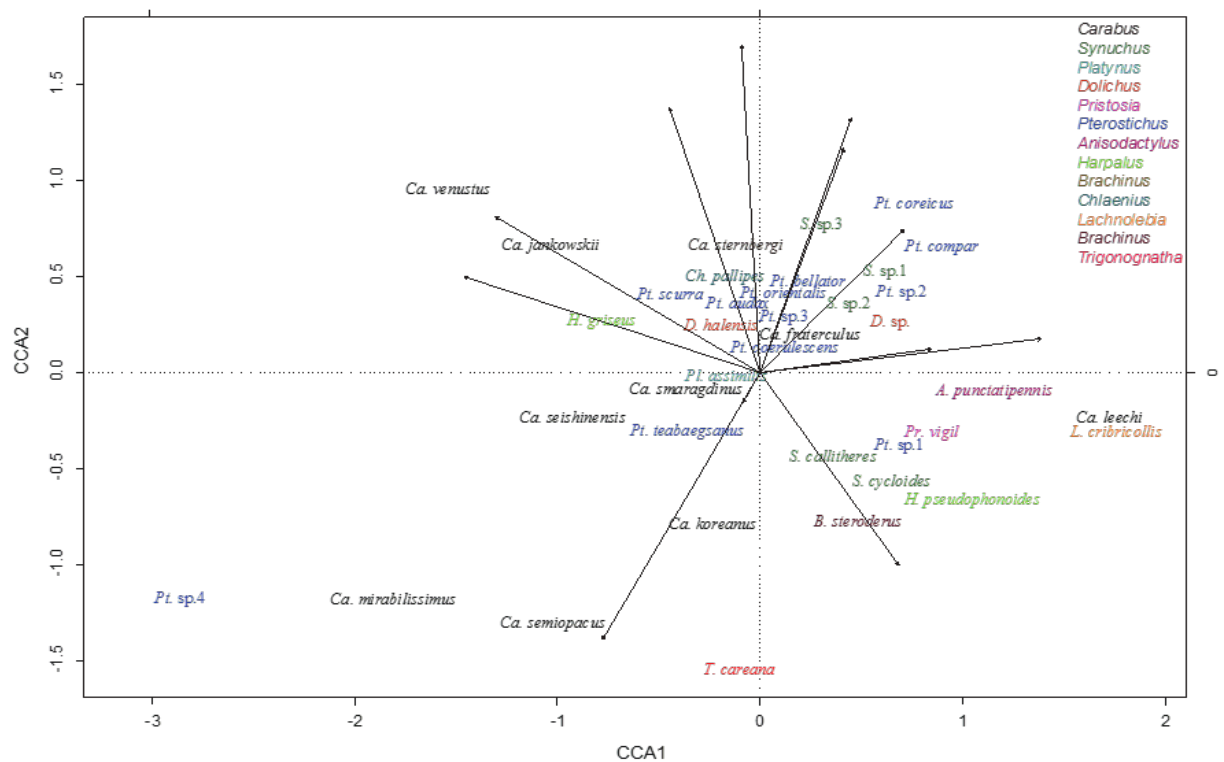


Figure 4-9. Canonical correspondence analysis (CCA) of associations between environmental conditions and carabid beetle community composition (Environmental preference of species; species with fewer than ten individuals are not shown).

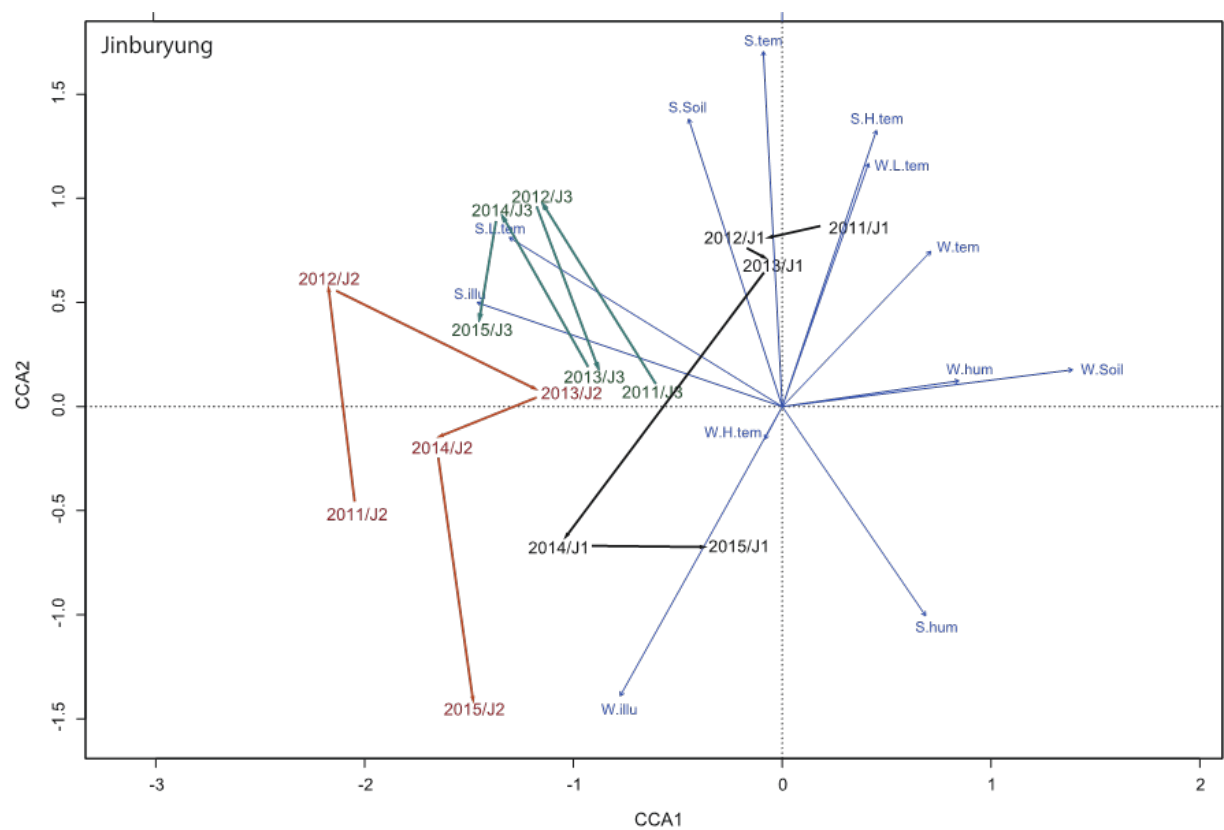


Figure 4-10. Canonical correspondence analysis (CCA) of temporal variations in communities in Jinburyung. Arrows are a rough indication of changes in carabid beetle community composition in each of the 5 years of sampling.

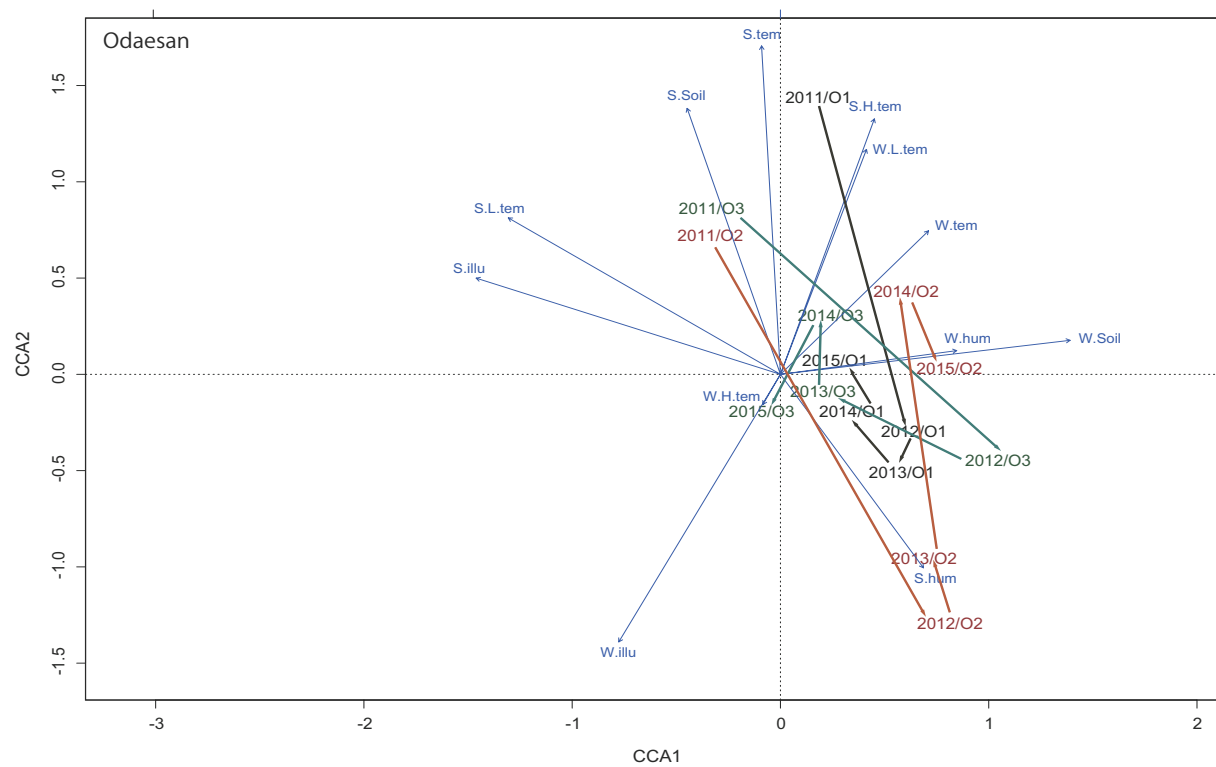


Figure 4-11. Canonical correspondence analysis (CCA) of temporal variations in communities in Odaesan. Arrows are a rough indication of changes in carabid beetle community composition in each of the 5 years of sampling.

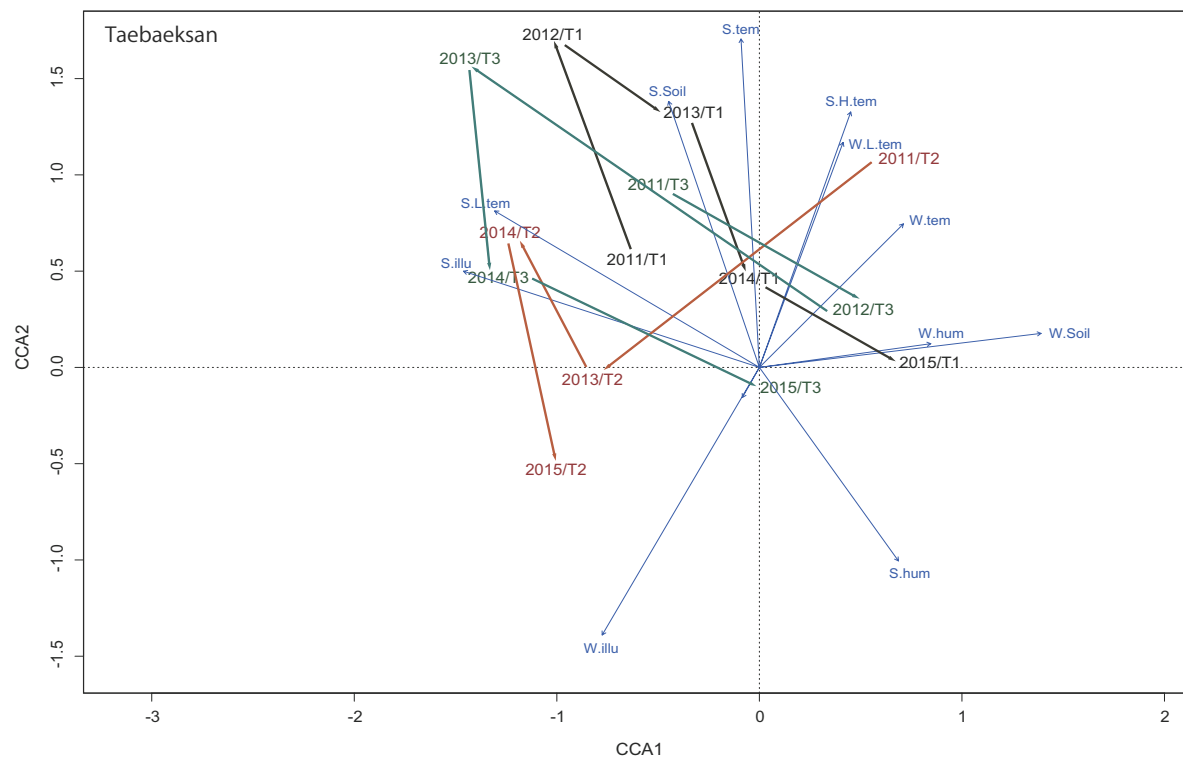


Figure 4-12. Canonical correspondence analysis (CCA) of temporal variations in communities in Taebaeksan. Arrows are a rough indication of changes in carabid beetle community composition in each of the 5 years of sampling.

Table 4-3. List of numbers of ground beetles found on Baekdudaegan Mountain Range, Korea, at three mountain, each sampled in 2 months each year over 5 years.

Species	Jinburyung					Odaesan					Taebaeksan					Total
	2011	2012	2013	2014	2015	2011	2012	2013	2014	2015	2011	2012	2013	2014	2015	
<i>Carabus (Eucarabus) sternbergi</i>	12	74	53	22	30	115	55	59	199	77	21	13	88	31	56	905
<i>Carabus (Leptocarabus) seishinensis</i>	69	31	41	62	53	25	29	34	61	41	22	1	41	87	63	660
<i>Carabus (Leptocarabus) semiopacus</i>	3	26	14	21	103		10	44	26	50			7	4	85	393
<i>Carabus (Leptocarabus) koreanus</i>				8										1		9
<i>Carabus (Morphocarabus) venustus</i>	1	27		26	22	4		7	8	3			13	13	2	126
<i>Carabus (Tomocarabus) fraterculus</i>	2			5	2	1		5	12	9	3	1		5	3	48
<i>Carabus (Coptolabus) smaragdinus</i>	5	7	3	2	6	7	3	5	11	13			3			65
<i>Carabus (Coptolabus) jankowskii</i>	1	8	12	3	6	3	9	5	4	7		1	25	35	17	136
<i>Carabus (Acoptolabus) mirabilissimus</i>	7					1	1		1			1		1		12
<i>Carabus (Acoptolabus) leechi</i>										1						1
<i>Synuchus callitheres</i>	4	9	19	1	57	23	56	74	100	97	2		10	19	86	557
<i>Synuchus cycloides</i>		3	3			10	53	112	66	82		4			101	434
<i>Synuchus nitidus</i>	29	31	41	23	59	4	65	83	259	115	22		29	50	88	898
<i>Synuchus sp.1</i>	44	2	1	7	10	31	22	5	67	38	31		12	10	5	285
<i>Synuchus sp.2</i>	3		2	5	4				95	39		1		14	10	173
<i>Synuchus sp.3</i>									44	14						58
<i>Platynus assimilis</i>	7		3		10	11	27	42	27	56	2		2		40	227
<i>Poecilus versicolor</i>	5	23	20	7	26	13	43	9	43	28		8		37	37	299
<i>Pterostichus orientalis</i>	2	12	7			5		41	30	40	7		7	11	18	180
<i>Pterostichus audax</i>	11	17	12	19	41	7	3	38	52	69	13		10	40	62	394
<i>Pterostichus scurra</i>	6	30	9	12	30	19	15	36	43	49	2		6	31	104	392
<i>Pterostichus compar</i>		14	11			8	31	5	31	29	4		10		66	209
<i>Pterostichus bellator</i>	1	10	8		6	27	19	33	31	42	3	6	7	8	25	226
<i>Pterostichus teabaegsanus</i>						1		10			1		1		4	17
<i>Pterostichus coreicus</i>						18										18
<i>Pterostichus sp.1</i>				5	5	1	14	6	16	20	2		2			71
<i>Pterostichus sp.2</i>						9	2	4	17	19						51
<i>Pterostichus sp.3</i>									4	5						9
<i>Dolichus halensis</i>		9		7	10	1	2	12	10	34	4			12	28	129
<i>Dolichus sp.</i>						10		6								16
<i>Pristosia vigil</i>	4	1	9	15	35	6	72	119	105	94	3	4	3	15	62	547
<i>Anisodactylus punctatipennis</i>						1		1		13					5	20
<i>Harpalus griseus</i>	1	1				3		2								7
<i>Brachinus stenoderus</i>							5	5								10
<i>Lachnolebia cribricollis</i>										3						3
<i>Chlaenius pallipes</i>						4		4			1					9
<i>Trigonognatha coreana</i>					1											1
Total	217	335	268	250	516	368	536	806	1,362	1,087	143	40	276	424	967	7,595

Table 4-4. Spatial and temporal variation in ground beetle communities. Plain and bold numbers indicate α - and β -diversity indices, respectively.

	Total (pooled for 5 years)	2011	2012	2013	2014	2015	Temporal β
Jinburyung (pooled for 3 sites)	1.19	0.96	1.11	1.08	1.08	1.14	0.367
J1	1.18	0.64	1.08	0.96	0.98	1.11	0.327
J2	1.04	0.81	0.77	0.93	0.85	0.96	0.326
J3	1.15	0.70	1.02	0.92	1.03	1.11	0.393
Spatial β within Jinburyung	0.239	0.318	0.352	0.340	0.293	0.327	-
Odaesan (pooled for 3 sites)	1.28	1.13	1.15	1.20	1.20	1.31	0.332
O1	1.24	1.02	1.01	1.13	1.06	1.13	0.327
O2	1.26	1.07	0.92	1.11	1.18	1.25	0.359
O3	1.24	0.62	1.00	1.16	1.10	1.22	0.324
Spatial β within Odaesan	0.254	0.407	0.431	0.486	0.430	0.475	-
Taebaeksan (pooled for 3 sites)	1.26	1.01	0.82	1.00	1.13	1.22	0.573
T1	1.20	0.87	0.36	0.86	1.11	1.07	0.568
T2	1.17	0.71	0.00	0.91	0.90	1.10	0.662
T3	1.19	0.65	0.76	0.77	0.96	1.17	0.562
Spatial β within Taebaeksan	0.270	0.354	0.321	0.317	0.389	0.374	-
Spatial β among mountains	0.442	0.446	0.594	0.450	0.520	0.404	-

Table 4-5. Variation partitioning of carabid community composition among explanatory variables. The factors with the first and second largest effects were shown in boldfaces and italics, respectively.

	Year	Mountain	Site within mountain	Error
Diversity	0.350**	<i>0.199</i>	0.044	0.407
Richness(McFadden)	0.336***	<i>0.302***</i>	0.034	0.329
Richness(Pearson)	0.327***	0.327***	0.048	0.298
Abundance (CoxSnell)	0.581***	<i>0.201***</i>	0.008***	0.210
Abundance (NagelKerke)	0.582***	<i>0.201***</i>	0.008***	0.209
Abundance (McFadden)	0.123***	<i>0.094***</i>	0.005***	0.775
Abundance (Pearson)	0.399***	<i>0.294***</i>	0.014***	0.293
CCA1	0.315***	0.162**	<i>0.179**</i>	0.344
CCA2	0.176	0.121	<i>0.122</i>	0.581

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Discussion

I attempted to quantify spatial and temporal variation in carabid beetle communities and its background environments in Baekdudaegan mountains in Korea based on continuous survey for 5 years. It was revealed that temporal variation was larger than spatial variation among sites and that among mountains in carabid beetle community compositions. In microclimate variables, spatial variation among sites within mountain represented the largest proportion of explained variation, and temporal variation was the second. These results indicate that temporal change provides significant component of variation in communities and environments, while it is often overlooked in the study of community and its dependence on environments.

What is a factor responsible for the observed temporal variation in carabid beetle communities? First, it could be due to insufficient survey. I used 200 traps for obtaining one community sample in one site and in one month. Although this amount of traps is quite larger than in related studies (e.g., Small *et al.* 2006; Riley & Browne 2011; Jung *et al.* 2012; Gillingham *et al.* 2012), it might not be sufficient to capture the composition of the beetle communities inhabiting each site. Insufficient survey can randomly bias the observed composition of the community, such as due to random dropout of species, and may introduce apparent temporal fluctuation of communities. However, the results indicate this may not be the case. When community samples were pooled for five years within site, α -diversity increased and spatial β -diversity among sites within mountain decreased (Table 4-4). This might be due to random dropout of species from community data in each site and year. By contrast, such a tendency was not observed in temporal β -diversity: it did not change after

pooling for three sites within mountain (Table 4-4). This inconsistency suggests that change in observed community composition among years within site was not at random but similar across sites. The results of CCA also support this notion: changes in community compositions showed a tendency to trace similar trajectories among sites (Fig. 4-4, 4-5 and 4-6). Thus, insufficient survey is not regarded as a major factor of temporal variation in carabid beetle communities.

Second, the change in local environment may cause temporal variation in communities. The results in Chapter 3 indicated that the spatial variation of the carabid beetle communities occurred due to changes in the local environmental factors. However, the results of this study differed in part from those of Chapter 3. The results of CCA showed no significant effects of environmental factors, and variance partitioning revealed that relative contribution of temporal variation differed between in environmental variables and carabid beetle community composition. It is possible that environmental factors that I did not investigate may influence carabid beetle communities. In addition, carabid beetles involve spring and autumn breeders: the former species reproduces in the spring and overwinters as adults, and the latter species reproduces in autumn and overwinters as larvae (Allen 1979; Luff 1987). Thus, the phenology of carabid beetles can be related to their life cycles. The phenology of most insects is influenced by temperature (Southwood 1978). Thus, the phenology in spring may be related to the time when temperatures are increasing, and that in autumn may be related to the time when temperatures are decreasing (French *et al.* 2001). My survey was conducted in July and August, the season with the highest temperature in Korea. Therefore, survey of carabid beetle communities in spring and autumn may detect significant effect of environmental variables.

Third, ecological processes other than responses to environmental factors may result in temporal variation in communities. The impact of interaction between species can

influence population dynamics of species. Resource competition is an interaction in which individuals of different species have a negative effect upon each other by affecting access to resources (Alley 1982; Welden & Slauson 1986; Connell 1990). Species can also negatively interact with each other through reproductive interference (Keddy & Shipley 1989; Gröning & Hochkirch 2008). Carabid beetles have traditionally been regarded as an example of the lack of competition in animal communities (Lindroth 1949; Thiele 1964, 1977; den Boer 1980, 1985), whereas reproductive interference is occasionally evident (Okuzaki *et al.* 2010). Further study is necessary to reveal the effect of interspecific interaction on temporal change in carabid beetle communities in this study area.

In conclusion, my results indicated that carabid beetle communities involved significant amount of temporal variation. This indicates the importance of conducting temporal surveys of communities at local scales. Such investigations are expected to reveal an additional fraction of variation in communities, and to provide information on the underlying processes that have been overlooked, especially in studies of global community patterns and changes. Since this data are relatively limited (5 years and three site in each three mountain), increases in temporal scale sample sizes would be beneficial, and would allow more general conclusions to be drawn. The geographical scale of this study was relatively narrow, within Baekdudaegan Mountain Range in Korean Peninsula. Survey in wider geographical scales may increase relative contribution of spatial variation and decrease that of temporal variation, warranting further study. In addition, the data may include variation in voltinism among species that can influence the results. However I treated all the species samely irrespective of possible variation in voltinism, because of only limited information about detailed life histories of carabids in Korea. Elucidation of life histories of individual species will benefit in further interpretation of this results.

Chapter 5.

General discussion

General discussion

Understanding the distributional patterns of biodiversity and the potential mechanisms that act along environmental gradients is one of the most important challenges in biogeography, conservation biology, ecology and evolution (Gaston 2000). This knowledge is critically important for biodiversity conservation, sustainable use and natural reserve area planning and management (Grytnes & Vetaas 2002). Species diversity is one of the most important features of biotic communities because it is closely related to other parameters of ecosystem functioning such as productivity, temporal variability and invasion resistance (Zhang *et al.* 2006; Acharya *et al.* 2011). Ecologists have recognized that biodiversity in an area is divided into three components such as alpha, beta and gamma diversity, alpha and gamma diversity are related to the species richness found in a single site or habitat, sharing the same characteristics and differentiated only by scale, while beta diversity is defined as the change in species composition among sites, habitat or gradients (Sfenthourakis & Panitsa 2012; Swenson *et al.* 2012). This species diversity-centric approach is a logical starting point in biodiversity studies and has been successful in contributing initial insights in to the distribution of biodiversity and the drivers governing these patterns (Swenson *et al.* 2012; Legendre *et al.* 2005).

One of the most important properties of biodiversity is its spatial variation (Rahbek 2005). In general, environmental drivers such as climate, temperature, humidity and illumination, regional area of a species pool, habitat heterogeneity, productivity and geological history contribute to this spatial distribution of biodiversity at broad geographic scales (Field *et al.* 2009), while at the local scale not only biotic factors such as competition and facilitation contribute to levels of biodiversity but also abiotic factors such as

geomorphological heterogeneity and disturbance make their own contribution (Gentili *et al.* 2013). In particular, general interest in the importance of regional-level patterns and the drivers that generate spatial variation in biodiversity have increased considerably during the last decades (Legendre *et al.* 2004). In particular, mountain ecosystems have received increasing attention from researchers examining ecological and biogeographical patterns as well as theories of biodiversity because they provide habitats for various organisms. In addition, a series of environmental gradients in mountain ecosystems are important factors affecting biodiversity and patterns of species distribution (Rahbek 1995; Grau *et al.* 2007).

Many studies have reported reduced abundance and species richness of carabid beetles in coniferous forests compared to mixed and deciduous forests (Butterfield *et al.* 1995; Fahy & Gormally 1998; Jukes *et al.* 2001; Kubota *et al.* 2001; Yu *et al.* 2006), although some of these studies (Jukes *et al.* 2001; Kubota *et al.* 2001; Yu *et al.* 2006) compared forest types of different successional phases. On the other hand, other studies (Niemelä 1993; Lee & Lee 1995; Koivula *et al.* 2002; Oxbrough *et al.* 2012) have found greater or equal beetle abundance and species richness in coniferous forests than in natural or mixed forests. These differences among studies may be in part due to different tree species at each study site (Yu *et al.* 2006). In addition, several environmental variables, such as temperature, humidity, illumination, elevation, and habitat complexity (e.g., number of tree species, canopy cover and leaf-litter depth), may also be more important factors affecting the distribution of carabid beetles (Koivula *et al.* 2002; Fuller *et al.* 2008; Oxbrough *et al.* 2012). Generally, large-bodied species suffer greater declines during environmental change than smaller ones possibly because of their lower reproductive and dispersal powers (Kotze & O'Hara 2003). In Korea, planted or regenerating forests are generally found throughout the nation, while primary forests are restricted to protected and higher mountainous areas, particularly national

parks. Many studies in Korea have reported greater diversity of brachypterous and/or large-bodied carabid beetles in deciduous forests in protected mountain forests (Lee & Lee 1995; Kubota *et al.* 2001; Jung *et al.* 2012). Although these studies have looked at biodiversity of various taxa and regions, few studies have comprehensively analyzed different components of diversity (i.e. spatial and temporal variations), and little attention has been paid to the response of different components of diversity along environmental gradients in mountain ecosystems.

My investigation has focused on which environmental parameters are responsible for variation in the carabid beetle communities, and how much variations are involved in spatial and temporal differences in carabid beetle communities. I found that environmental variables can be used to predict temporal changes in local carabid beetle communities, and responses in carabid beetle communities to microclimate variables differed between sites even within a relatively narrow area. I also found that temporal variation in carabid beetle community compositions was larger than spatial variation among sites and that among mountains. Thus, temporal change provides significant component of variation in communities, while it is often overlooked in the study of global climate change and its effect on communities.

My results suggest that prediction of community responses to ongoing global climate change involves a large amount of uncertainty. The response of local communities is determined by local environmental factors, and thus detailed observation of local climate factors is necessary for predicting temporal changes in local communities. However, such a prediction is difficult by snapshot data obtained in relatively short time scales and in relatively wider geographical ranges. Additionally, responses of local communities to microclimates differed among sites, suggesting difficulty in statistical modelling of community responses. A possible solution for these problems is to investigate how

environmental factors affect each species' population dynamics. In other words, if the environmental dependence of single species can be predicted by climate data, and such predictions can be made for all the species consisting of a community, it may be possible to predict the response of the community across a wide geographical range with spatially heterogeneous climatic conditions, as a set of responses of species belonging to the community. The results of this study consist of the data of population densities of all species involved in communities and background microclimates across 11 sites and for five years. This dataset can be helpful for realizing the above idea, and it will be my next study theme.

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