

Differences in Temporal Variation of Ground Beetle Assemblages (Coleoptera: Carabidae) between Two Well-Preserved Areas in Mt. Sobaeksan National Park

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Abstract

Understanding how future climate conditions will be impact on the biodiversity and species composition is important, because biodiversity becomes more important in environment assessment. To understand the biological changes including diversity and species composition over time (temporal variation within a year), the species diversity and composition of ground beetles were investigated in two well-preserved areas in the Sobaeksan National Park using pitfall traps. In addition, relationships between ground beetles and environmental variables were studied by considering temporal variation. We collected 2,146 ground beetle specimens representing 45 species, and individual-based rarefaction curves indicated that similar species richness was found between Geumseon Valley (GV) and Namcheon Valley (NV). The Bray-Curtis matrix comparisons between study sites were characterized by similar ground beetles sample heterogeneity, while temporal variations in abundance, species richness, and β -diversity of ground beetles showed rather difference over time according to location of study sites. In GV site, minimum temperature was selected as the best predictor for abundance, species richness, and β -diversity of ground beetles, while those relationships in NV site were more complicated. In conclusion, our study suggests that understanding the different response of ground beetles to climatic variables related to local habitat conditions is important to predict the effect of climate change on biological communities.

Key Words: carabid beetle, community structure, microclimate, β -diversity

Introduction

Forest ecosystem has been under threat due to the impacts of climate change and human disturbances (e.g., fragmentation and loss of habitat). In particular, climate change is predicted to alter tree phenology that could disrupt producer-herbivore dynamics (Visser and Holleman 2001; Hodkinson 2005), and is known to affect behaviour and physiology of predatory arthropods (Schmitz and Barton

2014). Therefore, understanding how future climate conditions will be impact on the biodiversity and species composition is important, because biodiversity becomes more important in environment assessment. There are some empirical studies in terms of temporal variations that have examined that population declines and phenological changes can be occurred under climate change (e.g., Roy and Sparks 2000; Pozsgai and Littlewood 2014).

To understand the biological changes including species

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diversity and composition over time (temporal variation within a year), we studied ground beetle assemblages (Coleoptera: Carabidae), because they constitute a taxonomically and ecologically diverse group. Ground beetles are one of most popular taxa in biodiversity monitoring because of their potential capability of bioindication under environmental changes (Thiele 1977; Lövei and Sunderland 1996; Rainio and Niemelä 2003) with comparative analyses in their abundance or community structure (Koivula 2011). Predatory arthropods are generally influenced by the degree of food limitation between sites, depending on habitat quality or landscape features (Östman 2005), although in case of ant assemblages some other factors, such as thermal tolerances relating to physiological traits or the coexistence and distribution of species, are known to be more important factors for the species turnover (β -diversity) along elevational gradients (Bishop et al. 2015). In general, the species turnover of community composition over space and time in terms of the metacommunity perspective, can be influenced by local environmental conditions (Penev 1996; Leibold et al. 2004; Holyoak et al. 2005).

Therefore, this study was conducted to investigate the species diversity and composition of ground beetles from two well-preserved areas in the Sobaeksan National Park. In addition, relationships between ground beetles and environmental variables were studied by considering temporal variation.

Materials and Methods

Study area

The flora of Sobaeksan National Park shows characteristics intermediate between northern and southern floras (KNPA 2007). The climate of Sobaeksan National Park is temperate to continental, with a dry, cold winter and hot, humid summer. In particular, the summer monsoon brings abundant moisture from the ocean and produces heavy rainfall. In Sobaeksan National Park, we selected two sites to investigate the community structure of ground beetles around Namcheon Valley (NV; Latitude, $37^{\circ} 02' 10.5''$; Longitude, $128^{\circ} 31' 04.1''$; Altitude, 285 m) on the northern slope, and around Geumseon Valley (GV; Latitude, $36^{\circ} 56' 25.7''$; Longitude, $128^{\circ} 29' 55.1''$; Altitude, 678 m) on the southern slope (Fig. 1a), in consideration of mountain's

topography, environmental characteristics and major vegetation structure.

For collecting temperature and relative humidity (R.H.), we installed HOBO data loggers in each site from middle January to early December. During study periods in 2016, annual mean temperatures in NV and GV sites were 16.4°C and 14.2°C , respectively, and annual means of R.H. in NV and GV sites were 80.8% and 85.6%, respectively.

Sampling

For ground beetle collection, pitfall traps were used. Pitfall trapping is a standard sampling method for comparing the abundance or community structure of ground beetles (Niemelä 1996; Koivula et al. 2003). The plastic pitfall traps (300 ml, 75 mm diameter, 100 mm depth) were un-baited, containing preservatives (200 ml, 95% ethyl-alcohol:95%:ethylene-glycol=1:1) as killing-preserving solution. A plastic roof was placed 3 cm above each trap to prevent the inflow of rainfall and litter.

Three study plots ($20 \times 20 \text{ m}^2$) were placed in each site and spaced 50 m apart from each other (Fig. 1b). In each plot, nine pitfall traps were placed in a grid of 3×3 traps.

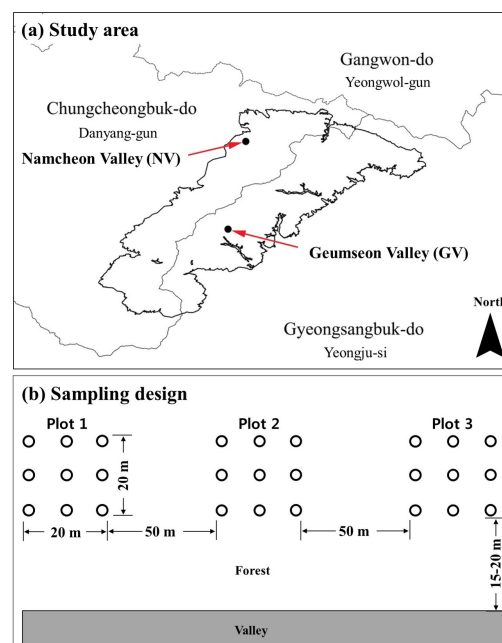


Fig. 1. Map of study area (a) and sampling design for collecting ground beetles in two study sites (b). In sampling design, opened-circles indicate pitfall trap.

Table 1. Species list of ground beetle assemblages in Geumseon and Namcheon valleys

Species	Geumseon valley	Namcheon valley
<i>Agonum xestus</i> (Bates, 1883)	63	26
<i>Amara congrua</i> Morawitz, 1862		2
<i>Amara</i> sp.1	1	
<i>Anisodactylus punctatipennis</i> Morawitz, 1862	1	3
<i>Aulonocarabus koreanus kyonilleeique</i> Deuve, 1992	1	7
<i>Aulonocarabus seishinensis seishinensis</i> Lapouge, 1931	6	
<i>Aulonocarabus semiopacus</i> Reitter, 1895	47	
<i>Brachinus scotomedes</i> L. Redtenbacher, 1867	10	6
<i>Chlaenius naeviger</i> Morawitz, 1862		4
<i>Chlaenius ocreatus</i> Bates, 1873		2
<i>Coptolabrus jankowskii jankowskii</i> Oberthur, 1883	8	10
<i>Coreocarabus fraterculus assimilis</i> Kwon et Lee, 1984	10	
<i>Cymindis collaris</i> Motschulsky, 1845	9	6
<i>Diplocheila zeelandica</i> (Redtenbacher, 1868)		4
<i>Dischissus mirandus</i> Bates, 1873		1
<i>Dolichus coreicus</i> Jedlička, 1936	9	1
<i>Eucarabus sternbergi sobaeksanensis</i> Kwon et Lee, 1984	28	15
<i>Galerita orientalis</i> Schmidt-Goebel, 1946		4
<i>Harpalus discrepans</i> Morawitz, 1862	6	45
<i>Harpalus niigatanus</i> Schauburger, 1929		2
<i>Harpalus roninus</i> Bates, 1873	21	
<i>Harpalus tridens</i> Morawitz, 1862	4	
<i>Harpalus vicarius</i> Harold, 1883	3	
<i>Nebria chinensis chinensis</i> Bates, 1872	18	29
<i>Nebria coreica</i> Solsky, 1875	1	
<i>Oxycentrus argutoroides</i> (Bates, 1873)		1
<i>Pheropsophus jessoensis</i> Morawitz, 1862		53
<i>Pristosia impunctata</i> Sasakawa, Kim, Kim&Kubota, 2006		13
<i>Pristosia vigil</i> (Tschitschérine, 1895)	112	6
<i>Pterostichus audax</i> Tschitschérine, 1895	330	27
<i>Pterostichus ishikawaoides</i> Sasakawa, Kim, Kim&Kubota, 2008	9	
<i>Pterostichus microcephalus</i> (Motschulsky, 1860)	1	1
<i>Pterostichus orientalis orientalis</i> Motschulsky, 1845	522	1
<i>Pterostichus scurrus</i> (Tschitschérine, 1901)	57	1
<i>Pterostichus subovatus</i> (Motschulsky, 1860)	1	
<i>Pterostichus sulcitaris</i> Morawitz, 1863		1
<i>Pterostichus vicinus</i> Park et Kwon, 1996	13	
<i>Synuchus agonus</i> (Tschitschérine, 1895)	100	45
<i>Synuchus arcuaticollis</i> Motschulsky, 1860	2	10
<i>Synuchus crocatus</i> (Bates, 1883)	41	191
<i>Synuchus cycloderus</i> (Bates, 1873)	29	27
<i>Synuchus melantho</i> (Bates, 1883)	55	20
<i>Synuchus nitidus</i> (Motschulsky, 1861)	1	13
<i>Synuchus</i> sp.1	2	5
<i>Trichotichmus</i> sp.1	17	26

Overall, 27 pitfall traps were placed in each study site, with a total of 54 pitfall traps used. Pitfall traps were replaced approximately every two weeks from March to November in 2016.

Collected ground beetles were brought to the laboratory, dried, mounted, and identified to species level under a dissecting microscope ($\times 63$). Identification was performed according to Habu (1967, 1973, 1978, 1987), Kwon and Lee (1984), Park and Paik (2001), and Park et al. (2014) and nomenclature was confirmed according to the lists of Korean Carabidae by Park and Paik (2001), Park (2004), and Park and Park (2013).

Data analysis

Species richness was measured by the total number of species collected during the sampling period, and abundance was measured by the total number of individuals collected in a set of traps for each study site. The species richness of ground beetles was estimated with individual-based rarefaction curves for each site. Rarefaction curves are based on random re-sampling of the pool of captured individuals, and are used to estimate expected richness in lower sample sizes (Gotelli and Colwell 2001). Rarefaction methods allow meaningful standardization and comparison of datasets (Gotelli and Colwell 2001).

To examine variation in sample heterogeneity (β -diversity) between study sites, we used a Bray-Curtis pair-wise sample dissimilarity matrix (Legendre et al. 2005; Anderson et al. 2006). We first selected matrix values for each of the GV and NV sites. Then we calculated average ground beetle catch for all sites within a given category, and for each site we calculated Bray-Curtis distance between the catch of a given site and the average catch of the corresponding study site. These distance were subjected to Levene's test to examine variance homogeneity. Then, one-way ANOVA was used to compare sample heterogeneity between the study sites.

To examine the relationship between ground beetle assemblages and environmental variables (temperature and relative humidity), stepwise multiple regressions were conducted to test the relative importance of all independent environmental variables in explaining the abundance, species richness, and β -diversity of ground beetles. For GV site, multiple linear regressions were conducted because of its

linear relationship between ground beetle assemblages and environmental variables. On the other hand, temporal variation of ground beetle assemblages in NV site showed double-humped distribution in general. Thus quadratic regressions were applied to NV site.

Rarefaction curves, Bray-Curtis dissimilarity indices, one-way ANOVA, and stepwise multiple regressions were conducted using the R version 3.0.2 (R Core Team 2013).

Results

Ground beetles in Geumseon and Namcheon valleys

We collected 2,146 ground beetle specimens representing 45 species (Table 1). Dominant species in Geumseon valley (GV) was *Pterostichus orientalis orientalis* (33.9% of the total catch) and *Pterostichus audax* (21.5%), while *Synuchus crocatus* (31.4%) and *Pheropsophus jessoensis* (8.7%) were dominant in Namcheon valley (NV). Ten and eleven species were unique to the GV and NV sites, respectively, and 22 species were shared between the two study sites.

Individual-based rarefaction curves indicated that similar species richness was found between GV and NV (Fig. 2). However, catches of all ground beetle species were significantly greater in GV, compared with NV (1538 vs 608 individuals).

Spatial and temporal variation of ground beetles diversity

The Bray-Curtis matrix comparisons between study sites

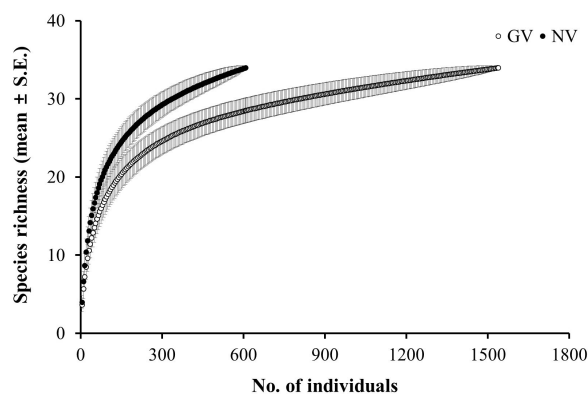


Fig. 2. Species richness estimation based on individual-based rarefaction curves in two study sites.

were characterized by similar ground beetles sample heterogeneity (Levene's test statistic=0.0009, $p=0.978$; ANOVA, $F_{1,4}=6.82$, $p=0.059$) (Fig. 3). On the other hand, temporal variations in abundance (Fig. 4a), species richness (Fig. 4b), and β -diversity of ground beetles (Fig. 4c) showed rather different over time according to location of study sites. In GV, abundance and β -diversity of ground beetles were relatively high during summer, while species richness was relatively high during late August and late September. Abundance, species richness, and β -diversity of ground beetles in NV showed two peaks in June and late September but not high during summer season. However, temporal variation of ground beetles between GV and NV showed significant difference in abundance only (rm-ANOVA, $F_{1,17}=4.88$, $p=0.041$), while it did not differ in species richness ($F_{1,17}=1.26$, $p=0.277$) and β -diversity ($F_{1,17}=0.88$, $p=0.361$).

Temporal patterns of ground beetle assemblages in both sites were relatively well predicted by environmental variables derived from temperature and relative humidity (Table 2). In particular, abundance ($F_{1,16}=27.16$, $p<0.001$), species richness ($F_{3,14}=25.49$, $p<0.001$), and β -diversity ($F_{1,16}=109.70$, $p<0.001$) of ground beetles in GV site were well predicted by minimum temperature with linear relationships, while in NV site minimum temperature squared and maximum relative humidity squared were relatively important ($F_{8,9}=5.92$, $p=0.008$).

Discussion

This study shows that temporal variation in environ-

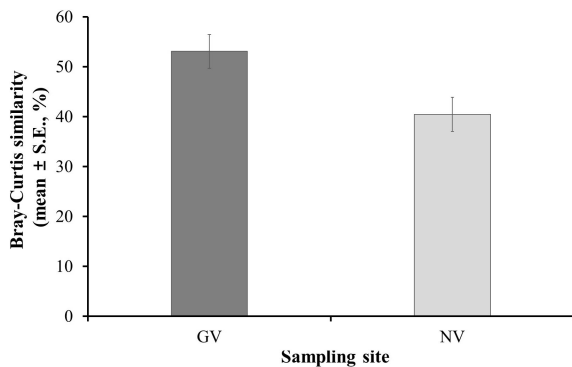


Fig. 3. Comparison of spatial variations of Bray-Curtis similarity (1-dissimilarity) of ground beetle assemblages between two study sites.

mental variables in terms of temperature and relative humidity is important to understand changes in ground beetle assemblages (abundance, species richness, and β -diversity). Therefore, microclimatic variables could be used to predict changes in communities in mountainous forest ecosystems. However, the patterns in temporal variations of ground beetles were also influenced by various combinations of environmental variables, depending on spatial locations.

As most plants and animals, temperature and rainfall are basically important for ground beetles in terms of habitat

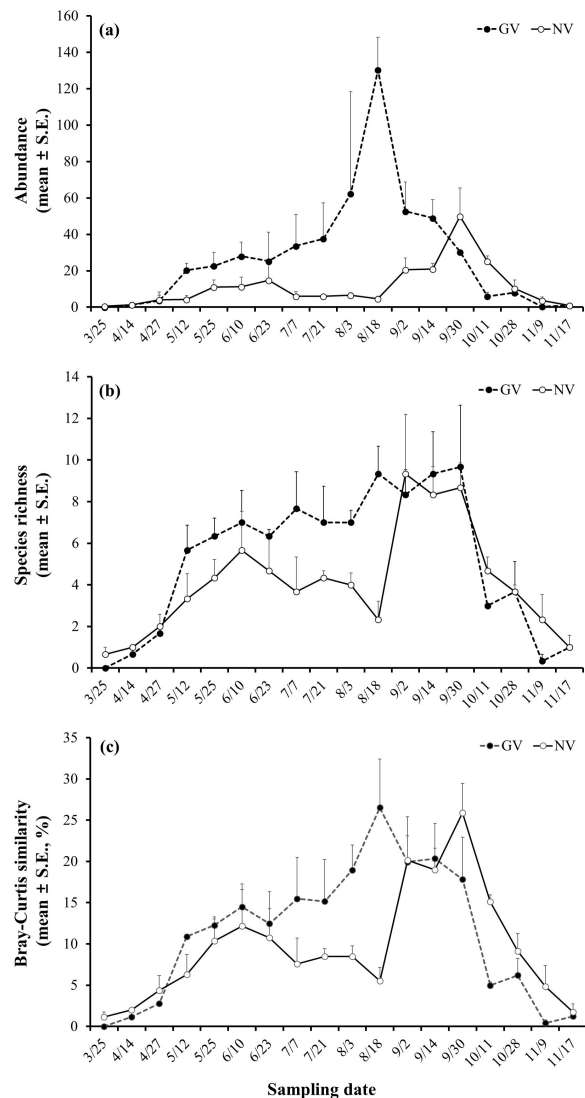


Fig. 4. Comparison of temporal variations of abundance (a), species richness (b), and Bray-Curtis similarity (1-dissimilarity), (c) of ground beetle assemblages between two study sites.

Table 2. Relationship between ground beetle assemblages (abundance, species richness, and β -diversity) and selected environmental variables as determined by stepwise multiple regression analyses. Multiple linear regressions were conducted to GV site because of its linear relationships between ground beetle assemblages and environmental variables. On the other hand, quadratic regressions were applied to NV site

Independent variables & statistics	Geumseon valley (GV)			Namcheon valley (NV)		
	Abundance	Species richness	β -diversity	Abundance	Species richness	β -diversity
Independent variables						
(intercept)	[†] ns -18.26	10.95	^{ns} -3.81	^{ns} -217.66	^{ns} -1081.00	*221.64
Avg. Temp.	[‡] N.E.	N.E.	N.E.	N.E.	N.E.	N.E.
Max. Temp.	N.E.	N.E.	N.E.	N.E.	^{ns} -2.24	^{ns} -9.29
Min. Temp.	***4.06	***0.45	***2.25	^{ns} 3.24	^{ns} 0.86	^{ns} 6.59
Avg. R.H.	N.E.	16.20	N.E.	^{ns} 831.58	^{ns} 255.10	^{ns} 560.67
Max. R.H.	N.E.	-32.74	N.E.	N.E.	^{ns} 2708.00	N.E.
Min. R.H.	N.E.	N.E.	N.E.	^{ns} -352.75	^{ns} -40.89	^{ns} -434.70
(Avg. Temp.) ²	-	-	-	^{ns} -0.11	^{ns} 0.16	^{ns} 0.61
(Max. Temp.) ²	-	-	-	N.E.	N.E.	N.E.
(Min. Temp.) ²	-	-	-	N.E.	^{ns} -0.14	*-0.66
(Avg. R.H.) ²	-	-	-	^{ns} -572.93	^{ns} 252.90	N.E.
(Max. R.H.) ²	-	-	-	N.E.	^{ns} -1556.00	*-457.06
(Min. R.H.) ²	-	-	-	^{ns} 380.08	N.E.	^{ns} 227.95
Statistics for final model						
<i>F</i>	27.16	25.49	109.7	3.29	3.97	5.92
<i>df</i>	1, 16	3, 14	1, 16	6, 11	9, 8	8, 9
<i>P</i>	< 0.001	< 0.001	< 0.001	0.042	0.033	0.008
Adjusted <i>R</i> ²	0.606	0.812	0.865	0.447	0.612	0.698

[†]Abbreviation of ns in superscript means that the given variable was included into the regression model with insignificant.

[‡]N.E. indicates that the given variable was not entered into the regression model.

Asterisks indicate statistical significant levels: **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

and microhabitat distributions (Lövei and Sunderland 1996; Antvogel and Bonn 2001), reproduction (Ernsting and Isaaks 2000), and population dynamics (Honěk 1997). In our study, annual mean temperature and relative humidity were relatively different between two study sites, and those differences were because of the different locations of study sites in terms of altitude, slope, and aspect. For these reasons, the distributional pattern of many ground beetle species or their relative abundance may also different according to location of study sites (Table 1). In general, distribution of ground beetles depends on biotic and abiotic factors, such as temperature, humidity, food availability, the presence of competitors, and life history (Lövei and Sunderland 1996). According to Jung et al. (2012), some species (for example, *Pterostichus orientalis orientalis* and *Synuchus cycloderus*) were gradually changes in their relative abundances along the altitudinal gradient in Sobaeksan National Park. Thus, species composition of ground beetles

in Sobaeksan National Park was divided in two groups, higher and lower altitudes. In fact, *P. orientalis orientalis* and *P. audax* in our study were dominant species in GV site, but not in NV site. Therefore, the difference in species composition due to the difference of environmental characteristics between two study sites seems to be the cause of temporal variations of ground beetle assemblages.

Differences in species composition can affect the predicted outcomes of temporal changes in ground beetle assemblages. In GV site, minimum temperature was only selected as best predictor for seasonal changes in abundance, species richness, and beta-diversity of ground beetles, but those relationships in NV site where double-humped patterns in carabid beetles was found along seasonal changes were more complicated (Fig. 4). These differences of temporal patterns in ground beetles between GV and NV sites may be because of the presence of *Pterostichus* species. In fact, 933 ground beetle individuals (7 species) were

caught in GV site, and their temporal variation is more similar to total ground beetle assemblages (data not shown). In NV site, on the other hand, very few ground beetles were caught (31 individuals belonging to 5 species). Thus, selected predictors for models are clearly different, although seasonal changes of temperature and relative humidity between two study sites were similar to each other. This result indicates that temporal variation of ground beetle assemblages can be altered by climate change, because the change of distributions and population dynamics of insect species to avoid future negative climate conditions is predicted in general. For example, some ground beetle species showed population declines and/or phenological changes based on short-term (Kiritani 2013) or long-term monitoring (Pozsgai and Littlewood 2014).

In conclusion, our study suggests that understanding the different response of ground beetles to climatic variables related to local habitat conditions is important to predict the effect of climate change on biological communities. However, the present data can involve some uncertainties because of short-term monitoring within a year. In addition, because environmental changes can also alter vegetation related variables and soil properties as well as temperature and relative humidity, investigation of other environmental variables would also be need.

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References

- Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecol Lett* 9: 683-693.
- Antvogel H, Bonn A. 2001. Environmental parameters and micro-spatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography* 24: 470-482.
- Bishop TR, Robertson MP, van Rensburg BJ, Parr CL. 2015. Contrasting species and functional beta diversity in montane ant assemblages. *J Biogeogr* 42: 1776-1786.
- Ernsting G, Isaaks A. 2000. Ectotherms, temperature, and trade-offs: size and number of eggs in a carabid beetle. *Am Nat* 155: 804-813.
- Gotelli NJ, Colwell RK. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4: 379-391.
- Habu A. 1967. Fauna Japonica, Carabidae truncatipennes group (Insecta: Coleoptera). Biogeographical Society of Japan, Tokyo.
- Habu A. 1973. Fauna Japonica, Carabidae: Harpalini (Insecta: Coleoptera). Keigaku Publishing Co. Ltd, Tokyo.
- Habu A. 1978. Fauna Japonica, Carabidae: Platynini (Insecta: Coleoptera). Keigaku Publishing Co. Ltd, Tokyo.
- Habu A. 1987. Classification of the Callistini of Japan (Coleoptera, Carabidae). *Entomol Rev Japan* 42: 1-36.
- Hodkinson ID. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol Rev Camb Philos Soc* 80: 489-513.
- Holyoak M, Leibold MA, Holt RD. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago.
- Honěk A. 1997. The effect of temperature on the activity of Carabidae (Coleoptera) in a fallow field. *Eur J Entomol* 94: 97-104.
- Jung JK, Kim ST, Lee SY, Park CG, Park JK, Lee JH. Community structure of ground beetles (Coleoptera: Carabidae) along an altitudinal gradient on Mt. Sobaeksan, Korea. *Journal of Asia-Pacific Entomology* 15: 487-494.
- Kiritani K. 2013. Different effects of climate change on the population dynamics of insects. *Appl Entomol Zool* 48: 97-104.
- KNPA. 2007. Research of the wildlife ecosystem in Sobaeksan National Park. Korean National Park Authority. (in Korean)
- Koivula M, Kotze DJ, Hiiisivuori L, Rita H. 2003. Pitfall trap efficiency: do trap size, collecting fluid and vegetation structure matter? *Entomol Fennica* 14: 1-14.
- Koivula MJ. 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *Zookeys* 100: 287-317.
- Kwon YJ, Lee SM. 1984. Classification of the subfamily Carabinae from Korea (Coleoptera: Carabidae). *Insecta Koreana*, Series 4, Editorial Committee of Insecta Koreana.
- Legendre P, Borcard D, Peres-Neto PR. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75: 435-450.
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7: 601-613.
- Lövei GL, Sunderland KD. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annu Rev Entomol* 41: 231-256.
- Niemelä J. 1996. From systematics to conservation-carabidologists do it all. *Ann Zool Fenn* 33: 1-4.
- Park JK, Choi IJ, Park J, Choi EY. 2014. Insect fauna of Korea, vol. 12, no. 16, Arthropoda: Insecta: Coleoptera: Carabidae: Chlaeniini, Truncatipennes group: Odacanthinae, Lebiinae.

- Junghaengsa, Inc., Incheon.
- Park JK, Paik JC. 2001. Family Carabidae. *Economic Insects of Korea* 12. Ins. Koreana Suppl. 19, Junghaeng-sa, Seoul.
- Park JK, Park J. 2013. *Insect fauna of Korea*, vol. 12, no. 13, Arthropoda: Insecta: Coleoptera: Carabidae: Pterostichinae. Junghaengsa, Inc., Incheon.
- Park JK. 2004. Subfamily Carabinae in Korea (Coleoptera: Carabidae). *Economic Insects of Korea* 23. Ins. Koreana Suppl. 30, Junghaeng-sa, Seoul.
- Penev L. 1996. Large-scale variation in carabid assemblages, with special reference to the local fauna concept. *Ann Zool Fenn* 33: 49-63.
- Pozsgai G, Littlewood NA. 2014. Ground beetle (Coleoptera: Carabidae) population declines and phenological changes: Is there a connection? *Ecol Indic* 41: 15-24.
- R Core Team. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rainio J, Niemelä J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers Conserv* 12: 487-506.
- Roy DB, Sparks TH. 2000. Phenology of British butterflies and climate change. *Glob Change Biol* 6: 407-416.
- Schmitz OJ, Barton BT. 2014. Climate change effects on behavioral and physiological ecology of predator-prey interactions: implications for conservation biological control. *Biol Control* 75: 87-96.
- Thiele HU. 1977. *Carabid beetles in their environments*. Springer, Berlin.
- Visser ME, Holleman LJ. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc Biol Sci* 268: 289-294.
- Östman Ö. 2005. Asynchronous temporal variation among sites in condition of two carabid species. *Ecol Entomol* 30: 63-69.