


ARTICLE

Winter sampling and seasonal variation in litter-dwelling beetle assemblages using a sifting method

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(Received 17 March 2021; accepted 12 August 2021)

Abstract

Litter-dwelling arthropods play an important role in maintaining forest ecosystem function. This study was designed to understand seasonal variations and diversity of litter-dwelling adult beetles, one of the most diverse groups of arthropods. Sampling was conducted in mixed-wood forests of South Korea between March and December 2019, covering all seasons, including winter. We used a sifting method and a Berlese funnel to collect arthropods living in leaf litter and soil. We collected a total of 5820 invertebrates representing six orders, of which 1422 were beetles representing 24 families and minimum 141 species. Beetle species richness was highest in spring and lowest in summer based on rarefaction and extrapolation. However, beetle abundance was lowest in spring, but abundance was similar among the other seasons. Beetle assemblage composition was correlated significantly with soil surface and atmospheric temperature. The assemblage composition differed among seasons, except between spring and winter, which overlapped slightly. The combined sifting–Berlese funnel method showed great advantages for investigating the diversity of overwintering arthropods. Continued study of the relationship between arthropods and the leaf-litter environment is essential to understand this microecosystem and will increase the chance of discovering new beetle species.

Introduction

Arthropods account for more than 80% of animal species, among which litter-dwelling invertebrates account for a large proportion of the world's biodiversity (Ødegaard 2000). They represent important food sources for many vertebrates and other predatory invertebrates (Pianka and Parker 1975; Redford 1987; McNabb *et al.* 2001). Beetles (Coleoptera) are among the most diverse group of arthropods (Hammond 1992; Rosenzweig 1995), live in a variety of habitats, and have a wide diet spectrum, from plant leaves, tree sap, animals, fungi to dead or decaying wood (Cott 1940; Ruppert *et al.* 2004). They play an important role in forest ecosystem services, recycling organic components and nutrients, affecting energy flow, and so on (Giller 1996; Artz *et al.* 2010; Roy *et al.* 2018).

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Subject editor: Jeff Battigelli

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Leaf litter is an important environment, harbouring many organisms, where interactions between litter-dwelling insects and the environment are ecologically important (Moore *et al.* 1988; Hughes *et al.* 2000; Jeffery and Gardi 2010). As leaf litter decomposes, it releases nutrients and moisture, promoting fungal growth and sporulation (Kerekes *et al.* 2013; Krishna and Mohan 2017). Litter-dwelling arthropods use this nutrient-rich environment and interact with each other (Seastedt and Crossley 1984). Leaf litter creates a variety of soil microhabitats that contain food resources, and it protects organisms from poor weather conditions and predators (Hamilton 2015). These microhabitats vary throughout the year and affect the availability of nutritional resources for species belonging to different feeding guilds (Fittkau and Klinge 1973; Hättenschwiler *et al.* 2005).

Changes in season or temperature affect the diversity and abundance of adult beetles that reside in leaf litter and soil (Pinheiro *et al.* 2002). The response of beetles to these changes differs worldwide, especially between temperate and tropical zones (Wolda 1978a, 1978b, 1980; Wolda and Broadhead 1985; McElravy and Resh 1987). In the temperate zone, where there are four seasons, for example, different species are active in different seasons (Scott and Epstein 1987). Summer in temperate regions is hot and humid, and the days are long. These environmental conditions are expected to increase the activity of adult beetles and increase their diversity and abundance (Whittaker and Tribe 1998; Frazier *et al.* 2006; Deutsch *et al.* 2008). Conversely, temperate-zone winters are cold and dry, with a short photoperiod, leading to decreased activity by adult beetles and a decline in species diversity and abundance (Mellanby 1939; Taylor 1963; Wolda 1988). Unfavourable cold environments also cause many insects to delay their development (Tauber *et al.* 1986; Saunders 2002), and many beetles enter diapause in an adult stage for winter (Danks 1987). Most adult beetles are sensitive to these environmental changes, and thus monitoring changes in diversity, abundance, and community structures of these organisms is highly important for biodiversity conservation (Agosti *et al.* 2000; Hilty and Merenlender 2000; Kime and Golovatch 2000; Longcore 2003; Bouyer *et al.* 2007; Siddig *et al.* 2016).

Several studies in Korea have investigated seasonal changes in insect biodiversity, including adult beetles. However, these studies have limited sampling periods and usually exclude the winter season. Furthermore, pitfall traps, light traps, or sweeping methods were typically used to collect insects (Lee *et al.* 2005; Byun *et al.* 2009a, 2009b, 2010; Lee *et al.* 2009; Park *et al.* 2010; Park *et al.* 2011; Lim *et al.* 2012; Kim and Kwon 2016). In the present study, we combined a sifting technique with Berlese funnel extraction to collect samples of litter-dwelling arthropods during all seasons because of the limited capability of other trapping methods for sampling overwintering arthropods. Because Berlese funnels direct constant high temperature and light towards litter samples, they can provide a strong signal to awaken insects from diapause (Saunders 2002). In this way, the use of Berlese funnels has the potential to collect insects and other soil arthropods in the winter season.

Few studies have addressed the full seasonal spectrum of litter-dwelling animals and their relationships with the environment. The present study investigated seasonal variations and diversity of litter-dwelling adult beetle assemblages. It is the first study to sample beetles using a sifting method in all seasons, including winter, in the temperate forests of Korea. For this study, we predicted that (1) adult beetle species richness and abundance would be highest in summer and lowest in winter because many adults may not overwinter in leaf litter (Leather *et al.* 1995) and (2) the adult beetle assemblage composition would differ among seasons because different species have developed various life-history strategies to deal with seasonality (Tauber and Tauber 1976; Wolda 1988). The results will provide important baseline data related to seasonal variations in the biodiversity of litter-dwelling beetles.

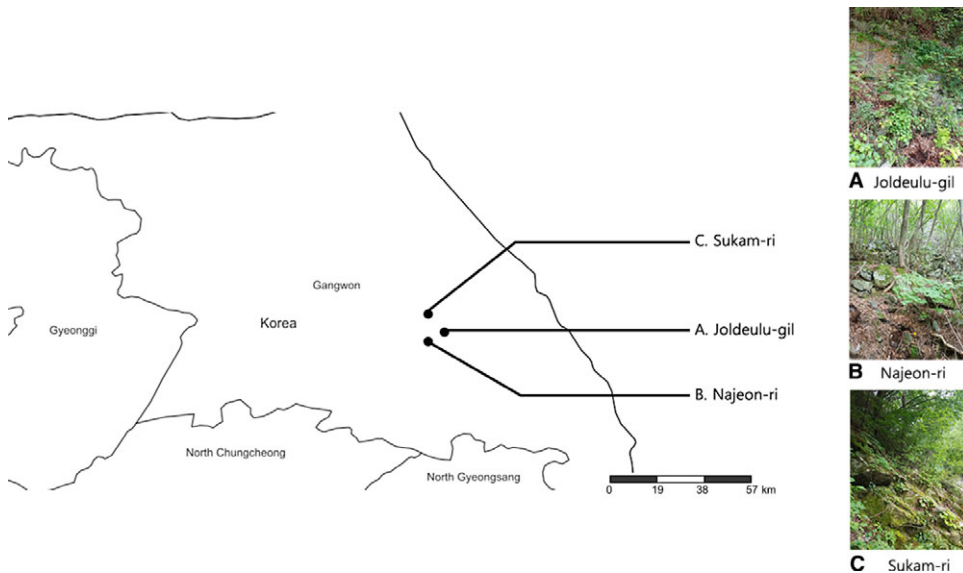


Fig. 1. Study sites in Bukpyeong-myeon, Jeongseon-gun, Gangwon-do, South Korea: **A**, Joldeulu-gil (37° 26' 53.8" N, 128° 38' 20.9" E, 384 m elevation); **B**, Najeon-ri (37° 26' 02.0" N, 128° 36' 57.0" E, 782 m elevation); and **C**, Sukam-ri (37° 29' 43.0" N, 128° 35' 00.0" E, 450 m elevation).

Materials and methods

Study sites

This study was conducted in Bukpyeong-myeon, Jeongseon-gun, Gangwon-do, South Korea, which is located in the southeastern part of Gangwon-do and the centre of the Mt. Taebaek Range. The average annual temperature in Jeongseon-gun is about 11 °C. August is the hottest month, with an average temperature of about 30 °C, and January is the coldest month, with an average temperature of −9.6 °C. Annual rainfall averages about 1100 mm, most of which falls in the summer (Korea Meteorological Administration 2020).

We selected three sites (site 1: Joldeulu-gil (Jol), 384 m elevation, 37° 26' 53.8" N, 128° 38' 20.9" E; site 2: Najeon-ri (Na), 782 m elevation, 37° 26' 02.0" N, 128° 36' 57.0" E; and site 3: Sukam-ri (Suk), 450 m elevation, 37° 29' 43.0" N, 128° 35' 00.0" E; Fig. 1). All sample areas were mixed-wood forests containing five dominant tree species: *Quercus mongolica* Fischer ex. Ledebour (Fagaceae), *Q. serrata* Murray (Fagaceae), *Pinus densiflora* Siebold & Zuccarini (Pinaceae), *P. koraiensis* Siebold & Zuccarini (Pinaceae), and *Betula platyphylla* Sukaczew (Betulaceae) (Heo and Lee 2015). At each site, we sampled soil and deciduous leaf litter near stream margins. The largest distance between sites was 6 km (between Jol and Suk), and the two closest sites were 2 km apart (Jol and Na).

Sampling methods

We sampled leaf litter once each season, March (spring), August (summer), October (autumn), and December (winter) 2019. Each seasonal collection was carried out for 1~2 days. A total of 31 samples were collected: seven samples each in spring, summer, and fall, and 10 samples in winter. To sample the frozen ground in winter, we first sifted the upper leaf litter and then tried to dig up the upper part of frozen soil that enabled the soil sample to be sifted. Although we collected more litter samples in winter than in the other seasons, the total volume of the samples was similar for each season and each location.

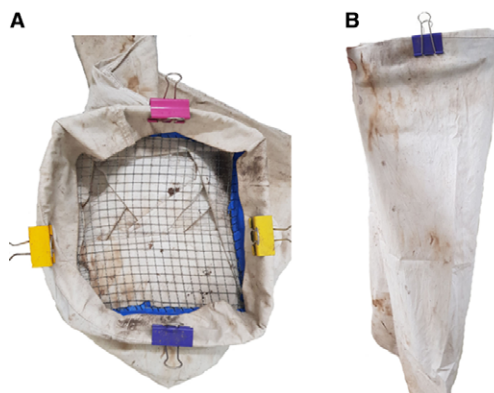


Fig. 2. Sifter and fabric bag: **A**, top view of the 25 × 25-cm-square, 1 × 1-cm-mesh sieve and **B**, side view.

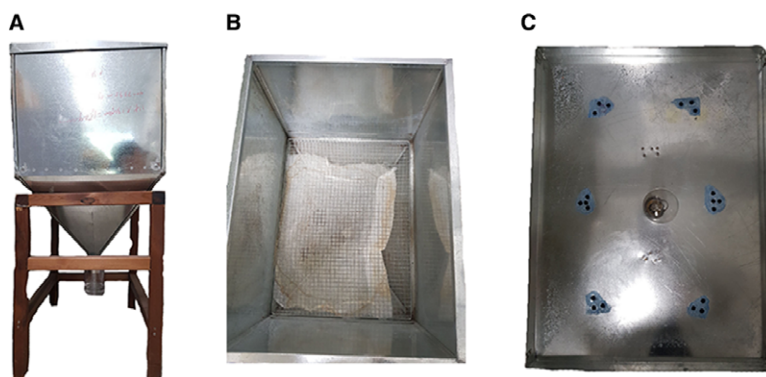


Fig. 3. Berlese funnel: **A**, external shape of the Berlese funnel attached to the wooden support frame; **B**, inside of the 42-cm-wide, 57-cm-long and 36-cm-high funnel; and **C**, the funnel's inner lid connected to a 100-Watt light bulb.

To standardise sifting, 3–4 L of mixed litter samples from *Pinus* and *Quercus* species were collected during each sampling using a sifter, which consisted of a 25 × 25-cm-square, 7-cm-deep, 1 × 1-cm-mesh sieve that fed into a fabric bag (Fig. 2). Small fragments of leaves and soil that included arthropods dropped into the fabric bag when leaf litter was shaken in the sifter. The sieved samples were brought to the laboratory in the fabric bags and placed in Berlese funnels to collect arthropods.

Berlese funnels take advantage of soil arthropods' behaviour to avoid light and dry environments, which, in the case of the funnel method, causes both overwintering and nonoverwintering arthropods to move earthwards out of litter samples and into a collection chamber below. The Berlese funnels used in the present study were constructed of tin, which does not rust, and measured 42 cm wide, 57 cm long, and 36 cm high. A piece of 30 × 40-cm rectangular 0.1 × 0.1-mm-mesh gauze was attached to a 1 × 1-cm metal sieve and placed inside the funnel. The funnel's top lid contained a 100-Watt incandescent bulb to emit light and heat. We operated the Berlese funnel for about a week for each litter sample. Arthropods dropped to the bottom of the funnel and were placed in a collecting jar with 70% ethanol (Fig. 3).

Whenever possible, adult beetles were identified to species level. However, due to the lack of taxonomic information on litter-dwelling beetles in Korea, some species were identified only to the genus level or multiple species were combined as a single species group and treated as one species for analysis (*e.g.*, Aleocharinae spp.). Adult beetles were identified using the keys in

taxonomic literature (e.g., Hayashi *et al.* 1984; Kurosawa *et al.* 1985; Ueno *et al.* 1985; Kurbatov 1991; Cho and Ahn 1999, 2001; Arnett and Thomas 2000; Kim and Ahn 2000a, 2000b; Park *et al.* 2012; Lee and Ahn 2015, 2019; Ahn *et al.* 2017; Kim *et al.* 2017; Jeong and Ahn 2018; Choi *et al.* 2020; Hoshina and Park 2020). We used a Garmin GPSmap 60CSx (Garmin Ltd., Schaffhausen, Switzerland) to measure geographic position and altitude, a Tenmars TM-183 meter to measure temperature and humidity (Tenmars Electronics Co., Taipei, Taiwan), and a Bosch Professional GIS 500 thermo detector (Bosch, Gerlingen, Germany) to measure soil temperature at each sampling site. Most specimens used for the study were deposited in the Chungbuk National University Insect Collection (Cheongju, South Korea).

Statistical analyses

We used permutational multivariate analysis of variance to test differences in species composition among season \times location combinations (Anderson *et al.* 2008). Bray–Curtis distances were calculated on square root transformed data, with 9999 permutations for the main test. We partitioned variation using the default type III sum of squares (Anderson *et al.* 2008). When the main tests were significant ($P < 0.05$), we performed 999 permutations for an *a posteriori* pairwise comparison. We used the PERMANOVA+ add-on package for Primer, version 7, for these analyses (Anderson *et al.* 2008; Clarke and Gorley 2015).

We used redundancy analysis (1) to visually understand the structures of adult beetle assemblage among season \times location combinations and (2) to determine the significant environmental variables underlying the variations in adult beetle assemblages among the above combinations. This method represents constrained ordination; thus, environmental variables directly influence the ordination process (Legendre and Legendre 2012). The environmental variables measured for this study were altitude, atmospheric temperature, humidity, and soil surface temperature. We included these variables in the initial model including the main factors (*i.e.*, season and location) and then selected the best-fit model to perform redundancy analysis with this final model. We used a Hellinger transformation on the species data to minimise the weight of rare species (Legendre and Gallagher 2001).

We used rarefaction and extrapolation to standardise uneven sampling efforts and to estimate species richness among seasons and locations. Rarefaction and extrapolation better characterise species richness than conventional individual-based rarefaction because it compares assemblages at a minimum coverage level in contrast with a minimum number of individuals (Chao *et al.* 2014a, 2014b). By doubling the reference sample size, extrapolation better predicts the presence of rare species (Budka *et al.* 2019). We visualised estimated species richness using the “ggiNEXT” function in R (Hsieh *et al.* 2016).

We used a generalised linear model, with residuals following a negative binomial distribution to analyse differences in abundance of adult beetles under different seasons and locations. We used Tukey’s honestly significant difference test for multiple comparisons of species richness and abundance when results from the generalised linear modelling were significant.

We used indicator species analysis to identify species associated with specific seasons and locations (Dufrêne and Legendre 1997). Indicator species analysis is an analytical method used to evaluate the statistical significance of relationships between species occurrence or abundance and any defined group (De Cáceres *et al.* 2010). We generated the “IndVal” function using 4999 permutations and calculated P -values for each species to ensure the results were different from random ($\alpha = 0.05$).

All analyses, except for permutational multivariate analysis of variance, were conducted using R, version 3.6.3 (R Core Team 2020), using the “Vegan” (Oksanen *et al.* 2019), “MASS” (Venables and Ripley 2002), “multcomp” (Hothorn *et al.* 2008), “iNEXT” (Hsieh *et al.* 2016), and “indicspecies” packages (De Cáceres and Legendre 2009).

Results

General results

A total of 5820 arthropods, representing six classes, were collected over four seasons (Supplementary material, Table S1). These arthropods included 4125 insects representing 11 orders (Supplementary material, Table S2). Among these insects, 1422 adult beetles representing 24 families and a minimum of 141 species were collected, with 73 singletons and 18 doubletons (Table 1, Supplementary material, Table S3). The minute hooded beetle, *Lewisium japonicum* (Corylophidae), was the dominant species collected among the beetles, with 376 individuals, and accounted for 26% of the total beetle catch. Two aleocharine rove beetles (Staphylinidae), *Atheta koreana* and *A. pasniki*, were the second- and the third-most common species, with 80 and 70 individuals, respectively (Table 1).

Beetle assemblage composition

Results of the permutational multivariate analysis of variance showed that adult beetle-assemblage composition differed significantly in terms of season (pseudo- $F = 2.35$, $P = 0.001$) and location (pseudo- $F = 1.50$, $P = 0.018$), but the results showed no interaction between season and location (pseudo- $F = 0.94$, $P = 0.676$; Table 2). Pairwise comparisons showed that beetle assemblage composition differed among seasons, except between spring and winter. In terms of location, assemblage composition was similar between Na and Suk, whereas the assemblage composition in Jol differed significantly from that of Na and Suk (Table 2).

According to the results of the redundancy analysis, the final model revealed significant differences across seasons ($F = 2.09$, $P = 0.005$) and locations ($F = 1.35$, $P = 0.035$). Overall assemblage structure was significantly correlated with soil surface temperature ($F = 2.74$, $P = 0.005$) and atmospheric temperature ($F = 2.16$, $P = 0.005$) along axis 1 (Table 3; Fig. 4). The model explained 31.6% of the total variance, with axes 1 and 2 accounting for 10.4% and 5.7% of the variance, respectively (Fig. 4). The permutational multivariate analysis of variance results were strongly supported by the redundancy analysis ordination, indicating that the assemblage composition differed among seasons except for a slight overlap during spring and winter. Also, the ellipse for summer assemblages was the largest, and the ellipse for winter assemblages was the smallest, suggesting that assemblages in summer and winter were the most heterogeneous and homogeneous, respectively (Fig. 4a). Two temperature variables seemed to drive seasonal differences of beetle assemblage structure along axis 1 (Fig. 4a). In terms of location, the redundancy analysis ordination showed that the assemblage composition was similar between Na and Suk (Fig. 4b). Furthermore, the ellipse for Jol assemblages was smallest, suggesting that the assemblages in Jol were more homogeneous than those in Na and Suk. Although it was not significant, altitude and humidity tended to drive regional variations of beetle assemblages along axis 2 (Fig. 4b).

Species richness and number of individuals

Estimated species richness of adult beetles was highest in spring and lowest in summer at 67.8% and 96.3% sample coverages, respectively, based on extrapolated curves (Fig. 5a). Estimated species richness was similar between fall and winter, both at 93.4% sample coverages, showing higher species richness than that in summer. However, species richness in fall and winter did not differ significantly from that in spring (Fig. 5a). Estimated species richness did not differ among locations, at 90.8%, 95.0%, and 92.8% sample coverages for Jol, Na, and Suk, respectively (Fig. 5b). However, Suk tended to be highest in species richness, whereas Jol tended to be lowest (Fig. 5b).

Table 1. List of adult beetles with the number of individuals collected in four seasons in Jeongseon-gun, Gangwon-do, Korea, using a sifting method followed by Berlese funnel extraction.

Scientific name	Feeding guild	Month				Total individuals
		Mar	Aug	Oct	Dec	
Anthicidae						
1 <i>Macratia</i> sp.1	Unknown				1	1
Carabidae						
2 <i>Bembidion scopulinum</i> Kirby	Predator	1				1
3 <i>Bembidion</i> sp.1	Predator		2			2
4 <i>Bradycellus</i> sp.1	Omnivore			1		1
5 <i>Colpodes</i> sp.1	Predator		1			1
6 <i>Nebria</i> sp.1	Predator		2			2
7 <i>Perigona nigriceps</i> Dejean	Unknown		5	2		7
8 <i>Pterostichus</i> sp.1	Unknown		2			2
9 <i>Trechus</i> sp.1	Unknown		1			1
10 <i>Trichotichnus congruus</i> (Motschulsky)	Omnivore	1				1
11 <i>Trichotichnus gerni</i> Noonan	Omnivore			2		2
12 <i>Trichotichnus</i> sp.1	Omnivore			1		1
Chrysomelidae						
13 <i>Agelasa nigriceps</i> Motschulsky	Herbivore			1	6	7
14 <i>Altica</i> sp.1	Herbivore				1	1
15 <i>Cassida fuscorufa</i> Motschulsky	Herbivore				1	1
16 <i>Cassida pallidicollis</i> Boheman	Herbivore				1	1
17 <i>Chrysochus chinensis</i> Baly	Herbivore				1	1
Ciidae						
18 <i>Cis</i> sp.1	Fungivore	1				1
Coccinellidae						
19 <i>Pseudoscymnus hareja</i> Weise	Predator	1				1
Corylophidae						
20 <i>Lewisium japonicum</i> Matthews	Fungivore	36	119	88	133	376
Cryptophagidae						
21 <i>Atomaria lewisi</i> Reitter	Fungivore		1		8	9
22 <i>Atomaria</i> sp.1	Fungivore			2		2
23 <i>Caenoscelis sibirica</i> Reitter	Fungivore				2	2
24 <i>Cryptophagus</i> sp.1	Fungivore	1	1	1		3
25 <i>Cryptophagus</i> sp.2	Fungivore	1	1	1		3
26 <i>Micrambe</i> sp.1	Herbivore	2				2
Curculionidae						
27 <i>Acallinus tuberculatus</i> Morimoto	Herbivore				1	1

(Continued)

Table 1. (Continued)

Scientific name	Feeding guild	Month				Total individuals
		Mar	Aug	Oct	Dec	
28 <i>Acicnemis luteomaculata</i> (Morimoto)	Herbivore				1	1
29 <i>Catabonops monachus</i> Roelofs	Herbivore	1				1
30 <i>Catabonops</i> sp.1	Herbivore				1	1
31 <i>Ceutorhynchus sinicus</i> (Voss)	Herbivore	1				1
32 <i>Cyrtepistomus castaneus</i> (Roelofs)	Herbivore				1	1
33 <i>Dryocoetes pini</i> Niisima	Herbivore		1			1
34 <i>Larinus</i> sp.1	Herbivore	1				1
35 <i>Lepidepistomodes fumosus</i> (Faust)	Herbivore				1	1
36 <i>Myosides chejuensis</i> Morimoto and Lee	Herbivore				5	5
37 <i>Nothomylocerus griseus</i> (Roelofs)	Herbivore		2			2
38 <i>Nothomylocerus illitus</i> (Reitter)	Herbivore				1	1
39 <i>Polygraphus</i> sp.1	Herbivore				1	1
40 <i>Ptochidius</i> sp.1	Herbivore		1			1
41 <i>Ptochidius tessellatus</i> Motschulsky	Herbivore	1			2	3
42 <i>Scepticus</i> sp.1	Herbivore	1				1
43 <i>Trachodes subfasciatus</i> Voss	Herbivore	1				1
Discolomatidae						
44 <i>Aphanocephalus hemisphericus</i> Wollaston	Fungivore			1	1	2
Elateridae						
45 <i>Ampedus</i> sp.1	Unknown			1		1
Endomychidae						
46 <i>Ancylopus pictus asiaticus</i> Strohecker	Fungivore		1			1
47 <i>Mycetina stackelbergi</i> Kryzhanowskij	Fungivore			1		1
Hydraenidae						
48 <i>Hydraena riparia</i> Kugelann	Omnivore			1		1
Hydrophilidae						
49 <i>Cercyon</i> sp.1	Saprophage		3	12		15
50 <i>Cercyon</i> sp.2	Saprophage		1			1
51 <i>Cercyon</i> sp.3	Saprophage		2			2
Latridiidae						
52 <i>Corticaria ornata</i> Reitter	Fungivore			1	2	3
53 <i>Corticarina lutea</i> Rücker	Fungivore			3		3
54 <i>Dienerella costulata</i> (Reitter)	Fungivore			1		1
55 <i>Stephostethus chinensis</i> (Reitter)	Fungivore	2		2		4
Leiodidae						
56 <i>Agathidium badium</i> Erichson	Fungivore				1	1

(Continued)

Table 1. (Continued)

Scientific name	Feeding guild	Month				Total individuals
		Mar	Aug	Oct	Dec	
57 <i>Agathidium merkli</i> Angelini	Fungivore				1	1
58 <i>Agathidium</i> sp.1	Fungivore			1		1
59 <i>Agathidium</i> sp.2	Fungivore			4		4
60 Leiodidae sp.1	Fungivore				8	8
61 Leiodidae sp.2	Fungivore				1	1
62 <i>Pseudocolenis hilleri</i> Reitter	Fungivore				3	3
63 <i>Typhlocolenis</i> sp.1	Fungivore			1		1
64 <i>Typhlocolenis</i> sp.2	Fungivore			2	2	4
Lucanidae						
65 <i>Platycerus hongwonpyoi</i> Imura & Choe	Herbivore				1	1
Melandryidae						
66 <i>Lederina</i> sp.1	Xylophage	1				1
67 <i>Lederina koreana</i> Choi, Park, Kim and Park	Xylophage			3		3
Nitidulidae						
68 <i>Eपुरaea oblonga</i> (Herbst)	Omnivore				1	1
69 <i>Eपुरaea hisamatsui</i> Nakane	Omnivore		1		1	2
70 <i>Meligethes flavicollis</i> Reitter	Unknown			2	2	4
71 <i>Pallodes</i> sp.1	Unknown			1		1
72 <i>Prometopia unidentata</i> Hisamatsu	Unknown				1	1
Ptiliidae						
73 <i>Acrotrichis lewisi</i> (Matthews)	Fungivore				5	5
74 <i>Acrotrichis</i> sp.1	Fungivore		4	1	15	20
75 <i>Baeocrara</i> sp.1	Fungivore			1	64	65
76 <i>Ptinella alisonae</i> Darby	Saprophage				7	7
77 <i>Ptinella</i> sp.1	Saprophage		16	52		68
Rhynchitidae						
78 <i>Aspidobyctiscus lacunipennis</i> (Jekel)	Herbivore				1	1
Silvanidae						
79 <i>Silvanoprus angusticollis</i> (Reitter)	Fungivore				1	1
80 <i>Psammoecus triguttatus</i> Reitter	Unknown				1	1
Sphindidae						
81 <i>Aspidiphorus japonicus</i> Reitter	Fungivore		1	1	1	3
82 <i>Aspidiphorus sakaii</i> Sasaji	Fungivore			2		2
Staphylinidae						
Aleocharinae						
83 <i>Aleochara</i> sp.1	Predator				5	5

(Continued)

Table 1. (Continued)

Scientific name	Feeding guild	Month				Total individuals
		Mar	Aug	Oct	Dec	
84 <i>Aleochara</i> sp.2	Predator				30	30
85 <i>Aleochara</i> sp.3	Predator				1	1
86 <i>Atheta koreana</i> Bernhauer	Predator				80	80
87 <i>Atheta pasniki</i> Lee & Ahn	Predator				70	70
88 <i>Atheta spinula</i> (Sawada)	Predator				1	1
89 <i>Atheta</i> sp.1	Predator	1		5	11	17
90 <i>Atheta</i> sp.2	Predator				1	1
91 <i>Atheta</i> sp.3	Predator				31	31
92 <i>Homalota sauteri</i> Bernhauer	Predator				1	1
93 <i>Leptusa</i> sp.1	Predator			1		1
94 <i>Paracyusa</i> sp.1	Predator	1				1
95 Aleocharinae spp.	Predator	2	53	123	1	179
Omaliinae						
96 <i>Geodromicus</i> sp.1	Unknown				1	1
97 <i>Lesteva</i> sp.1	Unknown	1				1
98 <i>Omalium</i> sp.1	Unknown			1		1
99 <i>Psephidonus</i> sp.1	Unknown			3		3
Osoriinae						
100 <i>Osorius taurus</i> Sharp	Saprophage			11		11
101 <i>Osorius</i> sp.1	Saprophage		9			9
Oxytelinae						
102 <i>Oxytelus</i> sp.1	Predator	1		2		3
103 Oxytelinae spp.	Unknown		37			37
Paederinae						
104 <i>Achenomorphus</i> sp.1	Predator			2		2
105 <i>Astenus</i> sp.1	Predator			1		1
106 <i>Leptacinus</i> sp.1	Predator			2		2
107 <i>Medon spadiceus</i> Sharp	Predator	1				1
108 <i>Nazeris rutilicarpus</i> Cho	Predator	1				1
109 Paederinae spp.	Predator		43			43
Piestinae						
110 <i>Siagonium</i> sp.1	Fungivore			1		1
Proteininae						
111 <i>Megarthus corticalis</i> Sharp	Fungivore				2	2
112 <i>Megarthus japonicus</i> Sharp	Fungivore				2	2
113 <i>Megarthus sawadai</i> Cuccodoro	Fungivore				7	7

(Continued)

Table 1. (Continued)

Scientific name	Feeding guild	Month				Total individuals
		Mar	Aug	Oct	Dec	
114 <i>Megarthus</i> sp.1	Fungivore	1		3		4
115 <i>Megarthus</i> sp.2	Fungivore			1		1
Pselaphinae						
116 <i>Batrisodes baejeongdoki</i> Nomura & Lee	Predator		5	1		6
117 <i>Bryaxis leechanyoungi</i> Nomura & Lee	Predator		16	11	2	29
118 <i>Bryaxis kimjongkuki</i> Nomura & Lee	Predator			2		2
119 <i>Euplectus domefactus</i> (Kurbatov)	Predator			1		1
120 <i>Pselaphogenius cornurus</i> (Nomura & Lee)	Predator				1	1
121 <i>Pselaphus striatus</i> Löbl	Predator			1		1
Scaphidiinae						
122 <i>Baeocera</i> sp.1	Fungivore				1	1
Scydmaeninae						
123 <i>Euconnus</i> sp.1	Predator			1	1	2
Staphylininae						
124 <i>Gabrius</i> sp.1	Predator	1				1
125 <i>Philonthus</i> sp.1	Predator			5	2	7
126 <i>Philonthus</i> sp.2	Predator				7	7
127 Staphylininae spp.	Predator		6			6
Steninae						
128 <i>Stenus</i> sp.1	Predator		2	8	1	11
129 <i>Stenus</i> sp.2	Predator		6			6
Tachyporinae						
130 <i>Sepedophilus germanus</i> Sharp	Fungivore	4	24			28
131 <i>Sepedophilus testaceus</i> (Fabricius)	Fungivore				6	6
132 <i>Sepedophilus</i> sp.1	Fungivore			30	6	36
133 <i>Derops coreanus</i> (Watanabe)	Unknown		10			10
134 <i>Ischnosoma</i> sp.1	Predator				1	1
135 <i>Nitidotachinus</i> sp.1	Predator			1		1
136 <i>Tachinus</i> sp.1	Predator				1	1
137 Tachyporinae sp.1	Unknown		1			1
Tenebrionidae						
138 <i>Tetraphyllus</i> sp.1	Saprophage	1				1
139 <i>Uloma bonzica</i> Marseul	Saprophage		1			1
140 <i>Misolampidius tentyrioides</i> Solsky	Saprophage		1			1
141 <i>Stenophanes mesostena</i> (Solsky)	Saprophage		1			1
Total 24 families, 100 genera, and minimum 141 species		68	383	410	561	1422

Table 2. Results of permutational multivariate analysis of variance testing for adult beetle species richness by season and location.

	<i>df</i>	SS	MS	Pseudo- <i>F</i>	<i>P</i> (PERM)	Pairwise comparisons
Season	3	19 785.0	6594.8	2.35	0.001	(Spring = Winter) ≠ Summer ≠ Fall
Location	2	8426.4	4213.2	1.50	0.018	Jol ≠ (Na = Suk)
Se × Lo	6	15 819	2636.4	0.94	0.676	Season and location, no interaction

Significant differences ($P < 0.05$) are highlighted in bold.

Abbreviations: *df*, degrees of freedom; Lo, location; MS, mean squares; PERM, permutational multivariate analysis of variance; Se, season; SS, sum of squares.

Table 3. Results of redundancy analysis testing for adult beetle assemblages by factors.

	<i>Df</i>	AIC	<i>F</i>	Pr (> <i>F</i>)
S.Temp	1	-13.998	2.7446	0.005
Season	3	-13.678	2.0937	0.005
Temp	1	-13.428	2.1663	0.005
Hum	1	-12.410	1.1599	0.190
Location	2	-12.055	1.3536	0.035
Alt	1	-11.995	0.7584	0.860

Significant differences ($P < 0.05$) are noted in bold.

Abbreviations: *df*, degrees of freedom; AIC, Akaike information criteria; S.Temp, soil surface temperature; Temp, atmospheric temperature; Hum, humidity; Alt, altitude.

Adult beetle abundance differed significantly among seasons (deviance = 50.7, $P < 0.001$), with the lowest abundance occurring in spring (Fig. 6a). However, beetle abundance did not differ significantly among locations (deviance = 37.8, $P = 0.108$; Fig. 6b).

Indicator species analysis

Nine and three species were identified as significant indicators of season and location, respectively. All indicators of season were members of Staphylinidae, except for the featherwing beetle, *Ptinella* sp.1 (Ptiliidae). In terms of season, Aleocharinae spp. showed the highest indicator value in fall (IndVal = 0.830), followed by *Sepedophilus germanus* (Sharp) in summer (IndVal = 0.782). *Philonthus* sp.1 was the only indicator in winter (IndVal = 0.579). No indicator species were found in spring (Table 4). Based on location, *Perigona nigriceps* Dejean showed the highest indicator value in Jol (IndVal = 0.612), followed by *Cryptophagus* sp.1 and *Meligethes flavicollis* Reitter, showing the same indicator value in Na (IndVal = 0.577; Table 4).

Discussion

Seasonal variations of adult beetle assemblage structure

The present study clearly showed that adult beetle assemblages differed among seasons, except between spring and winter, which partly overlapped. This similarity in assemblage structure between spring and winter is interesting. It is plausible that a large number of adult species overwintering under leaf litter emerged and were collected in spring, thereby displaying a similar assemblage structure between spring and winter (Burgess 1981; Bale and Hayward 2010). In addition, the dissimilarity of beetle assemblages between spring, summer,

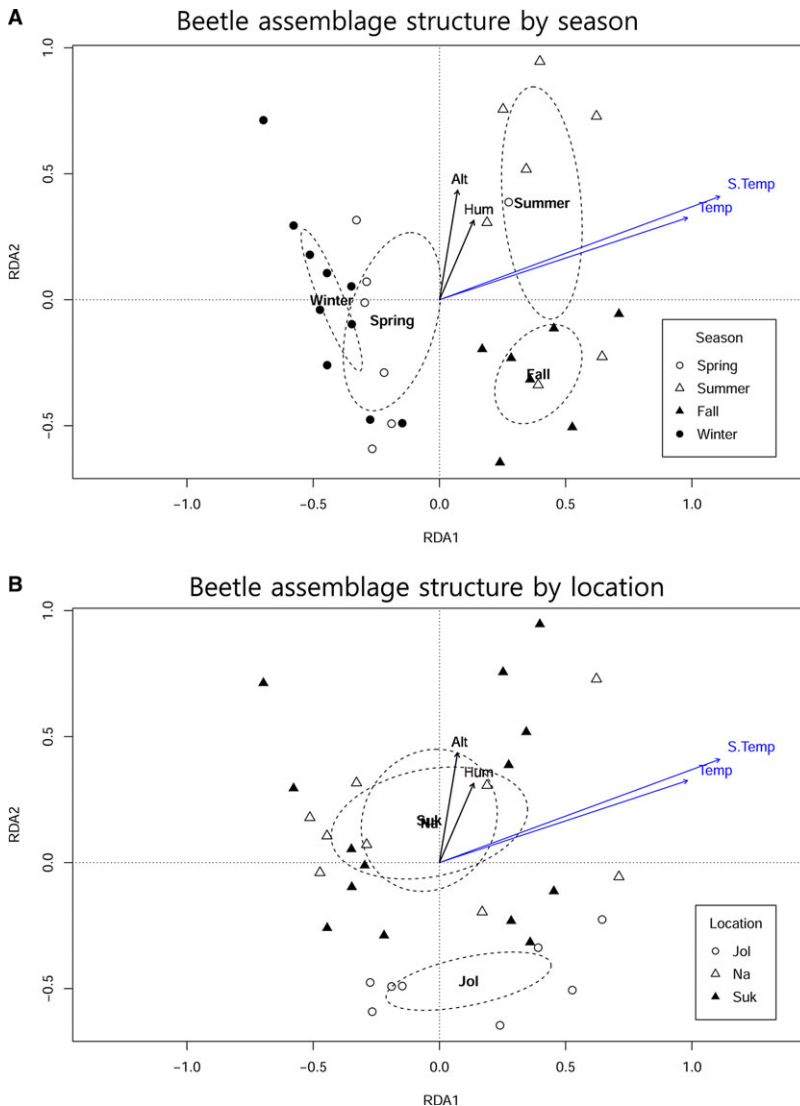


Fig. 4. Redundancy analysis (RDA) ordination of adult beetle assemblages by **A**, season and **B**, location. The model explained 31.6% of the total variance, and axis 1 and axis 2 explained 10.3% and 5.5% of the total variance, respectively. Arrows indicate environmental variables, with significant factors coloured blue. Abbreviations: Alt, altitude; Hum, humidity; S.Temp, soil surface temperature; Temp, atmospheric temperature.

and fall emphasises that each species has a different developmental plan, thereby emerging as adults in a different season. The distinct assemblage structure among seasons suggests the importance of sampling in different seasons to understand the total diversity of litter-dwelling beetles. A transition from dry to rainy seasons in summer may have produced different adult beetle assemblage structures due to environmental changes (Anu *et al.* 2009). Our study also revealed that the summer beetle assemblage was the most heterogeneous. Because of the high temperature in summer, activity and dispersibility of insects increase (Mellanby 1939; Taylor 1963), leading to structurally diverse summer communities. Winter assemblages were the most homogeneous, possibly due to low insect dispersibility and immobility or diapause (Bertram 1935; Mellanby 1939; Bale and Hayward 2010).

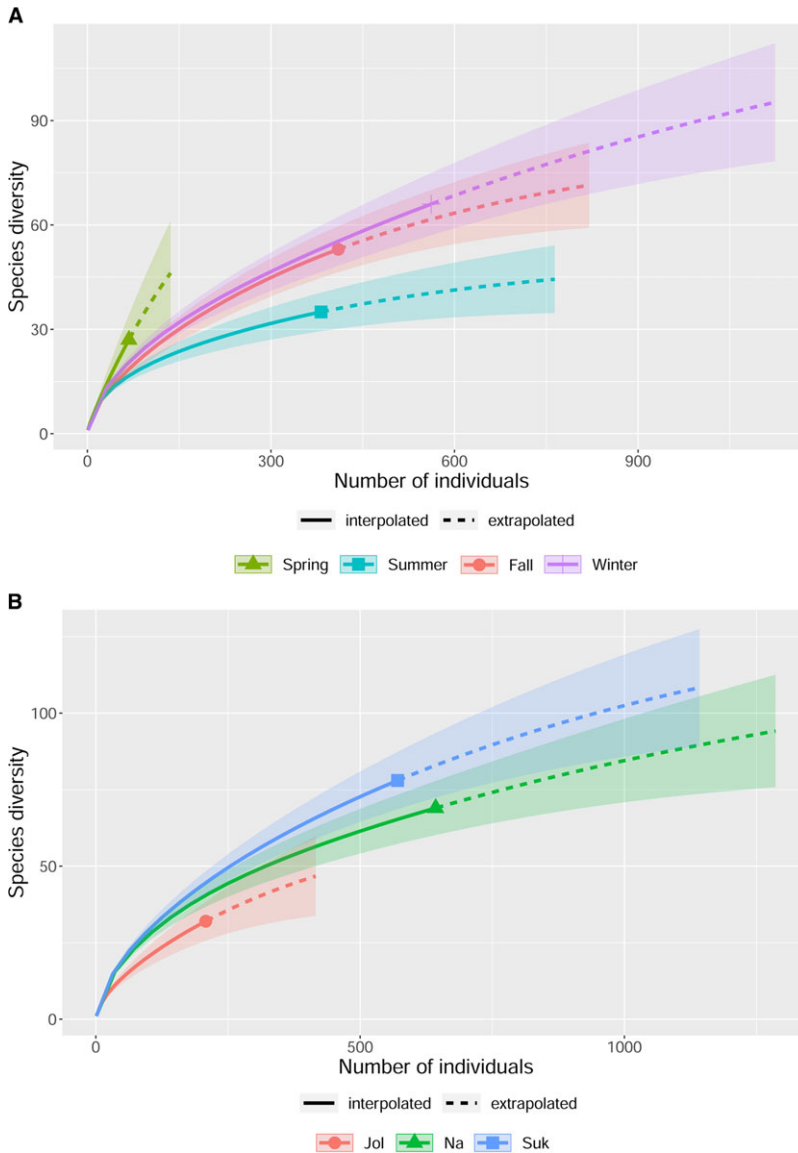


Fig. 5. Estimated species richness for **A**, season and **B**, location. Solid lines indicate interpolation, and dotted lines indicate extrapolation. Shaded areas indicate 95% confidence intervals.

Seasonal changes in species richness and abundance

Previous studies have shown the highest species richness and abundance of adult beetles occurred in either summer or fall in Korea (Byun *et al.* 2009a, 2009b, 2010; Park *et al.* 2011; Lim *et al.* 2011, 2012). Contrary to our prediction, the results of the present study showed that species richness was lowest in summer and that richness in winter was as high as that in spring and fall. In addition, abundance in winter was similar to values found for summer and fall, suggesting that winter sampling using a sifting method was highly effective for sampling adult beetles. Some species found in litter samples in winter may not be directly related to the soil and leaf-litter environment, as they use this habitat only for overwintering. The lowest abundance of adult beetles in spring may be attributed to dried leaf litter and soils that may

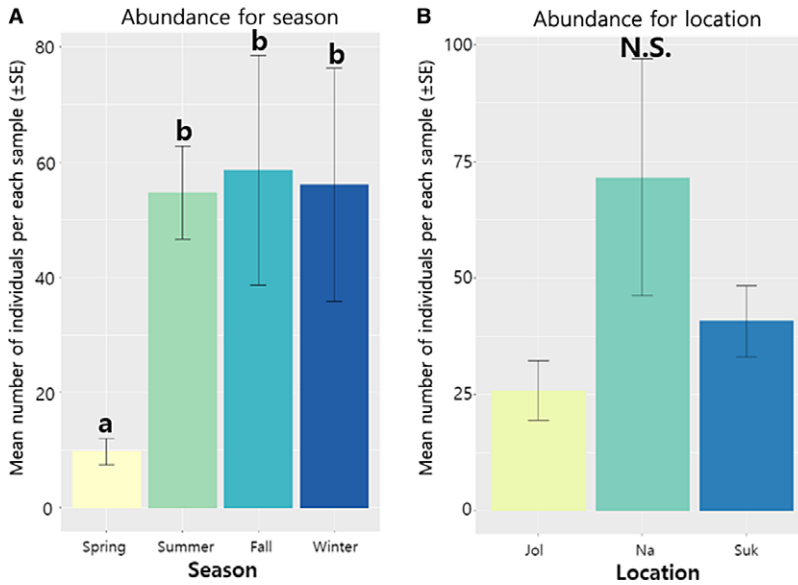


Fig. 6. Adult beetle abundance for **A**, season and **B**, location. Error bars represent the standard errors (SE) for each location. Different lowercase letters above error bars show significant post hoc results. N.S., nonsignificant *post hoc* result (Tukey's honestly significant difference test, $P < 0.05$).

Table 4. Significant indicator species of adult beetles for season and location.

Group	Family	Species	Feeding guild	IndVal*	<i>P</i>
Season					
Summer	Staphylinidae	<i>Sepedophilus germanus</i>	Fungivore	0.782	0.0020
Summer	Staphylinidae	<i>Oxytelinae</i> spp.	Unknown	0.756	0.0032
Summer	Staphylinidae	<i>Paederinae</i> spp.	Predator	0.756	0.0032
Summer	Staphylinidae	<i>Derops coreanus</i>	Fungivore	0.655	0.0228
Fall	Staphylinidae	<i>Aleocharinae</i> spp.	Predator	0.830	0.0056
Fall	Staphylinidae	<i>Osorius taurus</i>	Saprophage	0.756	0.0040
Fall	Ptiliidae	<i>Ptinella</i> sp.1	Saprophage	0.661	0.0402
Fall	Staphylinidae	<i>Philonthus</i> sp.1	Predator	0.579	0.0362
Winter	Staphylinidae	<i>Aleochara</i> sp.1	Predator	0.632	0.0116
Location					
Jol	Carabidae	<i>Perigona nigriceps</i>	Unknown	0.612	0.0130
Na	Cryptophagidae	<i>Cryptophagus</i> sp.1	Fungivore	0.577	0.0308
Na	Nitidulidae	<i>Meligethes flavicollis</i>	Omnivore	0.577	0.0298

*Indicator value

P-values were calculated after 4999 permutations.

cause beetles to move into more humid habitats, such as under logs or under bark (Janzen and Schoener 1968; Pinheiro *et al.* 2002). Most biodiversity studies in temperate forests use sweeping, light traps, Malaise traps, window, or pitfall traps to sample arthropods (Gadagkar *et al.* 1990; Recher *et al.* 1996; Hébert *et al.* 2000; Kai and Corlett 2002; Work *et al.* 2002; Park and

Cho 2007; Santos *et al.* 2007; Vasconcellos *et al.* 2010; Park *et al.* 2011; Lim *et al.* 2012; Dadmal and Khadakkar 2014; Saji and Al Dhaheri 2014; Kim and Kwon 2016; Wardhaugh *et al.* 2018). Because of this, it was difficult to directly compare the results for arthropod diversity and abundance of the present study with those of other studies due to the different sampling methods used by prior studies to collect biological data in the winter.

Only a few studies have used a combined sifting–Berlese funnel method to investigate insect biodiversity (Carlton and Robison 1998; Ferro *et al.* 2012a, 2012b). For example, Carlton and Robison (1998) observed the highest abundance of litter-dwelling beetles in spring and fall and the lowest abundance in early summer and winter. Ferro *et al.* (2012b) reported that both species richness and abundance of adult beetles were higher in spring than in fall. Differences between the present study and other studies were: (1) the types of material used during sifting, as they also sifted rotten deadwood together with leaf litters and soils; (2) the operation time for the funnel extraction (one week in the present study *versus* two days in the earlier studies); and (3) environmental factors, such as temperature, humidity, and rainfall in each sampling region.

Effects of environmental factors on beetle assemblage

Temperature affects insect abundance and assemblages (Wagner *et al.* 1985; Gilbert and Raworth 1996; Régnière *et al.* 2012). In our study, assemblage structures of adult beetles were affected by both soil surface and atmospheric temperatures, supporting previous findings that litter-dwelling beetles were sensitive to both soil surface temperature (Robinson *et al.* 2018) and atmospheric temperature (Ruggiero *et al.* 2009). Other factors, such as humidity and soil pH, showed no significant effects on variation in the assemblage structure.

Precipitation and humidity also significantly affect insect communities (Robinson and Robinson 1970; Smythe 1973; Wolda 1978a, 1978b; Rees 1983; Frith and Frith 1990; Pinheiro *et al.* 2002). However, in the present study, beetle assemblages were not affected by humidity. Characteristics of litter samples in our study areas were similar to each other, with wet soils and deciduous leaf litters. Soil pH in our study areas also did not affect beetle assemblage structure, supporting the results of Cameron and Leather (2012), who suggested that soil pH was unrelated to insect and carabid abundance. In our study areas, soil pH ranged between 6.7 and 7.0, showing no significant difference among seasons or locations. Additional environmental factors, such as vegetation, soil composition, and presence of deadwood, are better predictors of the structure of litter-dwelling arthropods and their environmental relationships (Ulyshen and Hanula 2009; Ashford *et al.* 2013).

Regional variations in adult beetle diversity and community structure

Both Na and Suk showed similar adult beetle assemblage structure despite these sites being the farthest apart. Beetle assemblages in Na and Suk were similarly heterogeneous, whereas those in Jol showed the maximum homogeneity. The lack of differences in annual average temperatures and soil surface temperatures at Na and Suk may help explain the similar beetle assemblage structures in these areas. Although we did not investigate plant species as an environmental variable, the different species composition of plants at each sampling area may have influenced the beetle assemblage composition (Andow 1991; Koricheva *et al.* 2000; Scherber *et al.* 2006).

The Jol site had lower species richness and abundance of adult beetles compared to the other sites. Since the sample area at Jol was narrower compared to those at Na and Suk, the least richness and abundance at Jol were expected. Conversely, Na tended to show high species richness and abundance of beetles. The average elevation at Na (782 m) was higher than at Jol (384 m) and Suk (450 m), and this difference likely affected the diversity and assemblage structure.

Previous studies have reported changes in diversity and assemblages along an elevational gradient (Lawton *et al.* 1987; Wolda 1987; Olson 1994; Sánchez-Reyes *et al.* 2014).

Advantages of sampling winter assemblages using a sifting method

Sampling litter-dwelling arthropods in winter is challenging because many of them enter diapause to survive the cold. Therefore, few collecting methods, such as sifting and pitfall traps, can be used to sample these overwintering arthropods. The sifting method has a great advantage in collecting higher species richness and individuals of insects than any other trapping method in winter because it enables collection of sedentary and overwintering invertebrates in diapause. In contrast, pitfall traps collect only arthropods that are winter active (Hamilton *et al.* 2018). As shown by our results, a sifting method combined with a Berlese funnel extraction can be used to effectively collect diverse arthropod taxa in winter, during which the biodiversity of beetles in leaf litter is surprisingly high. Furthermore, a sifting–Berlese funnel method allows sampling of very small invertebrates (less than 1 mm) and yields relatively undamaged and rare specimens, thereby providing better opportunities to find new species in this less-explored environment.

Acknowledgements. The authors thank Yeon-Jae Choi, Min-Sang Jang, Jun-Young Kang, Ji-Won Kang, Su-Ho Choi, Tae-Young Jang, and Ji-Wook Kim, who helped collect arthropods in the field, and Dr. Boo-Hee Jung, who helped provide ecological information of Tenebrionidae. They also thank Jeffrey Battigelli and three anonymous reviewers who provided valuable suggestions to improve the manuscript. This study was supported by two grants from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202002112 and NIBR202130202).

Author contributions. U.-J.B. and S.-I.L. contributed equally to this work.

Conflicts of interest. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.4039/tce.2021.54>.

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