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Distribution breadth and species turnover of night-flying beetles and moths on different mainland and island mountains

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Abstract Distribution breadth and species turnover rates of two night-flying insect groups (moths and beetles) were analyzed on two mountains in warm temperate forests of South Korea, Mt. Hallasan (range 278–1109 m) on Jeju island (HL) and Mt. Jirisan (range 319–1330 m) in southern Korea (JR). The goals of the study were to compare the spatial changes in the two insect groups on both mountains and to identify ecological factors influencing the diversity pattern. Insects were collected from 16 sites in two mountains from May to October of 2013 and 2014 using a UV light trap. Moths were generally more diverse on JR than on HL, but similarity among sites was higher on JR than on HL. However, beetles were not different between the two mountains in diversity and similarity of assemblages among sites. The distributional range of both moths and beetles were significantly narrower on HL than JR, while the distributional range curves peaked at mid-elevations, being positively skewed at HL and negatively skewed at JR. Whittaker's species turnover rates of moths and beetles were higher for HL than JR. On both mountains, latitude was a significant variable influencing moth species richness and abundance, while soil fertility and plant species richness were significant variables influencing beetle abundance. Geographic distance and elevation played a significant role in segregating insect assemblages on both mountains, except for moths in JR. The pattern and mechanism of spatial changes in night-flying insect assemblages on both mountains varied depending on insect group and location.

Keywords Distribution range · Turnover rate · Elevation · Coleoptera · Lepidoptera

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Introduction

Understanding spatial variation in diversity along environmental gradients and the underlying mechanisms responsible for these variations are important questions in ecology (Rosenzweig 1995; Kraft et al. 2011). Beta diversity, the pattern of variation in the community composition from place to place, is a critical component of biodiversity that reflects variations in species composition among local assemblages, as well as the relationship between local and regional diversity (Tuomisto 2010; Kraft et al. 2011; Tello et al. 2015). Globally, beta diversity generally increases from temperate to tropical regions (Koleff et al. 2003; Qian and Ricklefs 2007; Soininen et al. 2007; Myers et al. 2013), and from mainland to island populations (Stuart et al. 2012). The higher beta diversity in tropics than temperate regions could be attributed to the narrow breadth of species' distributional range (Buckley and Jetz 2008; McCain 2009; Melo et al. 2009; Jankowski et al. 2013; Stuart et al. 2012). The limited breadth of distributional range could be the result of relative differences in local community assembly processes, such as dispersal limitation, geographical distance, deterministic processes (e.g., environmental or habitat filtering) and stochastic processes that generate ecological drift (Qian and Ricklefs 2012; Stuart et al. 2012; Myers et al. 2013).

Elevational gradients of mountains have been widely adopted as models for understanding spatial variation because of their large and easily quantifiable shifts in abiotic conditions and habitat over small spatial scales (Jankowski et al. 2013). Mountain biota shows high spatial heterogeneity along elevational gradients owing to the structural complexity of forests (Mori et al. 2013), and this structural complexity plays an important role in maintenance of forest biodiversity. Furthermore, mountain biota on islands can contain taxa that have been isolated from their close relatives on other nearby islands (New 2007), resulting in a narrow distributional range and higher beta diversity. Comparison of moun-

tain biota on both island and mainland mountains could reveal differences in the ability of various organisms to colonize the habitat through temporal and environmental changes.

The present study was conducted to determine if spatial variations in moths and beetles were similar on two mountains with different locations, as well as to identify factors influencing the diversity pattern. To answer this question, we sampled night-flying insects from the highest mountainous areas in southern South Korea using UV light traps: Mt. Hallasan (HL) and Mt. Jirisan (JR). Mt. Hallasan is the highest mountain (1950 m, total area 149 km²) in South Korea and located on the nation's largest island Jeju-do (126°09'42"E–126°56'57"E, 33°11'27"N–33°33'50"N), a volcanic island that separated from the mainland of South Korea about 10,000 years ago (HL). About 550 vascular plants and 3000 animals are distributed on Mt. Hallasan (Koh 2006). The flora on Mt. Hallasan is characterized by its high endemism due to the long isolation from the mainland, the varying climate from aspect and elevation, and the complex topography of the mountain (Kong 2007). Mt. Jirisan is the second highest mountain (1915 m, total area 483.0 km², 127°43'50"E, 35°20'16"N) in South Korea and is characterized by a high species richness of flora (about 1450 vascular plants) and fauna (about 3000 animal species) (Jang et al. 2007). The rich biota on Mt. Jirisan has attributed to its geographic location and orientation: the location at the southern tip of the long north-to-south mountain ranges, Taebaek Mountains along the Korean peninsula acts as a corridor, while the east-to-west orientation of mountain acts as a barrier, harboring a variety of species with different distributional origins.

Thein and Choi (2016) sampled night flying insects from these two mountains using UV light traps and found the high species diversity, 10 and 14 insect orders from Mt. Hallasan and Mt. Jirisan, respectively. Among these insects, we selected two groups, moths and beetles since they are species rich and abundant in all survey sites. Coleoptera (beetles), which are strongly attracted to lights during night, represent about 25% of all recorded organisms, comprising 350,000–400,000 species, and the high diversity in numbers is assumed to be closely related to morphological, ecological and behavioral diversities (Hunt et al. 2007; Bouchard et al. 2011). When compared to beetles, the morphological and ecological diversity of moths is uniform, with two pairs of readily flying wings and wing pattern elements on each pair of wing that are mostly phytophagous during the immature stage (Wahlberg et al. 2013; Heikkilä et al. 2015).

Organisms with high dispersal ability have great potential to colonize appropriate habitats (Korhonen et al. 2010). Moths are good fliers that easily colonize islands, including those separated by great distances (Majerus 2002), while beetles have rather limited ability to colonize land or islands after local extinction because of habitat specificity (Roslin 2000). We hypothesized

that the species diversity of both moths and beetles would be higher on the mainland than the island since the immigration and extinction of species on island would be affected by the distance from the mainland through dispersal barriers such as the sea (distance effect) and space (area effect) (MacArthur and Wilson 1967).

In addition, we investigated whether the geographical, climatic and other ecological factors such as soil and plant composition would impact on nocturnal insect assemblages across southern South Korea. Climate-driven environmental variables such as plant productivity, temperature and precipitation are strongly influencing species richness in several elevational and latitudinal gradients (Evans et al. 2005; McCain 2009, 2010; Beck et al. 2017). Positive species richness and energy (or net primary productivity) relationship was well represented in multiple latitudinal gradients (Gaston 2000). While any single variable cannot be the main driver of elevational gradient patterns, the combined effect of temperature and precipitation has proven to play a significant role in explaining diversity patterns along elevation (Beck et al. 2017).

Increase of herbivorous insect diversity from temperate and tropical region appears driven largely by increasing plant diversity (Lewinsohn et al. 2005). In turn, plant diversity is positively related with soil organic matter (carbon and nitrogen storage and availability) and other nutrients such as calcium and potassium (Tilman et al. 2001; Bot and Benites 2005; Naples and Fisk 2010; Baribault et al. 2012). Therefore, we asked which environmental factors would influence the diversity pattern of both moth and beetle groups across two South Korean mountains.

Materials and methods

Study area

We sampled moths and beetles from a total of 16 warm temperate forest sites across two southern mountainous areas during nights (Fig. 1). We included eight sites on Mt. Hallasan (HL) (elevation range 278–1109 m, the longest distance being 15.54 km and the average distance between sites being 10.10 ± 0.92 km) and eight sites on Mt. Jirisan (JR) (elevation range 319–1330 m, the longest distance being 16.75 km and the average distance between sites being 8.50 ± 0.79 km) (Fig. 1).

Insect sampling and environmental data

Insect sampling was conducted monthly from May through October in two years (2013 and 2014). We set up a 22-Watt UV-light trap (BioQuip, USA) powered by a 12-volt battery at dusk for five hours. The UV light trap is a widely adopted method for sampling insects

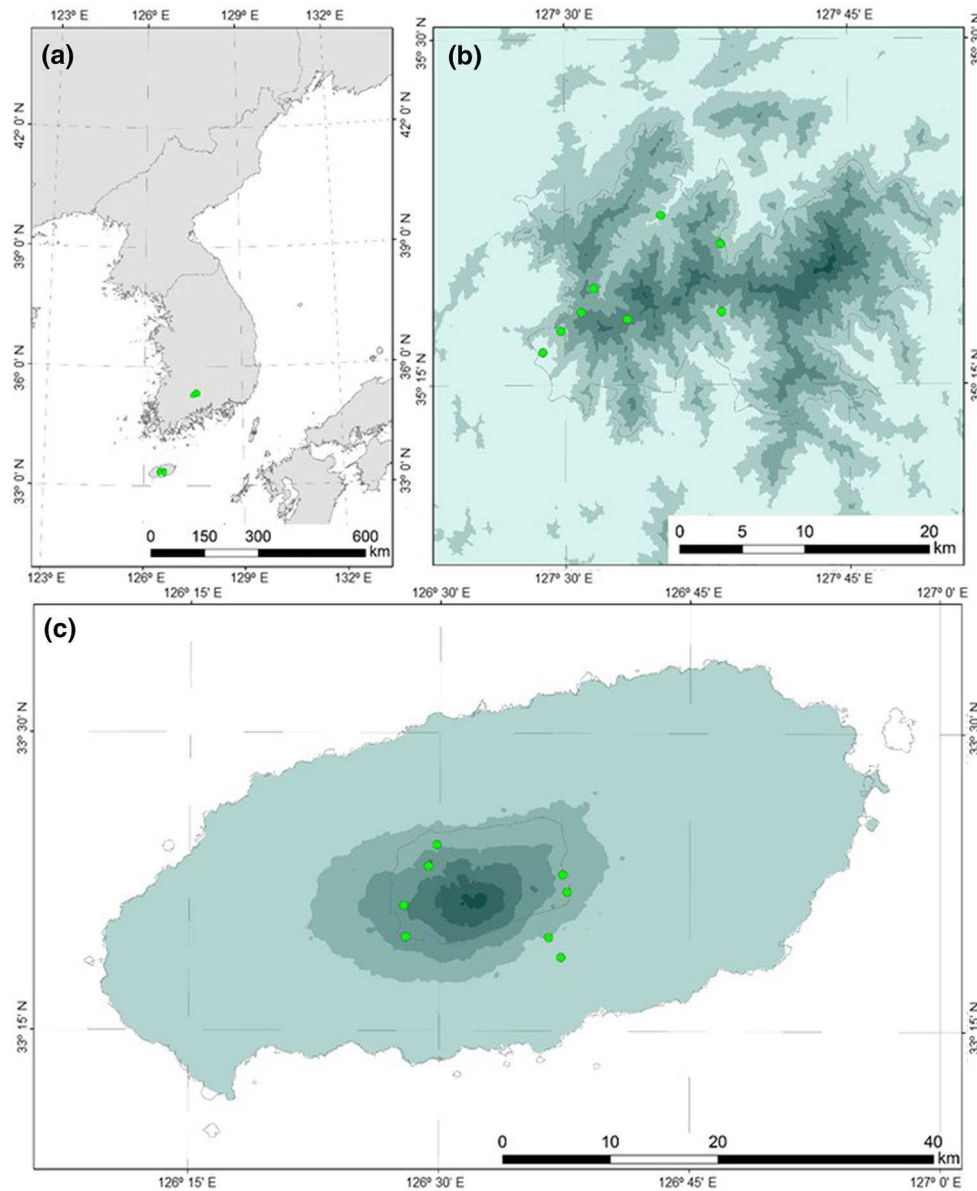


Fig. 1 Study sites **a** in South Korea. **b** Mt. Jirisan, (JR), **c** Mt. Hallasan (HL). Green dots on each mountain indicate the study sites. The original maps from National Geographic Information Institute, Korea were modified by the author (S.W. Choi)

such as moths and beetles since it is relatively unbiased and more efficient at sampling diverse insects attracted to light (Genung 1972; Wolda 1992; Kato et al. 2000; Hirao et al. 2008; Kishimoto-Yamada et al. 2009; Garcia-Lopez et al. 2011). Moths and beetles were killed using dichlorovos insecticide impregnated resin strips. All traps were emptied the following day, and the collected samples were sorted to moths and beetles that were identified to the species level, if possible, while unidentified species were coded as morphospecies. Moth identification and taxonomy referred to Kim et al. (2001), Kononenko et al. (1998), and Shin (2001). For beetle identification and taxonomy, we referred to Bouchard et al. (2011), Kim (2001), and Lawrence et al.

(2000). All voucher specimens have been deposited in the laboratory of Mokpo National University.

Environmental data comprised geography, weather, soil and plants. Geographic data included elevation, latitude and longitude. We collected weather data by installing a data logger (HOBO) to record air temperature ($^{\circ}\text{C}$) and relative humidity (%). We then summarized the annual mean temperature, January mean temperature, July mean temperature, and annual temperature range (highest to lowest mean temperature). If the data logger failed to obtain the data, we calculated the temperature based on $-0.65^{\circ}\text{C}/100\text{ m}$ using data from nearby sites.

We collected three random soil cores from each survey site and analyzed the samples at the soil analysis

laboratory of the Agritechnology Center of Muan County, Jeonnam. Soil sample analyses included pH, organic matter content, three major cations (K^+ , Ca^{2+} , Mg^{2+}), one anion (PO_3^-) and electrical conductivity (EC). Plant data included the abundance, richness, and density of trees and herbs within a 20×20 m square plot at each insect sampling site. Herb species were recorded from four 1×1 m² subplots at each site. Trees > 2 cm diameter at breast height (DBH) were counted. Host-plant data of moth species in Korea were compiled based on the available Korean literatures (e.g. Heo 2012, 2016). Numbers of host-plant families for each moth species at both mountains (HL and JR) were counted.

Data analysis

Data describing individual moths and beetles at each site over two years were pooled in this study. We obtained the observed species richness and abundance of night-flying moths and beetles at each site. The distribution range of each species of moth and beetle was calculated to investigate the breadth of each species on each elevational transect. Species occurring at more than two sites at each elevational transect were included for calculation of the distribution range: 82 (HL) and 92 (JR) beetles and 182 (HL) and 364 (JR) moths, respectively. The distribution range of each species on each mountain was the difference between the site of highest and lowest occurrence on the mountain.

Determining turnover rates at multiple scales can provide insight into species distributions related to ecosystem functions (Legendre et al. 2005; Soininen 2010). We calculated Whittaker's β partition [$\beta_w = (\text{total number of species in all samples } (\gamma) / \text{average number of species } (\bar{\alpha})) - 1$] to evaluate faunal changes in regional assemblages (Whittaker 1972). It is known that Whittaker's β_w measures beta diversity for a given area, but does not test for differences among areas (Anderson et al. 2006). To test differences in beta diversity of moths and beetles among regions, the similarity index was calculated based on the Chao–Sørensen–raw-abundance (CSRA) (Chao et al. 2005). This index is based on the probability that two randomly selected individuals (one from each of two samples) both belong to any of the species shared by the two samples. The index has been shown to better perform when assessing compositional similarities between samples that differ in size, are known or suspected to be under sampled, or are likely to contain numerous rare species (Chao et al. 2005). The CSRA similarity index was calculated for each insect group (moths and beetles) among eight sites of each mountain: moths_{HL} , moths_{JR} , beetles_{HL} , beetles_{JR} . In addition, the CSRA similarity index between eight sites of HL and eight sites of JR was calculated: moths_{HL-JR} and beetles_{HL-JR} . The magnitude of variance of the CSRA index was analyzed using the Chi squared test and the mean value of index between insect groups and locations was compared using the t test. The CSRA

index was calculated using the EstimateS software (Colwell 2016).

We conducted linear (Pearson) correlation analysis of geography, weather and soil variables to check the multicollinearity and excluded the variables longitude, annual temperature range, January, July and annual mean temperature, soil pH, Ca^{2+} , Mg^{2+} , PO_3^- , K^+ , electron conductivity and herb density. Seven variables (location, elevation, latitude, organic matter, tree basal area, tree richness, and herb richness) were used to identify significant determinants of moth and beetle assemblages across two southern South Korean mountains. Stepwise regression analyses were performed for moth and beetle assemblages after log transformation.

We used the nonmetric multidimensional scaling ordination (NMS) method with the Sørensen distance measure. Two multivariate analyses were conducted using 331 moth species and 108 beetle species across 16 sites after deleting rare species occurring at less than three surveyed areas. Deleting rare species is a useful way of reducing the bulk and noise in the data set without losing much information and of detecting of relationships between community composition and environmental factors (McCune and Grace 2002). Seven environmental variables (location, elevation, latitude, organic matter, tree basal area, tree richness, and herb richness) were used as a second matrix to correlate species assemblages and environmental variables. A bi-plot cutoff value of 0.3 was used to identify variables related to either axis. A multi-response permutation procedure (999 runs) (MRPP) based on the Sørensen distance measure was used to test differences among moth and beetle groups.

The Mantel test was applied to evaluate the relationship between each mountain insect assemblage and geographic distance among sites. The Sørensen distance measure for insect assemblages and Euclidian distance measure for sites were used. A total of 181 species (127 moth and 54 beetle) from HL and 320 species (257 moth and 63 beetle) from JR were implemented for the analyses. Additionally, the elevation difference between sites on each mountain and the similarity index based on the CSRA was calculated to check the dispersal ability along elevation on each mountain. Diet breadth of moth species on HL and JR was compared using Mann–Whitney test after calculating the proportion of the number of plant families. The NMS, MRPP and Mantel test were implemented using PC-ORD (version 6.0; McCune and Mefford 2011).

Results

Species composition and changes in lepidopterans and coleopterans on two mountains

We collected a total of 12,233 moths and 3,946 beetles that represented 695 and 261 species, respectively

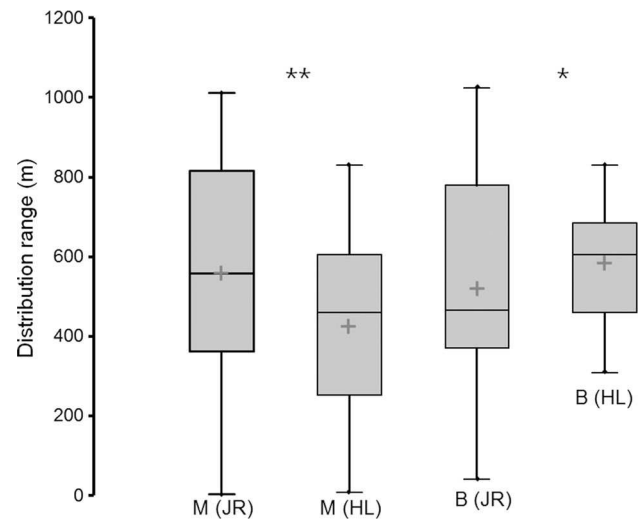
Table 1 Comparison of species richness, abundance, and spatial turnover rates of two study areas (HL. Mt. Hallasan and JR. Mt. Jirisan) in two years (2013 and 2014)

	Elevation	Moths		Beetles	
		Number of species	Number of individuals	Number of species	Number of individuals
HL	278	84	155	43	121
	503	87	252	60	447
	645	125	692	66	369
	752	122	565	44	184
	763	148	501	66	502
	954	121	536	32	102
	963	101	461	39	248
	1109	84	322	36	208
	Sum	337	3484	172	2181
	Whittaker turnover rate	2.09		2.55	
JR	319	169	772	35	103
	515	283	1653	59	178
	682	202	869	60	270
	686	240	1118	67	180
	736	253	1079	59	182
	931	155	589	53	246
	1073	190	1571	58	306
	1330	170	1098	44	300
	Sum	581	8749	179	1765
	Whittaker turnover rate	1.8		2.29	
Total sum		695	12,233	261	3946

(Table S1). The numbers of individuals and species of moths were higher in JR (581 species and 8749 individuals) than HL (337 species and 3484 individuals), while those of beetles showed the different pattern (179 species and 1765 individuals on JR and 172 species and 2181 individuals on HL) (Table 1). The number of moth families was higher at JR (18 families) than HL (12 families), whereas the number of beetle families was higher on HL (39 families) than JR (36 families).

The distribution range of each species of moths and beetles in the two mountains showed that the distribution ranges of insects on HL (moths 425.45 ± 219.09 m, beetles 431.04 ± 218.01 m) were much narrower than those of insects on JR (moths 560.33 ± 288.71 m, beetles 514.45 ± 252.76 m) (moths $t = 5.543$, $P < 0.0001$; beetles $t = 2.317$, $P < 0.05$) (Fig. 2). While distributional range curves of moths and beetles peaked at mid-elevations across both mountains (Fig. 3), these curves for beetles and moths on HL and JR were positively and negatively skewed, respectively.

Whittaker's species turnover rates (β_w) of moths and beetles among sites were higher for HL (2.09 for moths and 2.55 for beetles) than JR (1.80 for moths and 2.29 for beetles) (Table 1). The similarity index based on the Chao-Sorensen-raw-abundance showed significantly higher variability among beetles than moths (Table 2). The similarity index was slightly different among sites (Kruskal-Wallis test, $K = 7.946$, $P = 0.046 < 0.05$), but was higher within the mountains (HL and JR) than across different mountains (HL vs JR) (Kruskal-Wallis test, $K = 112.487$, $P < 0.00001$; Fig. 4). The magnitude of the deviation of the similarity index within JR was significantly higher in moths than beetles

**Fig. 2** Distribution ranges of moths (M) and beetles (B) from two mountains, Mt. Jirisan (JR) and Mt. Hallasan (HL) of South Korea. ** $P < 0.01$, * $P < 0.05$

($F = 3.420$, $P = 0.002$), but the magnitude of the deviation of index within HR was not different between moths and beetles ($F = 1.129$, $P = 0.755$) (Table 3). Moths showed a higher similarity index on JR than HL ($F = 2.177$, $P = 0.048$), but beetles showed no difference between locations ($F = 0.733$, $P = 0.427$) (Table 3).

The mean difference in geographic distance among sites at two locations did not differ significantly (t -test $t = -1.315$, $P = 0.194$). The Mantel test showed that the null hypothesis of no relationship between insects

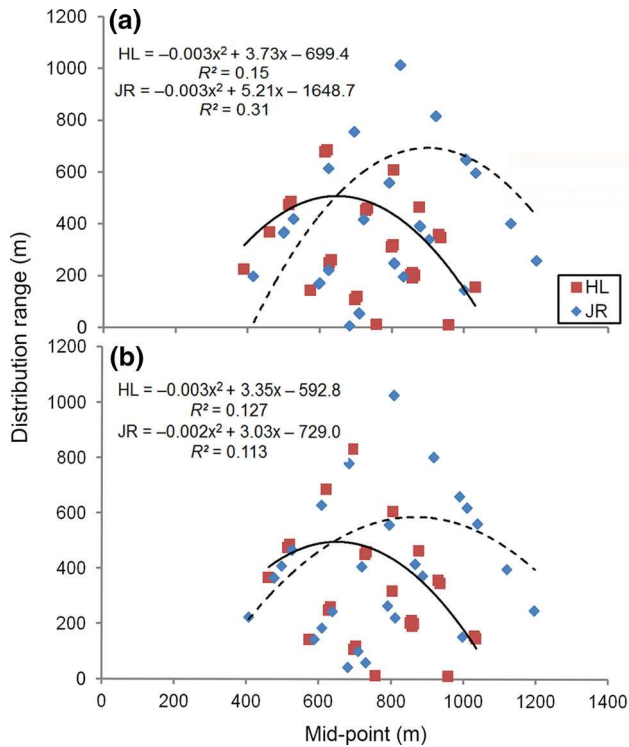


Fig. 3 Mid-point and distribution range of two insect groups across two elevational transects of South Korea, HL (Mt. Hallasan, dark squares with solid line) and JR (Mt. Jirisan, diamonds with dotted line). **a** Moths, **b** Beetles

Table 2 Summary of the similarity index (Chao–Sorensen–raw-abundance based) of each insect group among eight sites in two mountains [Mt. Hallasan (HL) and Mt. Jirisan (JR)] of South Korea

Mountain	Insects	Mean	SD	χ^2	<i>P</i>
JR	Beetles	5.977	1.579	67.356	< 0.0001
	Moths	6.986	0.854	19.693	0.313
HL	Beetles	6.359	1.339	48.409	0.014
	Moths	6.105	1.260	42.872	0.054

A test of variance of the value (χ^2) was produced
Significant *P* values (< 0.05) are italicized

and site distances on HL was rejected (combined $r = 0.298$, $P < 0.005$, moths $r = 0.213$, $P < 0.05$, beetles $r = 0.421$, $P < 0.001$), but the null hypothesis on JR was not rejected (combined $r = 0.025$, $P = 0.89$; moths $r = 0.053$, $P = 0.78$; beetles $r = -0.042$, $P = 0.82$). This suggested that two insect assemblages on the island's mountain (HL) were constrained by the geographic distance, but not on the mainland mountain (JR). Conversely, the relationship between the similarity index and elevation difference was significant for moths and beetles on HL and beetles on JR, but not for moths on JR, suggesting the moth assemblage on the mainland's mountain (JR) was not affected by elevation (Fig. 5).

The soil components showed that HL possessed higher organic matter (58.75 g/kg) than JR (45.33 g/

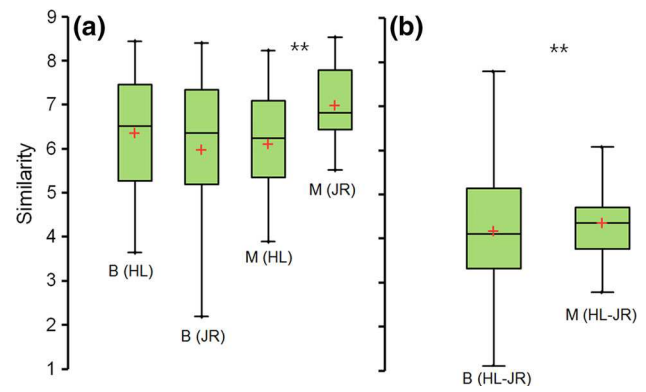


Fig. 4 Beta diversity deviations of moths and beetles within each mountain and between mountains of South Korea. Mt. Hallasan (HL), Mt. Jirisan (JR), beetles (B), and moths (M). ** $P < 0.01$. **a** Within each mountain **b** Between two mountains

Table 3 Summary of analyses testing for differences in community composition based on Chao–Sorensen–raw-abundance based similarity index attributable to landmass (island, HL and mainland, JR) and insects (moths and beetles)

Comparison	Variables	Model <i>F</i>	<i>t</i> value
Landmass	Beetles	0.733	0.975
(HL vs JR)	Moths	2.177*	- 3.061**
Insects	Hallasan (within HL)	1.129	- 0.730
(moths vs beetles)	Jirisan (within JR)	3.420**	2.972**
	Between HL and JR	3.198**	- 0.921

Significant *P* values (< 0.05) are italicized

Mt. Hallasan (HL), Mt. Jirisan (JR) * $P < 0.05$, ** $P < 0.01$

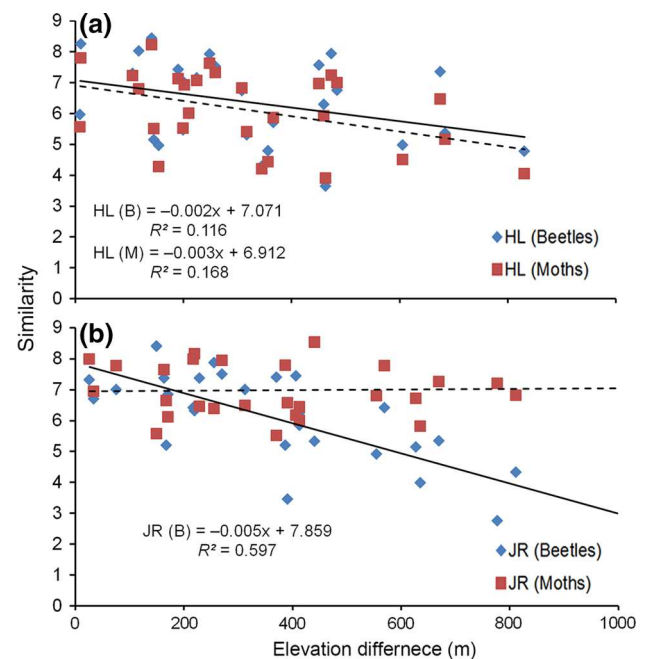


Fig. 5 Relationship between elevation difference from two sites on each mountain and the similarity index based on the Chao–Sorensen–raw-Abundance. **a** Mt. Hallasan (HL), beetles (B, solid line), moths (M, dotted line). **b** Mt. Jirisan (JR), beetles (B, solid line), moths (dotted line)

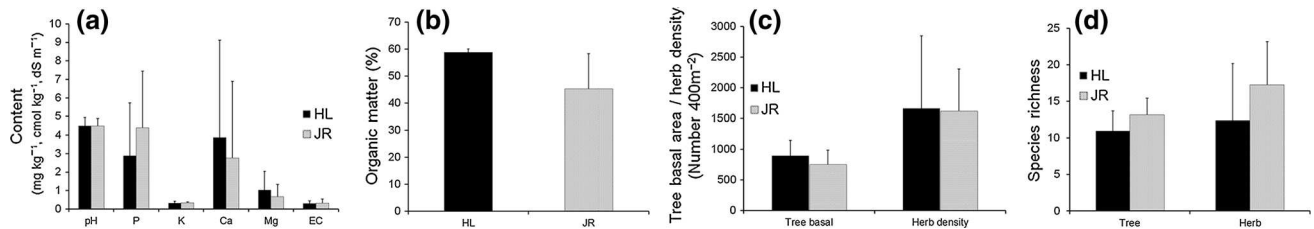


Fig. 6 Plant and soil characteristics in two regions: **a** pH, EC (electron conductivity, dS m^{-1}), cation (K^+ , Ca^{2+} , Mg^{2+} , cmol kg^{-1}), and anion (P , PO_3^- , mg kg^{-1}) contents (not significantly different); **b** soil organic matter ($P < 0.05$); **c** tree basal area and

herb density (not significantly different); **d** tree and herb species richness (not significantly different) (HL, Mt. Hallasan and JR, Mt. Jirisan). Lines above bars indicate standard deviation

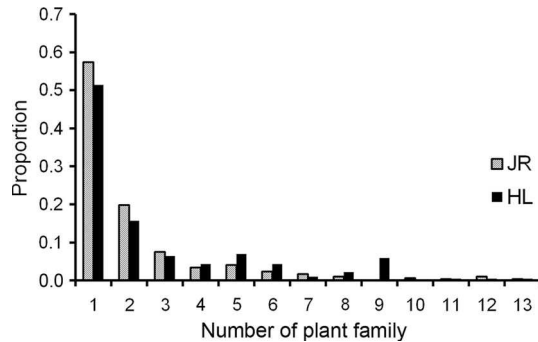


Fig. 7 Proportion of number of host plant families of moths from Mt. Hallasan (HL) and Mt. Jirisan (JR)

$\text{kg})(t\text{-test } t = 2.932, P < 0.05)$ (Fig. 6). Other soil components showed no differences between the two locations (Fig. 6). The average tree basal area (cm^2) and herb density were significantly higher on HL (1866.13 and 992.6) than JR (1453.3 and 603.7). Conversely, tree and herb richness were generally higher on JR than HL, but not significantly different. Host plant information of 291 (JR, 50%) and 185 (HL, 55%) moth species was available and diet breadth of moth species on HL and JR varied from one to thirteen plant families. More than half moth species on both mountains (JR 57%, HL 51%) feed on only one plant family. Comparison of proportion of host plant families between two moun-

tains was not different (Fig. 7; Mann–Whitney U-test, $U = 73.500, P = 0.590$).

Stepwise regression analyses showed different predictors for moths and beetles. Latitude and location were the significant variables influencing moth richness and abundance. Tree species richness and organic matter content were the significant variables influencing beetle abundance (Table 4). NMS analysis yielded two axes for the night-flying moth and beetle assemblages and explained 93% (moths) and 90% (beetles) of the total variance, respectively (Fig. 8). The variables most closely correlated ($r > 0.5$) with moth and beetle assemblages were the same: geography (latitude), elevation and organic matter content (Table 5). Two mountain areas grouped separately, and these groups were significantly different each other (MRPP: $A = 0.162, P < 0.0001$).

Discussion

Our study areas showed similar elevational breadth and distance among eight sites on each mountain (Mt. Hallasan, HL and Mt. Jirisan, JR), with the main differences being the location, mainland (JR) or island (HL). The magnitude of the deviation of beta diversity was no different between locations (Fig. 4), indicating the outcome of local community assembly processes is consis-

Table 4 Results of stepwise regression analysis for the abundance and richness of beetles and seven independent variables in two study areas (Mt. Hallasan and Mt. Jirisan) of South Korea

Dependent variables	R^2	F	Predictors
Beetles			
Ln (richness)	0.21	3.68	Intercept ($F = 151.95^{**}$) Tree species richness ($F = 3.68$)
Ln (abundance)	0.39	4.22*	Intercept ($F = 12.40^{**}$) Organic matter content ($F = 6.61^*$) Tree species richness ($F = 4.83^*$)
Moths			
Ln (richness)	0.9	36.18**	Intercept ($F = 19.12^{**}$) Location ($F = 17.84^{**}$) Latitude ($F = 20.24^{**}$)
Ln (abundance)	0.75	19.76**	Intercept ($F = 8.09^*$) Location ($F = 7.49^*$) Latitude ($F = 8.49^*$)

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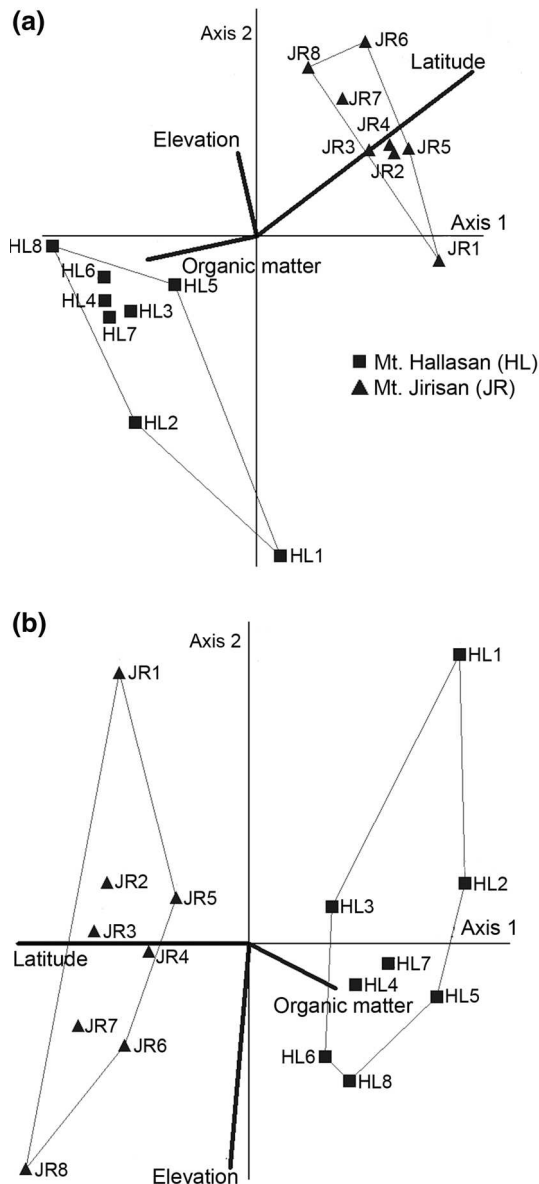


Fig. 8 Nonmetric multidimensional scaling (NMS) ordination using **a** 331 moth species (135° rotated) and **b** 108 beetle species (– 30° rotated) across 16 sites after deleting the species that occurring at less than three sites

tent for species on both mountains because of aggregation within local subplots. We showed that moths on HL on Jeju Island had a smaller pool size (small gamma diversity) and higher beta diversity than those on JR on the mainland. Unique historical processes can result in substantial differences in the sizes of species pools and beta diversity among regions with similar environmental conditions (Qian et al. 2005). Especially, high turnover rates in closed island areas can be explained through dispersal ability, habitat fragmentation and isolation (Feer and Hingrat 2005; Soininen 2010; Stuart et al. 2012). It should be noted that the relatively small size of the species pool of moths on HL could be the result of their limited ability to disperse because of isolation and the sea barrier (MacArthur and Wilson 1967).

Table 5 Variables of high correlation ($r > 0.5$) with two axes of NMS ordination of beetles and moths across two elevational transects (Mt. Hallasan and Mt. Jirisan) of South Korea

Variables axis	Beetles		Moths	
	1	2	1	2
Elevation	0.63	0.71		– 0.86
Latitude	0.78	– 0.56	– 0.98	
Organic matter content		0.75	– 0.55	
R^2 (%)	55.3	34.8	76.9	18.5

On the other hand, the pool size of nocturnal and light attracted beetles did not differ between the two mountains (HL and JR) (Table 1, Tables S2, S3). The species richness of beetles on JR was slightly larger than that of beetles on HL, while the abundance was 1.24 times larger on HL. Interestingly, the number of beetle families was larger on HL (39 families) than JR (36 families), and eight families were collected solely from HL, while five were only obtained from JR. These findings were opposite to those of moths (six moth families solely from JR and one family from HL), suggesting that a variety of beetle groups have colonized the island for a long time, regardless of dispersal limitation. The flora and butterfly fauna on Jeju Island comprised a variety of different origin, actively immigrated from southern China, Taiwan, Japan and mainland of Korea (Ju and Kim 2002; Kong 2007). Wepfer et al. (2016) suggested that climate and land connectivity during historical periods of low sea level (> 10,000 years) were the major drivers of ant diversity patterns in East Asia, including Jeju Island. Similar to ants, beetles were able to colonize Jeju Island for long time before the sea level rose, and this historical event likely preserved the relatively high number of unique beetle families on HL.

On the other hand, the mechanism responsible for maintenance of the relatively similar species richness of beetles on the island is not clear. It is noted that island systems differ from continents, but island system develops its own unique repeated patterns and processes (Losos and Ricklefs 2009). The taxon cycle (Wilson 1961) was suggested to explain the regular cycle of distributional changes following colonization of islands through the establishment of widespread and dispersive populations to many more restricted and specialized populations or species or the exploitation of a broad array of hosts from specialist phytophagous species (Gillespie and Roderick 2002). Compared to JR, beetles on HL showed the narrow distributional ranges and high turnover rates in spite of the similar richness and higher abundance. Additionally the family diversity of beetles on HL was slightly higher than JR. This unexpected pattern of beetles on HL could be explained by the taxon cycle that emphasized the dominance of more restricted and specialized species on island.

The Whittaker beta partition β_w for moths and beetles along eight elevation sites on HL generally had

higher turnover rates than those on JR. Both distributional range curves of beetles and moths showed a mid-peak unimodal pattern along two elevational transects (Fig. 3), while moths and beetles on JR generally favored high elevations (negatively skewed), and insects on HL favored low elevations (positively skewed). The distribution ranges of moths and beetles were much narrower on HL. We demonstrated that geographic distance was closely related to moth and beetle assemblages on HL, but that there was no relationship on JR. Low dispersal rate, high turnover rate, area size, habitat fragmentation, and colonization–extinction dynamics are the main factors that decrease the potential for species accumulation in one region relative to another (Romero-Alcaraz and Avila 2000; Yu et al. 2013; Zou et al. 2013). Although we only surveyed two mountains, the results of our study were consistent to the previous hypothesis that island fauna have larger turnover rates with narrower distribution ranges, and that insect assemblages are greatly affected by geographic distance (Buckley and Jetz 2008; McCain 2009; Melo et al. 2009; Jankowski et al. 2013; Wepfer et al. 2016). In addition, we found that moth and beetle assemblages on HL and beetle assemblages on JR were significantly negatively related to elevation (Fig. 5).

Organisms with high dispersal ability such as moths have high potential to colonize appropriate habitats (Majerus 2002; Korhonen et al. 2010). Our study showed that the moth diversity on JR was 1.7 times larger based on species richness and 2.5 times larger based on abundance than that on HL. The number of moth families was also higher on JR (18 families) than HL (12 families). Interestingly, the strong dispersal ability of moths was attributed to the lack of relationship between geographic distance and moth assemblages on JR (Mantel test) and the absence of influence of the elevation (Fig. 5). Diet breadth of moths on both mountains was not different (Fig. 7). While the moth assemblage on JR was not correlated with geographic distance and elevation, that on HL was strongly correlated with distance and elevation. The difference between the two mountains was only a result of location (latitude) and type of landmass (island vs mainland). This suggests that the moth community on Jejudo Island (HL) could be strongly constrained by island space.

Latitude and elevation had the greatest effect on assemblages of both moths and beetles (Table 5). It is known that latitude and elevation are not directly related, but are derived from covaried environmental variables, primarily temperature (Hawkins and Diniz-Filho 2004). Along with latitude, elevation has been noted as the primary predictor of the diversity of mountainous plants, vertebrates (birds) and invertebrate species (moths, beetles, etc.) (Hemp 2006; Axmacher and Fiedler 2009; Choi 2011; Cavarzere and Silveira 2012; Thein and Choi 2016). Even though there is no consensus pattern for elevational gradient, the lower productivity and harsh environment of higher elevations restrict species distributions, resulting in decreased insect

abundance and diversity at higher elevations (Rahbek 1995; Yu et al. 2013).

Organic matter content was also identified as a significant factor influencing beetle abundance. Specifically, HL, which possessed higher organic matter than JR (Fig. 6), was productive, with the highest tree basal area and plant density. Soil organic matter, which is well known as the major source of nutrients for plants, is produced by decomposing and reserving nutrients, especially nitrogen, phosphorus, sulfur and micronutrients (Bot and Benites 2005). High quality soil induces better performance of plant metabolism (Kos et al. 2015), and changes in soil components in response to vegetation structure (forest coverage) are known to change the main source of organic matter in an ecosystem (Erb et al. 2012). Aboveground herbivorous insects are involved in plant productivity, decomposition, and nutrient uptake via their selective feeding and excretion (Belovsky and Slade 2000; Weisser and Siemann 2004; Kagata and Ohgushi 2012). Yu et al. (2013) showed that litter cover with temperature and area are the major variables driving elevational gradients of epigeic beetles. Therefore, soil–plant interaction will influence plant–insect interactions, and the high abundance of beetles on Mt. Hallasan could be attributed to this interaction. Overall, our findings indicate that elevation and organic matter are the two primary factors influencing beetle assemblages.

We found that light traps were biased to moths, as indicated by their having twice the species richness and three times the abundance of beetles; specifically, 695 moth species in 19 families and 261 beetle species in 45 families. Although moths are the best known insects that are attracted to light (Majerus 2002), certain families of beetles are also well attracted to light (Genung 1972; Yahiro and Yano 1997; Hébert et al. 2000; Kato et al. 2000; Hirao et al. 2008; Garcia-Lopez et al. 2011). Even though the numbers of species and individuals of beetles were relatively smaller than those of moths, our study showed a high diversity of beetles that were attracted to lights (Scarabs group, Carabidae, Elateridae, Melandryidae, Scirtidae, Byturidae, Throscidae and Ptilodactylidae). On the other hand, it should be noted that beetle composition differs drastically between pitfall and light trap catches since beetles show great behavioral variations in response to food and their preferred environment. One-third of beetle assemblages collected using light traps were members of Melolonthinae in this study, while half of beetles collected using pitfall traps were Scarabaeinae (Lobo et al. 2007). We compared the beetle assemblages on Mt. Hallasan determined using pitfall traps (Yang et al. 2006) with the results of the current study and found that 15 families (about 40%), but only 18 species (about 8%) were shared between studies conducted using the two methods. Lee et al. (2014) reported no shared beetle species after surveys conducted using four different sampling methods (sweeping method, pitfall trap, Malaise trap and black light trap) on Mt. Gariwangsan, South Korea. In the

present study, we found that the relatively smaller diversity of beetles than moths and the large gap in beetle species composition could be due to the sampling method being biased for light attracted species.

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