



Pattern of ant diversity in Korea: An empirical test of Rapoport's altitudinal rule



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ABSTRACT

Two diversity patterns (hump-shaped and monotonic decrease) frequently occur along altitude or latitude gradients. We examined whether patterns of ant species richness along altitudes in South Korea can be described by these patterns and whether ranges of ant species follow Rapoport's altitudinal rule. Ants on 12 high mountains (>1100 m) throughout South Korea (from 33° N to 38° N) were surveyed using pitfall traps at intervals of 200–300 m altitude. The temperatures at the sampling sites were determined from digital climate maps. Ant species richness decreased monotonically along the altitudinal gradient and increased along the temperature gradient. However, species richness of cold-adapted species (highland species) showed a hump-shaped pattern along altitude and temperature gradients. The altitude and temperature ranges of ant species followed Rapoport's rule. Sampling site temperature ranges were significantly correlated with coldness. Therefore, Rapoport's rule can be explained by high cold-tolerance of species inhabiting high altitudes or latitudes.

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Introduction

Species richness patterns along latitudinal or altitudinal gradients have been the subject of debate for several decades (Rohde, 1999). It is generally accepted that diversity declines along latitudinal or altitudinal gradients (Stevens, 1989, 1992 and references therein; Colwell and Hurr, 1994; Allen et al., 2002) but such declines are not always straightforward, and evidence for mid-elevation (or latitude) peaks (hump shaped) has accumulated (McCoy, 1990; Olson, 1994; Rahbek, 1995; Lees et al., 1999). Explanations for the diversity patterns along gradients are generally either distribution range based (Stevens, 1989, 1992; Colwell and Hurr, 1994; Lees et al., 1999), or energy based (Allen et al., 2002). Rapoport (1982) reported that species at higher latitude have greater latitudinal range, and this phenomenon was defined as Rapoport's rule by Stevens (1989). Rapoport's rule was later extended to explain the finding that species at higher altitudes have wider altitudinal ranges (Stevens, 1992). Using these phenomena, Stevens (1992) devised a theorem to explain the decrease in species richness along latitude and altitude, which was defined as Rapoport's rescue effect. Rapoport's rescue effect was deduced from Rapoport's rule. Rapoport's rescue effect is one of several diversity theories that

explain the decrease in species richness that occurs with altitude or latitude. The Rapoport's rescue effect suggests that local species richness is strongly influenced by the proximity of the range margins of potentially interacting species, and that some species persist only through continued immigration from more suitable areas nearby (i.e., they are "rescued"). Since high elevation species have broader elevational ranges, more range margins occur in the lowlands compared to the highlands, inflating species richness there (Stevens, 1992).

When Colwell and Hurr (1994) developed one-dimensional species richness stochastic models to explain Rapoport's rule, they unexpectedly found that the species richness pattern within a domain produced a hump-shaped curve that declines symmetrically from the center towards the edges of the domain. This phenomenon was termed the mid-domain effect and has been used to explain the gradual decline in diversity that occurs from the equator to the poles without assuming impacts of abiotic or biotic factors (Colwell and Hurr, 1994). In the mid-domain effect, the stochastic process of geographical ranges within geometric constraints can lead to the development of species gradients in the absence of any environmental or historical gradients (Colwell et al., 2004). However, the applicability of using the mid-domain effect based on theoretical or empirical data has been the subject of debate (Hawkins et al., 2005b; Zapata et al., 2005). Thus, both theories are used to explain one of two diversity patterns. The rescue effect is used to describe the monotonic decline in local diversity, whereas the mid-domain effect is used to describe the hump-shaped pattern.

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There is no link between the two theories. Hence, these diversity theories cannot integrate the two prevalent diversity patterns along altitudinal or latitudinal gradients.

The rescue effect can be alternatively explained by overlap of ranges (Stevens, 1989). In thermally restricted organisms such as insects, distribution has been mainly determined by heat or cold tolerance (Addo-Bediako et al., 2000). Each species has an evolved thermal envelope (Brittain, 2008). It is hypothesized that the local combination of the thermal envelopes of coexisting species may lead to monotonic decline or hump-shaped patterns due to the linear change in temperature along an altitudinal or latitudinal gradient (Hypothesis 1). Rapoport's altitudinal rule may be formed by the ant thermal ranges (Hypothesis 2). Ants are abundant and diverse, have well-developed taxonomy, and are easily sampled throughout their active season almost anywhere in the world (Hölldobler and Wilson, 1990; Kaspari et al., 2003); therefore, they are useful for testing ecological theories (Sanders et al., 2007). Field survey was conducted to identify ant species richness patterns along altitudinal gradients on 12 mountains in South Korea. The two hypotheses were tested using ant data and temperature data, which were obtained from digital climate data.

Materials and methods

Sampling sites

This study was conducted on 12 high mountains (>1100 m) in South Korea (Fig. 1). The mountains were selected to represent altitudinal ant species richness gradients from 33° to 38° N. The study mountains included the three highest mountains (Mts. Hanlasan, Jirisan, and Seolaksan) in South Korea. Four to seven sampling sites were selected from the base to the top of each mountain with an interval of 200–300 m elevation. The undisturbed forests and bush lands (mountain tops) were selected as sampling sites to eliminate disturbance effects. Sampled forest sites were composed of trees >30 years

old and moderately dense grown understory vegetation. Of 62 sampling sites, 42 were deciduous forests, nine were coniferous forests, and 11 were bush land. Environmental information for each sampling site is given in Kwon et al. (2011a) and Kwon et al. (2012). Details regarding the climate, vegetation, and topography in Korea are shown in Kwon et al. (2011b).

Ant sampling and identification

Ants were collected in pitfall traps consisting of a plastic cup (depth, 6.3 cm; mouth diameter, 8 cm; bottom diameter, 6 cm). Ten pitfall traps were buried at each sampling site for 10 days during summer (July–August). Ant foraging is most active during the survey period (Kwon, 2010) because this period is the warmest during the year. One to four mountains were surveyed each year from 2006 to 2009. Each trap was placed 5 m from adjacent traps along a line, and about one-third of the trap filled with a preservative (polyethylene glycol). The species richness of ants collected by ten pitfalls for 10 days was about 44% (SD = 6%, $n = 30$, estimated SR = 25) of the total at an old deciduous forest study plot of 1 ha (Kwon unpublished data). The rates of species accumulation in samples 5 m apart are not different when compared with samples collected 10 or 15 m apart (Fisher, 1999b). All ant specimens were isolated from debris in the laboratory, and were stored in 80% ethanol.

Ant specimens were identified using taxonomic keys (Park, 2002; Imai, 2006; Lyu, 2006; Terayama and Kuboda, 2009; Japanese Ant Image Database, 2010). The ants, except two species of *Lasius*, were identified to the species or morphospecies levels. *Lasius japonicus* and *L. alienus* were the most common and abundant among the *Lasius* species. However, intermediate forms of the two species were frequently found, and the two species were treated as a species group (*Lasius* spp. (*japonicus* + *alienus*)). All specimens were deposited at the Forest Ecology Laboratory of the Korea Forest Research Institute.

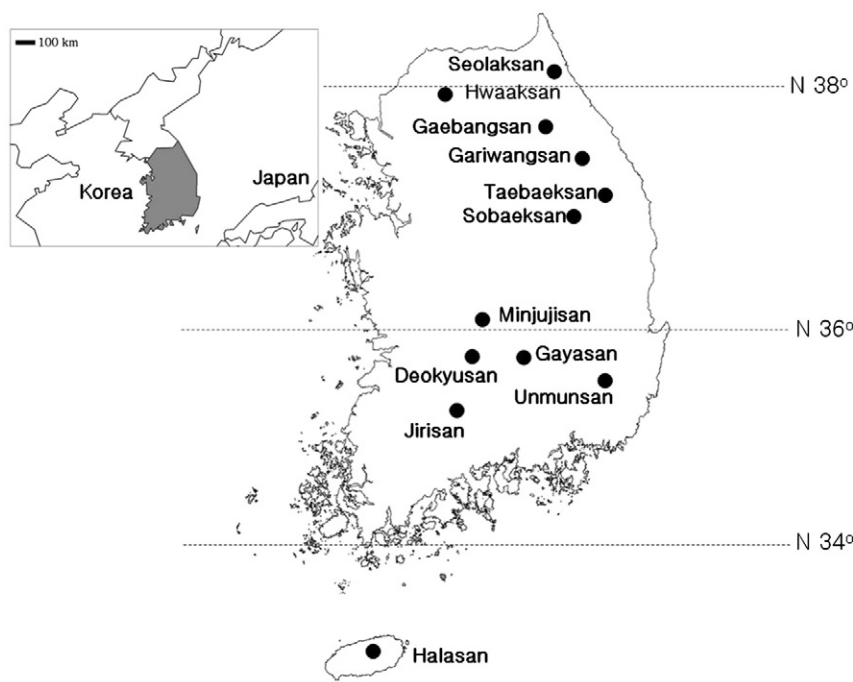


Fig. 1. Map of the study mountains in South Korea.

Grouping of ant species according to thermal range

During the preliminary analysis of ant distributions in 366 forests throughout South Korea, temperature was a key factor associated with ant distribution, and other factors such as rainfall and productivity (e.g. NDVI) were negligible (Kwon et al., 2011a). We used digital climate maps (Yun, 2010) produced by the Korea Meteorological Administration and National Center for Agrometeorology to extract the thermal parameters for each sampling site. Annual mean, maximum, and minimum air temperature were estimated based on observation data collected from 1971 to 2008. The spatial resolution of the gridded climate data was 30 m. Ant species were artificially grouped into warm-adapted species (WAS) and cold-adapted species (CAS) according to the average habitat temperature of each species occurred sites for testing the Hypothesis 1. Based on the temperature average values of occurred sites, ant species were grouped (Appendix A, Table A1). *Aphaenogaster japonica* (8.58 °C) are widely distributed from low elevations to mid elevations in South Korea (Kwon et al., 2012). Hence, the average temperature of 8.58 °C was chosen as the dividing point.

Analyses

The number of ant species collected at each sampling site was used to determine species richness. A generalized linear model (GLM) in STATISCA (ver. 6.1) was used to identify significant environmental factors for species richness, using mountains as a categorical variable, and altitude and latitude as continuous variables. Values of latitude were transformed to decimals for analyses. A regression analysis was used to identify the relationship between species richness (no. of species) and altitude at the study sites and between species richness and temperature (i.e., annual average). A quadratic polynomial regression was used, when patterns of species richness were hump-shaped. The level of significance was $p < 0.05$.

The altitudinal range of each ant species was plotted along their averages in order to test whether the ant species ranges followed Rapoport's altitudinal rule. Additionally, the ant species temperature ranges were also plotted along their averages (i.e., altitudinal averages of occurred sites) to test whether Rapoport's altitudinal rule may be caused by the temperature range (Hypothesis 2). Singleton species (sampled at one site, $n = 11$) were excluded in this analysis. Rapoport's rule assumes that environmental variations such as precipitation and temperature increase with high elevation or high latitude (Stevens, 1989, 1992). However, the temperature range at a site increases at high latitude due to the low minimum temperature (Addo-Bediako et al., 2000). Hence, Rapoport's rule may have arisen due to the increased coldness with increasing elevations or with increasing latitudes. To determine if this was the case, the annual range of temperature (maximum minus minimum) at the sampling sites was plotted with coldness (minus value of minimum of temperature) and with hotness (maximum temperature). A regression analysis was used to identify relationships.

Results

As a result of the GLM, altitude was significant only for species richness ($F_1 = 35.62$, $P \ll 0.0001$), whereas latitude and mountain influences were negligible (latitude, $F_1 = 1.191$, $P = 0.28$; mountain, $F_{11} = 1.76$, $p = 0.087$). Temperature was mainly explained by elevation ($F_{1,60} = 147.38$, $r^2 = 0.71$, $p \ll 0.0001$). When using two factors of elevation and latitude, the value of r^2 slightly increased ($r^2 = 0.86$). This low influence of latitude on species richness and temperature may be related with the narrow latitudinal range of South Korea. Therefore, the pooled data from all mountains were analyzed to identify the influence of elevation and temperature on species richness. In total, 4378 ants belonging to 32 species were collected during the ant surveys of 12 mountains (Appendix A, Table A1).

Ant species richness was negatively related with altitude (Fig. 2a; $r^2 = 0.42$, $P \ll 0.0001$). Species richness patterns were different between WAS and CAS. The former showed a decreasing pattern (Fig. 2c; $r^2 = 0.476$, $P \ll 0.0001$ in linear regression), whereas the latter showed a hump-shaped pattern (Fig. 2e; $r^2 = 0.248$, $P < 0.0001$ in quadratic polynomial regression). Temperature monotonically decreased along the altitudinal gradient as noted above. This negative relationship leads to symmetrical species richness patterns (Figs. 2a vs. b, and c vs. d) between the elevation and temperature gradients in all species and WAS. Species richness of all species and WAS increased gradually as temperature increased (Fig. 2b, d; $r^2 = 0.496$, $P \ll 0.0001$ in all species; $r^2 = 0.626$, $P \ll 0.001$ in WAS). When sites with CAS only were included, species richness at sites showed a hump-shaped pattern along temperature gradient (Fig. 2f; $r^2 = 0.334$, $P \ll 0.0001$ in quadratic polynomial regression).

The altitudinal ranges of the ant species were significantly correlated with the altitudinal averages (Fig. 3a; $r^2 = 0.312$, $P < 0.01$). These patterns indicate that species inhabiting higher altitudes may have a wider distribution range, supporting Rapoport's altitudinal rule. As temperature is highly related to altitude, the temperature range would follow Rapoport's rule, which was demonstrated in Fig. 3b ($r^2 = -0.262$, $p < 0.01$). The annual temperature range at the sampling sites was significantly correlated with coldness (Fig. 4b; $r^2 = 0.333$, $P \ll 0.0001$) but not significantly correlated with hotness (Fig. 4a; $r^2 = 0.055$, $P > 0.05$). This shows that wider ranges in temperature at higher altitude were primarily caused by increased coldness.

Discussion

In the present study, Rapoport's altitudinal rule was supported by the altitudinal ranges of Korean ant species. The wide environmental tolerances of organisms inhabiting high latitudes have been suggested to explain Rapoport's rule (Stevens, 1992). The five mechanisms (i.e., land area, climatic variability, differential extinction, competition, and biogeographical boundaries) for Rapoport's rule were compared by Gaston et al. (1998). They concluded that no single explanation is adequate for Rapoport's rule. However, in the present study the same patterns between altitudinal range and thermal range of ant species (Fig. 4) indicated that Rapoport's altitudinal rule may be mainly created by temperature tolerance. The wide range in temperature at high latitude and high elevation was primarily determined by the minimum temperature (cold) rather than the maximum temperature (heat) (Fig. 4). This is because maximum temperatures tend to be constant, whereas minimum temperatures decrease linearly, particularly at 10°–50° N and 10°–30° S (Addo-Bediako et al., 2000). Accordingly, it is likely that the wide environmental tolerance of organisms inhabiting high elevations and high latitudes reflects cold-tolerance. A revised analysis of insect tolerance to temperature revealed that heat tolerance (upper thermal limit) shows little geographical variation but that cold tolerance (lower thermal limit) increases with latitude (Addo-Bediako et al., 2000), supporting this prediction. Therefore, widening the temperature tolerance range caused by increased cold tolerance at high altitude (or latitude) explains the wider distribution of species in these areas, which was documented in detail by Ghalambor et al. (2006).

Ant species richness patterns also supported this finding. Ant species richness monotonically decreased along the altitudinal gradient at the 12 mountains in South Korea. However, the CAS richness pattern was hump-shaped, whereas the WAS richness monotonically decreased. Thus, overlap of two diversity patterns resulted in the monotonic decrease due to prevalence of WAS. A strong relationship between diversity pattern and evolution has been suggested recently by several researchers (Hawkins et al., 2005a, 2006, 2007; Harrison and Grace, 2007; Ackerly, 2009; Wiens et al., 2009; Buckley et al., 2010). High diversity in the tropics can be explained by evolutionary climate niche

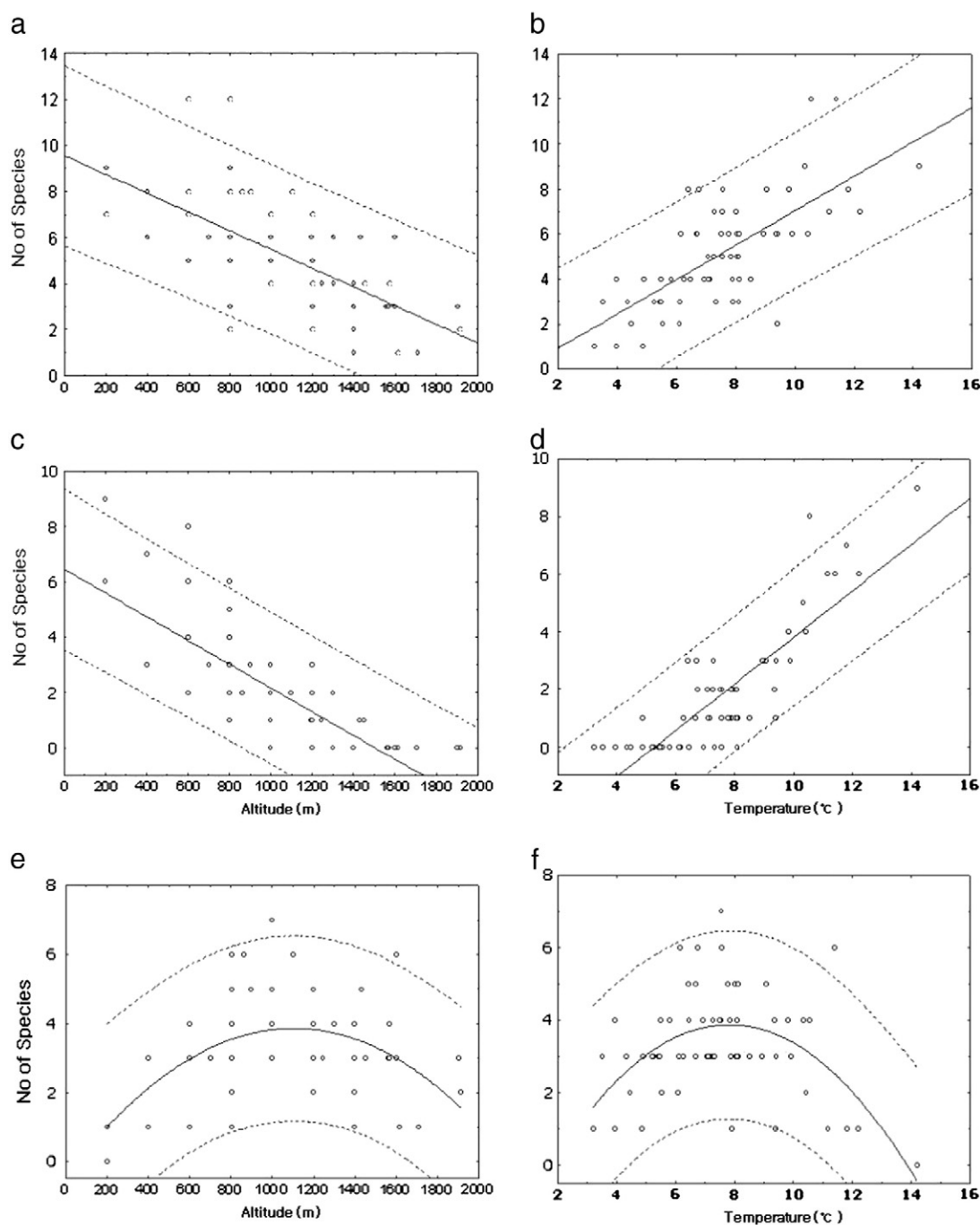


Fig. 2. Species richness (i.e., number of species collected at a site) of all species along altitudinal gradients (a), along temperature gradients (b), warm-adapted species along altitudinal gradients (c), cold-adapted species along altitudinal gradients (e), and along temperature gradients (f). The three lines in each figure indicate mean and 95% confidence intervals, which were predicted by the regression model (a–f, linear or quadratic). In the regression analysis, $F_{1,60} = 45.291$, $P < 0.0001$, $r^2 = 0.42$, $y = 1631.591 - 105.847 * x$ in a; $F_{1,60} = 60.999$, $P < 0.0001$, $r^2 = 0.496$, $y = 4.106459 + 0.661068 * x$ in b; $F_{1,60} = 56.457$, $P < 0.0001$, $r^2 = 0.476$, $y = 1262.8053 - 139.24908 * x$ in c; $F_{1,60} = 103.05$, $P < 0.0001$, $r^2 = 0.626$, $y = 6.351394 + 0.917256 * x$ in d; $F_{1,60} = 21.067$, $P < 0.0001$, $r^2 = 0.248$, $y = -0.4118 + 0.0077 * x - 3.5103E-6 * x^2$ in e; $F_{1,60} = 31.68$, $P < 0.0001$, $r^2 = 0.335$, $y = -2.6018 + 1.6556 * x - 0.1059 * x^2$ in f.

conservatism, in which temperate zones contain fewer species because many species that had adapted to the warmer climates of the early Tertiary have been exterminated by global-cooling (Hawkins et al., 2005a, 2006, 2007) or because of different evolutionary histories between tropical and temperate regions (Wiens et al., 2009; Buckley et al., 2010). Buckley et al. (2010) reported that the relationship between climate and species richness varies considerably between clades. They showed that many young clades have negative

richness-temperature slopes. Although ant species richness is higher in low latitudes (Ward, 2000; Kaspari et al., 2003), temperate-zone clades such as *Myrmica*, and *Formica* are rich at high latitudes (Cushman et al., 1993; Radchenko et al., 2006).

During the course of evolution, centers of origin may differ based on clades at different taxonomic levels. Differential radiation may result in diverse local spatial species richness patterns in various clades within a taxon. Hence, the pooled richness of component clades with different

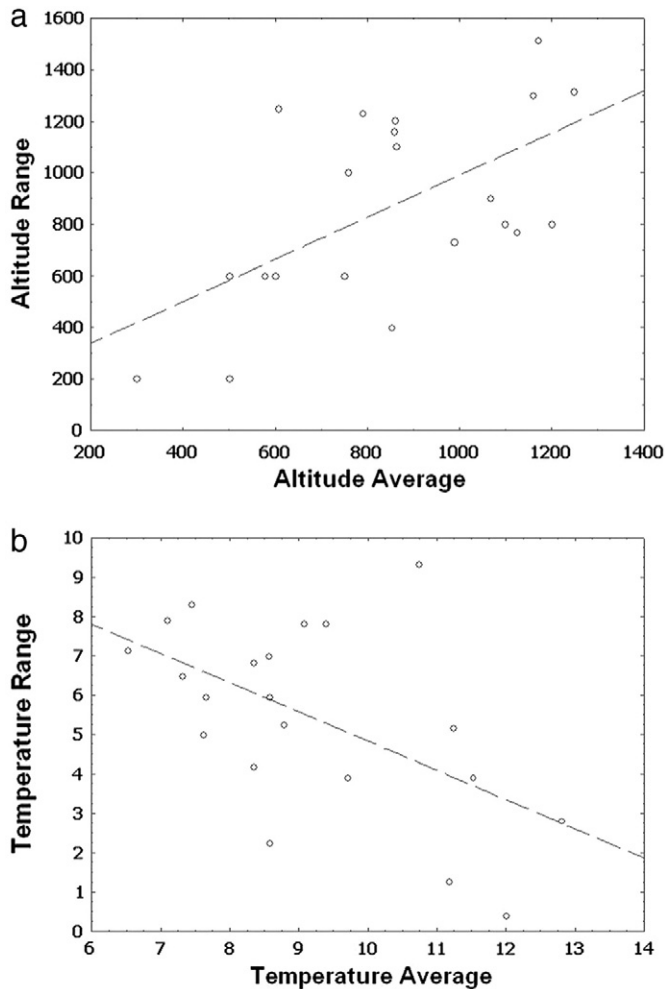


Fig. 3. Environmental range and average of ant species. Relationships between average and range in elevation (a), and temperature (b) are shown. Singleton species (sampled at one site, $n = 11$) were excluded in a and b. The temperature range in b is the difference between the highest and lowest annual average temperature at the sites where ant species occurred. In the regression analysis, $F_{1,19} = 10.09$, $P < 0.01$, $r^2 = 0.312$, $y = 174.86 + 0.8165 \times x$ in a; $F_{1,19} = 8.099$, $P < 0.01$, $r^2 = 0.262$, $y = 12.247 - 0.742 \times x$ in b.

geographical ranges may lead to hump-shaped or monotonic-decrease pattern shown in Fig. 2. The altitudinal diversity pattern may be related with the biogeography of a taxon which is highly dependent on the evolutionary origin. If richness of a taxon would monotonically decrease along altitudinal gradient in a region, more species of this taxa range more southerly (or warmer). However, this taxon may show a hump-shaped or monotonic increase pattern along elevation in more southerly located region. In Korean aquatic insects, diversity of Odonata, which have evolved in high temperature regions (Brittain, 2008), monotonically decreases with increasing elevation, whereas that of Plecoptera, which evolved in low temperature regions (Brittain, 2008), increases (Li et al., in press). These data were obtained at 501 sampling sites below 800 m of elevation.

In a worldwide survey of leaf litter ant diversity, species richness peaks at mid-elevations in the tropics but decreases continuously with elevation in temperate regions (references in Ward, 2000). In an ant survey of four mountains in Madagascar, the highest species richness occurred at mid-elevations of about 800 m (Fisher, 1999a,b). Fisher (1999a) suggested that mid-elevation species richness peaks are the result of mixing of two distinct lower and montane forest ant

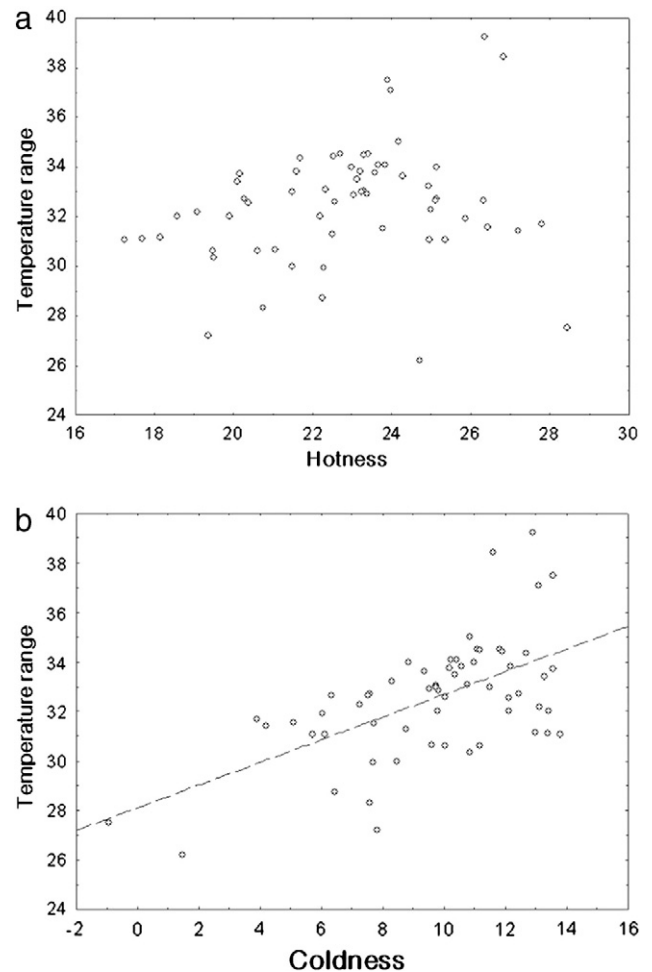


Fig. 4. Temperature range and hotness (a), and temperature range and coldness (b) at the sampling sites. In a and b, the temperature range (maximum temperature minus minimum temperature at each site) is plotted along hotness (the maximum temperature) and along coldness (minus value of the minimum temperature) at all the sampling sites. The hatched line indicates a significant relationship ($p < 0.05$). In the regression analysis, $F_{1,60} = 31.398$, $P \ll 0.0001$, $r^2 = 0.333$, $y = 28.10731 + 0.458 \times x$ in b.

assemblages. The lower elevation species was comparable with WAS, and the montane species was comparable with CAS. When ants were surveyed along an altitudinal gradient in deciduous forests in the Great Smoky Mountains National Park in the United States, species richness monotonically declined along the temperature gradient (Sanders et al., 2007) which might be negatively correlated with the altitudinal gradient. Sanders et al. (2007) suggested that temperature indirectly influences ant species diversity across spatial grains, perhaps by limiting access to resources. Ant diversity decreases monotonically along altitudinal and latitudinal gradients from 42°N to 45°N in North America (Gotelli and Ellison, 2002). Ant species richness monotonically declines along latitudinal gradient in northern Europe (49° to 70° N) (Cushman et al., 1993), which also occurs in North America from 0° N to 50° N (Kaspari et al., 2003).

Olson (1994) found strong mid-elevational peaks in litter arthropod fauna in a neotropical region. Additionally, dung beetles show mid-elevation peaks along elevation changes in low latitudinal areas of the Colombian Andes (Escobar et al., 2005). Furthermore, moth species richness in Costa Rica also shows hump-shaped patterns with elevation (Brehm et al., 2007). Similar to ants (Fisher, 1999a), butterflies in Madagascar show hump-shaped species richness patterns with changes in elevation and latitude, which are well matched by a null model based

on the mid-domain effect (Lees et al., 1999). Conversely, elevation and butterfly species richness are significantly negatively correlated in a mountain range in the central Great Basin in the United States (Fleishman et al., 1998). The prevalence of mid-elevation peaks in low latitudinal regions was also shown by several insects in a study conducted by McCoy (1990). Of 13 case studies showing a mid-elevation peak or a decrease with elevation, five mid-elevation peak cases and three decreasing cases were observed in low latitudinal regions (<30° north or south), whereas two mid-elevation peak cases and three decreasing cases were shown in high latitudinal regions (McCoy, 1990). Thus, the occurrence of a mid-elevation species richness peak along altitude is regionally dependent, and this is more pronounced in low latitudinal regions than in high latitudinal regions. This may be due to predominance of tropic-origin insect clades rather than temperate-origin insect clades. Therefore, it is expected that the mid-elevation peaks in temperate may occur more frequently in various insects such as springtails, aphids, mayflies, and alderflies, which had evolved from non-tropical regions (Stevens, 1989; McGavin, 2001) and are optimal in temperate.

Acknowledgments

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Appendix A

Table A1

Minimum, maximum, and average values of altitude, latitude, and temperature of ant species. Types, CAS: cold adapted species, and WAS: warm adapted species. Types are defined by the average value of temperature as explained in the text.

Species	Altitude (m)			Temperature (°C)			Type
	Min	Max	Avr	Min	Max	Avr	
<i>Aphaenogaster japonica</i>	200	1300	864	6.27	12.2	8.58	WAS
<i>Camponotus atrox</i>	700	1600	1066	5.47	11.4	7.65	CAS
<i>Camponotus japonicus</i>	400	600	500	10.55	11.8	11.18	WAS
<i>Camponotus kiusuensis</i>	600	1200	750	7.27	11.16	9.7	WAS
<i>Crematogaster osakensis</i>	200	800	500	11.4	14.21	12.8	WAS
<i>Crematogaster teranishi</i>	200	400	300	11.8	12.2	12	WAS
<i>Cryptone sauteri</i>	800	1600	1200	6.16	11.4	8.78	WAS
<i>Dolichoderus sibiricus</i>	600	600	600	8.06	8.06	8.06	CAS
<i>Formica japonica</i>	400	1915	1172	3.5	11.8	7.45	CAS
<i>Formica yessensis</i>	1400	1400	1400	6.94	6.94	6.94	CAS
<i>Hypoconer sauteri</i>	800	800	800	11.4	11.4	11.4	WAS
<i>Lasius</i> spp. (<i>japonicus</i> + <i>alienus</i>)	200	1430	790	6.42	14.21	9.07	WAS
<i>Lasius meridionalis</i>	800	1600	1100	6.16	10.33	8.35	CAS
<i>Lasius spathopus</i>	1100	1100	1100	6.76	6.76	6.76	CAS
<i>Leptothorax</i> sp. 1	700	1430	989	6.42	11.4	7.62	CAS
<i>Monomorium intrudens</i>	200	200	200	14.21	14.21	14.21	WAS
<i>Myrmecina nipponica</i>	400	1560	859	4.34	11.16	8.35	CAS
<i>Myrmica kotokui</i>	600	1900	1159	3.5	11.4	7.09	CAS
<i>Myrmica kurokii</i>	600	1915	1249	3.21	10.33	7.52	CAS
<i>Myrmica</i> sp. 1	1195	1195	1195	7.77	7.77	7.77	CAS
<i>Myrmica</i> sp. 3	1000	1000	1000	7.55	7.55	7.55	CAS
<i>Myrmica</i> sp. 4	1200	1200	1200	6.47	6.47	6.47	CAS
<i>Pachycondyla chinensis</i>	200	200	200	14.21	14.21	14.21	WAS
<i>Pachycondyla javana</i>	200	800	578	9.07	14.21	11.24	WAS
<i>Paratrechina flavipes</i>	200	1200	759	6.42	14.21	9.4	WAS
<i>Pheidole fervida</i>	200	1400	861	5.22	12.2	8.57	CAS
<i>Ponera scabra</i>	600	1000	852	7.58	9.82	8.57	CAS
<i>Pristomyrmex pungens</i>	200	200	200	14.21	14.21	14.21	WAS
<i>Stenamma owstoni</i>	800	1570	1125	3.96	10.43	7.3	CAS
<i>Strumigenys lewisi</i>	200	800	600	10.33	12	11.53	WAS
<i>Tapinoma</i> sp.	1567	1567	1567	5.43	5.43	5.43	CAS
<i>Vollenhovia emeryi</i>	200	1450	607	4.88	14.21	10.7	WAS

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