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ORIGINAL PAPER

Intra-annual variations in abundance and species composition of carabid beetles in a temperate forest in Northeast China

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Abstract In most habitats in temperate zones, species show clear intra-annual shifts in abundance and species composition. Here we aimed to present a comprehensive picture of community composition and seasonal dynamics of carabid beetles (Coleoptera: Carabidae) in broad-leaved Korean pine mixed forest in Northeast China, which harbors a large diversity. We sampled 23,336 individuals from 14 genera and 39 species with pitfall traps over more than 1 year in a 25-ha plot. The six most abundant species accounted for 76.65 % of all individuals. Species estimations for the 25 ha plot ranged from 40 to 45 species. Overall abundance, species diversity, community composition, and abundance of individual species varied seasonally. Most of the abundant species showed an activity pattern of single peak, and were most active between July and early September. Few species showed a bimodal seasonal activity pattern. Both temperature and precipitation significantly influenced the carabid community within a year. Hierarchical clustering indicated that carabid communities of ten consecutive sampling periods could be partitioned into three time-windows, respectively, corresponding with warm temperature-high rainfall season, warm temperature-low rainfall season, and cool and cold season. By using the extended method of indicator species analysis, 11 indicator species were identified for the three time-groups and their combinations, suggesting the existence of temporal niche partitioning among carabid species. We suggest that intra-annual patterns of carabid abundance and species composition can be explained by species responses to seasonal changes in hydrothermal conditions. Cost-effective sampling effort to assess native carabid diversity and assemblage was also discussed in this study.

Keywords Ground beetles · Species richness estimators · Sampling intensity · Seasonality · Population dynamics · Surface fitting

Introduction

Carabid beetles are important arthropod predators in natural and managed ecosystems, and are frequently used as environmental indicators at different spatial scales (Dufrêne and Legendre 1997; Rainio and Niemelä 2003; Kotze et al. 2011; Koivula 2011). Their biodiversity, population dynamics, spatial distributions, and trophic interactions have been extensively investigated in many parts of the world (especially in Europe; see Kotze et al. 2011). However, knowledge about Chinese carabid diversity is relatively scarce even today, despite the fact that China harbors at least 25 % of all Palaearctic carabid species (Schuldt et al. 2009). To provide new information for monitoring and conservation of China's carabid beetles, the present study on carabid ecology was conducted in

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Changbai Nature Reserve, Northeast China. As one of the earliest and largest biosphere reserves in China, Changbai Nature Reserve is well-known for its unique landscapes, natural ecosystems, and biodiversity of flora and fauna. Since the 1950s, hundreds of biological inventories and ecological studies have been conducted here, including a number of arthropod studies. However, because epigeal invertebrates were traditionally neglected by Chinese entomologists, these groups have not been well studied to date in Changbai Nature Reserve (but see a recent study by Zou et al. 2013) or even in the entire Northeast China. Hence, little is known about their phylogeny and biological and ecological features (e.g. life history, community composition, seasonal dynamics, reproductive phenology and habitat preference).

Understanding seasonal patterns of ground beetles in a given region is important for several reasons. Firstly, seasonal variations in abundance, richness and species composition emphasize the role of phenology and the influence of survey timing in studying carabid-habitat associations. Secondly, seasonal information of carabid beetles is essential to understand the relevant ecological processes and thus management aspects. For example, invertebrate pest predation (Traugott 1998; Suenaga and Hamamura 2001; Paill 2004) and seed consumption (Honek et al. 2003) by carabid beetles show seasonality due to their phenology; asynchronous seasonal cycles may attribute to the reduction of interspecific competition among carabids (Tauber and Tauber 1981; Werner and Raffa 2003). Thirdly, the lack of information on seasonal activity patterns of carabid beeltes is a major obstacle for carabid conservation, because species that are active during times of intensive management practices (e.g. pesticide application and soil cultivation) are predicted to be affected more than species that are active during times of less disturbance (Huusela-Veistola 1996; Fadl et al. 1996).

Many investigations in temperate and boreal forests indicated a distinct seasonality in carabid abundance (Niemelä et al. 1989; Epstein and Kulman 1990; Cartellieri and Lövei 2003; Yu et al. 2006). Previous studies have linked the seasonal activity rhythm of carabid beetles to their life history characteristics (e.g. reproductive activity, dormancy and diapause; Loreau 1985; Wallin 1989; Lys and Nentwig 1991; Hutchison 2007), prey availability (Loreau 1988; Niemelä et al. 1992), and seasonal variations in environment parameters (Kotze et al. 2011) such as temperature (Honek 1997), photoperiod (Tauber et al. 1986), rainfall (Paarmann and Stork 1987; Tauber et al. 1998), soil moisture (Niemelä et al. 1992; Lövei and Sunderland 1996), and the combinations of physical factors (e.g. photoperiod–temperature interaction; see Thiele 1969; Lopatina et al. 2011).

To obtain reliable biodiversity estimates for carabids requires large sampling efforts by either increasing sampling intensity and/or trapping duration when assessing spatial and temporal patterns of carabid beetles. However, due to the limitation of available resources (e.g. manpower, time and funding), it is important to determine a cost-effective sampling effort to adequately represent a local community.

Here we conducted a pitfall trapping survey in a 25-ha permanent forest plot from mid-June 2010 to early July 2011. Specifically, our study had three aims: (1) to examine intra-annual patterns of native carabids' abundance, species diversity and community composition; (2) to estimate the sampling effort required to get sufficient numbers of species to assess the local species diversity; and (3) to examine the relationship between seasonal weather conditions (air temperature and precipitation) and intra-annual patterns of carabid beetles.

Materials and methods

Study area

Changbai Mountain (also known as Baekdu Mountain) is located on the border between North Korea and China (128°03′18″E, 42°00′24″N), and is the highest mountain (2,691 m) in northeast Asia. The Changbai Nature Reserve (with a total area of 196,465 hm^2) was established in 1960 to protect ecosystems and natural resources in that region. In 1980, the Reserve joined the World Biosphere Network under the UNESCO Man and the Biosphere (MAB) Programme. There are four distinct vertical vegetation zones: the broad-leaved Korean pine mixed forest zone (the zonal vegetation in this region; 500–1,100 m asl), the evergreen coniferous forest zone (1,100–1,800 m asl), the Erman's birch (*Betula ermanii* Cham.) forest zone (1,800–2,000 m asl), and the tundra zone (above 2,000 m asl).

Our study site and the 25-ha permanent forest plot (42°23′N, 128°05′E; Fig. 1) is situated in the broad-leaved Korean pine mixed forest zone in the Changbai Nature Reserve, where mean annual temperature is 3.6 °C and mean annual precipitation is 695 mm (Guan et al. 2005). The vegetation in the study plot is representative of a late successional stage of broad-leaved Korean pine mixed forest and the mean age of the canopy trees is about 300 years. The eight most abundant tree species accounted for 83.4 % of the total individuals, including three overstory layer species (*Tilia amurensis*, *Pinus koraiensis*, and *Ulmus japonica*), three midstory layer species (*Acer mono*, *A. pseudo-sieboldianum*, and *Syringa reticulata*), and two understory layer species (*Corylus mandshurica* and *A.*

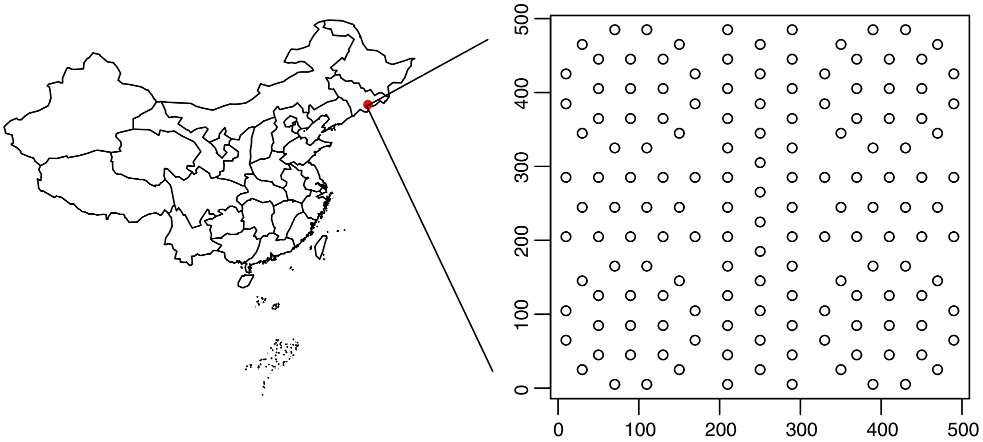

Fig. 1 Study site and the spatial arrangement of the 150 pitfall traps in the 25-ha temperate forest plot

barbinerve). See Hao et al. (2007) for more details about the plot and its plant communities.

Weather data collection and definition of seasons

To assess the relationship between seasonal weather conditions and temporal changes in carabid population and community, daily weather data was collected at an automatic weather station at the Changbai Mountain forest ecosystem research station, located about 3 km from our study stand. There is a difference between the meteorological seasons and the astronomical seasons, thus, to avoid confusion, we emphasized that the seasons in the texts of this paper refer to the astronomical seasons. Based on the astronomical definitions, in the northern hemisphere, spring begins on March 20–23, summer begins on June 20–23, autumn begins on September 20–23 and winter begins on December 20–23. We didn't use the meteorological seasons used by Chinese meteorologists that define the beginning of summer as when the mean temperature of five consecutive days rises above 22 °C, which is obviously not suitable for cold northern regions like our study site, where there are few days above 22 °C (e.g. only 4 days for 2010). According to the astronomical definitions of the seasons, the mean air temperature of winter, spring, summer, autumn of our study site is −12.9, 9.0, 17.7, and −1.5 °C (calculated based on meteorological observation data of 2010 and 2011).

Carabid sampling and identification

We used pitfall traps (depth = 145 mm, diameter 85 mm at the top) to collect carabid beetles. The traps were partly filled with 50 % propylene glycol and a few drops of ordinary detergent. Each trap was covered with a metal roof (15 × 15 cm) to protect from rain, litterfall and disturbance by animals. We installed 150 traps within the 25-ha temperate forest plot (6 trap/ha, for map see Fig. 1) on 15 June 2010, and the trapping continued until 7 July 2011. From 15 June to 18 October 2010 and from 5 May to 7 July 2011, the traps were emptied and refilled every 3 weeks. Beginning 18 October 2010, the pitfall traps with preserving liquid were left in situ and the captured beetles were not collected until 5 May 2011; during the long cold season, the captured individuals only accounted for 0.36 % of the total individuals collected during the entire study. In total, there were 10 consecutive sampling periods throughout the study. The start/end dates of the ten sampling periods, as well as the mean air temperature and accumulated precipitation in each sampling period are given in Table 1.

It is known that the catches from pitfall traps are not solely a reflection of population size but rather a combination of both abundance and activity (Halsall and Wratten 1988; Woodcock 2005; Hutchison 2007). Some authors believe that pitfall trapping can only be used to infer differences in population size for one species among habitats and should not be used to compare the relative abundance among species (see Dufrêne and Legendre 1997). However, it was considered that a large difference in the relative abundances of two species was enough to infer that one is more abundant than the other (see Woodcock 2005). Moreover, continuous sampling over the whole activity period or the whole year was considered to be able to provide reliable data for comparing relative population sizes among species (Baars 1979; Epstein and Kulman 1990). It is now acknowledged that pitfall trapping under standardized conditions was appropriate for comparing species richness and activity/abundance levels of larger (>5 mm) ground-dwelling beetles (see Riley and Browne 2011). Hence, the relatively long duration of pitfall trapping (about 13 months) and the comparatively large

Table 1 Start and end dates of the ten consecutive sampling periods

Codes of sampling periods	Start/end dates of each sampling period	Number of trap-days	Mean air temperature (°C)	Accumulated precipitation (mm)	Group of periods
T1	15 June[a]–5 July 2010	20	18.92	62	1
T2	5–26 July 2010	21	19.21	140	2
T3	26 July–17 August 2010	22	19.65	157.8	2
T4	17 August–8 September 2010	22	18.73	114	2
T5	8–28 September 2010	20	12.81	84.8	3
T6	28 September–18 October 2010	20	6.91	43	3
T7	18 October 2010–5 May 2011	199	−6.58	7.85	3
T8	5–27 May 2011	22	11.07	11.8	3
T9	27 May–18 June 2011	22	15.02	48	1
T10	18 June–7 July 2011	19	18.58	54.4	1

[a] 15 June 2010 is the date the pitfall traps were installed. The ten periods were classified into three time-windows in terms of carabid community data (using a hierarchical clustering; see "Data analysis" section for method details). Time-window 1 corresponded to the period from the end of May to early July (average daily temperature 17.4 °C and precipitation per day 2.7 mm), time-window 2 corresponded to the period from early July to early September (average daily temperature 19.2 °C and precipitation per day 6.3 mm), time-window 3 corresponded to the period from early September to the end of May in the following year (average daily temperature −2.58 °C and precipitation per day 0.8 mm) and represented the less active and the hibernating periods

sampling intensity used, to a large extent, allow this study to provide robust data for analyzing community structure and activity patterns of carabid beetles.

All the samples collected from each pitfall trap during each sampling period were brought back to laboratory at the Institute of Applied Ecology, Chinese Academy of Sciences, and stored in 70 % alcohol before further sorting and identification. All carabid beetles were identified to the species level. Species identification was confirmed or corrected by appropriate specialists (see Acknowledgements), and the voucher specimens were kept at IAE/CAS, Shenyang, China. Species in the larval stage were not considered in this classification and further statistical analysis.

Data analysis

As the number of trap-days in all sampling periods except for the 7th are very similar (19–22 trap-days; Table 1), the abundance data from each sampling period was not standardized to a certain value (e.g. 21 trap-days). All statistical analyses were performed in the R statistical environment (R Development Core Team 2011). A rank-abundance curve was calculated to determine the occurrence of dominant, common, and rare species of the entire study. The overall abundance of all carabid species, species diversity (species richness and Shannon diversity index), and community evenness (Pielou's evenness index) were calculated for each sampling period.

Because communities may change without affecting measures of alpha-diversity, similarity in carabid assemblages between any pair of sampling periods was assessed using principal coordinate analysis (PCoA) with Bray–Curtis distance (see note by Legendre and Legendre 2012: p. 311) using function *cmdscale* in stats package. A hierarchical clustering, Ward's minimum variance clustering, (function *hclust* in stats package) was used to partition the carabid communities of the ten consecutive sampling periods into few discrete groups. We conducted a Hellinger transformation (Legendre and Gallagher 2001) on the species data before this analysis. The species with significant association to one group or any combinations of time-groups were determined using function *multipatt* in indicspecies package (De Cáceres and Legendre 2009; De Cáceres et al. 2010). The function provides an extended method for indicator species analysis proposed by Dufrêne and Legendre (1997).

Relationships between ordination pattern and seasonal weather data were analyzed by fitting environmental vectors and surfaces to ordination patterns (using *envfit* and *ordisurf* functions in vegan package; Oksanen et al. 2011). For performing these analyses, mean air temperature and accumulated precipitation were calculated for each sampling period, except that the accumulated precipitation in sampling period 7 was calculated on a 21-day basis. We also performed PCoA ordination based on Sørensen coefficient (binary Bray–Curtis in vegan, which neglected the abundance information of species) to test for robustness of our results.

For each of the ten sampling periods, sample-based rarefaction curves (using function *specaccum* in vegan package) and Jackknife 1 estimator curves (using function *poolaccum* in vegan package) were created. The total extrapolated number of species occurring in and around the

Table 2 List of carabid species collected over the entire study, with relative abundance, relative frequency of occurrence (caught by how many traps) and code of each species given

Species names and their codes		Relative abundance (%)	Relative frequency of occurrence (%)	The association between species and combinations of time-groups[a]		
				IndVal	Adjusted *p*	Group of periods
s21	*Pterostichus orientalis* (Motschulsky)	15.187	100.00			
s22	*Pterostichus* sp. 1	14.810	92.00			
s23	*Pterostichus adstrictus* Eschscholtz	14.013	96.00			
s7	*Carabus billbergi* Mannerheim	11.604	99.33			
s17	*Pterostichus interruptus* (Dejean)	11.133	98.67	0.998	0.026	1 + 2
s11	*Leistus niger* Gebler	9.899	100.00			
s3	*Carabus granulatus* Linnaeus	6.505	94.00			
s1	*Carabus vietinghoffi* Adams	5.991	98.67	0.997	0.015	1 + 2
s2	*Carabus canaliculatus* Adams	2.515	80.00	0.996	0.015	1 + 2
s4	*Carabus venustus* Morawitz	2.228	40.00	1.000	0.004	1 + 2
s28	*Synuchus nitidus* (Motschulsky)	0.964	30.67	0.980	0.036	2
s35	*Pterostichus strenuus* (Panzer)	0.857	59.33			
s9	*Carabus constricticollis* Kraatz	0.793	60.00			
s20	*Pterostichus nigrita* (Paykull)	0.638	38.00			
s5	*Carabus seishinensis* Lapouge	0.514	16.67	1.000	0.004	1 + 2
s26	*Pristosia* sp. 1	0.497	35.33	0.971	0.018	2
s6	*Carabus fraterculus* Reitter	0.463	34.67			
s30	*Synuchus agonus* (Tschitscherine)	0.313	20.67			
s10	*Cychrus morawitzi coreicus* Breuning	0.253	26.00	1.000	0.004	1 + 2
s24	*Pterostichus gibbicollis* (Motschulsky)	0.146	11.33			
s19	*Pterostichus mandzhuricus* Lutshnik	0.116	12.00	1.000	0.004	1 + 2
s43	*Pterostichus horvatovichi* Kirschenhofer	0.094	10.67			
s32	*Synuchus nivalis* (Panzer)	0.086	10.67			
s8	*Carabus schrencki* Motschulsky	0.073	9.33			
s12	*Trechus ephippiatus* Bates	0.064	8.00			
s31	*Synuchus crocatus* (Bates)	0.064	6.67	0.918	0.036[a]	2
s25	*Agonum* sp. 1	0.051	4.00			
s14	*Amara congrua* Morawitz	0.047	6.00	1	0.011	1
s29	*Synuchus melantho* (Bates)	0.017	2.00			
s40	*Harpalus jureceki* (Jedlicka)	0.009	1.33			
s42	*Platynus* sp. 1	0.009	1.33			
s44	*Poecilus reflexicollis* Gebler	0.009	0.67			
s13	*Dyschirius* sp. 1	0.009	1.33			
s33	*Harpalus laevipes* Zetterstedt	0.009	1.33			
s41	*Pterostichus microcephalus* (Motschulsky)	0.004	0.67			
s15	*Harpalus ussuriensis* Chaudoir	0.004	0.67			
s34	*Trichotichnus* sp. 1	0.004	0.67			
s36	*Pterostichus subovatus* (Motschulsky)	0.004	0.67			
s38	*Pterostichus* (Nialoe) sp. 2	0.004	0.67			

[a] The species with significant associations to one group of periods or any combinations of time-groups (cf. Table 1 for the memberships of each group) were calculated using extended method of indicator species analysis and results are shown. The right three columns represent their indicator value (IndVal), the adjusted *p* value, and the time-groups for which they best match. Three species (s28, s26, s31) showed significant associations with time-group 2, one species (s14) best matched time-group 1, and seven species (s4, s5, s10, s19, s17, s1 and s2) were identified characteristic of time-group 1 + 2. No indicator species was identified for time-group 3

study plot was estimated using five species richness estimators. Two abundance-based estimators (Chao1 and ACE) were calculated using function *estimateR* in vegan package, and three incidence-based estimators (Chao2, first-order jackknife and bootstrap) were calculated using function *specpool* in vegan package. There is a wide range of species richness estimators available, but determining which of these estimators is least biased for a specific set of data is complex, and dependent on factors such as community evenness and sample sizes (Brose et al. 2003; Boonzaaier et al. 2007). Since datasets of different sampling periods differed in species abundance distributions, which might influence the performance of different estimators in different ways, all five of the above estimators were used for comparison.

According to Colwell (2009) and Colwell and Coddington (1994), the real utility of rarefaction species accumulation curves lies in its potential to predict species richness that can be obtained with much smaller samples. To assess the effects of sampling intensity, for the entire study period, we constructed both sample-based and individuals-based rarefaction curves (function *rarefy* in vegan package).

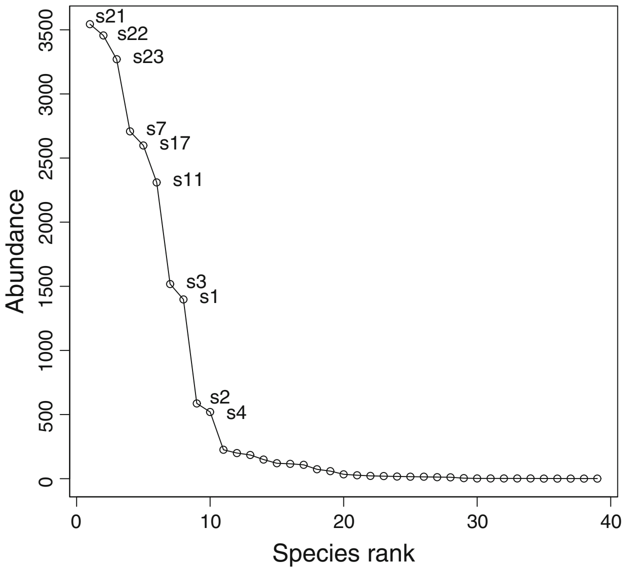

Fig. 2 Rank-abundance curve of the 39 carabid species recorded over the entire study period. s1, s22 … are the codes of species (cf. Table 1 for their latin names). The *long tail* of the curve indicates that there are many rare species and the carabid community has low evenness

Results

Species composition

In total, 23,336 adult carabid beetles from 14 genera and 39 species were caught throughout the study (Table 2). The rank-abundance curve (Fig. 2) and Table 2 indicates that the carabid community has low evenness, and there are obvious dominant species and many rare species, including 5 singletons and 5 doubletons. Of all 39 species, the 6 most abundant species accounted for 76.65 % of all individuals captured over the study (Table 2), and we considered them the dominant species. The next 4 abundant species together comprised 17.24 % of all catches and were considered common species. The remaining 29 species were considered rare species because they together accounted for 6.1 % of all captures and each species accounted for no more than 1 % of all specimens.

Seasonal activity of carabid beetles

A clear seasonal variation in total abundance were observed, and the results showed that it closely followed the fluctuations in air temperature (Fig. 3), as the largest and the lowest catches occurred during the hottest and the coldest time of the year respectively. Our analyses of carabid activity patterns showed that 4 of the 19 most abundant carabid species (specimens of each species was greater than 50) belonged to the two-peak activity pattern (Fig. 4), and the other 15 species belonged to the single peak activity pattern (among them, 12 species exhibited a single-peak in midsummer and 3 species showed a single-peak in early summer).

Species diversity and community evenness

Carabid diversity and evenness varied seasonally (Table 3). The estimated species richness for each sampling period and for the entire study are also listed in Table 3. By simply comparing the five species richness estimators in terms of their mean value and estimated error, we considered that the abundance-based coverage estimator (ACE) was the best estimator for this study because it always gave the intermediate estimate values with small estimated errors. According to the estimation by ACE, the ‘true’ species richness of the study site ranged between 42.93 ± 2.45 (i.e. 40–45 species; Table 3).

Carabid communities in different sampling periods

When performing ordination using Bray–Curtis (based on abundance data) and Sørensen (based on presence/absence data) distances, similar ordination patterns were obtained, except for the position of sampling period 5, which was closer to sampling period 2–4 in Fig. 5b but closer to sampling period 8 in Fig. 5a. This is because species abundance had greatly reduced from sampling period 4–5 but species richness and community composition didn’t change considerably (a time-lagged response to temperature variations).

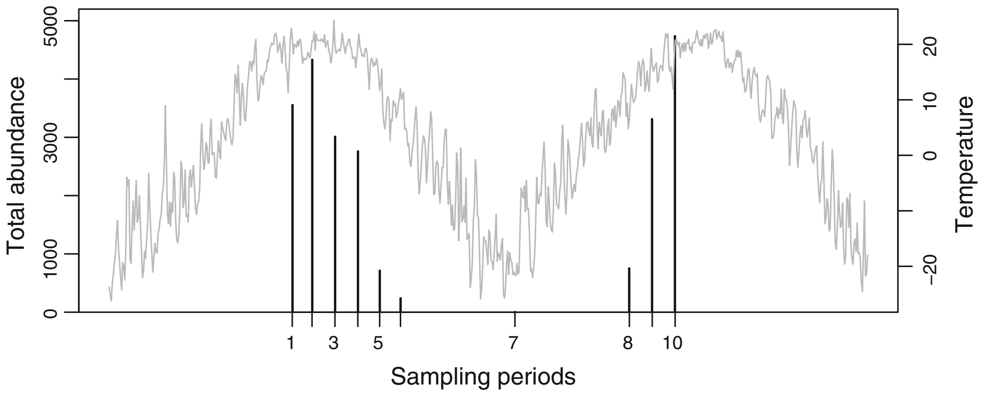

Fig. 3 The total number of carabid beetles captured (*bars*) in each of the ten sampling periods and the daily temperatures (°C; *grey line*) across 2010 and 2011. The abundance data were standardized to 21 trap-days. See Table 1 for start/end dates of each sampling period. The total catches increased rapidly from early May until it peaked in July, then slightly declined in August and decreased rapidly with the coming of autumn (September). The number of individuals captured in sampling period 7 was extremely low (85 individuals)

By applying Ward clustering, the carabid communities of the ten consecutive sampling periods could be partitioned into a different number of groups, but partitioning into three time-groups seems more meaningful, since each group corresponds with a distinct hydrothermal period: (1) warm temperature-low rainfall, (2) warm temperature-high rainfall, and (3) cool and cold season period (Table 1). By using the extended method of indicator species analysis, 11 indicator species were identified for the three time-groups and their combinations (Table 2).

When fitting environmental vectors on the ordination graph (PCoA based on Bray–Curtis distance; Fig. 5a), the result suggested a significant correlation between temperature and ordination pattern (vector fitting, $r^2 = 0.850$, p value $= 0.002$ based on 999 permutations). At the same time, a marginal significant correlation ($r^2 = 0.554$, p value $= 0.077$) between accumulated precipitation and ordination pattern was found. Figure 5a suggested that the role of precipitation was more important in warm seasons (time-group 1 and 2; Table 1). When excluding the data of time-group 3 (figure not shown), we found a significant relationship between precipitation and carabid communities ($r^2 = 0.926$, p value $= 0.027$) and a non-significant correlation between temperature and carabid communities (p value $= 0.166$). When performing ordination using Sørensen distance, we found both temperature ($r^2 = 0.936$, p value $= 0.003$) and precipitation ($r^2 = 0.773$, p value $= 0.011$) significantly correlated with carabid species composition (Fig. 5b).

Discussion

Community structure and species richness

Our finding that less than 15 % of species accounted for more than 75 % of the total individuals is consistent with most studies in temperate or boreal forests, where carabid communities are composed largely of few dominant species (Niemelä et al. 1988; Huber and Baumgarten 2005; Jung et al. 2012). 29 relatively rare species were identified in this study, but they are not necessarily the endangered species that should be given priority protection (see Müller and Goßner (2010) for a discussion on low-abundance species and endangered species). We conclude that the estimated 40–45 (42.93 ± 2.45) carabid species is the minimum number of species present in the broad-leaved Korean pine mixed forest because of the potential high β-diversity among stands (see the study by Müller and Goßner (2010) on saproxylic beetles). Compared to many studies in temperate or boreal forests, in which carabids were sampled across multiple habitats or over several years (e.g. Liebherr and Mahar 1979; Finch 2005; Huber and Baumgarten 2005; Klimaszewski et al. 2005; Latty et al. 2006; Jung et al. 2012), the 39 species that actually collected from the 25-ha plot seems a relatively high value for a temperate forest.

Activity patterns and life cycles

As an evolutionary strategy, carabid beetles (and probably all the land animals) may optimize and synchronize their life cycle with seasonal changes of the environment (Kotze et al. 2011). This, in combination with local climate characteristics (see mean air temperature of four seasons in M&M section) may explain why most of the abundant species concentrated their activities in the time period spanning from the end of May to early September, an expected result consistent with the general pattern of insect seasonality in the temperate zone, where most species are active during spring or summer (Wolda 1988).

Larsson (1939, see also Thiele 1977; Holland and Luff 2000) distinguished three types of life cycles for carabids

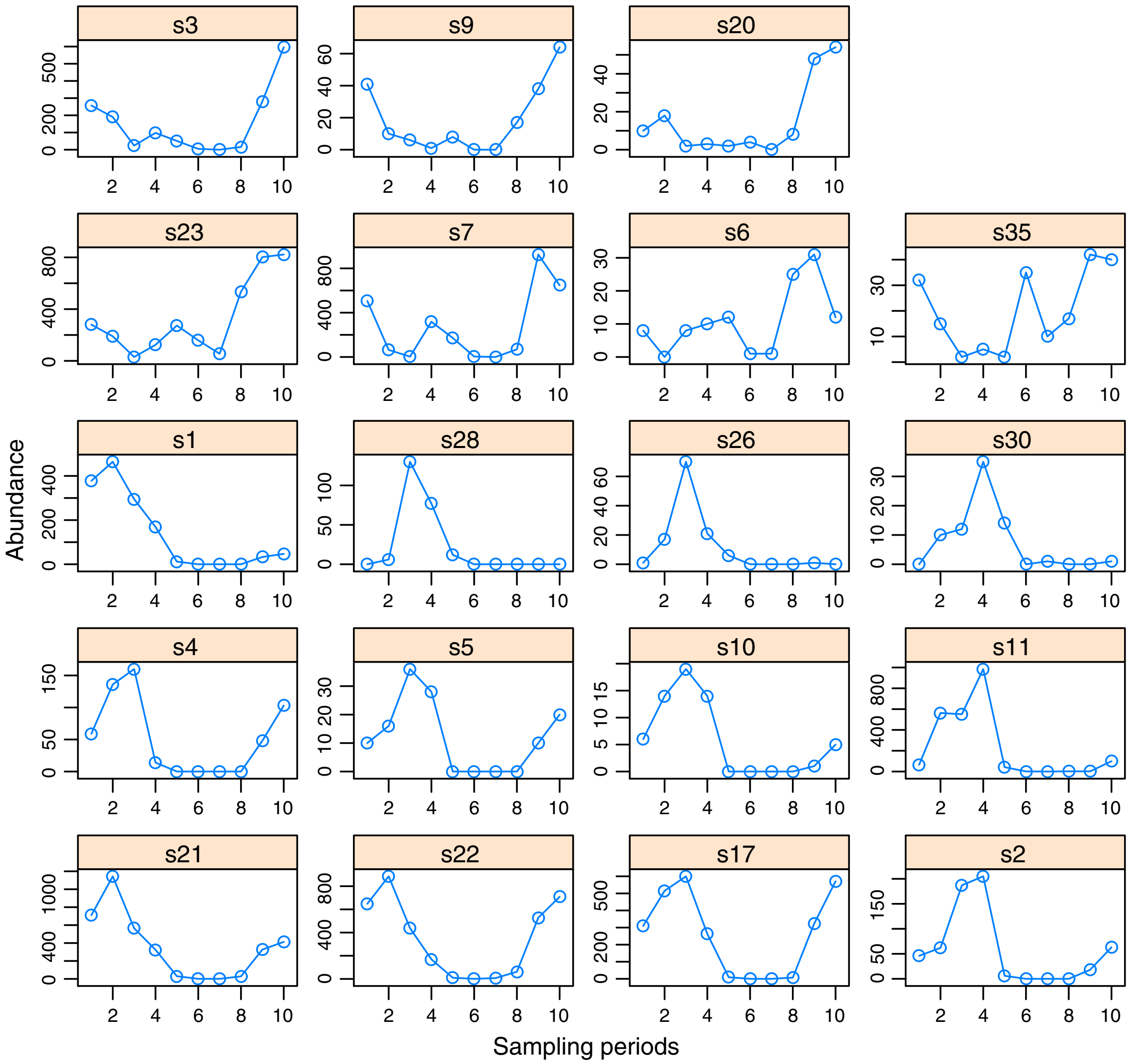

Fig. 4 Activity patterns of the 19 most abundant species (number of individuals for each species was greater than 50). Start/end dates of each sampling period were shown in Table 1. Three categories of activity pattern were distinguished. Category 1 corresponded to the species with a single-peak of abundance in midsummer (corresponding to sampling periods 2, 3 and 4), including 12 species (s21: *Pterostichus orientalis*; s22: *Pterostichus* sp. 1; s17: *P. interruptus*; s2: *Carabus canaliculatus*; s4: *C. venustus*; s5: *C. seishinensis*; s10: *Cychrus morawitzi coreicus*; s11: *Leistus niger*; s1: *C. vietinghoffi*; s28: *Synuchus nitidus*; s26: *Pristosia* sp. 1 and s30: *S. agonus*). Category 2 includes three species (s3: *C. granulatus*; s9: *C. constricticollis* and s20: *P. nigrita*), which has a single-peak of abundance in early summer (corresponding to sampling period 10). Category 3 included four species (s23: *P. adstrictus*; s7: *C. billbergi*; s6: *C. fraterculus* and s35: *P. strenuus*), and each has two activity peaks annually

in the temperate region: (1) ‘autumn-breeders’ that reproduce in autumn (or even from the middle of summer onwards) and hibernate as larvae; (2) ‘spring breeders with autumn activity’ who hibernate as adults, reproduce from spring to early summer, after which most of the beetles die off, with a new generation appearing in autumn; and (3) ‘spring breeders without autumn activity’ that reproduce at the same time as the other spring breeders, but the young beetles exhibit little activity following eclosion in autumn. In addition, some species have flexible reproductive periods or require more than 1 year to develop (Thiele 1977; Loreau 1985; Paarmann 1990; Fadl and Purvis 1998). It is known that the reproduction periods of carabid beetles often coincide with their activity peaks (Niemelä et al. 1992; Lövei and Sunderland 1996; French and Elliott 1999). According to this general rule, our results (Fig. 4) suggested that 4 of the 19 most abundant species (*Pterostichus adstrictus*, *Carabus billbergi*, *C. fraterculus* and *P. strenuus*) may be “spring breeders with autumn activity” because they showed bimodal seasonal peaks, a pronounced spring peak and a less pronounced peak between mid-summer and mid-autumn (see Niemelä et al. 1992 for a similar pattern); most of the other 15 species may be “spring breeders without autumn activity”. It was

Table 3 Shannon diversity index, Pielou's evenness index, and observed and estimated number of species of each sampling period and of the entire study

The codes of ten sampling periods	Shannon diversity index	Pielou's evenness index	Observed species richness	Species richness estimates ± standard errors of the estimators[a]				
				Chao1	ACE	Chao2	Jack1	Boot
T1	2.201	0.684	25	30 ± 17.14	29.24 ± 2.78	31.2 ± 7.55	29.97 ± 2.22	27.12 ± 1.18
T2	2.106	0.663	24	27 ± 11.66	29.50 ± 2.74	32 ± 11.66	27.97 ± 1.99	25.61 ± 1.02
T3	2.231	0.685	26	26.2 ± 1.03	27.03 ± 2.52	30 ± 5.29	29.97 ± 1.99	27.81 ± 1.18
T4	2.230	0.677	27	33 ± NaA	30.20 ± 2.72	27 ± 0	30.97 ± 1.99	28.64 ± 1.10
T5	1.965	0.627	23	23.25 ± 1.31	23.90 ± 2.38	24.5 ± 2.29	25.98 ± 1.72	24.62 ± 1.10
T6	1.154	0.464	12	22 ± NaA	18.56 ± 2.12	12 ± 0	16.97 ± 2.63	13.89 ± 1.31
T7	1.285	0.558	10	20 ± NaA	17.57 ± 2.30	10 ± 0	14.97 ± 2.22	11.93 ± 1.16
T8	1.302	0.493	14	14 ± 1.32	14.54 ± 1.84	14.17 ± 0.54	14.99 ± 0.99	14.77 ± 0.77
T9	2.018	0.644	23	25 ± 5.29	27.94 ± 2.68	27 ± 5.29	26.97 ± 1.99	24.84 ± 1.11
T10	2.208	0.678	26	27.5 ± 3.49	29.27 ± 2.42	28.67 ± 3.49	29.97 ± 1.99	27.93 ± 1.15
The entire study	2.419	0.660	39	40.67 ± 2.96	42.93 ± 2.45	43.50 ± 4.80	44.96 ± 2.43	41.78 ± 1.38

NaA not avaiable

[a] Richness estimator values represent the mean of 100 randomizations of sample order. See Table 1 for start/end dates of each sampling period

hypothesized that high proportion of spring breeders (with earlier reproduction strategy) occur in northern biomes to ensure their offspring have adequate time to develop before winter (Niemelä et al. 1992; Werner and Raffa 2003).

Previous studies indicated that annual activity rhythms and life cycle strategies of a certain carabid species may vary among years (Epstein and Kulman 1990; Suenaga and Hamamura 2001; Boivin and Hance 2003), or among habitats (e.g. along geographical or altitudinal gradients; Refseth 1980; Niemelä et al. 1989; Sota 1996; Butterfield 1996) which are mainly affected by climatic and microclimatic conditions. We inferred the types of life cycles of the 19 abundant species according to their activity data over 13 months, but more detailed information and observations on the biology of breeding and overwintering native carabids is needed to confirm the types of life cycles.

Graphs of annual activity patterns (Fig. 4) and the extended method of indicator species analysis (Table 2) suggested some species are significantly associated with certain periods of time, and a seasonal differentiation of activity cycles (asynchronous peaks of abundance) occurred between certain pair of species. In studies of carabid beetles (Niemelä et al. 1997; Werner and Raffa 2003) and some other insect species (Ahearn 1971; Whicker and Tracy 1987; Schultz 1989; Krasnov and Ayal 1995), researchers hypothesize that the asynchronous activity pattern or the temporal and seasonal niche partitioning may minimize competition among behaviorally similar species. Lundgren et al. (2009) further hypothesize that seasonal and diel niche partitioning may contribute to the maintenance of a diverse and abundant epigeal predator community.

Intra-annual dynamics and relationship to seasonal weather conditions

Temperature is a major factor influencing activity, flight, foraging behavior, and metabolism of carabid species (Lövei and Sunderland 1996; Saska et al. 2010). A number of studies have examined the effects of temperature fluctuations on carabid activity-density within a year (see Niemelä et al. 1989). For example, Niemelä et al. (1989) found the catches of 5-day periods follow the mean air temperature, and the correlation was especially pronounced in the period from May until mid July. In Honek's study (1997), a significant correlation between average daily temperatures and daily catches of carabid species occurred in spring, early summer and late summer, respectively. In the present study, we also found a significant positive correlation between carabid abundance and mean air temperature of each sampling period (Spearman's rank correlation: two-sided p value = 0.0184).

Moisture is also a major factor that influences insect life cycles and thus their seasonal ecology (Tauber et al. 1998). Niemelä et al. (1992) suggested that the early activity peak of carabids in central Alberta may be explained by soil moisture condition as it changed in early season. In a typical lowland rain forest, Paarmann and Stork (1987) suggested the seasonal reproductive rhythm of Carabidae species was a response to the seasonal rainfall patterns of the coastal areas. In a study on Tenerife Island, Gómez (2009) constructed the regression models to explore the effects of one of the three weather variables (minimum and maximum temperature, and precipitation) on activity density of ground beetles, and eventually found a positive

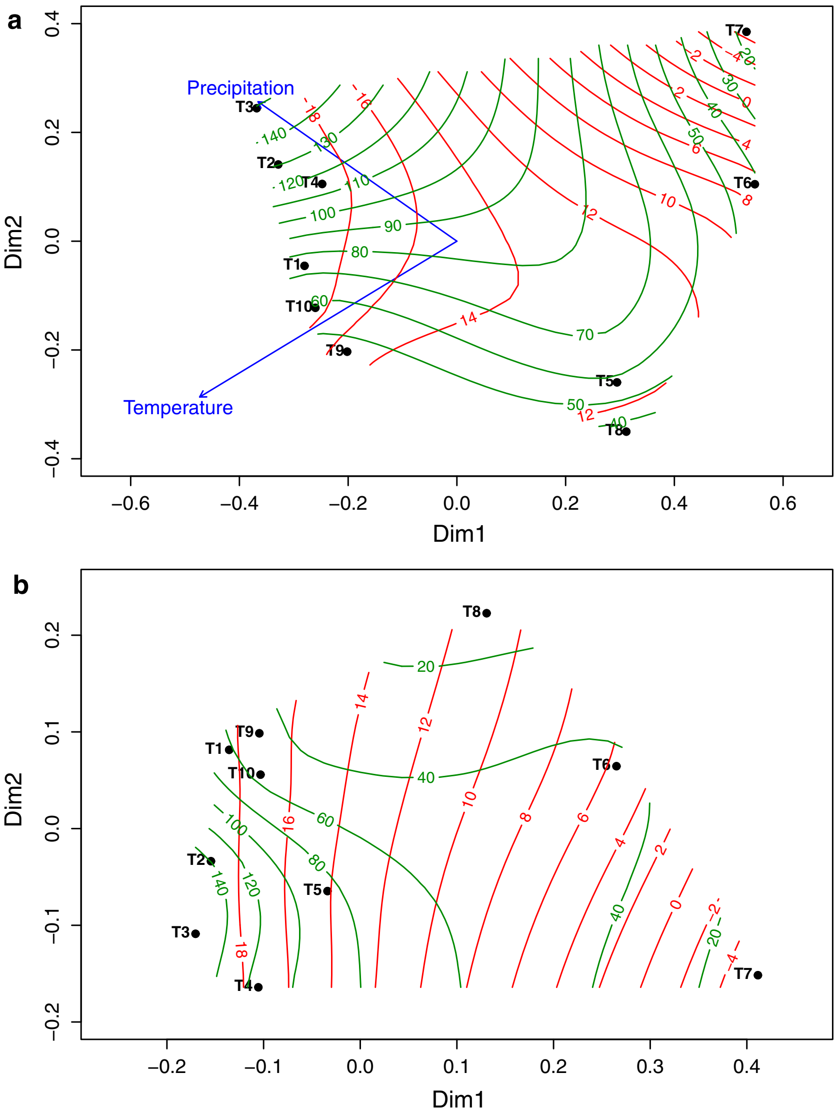

Fig. 5 Vector fitting (*blue lines*) and surface fitting temperature (*red lines*; unit = centi-degree) and precipitation (*green lines*; unit = millimeter) on ordination graphs, **a** PCoA ordination with Bray–Curtis distance, and **b** PCoA ordination with Sørensen distance. *T1–T10* represent sampling period 1–10 (cf. Table 1 for their start/end dates). The fitted vectors are displayed as *arrows*. The *arrow* points to the direction of most rapid change in the environmental variable, while the length of the *arrow* is proportional to the correlation between ordination and environmental variable. The significance of vector fits was determined using permutation tests (n = 999) at the $p = 0.05$ level. 'Precipitaiton' and 'Temperature' represent the accumulated precipitation and mean air temperature in each sampling period respectively; as an exception, the accumulated precipitation in sampling period 7 was calculated on a 21-day basis. Figure 4b suggested that the association between temperature and intra-annual patterns of carabid species composition was almost linear since the fitted contours were equally spaced *parallel lines*. For conciseness, *vector fitting lines* were not shown in Fig. 4b. (Color figure online)

influence of rainfall and a negative influence of temperature on carabid activity density. In our study, we did not find significant correlation between accumulated precipitation and the total catches for each sampling period (Spearman's rank correlation: two-sided p value >0.05).

Nevertheless, when analyzing at the community level, we found both temperature and precipitation significantly influenced the seasonal patterns of the carabid community (Fig. 4, ordination and surface fitting; Table 1, hierarchical clustering): temperature (axis 1) separated carabid communities of the ten consecutive sampling periods into two groups, an active period group which corresponded with warm seasons (combined time-window 1 and 2, Table 1) and an inactive period group that corresponded with cool and cold seasons (time-window 3, Table 1); precipitation (axis 2) further separated the active period group into two groups, coinciding with warm-humid hydrothermal period (time-window 2) and warm-low rainfall period (time-window 1), respectively. Therefore, we concluded that the seasonality in carabid beetles

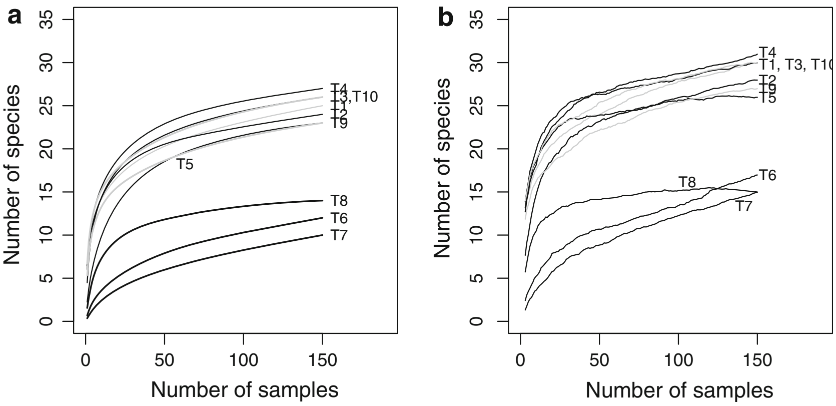

Fig. 6 Sample-based rarefaction curves **a** and Jackknife 1 estimator curves **b** for the ten sampling periods. The curves shows the mean of 100 randomizations. *T1–T10* represent sampling period 1–10 (cf. Table 1 for their start/end dates). The year-round sampling indicated that the total species pool is much larger than can be ascertained by sampling over a short period of time (e.g. 3 weeks)

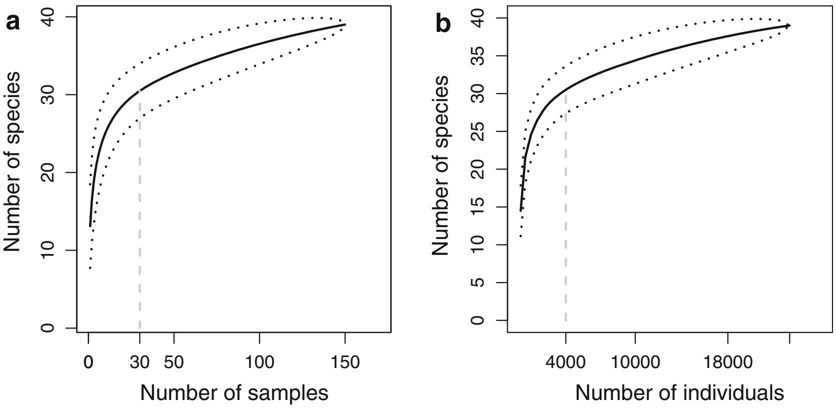

Fig. 7 Sample-based (**a**) and individual-based (**b**) rarefaction curves for the entire study

(including their activities and community composition) is a response to seasonal weather conditions (the combined effects of air temperature and precipitation). In addition, according to our results, we found that a daily mean temperature of 15–20 °C may provide the optimal thermal conditions for most of the native carabid beetles (consistent with previous reports; see Thiele 1977).

Cost-effective sampling efforts to assess native carabid diversity and assemblage

Our study suggested that sampling over a short period of time (e.g. 3 weeks, Fig. 6) may result in severe underestimations of species richness. However, it is unnecessary to sample throughout the year due to the extremely low captures in very cold seasons. The number of pitfall traps used for carabid sampling in a given area was highly variable in previous studies (see Woodcock 2005). Our results suggested that increasing the number of traps above 150 is still likely to catch additional species (Figs. 6, 7a). However, if using only 10 traps throughout a year, we may obtain up to 25.1 ± 2.6 species (Fig. 7a), which probably comprise most of the common species. This, to some extent, supported the statement by Obrtel (1971), who considered it likely to obtain reliable species data at a site from 12 pitfall traps when identifying common ground beetles in a deciduous lowland forest. However, using such small sample sizes poses a risk due to the potentially serious problem of trap losses (Kotze et al. 2011).

For the broad-leaved Korean pine mixed forest in northeastern China, our results suggested that one could perform samplings with 30 traps from May to September, or cumulatively collect about 4,000 specimens over a series of discrete periods within one growing season to obtain about 30 carabid species of the forest type (Fig. 7), which would include all the common species and a number of ‘rare’ species. Because the broad-leaved Korean pine mixed forest is the most complex forest type in the Changbai Nature Reserve, we believed that this sampling effort might be sufficient for each of the other forest type in the study region, and might be considered as a recommend sampling effort to assess native carabid diversity and assemblage at the local scale (e.g. for a specific habitat or forest type). Interestingly, however, in a recent study, Zou et al. (2013) obtained 30 carabid species with only 1,178 individuals captured in the broad-leaved Korean pine mixed forest in Changbai Nature Reserve, where beetles were sampled from 11 sampling plots across a large spatial range (with 4–8 pitfall traps for each plot) from early July to early August in 2011 and from late June to late August in

2012. This may support the suggestion by Atlegrim et al. (1997) that one should attempt to increase the number of sites (study plots) rather than increase the number of samples from a given area when study the impacts of forestry on invertebrates. For invertebrate field sampling, there is always a problem concerning trade-off between site replication and plot size (Pullen et al. 1992), and between sample size and length of sampling period (Lövei and Magura 2011). Usually, if one of them is limited, increasing the other may compensate for it. However, the actual situation is more complicated. For instance, Pullen et al. (1992) reported that there was an apparent positive correlation between plot size and the duration of insecticide's effects on non-target invertebrates (larger plot size, slower population recovery), suggesting that small experimental plots (despite using sufficiently high replications) may be questionable to predict the effects of hazardous compounds on a realistic scale.

Although large-scale forest research plot is often limited by lack of site replication, the present study indicated that by increasing the number of traps and extending the length of trapping period, large-scale forest plot may provide reliable data for assessing biodiversity and community composition of epigeal beetles in temperate forests.

In the near future, more studies and observations of the biology (e.g. life history and forage habits) of native carabid species (including the rare species) are needed. In addition, studies across various habitats and spatial scales with adequate sample sizes are greatly needed to identify the endangered carabid species and to develop a region-scale conservation strategy.

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