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The distribution patterns and temporal dynamics of carabid beetles (Coleoptera: Carabidae) in the forests of Jiaohe, Jilin Province, China

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Abstract Carabid beetles, predatory insects, are abundant in forests and sensitive to environmental changes. The distribution patterns and diversity of carabid beetles in several natural forests were studied to provide a basis for evaluating the importance of a forest in the protection of carabid beetle diversity. Carabids were captured by pitfall traps during their seasonal activity from 2012 to 2013 in a poplar-birch forest, ash-walnut forest and broad-leaved Korean pine forest. A total of 5252 individuals, representing 21 species, were collected. Carabid abundance was highest in the broad-leaved Korean pine forest and lowest in the ash-walnut forest.

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Carabus billbergi Mannerheim and Pterostichus pertinax (Tschitscherine) were the dominant beetle species in each stand. Carabus canaliculatus Adams was dominant in the poplar-birch and ash-walnut forests, and Leistus niger Gebler was dominant in the ash-walnut forest. The carabids were affected differently by stand factors. C. billbergi and P. pertinax was positively correlated with mean DBH. C. canaliculatus and L. niger were not positively correlated with any stand factors. The broad-leaved Korean pine forest with greater age, large DBH and thick leaf litter fostered a high diversity of carabid species. The main yearly activity period for most carabids was during July. Different carabid species responded differently to seasonality, and the activity period of several species was relatively late (August) in the year.

Keywords Carabid beetles \cdot Stand type \cdot Stand factors \cdot Temporal dynamics \cdot Distribution patterns \cdot Ordinal dates

Introduction

Carabid beetles (Coleoptera: Carabidae) are a diverse, species-rich family of insects. Most species are predatory and are natural enemies of other forest insects. They provide effective population control of a number of pests (Thiele 1977; Magura et al. 2000; Liu et al. 2004; Zhang et al. 2012). They often travel on the ground, directly exposed to environmental factors, and their responses can indicate environmental changes. Carabid beetles have been widely studied and used as environmental indicators (Chen et al. 2009; Gao and Fu 2009; Eyre et al. 2016).

Ground vegetation is the main habitat of carabid beetles and their distribution is influenced by ground characteristics; species composition is significantly affected by soil moisture content, vegetation cover and biomass, litter thickness, and cover (Tyler 2008; Wang et al. 2009; He et al. 2011; Moraes et al. 2013; Yanahan and Taylor 2014; Kostova 2015; Spake et al. 2016). However, the responses of species in different habitats to environmental factors may differ (Yang et al. 2015; Hang et al. 2016). The composition and distribution of species are closely related to forest habitat, and their diversity is influenced by forest type, age, density of the canopy, and area of distribution (Yu et al. 2006; Jung et al. 2018; Homburg et al. 2019; Koivula et al. 2019; Okatsu and Tsutsumi 2019). The responses of different species to forest habitats vary and some species only inhabit specific types of forests (Qin et al. 2018). The abundance of ground vegetation affects species distribution but the results have varied in different studies (Jouveau et al. 2020). Carabid beetle diversity tends to be lower in heavily managed forests but increases as recovery time increases (Latty et al. 2006). Forest heterogeneity also contributes to increased species richness (Zou et al. 2014; Yang et al. 2017). Diversity is higher in native and more diverse forests than in monoculture plantations. Carabids are also more diverse in mixed conifer-hardwood forests than in pure coniferous forests (Fuller et al. 2008; Jung et al. 2014; Sun et al. 2018). Forest age also affects the distribution of carabid beetles by influencing climate and vegetation factors (Yu et al. 2002; Negro 2014; Johansson et al. 2017; Sun et al. 2018). However, this has been infrequently reported at the species level, and there are relatively few reports on the effects of forest age, stand types and structure on carabid distribution at the species level. A continuous collection of carabids beetles throughout their adult activity period from different stands will provide a more comprehensive scope of their distribution patterns in different stands. This study of the distribution patterns of carabid beetles in broad-leaved Korean pine mixed forests and other deciduous broad-leaved mixed forests at different stages of succession can provide a basis for estimating the response of carabids to forest succession. The major objectives of this study are: (1) to determine the response of carabids to changes in stand types and stand factors; and, (2) to determine the influence of time on carabids abundance.

Materials and methods

Study area

The study area was located in the Administration Bureau of the Jiaohe experimental area in the Changbai Mountains forest region, Jilin Province, northeast China (127°35′–127°51′ E, 43°51′–44°05′ N). Altitude ranged from 330 to 1176 m a.s.l. This region has a temperate continental monsoon mountain climate, and average annual temperature is 3.8 °C. Temperatures are highest in July (average 21.7 °C) and most precipitation occurs from June to August. More than 1000 plant species have been identified in this area. The representative vegetation types mostly include broad-leaved Korean pine mixed forests and broad-leaved mixed forests at different successional stages. The experimental area is used for research and teaching, and the forest is older and the area larger because of less logging and reduced human interference (Wang and Qin 2012). The main tree species include Pinus koraiensis Siebold et Zucc., Picea jezoensis var. komarovii Cheng et L.K.Fu, Abies holophylla Maxim., Abies nephrolepis (Trautv. ex Maxim.) Maxim., Juglans mandshurica Maxim., Phellodendron amurense Rupr., Fraxinus mandshurica Rupr., Tilia mandschurica Rupr. et Maxim., Tilia amurensis Pupr., Acer mono Maxim., Acer mandshuricum Maxim., Acer pseudo-sieboldianum (Pax.) Komarov, Betula platyphylla Suk., Betula costata Trautv., Populus davidiana Dode, Quercus mongolica Fisch.ex Turca., Ulmus davidiana Planch., and Maackia amurensis Rupr. et Maxim. Common shrubs include Lespedeza bicolor Turcz, Rhamnus davurica Pall., Syringa reticulate var. mandshurica (Maxim.) Hara), Lonicera ruprechtiana Regel., and Sorbaria kirilowii (Regel) Maxim.

Samples setting and specimen collection

Four representative natural stands were selected as study sites, with a size of 300 m×400 m for each site (Table 1). Five 2 m×2 m plots were arranged at the center point and in four vertices in the four stands. At the center of each plot and 1 m from the four sides, a pitfall trap was established. The pitfall trap spacing was 1 m and the size was three rows and three columns. A total of nine pitfall traps were set up in each plot and 45 in each stand. Plastic water cups were used as pitfall traps (depth 90 mm, top diameter 70 mm) to collect carabid specimens. A small hole in the top of each plastic trap prevented the loss of specimens due to rain. All traps were filled with slightly salty water, vinegar and alcohol.

Collection times and identification of specimens

The adult carabids were collected from middle May to late August in 2012 and 2013, and the collection interval covered the entire active period of all carabid beetles in this region. Carabids were retrieved from the trap cups seven times per season, late May (T1), middle June (T2), late June (T3), middle July (T4), late July (T5), middle August (T6), and late August (T7). All specimens collected were pinned and identified in the Insect Laboratory at the Forestry College of Beihua University.

Data analysis

Dominant species represented more than 10% of the total number of individuals collected. CCA (canonical

 Table 1
 Stand information of the Jiaohe experimental area in the Changbai Mountains forest region, Jilin Province, northeast China

| Plots | Forest stand | Altitude (m a.s.l.) | Stand age group | Canopy | Main tree species |
|-------|---------------------------------------|---------------------|-------------------|--------|--|
| PBF | Poplar-birch forest | 430 m | Middle-age stand | 0.6 | Betula platyphylla Suk., Fraxinus mandshu- rica Rupr., Juglans mandshurica Maxim., Ulmus davidiana Planch., Populus davidi- ana Dode |
| AWF | Ash-walnut forest | 430 m | Near-mature stand | 0.7 | Fraxinus mandshurica Rupr., Juglans mandshurica Maxim., Betula platyphylla Suk., Ulmus davidiana Planch., Pinus koraiensis Siebold et Zucc., Picea jezoen- sis var. komarovii Cheng et L.K.Fu, Acer mono Maxim |
| BKP1 | Broad-leaved Korean pine mixed forest | 550 m | Mature stand | 0.8 | Pinus koraiensis Siebold et Zucc., Juglans mandshurica Maxim., Picea jezoensis var. komarovii Cheng et L.K.Fu, Fraxinus mandshurica Rupr., Tilia amurensis Pupr., Acer mono Maxim., Ulmus davidiana Planch., Populus davidiana Dode |
| BKP2 | Broad-leaved Korean pine mixed forest | 660 m | Mature stand | 0.8 | Pinus koraiensis Siebold et Zucc., Juglans mandshurica Maxim., Picea jezoensis var. komarovii Cheng et L.K.Fu, Fraxinus mandshurica Rupr., Tilia amurensis Pupr., Acer mono Maxim., Ulmus davidiana Planch., Betula costata Trauty |

correspondence analysis) and DCA (detrended correspondence analysis) were analyzed by Canoco 4.5 software (Biometris-Plant Research International, Wageningen, The Netherlands), and species and environmental data were transformed by square root. The collection times for each species were calculated quantitatively by ordinal date methods; the seven times were late May (T1) = 140, middle June (T2) = 150, late June (T3) = 170, middle July (T4) = 180, late July (T5) = 200, middle August (T6) = 210, late August (T7) = 230 (Hanks and Millar 2013; Liu et al. 2016). The number of species in different stands were statistically analyzed by one-way ANOVA.

Results

Species composition of carabid beetles

A total of 5252 carabid specimens representing 21 species were collected. Of these, 1130 were from the poplar-birch forest (PBF), 484 from the ash-walnut forest (AWF), 1802 from the broad-leaved Korean pine mixed forest 1 (BKP1), and 1836 from the broad-leaved Korean pine mixed forest 2 (BKP2). *Carabus billbergi* Mannerheim and *Pterostichus pertinax* (Tschitscherine) were the dominant species in each stand; *Carabus canaliculatus* Adams was dominant in PBF and AWF; *Leistus niger* Gebler was dominant in AWF (Table 2). *Pterostichus* (four species, 2996 individuals) and

Carabus (four species, 1103 individuals) were dominant genera.

The influence of stand factors on carabid species

Canopy density, litter thickness, herb coverage, trees/ha, shrub cover, and average DBH in each stand were recorded (Table 3). The number of individuals and the mean values of the six environmental factors were transformed by square root. Canonical correspondence analysis (CCA) was carried out with the number of individuals, four stand types and six factors in the different forests (Fig. 1). The contribution rate of the first axis was 73.8%, the contribution rate of the second was 15.6%, and cumulative contribution rate was 89.4% and the Monte Carlo Permutation Test P = 0.05, PBF was positively correlated with the first axis and negatively with the fourth axis in the fourth quadrant. AWF was in the first quadrant and positively correlated with both the first and second axes. In the second quadrant, BKP1 was negatively correlated with the first axis and positively correlated with the second axis. BKP2 was in the third quadrant and was negatively correlated with the first and second axes.

Among the six environmental factors, herb coverage (*X3*), trees per hectare (*X4*) and shrub coverage (*X5*) were positively correlated with the first axis; the correlation coefficients were 0.9766, 0.9958, and 0.9316. Canopy density (*X1*), litter thickness (*X2*), average DBH (*X6*) were negatively correlated with the first axis, and the correlation coefficients were -0.9836, -0.9056, and -0.997. BKP1 and BKP2 were strongly correlated with canopy density (*X1*),

Table 2Number of carabidbeetles in different stands

 Table 3
 Main stand factors of the Jiaohe experimental area in the Changbai Mountains forest region, Jilin Province, northeast

China

| Species | PBF | % | AWF | % | BKP1 | % | BKP2 | % | Total |
|---|------|------|-----|------|------|------|------|------|-------|
| Calosoma cyanescens Motschulsky | | | 1 | 0.2 | 3 | 0.2 | 9 | 0.5 | 13 |
| Carabus billbergi Mannerheim | 125 | 11.1 | 63 | 13.0 | 338 | 18.9 | 382 | 20.8 | 908 |
| Carabus canaliculatus Adams | 118 | 10.3 | 89 | 18.4 | 85 | 4.7 | 107 | 5.8 | 399 |
| Carabus constricticollus Kraatz | 7 | 0.6 | 2 | 0.4 | 8 | 0.4 | 7 | 0.4 | 24 |
| Carabus granulatus Linnaeus | 148 | 13.1 | 21 | 4.3 | | | | | 169 |
| Carabus seishinensis Lapouge | | | | | | | 2 | 0.1 | 2 |
| Carabus vietinghoffi Adams | 102 | 9.0 | 33 | 6.8 | 52 | 2.9 | 12 | 0.6 | 199 |
| Chlaenius sericimicans Chaudoir | 2 | 0.2 | 4 | 0.8 | 4 | 0.2 | 1 | 0.1 | 11 |
| Cychrus morawitzi Géhin | 3 | 0.3 | 1 | 0.2 | | | 1 | 0.1 | 5 |
| Cymindis sp. | 1 | 0.1 | | | 2 | 0.1 | 1 | 0.1 | 4 |
| Harpalus simplicidens Schauberger | 2 | 0.2 | | | | | | | 2 |
| Harpalus ussuriensis Chaudor | 3 | 0.3 | | | | | | | 3 |
| Leistus niger Gebler | 51 | 4.5 | 52 | 10.8 | 86 | 4.8 | 55 | 3.0 | 244 |
| Poecilus reflexicollis Gebler | 10 | 0.9 | 8 | 1.7 | 20 | 1.1 | 1 | 0.1 | 39 |
| Pristosia vigil Tschistcherine | 16 | 1.4 | 38 | 7.9 | 46 | 2.6 | 70 | 3.8 | 170 |
| Pterostichus interruptus (Dejean) | 56 | 5.0 | 9 | 1.9 | 17 | 0.9 | 7 | 0.4 | 89 |
| Pterostichus adstrictus Eschscholtz | 7 | 0.6 | 2 | 0.4 | 53 | 2.9 | 53 | 2.9 | 115 |
| Pterostichus pertinax (Tschitscherine) | 424 | 37.5 | 126 | 26.0 | 1033 | 57.3 | 1094 | 59.5 | 2677 |
| Pterostichus sp. | 38 | 3.4 | 20 | 4.1 | 38 | 2.1 | 19 | 1.0 | 115 |
| Synuchus sp. | | | | | | | 4 | 0.2 | 4 |
| Trichotichnus coruscus (Tschitscherine) | 17 | 1.5 | 15 | 3.1 | 17 | 0.9 | 11 | 0.6 | 60 |
| Total | 1130 | 100 | 484 | 100 | 1802 | 100 | 1836 | 100 | 5252 |

PBF Poplar-birch forest, AWF Ash-walnut forest, BKP1 Broad-leaved Korean pine mixed forest, BKP2 Broad-leaved Korean pine mixed forest

| Stands | Canopy den- sity (X1) | Litter thickness (mm, X2) | Herb cover- age (%, <i>X3</i>) | Tree numbers per hectare (X4) | Shrub coverage (%, <i>X5</i>) | Average DBH (cm, <i>X6</i>) |
|--------|--------------------------|------------------------------|------------------------------------|-------------------------------|--------------------------------|------------------------------------|
| PBF | 0.63 | 21.7 | 78.0 | 1267 | 45 | 16.1 |
| AWF | 0.72 | 19.3 | 75.3 | 1053 | 42 | 18.2 |
| BKP1 | 0.81 | 30.0 | 62.3 | 827 | 25 | 22.2 |
| BKP2 | 0.82 | 31.6 | 61.0 | 753 | 28 | 24.3 |

PBF Poplar-birch forest, *AWF* Ash-walnut forest, *BKP1* Broad-leaved Korean pine mixed forest, *BKP2* Broad-leaved Korean pine mixed forest

litter thickness (X2) and average DBH (X6). There was a strong correlation between PBF, AWF and herb cover (X3), trees per hectare (X4) and shrub cover (X5).

C. cyanescens (1) was strongly correlated with average DBH (X6), canopy density (X1), and litter thickness (X2). P. adstrictus (16), C. billbergi (2), Cymindis sp. (8), P. pertinax (17), P. vigil (14) showed a strong correlation with average DBH (X6). C. granulatus (3), C. morawitzi (7), P. interruptus (15) were correlated with number of trees per hectare (X4) and shrub coverage (X5). C. vietinghoffi (9) and Pterostichus sp. (18) were strongly correlated with herb cover (X3). Other species did not show obvious correlations with environmental factors.

Influence of stand type on the dominant species

In four stands, the number of *P. pertinax* was the highest of all species, reaching 51.0% of the total, and was significantly higher in BKP1 and BKP2 than in PBF and AWF (F=73.86; df=3, 16; P<0.001) (Fig. 2a). *C. billbergi* number reached



Fig. 1 Canonical correspondence analysis between carabid species, four stands, and six stand factors. 1: Calosoma cyanescens Motschulsky, 2: Carabus billbergi Mannerheim, 3: Carabus granulatus Linnaeus, 4: Carabus seishinensis Lapouge, 5: Carabus constricticollus Kraatz, 6: Chlaenius sericimicans Chaudoir, 7: Cychrus morawitzi Géhin, 8:Cymindis sp., 9: Carabus vietinghoffi Adams, 10: Harpalus simplicidens Schauberger, 11: Harpalus ussuriensis Chaudor, 12: Leistus niger Gebler, 13: Carabus canaliculatus Adams, 14: Pristosia vigil Tschistcherine, 15: Pterostichus interruptus (Dejean), 16: Pterostichus adstrictus Eschscholtz, 17: Pterostichus pertinax (Tschitscherine), 18: Pterostichus sp., 19: Poecilus reflexicollis Gebler, 20: Synuchus sp., 21: Trichotichnus coruscus (Tschitscherine), same to below

17.3% of the total, and was also significantly higher in BKP1 and BKP2 than in PBF and AWF (F = 53.60; df = 3, 16; P < 0.001) (Fig. 2b). *C. canaliculatus* was highest in AWF (F = 1.427; df = 3, 16; P > 0.05) (Fig. 2c), and *L. niger* was most common in BKP1 (F = 1.525; df = 3, 16; P > 0.05) (Fig. 2d).

Distribution of ordinal date of species

There were significant differences in the adult activity period of carabid beetles. The main month of activity of adults was July (Table 4). *C. billbergi, C. canaliculatus, C. vietinghoffi, P. interruptus, P. pertinax, Pterostichus* sp., and *P. vigil* were found in all seven collection times; and their activity periods were relatively long. Nine species were active in early spring from mid-May to the end of May. *C. constricticollus, L. niger, T. coruscus* were active from early June to late August. *H. ussuriensis, Synuchus* sp., *H. simplicidens, C. seishinensis* had small populations and a later active period mainly in August. The number of *C. billbergi, P. pertinax, P. vigil, P. adstrictus, T. coruscus* varied greatly in each sample period as indicated by the SD values (Table 4).



Fig. 2 Individuals (mean \pm S.E.) of a *Pterostichus pertinax*, b *Carabus billbergi*, c *Carabus canaliculatus*, d *Leistus niger* in different stands. Different small letters a, b indicate significant difference among stands

 Table 4
 Ordinal dates and individual numbers of 21 carabid species

| Species | Individual number (Mean±SD) | Ordina | Ordinal dates | | | | | | |
|---|--------------------------------|--------|---------------|-----|-----|-----|-----|-----|-----------------|
| | | 140 | 150 | 170 | 180 | 200 | 210 | 230 | $(Mean \pm SD)$ |
| Carabus billbergi Mannerheim | 129.7±110.6 | + | + | + | + | + | + | + | 183±33 |
| Carabus canaliculatus Adams | 57 ± 20.6 | + | + | + | + | + | + | + | 183±33 |
| Carabus vietinghoffi Adams | 28.4 ± 13.1 | + | + | + | + | + | + | + | 183±33 |
| Pterostichus interruptus (Dejean) | 12.7 ± 9.6 | + | + | + | + | + | + | + | 183 ± 33 |
| Pterostichus pertinax (Tschitscherine) | 382.4±232.6 | + | + | + | + | + | + | + | 183 ± 33 |
| Pterostichus sp. | 16.4 ± 11.0 | + | + | + | + | + | + | + | 183 ± 33 |
| Pristosia vigil Tschistcherine | 24.3 ± 27.9 | + | + | + | + | + | + | + | 183 ± 33 |
| Pterostichus adstrictus Eschscholtz | 19.2 ± 19.1 | + | + | + | + | + | + | | 175 ± 27 |
| Poecilus reflexicollis Gebler | 7.8 ± 5.4 | + | + | + | + | + | | | 168 ± 24 |
| Carabus constricticollus Kraatz | 4.0 ± 3.4 | | + | + | + | + | + | + | 190 ± 29 |
| Leistus niger Gebler | 40.7 ± 23.6 | | + | + | + | + | + | + | 190 ± 29 |
| Trichotichnus coruscus (Tschitscherine) | 10.0 ± 10.6 | | + | + | + | + | + | + | 190 ± 29 |
| Calosoma cyanescens Motschulsky | 4.3 ± 2.5 | | + | + | + | | | | 167 ± 15 |
| Chlaenius sericimicans Chaudoir | 2.2 ± 1.1 | | | + | + | + | + | + | 198 ± 24 |
| Cychrus morawitzi Géhin | 1.7 ± 0.6 | | | + | + | + | | | 183 ± 15 |
| Carabus granulatus Linnaeus | 42.3 ± 29.7 | | | | + | + | + | + | 205 ± 21 |
| Cymindis sp. | 1.3 ± 0.6 | | | | + | + | + | | 197 ± 15 |
| Harpalus ussuriensis Chaudor | 1.5 ± 0.7 | | | | | | + | + | 220 ± 14 |
| Synuchus sp. | 2.0 | | | | | | + | + | 220 ± 14 |
| Harpalus simplicidens Schauberger | 2.0 | | | | | | + | | 210 |
| Carabus seishinensis Lapouge | 2.0 | | | | | | | + | 230 |

"+" indicate species distribution in the ordinal date



Fig. 3 Detrended correspondence analysis between carabids and seven collection dates. T1 (late May), T2 (middle June), T3 (late June), T4 (middle July), T5 (late July), T6 (middle August) and T7 (late August), same to below

Detrended correspondence analysis between species and time

The individual numbers of 21 carabid species were square root transformed. Detrended correspondence analysis was established between the 21 species collected over the seven dates (Fig. 3). The contribution rate of the first axis was 63.1%, the second 10.9%, and the cumulative contribution rate was 74.0%. Early May, early and late June were in the second quadrant, negatively correlated with the first axis and positively correlated with the second. Early July and late July were in the fourth quadrant and positively correlated with the first axis and negatively correlated with the second. Early August and late August were in the first quadrant and positively correlated with both the first and second axes.

The relationship between late May (T1) and each carabid beetle were relatively weak. There was a strong correlation between August (T6 and T7) and *H. simplicidens* (10), *C. seishinensis* (4), *H. ussuriensis* (11), and *Synuchus* sp. (20). Compared with other species, the relationship between June (T2 and T3) and *P. adstrictus* (16), *C. billbergi* (2), *P. reflexicollis* (19), and *C. cyanescens* (1) were stronger. The relationship was stronger between July (T4 and T5) and *Cymindis* sp. (8), *C. morawitzi* (7), *C. constricticollus* (5),





C. sericimicans (6), *L. niger* (12), and *C. granulatus* (3). *C. canaliculatus* (13), *C. vietinghoffi* (9), *P. interruptus* (15), *P. pertinax* (17), *T. coruscus* (21), *Pristosia vigil* (14), and *Pterostichus* sp. (18) did not correspond with any collection time.

Dominant species temporal dynamics

There were large numbers of (a) *P. pertinax*, (b) *C. billbergi*, (c) *C. canaliculatus*, (d) *L. niger* collected at every sample time (Fig. 4). *P. pertinax* was the largest number, accounting for more than 50% of the total, and the number was unimodal. Its active peak period was in early July, followed by late July (Fig. 4a). The adult activity period of *C. billbergi* was mainly before early July; the peak period was late June (Fig. 4b). *C. canaliculatus* active period was from early July to late August, with a peak was in early July (Fig. 4c). *L. niger* active peak period was from late July to late August, with a peak was in late July (Fig. 4d).

Discussion

Forest ecosystems are an important habitat of carabid beetles. Forest type, tree species composition and structure affect their distribution by influencing the ground environment (Li et al. 2017; Vician et al. 2018). This study identified substantial differences in the composition of the carabid communities in broad-leaved Korean pine mixed forest, poplar-birch forest and ash-walnut forest in the Changbai Mountains. Carabid abundance was higher in the mature broad-leaved Korean pine mixed forest than in the poplar-birch and ash-walnut forests in earlier successional stages. This is consistent with the high abundance of beetles in mature forests (Zou et al. 2015; Liu et al. 2018b). The vegetation composition of the mature forest is complex which can increase the diversity of carabid beetle species, and the mature forest appears to play an important role in their protection (Fuller et al. 2008; Jung et al. 2014; Zou et al. 2019). We found that there were unique characteristics in the carabid composition in each stand. The number of *P. pertinax* was the largest, and *C.* billbergi, C. canaliculatus, and L. niger were also numerous. At the genus level, Carabus and Pterostichus were the main assemblages in the forests, which is consistent with other studies in which these genera were dominant (Gnetti et al. 2015; Sun et al. 2018).

In forest stands with reduced human interference, factors such as canopy density, litter thickness, herb cover, and number of trees per unit area, shrub cover and average DBH are closely related to stand composition and age. Differences in stand composition and structure leads to differences in stand factors. However, the influence of these on carabid species was also variable. Abundances of *P. pertinax*, *C. billbergi* and *P. vigil* were closely related to the average DBH of the stand. This increase in average stand diameter helped increase carabid species abundance, which is consistent with findings that large trees in a forest help to protect the diversity of carabid beetles and increase species abundance (Jouveau et al. 2020). Herb coverage affected the distribution of carabid communities, and the species and numbers of individual carabid species were greater in habitats with high herb cover (Eyre et al. 2004). Some species prefer to move into areas with high herb density (Brose 2003; Eyre et al. 2004; Tyler 2008). In this study, there was a strong correlation between herb cover and *C. granulatus*, *C. morawitzi*, *C. vietinghoffi*, and *Pterostichus* sp. This may be because these species prefer to feed and move in herbaceous areas.

Forest litter is the main factor that affects the distribution of carabid beetles. Litter helps to prevent the ground temperature from losing warmth and provides a habitat for beetles to hunt and hide (Luff et al. 1989; Irmler 2000). Litter thickness has a strong positive effect on carabid abundance (Sroka and Finch 2006), and mature stands with large diameter trees tend to accumulate a thick litter layer and have higher species abundance (Liu et al. 2018a). However, at the species level, the results of this study show that only some carabid species abundance were correlated with litter thickness. Of the four dominant species, only *P. pertinax* and *C. billbergi* were positively correlated while *C. canaliculatus* and *L. niger* were not correlated with environmental factors. This may be because carabid species exhibit diverse habitat preferences and adaptations at the species level.

Seasonality affects forest temperatures, humidities and ground vegetation, and thus influences the distribution patterns of carabid beetles. Only seven species were collected in all seven time periods from late May to late August, while the activity periods of the other species differed. Most studies have shown a significant positive correlation between carabid abundance and temperatures in the forest, with peak numbers occurring in July (Liu et al. 2018a; Sun et al. 2018). However, the four dominant species in this study responded differently to the season, which may reflect differentiated adaptability to seasonality at the species level (Yu et al. 2002). The activity peak of C. billbergi was relatively early (late June), consistent with its time distribution in the Changbai Mountain Reserve (Wang et al. 2014). This may be related to the biological characteristics of overwintering in adults (Jennings et al. 1986). When temperatures rise in the forest, the adults become active. The peak activity of P. pertinax and C. canaliculatus were in early July and related to higher forest temperatures and the abundance of edible animals and plants (Yu et al. 2002). Some studies have also shown that the higher ground temperatures at this time of year is an important reason for increased carabid abundance (Magura et al. 2004). The activity peak of L. niger was relatively late (late July) and was associated with a late emergence period. The temporal dynamics of the four dominant species were all unimodal, consistent with the finding that the activity period of most carabid species is unimodal in the forests of northern China (Wang et al. 2014).

Conclusion

As one of the representative vegetation types in this region, the broad-leaved Korean pine mixed forest is older, has less human disturbance, a larger diameter class and more litter accumulated, all of which have a positive effect on the abundance and richness of carabid beetles populations. Thus, the broad-leaved Korean pine mixed forest can play an important role in protecting the diversity of carabids. Carabids are more active in July, with different species sensitive to time changes. The results also suggest that the abundance and diversity of carabid beetles were affected by seasonal changes.

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