

***Carabus* (Coleoptera: Carabidae) assemblages of native forests and non-native plantations in Northern China**

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The effects of non-native plantation established after clear-cutting were studied in Dongling Mountain region, Northern China. Pitfall catches of *Carabus* beetles from a non-native larch plantation were compared with those from two native forests, an oak forest and a mixed broad-leaved forest. More individuals were captured from the mixed broad-leaved forest and the larch plantation than from the oak forest. For the three most abundant species in this area, *C. crassesculptus* peaked in abundance in the mixed broad-leaved forest; *C. manifestus* peaked in the larch plantation, and *C. sculptipennis* in the oak forest. Measured by PcoA using Bray-Curtis index of dissimilarity, species composition of the larch plantation was different from the two native forests, but overlapped remarkably with them. All the three abundant species showed a similar positive relationship between local distribution and abundance. Captures of abundant species were clumped within the forest, but the extent of aggregation among forests was different. Monthly catches of total *Carabus*, and *C. crassesculptus* alone, peaked in June–August in all the three forests, but *C. manifestus* peaked in June and again in August. Our results suggest that the planting of non-native larch does not have a detrimental effect on *Carabus* assemblages in general, but it changes the spatial distribution and abundance compared to the native forests.

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1. Introduction

Forestry practices, mainly clear-cutting and establishment of plantations, are causing increasing fragmentation in the northern forest zone of China. Since the 1960s, extensive plantations of non-native larch (*Larix*), pine (*Pinus*), arborvitae (*Platycladus*), spruce (*Picea*) and fir (*Abies*) species have been established in several mountain ranges in the warm temperature zone of Northern

China. This causes a significant loss of indigenous habitats (Chen & Huang 1997, MacKinnon & Xie 2001).

Previous studies in Central Europe indicate that logging and establishment of plantations greatly change forest faunas (Doberski & Lyle 1997, Magura *et al.* 2000). Clear-cutting has important effects on the environment and carabid communities (Lenski 1982, Jennings *et al.* 1986, Niemelä *et al.* 1993, Duchesne *et al.* 1999). Ad-

aptation to new habitats varies among different species, and introduction of new vegetation types may bring about changes in the composition and distribution of invertebrate communities (Duelli *et al.* 1990, Epstein & Kulman 1990, Niemelä *et al.* 1992, Kinnunen & Tiainen 1999).

Monitoring changes in the local fauna, and comparing communities of altered habitats are important in assessing human impacts on biological diversity (Lenski 1982, Humphrey *et al.* 1999, Hutcheson & Jones 1999, Kotze & Samways 1999). Ground beetles (Coleoptera: Carabidae) are an appropriate group for such studies, as they are ecologically and taxonomically well known and respond rapidly to habitat changes (Lenski 1982, Jennings *et al.* 1986, Eyre *et al.* 1996, Lövei & Sunderland 1996, Davies & Margules 1998).

The genus *Carabus* is a group of Carabidae, representatives have a large body size (Imura & Mizusawa 1996), and several studies have conducted on their habitat distribution, life history, morphological differentiation and molecular evolution (Sota 1985, 1986, Sota *et al.* 2000, Su *et al.* 1996, Kim *et al.* 2000, Yu *et al.* 2002, Takami 2003). In China, ca. 400 *Carabus* species or subspecies have been recorded, and most of them are associated with well-protected natural forests, meadows, and other special habitats (Imura & Mizusawa 1996, Brezina 1999). Fragmentation of *Carabus* habitats through harvesting of natural forests, and increased collecting by professional and amateur collectors, have drastically reduced the population density of many species. In fact, many species are facing extinction, and the State Forestry Administration of the People's Republic of China has included the subgenera *Coptolabrus* and *Apotomopterus* into the recent list of wild animals under national protection in China (Decree No.7 of the State Forestry Administration of the People's Republic of China 2002). Our study on *Carabus* assemblages, and how they are influenced by different plantations and forestry practices, can offer valuable knowledge about how to conserve this group of beetles.

Our earlier studies on *Carabus* in secondary plantations in Northern China suggest that these plantations do not always have low diversity (Yu *et al.* 2002). Indeed, some immature oak forests (coppices) may even have a similar composition

and abundance of *Carabus* species to mature oak forests in a well-protected area, suggesting that forest recovery by oak coppices can sustain a *Carabus* assemblage typical of native oak forests (Yu *et al.* 2002). In this study, we studied the *Carabus* assemblages of non-native plantation and two native forests with a focus on species abundance and composition, spatial distribution and seasonal dynamics.

2. Material and methods

2.1. Study site

This study was conducted at the Beijing Forestry Ecosystem Research Station (BFERS, ca. 114 km west of Beijing) in Dongling Mountain (40°00' N, 115°26' E, 800–2,300 m a.s.l.) that is a part of Taihang Mountain Ranges, North China. The area has a cool-temperature monsoon climate with an average annual temperature of +4.8° C (January –10.1° C, July +18.3° C). Precipitation amounts to 611.9 mm/yr, and 78% of the annual rainfall occurs between June and August (Chen & Huang 1997).

In this region, oak forest (*Quercus liaotungensis*) is the most extensive native forest association. At lower elevations, there are deciduous broad-leaved forests, dominated by e.g., *Acer mono*, *Betula dahurica*, *Juglans mandshurica*, *Fraxinus rhynchophylla*, *Populus davidiana*, *Quercus liaotungensis*, *Sorbus pauhuashanensis*, *Tilia mongolica* and *T. mandshurica*. In some areas, where the native forests have been logged 30 to 40 years ago, non-native coniferous plantations of larch (*Larix principis-rupprechtii*) and pine (*Pinus tabulaeformis*) have been established. All these forests have a closed canopy with tree height of 8–15 m (max 20 m).

Three plots were established in the core of the three forests studied: oak forest (ca. 30 ha), mixed (deciduous) broad-leaved forest (ca. 12 ha) and larch plantation (ca. 40 ha). Mature oak trees (50 years old) comprised 90% of the canopy in the oak forest. The understory vegetation coverage was relatively sparse (<20%), and the leaf litter layer was thin (<3 cm). In the mixed broad-leaved forest, deciduous trees (30–40 years old) comprised 70% of the total canopy. The shrub and

herb layer covered less than 60% of the ground, and the leaf litter layers were thick (8–10 cm). Larch plantation was dominated by larch (80% of canopy trees, 30 years old), with less than 40% coverage by shrubs and herbs under the canopy trees; its litter layer was dominated by needles (5–8 cm). The distances between the studied forests was ca. 2.0 km.

2.2. Sampling

Carabus beetles were captured in the three forests using pitfall traps. Although pitfall traps are biased to active forms and not a direct measure of absolute population density, this method is useful in monitoring and assessing local population changes (Baars 1979, Spence & Niemelä 1994). Traps were plastic beverage cups (400 ml, depth 9 cm, mouth diameter 7.5 cm). A small hole (diameter ca. 0.2 cm) was drilled on each trap ca. 2.5 cm below the upper brim, so that excess rainwater could flow out. Each trap was filled with ca. 100 ml of trapping fluid (vinegar: sugar: alcohol: water / 10 mL: 5 g : 5 mL: 20 mL) and the collected specimens were preserved in 70% alcohol for later identification. Because of the large body size of *Carabus* beetles (all the study species had a body size of 1.5 cm or larger), the method employed in this study was effective (Yu *et al.* 2002).

In 1999, sampling was conducted from April to October. Pitfall traps were set in two lines within each forest. The distance between the two trap lines in each forest was at least 100 m. Each trap line had 55 trap points (cups), with distance between trap points being ca. 2 m. The traps were serviced every 3 days from April to October.

According to the data in 1999 and the results of Yu *et al.* (2002), most *Carabus* species peak in abundance in June through August in the study region. Therefore, we arranged other field studies in June 2002 to investigate the activity density in the same three forests. To get statistically independent samples, we set traps in 20 groups, with 10 traps of each group, into each of the three forests. Trap groups were spaced 20 m apart, while trap points within each group were ca. 1 m apart and placed into a triangle. The contents of the traps in this study were serviced daily. In the mixed deciduous broad-leaved forest, the sam-

pling was carried out from June 8 to June 17. In the oak forest and larch plantation, the sampling period lasted from June 9 to June 16 and 17, respectively.

2.3. Statistical Analyses

Analysis of variance (ANOVA) was used to test for differences among the three forests of all *Carabus* beetles and the most abundant beetle species over the entire collecting period, after a square-root transformation. Regression analysis was used to examine the relationship of beetle abundance (logarithmic transformation) and trap occupancy, i.e. the fraction of trap groups ($n = 20$) occupied, for each species within each forest per one sampling day in 2002. Spearman rank correlation was used to compare the seasonal catches among the three forests for the dominant species in 1999. All the above analyses were done using SPSS (SPSS 1997).

Similarity among the assemblages of the three forests was calculated by Bray-Curtis index of dissimilarity and further studied by PCoA (Principal Coordinate Analysis) (Ludwig & Reynolds 1988) using the PAST package (Hammer *et al.* 2001). Morisita's index of aggregation (I_M , Morisita 1959, cited in Niemelä *et al.* 1992) was used to characterize the spatial distribution of the species among the trap groups within the forests in 2002. The index value of 1.0 indicates random distribution, values of <1.0 even, and values of >1.0 aggregated distribution. The deviation of the index from 1.0 (i.e. variance : mean ratio of 1.0) was tested by a chi-square test (Hurlbert 1990, Niemelä *et al.* 1992).

3. Results

3.1. Abundance and composition

A total of ten species was captured. In 1999, 983 individuals of *Carabus* were captured, and 960 in 2002. *C. manifestus* and *C. crassesculptus* were the predominant species, making up together 88% of the total sample in 1999 and 87% in 2002 (Table 1). *C. brandti* was not captured in 1999 and *C. granulatus* was not recorded in 2002.

Table 1. *Carabus* pitfall catches from three forests in Dongling Mountain region. The forests: Oak = oak forest; Mixed = mixed broad-leaved forest; Larch = larch plantation.

Species	Oak		Mixed		Larch		Total	
	1999	2002	1999	2002	1999	2002	1999	2002
<i>C. (Parhomopterus) manifestus</i>	147	70	159	162	244	215	550	447
<i>C. (Pagocarabus) crassesculptus</i>	59	3	77	279	178	103	314	385
<i>C. (Tomocarabus) sculptipennis</i>	16	51	20	3	1	15	37	69
<i>C. (Titanocarabus) sui</i>	31	11	6	22	6	5	43	38
<i>C. (Coptolabus) smaragdinus</i>	3	1	8	2	1	5	12	8
<i>C. (Piocarabus) vladimirskyi</i>	1	1	4	3	5	4	10	8
<i>C. (Aulonocarabus) canaliculatus</i>	2	1	–	–	7	–	9	1
<i>C. (Carabus) granulatus</i>	–	–	6	–	1	–	7	–
<i>C. (Morphocarabus) hummeli</i>	–	–	–	–	1	3	1	3
<i>C. (Cathaicus) brandti</i>	–	–	–	–	–	1	–	1
Species	7	7	7	6	9	8	9	9
Individuals	259	138	280	471	444	351	983	960

Seven species were recorded in the oak forest and in the mixed broad-leaved forest, and 10 species in the larch plantation (Table 1).

The total catch and the three most abundant species (with a catch of >5% of total) exhibited differences among the three forests in 2002 (Fig. 1). More individuals were sampled in the mixed broad-leaved forest and in the larch plantation than in the oak forest ($F = 18.52$; $d.f. = 2, 57$; $p < 0.001$). *C. crassesculptus* was abundant in the mixed broad-leaved forest samples, compared to the other two forests ($F = 32.36$; $d.f. = 2, 57$; $p < 0.001$). *C. manifestus* was less abundant in the oak forest, compared to the other two forests ($F = 11.99$; $d.f. = 2, 57$; $p < 0.001$). Significantly more individuals of *C. sculptipennis* were captured in the oak forest than in the mixed broad-leaved for-

est and in the larch plantation ($F = 15.61$; $d.f. = 2, 57$; $p < 0.001$).

Carabus assemblages of the oak forest and mixed broad-leaved forest were different from each other; the catches in the larch plantation showed a much higher variation, and its scores overlapped remarkably with those of the two native forests (Fig. 2).

3.2. Distribution and abundance among the forests

Beetle abundance and trap occupancy had a positive relationship across the three most abundant species, three forest types and 8–10 sample days in 2002 (Fig. 3). Of the 81 paired observations of

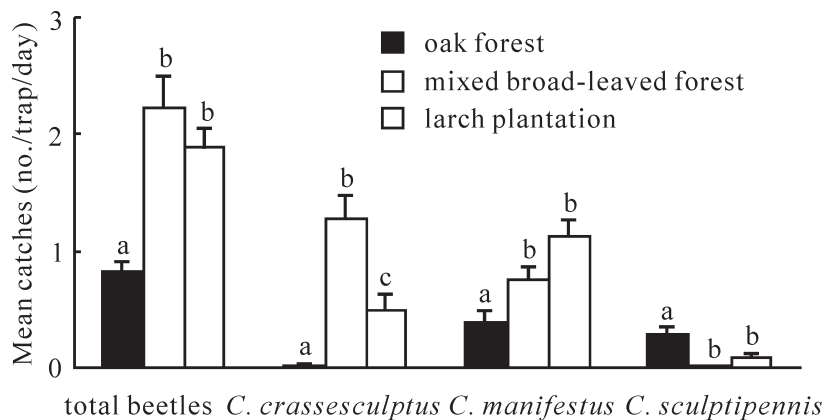


Fig. 1. Mean catches (\pm SE) per trap * day. Bars with the same letter are not significantly different at $\alpha = 0.05$.

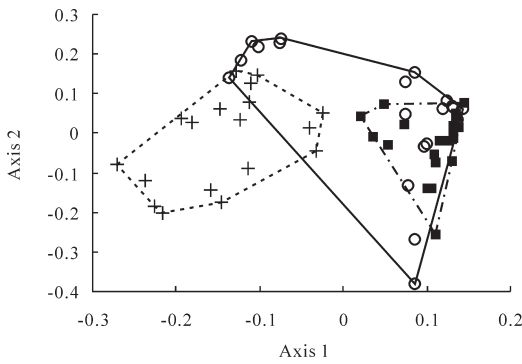


Fig. 2. Ordination plot (PCoA by Bray-Curtis index of dissimilarity) of the range of the catches of trap groups within each forest. Axes 1 and 2 explained 33.9% and 12.3% of the variation, respectively. (+) oak forest; (■) mixed broad-leaved forest; (○) larch plantation.

distribution and abundance, 38 fell along a curve that represented the case with a minimum number of individuals needed to occupy a given number of traps (dashed curve in Fig. 3). The remaining 43 of the 81 points occur above the minimum catch line, especially at higher values of abundance. Among these 43 points, there was a strong linear relationship (solid line, Fig. 3) between the abundance and trap occupancy ($r^2 = 0.88$; $F = 289.28$; $d.f. = 1, 41$; $p < 0.001$). Despite the species-specific responses of beetles to forest types and sampling date, all three species showed a similar positive relationship between local distribution and abundance.

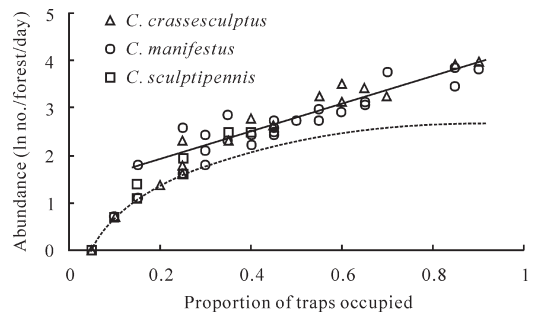


Fig. 3. Relationship between distribution (trap occupancy) and abundance (logarithmic transformation for mean catches per trap) for three most abundant species in three forests recorded during 8–10 days (a total of 81 observations). Trap occupancy is expressed as the fraction of trap groups ($n = 20$) occupied for each species within each forest at every sampling day. The dashed curve shows the minimum number of captures required to produce a given trap occupancy. The solid line shows a linear regression for 43 of the 81 observations that do not fall on the minimum catch line.

3.3. Spatial distribution of *Carabus* within forests

The value of Morisita index (I_M) of aggregation was >1.0 for most of the abundant species (including male, female and both sexes), indicating aggregated distributions within the study forests (Table 2). However, there were differences

Table 2. The Morisita index of aggregation (I_M) and the test of the deviation of variance : mean ratio from 1.0 (χ^2) of the abundant species (with a catch of >20 per forest, i.e. more than one individual per trapping group on the average) of the three forests in Dongling Mountain region in 2002. Statistical significance: **: $p < 0.01$; *: $p < 0.05$; ns: $p > 0.05$.

	Males		Females		Total	
	I_M	χ^2	I_M	χ^2	I_M	χ^2
Oak forest						
<i>C. manifestus</i>	1.460	35.111*	0.891	15.412ns	1.292	39.143**
<i>C. sculptipennis</i>	1.323	27.714ns	1.581	31.783*	1.412	39.588**
Mixed broad-leaved forest						
<i>C. manifestus</i>	1.208	38.340**	1.194	32.000*	1.184	48.617**
<i>C. crassesculptus</i>	1.334	57.448**	1.186	49.147**	1.278	96.412**
<i>C. sui</i>	2.909	38.091**	1.091	19.909ns	1.818	36.182*
Larch plantation						
<i>C. manifestus</i>	1.247	56.020**	1.190	31.000*	1.172	55.791**
<i>C. crassesculptus</i>	1.867	67.561**	1.797	54.870**	1.907	111.563**

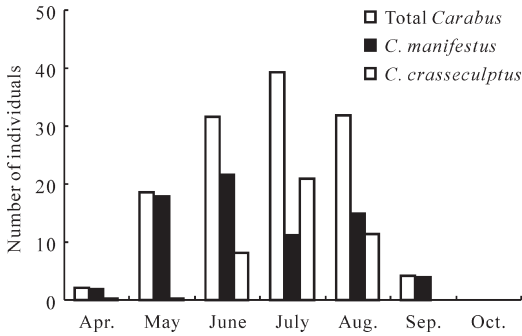


Fig. 4. Monthly catches (number of individuals per 100 traps) of total *Carabus* catch and two predominant species during the growing season of 1999 in the three forests.

among the forests in the extent to which captures were spatially clumped into particular traps. The males of *C. scultipennis* and the females of *C. manifestus* in the oak forest, and the females of *C. sui* in the mixed broad-leaved forest, did not show significant clumping, as the I_M for them did not deviate significantly from 1.0.

3.4. Temporal variation in the catches

The catches of total *Carabus* and *C. crassesculptus* alone, the predominant species, peaked in June–August in all the three forests (Fig. 4). *C. manifestus*, another abundant species, peaked in June and again in August (Fig. 4).

The monthly catches of *C. manifestus* correlated positively between the two native forests, but the correlations among the non-native larch plantation and the two native forests were not statistically significant (Table 3). The monthly catches of *C. crassesculptus* correlated positively among the three forests (Table 3).

4. Discussion

4.1. Species abundance and composition

Our results indicate that the non-native larch plantation differed from the two native forests regarding their *Carabus* assemblages. The management effects may be speculative, as only three forests (stands) were compared, and we have to

Table 3. Spearman rank correlation for the monthly catches among the three forests for two species with a catch of >5% of total individuals per forest in 1999. Oak = oak forest; Mixed = mixed broad-leaved forest. Statistical significance: ***: $p < 0.001$; **: $p < 0.01$; ns: $p > 0.05$.

	Oak	Mixed
<i>C. manifestus</i>		
Mixed broad-leaved forest	0.943**	
Larch plantation	0.714ns	0.600ns
<i>C. crassesculptus</i>		
Mixed broad-leaved forest	0.915**	
Larch plantation	0.915**	1.000***

pay attention to the effect of microhabitats within the forests included in the study. The understory in the native oak forest was sparse, with a thin leaf-litter layer, compared to the other two forests. Indeed, leaf litter was abundant in the native mixed broad-leaved forest. The larch plantation was managed regularly, encouraging the recolonization of herbs, shrubs and trees of native vegetation. Consequently, the shrubs and leaf litter were abundant. The coverage of leaf litter contributes significantly to carabid abundance, species richness and diversity by producing favourable micro-sites (Niemelä *et al.* 1992, Niemelä & Spence 1994, Magura *et al.* 2000). In the non-native managed larch plantation, the coverage of trees and herbs was rather similar to that of the mixed broad-leaved forest (contrary to the oak forest), as were the herb-species composition, structure and thickness of leaf litter.

These factors contribute to the microhabitat heterogeneity, which possibly induced the differentiation in the composition and abundance of *Carabus* assemblages among the forests of our study. Thus, planting larch for forest restoration may not have brought about great variation in species richness and abundance of *Carabus* assemblages, compared to the two native forests. However, the species composition of the *Carabus* assemblage in the larch plantation significantly differed from the two native forests. Thus, if the larch was chosen as the dominant tree species for forest restoration after clear-cutting, it may have led to a simplification of the *Carabus* assemblage of a larger area.

4.2. Spatial distribution

We showed a positive relationship between beetle distribution and abundance. Each of the three most abundant *Carabus* species in the study area changed among forests and sampling days from uncommon and narrowly distributed to common and widespread (Fig. 3). A positive relationship between local abundance and regional distribution among similar species is a general phenomenon (Hanski 1982, Gaston & Lawton 1990, Niemelä & Spence 1994). Our findings also indicate that this phenomenon was detectable at a local scale, in the short-term dynamics of abundance and trap occupancy within patches of habitats. This result corroborates the results of Crist & Ahern (1999), who studied different-sized mown patches in an old field over the summer, whereas we examined different forests and the seasonality of *Carabus* abundance. Niche specialization might be one explanation for the positive relationship between species distribution and abundance, suggesting that habitat generalists are more widespread than specialists (Gaston & Lawton 1990). Our previous findings have indicated that each of the three abundant species in the present study was most widespread and abundant in a different combination of habitats and time (seasons) (Yu *et al.* 2002).

On the smallest scale (trapping groups within a forest), the occurrence of abundant species was clumped but the extent of aggregation among forests was different. One possible explanation might be the similarity in responses to microhabitat differences that leads to aggregation of individuals (Niemelä & Halme 1992). In addition, behavioural responses involved in mating behaviour should also be considered as a possible explanation. However, the above two explanations could not be assessed directly with the present data, and further investigations should be conducted.

4.3. Temporal distribution

Temperature and humidity are two important factors that determine the quality and distribution of microhabitats, and influence the abundance and composition of carabid community (Lövei &

Sunderland 1996). Food availability is mainly determined by temperature and moisture, and may explain carabid seasonal activity. In the study area, temperature is higher in summer (June to August) than any other season, and nearly 78% of the annual rainfall occurs during that period (Chen & Huang 1997). Corresponding to the high temperature and humidity in the summer, our studies suggest that the total catches of all *Carabus* species had their main abundance peaks in June–August in the study area, but *C. manifestus*, as one of the dominant species, was deviated from this trend of seasonal dynamics. Because between-forest distances were ca. 2 km, the overall temperature and humidity conditions in the three forests were likely to be similar. Sota (1985) suggested that the life history patterns might be associated with seasonal dynamics in *Carabus*. Logically, the differences in life history pattern among different *Carabus* species may lead to different seasonal dynamics.

Undoubtedly the insignificant correlations of *C. manifestus* among the non-native larch plantation and the two native forests may have demonstrated asynchronous seasonal dynamics among the three forests. This result might be explained by microhabitat differentiation. The vegetation under the canopy in larch plantation is similar to the native mixed broad-leaved forest, but larch needles might create a ground cover different from that of the native forests.

In general, the non-native larch plantation was not remarkably different from the native forests regarding the composition and abundance of *Carabus* assemblages. Thus, if managed cautiously, the non-native larch plantations could even add to the landscape-scale indigenous species composition. However, because there was still some variation in species composition and spatial distribution between the larch plantation and the two native forests, planting larch instead of native forests after clear-cutting might lead to a simplification of the landscape-scale *Carabus* assemblage. So, although planting larch may contribute the post-harvest recovery of the forest environment without significantly deteriorating the abundance and composition of *Carabus*, the restoration of native trees is also necessary for maintaining the species diversity and abundance of *Carabus* in the study region. Moreover, addi-

tional information on the life cycles and dispersal of *Carabus* beetles would help to understand their seasonal distribution-abundance patterns in the warm temperate zone of North China.

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References

- Baars, M. A. 1979: Catches in pitfall traps in relation to mean densities of carabid beetles. — *Oecologia* 41: 25–46.
- Brezina, B. 1999: World catalogue of the genus *Carabus* L. — Pensoft, Sofia–Moscow.
- Chen, L. Z. & Huang, J. H. 1997: The study on structure and function of forest ecosystem in warm temperate zone. — Beijing Science Press, Beijing. [In Chinese with English abstract]
- Crist, T. O. & Ahern, R. 1999: Effects of habitat patch size and temperature on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in an old field. — *Environ. Entomol.* 28: 681–689.
- Davies, K. & Margules, C. R. 1998: Effects of habitat fragmentation on carabid beetles: experimental evidence. — *J. Anim. Ecol.* 67: 460–471.
- Decree No.7 of the State Forestry Administration of the People's Republic of China 2002: (The list of wild animals under national protection.) — The State Forestry Administration of the People's Republic of China. [In Chinese]
- Doberski, J. & Lyle, L. 1997: A study of the ground beetles (Carabidae) of Corsican pine plantations in Thetford Forest, eastern England. — *Entomologist* 116: 15–23.
- Duchesne, L. C., Lautenschlager, R. A. & Bell, F. W. 1999: Effects of clear-cutting and plant competition control methods on carabid (Coleoptera: Carabidae) assemblages in Northwestern Ontario. — *Environ. Monit. Assess.* 56: 87–96.
- Duelli, P., Studer, M., Marchand, I. & Jakob, S. 1990: Population movements of arthropods between natural and cultivated areas. — *Biol. Conserv.* 54: 193–207.
- Epstein, M. E. & Kulman, H. M. 1990: Habitat distribution and seasonal occurrence of carabid beetles in East-central Minnesota. — *Am. Midl. Nat.* 123: 209–225.
- Eyre, M. D., Lott, D. A. & Garside, A. 1996: Assessing the potential for environmental monitoring using ground beetles (Coleoptera: Carabidae) with riverside and Scottish data. — *Ann. Zool. Fennici* 33: 157–163.
- Gaston, K. J. & Lawton, J. H. 1990: Effects of scale and habitat on the relationship between regional distribution and local abundance. — *Oikos* 58: 329–335.
- Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001: PAST: Paleontological Statistics Software Package for Education and Data Analysis. — *Palaeontologia Electronica* 4: 9.
- Hanski, I. 1982: Dynamics of regional distribution: the core and satellite species hypothesis. — *Oikos* 38: 210–221.
- Humphrey, J. W., Hawes, C., Peace, A., Ferris-Kaan, J. R. & Jukes, M. R. 1999: Relationships between insect diversity and habitat characteristics in plantation forests. — *For. Ecol. Manage.* 113: 11–21.
- Hurlbert, S. H. 1990: Spatial distribution of montane unicorn. — *Oikos* 58: 257–271.
- Hutcherson, J. & Jones, D. 1999: Spatial variability of insect communities in a homogenous system: Measuring biodiversity using Malaise trapped beetles in a *Pinus radiata* plantation in New Zealand. — *For. Ecol. Manage.* 118: 93–105.
- Imura, Y. & Mizusawa, K. 1996: The *Carabus* of the world. — Mushi-sha, Tokyo. [In Japanese]
- Jennings, D. T., Houseweart, M. W. & Dunn, G. A. 1986: Carabid beetles (Coleoptera: Carabidae) associated with strip clear-cut and dense spruce-fir forest of Maine. — *Coleopt. Bull.* 40: 251–263.
- Kim, C. G., Zhou, H. Z., Imura, Y., Tominaga, O., Su, Z. H. & Osawa, S. 2000: Pattern of morphological diversification in the *Leptocarabus* ground beetles (Coleoptera: Carabidae) as deduced from mitochondrial ND5 gene and nuclear 28S rDNA sequences. — *Mol. Biol. Evol.* 17: 137–145.
- Kinnunen, H. & Tiainen, J. 1999: Carabid distribution in a farmland mosaic: the effect of patch type and location. — *Ann. Zool. Fennici* 36: 149–158.
- Kotze, D. J. & Samways, M. J. 1999: Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. — *Biod. Conserv.* 8: 1339–1363.
- Lenski, R. E. 1982: The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in southern Appalachians. — *Ecol. Entomol.* 7: 385–390.
- Lövei, G. L. & Sunderland, K. D. 1996: Ecology and behavior of ground beetles (Coleoptera: Carabidae). — *Ann. Rev. Entomol.* 41: 231–256.
- Ludwig, J. A. & Reynolds, J. F. 1988: Statistical ecology. — Wiley, New York.
- MacKinnon, J. & Xie, Y. 2001: Restoring China's degraded environment: the role natural vegetation. — China Forestry Publishing House, Beijing.
- Magura, T., Tóthmérész, B. & Bordán, Zs. 2000: Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. — *Biol. Conserv.* 93: 95–102.

- Morisita, M. 1959: Measuring of the dispersion of individuals and analysis of the distributional patterns. — *Memoirs Faculty of Science, Kyushu University, Series E, Biology* 2: 215–235.
- Niemelä J. & Halme, E. 1992: Habitat associations of carabid beetles in fields and forests on the Åland Islands, SW Finland. — *Ecography* 15: 3–11.
- Niemelä, J., Langor, D. & Spence, J. R. 1993: Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. — *Conserv. Biol.* 7: 551–561.
- Niemelä, J. & Spence, J. R. 1994: Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. — *Ecography* 17: 166–175.
- Niemelä, J., Spence, J. R. & Spence, D. H. 1992: Habitat associations and seasonal activity of ground-beetles (Coleoptera: Carabidae) in Central Alberta. — *Can. Entomol.* 124: 521–540.
- Sota, T. 1985: Life history patterns of carabid beetles belonging to the subtribe Carabidian (Coleoptera, Carabidae) in the Kinki district, western Japan. — *Kontyû* 53: 370–378.
- Sota, T. 1986: Effects of temperature and photoperiod on the larval development and gonad maturation of a carabid beetle, *Carabus yaconinus* (Coleoptera: Carabidae). — *Appl. Entomol. Zool.* 21: 89–94.
- Sota, T., Takami, Y., Kubota, K., Ujiiie, M. & Ishikawa, R. 2000: Interspecific body size differentiation in species assemblages of the carabid subgenus *Ohomopterus* in Japan. — *Popul. Ecol.* 42: 279–291.
- Spence, J. R. & Niemelä, J. K. 1994: Sampling carabid assemblages with pitfall traps: the madness and the method. — *Can. Entomol.* 126: 881–894.
- SPSS, Inc. 1997: SPSS base 7.5 for Windows user's guide. — SPSS Inc., Chicago.
- Su, Z. H., Ohama, T., Okada, T. S., Nakamura, K., Ishikawa, R., & Osawa, S. 1996: Phylogenetic relationship and evolution of the Japanese Carabidae ground beetles based on mitochondrial ND5 gene sequences. — *J. Mol. Evol.* 42: 124–129.
- Takami, Y. 2003: Experimental analysis of the effect of genital morphology on insemination success in the ground beetle *Carabus insulicola* (Coleoptera: Carabidae). — *Ethol. Ecol. Evol.* 15: 51–61.
- Yu, X. D., Zhou, H. Z. & Luo, T. H. 2002: Distribution patterns and their seasonal changes of *Carabus* beetles in Dongling Mountain region near Beijing. — *Acta Ecologica Sinica* 22: 1724–1733. [In Chinese with English abstract]