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ORIGINAL ARTICLE

Carabid beetles (Coleoptera: Carabidae) in several types of forests on Hokkaido, Japan, with implications for forest management practices and beetle preservation

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Abstract. This study of the role the environment in the composition of the communities of carabid beetles was carried out in several types of forests at Obihiro and Furano, Hokkaido, Japan. In addition, we analysed the altitudinal distributions of two forest specialists, *Damaster gehinii* (Faimaire) and *Procrustes kolbei* Roeschke, which occur in six mountain forests on Hokkaido. At Obihiro, the forest specialist, *P. kolbei* was found at only one site in a large area of broadleaf forest. A redundancy analysis indicated that the carabid assemblages were significantly different in the different types of forest, and that two species, *Leptocarabus arboreus arboreus* (Lewis) and *Leptocarabus opaculus opaculus* (Putzeys), were associated with broadleaf forests. At Furano, a forest specialist *D. gehinii* and a forest generalist *Cychrus morawitzi* Gehin were mainly collected in natural broadleaf and mixed forests, whereas the percentage made up of *L. o. opaculus* was very high (80.8%) in natural broadleaf forest. *Pterostichus thunbergii* Morawitz made up the highest percentage of the species in the conifer plantations. In the six mountain forests, *D. gehinii* was scarce and mainly occurred at low altitudes; however, *P. kolbei* was relatively abundant and mainly recorded at middle to high altitudes. The management of the forests on Hokkaido needed to maintain the diversity and abundance of carabid beetles is discussed.

INTRODUCTION

Japan is a country where two-thirds of the land is covered by forest of which 40% consists of plantations mainly composed of cryptomeria and Japanese cypress (Ministry of Agriculture, Forestry and Fisheries, 2018). On Hokkaido, more than 70% of the land is covered with forests, almost all of which are natural except at high altitudes where there are secondary broadleaf forests and conifer plantations (Hokkaido Government, 2018). In terms of forestry management, forest biota are not considered. Logging and reforestation fragment the landscape and can affect the composition of arthropod communities (Duchesne et al., 1999; Kotze & Samways, 1999; Werner & Raffa, 2000; Müller et al., 2002; Waltz & Covington, 2004; Koivula & Spence, 2006; Cobb et al., 2007). Reducing the effect of afforestation on arthropods in forest ecosystems is an important issue that needs to be considered by forest managers.

Carabid beetles (Coleoptera: Carabidae) are diverse and abundant, have relatively well known ecologies and systematics and are easy to collect using pitfall traps (Eyre et al., 1996; Lövei & Sunderland, 1996; Niemelä et al., 2000; Werner & Raffa, 2000). Moreover, they are sensitive to environmental factors and respond rapidly to habitat changes (Osawa et al., 2005; Shibuya et al., 2008, 2014), because they are poor at dispersing as they have vestigial hind wings (Niemelä, 1997; Duchesne et al., 1999; Yu et al., 2002, 2006). Thus, they are used as bio-indicators in investigations into the biodiversity in forests managed in different ways in Europe (Humphrey et al., 1999; Magura et al., 2000, 2001a; Koivula, 2002b; Finch, 2005; Lövei et al., 2006; Karen et al., 2008; Lange et al., 2014; Negro et al., 2014), Africa (Rainio & Niemelä, 2006), Central and North America (Klimaszewski et al., 2005; Ulyshen et al., 2006) and Japan (Fujita et al., 2008; Kaizuka & Iwasa, 2015).

Many studies on carabid assemblages in forests have been on various issues, such as age of forests and effect of replanting after logging and deforestation (Baguette & Gerard, 1993; Fahy & Gormally, 1998; Ings & Hartley, 1999; Baker, 2006); effects of fragmentation on assemblages (Halme & Niemelä, 1993; Fujita et al., 2008); effect of edges between forest and clear-cut grassland (Heliölä et al., 2001; Magura et al., 2001b; Magura, 2002) and comparison of conifer and broadleaf forests (Butterfield et al., 1995; Fuller et al., 2008; Yu et al., 2008). The differences between carabid assemblages in various landscapes are also reported in ecotones between natural forests and mature pine forests (Yu et al., 2010), urban landscapes (da Silva et al., 2008; Do et al., 2012) and farmland (Purtauf et al., 2005). The clear-cutting of native forests and planting non-native species of trees in clear-cut areas have unfavourable effects on the species diversity and abundance of carabids (Fahy & Gormally, 1998; Magura et al., 2000, 2002; Yu et al., 2006). However, the response of carabid beetles to changes in forests depends on their location. Further knowledge on carabid assemblages in various types of forests is required for conservation and management of forest. There is also little information on the altitudinal distributions of carabid. The aim of this study is to collect data on carabid beetles for evaluating the conservation value of typical forests on Hokkaido, Japan, and recommend how these forests should be managed in order to safeguard the carabid assemblages in mountain areas. First, the carabid assemblages in the secondary broadleaf forests, secondary mixed forests of broadleaf and conifer trees and the conifer (Sakhalin fir) plantations at Obihiro in eastern Hokkaido were recorded. All these sites were originally natural deciduous forests, which were felled and replanted. Second, we compared the composition of the carabid assemblage in a natural broadleaf forest, a natural mixed forest and conifer plantation at Furano in central Hokkaido. Third, the altitudinal distributions of two forest specialists (*Damaster gehinii* (Faimaire) and *Procrustes kolbei* Roeschke) that inhabit natural or mature forest on six mountains in central to eastern Hokkaido were analysed using insect collections in the Laboratory of Entomology at Obihiro University of Agriculture and Veterinary Medicine.

MATERIALS AND METHODS

Carabid beetles in secondary broadleaf forests, mixed forests and conifer plantations at Obihiro

Study area and sampling

The area studied is located at the foot of the Hidaka Mountain range in the suburbs of Obihiro City in the eastern part of Hokkaido, northern Japan. The area is mainly surrounded by secondary broadleaf forests, secondary mixed forests, and conifer plantations, and the Tottabetsu river and its tributaries. Three types of forests were sampled with three replicates in each: (1) secondary broadleaf forest, (2) secondary mixed forest and (3) conifer plantation (Table 1). The sample sites were located at an altitude of 425–650 m (Table 1). The areas were each between 0.9–30.2 ha in size: 2.7–30.2 ha for the secondary broad leaf forest, 0.9–4.9 ha for the secondary mixed forest and 1.1–2.5 ha for the conifer (Sakhalin fir) plantation and in terms of the age of the trees were between 40–50 years after regrowth or replanting of each site. Although there is a difference in the age of the trees at the different sites, stands of pine that are between 21–60 years old are usually regarded as in the same age class (Baguette & Gerard, 1993; Niemelä et al., 1994), so all the sites studied were considered to be in the same age class.

Ground beetles were sampled using baited pitfall traps (8 cm in diameter and 9.5 cm deep with two small holes high up on the sides to drain excess rainwater) containing 20 mL of a solution of water, brown sugar, acetic acid and ethanol in the ratio 6 : 2 : 1 : 1 (Kimoto & Yasuda, 1995). Six needles were fixed to the top of each trap to deter wild animals from damaging the traps. Fifteen traps were set at least 50 m from the forest edge in order to avoid "edge effects" (Magura et al., 2001b) with a distance of about 2–3 m between traps and with their openings level with the ground surface. During this survey, 135 traps were used. Samples were collected at 2-week intervals from 18 June to 26 August 2016. As the area studied was destroyed by 3 typhoons (17, 21, and 23 August), we only used the results recorded in the period prior to the first typhoon Carabid beetles collected at each site were pooled, and the number of beetles caught per trap was calculated only for traps that were not disturbed by wild animals. Pooled samples were identified to species according to Ueno et al. (1985). Some remarkable or representative species were categorized as "forest specialists" or "forest generalists" using habitat data of Kimoto & Yasuda (1995), Hori (2003) and Working Group for Biological Indicator Ground Beetles Database Japan (2015). According to Jukes et al. (2001), the two categories are defined as follows: forest specialist are species with a strong affinity for forest habitats such as natural or mature forest; forest generalist are those associated with a wider range of forest habitats, including scrub and hedgerows.

Environmental variables and analysis

Percentage understory cover and canopy cover were assessed at one point per site within a radius of 5 m in July 2016. Soil moisture was measured at a depth of approximately 5 cm in the

Table 1. Details of the sites where carabid beetles were sampled at Obihiro and Furano.

Forest types	n	Sites	Locations	Altitude (m)	Area (ha)	Canopy cover (%)	Understory cover (%)
Obihiro							
		1	42°42´59N, 142°52´53E	650	30.2	70	80
Secondary broadleaf forest (Bro)	3	2	42°44´29N, 142°52´10E	470	3.7	85	70
		3	42°43´59N, 142°53´26E	425	2.7	80	85
		1	42°43´54N, 142°52´53E	483	4.9	70	70
Secondary mixed forest (Mix)	3	2	42°44´26N, 142°52´10E	475	2.6	75	85
		3	42°44´10N, 142°52´58E	448	0.9	75	80
		1	42°44´03N, 142°52´56E	457	1.1	60	95
Conifer (Sakhalin fir) plantation (Con)	3	2	42°44´21N, 142°52´00E	495	2.5	65	90
		3	42°44´27N, 142°52´28E	458	1.5	55	100
Furano							
Natural broadleaf forest (NB)	1	—	43°12´44N, 142°28´22E	380	6.9	35	80
Natural mixed forest (NM)	1	—	43°12´49N, 142°28´27E	406	3.4	30	55
Conifer plantation (PL)	1	—	43°12´44N, 142°28´22E	355	4.3	85	10

Table 2. Locations and dominant species of trees in canopy and plants in the understory at sites sampled for carabid beetles on six mountains.

<table>
<tr><th rowspan="3">Mountain</th><th rowspan="3">Maximum altitude
Latitude
Longitude</th><th colspan="3">Dominant species of trees</th><th colspan="3">Dominant species of understory plants</th></tr>
<tr><th colspan="6">Altitudinal categories</th></tr>
<tr><th>Low
Below 700 m</th><th>Middle
700–1,400 m</th><th>High
Above 1,400 m</th><th>Low
Below 700 m</th><th>Middle
700–1,400 m</th><th>High
Above 1400 m</th></tr>
<tr><td>Tokachi-Poroshiri</td><td>1,846 m
42°41´44N
142°51´33E</td><td rowspan="5">Betulaceae
Alnus maximowiczii
Betula platyphylla
Pinaceae
Picea jezoensis
Abies sachalinensis
Salicaceae
Populus suaveolens</td><td rowspan="5">Betulaceae
Alnus maximowiczii
Betula ermanii
Pinaceae
Picea jezoensis
Picea glehnii
Abies sachalinensis
Fagaceae
Quercus crispula</td><td rowspan="6">Betulaceae
Betula ermanii
Pinaceae
Pinus pumila</td><td colspan="2" rowspan="3">Poaceae
Sasa senanensis</td><td rowspan="6">Ericaceae
Empetrum nigrum japonicum
Vaccinium vitis-udaea</td></tr>
<tr><td>Fushimi</td><td>1,792 m
42°46´34N
142°45´56E</td></tr>
<tr><td>Memuro</td><td>1,754 m
42°52´8N
142°47´7E</td></tr>
<tr><td>Shari</td><td>1,547 m
43°45´57N
144°43´3E</td><td colspan="2" rowspan="3">Poaceae
Sasa kurilensis</td></tr>
<tr><td>Yûbari</td><td>1,668 m
43°5´59N
142°15´4E</td></tr>
<tr><td>Rakko</td><td>1,471 m
42°16´20N
143°40´49E</td><td>Ulmaceae
Ulmus davidiana var. japonica
Sapindaceae
Acer pictum ssp. mono</td><td>Rosaceae
Sorbus commixta
Betulaceae
Betula platyphylla</td></tr>
</table>

centre of each site once a month during the sampling period using a ProCheck Handheld Reader (Decago Devices, Inc., Pullman, WA, USA).

We determined the associations between five environmental variables (canopy cover, understory cover, size of area, soil moisture and type of forest) and the numbers of species and individuals. We used generalized linear models (GLM) with Poisson error distributions and log link functions (glm function of package). In the GLM, the numbers of species and individuals were used as a response variables, and the five environmental variables as explanatory variables. Akaike's information criteria (AIC) were used to test the goodness of fit of the estimated statistical models. To remove the possible effects of variation in abundance among samples, a rarefaction method was used to standardize species richness per number of individuals. Redundancy analysis (RDA) was used to determine the relative importance of environmental variables associated with the carabid species assemblages. The significance of environmental variables associated with the carabid assemblage was tested using a permutation test (4,999 permutations). To reveal the significance of the relationship between environmental variables and assemblages, we chose the optimum model using the command "ordistep" in package "vegan". The "ordistep" selected two environmental variables "area" and "understory cover". The number of individuals in each species was $\log(x + 0.1)$ transformed in RDA. We used R4.0.2 software for these analyses (R Development Core Team, 2020).

Carabid beetles in natural broadleaf forest, natural mixed forest and conifer plantation at Furano

Study area and sampling

We investigated the distribution of carabid beetles in three types of forests located at Furano in central Hokkaido, northern Japan: (1) natural broadleaf forest, (2) natural mixed forest and (3) conifer plantation (Table 1). The areas were 6.9 ha for the natural broadleaf forest, 3.4 ha for the natural mixed forest and 4.3 ha for the conifer plantation. Ground beetles were sampled using the same methods as described above. Samples were collected at 2-week intervals from 16 June to 31 October 2008 and 6 June to 20 October 2009. Here, we focused on the species of carabid characteristic of each type of forest, because we only had one replicate for each types of forest.

Altitudinal distributions of two forest specialists in six mountain forests on Hokkaido

Study area and sampling

We analysed the altitudinal distributions of two forest specialists, *D. gehinii* and *P. kolbei*, which were collected from six mountain forests by the Laboratory of Entomology at Obihiro University of Agriculture and Veterinary Medicine. The six mountains and years sampled are as follows: (1) Mt. Tokachi-Poroshiri (1986), (2) Mt. Fushimi (1987), (3) Mt. Memuro (1983), (4) Mt. Shari (1983), (5) Mt. Yûbari (1981) and (6) Mt. Rakko (1995). These mountains are located in central and eastern Hokkaido (Table 2). We classified the samples collected into three groups based on their altitudinal distributions: (1) low altitudes (below 700 m) (Mt. Tokachi-Poroshiri: 2 sites, Mt. Fushimi: 1 site, Mt. Memuro: 2 sites, Mt. Shari: 2 sites, Mt. Yûbari: 2 sites, Mt. Rakko: 2 sites), (2) middle altitudes (701–1400 m) (Mt. Tokachi-Poroshiri: 5 sites, Mt. Fushimi: 4 site, Mt. Memuro: 4 sites, Mt. Shari: 4 sites, Mt. Yûbari: 2 sites, Mt. Rakko: 4 sites), (3) high altitudes (above 1,400 m) (Mt. Tokachi-Poroshiri: 3 sites, Mt. Fushimi: 4 site, Mt. Memuro: 2 sites, Mt. Shari: 4 sites, Mt. Yûbari: 1 site, Mt. Rakko: 1 site). When there were several sites for a group, the average number of individuals was divided by the number of sites. At low altitudes, the dominant vegetation making up the canopy was that of mixed forest consisting of broadleaf (*Alnus maxinowiczii* Callier, *Betula platyphylla* Sukaczev and *Populus suaveolens* Fisch) and coniferous trees [*Picea jezoensis* (Siebold et Zucc) and *Abies sachalinensis* (Fr. Schmidt)] except on Mt. Rakko where the broadleaf forests consist of *Ulmus davidiana* var. *japonica* Nakai and *Acer pictum subsp. mono* (Maxim.) (Table 2). The dominant vegetation making up the canopy at middle altitudes was mixed forest with broadleaf (*A. maxinowiczii*, *Betula ermanii* Cham., and *Quercus crispula* Blume) and coniferous trees [*P. jezoensis*, *A. sachalinensis* and *Picea glehnii* (Fr. chmidt)] except on Mt. Rakko where the broadleaf forests consist

Table 3. Species and numbers of carabid beetles collected in secondary broadleaf forest and mixed forests and conifer (Sakhalin fir) plantations at Obihiro.

Species	Bro	Mix	Con	Total
Cychrus morawitzi Gehin	61	31	5	97
Calosoma inquisitor cyanescens Motschulsky	10	1	0	11
Carabus conciliator hokkaidensis Lapouge	48	46	174	268
Leptocarabus arboreus arboreus (Lewis)	80	0	0	80
Leptocarabus opaculus opaculus (Putzeys)	938	404	84	1426
Procrustes kolbei (Roeschke)	2	0	0	2
Damaster blaptoides rugipennis Motschulsky	33	38	78	149
Pterostichus subovatus (Motschulsky)	2	2	0	4
Pterostichus adstrictus Eschscholtz	13	13	49	75
Pterostichus thunbergii Morawitz	171	226	819	1216
Pterostichus orientalis jessoensis Tschitscherine	22	17	82	121
Colpodes daisentsuzanus Nakane	4	1	1	6
Synuchus nitidus (Motshulsky)	1	0	2	3
Synuchus cycloderus (Bates)	6	0	0	6
Synuchus melantho (Bates)	2	8	2	12
Number of individuals	1393	787	1296	3476
Total number of species	15	11	10	15

Bro – secondary broadleaf forest; Mix – secondary mixed forest; Con – Conifer (Sakhalin fir) plantation.

of *Sorbus commixta* Hedl. and *B. platyphylla* (Table 2). At high altitudes, the dominant trees was *Betula ermanii* Cham. and *Pinus pumila* Regel (Table 2). The dominant species in the understory at low and middle altitudes was *Sasa senanensis* Rehder (Mt. Tokachi-Poroshiri, Mt. Fushimi and Mt. Memuro) and *Sasa kurilensis* Makino et Shibata (Mt. Shari, Mt. Yûbari and Mt. Rakko) (Table 2). The understory at high altitudes was dominated by *Empetrum nigrum japonicum* K. Koch and *Vaccinium vitis-udaea* L (Table 2). Ground beetles were sampled using the same methods as described above. Samples were collected at 2-week intervals from June to October each year.

RESULTS

Carabid beetles in secondary broadleaf forests, mixed forests and conifer plantations at Obihiro

Species richness and abundance

A total of 3,476 carabid beetles consisting of 15 species in 6 genera was caught (Table 3). The number of individuals was highest in the secondary broadleaf forests (1,393), followed by the conifer (Sakhalin fir) plantations (1,296) and the secondary mixed forests (787). We collected 15 species in the secondary broadleaf forests, 11 species in the secondary mixed forests and 10 species in the conifer (Sakhalin fir) plantations. *P. kolbei* was caught only in the largest broadleaf forests at the highest altitudes in the area studied. *Leptocarabus opaculus opaculus* (Putzeys) was the most abundant (1,426 individuals, 41.0% of the total catch), followed by *Pterostichus thunbergii* Morawitz (1,216 individuals, 35.0% of the total catch), together making up 76.0% of the total catch. *Leptocarabus opaculus opaculus* was most abundant in the secondary broadleaf forests and very rare in the conifer plantations. *Carabus conciliator hokkaidensis* Lapouge and *P. thunbergii* were abundant in the conifer plantations, accounting for 65.0% and 67.0% of the total catch in each, respectively.

Table 4. GLM results of the species richness and number of individuals of carabids.

Response variable	Estimate	Std. error	z value	Pr
No. of individuals				—
canopy	–0.817396	0.010237	–79.844	***
understory	–0.641410	0.004822	–133.020	***
moisture	3.116207	0.028425	109.628	***
area	0.498932	0.005282	94.465	***
forest type Mix	–1.125294	0.117318	–9.592	***
forest type Con	–5.618423	0.254746	–22.055	***
Species				
(NULL)	—	—	—	—

Forest type Mix – mixed forests; forest type Con – conifer plantations; *** – $p < 0.001$.

Environmental variables and carabid occurrence

The canopy cover was moderately thin (55–65%) in the conifer (Sakhalin fir) plantations but moderately dense (70–85%) in the secondary broadleaf forests and the secondary mixed forests (Table 1). The dominant species in the canopy cover were *A. sachalinensis* (Sakhalin fir) in the conifer plantations; *Q. crispula* and *Tilia japonica* Simonk in the secondary broadleaf forests; and *Q. crispula* and *A. sachlainensis* in the secondary mixed forests. The understory was dense (90–100%) in the conifer (Sakhalin fir) plantations and moderately dense (70–85%) in the secondary broadleaf forests and secondary mixed forests (Table 1). The dominant species in the understory was dwarf bamboo *S. senanensis* in all types of forest.

GLM models for species richness and numbers of carabids are presented in Table 4. All environmental variables were associated with the numbers of carabids. These results may be due to the large number of *L.o.opaculus* at one site in the broad leaf forest and *P.thunbergii* in conifer plantations. There were no environmental variables associated with the species richness of carabids. However, when the number of species recorded was standardized by rarefaction in terms of numbers of individuals, species richness in the secondary broadleaf forests was higher than in other types of forest (Fig. 1).

Carabid assemblages

A total of 72.2% of the carabid species-environmental associations was accounted for by two axes of the RDA. The study sites are located along the first and second axes

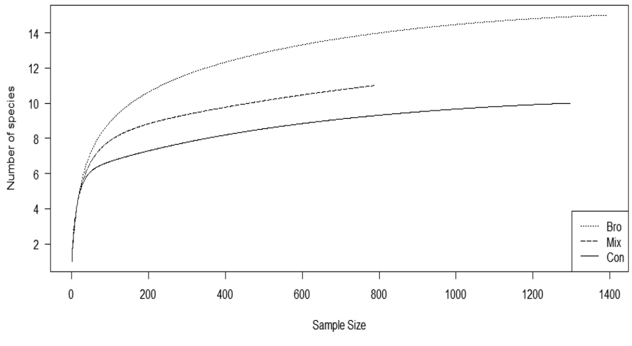

Fig. 1. Rarefaction curves of species richness for each type of forest at Obhiro. Bro – secondary broadleaf forest; Mix – secondary mixed forest; Con – conifer (Sakhalin fir) plantation.

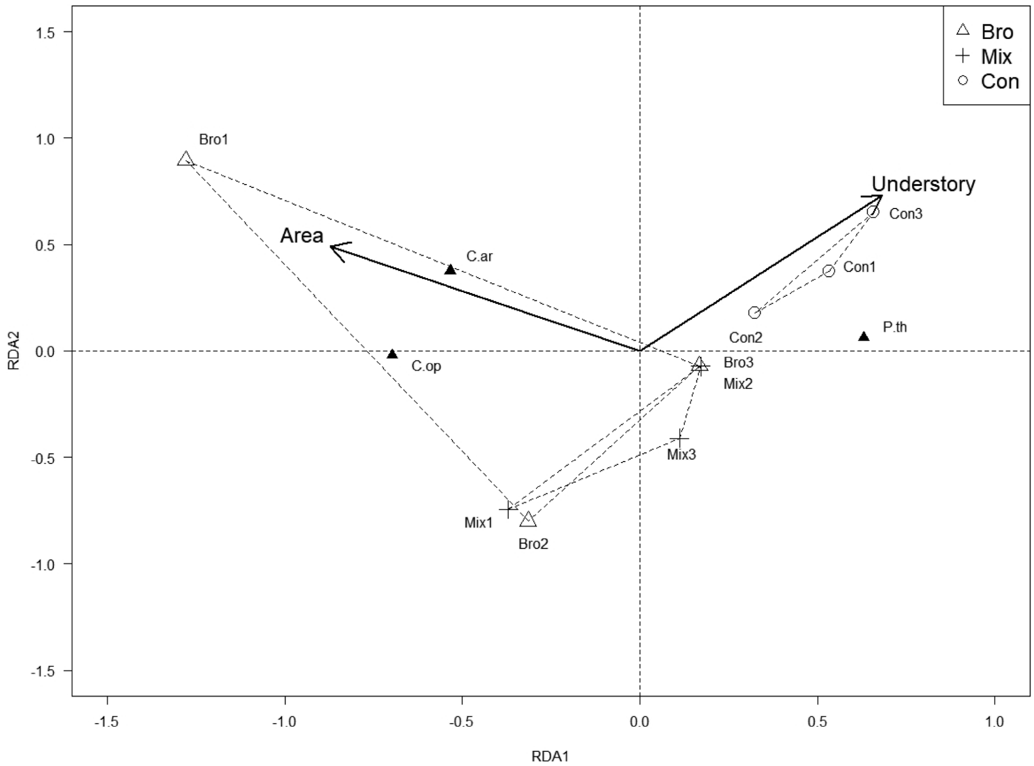

Fig. 2. Redundancy analysis (RDA) of carabid beetle-environmental variables biplot for Obihiro. L.ar – *Leptocarabus arboreus arboreus*; L.op – *Leptocarabus opaculus opaculus*; P.th – *Pterostichus thunbergii*; Bro – secondary broadleaf forest; Mix – secondary mixed forest; Con – conifer (Sakhalin fir) plantation.

in terms their area and understory cover (Fig. 2), with sites with large areas on the left of the diagram and those with high understory cover on the right. The RDA analysis indicates that the carabid assemblages differed significantly among the different types of forest ($p < 0.05$) and the structure of the carabid assemblages is significantly associated with area and understory cover ($p < 0.001$ and $p < 0.01$, respectively). The RDA diagram also indicates that two species [*Leptocarabus a. arboreus* (Lewis) and *L. o. opaculus*] are associated with area, and *P. thunbergii* with understory cover (Fig. 2).

Carabid beetles in natural broadleaf forest, natural mixed forest and conifer plantation at Furano

Species composition, species richness and abundance

A total of 2,684 individuals consisting of 21 species in 10 genera were caught at Furano (Table 5). The percentage of the total catch made up of the predominant species in the three types of forest is shown in Fig. 3. The percentage of the total catch made up of *Cychrus morawitzi* Gehin and *Damaster gehinii* was highest in both the natural broadleaf forest (59.5% and 53.0%, respectively) and natural mixed forest (31.6% and 44.8%, respectively) and low in the conifer plantation (8.9% and 2.2%, respectively). The percentages of the total catch made up of *L. o. opaculus* were remarkably high in the natural broadleaf forest (80.8%) and low in the natural mixed forest (10.9%) and conifer plantation (8.2%). The percentages of *P. thunbergii* were 51.6% in the natural mixed forest, 30.9% in the conifer plantation and 17.5% in the natural broadleaf forest.

The canopy cover was thin (35% and 30%, respectively) in the natural broadleaf forest and natural mixed forest. The dominant species of trees in the canopy were mainly *Acer pictum* Thunb and *Q. crispula* in the natural broadleaf for-

Table 5. Species and numbers of carabid beetles in natural broadleaf forest and mixed forest and conifer (Sakhalin fir) plantation at Furano.

Species	NB	NM	PL	Total
Cychrus morawitzi Gehin	94	50	14	158
Leptocarabus opaculus opaculus (Putzeys)	1050	142	107	1299
Damaster gehinii (Faimaire)	71	60	3	134
Damaster blaptoides rugipennis Motschulsky	154	217	54	425
Leistus niger alecto Bates	11	5	3	19
Pterostichus samurai (Lutshnik)	0	0	1	1
Pterostichus subovatus (Motschulsky)	9	0	7	16
Pterostichus adstrictus Eschscholtz	19	2	23	44
Pterostichus thunbergii Morawitz	191	564	338	1093
Pterostichus orientalis jessoensis Tschitscherine	10	12	29	51
Colpodes daisetsuzanus Nakane	57	4	2	63
Colpodes lampros Bates	1	0	0	1
Synuchus nitidus (Motschulsky)	203	144	259	606
Synuchus cycloderus (Bates)	10	20	30	60
Synuchus melantho (Bates)	17	37	38	92
Synuchus congruus (Morawitz)	0	3	3	6
Synuchus arcuaticollis (Motschulsky)	2	0	0	2
Amara sp.	1	0	0	1
Anisodactylus punctatipennis Morawitz	0	0	1	1
Harpalus quadripunctatus ainus Habu et Baba	8	0	1	9
Trichotichnus longitarsis Morawitz	1	0	0	1
Number of individuals	1406	816	462	2684
Number of species	18	13	17	21

NB – natural broadleaf forest; NM – natural mixed forest; PL – conifer plantation.

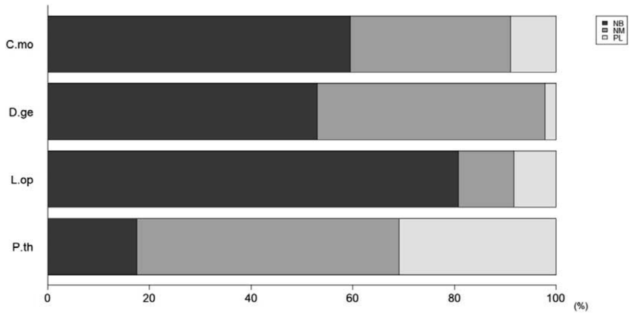

Fig. 3. The percentages of the total catch of four species carabids caught in the natural broadleaf forest, natural mixed forest and conifer (Sakhalin fir) plantation at Furano. C.mo – *Cychrus morawitzi*; D.ge – *Damaster gehinii*; L.op – *Leptocarabus opaculus opaculus*; P.th – *Pterostichus thunbergii*; NB – natural broadleaf forest; NM – natural mixed forest; PL – conifer plantation.

est; *A. sachalinensis* and *B. maximowicziana* in the natural mixed forest; and *A. sachalinensis* in the conifer plantation. The understory cover was dense (80%) in the natural broadleaf forest, moderately thin (55%) in the natural mixed forest and very thin (10%) in the conifer plantation. The dominant species in the understory were *Pachysandra terminalis* Siebold et Zucc and *S. senanensis* in the natural broadleaf forest and natural mixed forest, and *S. senanensis* in the conifer plantation.

Altitudinal distributions of two forest specialists in six mountain forests on Hokkaido

In our survey of the collections of two forest specialists in six mountain forests, the numbers of *D. gehinii* and *P. kolbei* were 174 (3.7%) and 4,525 (96.3%), respectively, with *D. gehinii* clearly the rarer. The percentage of these two forest specialists in the three categories of altitude in the six mountain forests are shown in Fig. 4. On the whole, the percentages of *D. gehinii* appears to be high at low altitudes (below 700 m). On Mt. Rakko, however, the percentages of *D. gehinii* were very low at low altitudes and comparatively high at high altitudes, this difference, however, may be associated with differences in the environmental conditions at the lowest altitudes on the six mountains. On the other hand, the percentages of *P. kolbei* were very high at middle (701–1,400 m) to high altitudes (above 1,400 m) and low at low altitudes (below 700 m).

DISCUSSION

Carabid assemblage composition, species richness, abundance and habitat preference

The species compositions recorded in the present study are similar to those previously reported on Hokkaido in broadleaf forests by Hori (2003) and conifer plantations by Kaizuka & Iwasa (2015). *Damaster gehinii* was caught at Furano but not Obihiro; this is mostly due to differences in the types of forest at Furano and Obihiro. According to Imura & Mizusawa (2013), *D. gehinii* occurs in a wide range of habitats and is abundant in broadleaf forests and mixed forests of broadleaf and coniferous trees. Hori (2003) classifies *D. gehinii* as a forest specialist and notes that it is rare, found only in large natural broadleaf forests. At Furano (Table 5, Fig. 3), this species primarily prefers both natural broadleaf forest and natural mixed forest. Forest specialist species disappear after logging of natural forests and replanting with coniferous trees (Magura et

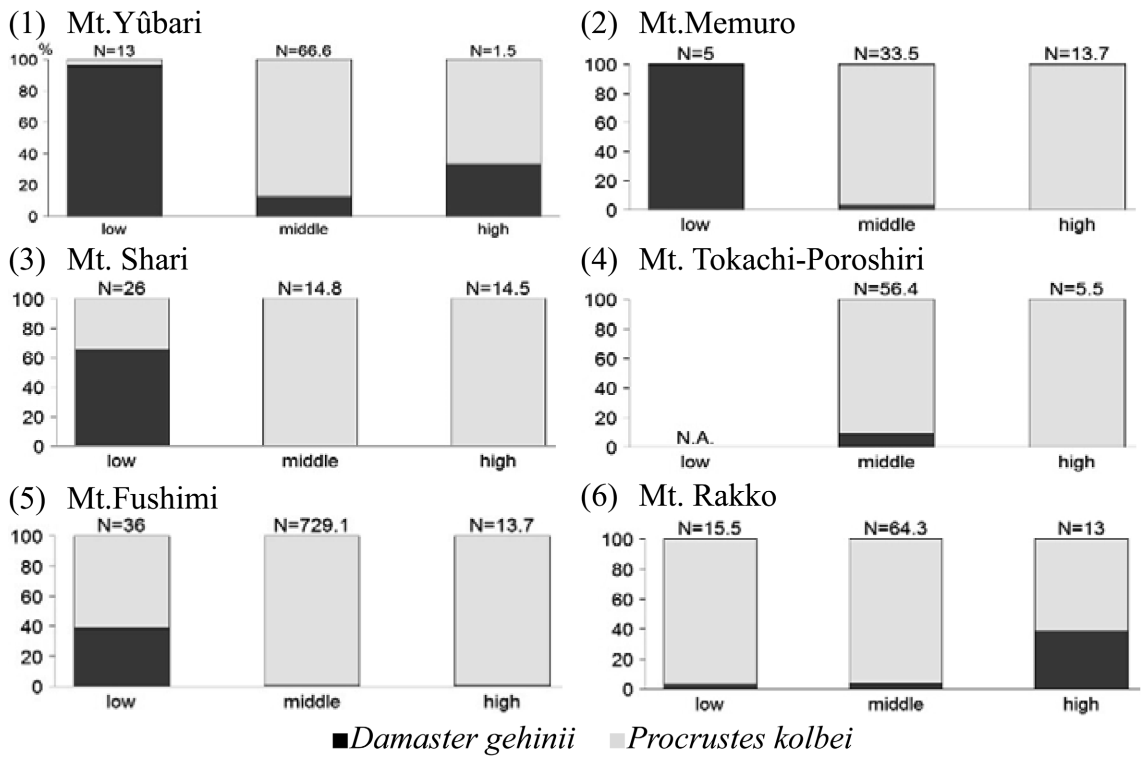

Fig. 4. The percentage of the catch that consisted of individuals of *D. gehinii* and *P. kolbei* at three different altitudes in six mountain forests. N.A. – not available; low – below 700 m; middle – 701 m–1,400 m; high – above 1,400 m.

al., 2002, 2003; Yu et al., 2006). The fact that *D. gehinii* was not caught at Obihiro indicates that this species is not able to survive in secondary forests on mountains at low altitudes, which were repeatedly logged and planted. *Procrustes kolbei* prefers mature forest (Imura & Mizusawa, 2013). Site 1 where *P. kolbei* was caught is located in a larger area of forest and at a higher altitude than the other sites (Table 1). In addition, this species was caught mainly at middle to high altitudes, with few caught at altitudes below 700 m (Table 5), whereas the main habitat of *D. gehinii* seems to be at low altitudes (Fig. 4). When evaluating carabid beetles in secondary broadleaf forest and secondary mixed forest of broadleaf and conifers in mountainous areas, attention should be paid not only to their diversity and abundance but also to the presence and altitudinal distributions of forest specialists.

Comparisons of the diversity of carabid assemblages in broadleaf forest and conifer plantations indicate a lower carabid diversity in conifer plantations (Butterfield et al., 1995; Fahy & Gormally, 1998; Magura et al., 2003; Yu et al., 2006). The rarefaction analysis (Fig. 1) confirms the above as the number of species was least in the conifer (Sakhalin fir) plantations. The mixed forests may be more suitable for some species than the conifer (Sakhalin fir) plantations. *Leptocarabus arboreus arboreus* and *L. o. opaculus* are forest generalists, which inhabit a wide range of forests (Kimoto & Yasuda, 1995; Imura & Mizusawa, 2013). However, Furuta (1983) shows that *L. o. opaculus* is more abundant in natural broadleaf forests than natural mixed forests and conifer (Sakhalin fir) plantations. The RDA results indicate that *L. a. arboreus* and *L. o. opaculus* were associated with secondary broadleaf forests at Obihiro (Fig. 2) and the latter was abundant in natural broadleaf forest at Furano (Fig. 3), therefore, it is likely that these species prefer broadleaf forest. The abundance of *P. thunbergii* in the conifer (Sakhalin fir) plantations at Obihiro (Table 3) indicates this species may not be sensitive to deforestation and can survive in conifer plantations. This is supported by the result that this species made up a relatively high percentage of the total catch in conifer (Sakhalin fir) plantation at Furano (Fig. 3).

Environmental variables and carabid occurrence

Niemelä et al. (1988) report no differences in the species assemblages in coniferous forests larger than 30 ha and smaller than 5 ha. The results presented on associations with forests of different sizes is similar to the above and may indicate there is no distinct difference in carabid assemblages recorded in forests of different sizes including broadleaf forests. However, strict forest specialists are found only in large, contiguous forests (Halme & Niemelä, 1993). Discovery of a forest specialist *P. kolbei* at only one site in a large broadleaf forest may indicate that area is an important factor for this forest specialist. That there are significant associations with large broadleaf forest for two forest generalist species (*L. a. arboreus* and *L. o. opaculus*) may be due to the high bio-productivity of large forests rather than area for these two species. It is reported that diversity and abundance of carabid beetles are associated with various environmental variables, such as, soil moisture (Butterfield et al., 1995), soil pH (Baguette & Gerard, 1993), vegetation structure (Ings & Hartley, 1999) and shad or openings in the canopy (Niemelä & Halme, 1992). Greenslade (1964) indicates that the presence of a dense understory inhibits the movement of carabid beetles. After logging and planting, bamboo grass is likely to invade disturbed areas on Hokkaido, potentially resulting in a dense understory, the cover of which is estimated to be greatly affected by canopy cover, which is dependent on the tree density in the plantation. *Pterostichus thunbergii*, which was associated with understory cover (Fig. 2), may be able to colonize conifer (Sakhalin fir) plantations where the understory cover is high. However, in a previous study (Kaizuka & Iwasa, 2015), some forest generalists such as *Pterostichus orientalis jessoensis* Tschitsherine and *Synuchus melantho* Bates are reported as very abundant in Sakhalin fir plantations where the understory cover is distinctly lower than that recorded in the present study, due to high tree density. Yasuda & Sato (1992) report that *Synuchus* sp. is very abundant in conifer (Sakhalin fir) plantations where the understory cover is very sparse. Thus, even in plantations of the same species of tree, carabid assemblages may differ because of difference in the understory cover. In particular, there may be an increase in the abundance of certain species in very dense conifer plantation due to a sparse understory cover.

Implications for conservation and forest management

The carabid assemblages are poorer in plantations consisting of only one species of tree (Magura et al., 2002, 2003) and biodiversity is higher in mixed tree plantings (Butterfield & Benitez-Malvido, 1992). In terms of the diversity of forest generalists, secondary mixed forests of broadleaf and conifer trees may be potential substitutes for secondary broadleaf forests. The forestry practice of leaving broadleaf forests or stands in conifer plantations may also provide a more favourable environment for carabids. However, it is important to maintain natural, semi-natural, or mature forests for some forest specialists. In mountain forests in the Hidaka range, where the sites studied at Obihiro are located, logging and afforestation mainly occurs at altitudes below about 700–800 m because forestry operations are difficult at high altitudes due to steep slopes. In particular, therefore, maintenance of natural or semi-natural broadleaf forests at low altitudes is essential for conserving the population of forest specialists, such as, *D. gehinii*. However, natural or semi-natural mixed forests of broadleaf and conifer trees at middle to high altitudes are an important habitat for *P. kolbei*.

Previous studies report that a mosaic of forest patches increases the diversity at the landscape level (Butterfield & Benitez-Malvido, 1992; Koivula, 2002a; Magura et al., 2002, 2003). In particular, in areas where forestry operations are frequent, maintenance of a connected mosaic of various habitats may result in a rich diversity and abundance of carabid beetles. Magura et al. (2000) indicate that creating gaps by thinning spruce stands encourages recolonization by the native understory. Forest management should also consider tree density, which affects both the understory and canopy cover. These management practices should protect the carabid populations and forest ecosystem.

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