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Effects of forest fragmentation on species richness and composition of ground

beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes

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Abstract

To clarify the effects of forest fragmentation in urban landscapes on the abundance, species richness,

dominance, and species composition of ground beetles (Coleoptera: Carabidae and Brachinidae), we compared

the beetles collected in 12 pitfall traps from April to July and from September to November between three

continuous suburban forests and eight isolated urban forests (0.06 - 1.02 ha), most of which were in the

precincts of shrines and temples in Hanshin District, Honshu, Japan. A total of 28 species and 4,178

individuals of ground beetles were collected. Segregation of urban forests from continuous suburban forests

changed the species composition and resulted in the loss of some large-sized forest species and the addition of

some non-forest species. Simpson's index of dominance (λ) also increased in the urban forests. The richness

of forest species markedly decreased with the reduction in forest area but not with the distance from

continuous forests, although the species richness of non-forest species did not change with them. Also species

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composition changed only with forest area. These indicate that continuous forests do not necessary serve as "a main land" for urban forest species and every urban habitat, even though small in size, plays a roll of temporary reservoir of species. In comparison with small-sized species, large-sized forest species appeared to

decline more easily during forest fragmentation.

studies.

Key words: arthropod biodiversity, body size, insect monitoring, pitfall trap, urbanization

INTRODUCTION

Urban forest remnants in the precincts of shrines and temples are precious habitats for plants and animals (Murakami et al. 2005; Hashimoto et al. 2005). As noted in the New National Biodiversity Strategy of Japan (Government of Japan 2002), restoring ecological networks along national land is essential for implementing biodiversity conservation, particularly in urbanized lowlands of Japan. To achieve this goal, a more comprehensive understanding of the ecological patterns and processes involved in urbanization is required (Niemelä 1999; Samways 2005). The effects of forest area and isolation on the species richness of woody plants (Murakami & Morimoto 2000), ferns and fern allies (Murakami et al. 2005), ants (Yui et al. 2001; Yamaguchi 2004), and birds (Hashimoto et al. 2005) have been examined in fragmented urban forests in lowland Japan; however, ground beetles (Coleoptera: Carabidae and Brachinidae) were not included in these

Ground beetles, which are carnivorous and consume insects and small animals or are occasionally herbivorous and subsist on seeds and roots of grasses, are considered to be good indicators of environment changes resulting from human activities (Thiele 1977; Ishitani 1996; Niemelä 2001; Rainio & Niemelä 2003; Slah et al. 2003; Purtauf et al. 2005); their abundance and species composition are easily monitored by using pitfall traps (New 1998; Isono 2005). Impacts of urbanization on ground beetle diversity have been studied under the GlobeNet worldwide research project (Niemelä et al. 2000). Niemelä et al. (2002), Ishitani et al. (2003) and Magura et al. (2004) discussed the changes in abundance, species richness and species composition of ground beetles across an urban-rural gradient based on data obtained from Europe, Canada and Japan. On

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the other hand, although the effects of forest fragmentation on ground beetle assemblages have been investigated, they have been mainly studied in forest patches that are surrounded by clear-cut areas or cultivated fields (Usher et al. 1993; Halme & Niemelä 1993; Burke & Goulet 1998; Niemelä 2001; Hori 2003). There is little information on the effects of size and isolation of urban forest patches on ground beetles, except for Sadler et al. (2006).

The aim of this study was to clarify the effects of forest fragmentation in urban landscapes on the abundance, species richness, dominance and species composition of ground beetles. In this study, assemblages of carabids and brachinids collected in pitfall traps were compared between continuous suburban forests (CSF), which connected to forests outside the city, and isolated urban forests (IUF) in lowlands of Japan. The effects of forest area and distance from continuous forests on species richness and composition of ground beetles were analyzed to test the assumption that continuous forest areas serve as "the mainland" and urban forests serve as "islands" in a sea of urban area. It could be predicted by the island biogeography theory (MacArthur & Wilson 1963) that the species richness of forest species decreases with the distance from continuous forests as well as with the reduction of forest area. Recently, Sadler et al. (2006) indicated the effects of woodland fragmentation on carabid assemblages in urbanization, which should be tested in our study. We also examined the prediction that large-sized and flightless species will decline easily in disturbed habitats (Halme & Niemelä 1993; Jennings & Tallamy 2006).

MATERIALS AND METHODS

Study area, plot design and sampling

We conducted the study in the urban and suburban areas of western Hanshin District in Honshu, Japan (Fig. 1).

We located three plots in continuous suburban forests (CSF) and eight plots in isolated urban forests (IUF, 0.06 – 1.02 ha) (Table 1). The plot T1 of CSF was an old-growth natural lucidophyllous forest dominated by Castanopsis cuspidata, Quercus glauca, Quercus phillyraeoides, and other evergreen broad-leaved tree species (Ishida et al. 1998). The plot T2 of CSF was a young secondary forest dominated by deciduous Quercus

secreta, and all other plots of CSF and IUF were secondary lucidophyllous forests dominated by *Q. glauca*, *Cinnamomum camphora*, and/or *C. cuspidata*. The CSF plots were surrounded or adjoined by continuous secondary forests of broad-leaved trees and pines, while the IUF plots were surrounded by residential areas, traffic roads, office buildings, and/ or partly farmlands. All the plots were in the precincts of shrines or temples except for T2, which had been managed for fuel-wood production. We measured the area of the forest patch and the minimum distance from continuous suburban forests on aerial photos that were taken in 1999. The location and stand variables of the study plots are summarized in Table 1.

We placed 12 pitfall traps within each plot with a distance of 10-20 m (with the exception of AN in which it was ca. 5 m) between neighboring traps. The traps were 10 cm in diameter, 11.5 cm in depth, and contained approximately 300 ml of propylene glycol as the preservative (Lemieux & Lindgren, 1999; Isono 2005). The opening was covered with a wood roof (15 cm by 15 cm) at a height of ca. 5 cm to block sunlight and rain. In 2003, from mid-April to mid-July and from early September to mid-November, adult carabids and brachinids were collected in the traps every two or three weeks. They were dried, mounted, and determined to species level. We measured the body length (from the apex of the labrum of the head to the tips of the elytra) of 10 or less individuals of each species. Voucher specimens will be deposited in the Museum of Nature and Human Activities, Sanda, Hyogo Prefecture.

Categorization of species

As shown in Table 2, we provisionally grouped the collected species into "forest species" and "non-forest species," based primarily on the habitat categorization proposed by Ishitani (1996) and the unpublished field experiences of the fourth author (N. Ito). We assumed that the "forest species" use woods or forests as the main habitat and may use non-forest lands occasionally; however, the "non-forest species" usually inhabit open lands or grasslands and do not require woody conditions. Categorizations by Ishitani (1996) and by N. Ito (unpublished) were largely consistent except in the case of *Diplocheila zeelandica* (Table 2). In this case, we treated *D. zeelandica* as a "forest species" as proposed by Ishitani (1996). The species were classified as small, middle and large sized based on the measured body size (Table 2). Flightless species without functional hind

wings (Carabus, Leptocarabus, and Damaster) were also observed (Table 2).

Data analyses

Abundance was measured based on the number of individuals collected in the 12 traps; species richness, based on the observed number of species; and dominance, using Simpson's index (λ) (Simpson 1949). Species composition was analyzed by correspondence analysis (CA) based on the number of traps in which each species was collected in every plot.

We used the Mann-Whitney U test to compare the abundance, species richness and dominance of all species, the species richness of "forest species" and "non-forest species", and the CA axis scores of plots between CSF and IUF, since the variance of most parameters could not be homogenized by any data-transformation.

We performed simple and multiple regressions of the abundance, species richness, and dominance of all species; the species richness of "forest species" and "non-forest species"; and the CA axis scores of plots on the stand variables (log forest area, log distance from continuous forests, and altitude) of isolated urban forests (IUF). Since there was a strong correlation between the altitude and log distance from continuous forests (r = -0.922, n = 8) that resulted in multicollinearity in multiple regressions, these two stand variables were not included in the same model.

The Pearson correlation coefficients between the log mean body length and CA axis scores were calculated for all species, "forest species," and "non-forest species." We also calculated the rank correlation coefficients between the forest areas of the IUF plots and the number of individuals for the dominant species that collected in three or more plots. All statistical analyses were performed with StatView 5.0 (SAS Institute Inc.), except for CA for which SPSS 11.5 (SPSS Inc.) was used.

RESULTS

A total of 28 species and 4,178 individuals of carabids and brachinids were recorded (Table 2). Three species, i.e., *Carabus yaconinus*, *Synuchus dulcigradus*, and *Synuchus nitidus*, accounted for 90% of all the individuals collected. *S. nitidus* was common to all except the smallest plot (AN). We collected *Damaster blaptoides*,

Pterostichus yoritomus, Synuchus agonus, and Haplochlaenius costiger only in CSF; three of these (with the exception of S. agonus) were "forest species." On the other hand, of the 14 species collected only in IUF (Leptocarabus kumagaii, Lesticus magnus, Pterostichus longinquus, P. microcephalus, Dolichus halensis, Amara spp., Harpalus spp., Trichotichnus congruous, Chlaenius bioculatus, and Aephnidius adelioides), 10 were "non-forest species," while four (L. kumagaii, L. magnus, P. microcephalus, and T. congruous) were "forest species."

Of the 28 species collected, 10 species and one subspecies were endemic to Japan (Loebl & Smetana 2003; N. Ito in preparation). Two (*D. blaptoides* and *P. yoritomus*) were only from CSF, five (*C. yaconinus*, *Pterostichus thorectoides, Synuchus arcuaticollis, S. dulcigradu*, and *Oxycentrus argutoroides*) were from both CSF and IUF, and four (*L. kumagaii*, *P. microcephalus*, *Amara macronota ovalipennis*, and *Harpalus niigatanus*) were only from IUF.

The abundance and species richness of all species were not significantly different between CSF and IUF (Tables 2, 3), but Simpson's index of dominance (λ) was significantly different between them and it was higher in IUF than in CSF. The species richness of "forest species" and "non-forest species" was not significantly different between CSF and IUF.

Fig. 2 shows the ordination of plots (a) and species (b) generated by CA. The percentages of inertial explained were 28.6% for the first axis and 17.7% for the second axis. The CSF plots (T1, T2, and KK) were all located on the lower half of the second CA axis; T1 and the smallest IUF plot (AN) were distinct from the other plots along this axis (Fig. 2a). The first CA axis was not significantly different but the second CA axis was significantly different between CSF and IUF (Table 3). In the ordination of species (Fig. 2b), the first CA axis was not significantly different between "forest species" (mean \pm SD, 0.01 \pm 1.05) and "non-forest species" (-0.29 \pm 1.45) ($F_{1,26} = 0.39$, P = 0.536), but the second CA axis was significantly different between "forest species" (-0.41 \pm 1.19) and "non-forest species" (0.91 \pm 0.89) ($F_{1,26} = 10.40$, P = 0.003).

The species richness of "forest species" increased significantly with the increase in forest area in isolated urban forests (IUF) as well as the abundance and species richness of all species did, although the species

richness of "non-forest species" did not increase with size of the forests (Table 4, Fig. 3). The second CA axis also varied significantly with the forest area (Fig. 4). The distance from the continuous forest and altitude were not significant in the prediction of any parameters. Further, none of the stand variables significantly predicted Simpson's index of dominance, the species richness of "non-forest species," and the first CA axis.

Correlations between the log mean body length and the first CA axis were not significant for all species (r = -0.225, n = 28, P = 0.253), "forest species" (r = -0.322, n = 16, P = 0.229), and "non-forest species" (r = -0.308, n = 12, P = 0.339). Those between the log mean body length and the second CA axis were significant for all species (r = -0.480, n = 28, P = 0.009), marginally significant for "forest species" (r = -0.468, n = 16, P = 0.067), and not significant for "non-forest species" (r = 0.042, n = 12, P = 0.900) (Fig. 5). This indicated that large-sized forest species declined more easily than small-sized species during forest fragmentation, which was reflected in the increase of the second CA axis (Fig. 4).

Of the eight dominant species collected in three or more IUF plots, seven showed a positive rank correlation between the forest area and the number of individuals (Table 2); the correlation was significant in two large-sized "forest species" (*C. yaconinus* and *L. magnus*) and one small-sized "non-forest species" (*P. longinguus*).

DISCUSSION

Our results suggest more than just a decline of ground beetles in urbanization. It seems that some large-sized "forest species" (*D. blaptoides* and *H. costiger*) have disappeared probably due to the segregation of forest patches from continuous forests, and other large- or middle-sized "forest species" (e.g., *C. yaconinus*, *D. zeelandica*, and *B. scotomedes*) are fading away as the forest area decreases, whereas many "non-forest species" (*P. longinquus*, *Amara* spp., and *Harpalus* spp.) and a few "forest species" (*L. magnus* and *P. microcephalus*) have been added or increased after forest segregation.

As shown by Halme & Niemelä (1993) in fragments of a coniferous forest in Finland, forest fragmentation usually changes the species composition of ground beetles because some species invade from surrounding

open habitats, often resulting in an increase in total species richness (Niemelä 2001; Warnaffe & Lebrun 2004). According to Magura et al. (2004), the overall species richness of carabid beetles was higher in urban areas than in suburban ones because of the increase in open-habitat species in Hungary. Matsumoto (2005) also reported that the species richness of ground beetles was higher in a managed arboretum than in a neighboring oak forest because *Harpalus* and other non-forest species were added in the arboretum in a suburban area of Japan. This was also observed in our study in isolated urban forests. Although several forest species have disappeared in isolated urban forests, the overall species richness in large forest patches has not decreased because of the addition of species probably from sparsely grown woods or open fields. In fact, several species that were collected only in isolated urban forests, such as *L. magnus*, *D. halensis*, *H. eous*, *H. niigatanus*, and *H. sinicus*, were abundant in the riverbeds and banks of the Yamato River, Osaka (Ishii et al. 1996). Some of these may only be transients from riversides or urban parks, while others would inhabit the edge of forest patches.

In spite of the addition of species from open habitats, the total species richness of ground beetles has decreased with the reduction in the urban forest area. As previously reported by Usher et al. (1993), Halme & Niemelä (1993), and Hori (2003) regarding ground beetles in forest patches surrounded by lawns, agricultural fields, and some residential areas, the results of our study also showed that an obvious positive effect of forest area on species richness with respect to the forest species present in urban forest remnants. However, as indicated for ants in urban forests (Yui et al. 2001; Yamaguchi 2004), there may a plateau of species richness in ground beetles over a forest area of approximately 1 ha, because the number of "forest species" in large forest patches (3-9 species) was not less than that in continuous forests (4-7 species).

We had also predicted that the species richness of forest species would decrease with the distance from continuous forests; however, such a negative effect of distance was not observed. This may indicate that the continuous forest area is not a single key source of species for rescue and that reciprocal rescue of species among urban forest habitats is important. However, it must be noted that some sporadic forest species, i.e., *L. kumagaii* and *O. argutoroides*, were collected only in the small forests (RH and TN) that were very close to

continuous forests, indicating that their main populations are present in continuous forests.

It might be noteworthy that the dominance index of species has evidently increased (thus the evenness of species has dropped) in isolated urban forests. The dominance of species measured by Simpson's index (λ) for ground beetles collected in non-baited pitfall traps in Japan is generally less than 0.3 (Ishii et al. 1996; Ishitani 1996). This is the same level as in our CSF plots; however, the index was more than 0.3 and up to 0.9 in IUF (Table 2). The same tendency of higher abundance of some dominant species in urban forests has also been reported in the GlobeNet project (Niemelä et al. 2002; Ishitani et al. 2003; Sadler et al. 2006). Difficulty in migration between forest fragments may cause an increase in the abundance of species that are less able to disperse. In fact, one of the most dominant species in large IUF plots, i.e., *C. yaconinus*, is flightless.

In our study, large-sized and often flightless forest species such as *C. yaconinus*, *D. blaptoides*, and *L. magnus* were easily affected by forest fragmentation. Further, there was a positive relationship between the ordinate axis of species composition along the progress of forest fragmentation and the body length, although it was just marginally significant in forest species. This is consistent with the findings of recent studies where it was shown that large and/or flightless species are vulnerable to natural and human disturbances (Holliday 1991; Halme & Niemelä 1993; Rainio & Niemelä 2003; Magura et al. 2004; Purtauf et al. 2005).

Semi-natural habitats still exist in hillsides and along large rivers even in the urbanized lowlands of Japan, but expanding city areas disconnect these. Eversham et al. (1996) have pointed out that manmade habitats support a rich fauna of ground beetles in Britain. Our results also indicate that forest remnants in the precincts of urban shrines and temples provide valuable habitats not only for forest species but also for some open-land species, including many species that are endemic to Japan. As "stepping stone" habitats (Samways 2005) that connect hilly forests and riverbanks, urban forests would play a role in maintaining landscape heterogeneity and connectivity of habitats for other groups of arthropods as well as ground beetles. Urban planning should encourage the appropriate management of such easily ignored habitats for the conservation of regional biodiversity.

Although ground beetles themselves are seldom targets for conservation, the distribution and abundance of

them reflects the degree of fragmentation and isolation of forest ecosystems due to anthropogenic disturbances (Niemelä 2001; Maleque et al. 2006). The monitoring of ground beetles, particularly of *Carabus* and other large-sized forest species, would provide useful information for urban planning and landscape restoration. Moreover, those well maintained in urban forests can be used for monitoring chemical pollution (Zödl & Wittmann 2003). Common carnivorous species that are only affected slightly by the reduction in forest area, such as *S. nitidus*, may be good candidates for such chemical monitoring.

In conclusion, the segregation of urban forests from continuous forests has changed the species composition of ground beetles, with the increase of dominance index; the reduction in forest area decreases the species richness of forest species; and large-sized forest species are rather easily affected by forest fragmentation. These conclusions are consistent with those of Sadler et al. (2006), while our study also indicates that continuous forests do not necessary serve as "a main land" for urban forest species. This may imply that every urban habitat, even though small in size, plays a roll of temporary reservoir of species. To promote the ecological network of habitats for ground beetles and other arthropods, further studies are necessary on the distribution and movement of species between assorted urban and suburban habitats, including riverbanks, private woods, or urban parks.

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Table 1 Location and stand variables of study plots in Hyogo Prefecture, Honshu, Japan

Code	Location ¹⁾	Forest area (ha)	Distance from continuous forests (km)	Altitude (m)	Vegetation type ²⁾
Contir	nuous suburban forests (CSF)				
T1	Taisanji Temple, KC			120	NL
T2	Near Taisanji Temple, KC			120	YS
KK	Kiyoshikojin-Seichoji Temple, TC			130	SL
Isolate	ed urban forests (IUF)				
NS	Nishinomiya-jinjya Shrine, NC	1.02	2.7	3	SL
HN	Hino-jinjya Shrine, NC	0.72	3.2	10	SL
ΚI	Koshikiwa-jinjya Shrine, NC	0.67	0.1	100	SL
MG	Minatogawa-jinjya Shrine, KC	0.63	1.1	5	SL
RH	Rokkohachiman-jinjya Shrine, KC	0.41	0.8	50	SL
ΜT	Matsuo-jinjya Shrine, TC	0.33	0.4	70	SL
TN	Tenma-jinjya Shrine, TC	0.25	0.6	70	SL
AN	Agenaruohachiman-jinjya Shrine, NC	0.06	6.0	2	SL

 ¹⁾ KC, Kobe City; TC, Takarazuka City; NC, Nishinomiya City.
 ²⁾ NL, natural lucidophyllous forest; YS, young secondary forest of deciduous and evergreen broad-leaved species; SL, secondary lucidophyllous forest.

Table 2 Abundance (number of individuals/number of traps) of carabid and brachinid species collected in 12 pitfall traps; the presumed habitat type of each species is also given

	Body size	Habitat type		Continuous suburban forests (CSF)		Isolated urban forests (IUF)										
Species	class ¹⁾	Ishitani ²⁾	Ito ³⁾	f/nf ⁴⁾	T1	T2	KK	NS	HN	KI	MG	RH	MT	TN	AN	τ 5)
Carabus yaconinus 6)	L	F/N	D	f	13 /6	2 /2		202 /12	1930 /12	118 /10		32 /6				0.73 *
Leptocarabus kumagaii 6)	L		W/D	f										2 /2		
Damaster blaptoides 6)	L	F/N	W	f	20 /8	5 /4	3 /3									
Trigonotoma lewisii	М		D	f						11 /3						
Lesticus magnus	L		D	f				8 /6	4 /3	9 /6						0.62 *
Pterostichus longinquus	S	N	Op	nf				9 /5	1 /1		1 /1					0.69 *
Pterostichus microcephalus	S	F/N	W/D/Op	f				1 /1	2 /2							
Pterostichus thorectoides	М		Op	nf		9 /5	20 /11						6 /3	27 /7		
Pterostichus yoritomus	М		W/D	f			4 /2									
Dolichus halensis	М	N	Op	nf									1 /1			
Synuchus agonus	S		Op	nf			1 /1									
Synuchus arcuaticollis	S	F	W/D	f		1 /1		37 /6	7 /3	6 /4	4 /3	10 /4			22 /5	0.33
Synuchus cycloderus	М	F	D	f			2 /2		1 /1	3 /2		1 /1	10 /6	3 /3		-0.20
Synuchus dulcigradus	S	F	W	f		3 /3		107 /10		17 /4	11 /3	77 /11				0.48
Synuchus nitidus	М	F	D	f	6 /3	13 /7	13 /7	2 /2	13 /6	348 /12	297 /12	288 /12	29 /10	216 /12		0.14
Amara congrua	S	N	Op	nf					4 /4						1 /1	
Amara macronota ovalipennis	М	N	Op	nf				44 /5	1 /1		0 (0	0 (0	4 /4		4 /4	0.45
Harpalus discrepans	М		Op	nf				14 /5	59 /12		8 /6	9 /6	1 /1		1 /1	0.45
Harpalus eous	М	N	Op	nf										1 /1		
Harpalus niigatanus	М	N	Op	nf					1 /1							
Harpalus sinicus sinicus	M	N	Op	nf									1 /1			
Trichotichnus congruus	S		D	f					1 /1							
Oxycentrus argutoroides	S		W/D	f	1 /1							2 /2				
Diplocheila zeelandica	М	F/N	Op	f	8 /4			8 /6		13 /6						
Haplochlaenius costiger	L	F/N	D	f	1 /1											
Chlaenius bioculatus	М		QΩ	nf					1 /1							
Aephnidius adelioides	S	N	Οp	nf							2 /2					
Brachinus scotomedes	М	F	Op	f	4 /3	1 /1		9 /4		42 /4						
Number of individuals					53	34	43	397	2021	567	323	419	48	249	24	
Number of species		7	7	6	10	12	9	6	7	6	5	3				
Simpson's index of dominance (λ)			0.23	0.23	0.31	0.34	0.91	0.43	0.85	0.51	0.41	0.76	0.84			
Number of "forest species"			7	6	4	8	7	9	3	6	2	3	1			
Number of "non-forest species"			0	1	2	2	5	0	3	1	4	2	2			

 $^{^{1)}\,\}text{S} \le 10~\text{mm} \,\leqq\, \text{M} \le 20~\text{mm} \,\leqq\, \text{L}$ in mean body length.

Main habitats according to Ishitani (1996): F, forest; N, non-forest (orchard, riverbank, vegetable field, residential area, urban area, etc.).

Main habitats according to isnitarii (1990): 1, 101est, 11, 1011 Totas (original at 1900): 10, 101est, 11, 1011 Totas (original at 1900): 10, 1019 Main habitats inferred from personal experience of N. Ito: W, wet wood; D, dry wood; O, open field.

3) Provisional categorization of species on habitat preference: f, "forest species"; nf, "non-forest species".

Frovisional categorization of species of manual preference. 1, Torest species 5 Rank correlation coefficient between the area of urban forests and the number of individuals. n = 8. *P < 0.05. 6 Flightless species.

	CS	SF (n = 3)	IU	Mann-		
Assemblage parameters	Median	Range	Median	Range	Whitney <i>U</i>	
Number of individuals	43	34 - 53	360	24 - 2021	4.0	
Number of species	7	6 – 7	6.5	3 - 12	12.0	
Simpson's index of dominance (λ)	0.23	0.23 - 0.31	0.64	0.34 - 0.91	0.0 *	
Number of "forest species"	6	4 – 7	4.5	1 – 9	10.0	
Number of "non-forest species"	1	0 – 2	2	0 - 5	5.5	
CA axis 1	-0.65	-1.8 - 0.09	0.36	-1.51 - 1.14	4.0	
CA axis 2	-0.57	-2.040.34	0.53	-0.36 - 1.79	1.0 *	

^{*}P < 0.05.

Table 4 Standardized coefficients of stand variables in simple and multiple regressions of the parameters of carabid and brachinid assemblages in isolated urban forests (IUF)

	Simple regressions			Multiple regressions					
Assemblage parameters	Simi	pie regressi	ons	Mod	el I	Model II			
	LFA LD		Al	LFA	LD	LFA	Al		
Log number of individuals	0.797 *	-0.138	0.014	0.834 *	0.120	0.800 *	-0.037		
Log number of species	0.916 **	-0.202	0.069	0.944 **	0.089	0.916 **	0.011		
Simpson's index of dominance (log λ)	-0.403	0.444	-0.403	-0.294	0.353	-0.379	-0.379		
Log number of "forest species"	0.866 **	-0.331	0.208	0.845 *	-0.071	0.857 *	0.154		
Log number of "non-forest species" 1)	-0.073	0.618	-0.594	0.130	0.658	-0.036	-0.592		
CA axis 1	0.043	0.516	-0.591	0.224	0.585	0.081	-0.596		
CA axis 2	-0.825 *	0.558	-0.443	-0.722 *	0.335	-0.800 **	-0.393		

Stand variables: Al, altitude; LFA, log forest area; LD, log distance from continuous forests.

¹⁾ Logarithm of the number of species + 0.5. $^*P < 0.05, ^{**}P < 0.01.$

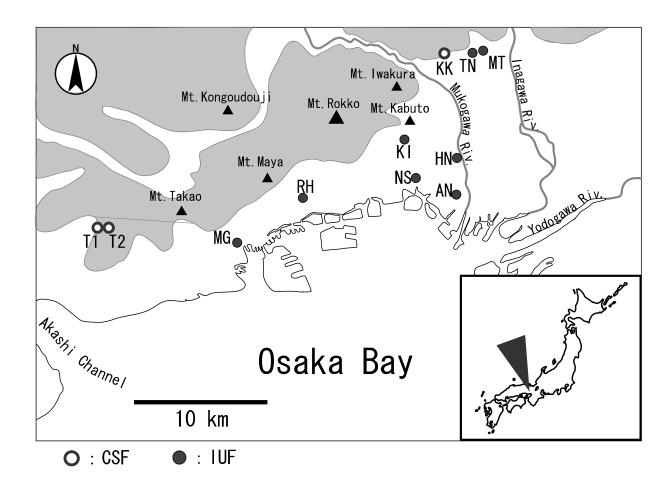


Figure 1 Location of the study plots in Hanshin District, Honshu, Japan. Shadow area indicates continuous forests, and plot codes refer to Table 1.

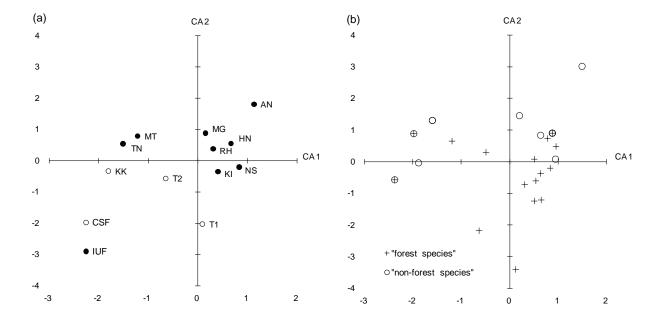


Figure 2 CA ordination of plots (a) and species (b). CSF, continuous suburban forests; IUF, isolated urban forests. Plot codes refer to Table 1.

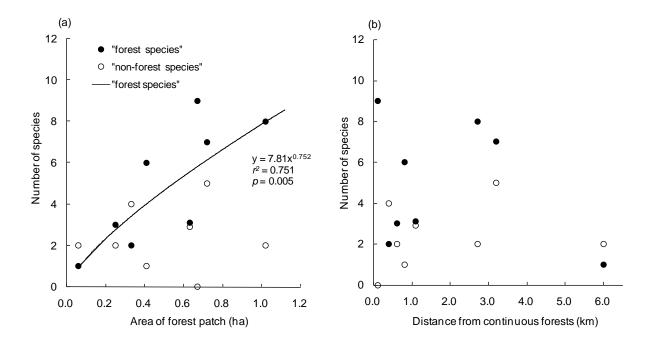


Figure 3 Regression of the species richness of "forest species" and "non-forest species" on the area of forest patch (a) and the distance from continuous forests (b). A significant regression model (a) is given for "forest species". See also Table 4.

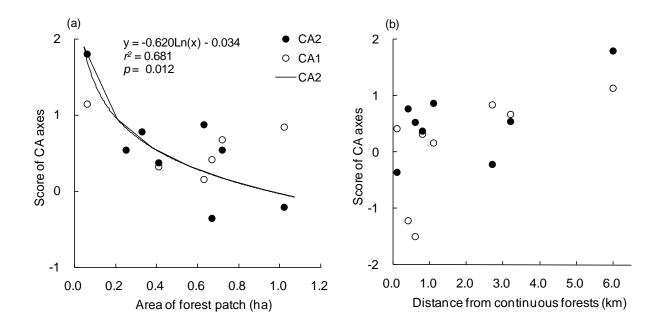


Figure 4 Regression of the score of CA axes on the area of the forest patch (a) and on the distance from continuous forests (b). A significant regression model (a) is given for the first CA axis. See also Table 4.

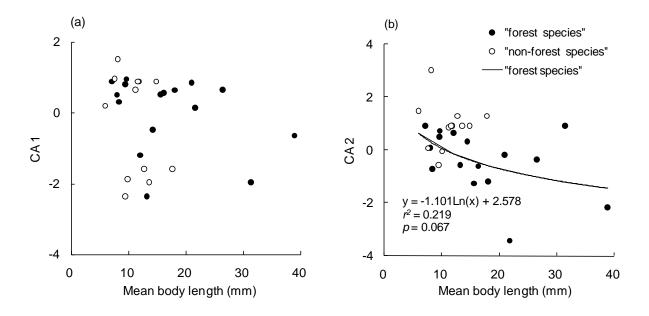


Figure 5 Relation between the log mean body length and the first (a) or second (b) CA axis of "forest species" and "non-forest species". A marginally significant regression model (b) is given for "forest species".