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Differential Sensitivity of Ground Beetles, *Eusilpha japonica* and Carabidae, to Vegetation Disturbance in an Abandoned Coppice Forest in Central Japan

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Abstract

We studied the responses of ground beetles to experimental disturbance of vegetation in an abandoned coppice forest in Saitama prefecture, central Japan, during 2004–2006. Experimental manipulations included tree cutting, clearing of ground vegetation, and litter removal, which we quantified by analyzing environmental variables. In parallel, ground beetles were sampled using pitfall traps. Overall, we analyzed 27 species of Carabidae and a single species of Silphidae (*Eusilpha japonica*). *E. japonica* dominated the ground beetle community and responded to vegetation disturbance in a way different from carabids. Carabids were most strongly affected by tree cutting but were insensitive to litter removal, whereas *E. japonica* was especially sensitive to litter removal. Our results show that *E. japonica* has high potential as a bioindicator since it is abundant, easily collectable, and selectively sensitive to litter accumulation, which is an indicator of abandonment of secondary forests. Both *E. japonica* and carabids were highly sensitive to vegetation disturbances, but responded to different types of vegetation manipulations. Such complementarity suggests that *E. japonica* and certain carabid species may be useful bioindicators if incorporated in a single integral monitoring system. However, further studies on the ecology on ground beetles will be needed to design effective monitoring protocols based on the differential sensitivity of ground beetle species to various kinds of vegetation disturbance.

Key words: carabidae, bioindicator, ground beetles, secondary forest, silphidae

Introduction

An important component of biodiversity in Japan is secondary (coppice) forests maintained by human management (Iida and Nakashizuka 1995; Takeuchi *et al.* 2003; Okubo 2005). However, the mass introduction of fossil fuels and chemical fertilizers in Japan since the 1960s has led to increasing abandonment of man-managed forests (Moriyama 1988; Fukamachi *et al.* 2001). Abandonment may reduce biodiversity in secondary forests (Brown and Yokohari 2003). Therefore, monitoring abandoned secondary forests is an issue of both theoretical and practical importance, as we need to be aware of changes occurring in abandoned forests in order to understand the ecological mechanisms in these forests and to intervene in a timely way to prevent loss of biodiversity.

The Carabidae are an abundant and widespread group of ground beetles that are sensitive to changes in their environment (Thiele 1977; Niemelä *et al.* 1993). Many studies conducted in Europe and North America have demonstrated the potential of carabid beetles as bioindicators (Irmiler 2003; Rainio and Niemelä 2003; Scott and Anderson 2003; Niemelä *et al.* 2007); however, few studies have been performed in Japan (Ishitani 1996; Ishitani *et al.* 2003).

Another abundant group of ground beetles with important functions in forests are the Silphidae, which

are largely considered carrion species, decomposing the carcasses of vertebrate animals (Leschen 1993; Ratcliffe 1996; Eggert and Müller 1997; Suzuki 2000; Wolf and Gibbs 2004). Probably one of the most common species of Silphidae in Japan is *Eusilpha japonica*; however, surprisingly, its ecology is poorly documented in the international scientific literature. Only a few studies on this species have been published in Japanese, and they either focus on *E. japonica* (Taniwaki *et al.* 2005) or compare it with other ground beetle species (Shimada 1985; Shimada *et al.* 1991). However, *E. japonica* is a special case among the Silphidae, as recent studies strongly suggest that it is not a carrion species but is a predator, like the Carabidae (Ikeda *et al.* 2007). In general, Silphidae are selective with respect to habitat type and structure (Werner and Raffa 2000; Wilhelm *et al.* 2001; Wolf and Gibbs 2004). The abundance of some species of Silphidae has been found to be affected by the intensity of human impact (Itoh and Aoki 1983), and it has been suggested that they could be used as bioindicators of human impact.

E. japonica is abundant and can easily be watched and sampled, and is sensitive to environmental changes in secondary forests. In suburban forests, Kuno *et al.* (2004) found a positive correlation between the abundance of *E. japonica* and litter accumulation, and

Table 1. Experimental design of vegetation disturbances.

Vegetation disturbances	Plot						
	P1	P1a	P2	P2a	P3	P4	P5
Ground vegetation ^a	Cut	Cut	Cut	Cut	Cut	Cut	Uncut
Tree ^b	Cut	Cut	Cut	Cut	Uncut	Uncut	Uncut
Litter ^c	Removed	Removed	Not removed	Not removed	Removed	Not removed	Not removed

a Ground vegetation cut in March 2004, 2006 at P1, P1a, P2, P2a, P3 and P4, and in July 2006 at P1a and P2a.

b Tree cut in March 2004 at P1, P1a, P2 and P2a.

c Litter removed in March 2004, 2006 at P1, P1a and P3.

Taniwaki *et al.* (2005) reported that the number of *E. japonica* beetles increased with the number of years since forest abandonment.

Like carabid beetles, *E. japonica* may be a useful bioindicator for monitoring secondary forests in Japan. The general goal of our study was to evaluate the potential of *E. japonica* as a bioindicator in secondary forests in Japan by comparing sensitivity to environmental changes between *E. japonica* and beetles of the family Carabidae. In particular, we were interested in studying environmental changes related to the traditional management of coppice forests. We therefore examined the responses of *E. japonica* and carabid species to the experimental manipulations of cutting down trees, ground floor vegetation, and removing litter, and analyzed the links between these types of vegetation disturbance and the behavior of the beetles.

Materials and Methods

Study site and experimental design

The study was conducted in Musashi-Kyūryō National Government Park in Namekawa-cho, Saitama Prefecture (36°04'N, 139°22'E, 40–90 m above sea level), a humid warm-temperate part of Japan with strong seasonality. The maximum summer temperature of 33°C occurs in August and the minimum winter temperature of –3°C in January; the mean annual temperature is 14.8°C and annual precipitation is 1479 mm (based on data collected in the territory of the park during 2004–2006). The park covers 304 ha and comprises a mosaic of abandoned and managed (by cutting of ground vegetation and litter removal) secondary forest patches. No trees were cut after the park was established in 1974. We selected a large patch of abandoned coppice forest (80 m × 100 m) in the center of this park. In this patch, an experimental site was established (40 m × 20 m) in March 2004. It was divided into four adjacent 10 m × 20 m plots (P1, P2, P3, P4) and one 10 m × 20 m control plot (P5) located 5 m from the experimental site (Table 1). In 2006, plots 1 and 2 were each divided into two plots, resulting in four plots, designated P1, P1a, P2, and P2a (Table 1). To reveal the effects of vegetation disturbances on the ground beetle community, different combinations of the following manipulations were applied to the plots (Table 1):

1. Tree cutting: all trees (woody vegetation >1.3 m tall) were cut 10 cm above the ground and removed from plots P1, P1a, P2 and P2a in March 2004.
2. Cutting of ground vegetation: dwarf bamboo (*Pleioblastus chino*), small trees (<1.3 m tall), and herbs were cut and removed from all plots except the control (P5) in March 2004, and were cut again in March 2006; the procedure was repeated in July 2006 but only in plots P1a and P2a.
3. Litter removal: Litter was removed in March 2004 from plots P1, P1a and P3, and was removed again in March 2006 from the same plots.

Before the experimental manipulations, the original conditions of the sites were documented by conducting a preliminary study of the plots that included sampling of the ground vegetation (10 randomly placed 1 m × 1 m quadrats) and a tree inventory (all trees in the plots). This preliminary survey revealed that dwarf bamboo dominated the ground vegetation (90% of the vegetation cover), with a mean density of 41 culms per m² and maximum and mean heights of 4.2 and 2.7 m, respectively. Examination of the tree inventory showed that a deciduous broad-leaved tree (*Quercus serrata*) dominated the site (Table 2).

Table 2. Original tree community structure on the plots before experimental manipulations.

	P1	P2	P3	P4	P5
Max height (m)	22	25	21	21	21
Max DBH (cm) ^a	31.0	29.5	42.7	30.2	23.3
Basal area (cm ² / 100 m ²) ^b	2272	2249	2844	2403	2574
Relative basal area (%)					
Species					
<i>Quercus serrata</i>	86.5	90.1	62.5	87.9	72.3
<i>Styrax japonica</i>	5.7		4.8		
<i>Eurya japonica</i>	4.4	1.4	3.0	7.2	4.9
<i>Ilex macropoda</i>	1.7	5.5	3.5	3.6	20.1
<i>Rhododendron kaempferi</i>	1.3	0.2	0.6	0.5	0.5
<i>Lyonia ovalifolia</i>	0.3	2.8		0.3	0.1
<i>Viburnum dilatatum</i>	0.1				0.1
<i>Prunus jamasakura</i>			25.2		
<i>Wisteria floribunda</i>			0.4	0.2	0.6
<i>Clerodendrum trichotomum</i>				0.3	
<i>Pourthiaea villosa</i>					1.4
Total	100	100	100	100	100

^a Diameter at breast height.

^b Basal area = $\pi (\text{DBH} / 2)^2$.

During the experiment, we cut 82 trees on plots P1 and P2 (density 0.2 individuals per m²). The cut trees were *Q. serrata* (36 individuals), *Rhododendron kaempferi* (22), *Eurya japonica* (12), *Ilex macropoda* (8), *Styrax japonica* (2), *Lyonia ovalifolia* (1), and *Viburnum dilatatum* (1). The annual rings of these trees at a height of 10 cm showed a maximum age of 43 years. This result suggests that there had been no tree cutting for more than four decades, during which *Q. serrata* and dwarf bamboo had become the dominant species in the canopy and ground layers, respectively.

Environmental variables

For the description of the tree canopy, the species of all individuals within the plots were identified, and diameter at breast height (DBH, 1.3 m above the ground) of individuals taller than 1.3 m was measured in February and March 2004. For each species, the basal area was calculated from the DBH data.

For the ground vegetation, all herbs and trees shorter than 1.3 m were sampled. The maximum height and total coverage (%) of each species within the plots were recorded. The sampling was performed in August and October 2004, and June and November 2006. Vegetation coverage in each plot (%) was monitored each month from January 2004 to November 2006. The above-ground biomass of a given species was measured as a 'volume', which is the maximum height of the species multiplied by its total projective coverage. Then these results were used to calculate the following diversity indices:

- overall richness (number of species)
- Pielou's evenness: ($H'/\log_2 S$, where H' is the Shannon index and S is the number of species; Pielou 1975)
- Simpson's diversity index: ($1/\sum p_i^2$, where p_i is the proportion of the total number of species accounted for by the i th species; Magurran 1988)

In addition, the annual maximum coverage and biomass of all ground vegetation, and the biomass and maximum height of dwarf bamboo were measured.

Litter mass on the plots was measured on a dry weight basis. Litter samples were collected from four small quadrats (0.3 m × 0.3 m) within each plot in March 2004 and 2006. The samples were oven-dried at 80°C for 48 h and then weighed to calculate a mean value for each sampled plot.

Soil water content (%) was measured at four locations within each plot every month from February to October using a Hydrosense CS 620 soil moisture measurement system (Campbell Scientific Inc., Logan, UT) with 20-cm probe rods. We used a TR 50 data logger (T&D Corporation, Nagano, Japan) to record the surface soil temperature (at a depth of 5 mm) and the temperature at a depth of 20 cm from April to December every hour. From these data, annual minimum values of soil water content at 20 cm depth and annual maximum temperature at the surface and 20 cm depth were calculated and used as data for subsequent analyses.

Canopy openness was measured from hemispherical

photographs taken 50 cm above the ground at four points within each plot in September 2004 and 2006, and mean openness (%) was calculated using CanopOn 2.02 software (<http://takenaka-akio.cool.ne.jp/etc/canopon2/>).

Ground beetle community

Pitfall traps (plastic cups: top diameter 6.5 cm, height 7.5 cm) were used to sample the ground beetles. Fourteen traps were buried at the center of each plot with 2 m distance between them. Traps were installed once per month from April to December 2004 and from May to November 2006. The traps were left in place for five consecutive days, then all trapped animals were identified and counted, and Carabidae and *E. japonica* analyzed excluding larval stages. The number of individuals was used to assess the abundance of each species and monitor their seasonal dynamics.

The major ground beetle species were determined by dominance analysis based on an abundance distribution method that was originally proposed for the analysis of plant communities (Ohsawa 1984; Kikvidze and Ohsawa 2002).

Correlation analysis and repeated-measures analysis of variance (RM-ANOVA) were used to reveal links among environmental variables and beetle abundances, using the software Statistix 8 (Analytical Software, Tallahassee, FL, USA).

Results

Environmental factors

Our experimental manipulations decreased the total basal area in the tree-cut plots (P1 and P2) to zero after logging in March 2004, in sharp contrast with the relatively high basal area (ca. 2500 cm² 100 m⁻²) in the tree-uncut plots (P3, P4, and P5, Appendix 1; see Table 1 for plot design).

Cutting ground vegetation allowed the invasion of early successional species and increased the species richness of the forest floor layer. Cutting the ground vegetation also reduced the biomass of dwarf bamboo drastically (Appendix 1).

The regeneration rate of the ground vegetation differed among the plots in both quality (number of species) and quantity (coverage) (Appendix 1). Ground vegetation regenerated rapidly, more so in tree-cut plots (P1 and P2) than in tree-uncut plots (P3 and P4). During the first year of manipulations after March 2004, the ground vegetation in the tree-cut plots had recovered to about 90% by October, whereas in the tree-uncut plots it recovered to no more than 50% in the same period. After the second cutting in 2006, ground vegetation recovery was again more rapid in the tree-cut (P1, P1a, P2, and P2a) than in the tree-uncut (P3 and P4) plots. Regeneration was also very fast after the third cutting of the ground vegetation in July 2006, which was performed only in plots P1a and P2a.

Litter removal from plots P1 and P3 in 2004 and from plots P1, P1a and P3 in 2006 caused great differences in litter dry weight among the plots (Appendix 1).

Table 3. Correlation matrix of environmental factors.

	Species number of trees	Basal area (cm ² /100 m ²)	Species number of ground vegetation	Pielou's evenness of ground vegetation	Simpson's index of ground vegetation	Annual maximum coverage of ground vegetation (%)	Biomass of all ground vegetation	Biomass of dwarf bamboo	Maximum height of dwarf bamboo (cm)	Litter weight (gram/100 m ²)	Water content (% up to 20 cm depth, annual minimum)	Temperature (°C at surface, annual maximum)	Temperature (°C at 20 cm depth, annual maximum)
Basal area (cm ² /100 m ²)	0.99 ^a												
Species number of ground vegetation	-0.51	-0.41											
Pielou's evenness of ground vegetation	-0.48	-0.43	0.74 ^b										
Simpson's index of ground vegetation	-0.35	-0.29	0.77 ^b	0.97 ^a									
Annual maximum coverage of ground vegetation (%)	-0.68 ^c	-0.72 ^b	-0.17	-0.12	-0.31								
Biomass of all ground vegetation	-0.04	-0.11	-0.39	-0.44	-0.47	0.49							
Biomass of dwarf bamboo	0.11	0.03	-0.57	-0.63 ^c	-0.66 ^c	0.45	0.96 ^a						
Maximum height of dwarf bamboo (cm)	0.37	0.28	-0.75 ^b	-0.79 ^b	-0.79 ^b	0.32	0.80 ^b	0.88 ^b					
Litter weight (gram/100 m ²)	0.34	0.24	-0.53	-0.20	-0.14	-0.13	0.42	0.44	0.43				
Water content (% up to 20 cm depth, annual minimum)	-0.59 ^c	-0.57	-0.01	0.26	0.06	0.60 ^c	-0.07	-0.06	-0.30	-0.14			
Temperature (°C at surface, annual maximum)	-0.91 ^a	-0.90 ^a	0.57	0.41	0.33	0.59 ^c	0.10	-0.08	-0.25	-0.38	0.25		
Temperature (°C at 20 cm depth, annual maximum)	-0.50	-0.46	0.07	0.25	0.06	0.49	-0.12	-0.09	-0.35	-0.31	0.95 ^a	0.15	
Sky openness (%)	-0.55	-0.52	0.70 ^c	0.43	0.45	0.20	0.06	-0.15	-0.18	-0.40	-0.27	0.80 ^b	-0.30

a: p<0.001, b: p<0.01, c: p<0.05

Soil water content at 20 cm depth was lower in the tree-uncut plots (P3, P4, and P5) than in the tree-cut plots (P1 and P2) from July 2004 onwards (Appendix 1).

Tree cutting caused an increase in maximum soil surface temperature compared with tree-uncut plots, although at 20 cm depth the difference was not noticeable (Appendix 1).

Vegetation manipulations also affected the sky openness: it was considerably higher in the tree-cut plots compared with the tree-uncut plots (Appendix 1).

Table 3 shows the correlation matrix for all environmental factors measured. Some variables showed significant correlation. Tree species richness and basal area were negatively related to ground vegetation cover. Similarly, soil water content and soil surface temperature were negatively correlated with tree species richness and basal area. The maximum height of dwarf bamboo was negatively related to ground vegetation diversity indices but positively correlated to ground vegetation biomass. Litter weight

did not show a significant correlation with any other environmental factor. Sky openness depended on ground vegetation species richness, and was positively correlated to soil surface temperature.

Ground beetle community

The total number of animals trapped in the pitfalls was 929 in 2004 and 2437 in 2006 (Appendices 2 and 3). The numbers of ground beetles totaled 476 and 1557, representing 51% and 64% of the all trapped animals in 2004 and 2006, respectively. Overall, we identified 28 ground beetle species (27 species of Carabidae and *E. japonica*).

The major species of ground beetles determined by the dominance analysis are presented in Fig. 1. The most abundant species in 2004 was *E. japonica* (Silphidae), followed by three carabid species (*Synuchus cycloderus*, *Carabus insulicola*, and *Chlaenius naeviger*). Carabid species became more diverse in 2006.

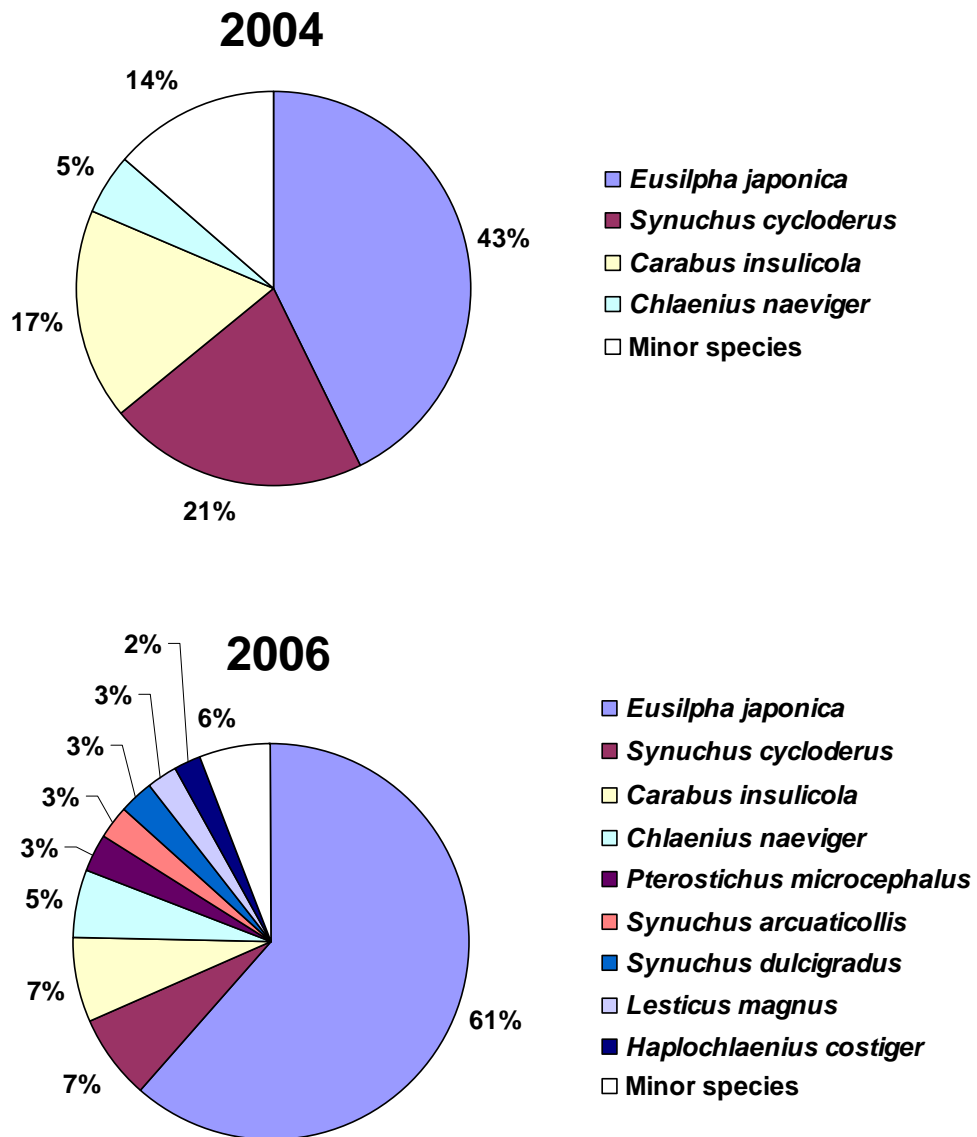


Fig. 1. Ground beetle community structure.

Differential responses of *E. japonica* and Carabidae to vegetation disturbance

We examined the seasonal changes in the numbers of *E. japonica* and carabids captured in the plots in 2004 and 2006 (Figs. 2 and 3). *E. japonica* responded to

vegetation disturbance in a different way than carabids; carabids were indifferent to litter removal, whereas this type of disturbance considerably reduced the abundance of *E. japonica*.

For a general analysis of correlations between the

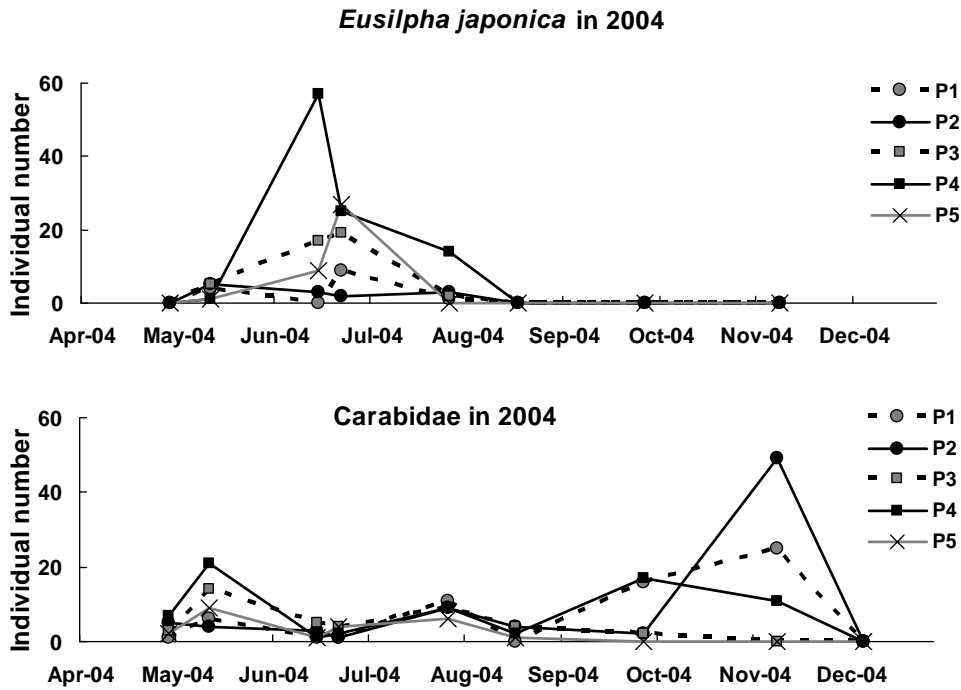


Fig. 2. Seasonal dynamics of *Eusilpha japonica* and Carabidae in 2004.

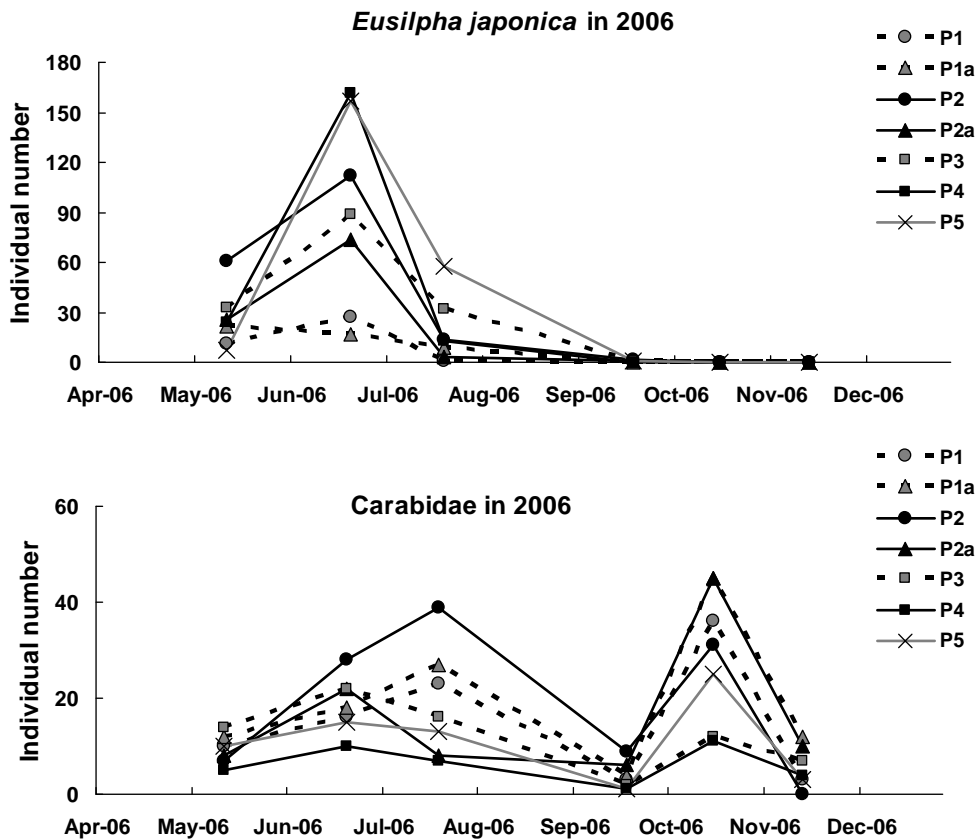


Fig. 3. Seasonal dynamics of *Eusilpha japonica* and Carabidae in 2006.

environmental factors and ground beetles, the data for 2004 and 2006 were pooled (Table 4). The abundance of *E. japonica* was positively correlated with litter dry weight in plots and negatively correlated to surface temperature and sky openness. In contrast, the abundance of Carabidae species showed strong negative correlations with tree diversity and basal area, and was positively correlated with ground vegetation coverage, soil water content, and soil temperature at 20 cm depth (Table 4). Because we performed the experimental manipulations twice (in 2004 and 2006),

RM-ANOVA is a more rigorous test of the responses of ground beetles to vegetation disturbance. This test confirmed the different effects of vegetation disturbance on *E. japonica* and carabid species: the interaction between beetles and vegetation disturbance was significant ($F = 5.32$, $df = 4$, $p = 0.0064$) (Fig. 4). Carabid species were strongly affected by tree cutting but showed no response to litter removal, whereas *E. japonica* responded more strongly to litter removal than to tree cutting (Fig. 4).

Table 4. Correlations of the abundance of *Eusilpha japonica* and Carabidae with environmental factors.

Environmental factors	<i>Eusilpha japonica</i>		Carabidae	
	<i>r</i>	P value	<i>r</i>	P value
Species number of trees	-	-	-0.737	0.006
Basal area (cm ² /100 m ²)	-	-	-0.720	0.008
Species number of ground vegetation	-	-	-	-
Pielou's evenness of ground vegetation	-	-	-	-
Simpson's index of ground vegetation	-	-	-	-
Annual maximum coverage of ground vegetation (%)	-	-	0.586	0.045
Biomass of all ground vegetation	-	-	-	-
Biomass of dwarf bamboo	-	-	-	-
Maximum height of dwarf bamboo (cm)	-	-	-	-
Litter weight (gram/100 m ²)	0.586	0.045	-	-
Water content (% up to 20 cm depth, annual minimum)	-	-	0.769	0.003
Temperature (°C at surface, annual maximum)	-0.675	0.016	-	-
Temperature (°C at 20 cm depth, annual maximum)	-	-	0.740	0.006
Sky openness (%)	-0.787	0.002	-	-

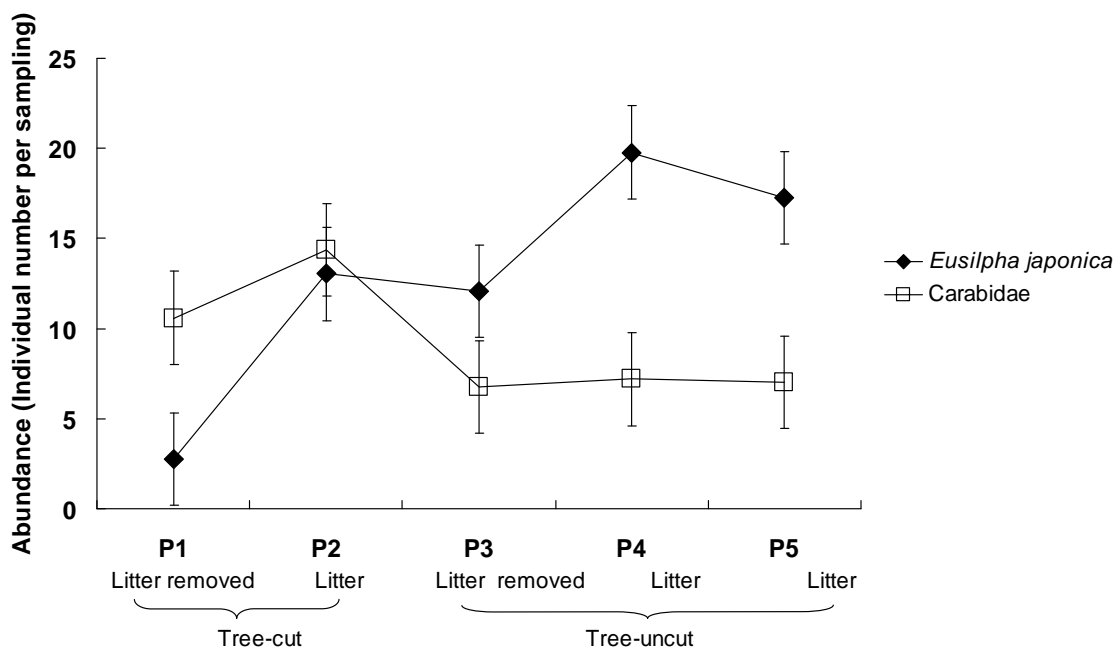


Fig. 4. Effect of vegetation manipulations on abundances of *Eusilpha japonica* and Carabidae.

Discussion

Our study demonstrated a strong link between *E. japonica* and litter mass in a secondary forest, and this finding agrees with early reports on *E. japonica*. Kuno et al. (2004) reported a positive correlation between the abundance of *E. japonica* and the amount of litter accumulated in unmanaged suburban forests, which probably led to an increase in the relative abundance of *E. japonica* with increasing number of years since abandonment of these forests.

Earthworms are the most common consumers of litter and are generally responsible for soil formation (Uchida et al. 2004). *E. japonica* was shown to be a predator of invertebrate species (Ikeda et al. 2007), and it is probable that earthworms are a usual prey of *E. japonica*. Such a food chain (litter → earthworms → *E. japonica*) may explain the effect of litter removal on *E. japonica*. In general, species of the genera *Silpha* and *Eusilpha* are considered mostly necrophagous, contributing considerably to the decomposition of dead biomass and soil formation (Leschen 1993; Ratcliffe 1996; Eggert and Müller 1997), which apparently is not the case with *E. japonica*. In managed forests, litter is regularly removed, but after forest abandonment, it accumulates, leading to an increase in the number of earthworms and subsequently an increase in the population of *E. japonica*.

Our study has found that carabid species were also sensitive to vegetation disturbance. However, in contrast with *E. japonica*, the abundance of carabid beetles responded primarily to tree canopy manipulations and positively correlated with ground vegetation cover, but showed no sensitivity to litter removal. The sensitivity of carabid beetles to forest disturbance has been demonstrated outside Japan (Butterfield et al. 1995; Brose 2003, Irmeler 2003; Rainio and Niemelä 2003; Scott and Anderson 2003; Niemelä et al. 2007) and in Japan (Ishitani 1996; Ishitani et al. 2003).

Our study shows that the responses of *E. japonica* and carabid species to vegetation disturbance are different, as *E. japonica* and Carabidae responded to different types of vegetation manipulations. Carabids were most strongly affected by tree cutting but were insensitive to litter removal, whereas *E. japonica* was especially sensitive to litter removal. Such complementarity suggests that *E. japonica* and certain carabid species may be useful bioindicators if they are incorporated in a single integral monitoring system (Shibuya et al., unpublished data). However, further studies on the ecology of ground beetles will be needed to design effective monitoring protocols based on the differential sensitivity of ground beetle species to various kinds of vegetation disturbance.

Overall, our results show that *E. japonica* has high potential as a bioindicator since this species is abundant, easily collectable, and selectively sensitive to litter accumulation, which is indicative of the abandonment of secondary forest. *E. japonica* is endemic to Japan and is especially common in the secondary forests of the central and eastern parts of the country. Therefore, our findings are most relevant to this region and we

should be cautious in asserting the bioindicative potential of *E. japonica* for other regions of Japan. However, there are other species of *Silpha* and *Eusilpha* (e.g., *S. longicornus*, *S. perforata*, and *E. jakowlewi*) that are phylogenetically and ecologically close to *E. japonica* (Ikeda et al. 2007). Such species can be found in a range of Far-Eastern forests, including those of east China and the Korean Peninsula (Uéno et al. 1985), and therefore deserve further study to assess their potential as bioindicators.

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Appendix 1. Environmental factors measured in plots in 2004 and 2006.

Environmental factors	2004					2006						
	P1	P2	P3	P4	P5	P1	P1a	P2	P2a	P3	P4	P5
Species number of trees	0	0	7	7	8	0	0	0	0	7	7	8
Basal area (cm ² /100 m ²)	0	0	2844	2403	2574	0	0	0	0	2844	2403	2574
Species number of ground vegetation	45	46	45	33	9	35	29	31	32	32	28	9
Pielou's evenness of ground vegetation	0.323	0.434	0.193	0.202	0.019	0.255	0.240	0.253	0.250	0.284	0.417	0.019
Simpson's index of ground vegetation	0.475	0.659	0.329	0.388	0.012	0.314	0.300	0.325	0.320	0.390	0.628	0.010
Annual maximum coverage of ground vegetation (%)	92	89	49	46	90	100	100	100	100	75	50	90
Biomass of all ground vegetation	123	151	61	31	115	85	73	104	88	33	21	273
Biomass of dwarf bamboo	87	84	50	23	114	70	63	85	75	26	7	272
Maximum height of dwarf bamboo (cm)	111	108	96	81	212	100	90	100	100	85	70	230
Litter weight (gram/100 m ²)	1600	27000	2800	29000	26000	0	0	27362	27036	0	36932	45874
Water content (% up to 20 cm depth, annual minimum)	15.0	16.7	12.0	11.0	12.0	25.5	25.5	25.8	28.0	22.8	20.0	18.0
Temperature (°C at surface, annual maximum)	62.0	60.0	37.0	34.0	35.0	48.0	55.4	45.0	53.0	28.0	27.0	27.0
Temperature (°C at 20 cm depth, annual maximum)	23.5	23.4	23.5	22.0	21.7	27.3	27.0	26.9	26.5	26.6	24.9	24.6
Sky openness (%)	27	26	18	13	15	14	16	14	15	12	10	8

