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## EFFECTS OF ANTHROPOGENIC DISTURBANCES ON THE FLOWERING PLANT – INSECT POLLINATOR SYSTEM IN KANAZAWA CASTLE PARK, KANAZAWA, JAPAN

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During last five years the Kanazawa Castle Park has been seriously disturbed by a park improvement project, including the creation of large flowerbeds. We monitored the pollination system there by a community approach with records of species, abundance and links of "all" flowering plants and flower-visiting insects during the period before (2000) and after (2001 and 2002) the flowerbed creation. Therefore, we could analyze the direct and indirect effects of the flowerbed creation on the pollination system. The direct effect was grassland destruction and the indirect effect was by garden plants planted in flowerbeds that took away pollinators from resident plants.

KEY WORDS: pollination, biodiversity, plant-insect link, conservation, disturbance.

**Д. Утсономия<sup>1)</sup>, К. Накамура<sup>1,2)</sup>. Эффект антропогенного воздействия на систему цветущие растения – насекомые-опылители в дворцовом парке Канадзавы, Япония // Дальневосточный энтомолог. 2006. N 162. С. 1-24.**

За последние пять лет дворцовый парк в центре г. Канадзава был существенно переделан в результате проекта реконструкции, включающего создание больших клумб. Авторами прослежены изменения в системе опыления растений с ис-

пользованием общих подходов к изучению сообществ: выявлен видовой состав, обилие и взаимосвязи всех цветущих растений и посещающих цветы насекомых перед (2000 г.) и после (2001-2002 гг.) разбивки клумб. Это позволило проанализировать непосредственное и опосредствованное влияние создания клумб на систему опыления. Непосредственный эффект заключается в разрушении лужаек, а опосредствованный – в том, что цветы на клумбах «оттягивают» на себя опылителей от давно произрастающих в парке растений.

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## INTRODUCTION

In pollination systems, flowering plants and flower-visiting insects utilize each other, *i.e.* plants provide rewards such as pollen and nectar to insects and receive pollination services from insects in return. Recently, much attention has been paid to the effect of disturbances by human activities, as well as natural ones, on pollination systems. Anthropogenic disturbances include both physical and biological aspects. The physical disturbances can occur more rapidly and include the destruction of habitats by logging and the fragmentation of habitat, of which the effects on pollination have been reported frequently (*e.g.* Jennersten, 1988; Ghazoul *et al.*, 1998; Steffan-Dewenter & Tscharntke, 1999). Flowering plants in fragmented habitats suffer reduced seed production through the reduction of diversity and the number of flower-visiting bees (Steffan-Dewenter & Tscharntke, 1999). In biological disturbances, the invasion of alien species, including intentional introduction, has drawn attention, *e.g.* alien pollinators may threaten native pollination systems (Kearns *et al.*, 1998). Introduced alien plants compete for pollinators with native plants (Richardson *et al.*, 2000; Brown & Mitchell, 2001; Moragues & Traveset, 2005). Combinations of alien plants and alien pollinators make their invasion easier (Stout *et al.*, 2002; Hanley & Goulson, 2003), and “super generalist” plants and pollinators have been shown to promote the invasion of alien pollinators and plants, respectively (Olsen *et al.*, 2002). In the creation of parks, a large number of exotic flowering plants with bright colours are often planted in flowerbeds, which may disturb the native pollination systems; however, such effects of flowerbeds have rarely been studied.

This study was carried out in Kanazawa Castle Park (KCP) located in the center of Kanazawa city (Fig. 1). The park, including a forest area with many mature trees and native plant species, was kept in a good condition for many years (Ohgushi, 1995). However, recently it has been seriously disturbed by a park improvement project, including the reconstruction of large historical buildings and the creation of flowerbeds with many exotic garden plants. These changes perturbed the ecosystem in KCP, resulting in the deterioration of biodiversity and ecological interactions of organisms (Nakamura, 2004). Compared to the early 1990’s, the following changes

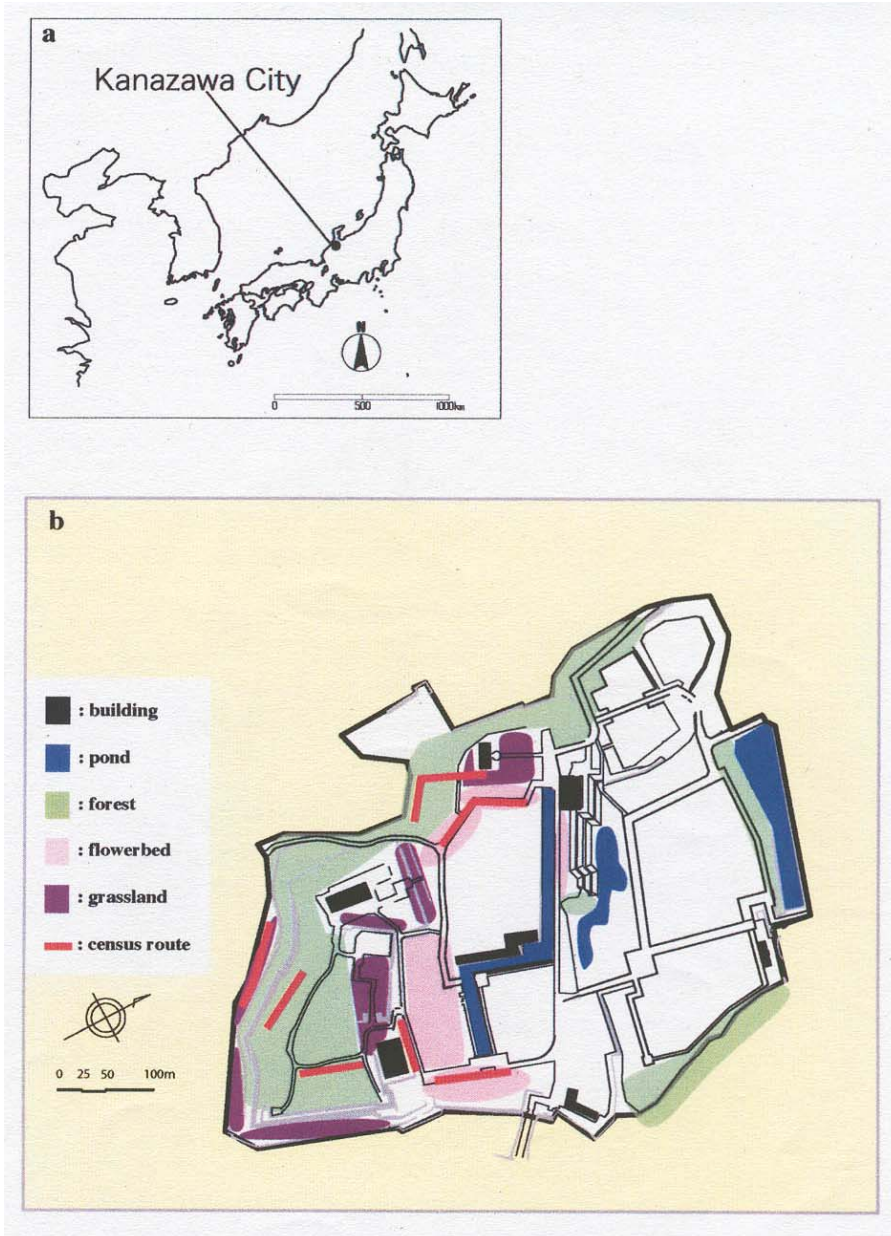


Fig. 1. Map showing the location of Kanazawa City (a), and a sketch map of Kanazawa Castle Park (b) with the census routes.

were reported: (1) total number of species recorded decreased from 1642 (including 1617 insect species) to 708 (608); (2) butterfly species (Lepidoptera: Diurna) decreased from 37 to 22 and Neuroptera from 19 to 7; (3) species of orthopteroid insects (Phasmatoptera, Mantoptera, Orthoptera) did not change but species composition changed drastically; (4) carabid beetles species (Coleoptera: Carabidae) increased due to the increase of species preferring disturbed habitats but the number of individuals decreased by three-quarters.

Long-term monitoring of pollination systems which deals with whole plant-insect links that coexist in a local biological community is necessary in order to analyze the causes and to predict the consequences of these changes. In the study, we monitored the change in pollination systems in KCP from 2000 to 2002. In the study area, we examined all flowering plant species and all flower-visiting insect species with abundance records of both flowers and insects. We also recorded the links between plants and insects. We could monitor the pollination system before (2000) and after (2001 and 2002) the flowerbeds were created. To analyze the direct and indirect effects of flowerbed creation on the pollination system separately, the direct effects created by the destruction of grasslands and indirect effects by garden plants planted in flowerbeds that took away pollinators from resident plants were observed.

### STUDY SITES

Figure 1 shows the location of Kanazawa City and a sketch map of KCP. In Kanazawa, the average annual temperature is 14.3°C and rainfall is 2470 mm. KCP is a green space (30 ha and 60 m altitude) with forest (about 4 ha), lawn, and building areas, isolated in the urban area of Kanazawa City.

History: Since the relocation of Kanazawa University to KCP in 1947, the forest area has been managed by the Botanical Garden of Kanazawa University in a conservation-oriented manner so as to recover the potential natural vegetation of the region. In the 1980's, the area became a biodiversity-rich area with many mature evergreen trees (e.g. *Castanopsis cuspidata* var. *sieboldii*, *Neolitsea sericea*) of more than 100 years old. After the university moved to Kakuma, a suburb of Kanazawa, about one third of the large trees were cut down from 1996 to 1999. Most grasslands were changed to bare grounds, lawns, and areas of the castle buildings were reconstructed in 2000 and 2001. In late August, 2001, large flowerbeds with exotic garden plants, which attracted insects to their brightly colored flowers, were constructed. In 2002, flowerbeds were used for the whole year for the first time.

Topography and ecosystem: KCP is located at the northern end of the foot of Mt. Hakusan, where a typical landscape of Japanese villages with paddy fields, secondary forests, and farmland (termed "satoyama" landscape) is found. It is isolated in the urban area, but narrow green strips (10-50 m width) run parallel along two rivers from the foot of Mt. Hakusan to nearby KCP (Fig. 1). The Utatsu hills, 2 km east of KCP, are the nearest satoyama area from KCP. The study site was originally a garden in KCP, so the forest in the study site included common trees: deciduous broad-leaved trees (e.g. *Celtis sinensis* var. *japonica*, *Quercus variabilis*, *Zanthoxylum ailanthoides*, *Swida macrophylla*) and evergreen trees, i.e. the potential natural

vegetation of the region (*Castanopsis cuspidata*, *Quercus myrsinaefolia*, *Neolitsea sericea*), and also tree species that were rare in the surrounding satoyama areas (e.g. evergreen: *Ternstroemia gymnanthera*, *Ilex integra*; deciduous: *Fagus crenata*, *Aesculus turbinata*) and garden species (maples and cherries). A rich flora of herbs and grasses, which are common in the surrounding satoyama areas, were found on the forest floors and grasslands in KCP (Akiyama *et al.*, 1973).

## CENSUS METHODS

**Census routes:** Figure 1 shows the locations of the census routes in KCP. The routes, total length 550 m, were established in 1999 in the forest area in the southern part of KCP, where the natural conditions are best preserved. The routes passed through a variety of habitats, including the interior and edges of forest and grasslands. In 2001, flowerbeds were constructed and a new census route (indicated in Fig. 1) was added to cover the flowerbeds. Observation of flowering plants and collection of flower-visiting insects were carried out within 2 m of both sides of the census routes.

**Census period and interval:** The census was carried out from April to November, for three years (2000-2002) at 7-10-day intervals. On a census day, all routes were surveyed three times (morning, noon and evening).

### Field data:

#### 1. Flowering plants

While walking slowly, records were kept of “flowering conditions” and “flowering abundance” for all flowering plant species, both resident and garden plants. In this study, “garden plants” refers to plants in flowerbeds, and all other plants including naturalized plants were classified as “resident”. Many resident herb species, which are common in the satoyama area in the suburbs of Kanazawa, were also found in KCP. “Flowering” was defined as the period from opening until dropping perianths, and for achlamydeous flowers, until the withering of stamens and/or pistil. The flower abundance index (*FAI*) was defined as the total number of individuals that flowered for tree and shrub species because sometimes it was impossible to count the number of flowers on tall trees and some shrub species had too many small flowers to count. *FAI* for herb plants was defined simply as the total number of flowers.

#### 2. Flower-visiting insects

While checking the plants, all insects found visiting flowers were collected, taken to the laboratory, and identified by the first author or sent to specialists for identification.

#### 3. Data analysis

##### 1. Similarity index

Similarity of the species compositions of flowering plants and flower-visiting insects was calculated by the Jaccard index (*CC*) as follows:

$$CC = a/(a+b+c),$$

where  $a$  is the number of species present during both analyzed years, and  $b$  and  $c$  are the number of species collected in either year. The  $CC$  value ranges from 0 to 1, and the higher the value is the higher the similarity.

The Bray-Curtis index ( $PS$ ), a similarity measure in which the relative abundance of each species is taken into account, was calculated as follows:

$$PS = 1 - 0.5 \sum | (n_{iA}/N_A - n_{iB}/N_B) |,$$

where  $n_{iA}$  and  $n_{iB}$  are  $FAIs$  of species  $i$  in years  $A$  and  $B$ , respectively, and  $N_A$  and  $N_B$  are total  $FAI$  in years  $A$  and  $B$ .

## 2. Quantitative food web

The links between flowering plants and flower-visiting insects were visualized by quantitative food webs. Right and left bars in Figure 6 were sectioned in proportion to the  $FAI$  of each plant species and the accumulated number of individuals for each insect species, respectively. Lines connecting both bars indicate the plant-insect links.

## RESULTS

### Flowering plants

#### *The whole study period*

The resident and garden plants that flowered during the study period are shown in the Tables 1 and 2. In resident plant species, 101 plant species (42 families and 87 genera) flowered during the study, including 12 tree and shrub species (12% of all species, 11 families and 12 genera) and 89 herb species (88%, 33 families and 76 genera). From 101 species, flower-visiting insects were collected from two shrub species (33%) and 47 herb species (48.5%). In garden plant species, 68 species (141 cultivars) flowered in 2001 and 2002, and flower-visiting insects were collected from 30 species (31 cultivars) (44.1%).

#### *Annual change*

##### Number of flowering plant species

Annual change in the total number of plant species that flowered in KCP from 2000 to 2002 was as follows: 72, 151, and 127 for all species combined (Fig. 2a), 4, 4, and 3 for tree species (Fig. 2b), 4, 4, and 4 for shrub species (Fig. 2c) and 65, 67, and 72 for herb species (Fig. 2d). For garden plants, 76 and 55 cultivars of garden plants flowered in 2001 and 2002, respectively (Fig. 2e). The changes were not large in resident tree and shrub species and herbs.

##### Flower abundance

Annual change in the flower abundance index ( $FAI$ ) of plant species from 2000 to 2002 was as follows: 7, 7, and 3 for tree species (Fig. 2b), 35, 17, and 56 for shrub species (Fig. 2c), 98960, 83295, and 164509 for herb species (Fig. 2d), and 66172 (2001) and 303566 (2002) for garden plants (Fig. 2e). In 2002, the species number of cultivars fell but larger numbers of the same cultivars were planted in flowerbeds.

Table 1

**List of the resident plant species that flowered on the census routes in KCP,  
with the flower abundance index (FAI) in each year**

Life form	Family	Species	FAI*		
			2000	2001	2002
TREE	Aceraceae	<i>Acer spp</i>	0	3	0
	Fagaceae	<i>Castanopsis sieboldii</i>	2	0	1
	Hippocastanaceae	<i>Aesculus turbinata</i>	2	2	1
	Leguminosae	<i>Robinia pseudoacacia</i>	2	0	0
	Rosaceae	<i>Prunus spp</i>	1	1	1
	Theaceae	<i>Camellia japonica</i>	0	1	0
SHRUB	Caprifoliaceae	<i>Sambucus racemosa</i>	0	1	0
	Cornaceae	<i>Aucuba japonica</i>	23	12	1
	Myrsinaceae	<i>Ardisia japonica</i>	1	0	0
	Rosaceae	<i>Duchesnea indica</i>	11	3	52
	Saxifragaceae	<i>Hydrangea serrata</i>	0	0	2
	Verveneaceae	<i>Callicarpa japonica</i>	0	1	1
HERB	Acanthaceae	<i>Justicia procumbens</i>	306	0	0
	Amaranthaceae	<i>Achyranthes bidentata</i>	410	1140	2802
	Araceae	<i>Arisaema serratum</i>	816	318	1049
	Boraginaceae	<i>Trigonotis peduncularis</i>	0	0	496
	Caryophyllaceae	<i>Myosoton aquaticum</i>	438	3360	4036
		<i>Sagina japonica</i>	73	0	0
		<i>Stellaria media</i>	0	78	23385
	Commelinaceae	<i>Commelina communis</i>	668	1173	1735
		<i>Pollia japonica</i>	0	5	87
	Compositae	<i>Adenocaulon himalaicum</i>	437	2603	10794
		<i>Anaphalis margaritacea</i>	0	32	0
		<i>Aster ovatus</i>	70	368	452
		<i>Bidens frondosa</i>	3	519	431
		<i>Carpesium abrotanoides</i>	0	13	4852
		<i>Cirsium japonicum</i>	2	1	0
		<i>Crassocephalum crepidioides</i>	33	1331	340
		<i>Erigeron philadelphicus</i>	370	0	0
		<i>Erigeron sumatrensis</i>	0	1179	2705
		<i>Gnaphalium affine</i>	2	59	22
	<i>Ixeris dentata</i>	0	6	0	

Table 1 (continued)

Life form	Family	Species	FAI		
			2000	2001	2002
HERB	Compositae	<i>Lactuca indica</i>	0	34	6
		<i>Lapsana humilis</i>	42	70	0
		<i>Picris hieracioides</i>	1	0	0
		<i>Senecio vulgaris</i>	0	0	742
		<i>Siegesbeckia orientalis</i>	0	867	480
		<i>Solidago virgaurea</i>	0	213	0
		<i>Sonchus asper</i>	2	0	0
		<i>Sonchus brachyotus</i>	3	10	20
		<i>Stenactis annuus</i>	513	3257	1440
		<i>Taraxacum albidum</i>	385	131	129
		<i>Taraxacum officinale</i>	34	10	9
		<i>Taraxacum spp</i>	183	0	0
		<i>Youngia japonica</i>	696	3393	9322
		Convolvulaceae	<i>Calystegia japonica</i>	12	0
	Cruciferae	<i>Cardamine scutata</i>	0	83	408
		<i>Rorippa cantoniensis</i>	0	16	54
	Cucurbitaceae	<i>Trichosanthes cucumeroides</i>	2	0	3
	Dioscoreaceae	<i>Dioscorea tokoro</i>	3	5	4
	Geraniaceae	<i>Geranium nepalense</i>	213	60	101
	Guttiferae	<i>Hypericum erectum</i>	0	4	0
	Iridaceae	<i>Sisyrinchium atlanticum</i>	3	0	0
	Labiatae	<i>Ajuga decumbens</i>	0	0	184
	Labiatae	<i>Clinopodium gracile</i>	63	68	435
		<i>Glechoma hederacea</i>	4357	820	1170
		<i>Lamium album</i>	6573	3773	7094
		<i>Mosla scabla</i>	409	2	26
		<i>Desmodium podocarpum</i>	4	185	543
	Leguminosae	<i>Medicago polymorpha</i>	34	50	0
		<i>Trifolium pratense</i>	154	45	0
		<i>Trifolium repens</i>	1192	436	13
		<i>Vicia angustifolia</i>	2	0	124
		Liliaceae	<i>Allium grayi</i>	4	3
<i>Cardiocrinum cordatum</i>	6		36	196	
<i>Liriope platyphylla</i>	46		60	365	
<i>Ophiopogon japonicus</i>	182		33	948	



Table 1 (continued)

Life form	Family	Species	FAI		
			2000	2001	2002
HERB	Liliaceae	<i>Ormithogallum umbellatum</i>	0	37	48
		<i>Polygonatum odoratum</i>	38	0	240
	Onagraceae	<i>Circaea mollis</i>	0	0	1819
	Orchidaceae	<i>Spiranthes sinensis</i>	123	303	6
	Oxalidaceae	<i>Oxalis corniculata</i>	1	87	219
	Papaveraceae	<i>Corydalis incisa</i>	434	148	1144
	Phytolaccaceae	<i>Phytolacca americana</i>	3	2	252
		Polygonaceae	<i>Antenoron filiforme</i>	277	0
	<i>Persicaria blumei</i>		0	0	5
	<i>Persicaria thunbergii</i>		1135	1099	1686
	<i>Persicaria yokusaiana</i>		58166	13086	10892
	Primulaceae	<i>Lysimachia japonica</i>	494	178	2063
	Ranunculaceae	<i>Ranunculus japonicus</i>	5759	2953	5340
		<i>Ranunculus sceleratus</i>	117	0	0
		<i>Ranunculus silerifolius</i>	48	50	0
	Rosaceae	<i>Agrimonia pilosa</i>	0	180	34
		<i>Duchesnea chrysantha</i>	218	239	1372
		<i>Geum japonicum</i>	0	131	90
		<i>Potentilla freyniana</i>	424	244	831
	Rubiaceae	<i>Paederia scandens</i>	42	0	0
	Saururaceae	<i>Houttuynia cordata</i>	703	2808	1208
	Scrophulariaceae	<i>Mazus miquelii</i>	144	642	439
		<i>Veronica arvensis</i>	0	13	0
		<i>Veronica persica</i>	20	117	4039
		<i>Veronica didyma</i>	0	26	0
	Solanaceae	<i>Solanum lyratum</i>	36	0	125
		<i>Solanum nigrum</i>	16	984	0
	Umbelliferae	<i>Anthriscus aemula</i>	10892	3311	17098
		<i>Chamaela decumbens</i>	0	29504	27585
		<i>Cryptotaenia japonica</i>	361	1035	1203
		<i>Osmorhiza aristata</i>	278	134	9460
	Violaceae	<i>Viola kusanoana</i>	288	136	10
		<i>Viola verecunda</i>	0	0	5
Vitaceae	<i>Cayratia japonica</i>	208	0	0	

\* Number of individuals for tree and shrub species and that of inflorescences or flowers for herb species, respectively.

Table 2

**List of the garden plant species that flowered on the census routes in KCP,  
with the number of cultivars and FAI\***

Family	Species	2001		2002	
		No. of cultivars	FAI	No. of cultivars	FAI
Amaranthaceae	<i>Celosia argentea</i>	-	-	1	3420
	<i>Celosia cristata</i>	2	1680	-	-
	<i>Celosia</i> cv.	-	-	1	3000
	<i>Gomphrena globosa</i>	2	952	2	20467
Amaryllidaceae	<i>Lycoris albiflora</i>	1	48	-	-
	<i>Lycoris aurea</i>	1	96	-	-
	<i>Lycoris radiata</i>	1	48	1	72
	<i>Nerine</i> cv.	1	192	-	-
Apocynaceae	<i>Catharanthus roseus</i>	4	736	3	6270
Asclepiadaceae	<i>Asclepias tuberosa</i>	-	-	1	3200
Balsaminaceae	<i>Impatiens walleriana</i>	5	736	2	4440
Begoniaceae	<i>Begonia senperflorens</i> × <i>cultorum</i>	2	2048	-	-
Campanulaceae	<i>Laurentia axillaris</i>	2	232	2	27000
Capparaceae	<i>Cleome sesquiorygalis</i>	-	-	1	4320
Caryophyllaceae	<i>Dianthus hybridus</i>	-	-	1	720
	<i>Dianthus</i> cv.	2	880	2	11400
Compositae	<i>Ageratm houstonianum</i>	3	4276	-	-
	<i>Ageratm</i> cv.	-	-	1	4245
	<i>Aster novi-belgii</i>	1	720	-	-
	<i>Bidens aurea</i>	1	152	-	-
	<i>Calllenda cv.</i>	-	-	1	1200
	<i>Chrysanthemum paludosum</i>	-	-	1	4872
	<i>Cosmos bipinnatus</i>	8	1804	2	4680
	<i>Cosmos sulpaureus</i>			1	6320
	<i>Eupatorium chinense</i>	1	40		
	<i>Felicia amelloides</i>	-	-	1	2250
	<i>Melampodium paludosum</i>	1	680	1	23040
	<i>Sanvitalis procumbens</i>	1	1212	-	-
	<i>Solidaster</i> cv.	1	12	-	-
	<i>Tagetes patula</i>	2	1424	1	1200
<i>Tagetes lemonii</i>	1	1060	-	-	
<i>Zinnia</i> cv.	1	1440	2	13080	

Table 2 (continued)

Family	Species	2001		2002	
		No. of cultivars	FAI	No. of cultivars	FAI
Convolvulaceae	<i>Evolvulus</i> cv.	1	720	1	11200
	<i>Ipomoea quamoclit</i>	2	60	-	-
Ericaceae	<i>Rhododendron</i> cv.	-	-	1	500
Gentianaceae	<i>Gentiana scabra</i>	1	1220	-	-
Iridaceae	<i>Crocus sativas</i>	1	5772	-	-
	<i>Crocus vernus</i>	-	-	1	8658
Labiatae	<i>Leonotis nepetifolia</i>	1	520	1	520
	<i>Mentha pulegium</i>	-	-	1	560
	<i>Salvia coccinea</i>	1	984	-	-
	<i>Salvia sinaloensis</i>	1	3600	-	-
	<i>Salvia splendens</i>	3	1272	-	-
	<i>Salvia farinacea</i>	2	4256	1	15920
	<i>Salvia madrensis</i>	1	12	-	-
	<i>Salvia leucantha</i>	1	188	-	-
	<i>Stachys byzantina</i>	1	608	1	1064
	<i>Thymus argenteus</i>	-	-	1	50
Leguminosae	<i>Trifolium</i> cv.	-	-	1	95
Liliaceae	<i>Colchicum</i> cv.	1	14788	1	11091
Melastomataceae	<i>Tibouchina urvilleana</i>	1	40	1	40
Onagraceae	<i>Gaura lindheimeri</i>	-	-	1	216
Oxalidaceae	<i>Oxalis variabilis</i>	2	880	2	880
Plumbaginaceae	<i>Limonium</i> spp.	-	-	2	3420
	<i>Plumbago auriculata</i>	-	-	1	400
Primulaceae	<i>Lysimachia nummlaria</i>	-	-	1	1056
Ranunculaceae	<i>Alyssum</i> cv.	-	-	2	4716
	<i>Anemone hupehensis</i>	1	40	1	40
	<i>Matthiola incana</i>	-	-	2	1790
Rubiaceae	<i>Pentas lanceolata</i>	1	116	1	2840
Scrophulariaceae	<i>Sutera cordata</i>	1	1040	1	1040
	<i>Torenia fournieri</i>	-	-	1	17490
Solanaceae	<i>Nierembergia caerulea</i>	-	-	1	2320
	<i>Petunia</i> cv.	5	2304	3	37040
Valerianaceae	<i>Patrinia scabiosifolia</i>	1	200	1	200
Verbenaceae	<i>Verbena</i> cv.	3	528	1	27080
Violaceae	<i>Viola sororia</i> × <i>wittrockiana</i>	-	-	4	6010
	<i>Viola tricolor</i>	-	-	1	2904

\* Explanations of FAI as in Table 1.

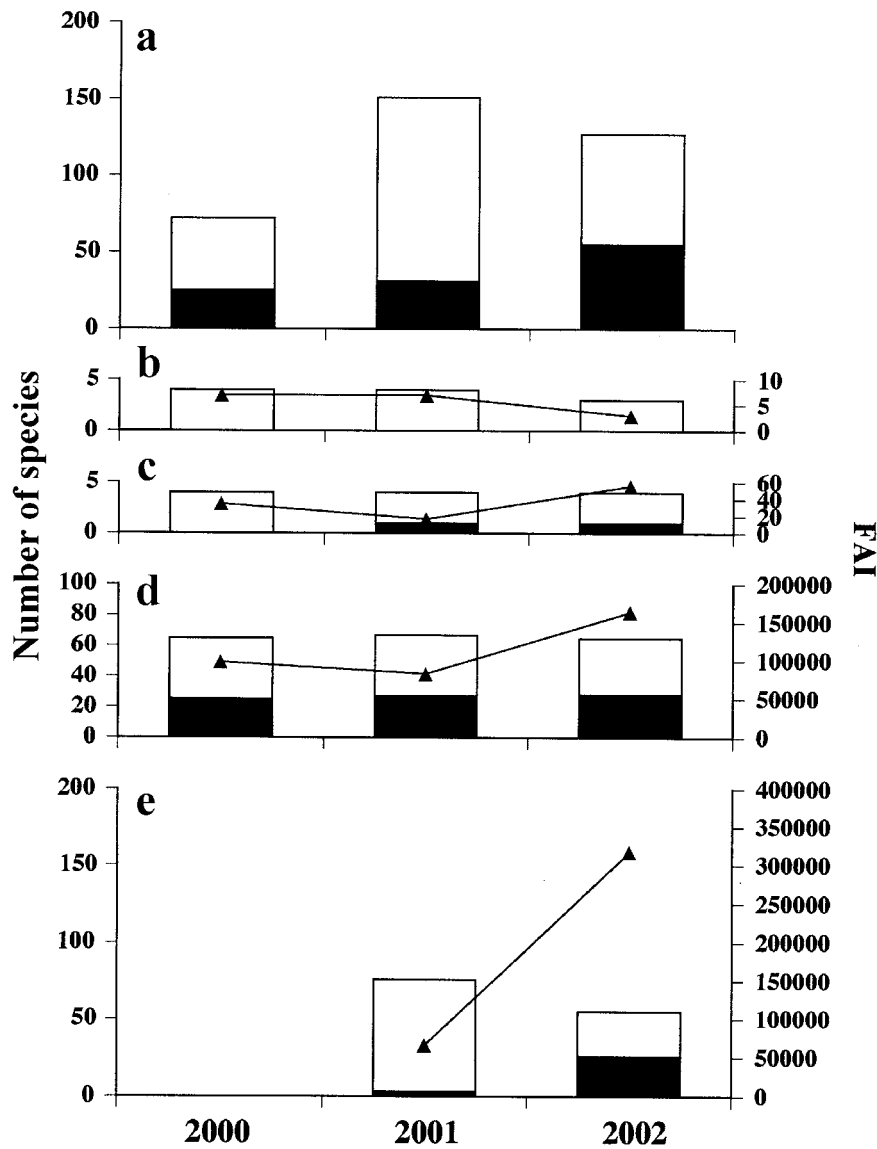


Fig. 2. Annual change in the total number of plant species and the flower abundance index of the plants (FAI) that flowered in Kanazawa Castle Park during the whole study period (2000-2002). Bar: number of species, line: FAI. a: all plant species, b: trees, c: shrubs, d: herbs, e: garden plants (cultivars). Shaded and unshaded bars refer to the species whose flowers were visited and not visited by insects, respectively.

### Number of flowering plant species visited by insects

These values changed within a narrow range from 2000 to 2002: no insect was collected from tree species during the study years (Fig. 3b). 0, 1 (25%), and 1 species (25%) for shrub plants (Fig. 2c); 25 (38.5%), 27 (40.3%), and 28 (38.9%) for herb species (Fig. 2d); and for garden plants, only 7 (9.2%) in 2001 because the flowerbeds were not ready until late August, and 26 (47.3%) in 2002 (Fig. 2e).

### Similarity between the two years

Figure 3 shows the overlap of resident plants that flowered from 2000 to 2002, indicating that, as a whole, 46 (45.5%) of 101 species flowered every year, 26 (25.8%) in two years, and 29 (28.7%) in only one year. The number of species that flowered in three, two, and one years was: four (33%), two (17%), and six (50%) for woody plants and 42 (47.2%), 24 (27%), and 23 (25.8%) for herb species, respectively. *CC* values ranged from 0.36-0.56 for trees and shrubs and from 0.57-0.69 for herbs (Fig. 4). *PS* values ranged from 0.17-0.55 for trees and shrubs and from 0.34-0.58 for herbs (Fig. 3). All garden plants except 17 cultivars were completely replaced from 2001 to 2002.

### **Flower-visiting insects collected from flowering plants**

#### *The whole study period*

The flower-visiting insects are shown in the Table 3. Figure 4 shows that 76 species (4 orders and 1395 individuals) of flower-visiting insects were collected during the study period. Among them, Coleoptera included 8 species (10.5%) and 565 individuals (40.6%), Diptera 22 species (28.9%) and 131 individuals (9.4%), Hymenoptera 34 species (44.7%) and 580 individuals (41.7%), Lepidoptera 12 species (15.8%) and 114 individuals (8.2%). Hymenoptera were the most abundant in terms of the number of species and individuals, followed by Diptera in the number of species and by Coleoptera in the number of individuals.

#### *Annual change*

#### Number of species and individuals

The number of species and individuals of flower-visiting insects from 2000 to 2002 were as follows: for all insects, 30 species (338 individuals), 31 (349), and 60 (708); for insects collected only from resident plants, 30 species (100%) because no garden plants were available in 2000, 23 (74.2%), and 26 (43.3%); for those collected only from garden plants, four species (12.9%) and 28 (46.7%) in 2001 and 2002, respectively (Fig. 4a, 4f). The total number of insect species collected only from resident plants decreased by only four species but the proportions of the number of species and individuals changed significantly due to a drastic increase in insects collected from garden plants.

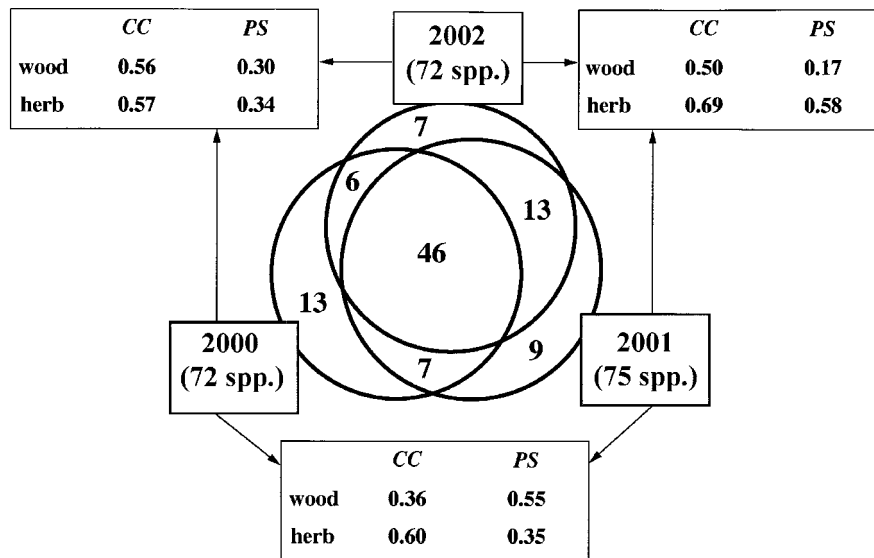


Fig 3. Diagram showing the overlap of the resident plants that flowered from 2000 to 2002. Numerals in shaded rectangles: total number of species that flowered each year. Numerals in circles: number of the overlapping species that flowered in two or three years. Jaccard and Bray-Curtis indexes are indicated in the unshaded rectangle for wood (tree and shrub) and herb species, respectively.

The change in each insect order from 2000 to 2002 was as follows:

**Coleoptera:** 1-6 species (3.2-10%) and the number of individuals decreased from 229 (67.8%) in 2000 to 129 (18.3%) in 2002. Almost all species were collected only from resident plants except for two species (five individuals) collected from garden plants in 2002 (Figs. 4b, 4g).

**Diptera:** The number of species and individuals increased every year: 10 species (33.3%) and 31 individuals (9.2%) to 14 species (23.3%) and 56 individuals (8%). All species were collected only from resident plants in 2000, but three species (25%) and seven individuals (16%) in 2001 and five species (36%) and 21 individuals (37%) in 2002 were collected from garden plants (Fig. 4c, 4h).

**Hymenoptera:** This was the most abundant order with 14-28 species (45.2-46.7%) and 65-437 individuals (18.6-62.2%). Hymenopteran insects drastically shifted from resident plants to garden plants from 2001 to 2002: a six-fold increase in species number (three species (21.4%) to 17 species (60.7%)) and 30-fold in the number of individuals (11 (16.9%) to 364 (83.3%)) (Figs. 4d, 4i).

**Lepidoptera:** No species was collected in 2000, but the number of species increased with the creation of the flowerbeds, four species and eleven in 2001 and 2002, respectively. Almost all species (10 of 12) were collected only from the garden plants (Fig. 4e, 4j).

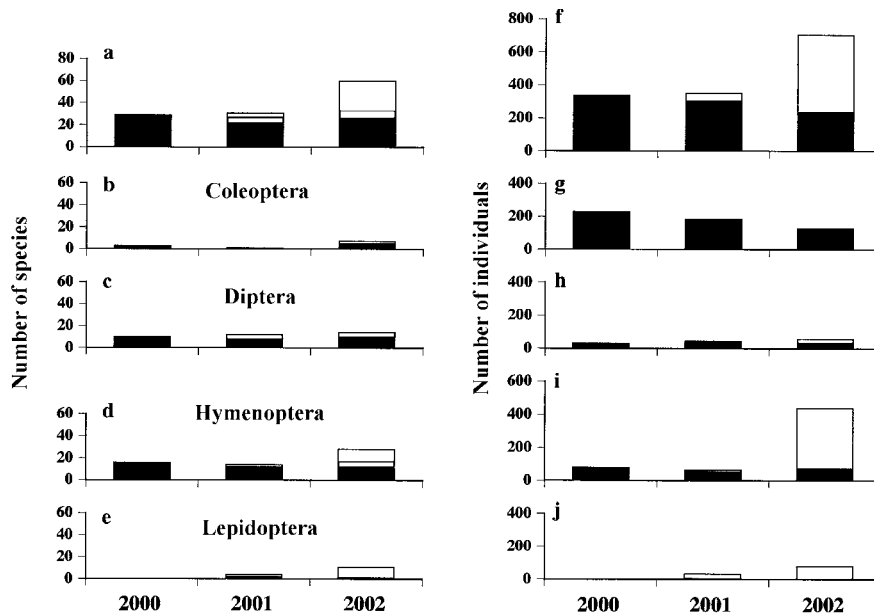


Fig 4. Annual change in the number of insect species and individuals of different orders that visited flowering plants in KCP. a-e: annual change in the number of species; f-j: annual change in the number of individuals. a and f: all species; b and g: Coleoptera; c and h: Diptera; d and i: Hymenoptera; e and j: Lepidoptera. ■ – visited only resident plants; ▒ – visited both resident and garden plants; □ – visited only garden plants.

#### Similarity between the two years

Figure 5 shows the overlap of flower-visiting insects between 2000 and 2002, indicating that, as a whole, 11 species (14.5%) of 76 were collected every year, 23 (30.2%) in two years, and 42 (55.3%) in just one year. The number of species that were collected in three, two, and one years was: one (12.5%), one (12.5%), and six (75%) in Coleoptera; three (13.6%), eight (36.4%), and 11 (50%) in Diptera; seven (20.6%), 10 (29.4%), and 17 (50%) in Hymenoptera; 0 (0%), four (33.3%), and eight (66.7%) in Lepidoptera. More than half of the species in all orders were collected only in one year. Seven of 11 species that were collected in all three years were Hymenoptera. *CC* values were low, ranging from 0.28-0.31, indicating that the composition of flower-visiting insects changed significantly each year. The *PS* value was high, 0.63, between 2000 and 2001, reflecting the predominant abundance of *Meligethes astacus* (Coleoptera) in both years, while it was low, 0.22, between 2002 and the other two years, because *Anthophora plumipes*, a large size bee, increased the number of individuals from 35 in 2000 and seven in 2001 to 123 in 2002. *Apis cerana japonica* also increased from only one in 2000 to 108 in 2002.

Table 3

**List of insects that visited the flowering plants on the census routes in KCP,  
with the total number of individuals collected in each year**

Order	Family	Species	Number of individuals		
			2000	2001	2002
Coleoptera	Byturidae	<i>Byturus atricollis</i>	0	0	1
		Chrysomelidae	<i>Aphthona perminuta</i>	0	0
	<i>Aulacophora femoralis</i>		0	0	4
	<i>Nonarthra tibiale</i>		54	0	0
	Nitidulidae		<i>Epuraea mandibularis</i>	0	0
		<i>Meligethes astacus</i>	172	207	37
	Phalacridae	<i>Olibrus particeps</i>	0	0	1
Scarabaeidae	<i>Popillia japonica</i>	3	0	1	
Diptera	Syrphidae	<i>Baccha maculata</i>	1	1	0
		<i>Betasyrphus serarius</i>	0	0	4
		<i>Brachyopa</i> sp.	0	0	1
		<i>Epistrophe shibakawae</i>	0	1	0
		<i>Episyrphus baltaetus</i>	10	9	30
		<i>Eupeodes bucculatus</i>	1	0	1
		<i>Eristalis kyokoae</i>	0	0	1
		<i>Eumerus japonicus</i>	0	3	1
		<i>Helophylus virgatus</i>	0	3	1
		<i>Megaspis zonata</i>	0	2	7
		<i>Melanostoma mellinum</i>	1	0	1
		<i>Melanostoma scalare</i>	0	1	4
		<i>Melanostoma</i> sp.	1	1	2
		<i>Paragus haemorrhous</i>	4	5	2
		<i>Rhingia laevigata</i>	0	1	0
		<i>Sphaerophoria macrogaster</i>	7	16	1
		<i>Sphaerophoria philanthus</i>	0	1	0
		<i>Syrphidae</i> sp. 8	4	0	0
		<i>Syrphidae</i> sp. 10	1	0	0
		<i>Syrphidae</i> sp. 11	1	0	0
Hymenoptera	Andrenidae	<i>Andrena brassicae</i>	0	1	0
		<i>Andrena knuthi</i>	1	0	5
		<i>Andrena minutula</i>	0	2	0
		<i>Andrena watasei</i>	2	2	4
	Anthophoridae	<i>Anthophora plumipes</i>	35	7	123
		<i>Ceratina flavipes</i>	2	0	8
		<i>Eucera spurcatipes</i>	2	0	2
		<i>Nomada reingio</i>	0	0	1
		<i>Tetralonia nipponensis</i>	2	2	5



Table 3 (continued)

Order	Family	Species	Number of individuals		
			2000	2001	2002
	Anthophoridae	<i>Xylocopa appendiculata</i>	0	2	13
	Apidae	<i>Apis cerana</i>	1	0	108
		<i>Apis mellifera</i>	2	11	5
		<i>Bombus ardens ardens</i>	2	0	0
		<i>Bombus diversus</i>	0	0	2
		<i>Bombus ignitus</i>	0	1	5
	Eumenidae	<i>Anterhynchium flavomarginatum micado</i>	0	0	2
		<i>Stenodynerus tokyanus</i>	0	0	1
	Halictidae	<i>Halictus aerarius</i>	13	5	1
		<i>Lasioglossum japonicum</i>	7	15	22
		<i>Lasioglossum kuroshio</i>	0	0	1
		<i>Lasioglossum mutilum</i>	1	1	0
		<i>Lasioglossum occidens</i>	0	1	3
		<i>Lasioglossum pallilomum</i>	2	0	6
		<i>Lasioglossum proximatum</i>	0	1	0
		<i>Lasioglossum scitulum</i>	1	0	1
		<i>Lasioglossum taeniolillum</i>	0	0	1
		Megachilidae	<i>Coelioxys yanonis</i>	0	0
	<i>Megachile willughbiella munakatai</i>		0	0	23
	<i>Megachile kobensis</i>		0	0	75
	<i>Megachile tsurugensis</i>		1	0	0
		<i>Osmia cornifrons</i>	0	0	1
	Scoliidae	<i>Campsomeris prismatica</i>	4	14	16
	Vespidae	<i>Vespa simillima xanthoptera</i>	0	0	1
		<i>Vespula flaviceps lewisii</i>	0	0	1
Lepidoptera	Hesperiidae	<i>Parnara guttata</i>	0	28	55
	Lycaenidae	<i>Celastrina argiolus radonides</i>	0	3	5
		<i>Lycaena phlaeas daimio</i>	0	0	2
	Nymphalidae	<i>Cynthia cardui</i>	0	0	7
		<i>Nymphalis xanthomelas japonica</i>	0	0	1
	Papilionidae	<i>Graphium sarpedon nipponum</i>	0	0	5
		<i>Papilio helenus nicconicolens</i>	0	1	0
		<i>Papilio xuthus</i>	0	0	4
	Pieridae	<i>Anthocharis scolymus</i>	0	0	1
		<i>Eurema hecabe mandarina</i>	0	0	1
		<i>Pieris rapae crucivora</i>	0	0	2
	Satyridae	<i>Ypthima argus</i>	0	1	3
	Total	20	76	338	349

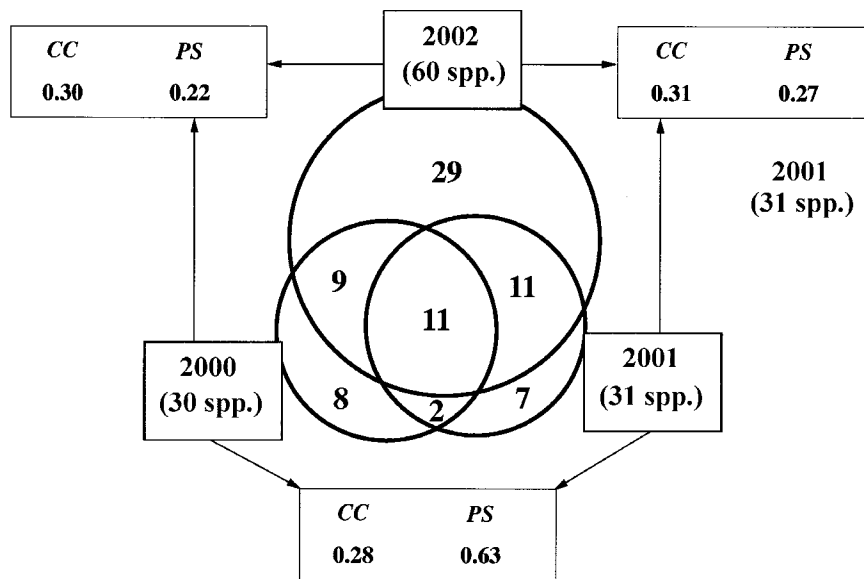


Fig. 5. Diagram showing the overlap of flower-visiting insect species in KCP. Numerals in shaded rectangles: total number of insect species in each year. Numerals in circles: number of overlapping species in two or three years. Jaccard and Bray-Curtis indexes are shown in unshaded rectangles.

### Plant-insect links

#### *The whole study period*

A total of 254 links were recorded during the study. Among them, in resident plants, the number of links was: 0, 5, 157 in tree, shrub and herb species, respectively. In garden plants, which were cultivated in large flowerbeds in 2001 for the first time, and were completely replaced the next year, 92 links were recorded (Fig. 6). Figure 6 shows that more than 85% of the links were recorded only in one year during the study: five links (100%) in shrubs, 140 (89%) in herbs and 90 (98%) in garden plants. The links were highly variable in both resident and garden plants.

#### *Annual change of links*

Figure 7 shows the annual change in the links during the study period. The total number of links was 58, 83 and 155 in 2000, 2001 and 2002, respectively (Fig. 7). Annual change in each insect order was as follows: in Coleoptera, the number of the links ranged from 10 to 13. The number of individuals of Coleoptera collected decreased year by year. All coleopteran species except two species in 2002 were collected from resident plants. In Diptera, 21, 29 and 30 links were recorded with

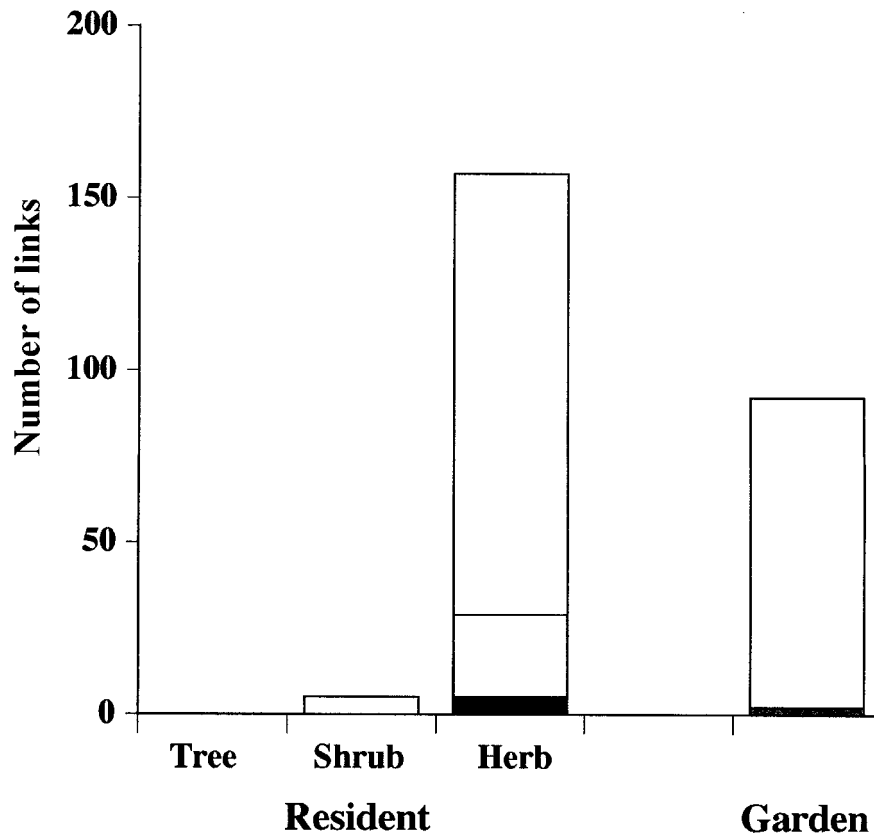


Fig. 6. Total number of flowering plant-flower-visiting insect links recorded in KCP. The number was counted separately for resident trees, resident shrubs, resident herbs and garden plants. ■ – three years; ■ – two years; □ – one year.

resident plants from 2000 to 2002, while five and nine links were recorded with garden plants in 2001 and 2002. In Hymenoptera, 28, 27 and 29 links were recorded with resident plants from 2000 to 2002. Five and 49 links were recorded with garden plants. Twenty species, including *Apis cerana* and *Anthophora plumipes*, were attracted to garden plants, but 14 species were collected only from resident plants, which accounted for the high stability of the link number with resident plants. Two species of Lepidoptera were collected from resident and garden plants (each two links) in 2001 for the first time. In 2002, two and 23 links were recorded with resident and garden plants, respectively.

The attraction of insects by garden plants, as shown above (Fig. 7), resulted in an increased number of links. Two processes were involved in this process: first, attraction of new insect species, and second, take over of pollinator insects from resident plants

by garden plants. In 2001, five species from 15 new insect species linked up with garden plants (each two species of Hymenoptera and Lepidoptera were exclusively collected from garden plants). In 2002, when the number of links drastically increased, 28 new species, including 12 and eight Hymenoptera and Lepidoptera species, respectively, were collected. Of the 28 species, 19 formed 30 links with garden plants, including 13 links by eight Hymenoptera species and 14 by eight Lepidoptera species, respectively. From 2001 to 2002, Hymenoptera and Lepidoptera, which were collected from garden plants, increased the number of species, individuals and number of links per insect species. In the latter case, from 25 insect species, which were collected exclusively from resident plants in 2000 and/or 2001, 10 species, forming 31 links, were collected from garden plants in 2002. In particular, *A. cerana*, which had only one link with resident plants in 2000, were collected from 14 garden plant species. In Hymenoptera, *Anthophora plumipes* was most abundantly collected (29 bees out of 35) from *Lamium album*, a resident herb, in 2000. In 2002, 111 out of 123 bees collected were obtained from garden plant species, and only one from *L. album*. This is a case of complete switching from resident plants to garden plants. In this study, we could obtain the detailed data on the shift of plant-insect links by using a community approach. Changes in flower visitation by individual insect pollinator species and that in flower-visiting insect assemblage on each plant species will be presented elsewhere.

## DISCUSSION

### Community-level studies on pollination systems and features of this study

In Japan, community-level studies of plant-pollinator interactions have been executed in many localities of different vegetation and altitudes. In the 1970's, Sakagami's Hokkaido University group proposed a standardized bee survey system with rather quantitative records of faunal makeup, phenology, and flower visits (*e.g.* Sakagami *et al.*, 1974). In the 1980's, Inoue's Kyoto University group developed the bee survey system into a more expanded method as follows: (1) collection of all flower-visiting insects and other organisms on each plant species for 10 minutes along the fixed census route; (2) multivariate analysis using cluster analysis and DCA (*e.g.* Kato *et al.*, 1990). These study systems are useful to clarify the basic pattern of pollination systems at a community level. However, they have limitations in analyzing the effects of disturbance on a pollination system at a particular site and/or during a particular period, because their studies (1) dealt only with bees; (2) spanned only one or two years; (3) pooled data for more than one year; (4) dealt with plant-pollinator links, but the abundance of flowers and pollinators were not quantified in each year. In contrast, in this study, we examined all flowering plant species and all flower-visiting insect species with abundance records of flowers and insects over the period spanning before (2000) and after (2001 and 2002) the creation of flowerbeds. We also carried out a comparative study in the Kakuma hills, a satoyama area (see below), during the same period (2000-2002), using exactly the same methods. Moreover, the results of previous bee surveys, which were carried out using Sakagami's methods in 1975 (Negoro, 1980) and 1987 (Utsumi, unpublished data) are available to discuss the long-term change of the pollination system in KCP.

### Comparison of pollination systems between KCP and Kakuma

There have been few comparable data to evaluate the structure and stability of the pollination system in KCP, because the pollination system in a particular location has been rarely studied using a community approach similar to this study. Below we compare the results obtained from KCP with those of Kakuma (detailed results from Kakuma will be presented elsewhere). The Kakuma hills (150 m altitude), a former satoyama area, are located 5 km southeast of KCP and are covered with deciduous forests dominated by native oak trees (*Quercus serrata* and *Q. variabilis*). The satoyama forest at Kakuma has been free from management for almost 30 years. Before modern urbanization, the environs of the central part of Kanazawa City, which has never been heavily industrialized, were similar to Kakuma. Compared to KCP, Kakuma apparently has more stable environmental conditions and much greater biodiversity. In Kakuma, the routine census was carried out along a fixed route (500 m) with exactly the same method as in KCP for 3 years (2000-2002).

The results from Kakuma indicated that the flowering plants were 36 species (1920 individuals) and 92 species (110434 flowers) of woody and herb plants, respectively, and their insect visitors included 5 orders, 42 families, and 160 species. The comparative values in KCP were: 12 species and 89 species of woody and herb plants, respectively, and of insects 4 orders, 20 families, and 76 species. In KCP, woody plant species showed a much lower number of flowering plant species and flowering individuals, one third and one tenth, respectively, of Kakuma. In terms of herb species, in KCP, the total number of species was the same as Kakuma but the total number of flowers was about three times larger than Kakuma. The *PS* value of KCP was lower than that of Kakuma (0.34-0.58 vs. 0.56-0.66), because in KCP the dominant plant species changed each year due to human interference. KCP had a lower number of insect species than Kakuma due to differences in the number of coleopteran species (8 vs. 80). In Kakuma, more than 75% of coleopteran species and individuals visited woody plants. Compared to Kakuma, bees, important pollinators, in KCP were poorer in species diversity and abundance (five families, 29 species, and 541 individuals vs. six families, 43 species, and 547 individuals). Regarding the similarity in insect species compositions between the two years, it was low in KCP (55.3% of the species were recorded only in one year and just 14.5% in all three years, Fig. 5). A similar tendency was also observed in Kakuma (53.8% and 16.2%). The *PS* value in KCP was extremely low (0.22, 0.29, and 0.63 from 2000 to 2002), but it ranged from 0.36 to 0.49 in Kakuma, indicating that the yearly change of insect species composition in KCP was larger than in Kakuma.

The plant-insect links in KCP (58 to 155) were much fewer than in Kakuma (133 to 233), indicating that the structure of the pollination system in KCP was much simpler than in Kakuma, resulting from the low number of flowering woody plant species in KCP (Fig. 2). About 70% and 65% of total links in KCP and Kakuma, respectively, were recorded only one out of three years, indicating that plant species changed insect partners yearly. In summary, the pollination system in KCP had less diversity and stability than Kakuma, due to its isolated condition in the urban area and the human disturbance.

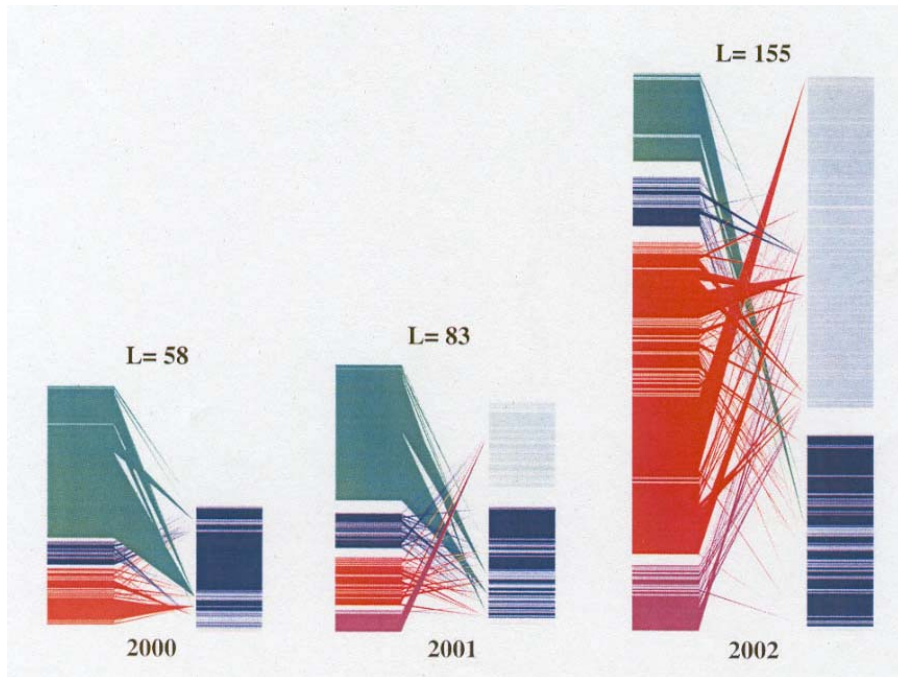


Figure 7. Diagram showing the flowering plants-flower-visiting insect links for each year. Right bar: flowering plants. Left bar: flower-visiting insects. Bars are sectioned in proportion to the flower abundance index (FAI) for each plant species and accumulated number of individuals for each insect species, respectively. For the insects: green – Coleoptera; blue – Diptera; red – Hymenoptera; purple – Lepidoptera. For the plants: red – tree; green – shrub; blue – herb; gray – garden species. L – total number of links.

#### **Long-term change in the pollination system in KCP: comparison of these results with those obtained in the 1970's and 1980's**

In KCP, bee surveys were performed in 1975 (Negoro, 1980) and 1987 (Utsumi, unpublished data) using Sakagami's system, *i.e.* all bees were collected at regular intervals during the flowering seasons. It should be noted that they did not record *Apis* and collected insects during flight as well as from flowers. Negoro (1980) collected six families, 77 species, and 2809 individuals from a wider area than this study, and Utsumi (unpublished data) collected six families, 49 species, and 933 individuals from the same areas as this study (the route was 100 m longer than in this study). In this study, 541 individuals from five families of 29 species were collected during the three-year study period. The total number of individuals collected was smaller than the two former studies, possibly because in this study insects were not collected in flight and all insects were collected so that the efficiency

of bee collection was lower. To compare the taxonomic composition of the bees between this and previous studies, it should be noted that (1) at a family level, Halictidae, Anthophoridae, and Megachilidae were dominant in all studies; (2) total number of species in each bee family except Apidae was smaller by 4-12 species; at a species level, 20 and 22 out of 27 species that were recorded in this study were also recorded in Negoro (1980) and Utsumi (unpublished data), respectively, and only two species were newly recorded in this study. These findings indicated that most of the species recorded in this study were identified in previous studies and seemed to survive serious disturbances caused by human activities such as logging and the construction of flowerbeds.

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### REFERENCES

- Akiyama, H., Kashitani, H., Kitagawa, H., Kinoshita, E. & Shimizu, T. 1993. Faunistic observations on the site of old Kanazawa Castle situated in the center of Kanazawa City. – University extension journal of Kanazawa University 13: 71-105. (In Japanese).
- Brown, B.J. & Mitchell, R.J. 2001. Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. – *Oecologia* 129: 43-49.
- Ghazoul, J., Liston, K.A. & Boyle, T.J.B. 1998. Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. – *Journal of Ecology* 86: 462-473.
- Hanley, M.E. & Goulson, D. 2003. Introduced weeds pollinated by introduced bees: cause or effect? – *Weed Biology and Management* 3: 204-212.
- Jennersten, O.L.A. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. – *Conservation Biology* 2: 359-366.
- Kato, M., Kakutani, T., Inoue, T. & Itino, T. 1990. Insect-flower relationship in the primary beech forest of Ashu, Kyoto: an overview of the flowering phenology and the seasonal pattern of insect visits. – *Contributions from the biological laboratory, Kyoto University*. 27: 309-375.

- Moragues, E. & Traveset, A. 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. – *Biological Conservation* 122: 611-619.
- Negoro, H. 1980. A wild bee survey in the campus of Kanazawa University, Hokuriku, Japan. – *Bulletin of the Toyama Science Museum* 2: 23-34. (In Japanese).
- Ohgushi, R. 1995. Natural history of a forest in old Kanazawa Castle from the viewpoint of animal communities. *Jugatsusha*. Kanazawa, Japan. (In Japanese).
- Olesen, J.M., Eskildsen, L.I. & Venkatasamy, S. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. – *Diversity and Distributions* 8: 181-192.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Remànek, M. 2000. Plant invasions - the role of mutualisms. – *Biological Review* 75: 65-93.
- Nakamura, K. (ed.). 2004. Effects of deforestation and other disturbance on the biodiversity and ecosystem in Kanazawa Castle Park. Research group for conservation of the ecosystem in Kanazawa Castle Park. Kanazawa, Japan. (In Japanese).
- Sakagami, S. H., Fukuda, H. & Kawano, H. 1974. Biofaunistic survey of wild bees: problems and methods, with results taken at Mt. Moiwa, Sapporo. – *Materials F. Biol. Educ.* 9: 1-60. (In Japanese).
- Steffan-Dewenter, I. & Tschamntke, T. 1999. Effects of habitat isolation on pollinator communities and seed set. – *Oecologia* 121: 432-440.
- Stout, J.C., Kells, A.R. & Goulson, D. 2002. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. – *Biological Conservation* 106: 425-434.