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ORIGINAL PAPER

Relationship of butterfly diversity with nectar plant species richness in and around the Aokigahara primary woodland of Mount Fuji, central Japan

Masahiko Kitahara · Mitsuko Yumoto · Takato Kobayashi

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Abstract We examined the relationships between the diversities of vegetation, adult nectar plants, and butterflies in and around the Aokigahara primary woodland on the northwestern footslopes of Mount Fuji, central Japan. The results showed that the nectar resource utilization by adult butterflies was significantly biased to herbaceous plants, especially to perennials, compared to woody species, although most of the study area was in and near a primary woodland. There were greater nectar plant species in sites with greater plant species richness. Among the butterfly community indices analyzed, the strongest correlation was detected between butterfly species richness and nectar plant species richness at each site. Another close correlation was detected between the species richness of nectar plants and herbaceous plants at each site. These results suggest that herbaceous plant species richness in a habitat plays a central role in its nectar plant species richness, and the nectar plant richness is a highly important factor supporting its adult butterfly species richness. Consequently, we propose that the maintenance and management of herbaceous plant species richness in a butterfly habitat, which lead to those of its nectar plant species richness, are very important for conservation of butterfly diversity even in and around woodland landscapes of temperate regions.

Keywords Adult nectar plants · Butterfly diversity · Herbaceous plants · Plant–butterfly relations · Species richness · Vegetation · Woodland habitats

Introduction

To search for the factors governing the diversity patterns of biological communities is one of the central aims of community ecology (MacArthur 1972; Pianka 1988; Begon

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et al. 1996). This kind of study and information is also vital for the conservation of biodiversity (Primack 1993, 1995). Up to now, butterflies have been well examined as to variation in diversity patterns along a variety of environmental gradients (e.g. Ishii et al. 1991; Spitzer et al. 1993, 1997; Kitahara and Fujii 1994, Blair and Launer 1997; Natuhara et al. 1999; Kitahara et al. 2000; Kocher and Williams 2000; Natuhara 2000; Inoue 2003; Hogsden and Hutchinson 2004). In addition, they have been extensively examined as to their ecological attributes and biotope occupancy (e.g. Dennis et al. 2000; Shreeve et al. 2001; Dennis et al. 2004, 2005), and therefore, repeatedly used in studies of conservation biology as an important bioindicator for environmental assessment (e.g. Sakuratani and Fujiyama 1991; Kremen 1992; Schmitt 2003). Thus, butterflies are one of the most suitable organisms for the studies of biological diversity and conservation biology.

In general, as almost all butterflies utilize species-specific plant resources in both larval and adult stages, it is believed that the diversity of plants influences the diversity of butterflies. In fact, the positive correlation between plant and butterfly diversities has been reported or pointed out in many previous studies (e.g. Erhardt 1985; Sparks and Parish 1995; Ishii 1996; Kitahara and Watanabe 2001, 2003; Simonson et al. 2001; Croxton et al. 2005). However, there have been a few studies (Väisänen 1992; Holl 1996; Kitahara 2004) in which the correlation is weak between butterfly diversity and vegetational community composition or species richness. In another study (Hawkins and Porter 2003), it was pointed out that, although plant and butterfly diversities are positively correlated, plant diversity does not directly influence butterfly diversity but that both are probably responding to similar environmental factors. Thus, the actual relationship between butterfly and plant diversities and their causal mechanisms are not yet clear.

On the other hand, it is generally thought that a greater diversity of resources should support a greater diversity of consumers. Indeed, it has been known that a greater abundance and/or diversity of nectar resources are associated with a greater abundance and/or diversity of butterflies (Murphy and Wilcox 1986; Kremen 1992; Munguira and Thomas 1992; Holl 1995; Ishii et al. 1995; Loertscher et al 1995; Steffan-Dewenter and Tscharntke 1997; Hardy and Dennis 1999; Clausen et al. 2001; Ries et al. 2001; Schneider and Fry 2001; Simonson et al. 2001; Pryke and Samways 2003; Pywell et al. 2004), although an association is absent in a few studies (e.g. Sharp et al. 1974). Schneider and Fry (2001) advocated that the availability of both nectar sources and larval food plants are important in determining butterfly diversity. However, at least in temperate Japan, few studies have been conducted on butterfly species and their nectar plant relationships, and almost no information is available on the conservation value of flowering nectar plants for butterfly abundance and diversity.

Recently, the importance of a resource-founded definition of habitat and approach based on the accurate identification of the spatial and temporal existence of resources in a landscape has been emphasized for butterfly conservation (Dennis et al. 2003, 2006). In addition to this, the need for the development of a resource database on butterfly biology necessary to adopt the resource-based approach has been proposed (Dennis et al. 2003). Thus, in the present study, considering the accumulation of new data on adult nectar resources, we examined the relationship between butterfly species and their nectar plant species richness in and around the Aokigahara primary woodland at the northwestern foot

Table 1 Characteristics of six study sites

Study site	Altitude (m)	Landscape and landscape element (open land)	Main plant (Phanerogamae) species			Type of human disturbance (mainly in open land)
			Trees	Small trees and shrubs	Herbs	
FI-1	1030	Woodland	*Quercus mongolica* var. *crispula*	*Ilex pedunculosa*	*Polygonum cuspidatum*	
			Clethra barbinervis	*Acer micranthum*	*Maianthemum dilatatum*	
			Acanthopanax sciadophylloides	*Sorbus americana* ssp. *japonica*		
			Acer sieboldianum	*Rhus trichocarpa*		
			Pinus densiflora	*Enkianthus campanulatus*		
			Chamaecyparis obtusa	*Rhododendron dilatatum*		
				Skimmja japonica f. repens		
FI-2	1020	Woodland	*Tsuga sieboldii*	*Ilex pedunculosa*	*Oplismenus undulatifolius*	
			Chamaecyparis obtusa	*Callicarpa japonica*	*Plantago asiatica*	
			Clethra barbinervis	*Prunus incisa*	*Artemisia princeps*	
			Acer distylum	*Lindera obtusiloba*	*Maianthemum dilatatum*	
			Cornus controversa	*Euonymns macropterus*	*Erigeron annuus*	
			Quercus mongolica var. *crispula*	*Skimmja japonica f. repens*	*Corydalis incisa*	
			Quercus serrata			

Table 1 continued

Study site	Altitude (m)	Landscape and landscape element (open land)	Main plant (Phanerogamae) species			Type of human disturbance (mainly in open land)
			Trees	Small trees and shrubs	Herbs	
FE-1	1025	Woodland	*Quercus mongolica* var. *crispula*	*Prunus incisa*	*Miscanthus sinensis*	Mowing
		Open land	*Quercus serrata*	*Lonicera japonica*	*Boehmeria tricuspis* ssp. *paraspicata*	Cultivation
		Secondary grassland	*Castanea crenata*	*Malus toringo*	*Cirsium nipponicum* var. *incomptum*	Fertilization
		Conifer plantations	*Pinus densiflora*	*Rosa multiflora*	*Lysimachia clethroides*	
		Vegetable plots	*Larix kaempferi*	*Deutzia crenata*	*Agrimonia pilosa*	
		Abandoned arable land	*Alnus hirsuta*	*Hydrangea paniculata*	*Sanguisorba officinalis*	
		Sparse forest	*Magnolia obovata*		*Vicia cracca*	
			Abies firma		*Vicia unijuga*	
					Picris hieracioides ssp. *japonica*	
					Erigeron annuus	
FE-2	1010	Woodland	*Quercus serrata*	*Acer crataegifolium*	*Miscanthus sinensis*	Mowing
		Open land	*Pinus densiflora*	*Lindera obtusiloba*	*Oplismenus undulatifolius*	Cultivation
		Conifer plantations	*Larix kaempferi*	*Enkianthus campanulatus*	*Campanula punctata*	Fertilization
		Secondary grassland	*Alnus hirsuta*	*Rhododendron dilatatum*	*Cirsium nipponicum* var. *incomptum*	
		Sparse forest	*Acer capillipes*	*Euonymns macropterus*	*Kalieris pinnatifida*	
		Bare site	*Zelkova serrata*	*Spiraea japonica*	*Lysimachia clethroides*	
			Prunus maximowiczii	*Ligustrum obtusifolium*	*Polygonum cuspidatum*	
			Clethra barbinervis		*Trifolium repens*	
					Astilbe microphylla	
					Picris hieracioides ssp. *japonica*	

Table 1 continued

Study site	Altitude (m)	Landscape and landscape element (open land)	Main plant (Phanerogamae) species			Type of human disturbance (mainly in open land)
			Trees	Small trees and shrubs	Herbs	
OL-1	990	Open land			*Oxalis corniculata*	Heavy trampling
		Athletic fields and open areas with grassland			*Taraxacum officinale*	Intensive mowing
					Geramium thumbergii	Land readjustment
					Vicia cracca	
					Trifolium repens	
					Cerastium fontanum ssp. *japonica*	
					Poa annua	
					Ambrosia artemisiifolia var. *elatior*	
					Kummerovia striata	
OL-2	1025	Open land		*Morus australis*	*Rorippa indica*	Intensive cultivation
		Farmland consisting of cabbage, potato, and strawberry plots		*Pinus densiflora*	*Miscanthus sinensis*	Tilling
				Cornus controversa	*Plantago asiatica*	Intensive mowing
				Salix bakko	*Oxalis corniculata*	Intensive fertilization
				Pieris japonica	*Taraxacum officinale*	Insecticide spraying
				Celastrus orbiculatus	*Rumex crispus* ssp. *japonicus*	
				Rosa multiflora	*Agrimonia pilosa*	
					Calystegia japonica	
					Trifolium pratense	
					Vicia unijuga	
					Hemerocallis fulva var. *Kwanso*	

of Mount Fuji, central Japan. Our objectives are (1) to clarify the relationships between the diversities of vegetation, adult nectar plants, and butterfly communities, (2) to examine the role nectar resources play in determining butterfly diversity, and (3) to evaluate the conservation value of flowering adult nectar plants for butterfly diversity.

Materials and methods

Study sites

The study was carried out at an altitude of ca. 1000 m in and around the Aokigahara primary woodland on the northwestern foot of Mt. Fuji in central Japan. Six study sites were selected comprising three habitat types: forest interior, forest edge, and open land adjacent to the forest. All study sites were similar in terms of altitude and topography (almost flat or gently sloping land), and were located inside an area measuring 2.4 km east to west and 0.63 km north to south. In each site, a fixed 300-m-long census route was established. The characteristics of the six study sites (named FI-1, FI-2, FE-1, FE-2, OL-1, and OL-2) are as follows and are summarized in Table 1.

Sites FI-1 and FI-2 were in the forest interior, consisting of natural forest established on the Aokigahara lava flow, which originated in AD 864 eruption of Mount Nagao (located halfway up Mount Fuji). Each census route was established along a path crossing the site's interior. It is believed that this forest has never been subjected to large-scale human disturbance. Average tree age is ca. 150 years and the highest ever ages recorded for the dominant tree species are 356 years for *Tsuga sieboldii* and 240 years for *Chamaecyparis obtusa* (Seido 1991). Comparison of FI-1 and FI-2 showed that the latter was dominated by evergreen coniferous trees such as *T. sieboldii* and *C. obtusa*, with herb species present in some parts of the understory, while about half of FI-1 was dominated by broad-leaved deciduous trees such as *Q. mongolica* var. *crispula*, with very few herb species. Almost no human land use or disturbance was evident.

Sites FE-1 and FE-2 were at the edge of the forest. Census routes were established mostly along the forest boundary. A small part of the route in site FE-1 ran through a grassland area near the forest boundary. Both sites consisted mainly of natural forest (usually along one side of the census route), and secondary grassland, conifer plantations, vegetable plots, abandoned farmland, and scattered forest (these usually on the other side of the census route). Forest structure and composition was similar to that of sites FI-1 and FI-2 described above, except for the presence of more broad-leaved deciduous trees (probably due to the greater access to sunlight along the forest's edge). There were few major differences between FE-1 and FE-2, except for in the composition of plant species. In the open areas of these sites, there was abundant evidence of human land use (e.g. plantations and vegetable plots) and disturbance (e.g. mowing and cultivation). In contrast, forested parts, which comprised about half the area of each site were relatively undisturbed. Taken as a whole, these sites were classed as having intermediate levels of human disturbance.

Sites OL-1 and OL-2 were in open land near the woodland. Census routes ran through the middle of each site. Site OL-1 consisted mainly of fields and open areas of turf for track and field sports, with almost no trees or shrubs. Site OL-2 consisted of agricultural fields of cabbage, potato, strawberry, and *Sanguisorba officinalis*. OL-2 contained some trees, shrubs and herbs in areas surrounding the agricultural fields and along farm tracks. Levels of human land use (e.g. for sports, recreation, and farming) and disturbance (e.g. trampling, mowing, pesticide spraying, fertilizer application, cultivation) were generally high, and these sites were classed as having the highest level of human disturbance.

Census methods

Butterfly communities were monitored using the line transect method (Pollard 1977, 1984; Thomas 1983; Gall 1985; Pollard and Yates 1993). This method is now extensively used to survey and monitor butterfly populations and communities (e.g. Shreeve and Mason 1980; Erhardt 1985; Pollard and Yates 1993) and is of considerable value when investigating differences in species abundance between sites (Gall 1985; New 1991, 1997). Transect counts were conducted twice a month usually during the adult flight season (from April to November 1999) and between 10:00 and 15:00 h local time under suitable weather conditions. Walking at a steady pace along the transect line, the number of adult individuals of each butterfly species sighted was recorded within a belt approximately 10 m wide. Individuals that could not be identified immediately were netted, identified, and released. In the field, it is not possible to distinguish between *Pieris melete* and *Pieris napi*. Therefore, these two congeneric species complexes were treated as *Pieris* spp. for the analysis.

Recently, several problems on butterfly distribution maps have been discussed (Dennis et al. 1999). In particular, it is pointed out that these maps fail to distinguish the status of records, that is, whether they are observations of breeding populations or vagrant individuals (Cook et al. 2001; Dennis 2001). Thus, it is very important to know whether records relate to breeding populations in favorable habitats or not, especially for conservation purposes. The same is true for transect data on recording adult individuals. In addition, it is pointed out that simultaneous collection of biotope, resources, and behavioral data is needed for monitoring affinities of butterflies to vegetation structures and using butterflies as indicators of environmental changes (Dennis 2004). Thus, in the present study, we recorded all adult feeding behaviors and their diet resource items (e.g. species name of nectaring plants) observed simultaneously with adult butterfly monitoring during each transect survey at every site. Weather conditions, light conditions, and human disturbance-related events such as mowing and cultivation were recorded at the same time during each transect survey.

At all butterfly study sites surveyed using the transect method, the vegetation was surveyed within 10-m wide corridors along each transect route using the belt-transect method (Lincoln et al. 1998); to record as many plant species as possible, separate surveys were conducted on 12 June and 27 August, 1999. We recorded all species of plants (belonging to Phanerogamae) sighted along each route in the respective survey days. Only Phanerogammic species were surveyed because most butterflies in the study area utilize such plants in both the larval and adult stages.

Data analysis

We analyzed butterfly community structure at each site using the following ecological parameters: population density, total population density, species richness, and species diversity. The population density of each butterfly species at each study site was calculated as follows. The monthly count was determined as the mean of twice-monthly counts conducted in May–September or as the value of single counts in April, October, and November. The mean monthly count over the season was then calculated using only those months when the species was observed to minimize the effect of variable voltinism between species. Finally, the population density (number of adults/month/km) was obtained by dividing the mean monthly count by 0.3 km (the length of each census route). The total population density at each site was the sum of population densities of all component butterfly species observed in each site. The species richness at each site was the total number of butterfly species observed in each site during the study period. The species diversity at each site was expressed by both Shannon-Wiener function, $H' = -\sum_{i=1}^{s} p_i \ln p_i$, where s is the total number of species recorded, and p_i is the proportion of the population density of the i-th species, and Simpson's index of diversity (Simpson 1949), $1 - \lambda$, where $\lambda = \sum_{i=1}^{S} n_i(n_i - 1)/N(N - 1)$, n_i is the population density of the i-th species, and N is the total population density of all component species in each site.

Concerning the vegetation at each study site, we used the following seven parameters in the analyses: the numbers of (1) all plant species (belonging to Phanerogamae), (2) herbaceous plant species, (3) woody plant species, (4) annual plant species, (5) perennial plant species, (6) shrub plant species, and (7) tree plant species observed in the two vegetation surveys.

To estimate the abundance of diet resources for adult butterflies, we obtained the number of adult nectar plant species in each study site as follows. First, we listed up all species of nectar plants used by adult butterflies observed through all study sites during the study period. Second, we determined the presence or absence of these nectar plant species in each study site based on the results of the vegetation survey stated above. The distribution record of each nectar plant species in each study site is shown in the Appendix. We used the following seven parameters in the analyses: the numbers of species of (1) all nectar plants, (2) herbaceous nectar plants, (3) woody nectar plants, (4) annual nectar plants, (5) perennial nectar plants, (6) shrub nectar plants, and (7) tree nectar plants recorded in each study site.

Results

Vegetation and adult nectar plants

The values of various indices of butterfly communities, vegetation represented by plants belonging to Phanerogamae, and nectar plants utilized by adult butterflies in each of all the six study sites are shown in Table 2.

Table 3 shows the species composition of all plants (belonging to Phanerogamae) and adult nectar plants recorded all over the study sites. Out of all 221 plant species (Phanerogamae) recorded in this study, their utilization as a nectar resource by adult butterflies was observed in 38 plant species (17.2%). Of all 127 herbaceous and 84 woody species, the proportion used as a nectar resource by adult butterflies was substantially higher in

Table 2 The values of various indices of butterfly communities, vegetation, and nectar plants recorded in the six study sites

Study site	OL-1	OL-2	FE-1	FE-2	FI-1	FI-2
Butterfly community						
Total population density	74.76	121.87	269.53	162.92	10.83	9.44
Total number of species	18	23	43	39	3	3
Species diversity (H')	2.633	2.659	3.240	3.364	1.058	1.028
Species diversity ($1-\lambda$)	0.920	0.900	0.930	0.960	0.700	0.700
Vegetation (Phanerogamae)						
No. of all plant species	52	60	106	136	37	64
No. of woody plant species	1	16	35	55	34	42
No. of tree species	0	6	16	31	20	22
No. of shrub species	1	9	15	20	13	17
No. of herbaceous plant species	50	42	69	77	2	21
No. of perennial species	23	24	48	55	2	17
No. of annual species	27	18	18	20	0	3
Adult nectar plants						
No. of all nectar plant species	17	19	28	28	3	8
No. of woody nectar plant species	1	2	3	4	3	4
No. of tree nectar species	0	1	1	1	2	2
No. of shrub nectar species	1	1	2	3	1	2
No. of herbaceous nectar plant species	16	17	25	24	0	4
No. of perennial nectar species	11	12	17	16	0	3
No. of annual nectar species	5	5	8	8	0	1

herbaceous (33 spp., 26.0%) than woody (6 spp., 5.9%) plants. This trend is shown in Fig. 1. The chi-square test for goodness of fit showed that the proportions of number in the woody and herbaceous plant species recorded in the study area (i.e. expected proportions) differed significantly from those of number of woody and herbaceous adult nectar plant species used (i.e. observed proportions) ($\chi^2 = 26.333$, df = 1, $P < 0.0001$). In more detailed analysis, the chi-square test for goodness of fit showed that the proportions of number in the species of trees, shrubs, perennials, and annuals recorded in the study area (i.e. expected proportions) differed significantly from those of number of adult nectar species of trees, shrubs, perennials, and annuals used (i.e. observed proportions) ($\chi^2 = 27.246$, df = 3, $P < 0.0001$). These results indicate that, in the study area, the nectar

Table 3 Number of species of plants belonging to Phanerogamae and the number of nectar plant species among them recorded across all study sites

	Herbaceous plants			Woody plants			Other plants	Total
	Annuals	Perennials	Total	Shrubs	Trees	Total		
Plants belonging to Phanerogamae	43	84	127	40	44	84	10	221
Adult nectar plants	11	22	33	3	2	5	0	38

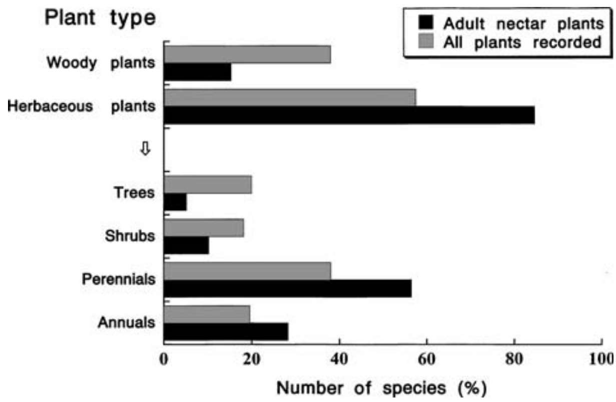

Fig. 1 The number of species (%) of the respective plant types in all plants belonging to Phanerogamae and in adult nectar plants among them recorded in all the study area

Table 4 Correlation coefficients of the number of species between various plant types and adult nectar plants recorded in each study site

	All plants	Herbaceous plants	Annual plants	Perennial plants	Woody plants	Tree plants	Shrub plants
Nectar plants	0.843*	0.983**	0.767	0.958**	0.140	0.061	0.161

* $P < 0.05$

** $P < 0.001$

resource utilization by adult butterflies is biased heavily to herbaceous plants especially perennials, compared to woody plants.

A significant positive correlation in the number of species was detected between adult nectar plants and all, herbaceous, and perennial plants belonging to Phanerogamae recorded at each study site (Table 4). In particular, the correlation was strong in both herbaceous and perennial plants.

Butterfly communities and adult nectar plants

All butterfly community indices (total population density, total number of species, species diversities H' and $1 - \lambda$) were positively and highly significantly correlated with the number of species of all adult nectar plants recorded at each study site. In particular, the strongest correlation was detected with butterfly species richness (total no. of species) (Table 5). On the other hand, similar to the above results, all butterfly community indices were positively and highly significantly correlated with the number of species of herbaceous adult nectar plants recorded in each study site. However, no significant correlations were detected between all butterfly community indices and the number of species of woody adult nectar plants recorded at each study site.

Table 5 Correlation coefficients between various butterfly community indices and the numbers of nectar plant species in the six study sites

	Butterfly community index			
	Total population density	Total number of species	Species diversity (H')	Species diversity ($1 - \lambda$)
All nectar plants	0.915**	0.979***	0.970***	0.926***
Herbaceous nectar plants	0.907**	0.968***	0.986***	0.958***
Woody nectar plants	0.016	0.045	− 0.198	− 0.328

** $P < 0.01$

*** $P < 0.001$

Discussion

Resource utilization patterns of adult butterflies

In the present study, we have shown that the nectar resource utilization by adult butterflies is heavily biased to herbaceous plants, especially to perennials, compared to woody species, although most of the study area was in and near a primary woodland. Such biased herb resource utilization by adult butterflies has been observed by several previous authors (Kitahara 2000; Kamimura 2004; Mano 2004; Tiple et al. 2006). Also, in arable field margins of Britain, the importance of perennial nectar sources rather than annual ones was pointed out for butterfly conservation (Dover 1996). In this study, the highest number of adult butterfly species was recorded in woodland edge study sites, intermediate in open land sites, and lowest in woodland interior sites (Kitahara and Watanabe 2003). It is also a general observation that most adult butterflies avoid shade and are often encountered in open sunny places (Douwes 1975; Dennis and Bramley 1985; Warren 1985; Pivnick and McNeil 1987). Thus, one possible reason for biased herb resource use by adults is that most adult butterflies indeed prefer flowers of herbaceous plants to those of woody ones, or that herb abundance and density are simply much higher in open sunny spaces such as woodland edges and open land sites with abundant adult butterflies. Concerning butterfly conservation, the biased herb resource use by adults suggests that the maintenance of herbaceous plant species richness and diversity in their habitats is important for ensuring the nectar resources of adult butterflies.

Relationship between vegetation and adult nectar plants

The number of species of adult nectar plants in each site was significantly and positively correlated with that of all plants belonging to Phanerogamae. Thus, there were greater nectar plant species in sites with greater plant species richness. In more detail, the number of species of adult nectar plants at each site was more strongly correlated with that of herbaceous or perennial plants than with that of all plants belonging to Phanerogamae, suggesting that the numbers of species of herbaceous and perennial plants are both good predictors for adult nectar plants at the respective study sites. Probably, the strong correlations in numbers of species between adult nectar plants and both herbaceous and perennial plants at each site are caused by bias in herb resource utilization of adult butterflies. The relationships between vegetation and adult nectar plants suggest that the maintenance and management of habitats for species richness and diversity of herbaceous plants is important for the supply and availability of adult nectar resources.

Relationship between butterfly diversity and adult nectar plants, and conservation implications

In the present study, we showed that butterfly community indices were all positively correlated with the number of nectar plant species at each site. Among them, the strongest correlation was detected between butterfly species richness (total no. of species) and nectar plant species richness ($r = 0.979$, $P < 0.001$). This correlation with the number of species of nectar plants is much stronger than that with the number of species of all plants (belonging to Phanerogamae) recorded at each site ($r = 0.842$, $P < 0.05$) shown in a previous study (Kitahara and Watanabe 2001). These results suggest that nectar plant species richness is an important factor governing adult butterfly species richness at each site rather than total species richness of plants (Fig. 2). The importance of nectar plant abundance for butterfly abundance and diversity has been pointed out in many previous studies (Murphy and Wilcox 1986; Kremen 1992; Munguira and Thomas 1992; Holl 1995; Ishii et al. 1995; Loertscher et al 1995; Steffan-Dewenter and Tscharntke 1997; Hardy and Dennis 1999; Clausen et al. 2001; Ries et al. 2001; Schneider and Fry 2001; Simonson et al. 2001; Pryke and Samways 2003; Pywell et al. 2004), although the reverse has emerged in a few studies (Sharp et al. 1974). A number of population and community studies of butterflies suggest that adult distribution patterns are more affected by the availability of nectar resources than the presence of larval host plants (Ehrlich and Gilbert 1973; Gilbert and Singer 1973; Murphy 1983; Grossmueller 1987; Feber et al. 1996; Hardy and Dennis 1999).

In addition, it has been known in some studies (Thomas and Mallorie 1985; Holl 1996) that butterfly species richness is positively correlated with herbaceous cover. Our study also showed that butterfly community indices were all strongly correlated with the species

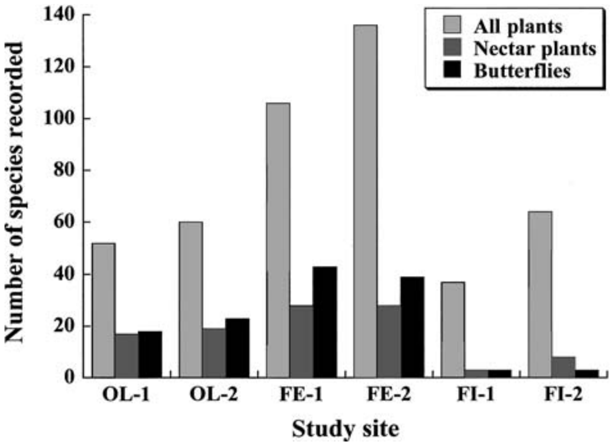

Fig. 2 Number of species of all plants belonging to Phanerogamae, adult nectar plants and butterflies recorded in each study site

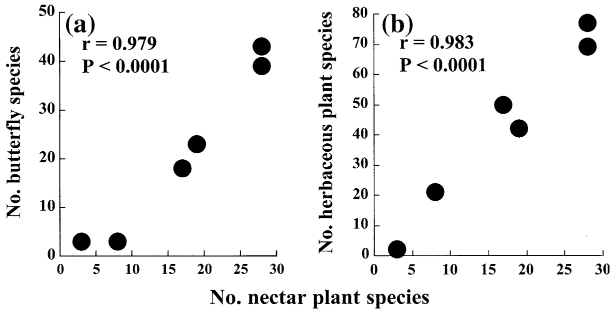

Fig. 3 Relationships between the number of nectar plant species and the number of butterfly species (**a**), and the number of herbaceous plant species (**b**) recorded in each study site

richness of herbaceous nectar plants at each site, but not with that of woody nectar plants. This indicates that the richness of herbaceous nectar plant species is one of the most important factors determining the community structure and attributes of adult butterflies. Yet, most of the present study area was in and near a primary woodland; nevertheless, the richness of woody nectar plant species has almost no effects on the determination of adult butterfly community structure. The importance of herbaceous plant species richness even within woodlands for herbivore diversity is also known for moths (Usher and Keiller 1998).

Two key correlations are found, one between the species richness of butterflies and nectar plants, and another between the species richness of nectar plants and herbaceous plants at each site (Fig. 3). These results suggest that herbaceous plant species richness in a habitat has a central role in its nectar plant species richness, and that nectar plant richness is a highly important factor governing and supporting its adult butterfly species richness. Consequently, we propose that the maintenance and management of herbaceous plant species richness in a butterfly habitat, which underlies nectar plant species richness, is very important for the maintenance and conservation of butterfly species richness and diversity even in and around woodland landscapes of temperate regions, as Tudor et al. (2004) claim that management of woodland sites for butterfly conservation should give as much consideration to nectar sources as to host plant sources.

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Appendix List of nectar plant species recorded in the present study, their observed sites (○), the number of butterfly species which utilized the respective nectar plants, and the species name of butterflies, which utilized the respective nectar plants

Species of nectar plants	Type		Study site observed						No. of sites observed	No. of butterfly species which utilized the plant	Butterfly species which utilized the plant as a nectar resource (No. of adults observed which utilized the plant in parenthesis)	
			OL-1	OL-2	FE-1	FE-2	FI-1	FE-2				
Taraxacum spp. (*officinale* or *platycarpum*)	Herbaceous	Perennial	○	○	○	○			4	10	*Colias erate* (Esper) (16) *Eurema hecabe* (Linnaeus) (5) *Pieris* (*m.* or *n.*) sp. (2) *Pelopidas mathias* (Fabricius) (1) *Lycaena phlaeas* (Linnaeus) (1)	*Pieris rapae* (Linnaeus) (12) *Polygonia c-aureum* (Linnaeus) (3) *Ypthima argus* (Butler) (2) *Gonepteryx rhamni* (Butler) (1) *Inachis io* (Stichel) (1)
Trifolium repens Linnaeus	Herbaceous	Perennial	○	○	○	○			4	8	*Colias erate* (Esper) (5) *Lycaeides subsolanus* (Eversmann) (2) *Leptalina unicolor* (Bremer & Grey) (1) *Everes argiades* (Pallas) (1)	*Pieris* (*m.* or *n.*) sp. (2) *Cynthia cardui* (Linnaeus) (2) *Parnassius glacialis* (Butler) (1) *Pieris rapae* (Linnaeus) (1)
Erigeron annuus Linnaeus	Herbaceous	Winter annual	○	○	○	○		○	5	7	*Colias erate* (Esper) (8) *Pieris* (*m.* or *n.*) sp. (4) *Lycaena phlaeas* (Linnaeus) (1) *Minois dryas* (Scopoli) (1)	*Pieris rapae* (Linnaeus) (4) *Eurema hecabe* (Linnaeus) (1) *Polygonia c-aureum* (Linnaeus) (1)

Appendix continued

Species of nectar plants	Type		Study site observed						No. of sites observed	No. of butterfly species which utilized the plant	Butterfly species which utilized the plant as a nectar resource (No. of adults observed which utilized the plant in parenthesis)	
			OL-1	OL-2	FE-1	FE-2	FI-1	FE-2				
Lespedeza bicolor Turcz. var. *japonica* Nakai	Herbaceous	Semi-shrub			○	○			2	7	*Eurema hecabe* (Linnaeus) (4) *Everes argiades* (Pallas) (3) *Pieris* (*m.* or *n.*) sp. (1) *Lampides boetieus* (Linnaeus) (1)	*Polygonia c-aureum* (Linnaeus) (4) *Choaspes benjaminii* (Murray) (1) *Celastrina argiolus* (Linnaeus) (1)
Cirsium nipponicum var. *incomptum* Kitamura	Herbaceous	Perennial	○		○	○		○	4	6	*Eurema hecabe* (Linnaeus) (7) *Choaspes benjaminii* (Murray) (1) *Argyronome ruslana* (Motschulsky) (1)	*Parnara guttata* (Bremer et Grey) (4) *Polygonia c-aureum* (Linnaeus) (1) *Minois dryas* (Scopoli) (1)
Aster ageratoides Turcz. var. *ovatus* Nakai	Herbaceous	Perennial			○	○			2	6	*Polygonia c-aureum* (Linnaeus) (4) *Lycaena phlaeas* (Linnaeus) (3) *Pieris rapae* (Linnaeus) (2)	*Colias erate* (Esper) (3) *Ypthima argus* (Butler) (3) *Eurema hecabe* (Linnaeus) (1)
Polygonum sagittatum var. *sibiricum* Maxim.	Herbaceous	Annual			○	○			2	5	*Eurema hecabe* (Linnaeus) (2) *Celastrina argiolus* (Linnaeus) (1) *Polygonia c-aureum* (Linnaeus) (1)	*Pieris* (*m.* or *n.*) sp. (1) *Lampides boetieus* (Linnaeus) (1)

Appendix continued

Species of nectar plants	Type		Study site observed						No. of sites observed	No. of butterfly species which utilized the plant	Butterfly species which utilized the plant as a nectar resource (No. of adults observed which utilized the plant in parenthesis)	
			OL-1	OL-2	FE-1	FE-2	FI-1	FE-2				
Trifolium pratense Linnaeus	Herbaceous	Perennial	○	○					2	4	*Colias erate* (Esper) (9) *Eurema hecabe* (Linnaeus) (3)	*Cynthia cardui* (Linnaeus) (4) *Pieris rapae* (Linnaeus) (1)
Geranium nepalense Sweet	Herbaceous	Perennial	○	○	○	○		○	5	4	*Parnara guttata* (Bremer et Grey) (1) *Pieris* (*m.* or *n.*) sp. (1)	*Leptidea amurensis* (Menetries) (1) *Ypthima argus* (Butler) (1)
Stachys Riederi var. *intermedia* Kitamura	Herbaceous	Perennial	○		○				2	3	*Pieris* (*m.* or *n.*) sp. (3) *Leptidea amurensis* (Menetries) (1)	*Parnara guttata* (Bremer et Grey) (2)
Patrinia villosa Juss.	Herbaceous	Perennial				○			1	3	*Choaspes benjaminii* (Murray) (1) *Ypthima argus* (Butler) (1)	*Parantica sita* (Moore) (1)
Vicia unijuga A. Br.	Herbaceous	Perennial	○	○	○	○			4	3	*Parnara guttata* (Bremer et Grey) (1) *Lampides boetieus* (Linnaeus) (1)	*Eurema hecabe* (Linnaeus) (1)
Polygonum thunbergii Sieb. et Zucc.	Herbaceous	Annual				○			1	2	*Celastrina argiolus* (Linnaeus) (1)	*Polygonia c-aureum* (Linnaeus) (1)
Kalimeris pinnatifida Kitamura	Herbaceous	Perennial	○	○	○	○		○	5	2	*Lycaena phlaeas* (Linnaeus) (2)	*Parnara guttata* (Bremer et Grey) (1)

Appendix continued

Species of nectar plants	Type		Study site observed						No. of sites observed	No. of butterfly species which utilized the plant	Butterfly species which utilized the plant as a nectar resource (No. of adults observed which utilized the plant in parenthesis)	
			OL-1	OL-2	FE-1	FE-2	FI-1	FE-2				
Polygonum erecto-minus Makino	Herbaceous	Annual		○	○				2	2	*Parnara guttata* (Bremer et Grey) (1)	*Colias erate* (Esper) (1)
Deutzia crenata Sieb. et Zucc.	Woody	Shrub			○	○		○	3	2	*Nephargynnis anadyomene* (Bremer) (1)	*Fabriciana adippe* (Butler) (1)
Lysimachia clethroides Duby	Herbaceous	Perennial			○	○			2	2	*Pieris rapae* (Linnaeus) (1)	*Pieris* (*m.* or *n.*) sp. (1)
Metaplexis japonica Makino	Herbaceous	Perennial				○			1	2	*Parnara guttata* (Bremer et Grey) (1)	*Papilio maackii* (Menetries) (1)
Vicia cracca Linnaeus	Herbaceous	Perennial	○	○	○	○			4	2	*Lampides boetieus* (Linnaeus) (3)	*Everes argiades* (Pallas) (1)
Astilbe microphylla Knoll	Herbaceous	Perennial		○	○	○			3	2	*Neptis sappho* (Pallas) (1)	*Araschnia burejana* (Bremer) (1)
Elsholtzia ciliata Hylander	Herbaceous	Annual	○						1	2	*Parnara guttata* (Bremer et Grey) (1)	*Eurema hecabe* (Linnaeus) (1)
Rubus parvifolius Linnaeus	Woody	Shrub	○	○	○	○			4	2	*Pieris* (*m.* or *n.*) sp. (1)	*Lycaeides subsolanus* (Eversmann) (1)
Clethra barbinervis Sieb. et Zucc.	Woody	Tree				○	○	○	3	2	*Argynnis paphia* (Linnaeus) (1)	*Polygonia c-aureum* (Linnaeus) (1)
Rhododendron japonicum Suringer	Woody	Shrub				○	○	○	3	2	*Papilio macilentus* (Janson) (1)	*Pieris* (*m.* or *n.*) sp. (1)
Bidens frondosa Linnaeus	Herbaceous	Annual	○						1	1	*Lampides boetieus* (Linnaeus) (1)	

Appendix continued

Species of nectar plants	Type		Study site observed						No. of sites observed	No. of butterfly species which utilized the plant	Butterfly species which utilized the plant as a nectar resource (No. of adults observed which utilized the plant in parenthesis)
			OL-1	OL-2	FE-1	FE-2	FI-1	FE-2			
Rorippa indica Hiern.	Herbaceous	Perennial	○	○					2	1	*Colias erate* (Esper) (1)
Oxalis corniculata Linnaeus	Herbaceous	Perennial	○	○		○			3	1	*Colias erate* (Esper) (1)
Sedum kamtschaticum Fisch.	Herbaceous	Perennial			○	○			2	1	*Pieris rapae* (Linnaeus) (1)
Agrimonia eupatoria L. var. *pilosa* Makino	Herbaceous	Perennial		○	○	○			3	1	*Lampides boetieus* (Linnaeus) (1)
Picris hieracioides L. var. *japonica* Regel	Herbaceous	Winter annual	○		○	○			3	1	*Eurema hecabe* (Linnaeus) (1)
Commelina communis Linnaeus	Herbaceous	Annual		○	○	○			3	1	*Parnara guttata* (Bremer et Grey) (1)
Adenophora triphylla A. var. *japonica* Hara	Herbaceous	Perennial			○				1	1	*Parnara guttata* (Bremer et Grey) (1)
Mazus japonicus O.Kuntze	Herbaceous	Annual	○		○	○			3	1	*Eurema hecabe* (Linnaeus) (1)
Oenothera biennis Linnaeus	Herbaceous	Winter annual		○	○	○			3	1	*Colias erate* (Esper) (1)
Amphicarpaea edgeworthii Benth. var. *japonica* Oliver	Herbaceous	Annual		○	○				2	1	*Parnara guttata* (Bremer et Grey) (1)

Appendix continued

Species of nectar plants	Type		Study site observed						No. of sites observed	No. of butterfly species which utilized the plant	Butterfly species which utilized the plant as a nectar resource (No. of adults observed which utilized the plant in parenthesis)
			OL-1	OL-2	FE-1	FE-2	FI-1	FE-2			
Eupatorium lindleyanum DC.	Herbaceous	Perennial			○				1	1	*Minois dryas* (Scopoli) (3)
Sanguisorba officinalis Linnaeus	Herbaceous	Perennial		○	○	○			3	1	*Polygonia c-aureum* (Linnaeus) (1)
Betula platyphylla Sukatchev var. *japonica* Hara	Woody	Tree		○	○		○	○	4	1	*Polygonia c-aureum* (Linnaeus) (2)

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