

**The Analysis and Understanding of Butterfly
Community Structure Based on the Concept of
Generalist vs. Specialist Strategies:
A New Approach to Biological Community Analysis**

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Abstract

The search for patterns is an important component of ecological research, and has probably been the most important step in the development of community ecology. Up to the present, biological communities have been analyzed mainly from the viewpoint of biotic interactions such as interspecific competition and predation, niche theory, and species diversity. However, few attempt has been made to analyze natural community structure in terms of life-history strategies (e.g., generalist and specialist strategies) of its component species. On the other hand, the verification of the generalist/specialist (r/K) concept has been examined mainly among populations of a species, or of closely related species. However, little attempt has yet been made to verify the concept among many species at the community level.

In the present study, I examine temperate butterfly communities subjected to different degrees of human disturbance, and apply the generalist/specialist concept to analyze butterfly community structure. Butterflies are the most suitable organisms for the study of the structure and dynamics of biological populations and communities. The adults can be identified easily in the field and their life-histories are already well known in Japan. The series of my studies are composed of the following four chapters.

Chapter 1: *Patterns in the structure of butterfly communities along an environmental gradient of human disturbance based on the concept of generalist vs. specialist strategies*

I monitored nine butterfly communities with varying degrees of human disturbance by conducting a census twice a month during 1980 by the line transect method in and around Tsukuba City, central Japan. I analyzed the community structures using the generalist/specialist concept. The site (community) order based on decreasing human disturbance was positively correlated with butterfly species diversity (H'), species richness (the total number of species), and the number of specialist species in a community, but not with the number of generalist species. The number of generalist species was rather constant, irrespective of the degree of human disturbance. Thus, both the butterfly species diversity and species richness were more dependent on the specialists than the generalists. The analyses also showed that the generalist species were distributed widely over the communities, and they maintained high population densities, resulting in high rank status in abundance in a community, with more spatial variation in density per species. Specialist species showed the opposite trends. These results demonstrate that the

generalist/specialist concept is a powerful tool applicable to analyze structure of natural communities.

Chapter 2: Reexamination of the butterfly community patterns based on the generalist/specialist concept along a grassland habitat gradient of human disturbance in a different region

In the previous chapter, I analyzed the butterfly communities along a gradient of human disturbance by applying the generalist/specialist concept. Butterfly species were classified into generalist or specialist species based on their voltinism (seasonal time dimension) and potential larval resource breadth (food dimension). The community structure and species composition showed the systematic changes along the gradient. To verify the generality of those trends, I chose another butterfly community data (Sei 1986a,b) obtained by monitoring five grassland butterfly communities with varying degrees of human disturbance twice a month during 1985 by the line transect method at the foot of Mt. Fuji, central Japan, and analyzed their structure in a manner similar to that employed in the previous chapter. Most results were consistent with the patterns recognized in the previous chapter. The route (community) order based on increasing human disturbance was strongly and negatively correlated with butterfly species richness but with neither butterfly species diversity (H') nor evenness (J'). Also, the degree of human disturbance was significantly and negatively correlated with the number of specialist species, but not with that of generalists, in a community. Butterfly species richness was more strongly correlated with the number of specialist species than with that of generalists. The analyses also showed that the generalist species were distributed more widely over the communities than were the specialists. However, in contrast to the trend revealed in the previous chapter, there was no significant difference in the population densities and in the spatial population variability between the two species groups. As a whole, the present analyses confirmed the consistency of most community patterns detected in the previous chapter. The causes of the inconsistencies in some patterns were thought to be mainly due to the present habitat conditions with a relatively short growing season at high altitudes.

Chapter 3: Analyses of butterfly community structure and composition through multivariate approaches and the concept of generalist/specialist strategies, and conservation implications

In this chapter, I analyzed the community structure of the butterfly data in Chapter 1 using multivariate analyses. The present analyses are in sharp contrast to my previous analyses (Chapter 1) in which each butterfly species was assigned, prior to data analyses, either generalist, intermediate, or specialist based on their larval food plant and voltinism in

accordance with the generalist/specialist concept. The present results of principal components analysis (PCA) showed that the butterfly community was composed of two species groups (I and II). This species grouping was also supported by the results of the cluster analysis (unweighted pair-group method using arithmetic average (UPGMA)). Comparing the present results with species classification used in Chapter 1, the butterfly community was found to be composed of five species groups (specialists, intermediates I and II, and generalists I and II), which differed from each other in their ecological characteristics. Through the comparisons of their characteristics among the five species groups, it was suggested that, in the butterfly community, the positions of the specialist group and the generalist group II are the endpoints on the generalist-specialist selection spectrum, and the three other groups are positioned between these two extremes. The results of the multivariate analyses showed that, among the specialist, intermediate, and generalist groups classified a priori in the previous study, only the specialist group could be discriminated well in one group, and the generalist and intermediate groups were both divided further into two subgroups (I and II) with different characteristics. The multivariate approaches also succeeded in extracting a typical generalist group (i.e., generalist II) from the butterfly community. I propose and recommend the synergetic application of the generalist/specialist (r/K) concept and multivariate approaches to the detailed analysis and deeper understanding of community structure and composition. The present results also suggest that the approach employed in this study is much effective and helpful to identify and find out priority or target species for local butterfly conservation.

Chapter 4: *Application of the community analysis based on the generalist/specialist concept to the environmental evaluation of habitat islands: The island biogeographical analysis of butterfly community structure in the newly designed parks of Tsukuba City*

I analyzed the butterfly communities in the newly designed city parks (area C), "newly opened habitat islands", of Tsukuba City, central Japan. The area constituted a natural ecological experiment on the mainland for clarifying the pattern and process of faunal immigration. I compared butterfly communities in area C with those in two other areas in the light of the theory of island biogeography and the concept of generalist/specialist. The results showed the following: (1) Fewer species were found in area C than in other areas, due largely to the absence of many specialist types, restricted and habitat specialists, and/or low density species in the area. Generalist types, widespread and habitat generalists, and/or high density species predominated in area C. (2) The difference in the species numbers among the three sections within area C could be explained by the habitat structure in and around the respective sections. (3) The densities of many species were low in area C, probably due to its man-modified habitat structure.

In particular, several species occurred at extremely low densities in area C, but at high densities in other areas. (4) The internal structure of the habitat island butterfly community in area C was almost perfectly consistent with that of "quasi-equilibrium" communities that appear during the colonization of an island. These results demonstrate that the synergetic application of the generalist/specialist concept and the island biogeography theory is effective for the understanding of the patterns and structures of habitat island communities.

Overall, I conclude that (1) the patterns in the structure of butterfly communities along an environmental gradient of human disturbance based on the generalist/specialist concept found in the present studies are both robust and general ones, probably common to various types of habitats, environments, and ecosystems, (2) even relatively stable environments usually have heterogeneous structure with stability and unstability, and therefore, support the mixture of specialists and generalists and the resultant high species richness and diversity, and (3) the analytical approach based on the generalist/specialist concept is a highly operational method with good predictive and explanatory powers much applicable to the analysis of various types of biotic communities, in spite of a variety of criticism of the concept.

Key words: Butterfly communities, Community patterns, Community structure, Conservation priority, Environmental disturbance, Generalist-Specialist selection continuum, Generalist and Specialist strategy, Habitat island, Human disturbance, Island biogeography theory, Island patterns, Lepidoptera, Principal components analysis (PCA), Route order, Species characteristics, Species classification, Species composition, Species distribution, Species richness, Temperate butterfly species.

General Introduction

"To do science is to search for repeated patterns, not simply to accumulate facts." (MacArthur 1972). The search for patterns is an important component of ecological research (May 1984; Wiens 1984; Southwood 1987), and has probably been the most important step in the development of community ecology (Cody and Diamond 1975; May 1981; Strong *et al.* 1984; Diamond and Case 1986; Kikkawa and Anderson 1986; Gee and Giller 1987; Ricklefs 1990). Further, the recognition of patterns leads in turn to the formation of hypotheses about the causes of these patterns (Begon *et al.* 1990, p. 614). This kind of information is also vital for the conservation of biodiversity (Ehrlich 1992).

The structure and functions of a biological community are molded by the characteristics, life-histories, and interactions of its constituent species (Holmes *et al.* 1979). Up to the present, communities have been analyzed mainly from the viewpoint of biotic interactions such as interspecific competition (e.g., MacArthur 1972; Cody 1974; Pianka 1974; Cody and Diamond 1975) and predation (e.g., Paine 1966, 1980; Sih *et al.* 1985), niche theory (e.g., Hutchinson 1957; MacArthur 1968; Pianka 1973, 1981, 1988; Schoener 1974), and species diversity (e.g., MacArthur 1965; Whittaker 1972, 1975; Peet 1974; May 1975, 1981; Pielou 1975; Huston 1979; Brown 1988). Also the analyses of natural communities from their guild structures (Root 1967) have so far received much attention (e.g., Holmes *et al.* 1979; Pianka 1980; reviewed by Terborgh and Robinson 1986). Compared to these, some attempts have been made to analyze natural community structure in terms of adaptive strategies (e.g., generalist/specialist strategy) of its component species.

In contrast, the concept of generalist vs. specialist strategies associated with niche breadth or width (MacArthur and Levins 1967; Levins 1968; MacArthur 1972; Pianka 1988; Odum 1989; Novotny 1991; Leps *et al.* 1998) has been one of the central concepts in evolutionary ecology (Cockburn 1991). To date, studies on the generalist/specialist concept have been primarily concerned with an understanding of the evolution of generalization and specialization in different environmental conditions (e.g., MacArthur and Levins 1967; MacArthur 1972; Roughgarden 1972, 1974; Futuyma, and Moreno 1988) and their effect on resource partitioning and the resultant species diversity (e.g., Giller 1984; Pianka 1988). Also, the positive correlation across species between local abundance and distribution has been interpreted in terms of niche breadths along different axes (Brown 1984) and the effect of feeding specialization on local population variability

has been discussed (MacArthur 1955; Watt 1964; Gaston and Lawton 1988a, b; Redfearn and Pimm 1988; Pimm 1991). However, the comparative characteristics of generalist and specialist species at the community level have seldom been quantitatively analyzed.

In community ecology, environmental disturbance has been repeatedly considered to be the ultimate factor governing the distribution and abundance of species and to be one of the most important determinants of natural community structure and composition (Pianka 1970, 1988; Southwood. 1977, 1988; Grime 1979; Greenslade 1983; Spitzer *et al.* 1993; Huston 1994). The generalist/specialist (r/K) strategy (Levins 1968; Odum 1983, 1989; Novotny 1991; Leps *et al.* 1998) is generated along a continuum of selection pressures associated with different levels of disturbance (MacArthur and Wilson 1967; Pianka 1970; Wilson 1975; Southwood 1977, 1981, 1988). The verification of the generalist/specialist (r/K) concept has been examined mainly among populations of a species (e.g., Solbrig & Simpson 1974; Law *et al.* 1977), or of closely related species (e.g., McNaughton 1975). However, little attempt has yet been made to verify the concept among many species at the community level. For butterflies also, with the exception of a few studies such as that of closely related *Pieris* (Ohsaki 1982) and *Mycalesis* species (Braby 2002), the verification of the generalist/specialist (r/K) concept has rarely been examined especially at the community level.

On the other hand, Ehrlich (1992), after more than three decades of work on checkerspot butterflies (*Euphydryas*) populations, suggested that insights obtained from long-term species-focused research have a limited future in conservation biology and a new strategy is required for the overall goal of saving ecosystems, which does not focus on any one species at a time.

In the following studies, I examine temperate butterfly communities subjected to different degrees of human disturbance, and apply the generalist/specialist concept to analyze butterfly community structure. As Ehrlich (1992) also pointed out, butterflies are the most suitable organisms for the study of the structure and dynamics of biological populations and communities. The adults can be identified easily in the field and their life-histories are already well known in Japan (e.g., Fukuda *et al.* 1982, 1983, 1984a, 1984b). Thus, I classified the butterfly species observed in this study a priori into generalist and specialist species based on their two representative life-history traits, voltinism (number of generations per year) and larval resource breadth (range of hostplant species used by larvae). I shall deal with this in more detail later in the section of the chapter 1 "The classification of the butterfly species into generalist and specialist species".

The following studies are composed of four chapters, and their main objectives and approaches are as follows:

Chapter 1: *Patterns in the structure of butterfly communities along an environmental gradient of human disturbance based on the concept of generalist vs. specialist strategies*

I try (1) to analyze butterfly community structure based on the generalist/specialist concept, (2) to search for patterns in the structure of butterfly communities along an environmental gradient of human disturbance, (3) to verify the concept at the community level, and (4) to evaluate the applicability of the concept to butterfly community analyses.

Chapter 2: *Reexamination of the butterfly community patterns based on the generalist/specialist concept along a grassland habitat gradient of human disturbance in a different region*

To verify the generality and robustness of the patterns in the structure of butterfly communities along an environmental gradient of human disturbance detected and found in Chapter 1 and to reevaluate the applicability of the concept at the community level, I try again to examine butterfly community structure based on the generalist/specialist concept in the same manner as that employed in Chapter 1, using the community data collected in a different habitat type and in a distant region from those in Chapter 1.

Chapter 3: *Analyses of butterfly community structure and composition through multivariate approaches and the concept of generalist/specialist strategies, and conservation implications*

To assess the validity of the analytical manner (a priori approach) and results obtained in Chapter 1, I reanalyze the same butterfly community data in Chapter 1 by using multivariate analyses (a posteriori approach). In addition, by combining a priori species classification and the multivariate approaches, I try to analyze and understand the species composition and characteristics of the butterfly community more deeply than in the previous chapters.

Chapter 4: *Application of the community analysis based on the generalist/specialist concept to the environmental evaluation of habitat islands: The island biogeographical analysis of butterfly community structure in the newly designed parks of Tsukuba City*

In this chapter, by applying the generalist/specialist concept to the analysis of butterfly community structure in the newly designed city parks, I try to perform the environmental assessment of city parks. In this chapter, by considering the city parks as habitat islands, I try to analyze the butterfly community structure of city parks based on the theory of island biogeography.

Chapter 1. Patterns in the structure of butterfly communities along an environmental gradient of human disturbance based on the concept of generalist vs. specialist strategies

INTRODUCTION

Environmental disturbance is thought to be one of the most important determinants of ecological community structure and composition (Pianka 1970, 1988; Southwood 1977, 1988; Grime 1979; Greenslade 1983; Spitzer *et al.* 1993; Huston 1994). The generalist/specialist (r/K) strategy (Levins 1968; Odum 1983, 1989; Novotny 1991; Leps *et al.* 1998) is generated along a continuum of selection pressures associated with different levels of disturbance (MacArthur & Wilson 1967; Pianka 1970; Southwood 1977, 1988). The verification of the generalist/specialist (r/K) concept has been examined mainly among populations of a species (e.g., Solbrig & Simpson 1974; Law *et al.* 1977), or of closely related species (e.g., McNaughton 1975; Ohsaki 1982). However, little attempt has yet been made to verify the concept among many species at the community level. In particular, no attempt has been known to analyze and understand natural community structure using a priori approach based on the predictions of the generalist/specialist concept.

In this chapter, I try (1) to search for patterns in the structure of butterfly communities under varying degrees of human disturbance based on the generalist/specialist concept, (2) to clarify quantitatively the comparative characteristics of generalist and specialist species at the community level, (3) to verify the generalist/specialist concept at the community level, and (4) to evaluate the applicability of the generalist/specialist concept to an understanding of community structure.

STUDY AREA AND METHODS

Study area

I chose three areas (areas A, B and C) in and around Tsukuba City, Ibaraki Prefecture, central Japan. The degree of human disturbance of the three areas increased from area A

to C as detailed below. I established nine census routes in these areas. The description of the environmental and vegetational types of each area and site follows.

Area A (secondary natural forest on the gentle south slope of Mt. Tsukuba (alt. 875.9 m) at an altitude of 150-200 m) - In this area, I established two census routes along the forest path (A-1 and A-2). Most of this area was occupied by deciduous broad-leaved forests composed mainly of *Quercus acutissima* and *Q. serrata*, coniferous forests dominated by *Pinus densiflora*, and mixed forests of deciduous and evergreen broad-leaved trees (genus *Castanopsis* and *Quercus*) and coniferous trees. A part of this area contained tree stands of *Phyllostachys* spp. and patches of grasses. The lengths of routes A-1 and A-2 were 530 m and 330 m, respectively. Typical environmental differences between the two routes were as follows. (1) Route A-2 was more open than route A-1. (2) The forests along route A-2 were more fragmentary than those along route A-1. (3) There were cultivated areas of *Morus bombycis* and *Prunus mume* for part of route A-2. (4) There were also some bushes in a part of route A-2. The extent of human disturbances was higher in route A-2 than in route A-1.

Area B (cultivated lands and villages from 50 to 100 m in altitude at the foot of Mt. Tsukuba) - I established four census routes (B-1, B-2, B-3-1, and B-3-2). Route B-1 (360 m in length) ran through paddy fields, cultivated vegetable and *M. bombycis* fields, and a farm village. Small clusters of deciduous broad-leaved trees remained along the paddy fields. One side of route B-2 (280 m in length) was predominantly cultivated lands (paddy fields, *M. bombycis* and lotus (*Nelumbo nucifera*) fields), while the other side was deciduous broad-leaved forests (mostly of *Q. serrata*). Planted forests of *Chamaecyparis obtusa* were present along a part of this route. Route B-3-1 (310 m in length) was surrounded predominantly by secondary forests of evergreen (genus *Castanopsis* and *Quercus*) and deciduous (*Q. acutissima* and *Q. serrata*) broad-leaved trees and planted woods of *Cryptomeria japonica* and *C. obtusa* near the village. The clusters of *Phyllostachys* spp. were also partially present along the route. A part of the route was covered by tree canopy. Route B-3-2 (330m in length) was situated in predominantly *M. bombycis* fields and planted forests of *P. densiflora*, *C. obtusa*, and *C. japonica*, with two houses along the route. The extent of human disturbances decreased in the order of B-1, B-3-2, B-2 and B-3-1.

Area C (newly designed city parks and the connecting pedestrian road with transplanted trees at an altitude of 25 m in Tsukuba City) - The area was occupied mainly of patchy forests, lawns, paved roads, and man-made ponds. Most trees in the area were transplanted when the parks were designed. These forests were mixtures of various tree species belonging to deciduous and evergreen broad-leaved trees and coniferous trees. Most of the forest floors were covered by lawns and grasses. The vegetation of this area

was very different from those of the other areas. The human activities (mowing, pruning, and disinfection) by park management were frequently conducted aperiodically. Therefore, in this area, the progress of succession was almost stopped by human activities.

I established three census routes (C-1, C-2, and C-3). Some patches of secondary forests remained along the route C-1 (510m in length, in Akatsuka Park). The park was surrounded mainly by cultivated fields and residential area. Route C-2 (900 m in length, a pedestrian road about 20 m wide, connecting C-1 and C-3) was next to the remaining forests dominated mainly by deciduous broad-leaved trees and *P. densiflora*. Most trees along route C-3 (1200 m in length, in Doho park) had been transplanted. There was no forest in the surrounding area. The extent of human disturbances was highest in route C-3, followed by routes C-1 and C-2.

In the above site description, I described mainly the representative landscape of vegetation seen around each census route. However, I note that there were sleeve communities composed mainly of herbs and grasses on both sides of each census route, because all census routes were set up along road or path in each study area. In addition, in the areas including woodland, the census route was set up along forest edge landscape often including mantle communities composed mainly of shrubs and climbing plants. Therefore, even in the areas dominated by secondary woodland such as area A, I emphasize that there were relatively open and bright spaces along the census route.

Although the routes within each area were continuous, each route was characterized by sudden change in vegetation as described above. Thus, in the following analyses, I treated each route as a distinct community. Based on my observation, I ranked and numbered the degree of human disturbance of the census routes in the following decreasing order; C-3(1), C-1(2), C-2(3), B-1(4), B-3-2(5), B-2(6), B-3-1(7), A-2(8), and A-1(9).

It is usually thought that the degree of human disturbance in a given site is closely related with the number of persons acting or working in the site. In fact, the above order of census routes based on the degree of human disturbance was also evidenced by the approximate number of persons I met at each census route during the study period. This reinforces the validity of the route order based on the degree of human disturbance used in the present study.

Census methods

I censused butterfly communities by a line transect method (Pollard 1977, 1984; Thomas 1983; Gall 1985; Pollard *et al.* 1986; Pollard and Yates 1993). The method is now being extensively used in surveying and monitoring butterfly populations and communities (e.g.,

Shreeve and Mason 1980; Erhardt 1985; Pollard *et al.* 1986; Warren *et al.* 1986; Pollard 1991; Pollard and Yates 1993). This is a relative method of considerable value when differences in species abundance among sites are being investigated (Gall 1985; New 1991; Warren 1992). I conducted the transect counts along the route twice a month during the adult flight season (from March to November 1980), within the period from ca. 10:00 to 15:00 under fine weather conditions. I recorded the species and the number of individuals for all adult butterflies sighted within 10 m of either side of the route. I captured individuals by an insect net which I could not identify by sight, and released them after identification. Some individuals sighted but not identified were recorded as uncertain taxa such as *Japonica* spp. and *Limenitis* spp.

I first calculated the monthly density (no. of adults observed per 100 m) for each species for each census route during the observation period. These were the means of the two observations in each month. Then, to obtain the monthly mean density for each species for each census route (see **Appendix 1**), I averaged the monthly densities only when the butterfly species were found. Exclusion of months when no butterflies were observed minimized the effect of different voltinism of butterfly species on the yearly abundance estimate (i.e., monthly mean density). I treated each *Pieris* spp. (*melete* and *napi*; two species) and *Neope* spp. (*goschkevitschii* and *niphonica*; two species) as a single species because of the difficulty in distinguishing them in field censuses, especially in their flight.

I analyzed the butterfly community structure using the following ecological parameters; monthly mean population density, species richness, and species diversity. Species richness was expressed by the number of species recorded in each census route during the period. Species diversity was expressed by Shannon-Wiener function,

$$H' = - \sum_{i=1}^s p_i \ln p_i, \text{ where } s \text{ is the number of species recorded, and } p_i \text{ is the proportion of the}$$

monthly mean density of the *i*-th species. In the calculations of the total number of species and the number of generalist or specialist species in a community, I included the values of the uncertain taxa unable to be classified into species in field censuses (see above) in order to make estimates as accurate as possible.

The classification of the butterfly species into generalist and specialist species

Generalization and specialization must be defined with reference to particular axes (Futuyma and Moreno 1988). I classified the butterfly species observed in the present study into generalist or specialist based on their resource utilization patterns in two fundamental niche dimensions (time and food), which could be determined from the

detailed information available in the literature.

First, as Price (1984) pointed out, time is a more limiting resource for specialists than for generalists because the resources are ephemeral. Thus, I used voltinism (number of generations per year) as an indicator of the niche breadth in a seasonal time dimension. Voltinism in insects, as well as larval diet breadth, is subject to natural selection and is one of the most important life-history traits strongly associated with their adaptive strategies and efficient uses of resources (Shapiro 1975). In general, multivoltine species have a longer adult flight period (season) than oligovoltine species (see Glassberg 1993), and the time of adult appearance of oligovoltines is more specialized in particular seasons than that of multivoltine species. Therefore, when we consider their adult flight periods and times of appearance in a seasonal time dimension, we can think of multivoltine species as seasonal generalists, and oligovoltines as seasonal specialists. Voltinism was based on Unno and Aoyama (1981) and Fukuda *et al.* (1982, 1983, 1984a, 1984b), and also on the actual data of seasonal changes in the observed number of individuals of each species in the present study. In this study, I defined "uni- or bivoltine species" as "species with seasonal specialty" and "multivoltine (more than bivoltine) species" as "species with seasonal generality". Actually, in the present study, the mean value of the numbers of months observed in each route of all uni- and bivoltine species combined ($\bar{x} = 1.606$, $n = 34$) was significantly smaller than that of multivoltine (more than bivoltine) species ($\bar{x} = 3.134$, $n = 28$; $t = 3.868$, $P < 0.001$). This shows that the adult emergence period was much longer in multivoltines than in oligovoltines.

Second, I used the degree of polyphagy (range of host plant species used by larvae) as an indicator of the niche breadth in a larval food dimension. The degree of polyphagy (larval resource breadth) was based on Endo and Nihira (1990) and Fukuda *et al.* (1982, 1983, 1984a, 1984b). In this paper, referring to Scriber (1973), Beaver (1979) and others, I expediently define "species whose larvae had been reported to feed on 10 or less plant species belonging to one taxonomic family" as "species with feeding specialty", and "species the larvae of which feed on more than 10 plant species belonging to one taxonomic family, or on a variety of host plants belonging to two or more taxonomic families" as "species with feeding generality".

Then, I classified "the species with both seasonal and feeding specialty" into "specialist species", and "those with both seasonal and feeding generality" into "generalist species" (**Table 1**). With these criteria, out of 62 butterfly species identified, I classified 20 species (32.3%) as generalists, and 17 (27.4%) as specialists. The remaining 25 species (40.3%) could not be classified into either category. They were the species with either seasonal generality and feeding specialty, or seasonal specialty and feeding generality, and treated as "intermediate species". These species show a negative relationship in two

fundamental niche dimensions (voltinism and larval feeding specialization) and are not consistent with the prediction of the generalist/specialist concept that species with multivoltinism and polyphagy prevail in unstable (disturbed) habitats, whereas those with oligovoltinism and oligophagy do so in stable (undisturbed) habitats (Pianka 1970, 1988; Southwood 1977). Thus, in this chapter, I did not take these species into account when I discussed the result in terms solely of the generalist/specialist concept. See **Appendix 1** for the list of butterfly species observed and their characteristics.

Table 1. The criteria used for the classification of the butterfly species into generalists, specialists, or intermediates.

	Voltinism	Uni- or bivoltine	Multivoltine (more than bivoltine)
Larval resource breadth		(seasonal specialist)	(seasonal generalist)
Feeding specialist† (Oligophagous)		Specialists	Intermediates
Feeding generalist† (Polyphagous)		Intermediates	Generalists

^asee text for exact criteria.

The theoretical predictions of the relationships between the degree of disturbance and generalists and specialists

According to the generalist/specialist concept, the following relationships can be expected among the degree of disturbance and life history characteristics. The degree of disturbance and voltinism (number of generations) are positively related; multivoltines are associated with more disturbed (unstable) habitats, whereas oligovoltines are associated with less disturbed (stable) habitats. In addition, the relationship between the degree of disturbance and food niche width is also positive; diet generalists are associated with more disturbed (unstable) habitats, while diet specialists are associated with less disturbed (stable) habitats.

Thus, the concept predicts that the relationship between the degree of disturbance and species richness (the number of species) is positive for the generalist species (with multivoltinism and polyphagy), and is negative for the specialist species (with oligovoltinism and oligophagy). In other words, as the degree of disturbance increases, the number of generalist species increases, whereas the number of specialist species decreases.

RESULTS

Relationship between the degree of human disturbance and butterfly species diversity or butterfly species richness

There was a highly significant positive correlation between the order of census routes based on decreasing human disturbance (see the section of "Study Area") and butterfly species diversity (H') (**Fig. 1a**; Spearman's rank correlation coefficient, $r_s = 0.983$, $P < 0.01$). Also, a significantly positive correlation was recognized between decreasing human disturbance and butterfly species richness (the total number of species in a community) (**Fig. 1b**; $r_s = 0.867$, $P < 0.01$).

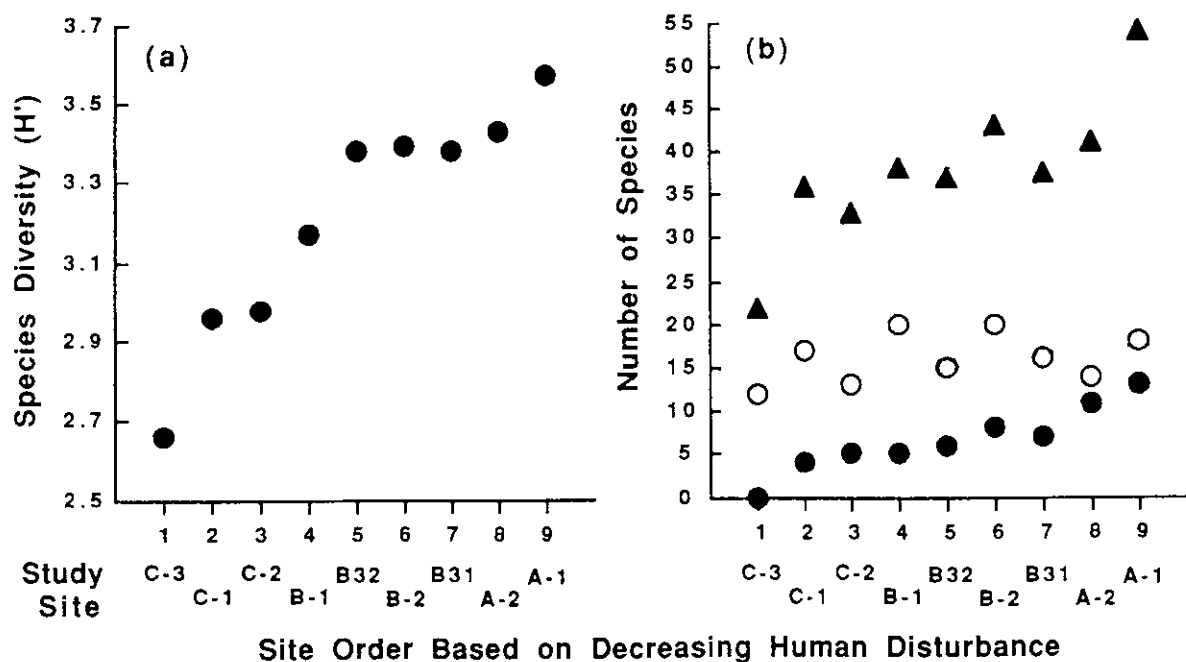


Fig. 1. Relationships of (a) species diversity (H'), and (b) the number of species in a community with the order of census routes based on decreasing human disturbances for nine butterfly communities. (a) $r_s = 0.983$, $P < 0.01$, (b) \blacktriangle : total no. of species ($r_s = 0.867$, $P < 0.01$); \circ : no. of generalist species ($r_s = 0.351$, $P > 0.05$); \bullet : no. of specialist species ($r_s = 0.966$, $P < 0.01$).

Relationship between the degree of human disturbance, and the number of generalist or specialist species in a community

A highly significant positive correlation was detected between the order of decreasing human disturbance and the number of specialist species in a community (**Fig. 1b**; $r_s = 0.966$, $P < 0.01$). But, the relationship between the site order and the number of generalist species in a community was not significant (**Fig. 1b**; $r_s = 0.351$, $P > 0.05$). The numbers of generalist species in a community were relatively constant among the communities irrespective of the degree of human disturbance.

Relationship between butterfly species richness or diversity, and the number of generalist or specialist species in a community

Butterfly species richness (the total number of species) was significantly and positively correlated with the number of specialist species in a community ($r = 0.916$, $t = 6.041$, $P < 0.001$), but not with that of generalist species ($r = 0.643$, $t = 2.221$, $P > 0.05$) (**Fig. 2**). As well, species diversity (H') was significantly and positively correlated with the number of specialist species in a community ($r = 0.935$, $t = 6.975$, $P < 0.001$), but not with that of generalist species ($r = 0.485$, $t = 1.467$, $P > 0.05$). These results suggest that the differences in the butterfly species richness and diversity in each community were more dependent on the number of specialist species than generalists in each community.

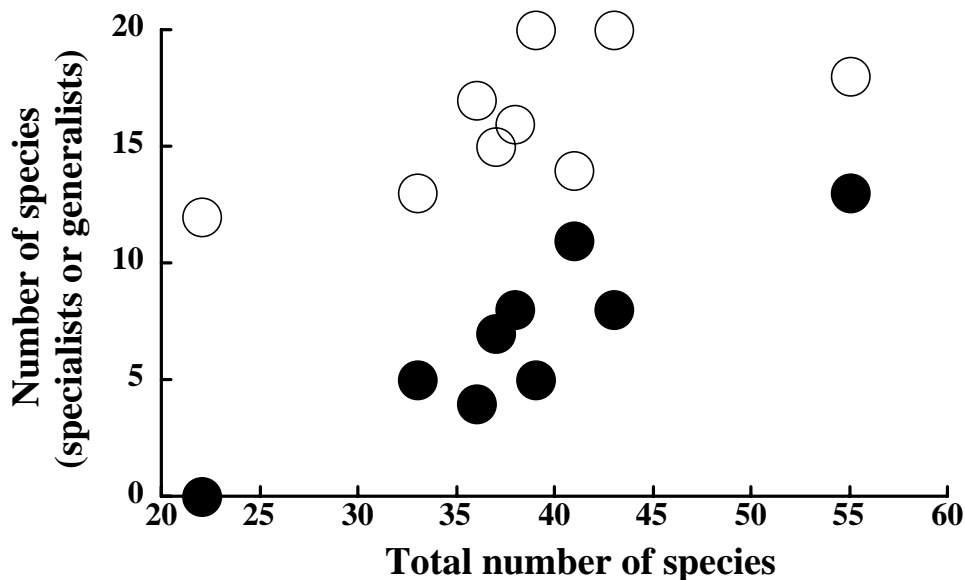


Fig. 2. Relationship of the number of generalist or specialist species in a community with species richness (the total number of species) for nine butterfly communities. : generalists ($r = 0.643$, $P > 0.05$); : specialists ($r = 0.916$, $P < 0.001$).

The distribution patterns of generalist and specialist species among the communities

Figure 3 shows the frequency distributions of generalist and specialist species against the number of census routes in which each species was observed during the period. For example, seven species of specialists were present only in one route, and eight species of generalists were observed in all nine census routes. Kolmogorov-Smirnov two sample test showed a highly significant difference between the two distributions ($D = 0.641$, $\chi^2 = 15.103$, $P < 0.001$). These results show that generalists are widely distributed throughout the study areas, but specialists are locally restricted.

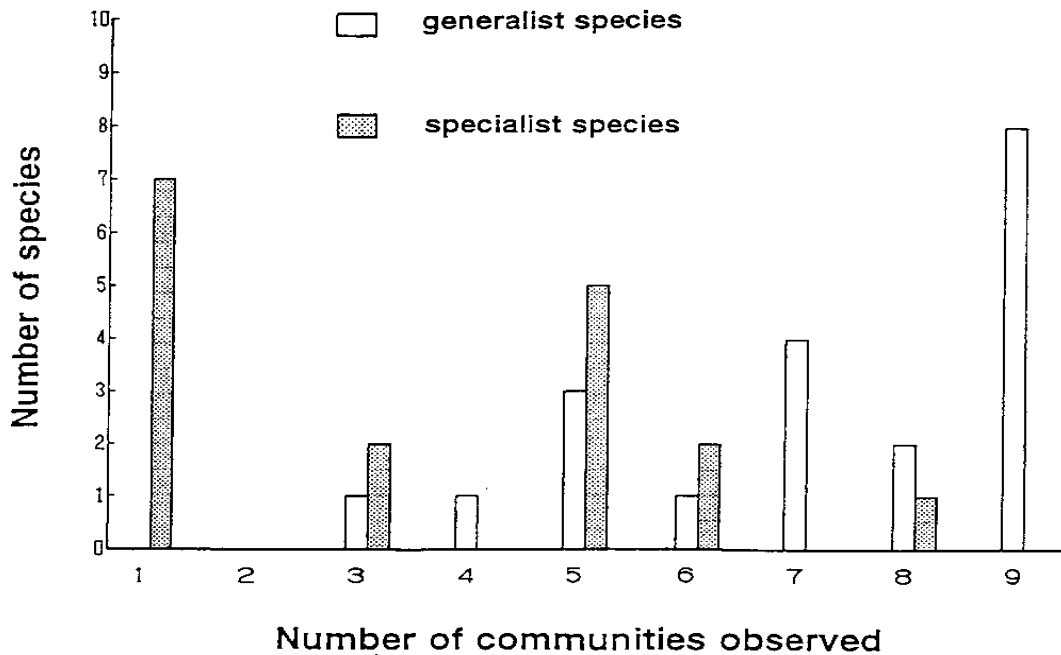


Fig. 3. Frequency distributions of generalist and specialist butterfly species against the number of communities (i.e., census routes) in which they were found.

The characteristics of generalist and specialist species at the community level

Figure 4 shows three typical examples of species-relative abundance curves. The ranks of generalist species within a community were usually higher (more important) than those of specialists. In particular, higher rank position of generalists in a community was detected even in the less disturbed sites such as A-1 and A-2.

The same tendency was also recognized when the data of all census routes were combined (**Fig. 5**). The mean value of the overall monthly mean densities (i.e., the mean of monthly mean densities at nine routes) of all generalist species (0.508/100 m) was significantly higher than that of all specialists (0.287/100 m; $t = 2.503$, $P < 0.05$).

Although the values were not significantly different ($t = 1.280$, $P > 0.05$), the mean value of coefficient of variations (C.V.) of monthly mean population densities among nine routes was higher in generalists (67.37) than in specialists (54.18). The coefficient of variation of monthly mean densities per species among the nine routes was larger in generalists (50.93) than in specialists (45.14) (**Fig. 6**). This means that the population density per species of generalists was rather variable among census routes, while that of specialists was relatively constant. **Table 2** summarizes those results stated above.

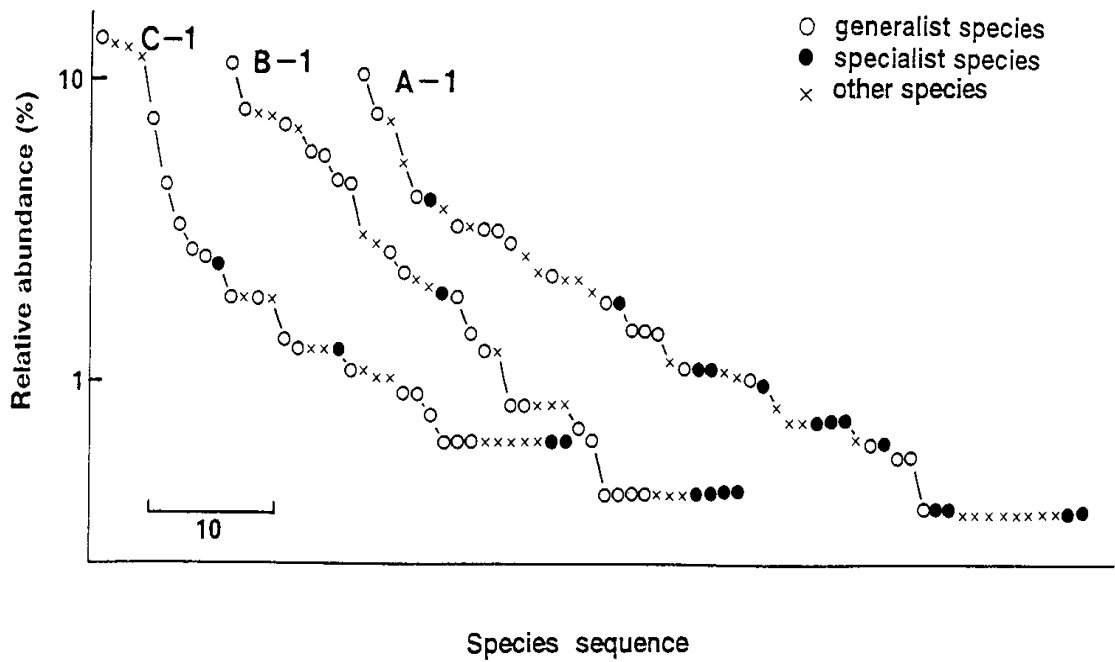


Fig. 4. Examples of species-relative abundance curves in three different butterfly communities.

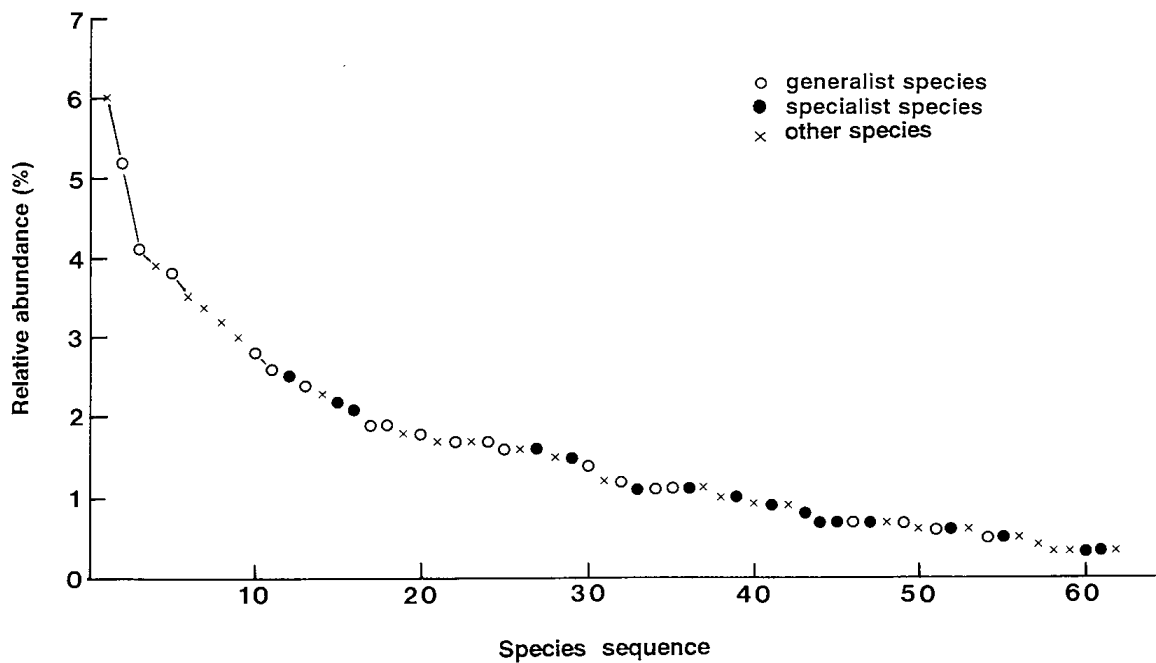


Fig. 5. A species-relative abundance curve for all 62 butterfly species observed in the present study when nine butterfly communities are pooled.

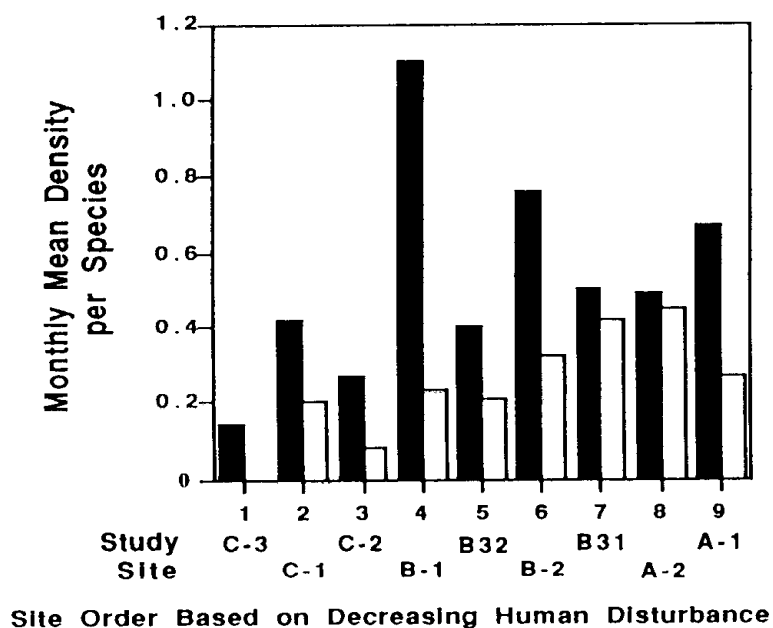


Fig. 6. Fluctuations in the monthly mean density per species of generalists () and specialists () among nine butterfly communities.

Table 2. Comparisons of the observed characteristics between generalist and specialist species at the community level.

	generalists	specialists
Distribution pattern	Wide and continuous	Locally restricted and fragmented
Population density	High	Low
Status (relative position) in a community	High dominant spp.	Low rare spp.
Spatial variation in density per species	Large	Small

DISCUSSION

Relationship between human disturbance, butterfly community structure and biodiversity

In the present study, I found several important patterns with respect to butterfly community structure and biodiversity in a gradient of human disturbance. First, both the butterfly species diversity (H') and the species richness (the total number of species) in a community were highly correlated with route order based on decreasing human disturbance (**Fig. 1**). Increasing species diversity and species richness closely corresponded to decreasing degrees of human disturbance. This result concurs with one general hypothesis for the determination of species diversity; more stable and predictable environments with less

disturbance (which allow evolution of fine specialization and narrow niches) promote high species diversity, whereas unstable and unpredictable ones with frequent disturbance (which demand broad tolerance limits and broad niches) result in low species diversity (e.g., Pianka 1966, 1988; Margalef 1968; Odum 1971; MacArthur 1972; Giller 1984; Ehrlich and Roughgarden 1987). However, since the butterfly community in route A-1, which was the least disturbed area in the present study, has not yet reached its climax stage, but rather appeared to be in a middle stage of ecological succession, we cannot, at present, reject the Connell's "Intermediate Disturbance hypothesis" (1978, 1979) which states that a community is of simple structure and low diversity under frequent, large disturbance, and the greatest diversity of the community occurs at intermediate levels of disturbance before the community moves to equilibrium with infrequent, small disturbances. Nor can we reject the concept of "ecological succession" that the highest diversity often occurs at pre-late (pre-climax) stages of succession (Whittaker 1972; Odum 1983, 1989; Giller 1984; Sousa 1984). To examine this possibility, more detailed study on the equilibrium and climax community under conditions with less frequent and smaller disturbances is needed.

Second, the route order based on decreasing human disturbance was strongly correlated with the number of specialist species in a community, but not with that of generalists (**Fig. 1b**). In addition, both the butterfly species richness (the total number of species in a community) and species diversity (H') were more dependent on the specialists than on the generalists (**Fig. 2**). The positive relationship between the decreasing degrees of human disturbance and the increasing number of specialists in a community can be explained well by the above mentioned hypothesis for the determination of species diversity. In addition, it is usually predicted that the increase in human disturbance (the impact of man) in a given habitat promotes a decrease in its host plant species diversity (poor numbers of host plant species), and as a result, will not allow specialists characterized by the exploitation of specialized host plants species to exist in the habitat. In contrast, generalists with a broad larval diet breadth can successfully establish in a variety of habitats, irrespective of the extent of its host plant species diversity. In fact, an almost constant number of generalist species was usually present, irrespective of the degree of human disturbance (**Fig. 1b**). However, the view that more generalists prevail mainly in unstable and/or unpredictable habitats with relatively frequent, large disturbance can be clearly dismissed in the present study.

How can we interpret this result? One possible explanation is that, as stated in the section of "Study area", there were open and light, so relatively unstable spaces along the census route in all study sites, even in ones predominated by secondary forest such as A-1 and A-2. This situation may have enabled nearly constant number of generalist species to exist in all study sites. In addition, the modern disturbance theory including the

patch-dynamics concept (e.g., Connell 1978, 1979; Huston 1979; White 1979; Sousa 1979 1984; Pickett and White 1985; Begon *et al.* 1990) can provide another possible explanation. According to the theory, natural disturbance that opens up gaps for colonization by species that are unable to survive in an undisturbed community, is common in all kinds of community (Begon *et al.* 1990), and all natural communities are usually spatially heterogeneous (Sousa 1984). Indeed, even stable climax communities such as tropical rain forests have an internally heterogeneous structure. They comprise a mosaic of patches at different stages of ecological succession and are in a shifting mosaic steady state of dynamic equilibrium (Bormann and Likens 1979; Remmert 1991). These communities show the mixture of pioneer species (early successional, with high colonizing ability; usually more generalistic) and climax species (late successional, competitively stronger; usually more specialized) (Watt 1947; Forcier 1975; Whitmore 1984, 1989, 1990; Brokaw 1985; Hubbell and Foster 1986; Kricher 1989; Terborgh 1992). Periodic disturbance that promotes the spatial heterogeneity in a habitat and can result in catastrophic density-independent mortality, seems more frequent in the temperate zones than in the tropics (e.g., MacArthur 1972). In the present study area, the features mentioned above (i.e., a mosaic of patches at different stages of succession and the resultant spatial heterogeneity) were thought to characterize all the study sites, including such relatively stable and predictable ones as A-1 and A-2. This condition may allow the almost constant number of generalist species (with good colonizing and high dispersal abilities) to invade and settle in unstable and unpredictable patches (e.g., gaps and margins of forests in A-1 and A-2). Also, generalists by definition typically have broad tolerance limits and large niches (Pianka 1988). As a result, they have more flexible habitat requirements and can occupy various types of habitats. Therefore, as the present results show, the number of generalist species can be expected to saturate in a variety of habitats irrespective of habitat complexity.

In temperate regions, having a mixture of both generalists and specialists may play an important role in the maintenance of high species diversity in natural communities.

The characteristics of generalist and specialist species at the community level

In the present study, I found three correlates of the characteristics of generalist and specialist species at the community level. First, generalists had wide distribution, whereas specialists were locally restricted (**Fig. 3**). A similar tendency was also demonstrated in the concept of the taxon cycle (Wilson 1961; MacArthur and Wilson 1967; Ricklefs and Cox 1972, 1978; Pianka 1988; Ricklefs 1990). A species at the early stage of the taxon cycle (which almost corresponds to an *r*-strategic generalist) is widespread and occurs on many islands, while a species at the late stage of the taxon cycle (corresponding to

K-strategic specialist) becomes more restricted and its geographic range is fragmented. In fact, Wilson (1959) recognized that stage I ant species (corresponding to generalist) were evidenced by their expansion and continuous ranges. They occupied a wide range of habitats on the mainland. The difference in distribution patterns of generalist and specialist species observed in this study can be explained well by the operational definition of each strategist (see Pianka 1988). Typical generalist characteristics (e.g., broad tolerance limits, exploitation of more food types, flexible habitat requirements, and strong dispersal and colonizing abilities) allow them to occupy more habitats and to be distributed widely and continuously. On the other hand, the typical specialist characteristics (e.g., narrow tolerance limits, more specialized food types, very specific habitat requirements, and poor dispersabilities) would force them to rely on a particular habitat and to be locally restricted.

Second, generalists existed at higher population densities than specialists. As a result, the status (relative position) of generalists in a community was higher than that of specialists (**Figs. 4 and 5**). This result is perfectly consistent with Pianka's (1988, p. 254) argument. Such a difference in population levels between generalists and specialists is probably due to their reproductive potential and the niche breadths of the respective strategist. A high density of generalists may result from their high potential rates of increase evidenced by multivoltinism and wide niches (broad larval diet breadth). By contrast, a low density of specialists may result from their low reproductive ability and narrow niches. A related phenomenon, a positive correlation between local species abundance and regional distribution, has been detected. That is, widespread species are more locally abundant than geographically restricted species (Hanski 1982; Bock and Ricklefs 1983; Brown 1984; Lacy and Bock 1986; Bock 1987; Schoener 1987; Gaston 1988; Gaston and Lawton 1988a, 1988b; Ricklefs 1990; Cockburn 1991). Brown (1984) interpreted this correlation as the result that widespread species are more flexible in their use of resources (i.e., more generalistic) than restricted species. In the present study, most of generalist species showed widespread distributions and higher population densities, while most of the specialists had restricted distributions and lower densities (**Figs. 3, 4 and 5**). These results concur well with the above positive distribution-abundance relationship. Thus, the result can explain the positive distribution-abundance relationship quantitatively in terms of the generalist/specialist concept and can strongly support the Brown's (1984) interpretation for the relationship mentioned above.

Third, the density per species of generalists was more variable among the communities (census routes) than that of specialists (**Fig. 6**). The habitat condition of generalists was likely to vary from route to route in response to the degree of disturbance (which almost corresponds to the habitat template; Southwood 1988), and as a result, they

must have been more variable in space because of their potential for population explosions in favorable habitats. On the other hand, specialist habitats with a constant suitability (corresponding roughly to the *K*-habitat template; Southwood 1988) seem to result in spatially less variable specialist densities.

Relationship between the generalist/specialist concept and the *r/K* concept

The intrinsic rate of natural increase (*r*) is one of the better indicators of an organism's position along *r-K* selection continuum (Pianka 1988), and is more influenced by generation time than fertility (Cole 1954; Ohsaki 1982). We know that the generation time is strongly and negatively correlated with both the value of *r* (e.g., Smith 1954; Pianka 1970, 1988; Heron 1972; Southwood 1981; Stiling 1992) and voltinism (number of generations per year). Thus, the intrinsic rate of natural increase (*r*) is positively correlated with voltinism, and consequently, there is a general correlation of multi- and univoltinism with higher *r* (*r*-selection) and lower *r* (*K*-selection), respectively (e.g., Shapiro 1975). In a related argument, Cody and Diamond (1975) state that *K*-selected butterfly species have a single annual peak flying time, while *r*-selected species have several peaks.

In contrast, it is suggested that *K*-selecting environments allow finer specialization and narrower niches, whereas *r*-selecting environments demand generalization and broader niches (e.g., Giller 1984; Pianka 1988). Thus, *r*- and *K*-selection are closely related with generalization and specialization, respectively (e.g., Levins 1968; Margalef 1968; Odum 1971, 1983; Shapiro 1975; Wilson 1975; Conway 1981; Smith 1990).

Based on these arguments, the present "generalists" (species with multivoltinism and broad larval diet breadth) and "specialists" (species with oligovoltinism and narrow larval diet breadth) can correspond well to "*r*-type species" and "*K*-type species", respectively. Thus, we can also interpret these results based on the generalist/specialist concept on the basis of the concept of *r*- and *K*-strategists, too. We may replace all the words "generalists" in the present study with *r*-strategists, and "specialists" with *K*-strategists (MacArthur and Wilson 1967; Pianka 1970, 1988; Gadgil and Solbrig 1972; MacArthur 1972; Southwood *et al.* 1974; McNaughton 1975; Wilson 1975; Southwood 1977, 1981; Horn 1978; Conway 1981; Horn and Rubenstein 1984; Begon *et al.* 1990).

I conclude that the concept of generalist and specialist strategy (MacArthur and Levins 1967; Levins 1968; MacArthur 1972; Pianka 1988), or *r*- and *K*-strategy, is robust, helpful, and useful in understanding the structure and function of natural communities. The concept is well worth applying to the analyses of biodiversity and community structure.

Chapter 2. Reexamination of the butterfly community patterns based on the generalist/specialist concept along a grassland habitat gradient of human disturbance in a different region

INTRODUCTION

In Chapter 1, I studied the butterfly communities in several types of habitats (secondary forest, farmland, and city parks) in and around Tsukuba City, central Japan, and analyzed the community structure along a gradient of human disturbance by applying the generalist/specialist (r/K) concept. The study clearly showed the systematic changes of the community structure along the gradient and found that the degree of human disturbance at each site was significantly correlated with species diversity, total species richness, and specialist species richness, but not with generalist species richness, of the butterfly community. Also, the generalist species had locally wider distributions and larger population sizes with more spatial variation than the specialists. These community patterns were mostly consistent with the prediction of the concept, suggesting that the concept has good explanatory powers for the understanding of community structure, and thus that the patterns obtained are of much ecological importance with a potential of generality and robustness applicable to other natural communities. Another point of importance in these patterns is that they are useful for reexamining the generality and robustness for the various types of butterfly communities.

Ecologically important community patterns must be those with generality and consistency applicable to a wide variety of ecological or natural communities, irrespective of the different types of component species, habitats, and localities where they exist, and also must be useful and helpful in the understanding of the community structure (MacArthur 1972). Thus, to verify the generality and robustness of the patterns found out through the analysis of a community structure, we need to examine whether those patterns are repeatedly detectable in the various types of natural communities in different regions or habitats (Begon *et al.* 1990, p. 614).

In this chapter, to examine the generality and consistency of the community patterns detected in Chapter 1 as just stated, and the usefulness of the generalist/specialist concept in the analysis of community structure, I again paid attention to human disturbance as an environmental gradient and applied the concept to analysis of the butterfly

communities in a considerably different habitat type (grassland) and in a distant region (the Asagiri Plateau near Mt. Fuji) from those of the previous study. The main goals in this chapter are (1) to search for patterns in the structure of grassland butterfly communities along a gradient of human disturbance in the light of the generalist/specialist concept, (2) to compare these patterns with those detected in the previous study (Chapter 1) and to confirm the consistency of the patterns, and (3) to infer the causes about the differences, if any, between the two studies.

MATERIALS AND METHODS

Data set analyzed

In the present study, I chose and analyzed a butterfly community data set (Sei 1986a, b) already published. The butterfly community data were collected as follows.

Study area: Five census routes (A, B, C, D, and E) were established in five different grassland areas with varying degrees of human disturbance on the Asagiri Plateau at the western foot of Mt. Fuji, Shizuoka Pref., central Japan. The design of the field studies used here makes it possible to distinguish the influence of human disturbance on butterfly communities from the effect of other physical factors affecting the distribution of butterfly species; that is, all five grassland areas were situated at an altitude of about 900 m and located within a range of 1.7 km from east to west and 2.4 km from north to south. The length of each census route was about 1 km. Detailed descriptions of each area studied are shown in **Table 1**.

Human disturbances detected in the study areas during the study period were mowing, fertilization, cultivation, trampling by humans or livestock grazing, etc. (**Table 1**). The magnitude and frequency of the disturbances in each study area are listed in **Table 1**. By comparing the type of disturbance and its magnitude and frequency among the study areas, I assumed that the extent of human disturbances increased qualitatively and quantitatively in the order of A, B, C, D, and E. Thus, for the following analyses, I ranked the degree of human disturbance of the census routes in increasing order, as follows: A(1), B(2), C(3), D(4), and E(5).

Census methods: The observations were made using a line transect method (Pollard 1977, 1984; Thomas 1983; Gall 1985; Pollard and Yates 1993). The transect counts were done twice a month during the adult flight season (from April to October, 1985), within the period from about 10:30 to 12:00 local time under fine weather conditions. Walking at a steady pace along a transect line, the species and the number of individuals were recorded for all adult butterflies sighted within a maximum distance of about 5 m. The observer captured by net those individuals that he could not identify by sight, and

released them after identification.

Table 1. Characteristics of study areas

Census route	Habitat type	Altitude (m)	Vegetation		Type of disturbance (frequency or magnitude)	Degree of disturbance
			Main component species	Dominant species		
A	Secondary natural grassland	900	<i>Miscanthus sinensis</i> <i>Hosta sieboldiana</i> <i>Cirsium japonicum</i> <i>Geranium krameri</i> <i>Astilbe microphylla</i> <i>Scabiosa japonica</i> <i>Patrinia scabiosaefolia</i> <i>Cirsium nipponicum</i>		Mowing (all of the area) (once a year)	Decreasing ↑ ↓ Increasing
B	Secondary natural grassland (including villa place)	870–890	<i>Miscanthus sinensis</i> <i>Aster ageratoides</i> <i>Artemisia vulgaris</i> <i>Scabiosa japonica</i> <i>Patrinia scabiosaefolia</i>	<i>Miscanthus sinensis</i>	Mowing (all of the area) (1–2 times per year)	
C	Vegetable field	890	<i>Brassica oleracea</i> ^a <i>Raphanus sativus</i> ^a <i>Plantago asiatica</i> <i>Artemisia princeps</i> <i>Trifolium repens</i> <i>Zinnia elegans</i> ^b <i>Cosmos bipinnatus</i> ^b	<i>Brassica oleracea</i> ^a	Mowing and cultivation (3–4 per year) Fertilization (4 per year)	
D	Cultivated meadow	900	Poaceae species ^c <i>Capsella bursa-pastoris</i> <i>Rumex</i> sp. <i>Humulus scandens</i> <i>Erigeron annuus</i> <i>Oenothera erythrosepala</i> <i>Trifolium repens</i> <i>Aster ageratoides</i>	Poaceae species ^c	Livestock grazing (10–12 times for 1–2 days per year) Trampling (by 500–600 cattle per year) Mowing (2–3 times per year) Fertilization (3–4 times per year)	
E	Golf course	940–960	<i>Zoysia japonica</i> ^d <i>Salvia officinalis</i> ^b <i>Taraxacum officinale</i> <i>Humulus scandens</i>	<i>Zoysia japonica</i> ^d	Heavy trampling [by 40000 people (players and caddies) per year] Intensive mowing (more than 15 times per year) Intensive fertilization (8–20 times per year)	

^aVegetable plant

^bDecorative plant

^cPasture plant

^dGolf lawn plant

Data analysis

I first calculated the adult butterfly density (number of adults observed/kilometer) for each species for each census route on each observation date. Then, to obtain the mean monthly density for each species for each census route, I averaged the two densities only when the butterfly species were found. Then I calculated the mean annual density averaging the mean monthly densities with more than 0. Exclusion of census periods when no butterflies were observed minimized the effect of different voltinism of butterfly species on the yearly abundance estimate (i.e., mean annual density). The average abundance (see **Appendix 2**) of each species over the five census routes was obtained by averaging the mean annual densities only where the butterfly species were found. Exclusion of census routes where no butterflies were observed minimized the effect of different distribution patterns (widespread or restricted) of butterfly species on the average abundance.

I analyzed the butterfly community structure using the following ecological parameters; mean annual population density, species richness, species diversity, species evenness, and dominance in each census route. Species richness was expressed by the

number of species recorded in each census route during the period. Species diversity was expressed by Shannon-Wiener function, $H' = -\sum_{i=1}^s p_i \ln p_i$, where s is the number of species recorded, and p_i is the proportion of the mean annual density of the i -th species. Species evenness was expressed by the Shannon equitability index, $J' = H' / \ln S$, where H' is the Shannon-Wiener function and S is the number of species recorded. Dominance was estimated by the McNaughton's dominance index, $DI = (n_1 + n_2)/N$, where $N = \sum_{i=1}^s n_i$, and n_1 and n_2 are the mean annual density of the 1st and 2nd dominant species, respectively.

The classification of the butterfly species into generalist and specialist species

Generalization and specialization must be defined with reference to particular axes (Futuyma and Moreno 1988). Following the previous study (Chapter 1), I classified the butterfly species into generalist or specialist based on their resource utilization patterns in two fundamental niche dimensions (time and food), which could be determined from the detailed information available in the literature.

First, I used voltinism (number of generations per year) as an indicator of the niche breadth in a seasonal time dimension. I thought of multivoltine (more than bivoltine) species as seasonal generalists, and oligovoltines (uni- or bivoltines) as seasonal specialists. Voltinism was based on Unno and Aoyama (1981), Fukuda *et al.* (1982, 1983, 1984a,b), and Sei (1986). Second, I used the degree of polyphagy (range of potential host plant species used by larvae) as an indicator of the niche breadth in a larval food dimension. I defined "species whose larvae had been reported to feed on ten or fewer plant species belonging to one taxonomic family" as larval feeding specialists, and "species the larvae of which feed on more than ten plant species belonging to one taxonomic family, or on a variety of host plants belonging to two or more taxonomic families" as larval feeding generalists. The degree of polyphagy (number of potential host plant species) was based on Endo and Nihira (1990) and Fukuda *et al.* (1982, 1983, 1984a,b).

Using the foregoing two axes, I classified the species belonging to both multivoltines (seasonal generalists) and larval feeding generalists into "generalist species" and those belonging to both oligovoltines (seasonal specialists) and larval feeding specialists into "specialist species." With this criteria, of 39 butterfly species reported, I classified 14 species (35.9%) as generalist species and 12 species (30.8%) as specialist species. The remaining 13 species (33.3%) were in the intermediate category; these were species with either multivoltinism and larval feeding specialty, or oligovoltinism and larval feeding generality. Following Chapter 1, I did not take these remaining species into account when I discussed the result in terms solely of the generalist/specialist concept.

See **Appendix 2** for the list of butterfly species observed and their characteristics.

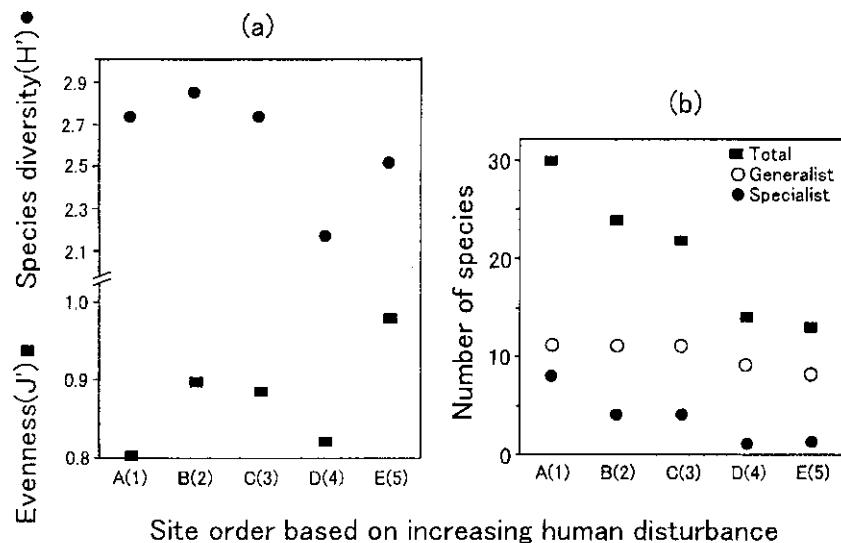
RESULTS

Relationship between the degree of human disturbance and butterfly species diversity or butterfly species richness

The values of species diversity (H'), species richness (the total number of species), species evenness (J'), and dominance index (DI) of each census route are summarized in the **Appendix 2**. The order of census routes based on increasing human disturbance was only weakly correlated with butterfly species diversity (H') (Spearman's rank correlation coefficient; $r_s = -0.800$, $P = 0.10$) (**Fig. 1a**).

Also, the correlation between the route order and species evenness (J') was not significant ($r_s = 0.600$, $P > 0.10$) (**Fig. 1a**). Butterfly species richness (the total number of species in a community) was highly significantly correlated with the route order of increasing human disturbance ($r_s = -1.000$, $P = 0.01$) (**Fig. 1b**).

Fig. 1. Relationships of (a) species diversity (H') and evenness (J') and (b) the number of species in a community with the order of census routes based on increasing human disturbances for five butterfly communities. **a** ●, species diversity (H') ($r_s = -0.800$, $P = 0.10$); ■, evenness (J') ($r_s = 0.600$, $P > 0.10$). **b** ■, total no. of species ($r_s = -1.000$, $P = 0.01$); ○, no. of generalist species ($r_s = -0.894$, $P < 0.10$); ●, no. of specialist species ($r_s = -0.949$, $P < 0.05$)



Relationship between the degree of human disturbance and the number of generalist or specialist species in a community

A significant negative correlation was detected between the route order of increasing human disturbance and the number of specialist species in a community ($r_s = -0.949$, $P < 0.05$) (**Fig. 1b**). However, the numbers of generalist species in a community were rather constant among the communities (**Fig. 1b**), and the relationship between the route order and the number of generalist species in a community was only weakly significant ($r_s =$

-0.894, $P < 0.10$).

Butterfly species richness (the total number of species) was more correlated with the number of specialist species in a community ($r = 0.976$, $P < 0.01$) than that of generalist species ($r = 0.893$, $P < 0.05$), although the both correlations were positive and significant (**Fig. 2**). These results suggest that the variation in butterfly species richness among the communities was accounted for more by the number of specialist species than generalists in each community.

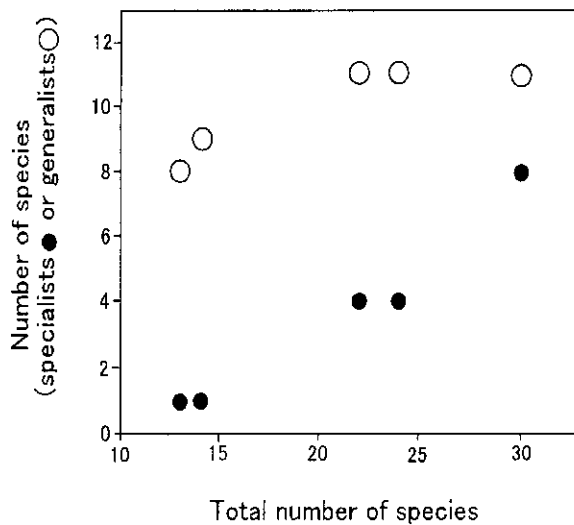


Fig. 2. Relationship of the number of generalist or specialist species in a community with butterfly species richness (the total number of species) for five butterfly communities. ○, generalists ($r = 0.893$, $P < 0.05$); ●, specialists ($r = 0.976$, $P < 0.01$)

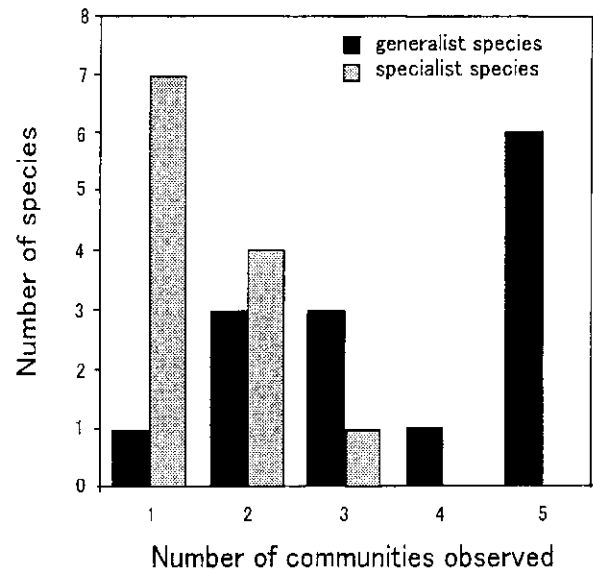


Fig. 3. Frequency distributions of generalist (dark bars) and specialist (light bars) butterfly species against the number of communities (i.e., census routes) in which they were found

The distribution patterns of generalist and specialist species among the communities

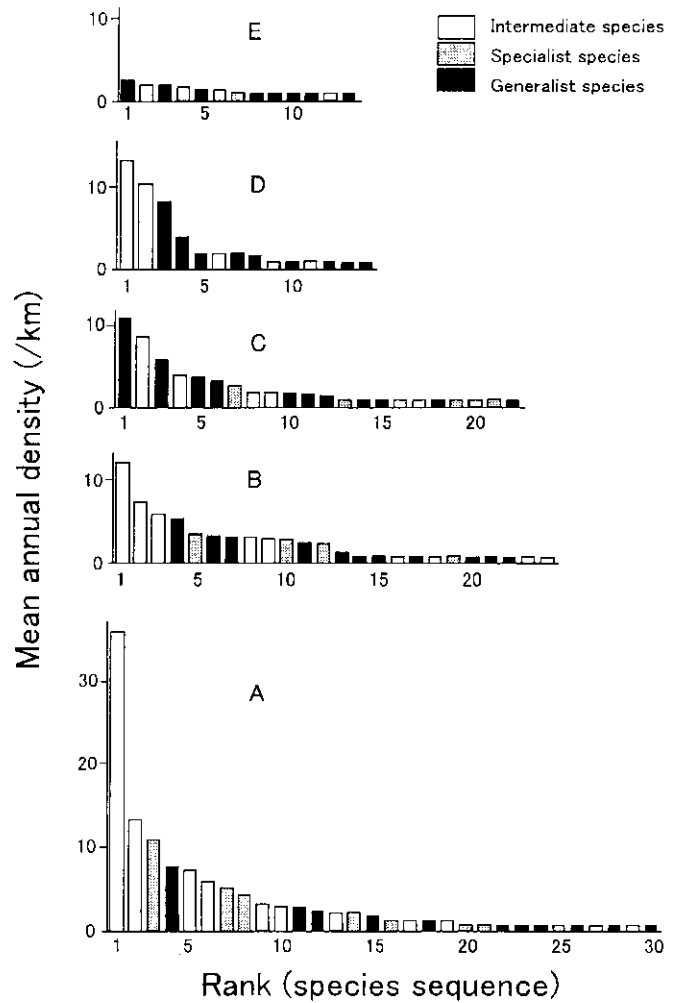
Figure 3 shows the frequency distributions of generalist and specialist species against the number of census routes in which each species was observed during the period. For example, seven species of specialists were present only in one census area, and six species of generalists were observed in all five areas. A Kolmogorov-Smirnov two sample test showed a highly significant difference between the two distributions ($D = 0.631$, $\chi^2 = 10.288$, $P < 0.01$). These results show that generalists are widely distributed throughout the study areas, but specialists are locally restricted.

Comparison of the characteristics between generalist and specialist species at the community level

Figure 4 shows the rank (species sequence)-abundance (mean annual density) relationships for five butterfly communities. The mean rank order within a community was higher (more important) for generalist species than for specialists in the more disturbed areas, E (generalists: $\bar{x} = 5.38$, specialists: $\bar{x} = 7.00$), D (generalists: $\bar{x} = 6.78$, specialists: $\bar{x} =$

9.00),

Fig. 4. Rank (species sequence)–abundance (mean annual density) diagrams for five grassland butterfly communities



and C (generalists: $\bar{x} = 8.91$, specialists: $\bar{x} = 11.50$). On the other hand, the opposite trend was recognized between their mean rank orders in the less disturbed areas, A (generalists: $\bar{x} = 16.27$, specialists: $\bar{x} = 13.38$) and B (generalists: $\bar{x} = 11.36$, specialists: $\bar{x} = 10.00$).

The mean density of all generalist species over five census routes (1.917/km) was not significantly different from that of all specialists (2.113/km) ($t = 0.296$, $P > 0.05$). Also, the mean values of coefficient of variations (CV) of mean annual densities among five census routes were not significantly different between all generalists ($\bar{x} = 29.062$) and all specialists ($\bar{x} = 28.250$) ($t = 0.062$, $P > 0.05$). These results show that both population size and spatial population variability were not different between generalist and specialist species.

The mean of mean annual densities of the specialist species observed only in one census area (1.071/km) was significantly less than that of specialists observed in two or more census areas (3.570/km) ($t = 2.899$, $P < 0.05$). Thus, the specialist species may be further divided into "restricted and less abundant specialists" and "wide-ranging and

abundant specialists."

DISCUSSION

I analyzed the grassland butterfly communities in a manner similar to that employed in the previous chapter. **Table 2** summarizes the present results together with the previous results (Chapter 1) for comparison.

Significance of the classification into generalist and specialist groups

To analyze the butterfly communities, I classified their component butterfly species into three groups (generalist, specialist, and intermediate) according to their voltinism and larval host plant. In the Tsukuba area of the previous study (Chapter 1), which is located about 160 km east of the present study area, 62 butterfly species were classified into three groups, roughly one-third each (**Table 2**). Applying the same criteria, I could classify 39 species found in the present area into three groups, again with roughly one-third each. The fewer total number of species found in the present area reflects the difference in habitat conditions in the two study areas.

It is quite noteworthy that all 14 generalist species in this study were found also in the Tsukuba area. On the other hand, of the 12 specialist species in this study, only 3 species were observed in the Tsukuba area. This result shows that the classification of butterfly species into generalist and specialist groups based on their voltinism (seasonal time dimension) and potential larval host plant (food dimension) can be also well justified in terms of their geographic distribution pattern (large scale spatial dimension), not only in a local scale but also geographically.

Superficially, the present generalist and specialist classification of the species may look similar to core and satellite species in the metapopulation analysis (Hanski 1982). However, there is a fundamental difference in the two classifications. My classification is based on a priori assumption based on the voltinism and larval food resource of the butterflies. On the other hand, core and satellite species are often named a posteriori; typically, the data are first analyzed in a similar manner as my **Fig. 3** but without a priori classification, and then the widespread species and locally restricted species are classified into core and satellite species, respectively. Thereafter, the characteristics of these two groups are explored (Cornell 1985; Collins and Glenn 1991; Pollard and Eversham 1995). I believe that a priori classification and analytical approach based on the generalist/specialist concept provides more predictive power for the analysis of community patterns.

Relationship between the degree of human disturbance and butterfly community

structure (species diversity and species richness)

The previous study (Chapter 1) showed that the degree of human disturbance was highly

Table 2. Comparison of the various community characteristics between the present study and the Tsukuba area

	Tsukuba area	This study	Common ^a
No. of species found	62	39	24
No. of generalist species	20 (32%)	14 (36%)	14
No. of specialist species	17 (27%)	12 (31%)	3
No. of intermediate species	25 (40%)	13 (33%)	7
Human disturbance vs. H'	–	(–)	
Human disturbance vs. species richness	–	–	
Human disturbance vs. J'	–	ns	
Human disturbance vs. no. of generalist species	ns	(–)	
Human disturbance vs. no. of specialist species	–	–	
Species richness vs. no. of generalist species	(+)	+	
Species richness vs. no. of specialist species	+	+	
Spatial distribution (generalists)	Wide	Wide	
Spatial distribution (specialists)	Restricted	Restricted	
Population density	G > S	ns	
Spatial variation	(G > S)	ns	
Rank order	G > S	G > S (Disturbed areas) S > G (Undisturbed areas)	

G, generalist species; S, specialist species

+, significant ($P < 0.05$) positive correlation; (+), weak ($P \leq 0.10$) positive correlation; –, significant ($P < 0.05$) negative correlation; (–), weak ($P \leq 0.10$) negative correlation; ns, no correlation

^a Common, no. of common species (i.e., no. of species found in both studies)

correlated with both butterfly species diversity (H') and butterfly species richness (the total number of species in a community) (**Table 2**). In the present study, however, the degree of human disturbance was only weakly correlated with butterfly species diversity (H') (**Fig. 1a**), although it was strongly correlated with butterfly species richness (**Fig. 1b**). This finding is closely related to the positive, but non-significant, relationship between the degree of human disturbance and species evenness (J') (**Fig. 1a, Table 2**). This positive trend was caused mainly by both the highest evenness in the most disturbed area, E, due to the absence of extremely dominant species (also revealed by its lowest dominance index), and the lowest evenness in the least disturbed area, A. The high degree of equitability in the highly disturbed area can be attributed largely to its low resource availability (which provides smaller niches), caused by the extremely high degree of human disturbances. This situation may not have allowed dominant species to prevail in the area. Thus, the previous findings that the higher the disturbance, the lower the species diversity, may not apply when the disturbance is too frequent and too high, as in route E in this study.

In the present study, the degree of human disturbance was strongly correlated with the number of specialist species in a community, but only weakly with that of generalists (**Fig. 1b**). In addition, butterfly species richness was significantly correlated with both the number of specialist and generalist species in a community (**Fig. 2**). These results are

generally consistent with the patterns detected in the previous study (**Table 2**). The study area of the previous study consisted of secondary forest, farmland, and newly designed city parks, while the present study areas covered various types of grasslands. The fact that almost identical community patterns were detected in the two distant and completely different habitat localities deserves special attention. This result strongly suggests that the aforementioned patterns of community structure along a gradient of disturbance are both robust and general.

The negative correlation between the degree of human disturbance and the number of specialist species in a community (**Fig. 1b**) can be entirely accounted for in terms of the generalist/specialist concept (MacArthur and Levins 1967; Levins 1968; Pianka 1988). Generalist/specialist concept predicts that generalists will be advantageous in fluctuating environments, whereas specialists should be found in relatively constant environments. The present analysis also demonstrates that the major factor determining butterfly species richness was the number of specialist species in a community (**Fig. 2**). On the other hand, more generalist species were present in the more species-rich communities of less disturbed (thus more stable) habitats (**Fig. 2**). This positive correlation, though weak, between butterfly species richness and the number of generalist species in a community contradicts the generalist/specialist concept but has received little attention so far. One possible explanation may be derived from the patch-dynamics concept of community structure (e.g., Pickett and White 1985), as discussed in detail in the previous chapter.

In the present study, I tried to explain the patterns of adult butterfly distribution in terms of the environmental disturbance, but not in terms of the larval host plant distribution. Erhardt (1985) found that various types of human disturbances have strong influences on species richness both of Lepidoptera and of vascular plants. Similarly, Novotny (1995) showed that the difference in disturbance intensity among various habitats was reflected by differences in the life history syndromes of both plants (ruderal vs. competitive and stress-tolerant) and leafhoppers. Thus, in the present study, it is possible that the increase in human disturbance in the habitat promoted a decrease in its habitat components for butterflies (e.g., host plants) and, as a result, did not allow many butterfly species (especially specialists) to exist in the habitat. In the future, further work on the relationships among the habitat components of butterflies, the degree of disturbance, and butterfly community structure are greatly needed to understand the proximate (direct) factors affecting the differences in butterfly community structure among different habitats.

The characteristics of generalist and specialist species at the community level

The present trend that generalist species had wide distribution, while specialist species were locally restricted (see **Fig. 3**), was perfectly consistent with the finding in the previous study.

This result suggests that the repeated distribution pattern of the two species groups is a consistent one, detected widely across different habitat types and regions.

The previous study showed that the ranks of generalist species within a community were higher (more important) than those of specialists, irrespective of the degree of human disturbance. In this study, however, higher rank position (predominance) of specialists in a community was detected in less disturbed (thus more constant) areas such as A and B (see **Fig. 4**). On the other hand, the previous study also showed that generalist species existed at higher population densities and had larger spatial variation in density per species than specialists. In the present study, however, there were no such differences either in the population density or in the spatial population variability between the two species groups. This difference probably was the result of the present habitat condition, which has a shorter growing season at higher altitude compared with the study area of the previous study. Under such a habitat condition, it is expected that the population growth rate (r) of generalists will decrease, leading to lower population size, whereas the efficiency of resource utilization by specialists will increase, leading to higher population size. Thus, the community patterns detected in the previous study based on the generalist/specialist concept in long growing season environments may not necessarily apply to natural communities in environments with a short growing season. It is quite important to take into account environmental quality when we try to understand community structures in terms of the generalist/ specialist concept.

Chapter 3. Analyses of butterfly community structure and composition through multivariate approaches and the concept of generalist/specialist strategies, and conservation implications

INTRODUCTION

In Chapter 1, I analyzed the butterfly communities in nine types of habitats different in their degrees of disturbance, in and around Tsukuba City, central Japan. Prior to data analyses, I classified the component species into three categories, generalist, intermediate, and specialist, based on their voltinism and larval diet breadth according to the generalist/specialist (*r/K*) concept. Then I analyzed the community structure along a gradient of human disturbance on the basis of the species classification. I found several ecological community patterns based on the concept, and clearly showed the systematic changes of the community structure along the gradient and the differences in the ecological characteristics between generalist and specialist species at the community level. The community patterns obtained were mostly consistent with the predictions of the concept, suggesting that the concept has good explanatory powers for the understanding of community structure.

In Chapter 2, to verify the generality and consistency of those community patterns and the usefulness of the generalist/specialist concept in the analysis of community structure, I analyzed the butterfly community structure along a disturbance gradient in the same manner as that employed in Chapter 1, using the community data collected in a different habitat type and in a distant region (the Asagiri Plateau near Mt. Fuji) from those in Chapter 1. The analyses confirmed the consistency and robustness of most community patterns detected in Chapter 1 and the high applicability of the generalist/specialist concept to the analysis of butterfly community structure.

However, to evaluate the validity and generality of species classification based on the generalist/specialist concept (i.e., a priori approach) and the community patterns observed in those studies more objectively, we further need to analyze the same data set by different approaches.

In this chapter, to confirm whether the approach based on the generalist/specialist

concept employed in the previous chapters is appropriate or not, and to obtain new insight into butterfly community structure and composition, I reanalyze the same butterfly community data used in Chapter 1 by multivariate analyses. In this chapter, by combining a priori species classification and multivariate approach, I try to understand the butterfly community structure more deeply than in the previous studies. In addition, I discuss the relevance of the results revealed in the present study to local butterfly conservation.

MATERIALS AND METHODS

Data set analyzed

In this study, I used the data collected in my previous study (Chapter 1) (see **Appendix 1**). The details of the census areas and routes within, and the census methods were described in Chapter 1.

I chose three areas (areas A, B and C) in and around Tsukuba City, Ibaraki Prefecture, central Japan. The degree of human disturbance of the three areas increased from area A to C. I established nine census routes in these areas. Based on my observation, I ranked and numbered the degree of human disturbance of the census routes in the following decreasing order; C-3(1), C-1(2), C-2(3), B-1(4), B-3-2(5), B-2(6), B-3-1(7), A-2(8), and A-1(9).

Data analysis

Data matrix (62 (species) by 9 (census routes)) based on the population abundance (monthly mean density) of each species at each census route (see **Appendix 1**) was subjected to the multivariate analyses. Species grouping and ordination were carried out by principal components analysis (PCA) based on the variance-covariance matrix, using the program NTSYS, ver. 2.02J (Rohlf 2000). The validity of the species grouping was also examined by the cluster analysis (unweighted pair-group method using arithmetic average (UPGMA)) based on 62 by 62 Euclidean distances matrix, using the program NTSYS, ver. 2.02J (Rohlf 2000).

To examine the relationship between the species groupings based on the generalist/specialist concept and those on the multivariate analyses, I classified the component butterfly species into generalist, intermediate, or specialist species based on their voltinism (seasonal time dimension) and potential larval diet breadth (food dimension). The criteria used for the species classification are detailed in the Chapter 1, and the classified category of each component species is seen in **Appendix 1**. The examination of the biological characteristics (larval hostplant and adult habitat types) of butterfly species was based on Unno and Aoyama (1981) and Fukuda et al. (1972, 1982, 1983, 1984a, b).

To clarify which species group discriminated in the present study was associated

with high local extinction probability, I counted the number of Red List species included in each species group. For this analysis, I used the Red Data list of butterflies in Ibaraki Prefecture in the year 1992 (Yata and Ueda 1993), when 12 years have passed since the data collection was performed. Registered species on the Red Data list are shown in **Appendix 1**.

RESULTS

Species ordination by PCA analysis

Distribution of the butterfly species observed on major- and minor-axes plane by PCA based on the variance-covariance matrix is shown in **Fig. 1**. Intuitively, we notice that there are two major distinct groups: One tightly packed species group (hereafter refer to as I) distributes on the left side of the first axis, and another species group (hereafter refer to as II) distributes sparsely on the right side of the first axis. All specialist butterfly species belong to group I. On the other hand, intermediate and generalist species are both divided into the two distinct groups, each of which corresponds to either group I or II (hereafter referred to as intermediate I or II, or generalist I or II).

The cumulative contribution by the first and second principal components was 76.0 % (**Table 1**). In the first axis, the values of eigenvectors were all positive, and the routes B-1 and B-2, which showed higher total population abundances, had higher eigenvector values (> 0.5), while the routes C-3 and C-2, which showed lower total population abundances, had lower eigenvector values (< 0.15) (**Table 1**). Thus, these results suggest that the first axis reflects total population size of the butterfly species. In the second axis, the eigenvector value of only route B-1, which was the areas of arable fields almost without trees and woods, was negative (**Table 1**). Other routes included at least areas of forests or woodland within, although the proportion of the areas differed among routes. The routes A-1 and A-2, which were located in secondary woodland, had higher eigenvector values (> 0.3), while the routes that were located in transitional (ecotonal) areas (e.g., arable fields contiguous to secondary and/or artificial forests) such as B-2 and B-3-2 showed intermediate eigenvector values (0.15-0.20). Thus, it is suggested that the second axis reflects a gradient from open zone via transition to forest zone.

The evaluation of PCA species grouping by cluster analysis

Figure 2 shows the community dendrogram based on Euclidean distances between all butterfly species. In this analysis (UPGMA), I obtained a high value of the normalized Mantel statistic of $r = 0.950$ (cophenetic correlation) for the association between the original and tree distance matrices. Approximate Mantel t -test showed $t = 8.806$, which

yielded a probability of $p = 1.000$ that randomized Z -values are lower than observed ones.

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Fig. 1. Scattergram of 62 butterfly species along the first and second principal component axis by PCA ordination. The numerals in the figure represent the following species: 1. *Erynnis montanus*, 2. *Daimio tethys*, 3. *Thoressa varia*, 4. *Isoteinon lamprospilius*, 5. *Ochlodes ochracea*, 6. *Potanthus flavum*, 7. *Polytremsis pellucida*, 8. *Pelopidas mathias*, 9. *Parnara guttata*, 10. *Atrophaneura alcinous*, 11. *Graphium sarpedon*, 12. *Papilio machaon*, 13. *Papilio xuthus*, 14. *Papilio macilentus*, 15. *Papilio protenor*, 16. *Papilio helenus*, 17. *Papilio bianor*, 18. *Eurema hecabe*, 19. *Eurema laeta*, 20. *Colias erate*, 21. *Anthocharis scolymus*, 22. *Pieris rapae*, 23. *Pieris (m. or n.) sp.*, 24. *Narathura japonida*, 25. *Japonica lutea*, 26. *Japonica saepestriata*, 27. *Antigius attilia*, 28. *Neozephyrus japonicus*, 29. *Favonius orientalis*, 30. *Rapala arata*, 31. *Callophrys ferrea*, 32. *Lycaena phlaeas*, 33. *Taraka hamada*, 34. *Lampides boeticus*, 35. *Pseudozizeeria maha*, 36. *Celastrina argiolus*, 37. *Everes argiades*, 38. *Curetis acuta*, 39. *Argyronome ruslana*, 40. *Argynnis paphia*, 41. *Nephargynnis anadyomene*, 42. *Damora sagana*, 43. *Limenitis camilla*, 44. *Limenitis glorifica*, 45. *Neptis sappho*, 46. *Neptis philyra*, 47. *Polygonia c-aureum*, 48. *Polygonia c-album*, 49. *Kaniska canace*, 50. *Nymphalis xanthomelas*, 51. *Cynthia cardui*, 52. *Vanessa indica*, 53. *Dichorragia nesimachus*, 54. *Apatura metis*, 55. *Hestina persimilis*, 56. *Sakakia charonda*, 57. *Ypthima argus*, 58. *Minois dryas*, 59. *Lethe sicelis*, 60. *Neope (g. or n.) sp.*, 61. *Mycalesis gotama*, 62. *Mycalesis francisca*.

Table 1 Eigenvalues and eigenvectors of the variance-covariance matrix used for PCA analysis of the butterfly community.

		Principal component	
		Axis 1	Axis 2
Eigenvalue		1.4629	0.284
Contribution to community variance (%)		63.61	12.35
Cumulative %		63.61	75.97
Eigenvector	A-1	0.3029	0.3497
	A-2	0.1805	0.3384
	B-1	0.6263	-0.7315
	B-2	0.5341	0.1805
	B-3-1	0.2369	0.2467
	B-3-2	0.2112	0.1816
	C-1	0.2797	0.2665
	C-2	0.1256	0.1722
	C-3	0.0588	0.0293

Thus, the results of the UPGMA are highly valid. Although the value chosen is necessarily arbitrary, when the level of Euclidean distance 0.60 was adopted for grouping, there were three major clusters (A, B, and C in **Fig. 2**). The appropriateness of this clustering is well supported by the fact that the respective clusters almost corresponded to the species groups with different density levels, that is, the density levels of the clusters A, B, and C were < 0.5 , $0.5 < \dots < 0.7$, and > 0.7 , respectively (cf. **Appendix 1**).

All but two species belonging to group I in the PCA were included in the cluster A. As well, all the species in group II in the PCA were included in either cluster B or C. These results by cluster analysis suggest that the species grouping and classification revealed by the PCA (i.e., the presence of groups I and II) was valid and reasonable.

Correlations between species diversity or richness and the number of the respective component species in the butterfly communities

Figure 3 shows the distribution of the numbers of species against species diversity or species richness of each census route. Species diversity was expressed by Shannon-Wiener function, $H' = - \sum_{i=1}^s p_i \ln p_i$, where s is the number of species recorded, and p_i is the proportion of the monthly mean density of the i -th species. Species richness was expressed by the number of species recorded in each route during the period.

The number of specialist species in each route (**Fig. 3a**) was highly correlated with both species diversity ($r = 0.942$, $p < 0.0001$) and species richness ($r = 0.909$, $p < 0.001$). As well, the number of group I intermediate species in each route was significantly correlated with both species diversity ($r = 0.675$, $p < 0.05$) and species richness ($r = 0.898$, $p < 0.001$) (**Fig. 3b**). However, the number of group II intermediate species in each route was not significantly correlated with either species diversity ($r = 0.648$, $p > 0.05$) or species richness ($r = 0.392$, $p > 0.05$) (**Fig. 3b**). The numbers of group I and II generalist species in each route were both not significantly correlated with species diversity (generalists I : $r = 0.496$, $p > 0.05$, generalists II : $r = 0.181$, $p > 0.05$) nor with species richness (generalists I : $r = 0.640$, $p > 0.05$, generalists II : $r = 0.216$, $p > 0.05$) (**Fig. 3c**).

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Fig. 2. Dendrogram of 62 butterfly species classified by the cluster analysis (UPGMA) based on 62 by 62 Euclidean distances matrix. See the caption of Fig. 1 for species numbers.

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Fig. 3. Relationships of the number of the respective component species (specialists (a), intermediates I and II (b), and generalists I and II (c)) with species diversity (H') and species richness (the total number of species) for the butterfly communities of the nine census routes.

Table 2 The number (and proportion) of species in each group classified into larval hostplant and adult habitat types, based on Unno and Aoyama (1981).

Species group	Larval hostplant type			Adult habitat type		
	Herbaceous and grassy	Woody	Carnivorous	Grassland	Forest edge	Forest inside
Specialist	6 (35.3%)	11 (64.7%)	0 (0.0%)	1 (5.9%)	15 (88.2%)	1 (5.9%)
Intermediate I	8 (42.1%)	11 (57.9%)	0 (0.0%)	3 (15.8%)	15 (78.9%)	1 (5.3%)
Intermediate II	5 (83.3%)	0 (0.0%)	1 (16.7%)	2 (33.3%)	2 (33.3%)	2 (33.3%)
Generalist I	8 (61.5%)	5 (38.5%)	0 (0.0%)	5 (38.5%)	8 (61.5%)	0 (0.0%)
Generalist II	6 (85.7%)	1 (14.3%)	0 (0.0%)	0 (0.0%)	7 (100.0%)	0 (0.0%)

Larval hostplant and adult habitat types of component species

Table 2 shows the larval hostplant type and adult habitat type of each species group. In species group I, specialist and intermediate I species showed the highest proportion of the woody type of larval hostplants, and only generalists I species showed the highest proportion of the herbaceous and grassy type. On the other hand, all species in group II showed the highest proportion of the herbaceous and grassy type of larval hostplants. For adult habitat types, all but group II intermediates showed the highest proportion of forest edges. No generalist groups included the species for their adults' habitat types to be forest inside.

Number of Red List species included in each species group

The number of the Red List species in Ibaraki Pref. included in each species group is shown in **Table 3**. Only the specialist and intermediate I groups included the Red List species, five (62.5 %) and three (37.5 %) species, respectively. It is predicted that these species groups are subjected to higher local extinction probability than the other species groups.

DISCUSSION

Butterfly community structure and the concept of generalist/specialist strategies

In this study, the results of the PCA showed that the butterfly community was composed of two major species groups (I and II). This species grouping was also supported by the results of the UPGMA. Further, when we added a priori criteria of species classification based on the generalist/specialist concept used and developed in Chapter 1, the butterfly community was found to be composed of 5 species groups (i.e., specialists, intermediates I and II, and generalists I and II) which differed from each other in their characteristics (**Table 3**).

Table 3 The summary of the characteristics of the six species groups in the butterfly community.

Characteristics	Species group				
	Specialists	Intermediates		Generalists	
		group	group	group	group
Voltinism	Oligovoltine	Multi- or oligovoltine		Multivoltine	
Larval diet breadth	Narrow	Broad or narrow		Broad	
PCA (population size)	Small	Small	Large	Small	Large
PCA (open-transition-forest gradient (habitat breadth))	Transition (narrow)	Transition-forest (intermediate)	Transition-forest (intermediate)	Open-transition (intermediate)	Open-forest (broad)
Correlation ⁵ with species richness	++	++	NS	NS	NS
Correlation ⁵ with species diversity (H')	++	+	NS	NS	NS
Larval hostplant type	Woody (64.7%)	Woody (57.9%)	Herbaceous (83.3%)	Herbaceous (61.5%)	Herbaceous (85.7%)
Adult habitat type	Forest edge (88.2%)	Forest edge (78.9%)	Grassland (33.3%) Forest edge (33.3%) Forest inside (33.3%)	Forest edge (61.5%)	Forest edge (100.0%)
No. Red List species included	5	3	0	0	0

¹) Oligovoltine: uni- or bivoltine, Multivoltine: more than bivoltine.

²) Narrow: feeding specialist, Broad: feeding generalist. See the criteria used for the species classification in Chapter 1.

³) First principal component.

⁴) Second principal component.

⁵) ++: $P < 0.01$, +: $P < 0.05$, NS: not significant,

⁶) Only an item which was the largest proportion is shown.

⁷) Based on Yata and Ueda (1993). See Appendix 1.

The species classified as a specialist by a priori criteria were all included in the group I in PCA, and they were characterized by small population size, narrow habitat breadth, number of species highly correlated with butterfly species diversity (H') and richness, leading to the association with less disturbed habitats with high species richness and diversity, and high proportions of woody type of larval hostplants associated with later successional stages. These characteristics are well consistent with the theoretical and empirical predictions of the generalist/specialist concept (MacArthur & Wilson 1967; Pianka 1970, 1988; Gadgil & Solbrig 1972; Southwood 1977, 1988; Spitzer & Leps 1988). These results also show that specialist species in the butterfly community could be discriminated well by a priori species classification based only on their voltinism and larval diet breadth. On the other hand, the species classified as an intermediate and generalist by a priori criteria were both divided further into two species groups by the present multivariate analyses. This implies that, in contrast to specialist species, the determinations of both the intermediate and generalist species groups by a priori criteria based only on their voltinism and larval diet breadth were not sufficient to characterize the species classification. Particularly, at least in butterfly communities, a priori species classification based only on their voltinism and larval diet breadth cannot discriminate a typical generalist group. In the process of species classification, other life-history traits strongly influenced by generalist-specialist selection pressures should be considered to discriminate a typical generalist group in a community.

When we compare the characteristics of intermediate and generalist species groups (**Table 3**), we notice that both species groups include those with features similar to specialist species (intermediate I and generalist I species groups) and those with features similar to typical generalist species (intermediate II and generalist II species groups). The generalist/specialist concept states that the dichotomy is invariably comparative, and a given organism is positioned along a generalist-specialist selection continuum (Pianka 1970, 1988). Southwood *et al.* (1974) also suggested that, even among a closely related species group, there are species seemed to be relatively *r*-selected and those to be relatively *K*-selected. Thus, the fact that the generalist and intermediate species groups both included different subgroups with features similar to generalists or specialists does not contradict the predictions of the concept. Further, in the two generalist subgroups, only the generalist II can be thought of as true or typical generalist group in terms of its characteristics (large population size, broad habitat breadth, number of species unrelated with butterfly species diversity and richness, and high proportions of herbaceous and grassy type of larval hostplants associated with earlier successional stages). Probably, in the butterfly community, the positions of the specialist species group and the generalist group II are both the endpoints on the generalist-specialist selection spectrum, and the remaining three species groups are positioned between these two extremes. However, when we compare the characteristics of group II intermediates with those of group I generalists, the relationship of the exact positions of the two groups along the generalist-specialist selection continuum is equivocal.

The multivariate analyses used as a posteriori approach in this study clearly showed that a priori classification into the generalist and intermediate species groups based only on their voltinism and larval diet breadth in Chapter 1 were both further divided into two species subgroups with different characteristics. Present analyses also succeeded in extracting a typical generalist species group in the butterfly community. This suggests that the multivariate approach is much effective, appropriate, and helpful to classify the component species more exactly and to analyze community structure and composition in more detail. In conclusion, I propose and recommend the synergetic application of the generalist/specialist (*r/K*) concept and multivariate approaches for the detailed analysis and deeper understanding of community structure and composition. Similar analyses for a wide range of different habitats and organisms are much welcome to test the generality of the community patterns obtained and the applicability of the analytical approaches used in the present study.

Butterfly community composition based on the generalist/specialist concept and conservation implications

The previous studies (Chapters 1 and 2) showed that the number of specialist-type species was negatively correlated with the degree of human disturbance, while that of generalists was not correlated with disturbance. This implies that the specialist-type species would disappear or become extinct in the environment with high human disturbances. In addition, the present study showed that the component species registered on the Red Data list in Ibaraki Prefecture (Yata & Ueda 1993) were all included in either specialist or intermediate I group, suggesting that these species groups are associated with relatively high local extinction probability. These species groups were characterized mainly by such ecological traits as oligovoltinism, narrow larval diet breadth, small population size, and narrow habitat breadth (Table 3). Primack (1993) pointed out that species with univoltinism, narrow diet or habitat breadth and/or low population densities are usually vulnerable to extinction. Kitahara and Sei (2001) also showed that, in grassland habitats, butterfly species of oligovoltinism, low population abundance and restricted local distribution are prone to extinction through human land use and modification. Thus, it is predicted that these specialist-type species revealed in the present analyses are vulnerable to extinction, and these species are thought to be the priority and target species on local butterfly conservation.

I conclude that the present approach based on the generalist/specialist concept and multivariate analyses is also much effective and helpful to identify priority or target species on local biological conservation. To maintain local butterfly diversity, we need to carefully monitor and manage specialist-type species identified through such analytical approaches.

Chapter 4. Application of the community analysis based on the generalist/specialist concept to the environmental evaluation of habitat islands: The island biogeographical analysis of butterfly community structure in the newly designed parks of Tsukuba City

INTRODUCTION

The studies of island plant and animal communities have played an important role in the development of evolutionary and ecological thought (e.g., MacArthur and Wilson 1963, 1967; MacArthur 1972; Simberloff 1974; Cody and Diamond 1975; Gorman 1979; Diamond and May 1981; Pianka 1988). Islands have definite boundaries and come in many different sizes, heights, and degrees of isolation, and therefore constitute some of the finest of natural ecological experiments (Diamond and May 1981; Pianka 1988).

Some mainland habitats which are effectively isolated from each other (e.g., a patch of forest, isolated lakes, alpine mountaintops, recent fire burns, and gaps in a forest canopy) can also be regarded as habitat islands (Wilson and Bossert 1971; MacArthur 1972; Diamond and May 1981; Giller 1984; Pianka 1988; Begon *et al.* 1990). As Wilson (1992) noted, habitat islands are subject to the same ecological and evolutionary processes as real islands. Up to the present, some progress has been made in applying the equilibrium theory of island biogeography (MacArthur and Wilson 1967) to such habitat islands (e.g., Vuilleumier 1970; Brown 1971; Gorman 1979). However, the mainland habitats usually form very complex mosaics. As a result, diversity patterns on the habitat islands cannot so easily be studied and our understanding is much less advanced than those on real islands (Cody 1975; Gorman 1979; Giller 1984).

The usefulness of the island biogeography theory in conservation biology has been claimed (e.g., Spellerberg 1991; Primack 1993; Hunter 1996). However, little attempt has yet been made to evaluate the simultaneous applicability of the generalist/specialist concept and the island biogeography theory in order to analyze habitat island ecological communities. In particular, we do not know any attempt of applying the generalist/specialist concept directly to the actual component species of habitat island communities.

In Chapter 1, I treated the newly designed parks in Tsukuba City, central Japan, mainly as the most human-disturbed site of all the study areas. In addition to this high

degree of human disturbance, these parks were also newly established after intensive ground preparation, and most of the vegetation was transplanted from other areas. Thus, their environmental structures are very different from the surrounding habitats. Most animal species present there seem to have immigrated from adjacent habitats after the birth of the parks. Thus, we can think of these parks as "habitat islands" with newly established faunas, surrounded by habitats with relatively old faunas. These parks can constitute one of the finest of natural ecological experiments on the mainland for clarifying the patterns and processes of faunal immigration into the newly established habitat islands.

Schaefer (1982) demonstrated that, in studying the structure and function of green urban ecosystems, it is important to compare these ecosystems with semi-natural ones in the surroundings of the urban area (also see Frankie and Ehler 1978). Thus, in the present study, to analyze the patterns of the habitat island communities, I used data from not only the butterfly communities in these parks, but also from two other butterfly communities in more natural habitats in the surrounding areas, and compared them in the light of the theory of island biogeography and the concept of generalist/specialist. Butterflies are the most suitable organisms for the study of the structure and dynamics of biological populations and communities (Ehrlich 1992). The adults can be identified easily in the field and their life-history information (e.g., hostplants, voltinism) are already well known in Japan (e.g., Fukuda et al. 1972).

In the previous Chapters 1 and 2, I analyzed butterfly community structures based on the classification of their component species into generalist, specialist, and intermediate species. In this study, I analyze butterfly community structures in more detail based on the more exact classification of the component species as detailed in the section "Definitions". The goals of this study were (1) to search for butterfly community patterns in newly designed parks by comparing them with those in two other areas with relatively old faunas, (2) to understand the habitat island community patterns detected in the light of the generalist/specialist concept and the island biogeography theory, and (3) to evaluate the synergetic effectiveness of both the concept and the theory for the analysis of habitat island community patterns.

STUDY AREA AND METHODS

In this study I used the data collected in the previous study (Chapter 1), and the details of the census areas and sections within were described in Chapter 1. Only short descriptions follow.

I established three census routes (in areas A, B, and C) in and around Tsukuba City,

Ibaraki Pref., central Japan. Route A was established in area A located in secondary natural forest on the gentle south slope of Mt. Tsukuba (alt. 875.9 m) at an altitude of 150-200 m. It was 860 m in length and divided into two sections (A-1 and A-2). Route B was established in area B located in cultivated lands and villages from 50 to 100 m in altitude at the foot of Mt. Tsukuba. It was 1280 m in length and divided into four sections (B-1, B-2, B-3-1 and B-3-2). Route C, which was 2610 m in length, was established in area C located in newly designed city parks with transplanted trees and a connecting pedestrian road at an altitude of 25 m in Tsukuba City.

Area C was occupied mainly by patchy forests, lawns, paved roads, and man-made ponds. Most forest trees were transplanted when the parks were designed. These forests were mixtures of various tree species belonging to deciduous and evergreen broad-leaved trees and coniferous trees. Most of the forest floors were covered by lawns and grasses, and the rest was bare ground. Human activities (mowing, pruning, and insecticide spraying) by park management were frequently conducted aperiodically. Thus, succession was almost prevented by human activities, and the environmental structure was very different from those of the surrounding areas. When I studied the butterfly community of area C in the year 1980, several years had passed since the birth of the parks. Route C was divided into three census sections, C-1 (510 m), C-2 (900 m) and C-3 (1200 m) based on the different vegetation and environmental structures within and around each section. C-1 was located in Akatsuka Park in which some patches of secondary forest remained. The park was surrounded mainly by cultivated fields and residential area. C-2 was located along a pedestrian road about 20 m wide, connecting C-1 and C-3. It was situated next to remaining forests dominated mainly by deciduous broad-leaved trees and *Pinus densiflora*. C-3 was located in Doho Park in which most trees had been transplanted. There was no forest in the surrounding area.

I censused butterfly communities twice a month during the adult flight season (from March to November, 1980) by line transect method (Pollard 1977; Thomas 1983 ; Gall 1985; Pollard and Yates 1993). Details of the census method are described in Chapter 1. I analyzed the butterfly community structure using the following ecological indices; monthly mean population density, species richness, species diversity, equitability (evenness), and dominance. Definitions and formulae of these indices are detailed in Chapters 1 and 2. The overall monthly mean density of each species for each area (A, B and C) was calculated by averaging the monthly mean densities of the sections within each area only where butterfly species were recorded. Exclusion of census sections where no butterflies were recorded minimized the effect of different distribution patterns (widespread or restricted) of butterfly species on the overall monthly mean density.

DEFINITIONS

Classification of the component butterfly species based on their voltinism and larval resource

Generalization and specialization must be defined with reference to particular axes (Futuyma and Moreno 1988). I classified the butterfly species observed into generalist and specialist species based on their resource utilization patterns in two fundamental niche dimensions (time and food), which could be determined from the detailed information available in the literature. In this study, I adopted more detailed species classifications based on the generalist/specialist concept than those in the previous study (Chapter 1) as follows.

First, I used voltinism (number of generations per year) as an indicator of the niche breadth in a seasonal time dimension. When we consider their adult flight periods and times of appearance in a seasonal time dimension, we can think of multivoltine species as seasonal generalists, and oligovoltines as seasonal specialists. In this study, I defined uni- or bivoltine species as "seasonal specialists (hereafter SS)" and multivoltine (more than bivoltine) species as "seasonal generalists (hereafter SG)". Voltinism was based on Unno and Aoyama (1981) and Fukuda *et al.* (1982, 1983, 1984a, 1984b), and also on the actual data of their seasonal dynamics in the study areas. Out of 62 butterfly species observed, 34 species (54.8 %) were classified as SS species, and 28 species (45.2 %) as SG species (see **Table 1a**).

Second, I used the degree of polyphagy (range of hostplant species used by larvae) as an indicator of the niche breadth in a larval food dimension. In this study, I defined species whose larvae had been reported to feed on 10 or less plant species belonging to one taxonomic family as "feeding specialist (hereafter FS)", and species the larvae of which feed on more than 10 plant species belonging to one taxonomic family, or on a variety of hostplants belonging to two or more taxonomic families as "feeding generalists (hereafter FG)". The degree of polyphagy (larval diet breadth) was based on Endo and Nihira (1990) and Fukuda *et al.* (1982, 1983, 1984a, 1984b). Out of 62 butterfly species observed, 25 species (40.3 %) were classified as FS species, and 37 species (59.7 %) as FG species (**Table 1a**).

I then classified the species which belonged to both SS and FS as "typical specialists (hereafter TS)", those belonging to both SG and FS as "rebound specialists (hereafter RS)", those belonging to both SG and FG as "typical generalists (hereafter TG)", and those belonging to both SS and FG into "tolerant generalists (hereafter ToG)", expediently. With these criteria, out of 62 butterfly species found in the study areas, I classified 17 species (27.4 %) as TS species, 8 species (12.9 %) as RS species, 20 species

(32.3 %) as TG species, and 17 species (27.4 %) as ToG species (**Table 1a**). The characteristics (voltinism and larval diet breadth) and adaptive strategy of each butterfly species thus classified are described in **Appendix 3**.

Table 1. The criteria used for the classification of the butterfly species into various types. The number and the proportion (%) of each category of butterfly species are also shown.

(a) Voltinism and larval resource.

Larval resource breadth	Uni- or bivoltine (Seasonal specialist: SS) 34 (54.8%)	Multivoltine (more than bivoltine) (Seasonal generalist: SG) 28 (45.2%)
Oligophagous ^{a,b} (Feeding specialist: FS) 25 (40.3%)	Typical specialist: TS 17 (27.4%)	Rebound specialist: RS 8 (12.9%)
Polyphagous ^a (Feeding generalist: FG) 37 (59.7%)	Tolerant generalist: ToG 17 (27.4%)	Typical generalist: TG 20 (32.3%)

^a See text for exact criteria.

^b *Taraka hamada* (carnivorous) was treated as an oligophagous species.

(b) Distribution pattern

Present in all three areas	Present in two areas	Present only in one area
Widespread species 39 (62.9%)	Intermediate species 11 (17.7%)	Restricted species 12 (19.4%)

(c) Population density

≥ 0.5	The mean value of overall monthly mean density (/100m) 0.5~0.2	<0.2
High density species 15 (24.2%)	Intermediate density species 27 (43.5%)	Low density species 20 (32.3%)

Classification of the component butterfly species based on their distribution and habitat usage patterns

In this study, I censused the butterfly communities in three geographically distant and different habitats (i.e., area A: secondary natural woodland; area B: agricultural land and villages; area C: newly designed city parks). Based on their distributions and habitat usage patterns among the three areas, I classified the butterfly species into three types. I defined the species recorded in all three areas A, B, and C as geographically widespread and broad habitat usage species (hereafter "widespread" species), those recorded in two areas among the three as intermediately distributed species (hereafter "intermediate" species), and those recorded only in one area as geographically restricted and narrow habitat usage species (hereafter "restricted" species) (**Table 1b**).

With these criteria, I classified 39 species (62.9 %) as widespread, 11 (17.7 %) as intermediate, and 12 (19.4 %) as restricted species (cf. **Appendix 3**).

Classification of the component butterfly species based on their population densities

In order to analyze the butterfly community structure in the light of the population densities of the component species, I divided the butterfly species into three types based on their

overall monthly mean densities observed in this study. Expediently, I defined the species which occurred at high densities (the mean value of overall monthly mean densities 0.5/100 m) as "high" density species, those which occurred at 0.2-0.5/100 m as "intermediate" density species, and those which occurred at <0.2/100 m as "low" density species (Table 1c). With these criteria, I classified 15 species (24.2 %) as "high", 27 (43.5 %) as "intermediate", and 20 (32.3 %) as "low" density species.

RESULTS

Comparison of butterfly community structure among the three areas A, B, and C

Fifty seven butterfly species were recorded in area A, 51 in area B, and 43 in area C (Table 2). The proportion of TG species was highest in area C (41.9 %), followed by area B (39.2 %), and area A (31.6 %). The coefficients of determination (r^2) between the total number of species and the number of TG, ToG, RS, and TS species in each area were 0.006, 0.279, 0.817, and 0.980, respectively (Fig. 1a). In addition, the increase in the number of species in the order of the areas C, B, and A was much larger in TS (range, 10 spp.) than in RS (range, 1 sp.) species. These results suggest that the variation in the total number of

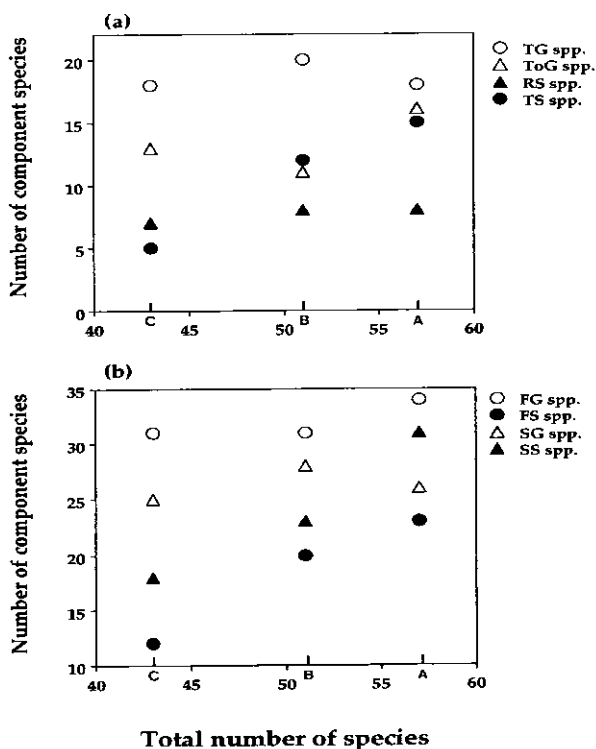


Fig. 1. (a) Relationship between the total number of species (species richness) and the number of typical generalist (TG), tolerant generalist (ToG), rebound specialist (RS), or typical specialist (TS) species in a community at three areas A, B, and C. (b) Relationship between the total number of species and feeding generalist (FG), feeding specialist (FS), seasonal generalist (SG), or seasonal specialist (SS) species in a community at three areas A, B, and C.

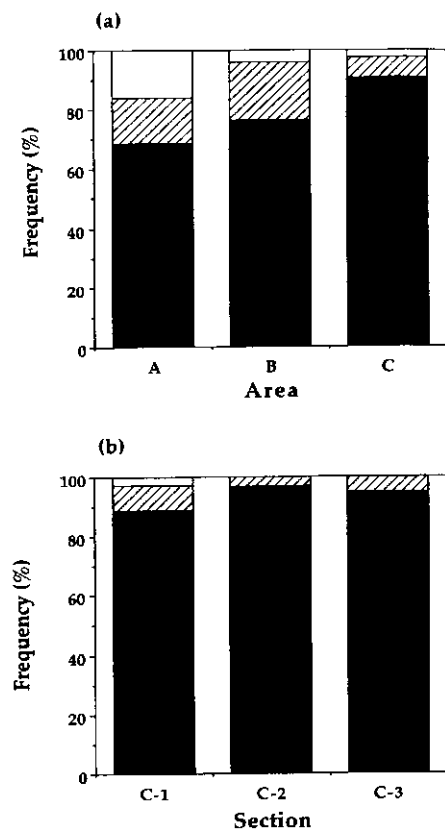


Fig. 2. Frequency distributions of widespread (■), intermediate (▨), and restricted (□) species in each of three areas A, B, and C (a), and of three sections C-1, C-2, and C-3 within area C (b).

species among the areas was accounted for mostly by the number of TS species. The fewer species in area C depended almost entirely on the scantiness of typical specialist (TS) species.

Table 2. The numbers (percent in parentheses) of respective component species in each butterfly community at each study area or section.

Study area Section	Number of species (species richness)								Total
	Typical generalist	Tolerant generalist	Rebound specialist	Typical specialist	Feeding generalist	Feeding specialist	Seasonal generalist	Seasonal specialist	
A	18(31.6)	16(28.1)	8(14.0)	15(26.3)	34(59.6)	23(40.4)	26(45.6)	31(54.4)	57
B	20(39.2)	11(21.6)	8(15.7)	12(23.5)	31(60.8)	20(39.2)	28(54.9)	23(45.1)	51
C	18(41.9)	13(30.2)	7(16.3)	5(11.6)	31(72.1)	12(27.9)	25(58.1)	18(41.9)	43
C-1	17(47.2)	9(25.0)	6(16.7)	4(11.1)	26(72.2)	10(27.8)	23(63.9)	13(36.1)	36
C-2	12(38.7)	8(25.8)	7(22.6)	4(12.9)	20(64.5)	11(35.5)	19(61.3)	12(38.7)	31
C-3	12(60.0)	5(25.0)	3(15.0)	0(0)	17(85.0)	3(15.0)	15(75.0)	5(25.0)	20

On the other hand, the coefficients of determination (r^2) between the total number of species and the number of FG, FS, SG, and SS species in each area were 0.676, 0.970, 0.163, and 0.955, respectively (**Fig. 1b**). The maximum difference in the number of species among the areas was much larger in FS (11 spp.) and SS (13 spp.) than in FG (3 spp.) and SG (3 spp.) species. These results suggest that the variation in the total number of species among the areas was accounted for mostly by the number of FS and SS species. The poor species richness in area C was mostly due to the scantiness of both feeding specialist (FS) and seasonal specialist (SS) species. Thus the community structure of area C was characterized by both the predominance of FG and TG species and the paucity of specialist (TS, FS, and SS) species.

Figure 2a shows the frequency distributions of widespread, intermediate, and restricted species in each area. The butterfly community structure in the habitat island (area C) was characterized by the predominance of widespread species (90.7 %).

Figure 3a shows the relationship between the total number of butterfly species and the number of high, intermediate, or low density species in a community at the three areas. The coefficients of determination (r^2) between the total species number and the number of high, intermediate, and low density species in a community were 0.007, 0.961, and 0.811, respectively. This indicates that the variation in the total species number among the areas was accounted for mostly by the number of intermediate and low density species. The lowest species richness in the habitat island (area C) was dependent largely on the paucity of intermediate and low density species. The number of high density species was almost constant among the three areas.

The total overall monthly mean density of all butterfly species was much lower in area C (10.55) than in areas A (25.93) and B (30.00). Also, the species diversity (H') was

much lower in area C (3.383) than in areas A (3.716) and B (3.664). A similar trend was also recognized in the equitability index (J'). The dominance index was highest in area C (0.204), followed by area B (0.147), and area A (0.125) (Table 3). These results show that the relatively low species diversity in area C resulted from both low species richness (fewer species) and low equitability (higher concentration of the dominant species).

Comparison of butterfly community structure among three census sections in area C

Thirty six species were recorded in section C-1, 31 in section C-2 and 20 in section C-3 (Table 2). Section C-3 with the lowest species richness was characterized by the predominance of species belonging to generalist groups (i.e., TG (60.0 %), FG (85.0 %), and SG (75.0 %)) and poorness of the species belonging to specialist groups (i.e., TS (0 %),

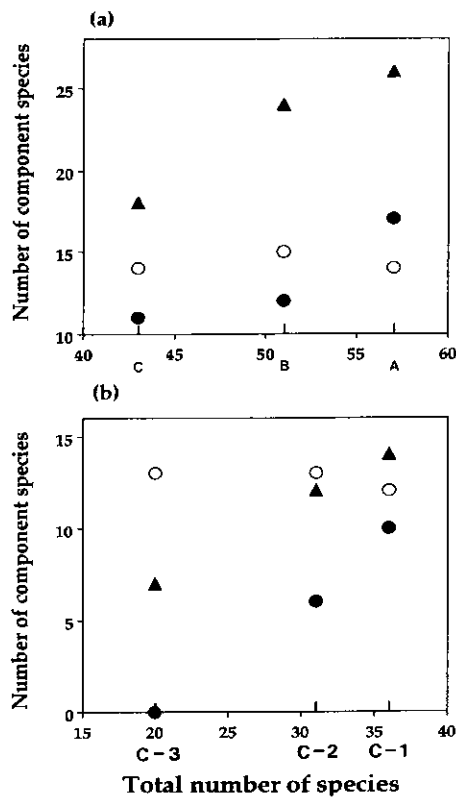


Fig. 3. Relationships between the total number of species (species richness) and the number of high density (\circ), intermediate density (\blacktriangle), and low density (\bullet) species in a community at three areas A, B, and C (a), and at three sections C-1, C-2, and C-3 within area C (b).

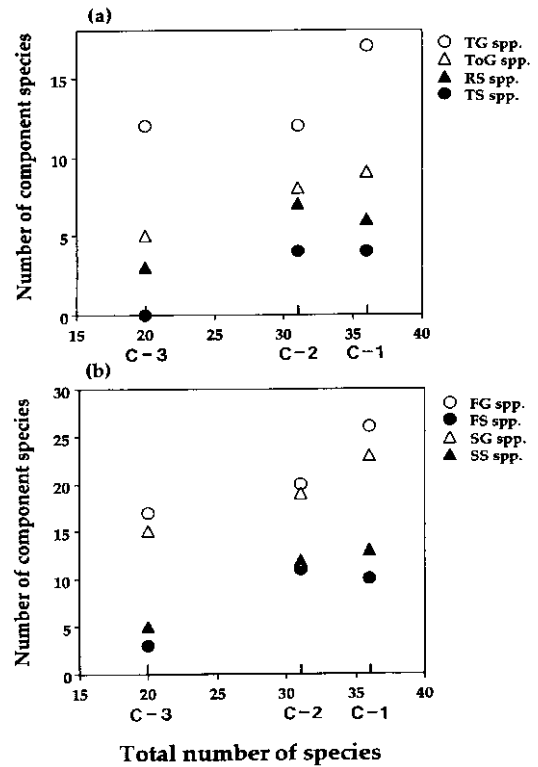


Fig. 4. Relationship between the total number of species (species richness) and the number of typical generalist (TG), tolerant generalist (ToG), rebound specialist (RS), or typical specialist (TS) species in a community (a), and that of feeding generalist (FG), feeding specialist (FS), seasonal generalist (SG), or seasonal specialist (SS) species in a community (b) at three sections C-1, C-2, and C-3 within area C.

RS (15.0 %), FS (15.0 %), and SS (25.0 %)) (Fig. 4, Table 2). The intermediate species richness of section C-2 was caused mainly by the increased number of specialist species (i.e., TS, RS, FS, and SS) and a similar number of generalist species (i.e., TG, FG, and SG) compared with section C-3 (Fig. 4). The highest species richness of section C-1 was caused mainly by an increased number of generalist species (i.e., TG, FG, and SG) compared with section C-2 (Fig. 4).

Five TS species (e.g., *Erynnis montanus* and *Papilio bianor*), nine FS species (e.g., *Taraka hamada*, *Limenitis camilla*, and *Daimio tethys*), and 13 SS species (e.g., *Antigius attilia*, *Nymphalis xanthomelas*, and *Apatura metis*) were recorded in sections C-1 and C-2, but not in C-3 (**Appendix 3**). All (15 species, 88.2 %) of these specialist (TS, FS, and SS) species except for *Polygonia c-aureum* and *Anthocharis scolymus* are closely associated with secondary natural (mostly broad-leaved) woodland and its margin habitats, where their hostplants are usually distributed (cf. Fukuda *et al.* 1972).

On the other hand, the group of generalist (TG, FG, and SG) species found only in section C-1 included eight species (**Appendix 3**). Of these species, half of them (e.g., *Vanessa indica*, *Cynthia cardui*, and *Graphium sarpedon*) are representative species of cultivated land and/or residential areas, in which their hostplants are frequently distributed (cf. Fukuda *et al.* 1972). The rest of the species (e.g., *Antigius attilia*, *Nymphalis xanthomelas*, and *Apatura metis*) are closely associated with secondary natural wood and its margin habitats (cf. Fukuda *et al.* 1972).

Figure 2b shows the frequency distributions of widespread, intermediate, and restricted species in the three sections. All butterfly communities in these sections were dominated by widespread species (C-1: 32 species (88.9 %); C-2: 30 species (96.8 %); C-3: 19 species (95.0 %)). Only one restricted species (2.8 %) was observed in C-1.

Figure 3b shows the relationship between the total number of butterfly species and the number of high, intermediate, or low density species in a community at the three sections. The coefficients of determination (r^2) between the total species number and the number of high, intermediate, and low density species in a community were 0.549, 0.999, and 0.990, respectively. Also, the maximum difference in the number of species among the areas was much larger in intermediate (7 spp.) and low (10 spp.) density species than in high density species (1 sp.). These results indicate that the variation in the total species number among the three sections was accounted for almost completely by that in the number of intermediate and low density species. The highest species richness in section C-1 was almost completely due to its richness of intermediate and low density species. The number of high density species was nearly constant among the three sections.

The total monthly mean density of all butterfly species was highest in section C-1 (15.94), followed by C-2 (7.37) and C-3 (2.94). Species diversity (H') was highest in section C-2 (3.008), followed by section C-1 (2.972), and section C-3 (2.668), whereas the equitability index (J') was highest in section C-3 (0.891), followed by sections C-2 (0.876) and C-1 (0.829) (**Table 3**). These results show that the highest species diversity in section C-2 was largely due to its higher equitability caused by the lowest dominance (0.235) of high density species. In contrast, the lowest species diversity in section C-3 was mainly due to the lowest species richness among the three sections.

Table 3. The values of various ecological indices of each butterfly community at each study area or section.

Study area Section	Total monthly mean population density of all species	Species diversity ^a (H')	Equitability index ^b (evenness)	Dominance index ^c
A	25.93	3.716	0.919	0.125
B	30.00	3.664	0.932	0.147
C	10.55	3.383	0.899	0.204
C-1	15.94	2.972	0.829	0.263
C-2	7.37	3.008	0.876	0.235
C-3	2.94	2.668	0.891	0.292

^a Shannon-Wiener function: $H' = -\sum p_i \ln p_i$.

^b Pielou's index of equitability: $J' = H' / \ln S$ (Pielou 1969).

^c McNaughton's dominance index: $DI = (n_1 + n_2) / N$.

Comparison of overall monthly mean densities of component butterfly species among the three areas A, B, and C

Thirty species (76.9 %) out of 39 species recorded in all three areas showed the lowest densities in area C (**Appendix 3**). Of these species, 11 species (overall percentage: 28.2 %) (e.g., *Lethe sicelis* and *Neptis sappho*) were observed at highest densities in area A, followed by B and C (*Kaniska canace* was observed at the same densities in areas A and B, followed by area C). Nineteen species (48.7 %) (e.g., *Ypthima argus*, *Lycaena phlaeas*, and *Mycalesis gotama*) were at highest densities in area B, followed by A, and C. Only 2 species, *Celastrina argiolus* and *Vanessa indica*, occurred at the highest densities in area C.

The relationship between the mean value of overall monthly mean population densities at the three areas and its coefficient of variation is shown in **Fig. 5** for the species recorded at high densities (mean value > 0.2/100 m) in all the three areas (cf. **Appendix 3**). The species above the regression line represent those with relatively large variations of population densities among the areas, six (35.3 %) of which are TG species. Referring to the Appendix, we notice that most species (15 species, 88.2 %) of this group (e.g., *Ypthima argus*, *Eurema laeta*, and *Lycaena phlaeas*) were at high densities in areas A and B, but at extremely low densities in area C. These species were feeding specialists (FS) (e.g., *Lycaena phlaeas* and *Eurema laeta*) and/or representative dominant species of agricultural land (cf. Fukuda *et al.* 1972) such as in area B in this study (e.g., *Ypthima argus*).

On the other hand, the species below the regression line (14 species) represent those with relatively similar population densities among the areas. These species were feeding generalists (FG) (e.g., *Polytremis pellucida*, *Eurema hecabe*, and *Parnara guttata*) and/or those whose larvae feed mainly on woody plants (e.g., *Papilio xuthus*, *Papilio protenor*, and *Papilio bianor*) (cf. Fukuda *et al.* 1972).

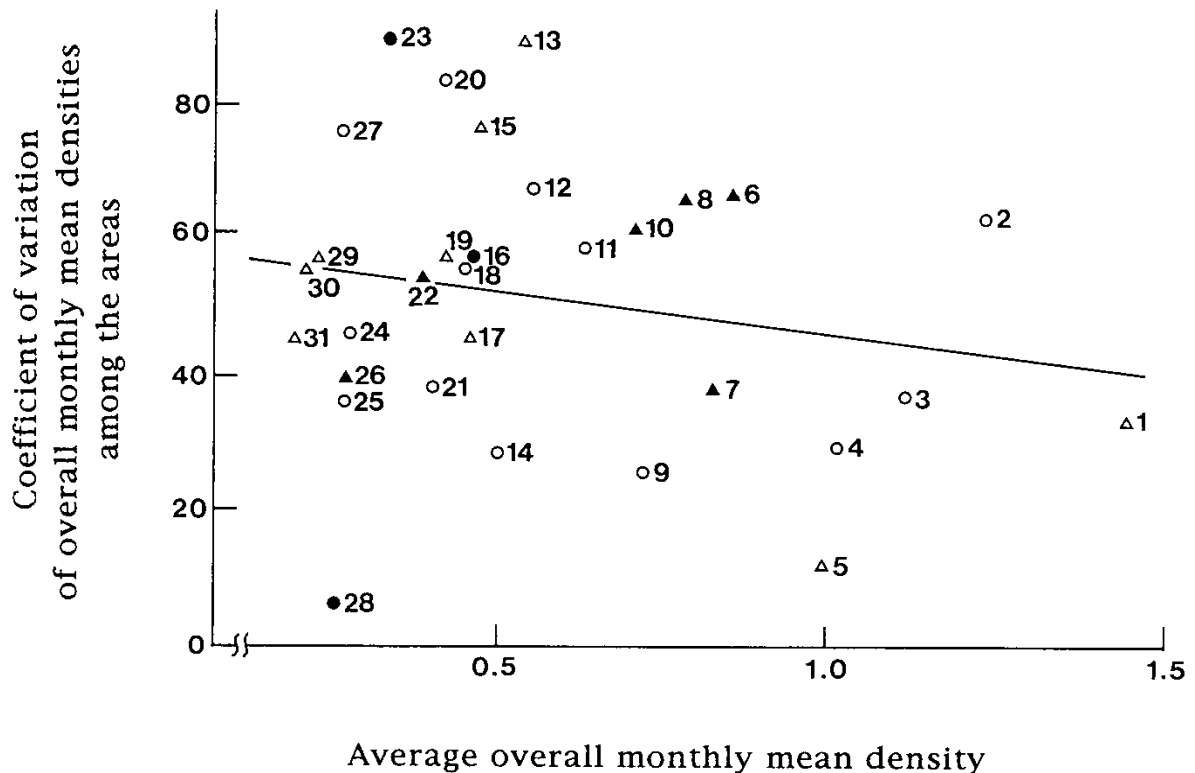


Fig. 5. Relationship between the mean value of overall monthly mean densities at the three areas and its coefficient of variation for the species occurring at higher densities (mean value $>0.2/100$ m) in all three areas. ○, typical generalist (TG); ●, typical specialist (TS); △, tolerant generalist (ToG); and ▲, rebound specialist (RS) species. The numerals in the figure represent the following species: 1, *Polytremis pellucida*; 2, *Ypthima argus*; 3, *Eurema hecabe*; 4, *Parnara guttata*; 5, *Neope* spp.; 6, *Eurema laeta*; 7, *Pseudozizeeria maha*; 8, *Lycaena phlaeas*; 9, *Celastrina argiolus*; 10, *Taraka hamada*; 11, *Everes argiades*; 12, *Mycalesis gotama*; 13, *Minois dryas*; 14, *Papilio xuthus*; 15, *Thoressa varia*; 16, *Hestina japonica*; 17, *Lethe sicelis*; 18, *Neptis sappho*; 19, *Antigius attilia*; 20, *Pelopidas mathias*; 21, *Curetis acuta*; 22, *Polygonia c-aureum*; 23, *Erynnis montanus*; 24, *Papilio machaon*; 25, *Papilio protenor*; 26, *Limenitis camilla*; 27, *Colias erate*; 28, *Papilio bianor*; 29, *Apatura metis*; 30, *Narathura japonica*; 31, *Anthocharis scolymus*.

DISCUSSION

In the following, I discuss how well we can understand the butterfly community patterns detected in area C, the newly opened habitat island, in the light of the generalist/specialist concept (MacArthur and Levins 1967; MacArthur and Wilson 1967; MacArthur 1972; Pianka 1988) and the theory of island biogeography (e.g., MacArthur and Wilson 1963, 1967; MacArthur 1972).

The habitat island community patterns detected in area C, newly designed parks

It has long been recognized for a variety of organisms that fewer species occur in real oceanic islands than in apparently comparable pieces of mainland (e.g., Crowell 1962;

Diamond 1969; Karr 1971; MacArthur 1972; Gorman 1979; Yukawa 1984b,c; Begon *et al.* 1990). These species-poor island communities are largely due to the absence of closely related species and/or particular species or taxa of organisms. The former is mainly due to interspecific competition (e.g., Karr 1971; MacArthur 1972; Higuchi 1979), and the latter is to their poor ability of dispersal, low reproductive potential, and/or specialized habitat requirements and food preferences (e.g., Higuchi 1979).

In the present study, area C supported a butterfly community of fewer species than other areas and showed a simpler community structure (with lowest species diversity) (**Tables 2 and 3**), showing the same pattern as seen in true oceanic islands. The fewer species in area C was mostly due to the absence of many species of specialist groups (TS, FS, and SS) (**Fig. 1**), the restricted group (**Fig. 2a**), and/or low and intermediate density groups (**Fig. 3a**). This probably happened due to their lower colonizing abilities evidenced by lower r resulting from oligovoltinism (for SS species), particular hostplant preferences (for FS species), or both (for TS species). Another possible reason for colonization failure by the above specialist species into area C may be due to its unstable and unpredictable habitat caused by aperiodical but frequent human disturbances. Furthermore, it is generally accepted that there is a positive relationship between the dispersal ability of a species and its range size within a taxonomically defined assemblage (e.g., Reaka 1980; Hedderson 1992; Oakwood *et al.* 1993; also see Gaston 1994 references therein), and that rare species tend to have poorer dispersal abilities than common species (e.g., Gaston 1994). Therefore, it is suggested that the paucity of restricted species and low and intermediate density species in the habitat island (area C) was a result of their poorer dispersal abilities (for both species types) and specialized habitat requirements (for the former species type).

The present analyses also showed that typical generalists (TG) (**Fig. 1a**), widespread (**Fig. 2a**), and/or high density (**Fig. 3a**) species predominated in area C, compared with other areas. Similar trends have been often demonstrated in real oceanic islands (Wilson 1959,1961; MacArthur 1972; Diamond 1975; Ricklefs 1990). For example, Karr (1971) found that most land birds of Puerco island were from low second growth on the mainland (which corresponded well to generalists) and that these successful colonists were characterized by their adaptation to changing habitats and tolerance for various environmental conditions. The present result can be explained by the concept of generalist/specialist (MacArthur and Wilson 1967; Pianka 1970) which suggests that in newly opened and uncrowded environments, r -selection should prevail and generalists would successfully establish (almost a synonym of supertramp strategists conceived by Diamond (1975)). In area C, a newly opened virgin habitat, r -selection should have prevailed and TG species with higher reproductive potential (evidenced by multivoltinism)

must have more easily migrated from the surrounding areas. Also, their broad larval diet breadth must have strongly favored their colonization into the area C dominated by many trees transplanted from other areas. The unstable habitat conditions in area C due to aperiodic human disturbances must also have been advantageous for TG species to establish themselves there. Furthermore, the successful colonization of many widespread, and high density species may be partly due to their suggested higher dispersal abilities and/or broad habitat requirements. In practice, the features of these species were consistent with many of the generalized characteristics of invasive species (e.g., high reproductive rate, short generation time, broad diet, broad native range, habitat generalist) summarized by Lodge (1993) and Meffe *et al.* (1994).

The differences in the number of species among three sections in area C

MacArthur and Wilson (1967) pointed out that the number of species on an island is correlated with and is a function of its area and its distance from colonization sources. In my results, the sections C-1 and C-2 contained more species than section C-3 which had the longest census route (**Table 2**). Thus, in this study, the correlation between the species number and area of each section was not established.

The above expectation stands on the assumptions that each island differs only in size but has a similar habitat structure and the same distance from the common pool. In the present habitat islands, the habitat structures in and around each island differed to some extent among the three, although their basic habitat structures (e.g., the patches of intensively managed transplanted trees and lawns, paved roads, and aperiodic human disturbances) were common to all. Thus the number of species observed in each habitat island is expected to be associated with the habitat structure unique to each section. The probable explanations are as follows: The predominance of generalists and the poorness of specialists in section C-3 with the lowest species richness (**Fig. 4**) can be interpreted in terms of its surroundings with no secondary forests. The increased number of specialist species in section C-2 compared with section C-3 (leading the C-2 to intermediate species richness) (**Fig. 4**) can be interpreted in terms of the presence of surrounding secondary natural woods which served as colonization sources. In fact, most specialist species (TS, FS, and SS) found in section C-2, but not in C-3 were those closely associated with secondary natural woodlands and their margin habitats (see Results). The highest species richness in section C-1 was caused mainly by the increased number of generalist species and the similar number of specialist species compared with section C-2 (**Fig. 4**). In section C-1, the presence of remaining secondary woods and the surrounding cultivated and residential areas must have allowed the above specialist and/or generalist species to be present or settle in the section. This is supported by my observations that the specialist

(TS, FS, and SS) species found in section C-1, but not in C-3 are those closely associated with secondary natural woods, and the generalist (TG, FG and SG) species found only in section C-1 are either those associated with secondary natural woods, or those commonly seen in cultivated land and/or residential areas (see Results).

Regarding the positive relationships between the total number of species and the numbers of intermediate and low density species in a community at the three sections (**Fig. 3b**), almost the same argument as above can be drawn based on the differences in their habitat structures in and around the three sections. On the other hand, the predominance of widespread species in all three sections (**Fig. 2b**) may be explained well by their suggested advantageous attributes for invasion and colonization such as higher dispersal abilities and generalized habitat requirements.

As discussed above, the difference in the species numbers among the three sections in area C could be explained by the habitat structure within and around the respective section. It is noteworthy that we can interpret the differences in the species numbers among the habitat islands in terms of simple qualitative habitat information and descriptions such as the presence or absence of secondary natural forest without detailed quantitative data. Thus, the species number in each section (habitat island) seemed to be more closely related to the diversity of the habitat, as often pointed out in true oceanic islands (MacArthur 1972). A similar result is obtained for Schaefer's (1982) empirical study on arthropod communities in urban ecosystems. He also points out that the most important factor affecting the number of species is the structural complexity and the degree of perturbation of the habitats rather than the size of area.

Characteristics of component species and the predicted status in the habitat island butterfly community

It has been often observed that the densities of island populations are much higher than those of mainland ones, and often lead to population explosions (e.g., Crowell 1962; Grant 1966; Karr 1971; Cody and Cody 1972; Cody 1974; and Higuchi 1976 for birds; MacArthur 1972 for lizards; Iwamoto 1986 for rats; Yukawa 1984a for scale insects; Yukawa 1984b for fruit flies). These higher densities in island populations are presumably due (1) to a release from competition and predation (e.g., MacArthur 1972; Cody 1974; Ehrlich and Roughgarden 1987), (2) to relatively *K*-selecting island habitats resulting from a more equable climate (MacArthur and Wilson 1967), and/or (3) to their good adaptation to new, empty island habitats as virgin resources (Elton 1958). On the other hand, it is also frequently known that some species which commonly distribute in the mainland cannot be found or are at very low densities on the island (e.g., MacArthur 1972; Yukawa 1984c).

In this study, the results showed that most species found in all the areas A, B, and

C exhibited much lower monthly mean densities in area C (habitat island) than in other areas, almost consistent with the latter trend stated above. This result can be explained by the unique habitat structure of area C, which contained both uninhabitable sites such as paved roads, and vegetation structure unsuitable for many butterflies (e.g., the absence or shortage of natural grass and shrub layer on the ground and forest floors, which provide many hostplants). The man-modified environment in area C may provide a relatively small quantity of resources available to butterfly populations, which affects the population size of given species (Price 1984).

In particular, the community of area C contained 15 species which were present at high densities in areas A and B, but at extremely low densities in area C (**Fig. 5**). These species belonged to either feeding specialist (FS) or representative species of agricultural land. Their low densities in area C were almost certainly a result of the absence or shortage of their particular hostplants or the lack of agricultural habitats there. On the other hand, the community of area C contained 14 species which occurred at similar densities to those in other areas (**Fig. 5**). These species belonged to either feeding generalist (FG) or species whose larvae feed mainly on woody plants. Thus, they could well utilize a variety of transplanted trees as virgin resources in area C. They can be thought of as good colonizers.

According to the island biogeography theory, "quasi-equilibrium" communities are composed mostly of "tramp" species (corresponding to generalists) and equilibrate with fewer species, while equilibrium communities are predominated by well-adapted species (corresponding to specialists) and have more species (e.g., Wilson and Taylor 1967). In this study, the butterfly community of area C was characterized by (1) fewer species, (2) the predominance of generalists, (3) the almost saturated number of generalist species, and (4) the paucity of specialists. Thus, the internal structure of the butterfly community in area C was almost perfectly consistent with that of usual quasi-equilibrium communities. Or, the butterfly community in area C can be thought of as a "plagioclimax" community, in which succession is halted more or less permanently because of continued management (e.g., Morris 1991; Thomas 1995). In area C, the environmental condition was unstable due to aperiodic, but continued human disturbances and the habitat structure was maintained by intensive park management, preventing succession from occurring in the area. Probably, the status of the community in area C will be maintained permanently as it is, as long as human disturbances and park management continue.

In conclusion, the present results demonstrate that the synergetic application of the generalist/specialist concept and the island biogeography theory are effective and valid for the understanding of the patterns and structures of habitat island communities.

Concluding Remarks

The generality and validity of the patterns found in the structure of butterfly communities along an environmental gradient of human disturbance based on the generalist/specialist concept

In Chapter 1, I showed that, as the level of human disturbance in a habitat is enhanced, the species richness of butterfly communities and the number of specialist species in a community decreases, whereas the number of generalist species is almost constant irrespective of habitat stability. In other words, the decrease in the total number of butterfly species based on the enhancement of habitat disturbance was dependent more on the decrease in the number of specialist species in a community than that of generalists. Almost identical community patterns were also recognized in the following study (Chapter 2), which was conducted in a considerably different habitat type and in a distant region from those of the previous study (Chapter 1). This strongly supports that this community pattern detected between habitat disturbance and butterfly community structure is rather general and valid in the ecosystems of temperate zone such as those of the present studies.

In addition, these community patterns are also evidenced by several recent butterfly studies. In British butterflies, Warren *et al.* (2001) clearly showed that habitat degradation and climate change promoted the increase in the distribution sites of mobile and habitat generalists, whereas the decline in the distribution size of most habitat specialists, and therefore, the dual forces of habitat modification and climate change are likely to cause specialists to decline, leaving biological communities with reduced number of species and dominated by mobile and widespread habitat generalists. Even in tropical rainforests, Hamer *et al.* (2003) reported that, in tropical Satyrinae and Morphinae butterflies, the species with higher shade preferences and narrow geographical distributions (almost corresponding to specialists) were most adversely affected by forest disturbance (i.e., logging), whereas cosmopolitan species with high light preferences (almost corresponding to generalists) benefited from forest disturbance.

From aforementioned discussion, I conclude that the patterns in the structure of butterfly communities along an environmental gradient of human disturbance based on the generalist/specialist concept found in the present studies are both robust and general ones probably common to various types of habitats, environments, and ecosystems.

The verification of the generalist/specialist concept at the community level, and a suggestion on habitat structure concerning to environmental stability

The present studies clearly showed that the degree of habitat disturbance was negatively correlated with the number of specialist species in a community, but not with that of generalist species. The number of generalist species in a community was rather constant irrespective of the environmental gradient of habitat disturbance. The relationship between habitat disturbance and the specialists was perfectly consistent with the prediction of the generalist/specialist concept, but that of the generalists was not compatible with the concept. That is, at the community level, the changing patterns of the specialists on the environmental gradient of disturbance can be explained well by the prediction of the concept, but those of the generalists cannot. The fact that the relationship between habitat disturbance and the generalists was not compatible with the prediction of the concept may be caused rather by the microhabitat structure of the present study areas, than by the mis-prediction of the concept, as the following discussions suggest.

The present studies clearly showed that, in more disturbed, so unstable habitats, the butterfly communities were composed of fewer species and almost dominated by generalists, whereas in less disturbed, so stable habitats, those were composed of more species with the mixture of specialists and generalists. This result strongly suggests that relatively unstable habitats had homogeneous structure in instability, whereas relatively stable habitats did heterogeneous structure with the mixture of relatively stable and unstable patches. In general, it is accepted that, even in relatively stable woodland habitats regarded as later successional stage, there are forest gaps and margins with instability and unpredictability (e.g., Whitmore 1984, 1989, 1990). This situation may enable generalist species to coexist with specialists in such relatively stable and predictable habitats as a whole. In fact, recent butterfly studies in tropical rainforests (Hill *et al.* 2001; Hamer *et al.* 2003) confirmed this phenomenon. These studies clearly showed that tropical rainforest gaps were ephemeral and patchily distributed within forest areas, and the closed-canopy sites contained mostly species with higher shade preferences and more restricted geographical distributions (almost corresponding to specialists), whereas the forest gap communities mostly comprised of more widespread, mobile species with light preferences (almost corresponding to generalists).

From these results, I conclude that even relatively stable environments usually have heterogeneous structure with stability and instability, and therefore, support the mixture of specialists and generalists and the resultant high species richness and diversity.

The applicability of the generalist/specialist concept to biological community analyses and other environmental sciences

The present studies demonstrated that the generalist/specialist (r/K) concept is much useful and helpful in searching for community patterns along an environmental gradient and in the analysis and understanding of biological community structure and composition. In particular, it is emphasized that the community analysis based on the generalist/specialist concept employed in the present studies is a highly scientific method based on a priori approach from hypothesis via prediction to verification. In this respect, the method is a very significant and important one in the research area of general ecology usually predominated by analyses a posteriori. For instance, this method can analyze community structure more predictably and explicably than other a posteriori community analytical method such as the core and satellite species hypothesis (Hanski 1982).

In addition, the present studies also demonstrated that the combination of the method with other theory or analytical approaches lead to the detailed understanding of community structure or the contribution to applied environmental sciences. That is, the synergetic application of a priori method based on the generalist/specialist concept and multivariate analyses used as a posteriori led to the more detailed analysis and deeper understanding of butterfly community structure (Chapter 3). Furthermore, the synergetic application of the generalist/specialist concept and the theory of island biogeography was effective and valid for the understanding of the patterns and structures of habitat island butterfly communities, and contributed much to the environmental assessment of newly designed city parks (Chapter 4).

Thus, from aforementioned discussion, I conclude that the analytical approach based on the generalist/specialist concept is a highly operational method with good predictable and explanatory powers much applicable to the analysis of various types of biotic communities, in spite of a variety of criticism of the concept (e.g., Stearns 1976, 1977; Ito 1980; Parry 1981; Boyce 1984).

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Appendix 1. List of the butterfly species observed in the present study (chapter 1), their monthly mean density, and their characteristics.

Species	Monthly mean density (No. adults/100m/month)										Characteristics			Status in a Red Data list ⁴⁾
	A-1	A-2	B-1	B-2	B-3-1	B-3-2	C-1	C-2	C-3	Average	Volturnism ¹⁾	Host plant ²⁾	Strategy ³⁾	
Hesperiidae														
<i>Erynnis montanus</i>	0.47	1.06	0.14	0.00	0.16	0.00	0.00	0.11	0.00	0.39	1	O	S	
<i>Daimio tethys</i>	0.31	0.15	0.00	0.24	0.16	0.15	0.16	0.06	0.00	0.18	M	O	I	
<i>Thoressa varia</i>	0.21	0.15	0.97	0.98	0.97	1.06	0.00	0.50	0.04	0.61	2	P	I	
<i>Isoteinon lamprospilus</i>	1.04	0.46	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.56	1	O	S	
<i>Ochlodes ochracea</i>	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	2	P	I	
<i>Potanthus flavum</i>	0.09	0.15	0.00	0.18	0.00	0.15	0.00	0.06	0.00	0.13	2	P	I	
<i>Polytremis pellucida</i>	1.89	0.23	2.53	3.32	1.94	0.85	2.06	0.97	0.44	1.58	2	P	I	
<i>Pelopidas mathias</i>	0.38	0.15	1.94	0.36	0.00	0.46	0.15	0.00	0.07	0.50	M	P	G	
<i>Parnara guttata</i>	1.98	0.66	2.67	0.95	0.53	0.40	1.14	0.24	0.42	1.00	M	P	G	
Papilionidae														
<i>Atrophaneura alcinous</i>	0.52	0.30	0.14	0.90	0.16	0.00	0.00	0.00	0.00	0.40	M	O	I	
<i>Graphium sarpedon</i>	0.14	0.00	0.14	0.18	0.33	0.00	0.15	0.00	0.00	0.19	M	P	G	
<i>Papilio machaon</i>	0.28	0.38	0.77	0.48	0.16	0.27	0.17	0.06	0.09	0.30	M	P	G	
<i>Papilio xuthus</i>	0.83	0.52	0.64	0.54	0.48	0.53	0.52	0.31	0.11	0.50	M	P	G	
<i>Papilio macilentus</i>	0.16	0.46	0.14	0.36	0.16	0.15	0.00	0.00	0.00	0.24	2	O	S	
<i>Papilio protenor</i>	0.26	0.23	0.49	0.42	0.35	0.00	0.29	0.06	0.00	0.30	M	P	G	
<i>Papilio helenus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.10	2	P	I	
<i>Papilio bianor</i>	0.28	0.30	0.14	0.30	0.27	0.25	0.39	0.11	0.00	0.26	2	O	S	
Pieridae														
<i>Eurema hecabe</i>	2.64	0.61	1.56	1.45	0.55	1.02	0.72	0.68	0.39	1.07	M	P	G	
<i>Eurema laeta</i>	1.37	1.87	0.00	0.18	0.00	1.21	0.17	0.25	0.36	0.77	M	O	I	
<i>Colias erate</i>	0.14	0.00	0.90	1.01	0.16	0.15	0.00	0.13	0.11	0.37	M	P	G	
<i>Anthocharis scolymus</i>	0.09	0.00	0.28	0.36	0.48	0.15	0.20	0.00	0.00	0.26	1	P	I	
<i>Pieris rapae</i>	0.00	0.00	1.51	0.51	0.24	0.15	0.12	0.00	0.11	0.44	M	P	G	
<i>Pieris (m. or n.) sp.</i>	0.38	0.20	0.23	0.61	0.74	0.00	0.00	0.00	0.00	0.43	M	P	G	
Lycaenidae														
<i>Narathura japonica</i>	0.17	0.15	0.00	0.00	0.16	0.61	0.00	0.11	0.00	0.24	2	P	I	
<i>Japonica lutea</i>	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	1	O	S	
<i>Japonica saepestriata</i>	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.14	1	O	S	
<i>Antigius attilia</i>	0.09	0.91	0.69	0.00	0.00	0.00	0.10	0.00	0.00	0.45	1	P	I	
<i>Neozeephyrus japonicus</i>	0.00	0.00	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.65	1	O	S	R
<i>Favonius orientalis</i>	0.19	0.00	0.00	0.36	0.00	0.15	0.20	0.06	0.00	0.19	1	O	S	
<i>Rapala arata</i>	0.09	0.00	0.00	0.00	0.00	0.00	0.29	0.06	0.00	0.15	2	P	I	
<i>Callophrys ferrea</i>	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	1	P	I	
<i>Lycaena phlaeas</i>	0.69	1.04	2.30	1.91	0.43	0.91	0.20	0.06	0.12	0.85	M	O	I	
<i>Taraka hamada</i>	0.97	0.84	0.00	1.96	0.89	0.53	0.00	0.11	0.00	0.88	M	C	I	
<i>Lampides boeticus</i>	0.38	0.00	0.14	0.54	0.00	0.15	0.00	0.00	0.00	0.30	M	P	G	
<i>Pseudozizeeria maha</i>	0.27	0.73	2.58	0.60	1.08	0.80	1.86	0.17	0.15	0.92	M	O	I	
<i>Celastrina argiolus</i>	0.75	0.46	0.28	0.71	0.89	0.42	2.13	0.76	0.11	0.72	M	P	G	
<i>Everes argiades</i>	0.81	1.09	1.86	0.49	0.49	0.58	0.10	0.00	0.13	0.69	M	P	G	
<i>Curetis acuta</i>	0.58	0.23	0.42	0.75	1.01	0.25	0.30	0.14	0.00	0.46	M	P	G	
Nymphalidae														
<i>Argyronome rustana</i>	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	1	O	S	R
<i>Argynnis paphia</i>	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	1	O	S	
<i>Nephargynnis anadyom</i>	0.10	0.15	0.00	0.18	0.16	0.15	0.00	0.00	0.00	0.15	1	O	S	
<i>Damora sagana</i>	0.10	0.30	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.18	1	O	S	R
<i>Limenitis camilla</i>	0.19	0.46	0.14	0.39	0.48	0.53	0.16	0.09	0.00	0.31	M	O	I	
<i>Limenitis glorifica</i>	0.00	0.15	0.00	0.36	0.32	0.00	0.10	0.06	0.00	0.20	2	O	S	
<i>Neptis sappho</i>	0.80	0.61	0.21	0.79	0.81	0.33	0.22	0.07	0.06	0.43	M	P	G	
<i>Neptis philyra</i>	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	1	P	I	R
<i>Polygonia c-aureum</i>	0.57	0.46	1.03	0.47	0.38	0.42	0.10	0.09	0.00	0.44	M	O	I	
<i>Polygonia c-album</i>	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	2	P	I	
<i>Kaniska canace</i>	0.16	0.25	0.28	0.18	0.16	0.00	0.10	0.06	0.00	0.17	M	P	G	
<i>Nymphalis xanthomelas</i>	0.09	0.00	0.28	0.00	0.00	0.00	0.10	0.00	0.00	0.16	1	P	I	
<i>Cynthia cardui</i>	0.00	0.00	0.14	0.18	0.00	0.00	0.10	0.00	0.00	0.14	M	P	G	
<i>Vanessa indica</i>	0.10	0.00	0.14	0.18	0.00	0.15	0.20	0.00	0.00	0.15	M	P	G	
<i>Dichorragia nesimachus</i>	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	2	O	S	
<i>Apatura metis</i>	0.19	0.00	0.42	0.00	0.00	0.00	0.10	0.00	0.00	0.24	2	P	I	V
<i>Hestina japonica</i>	0.25	0.91	0.00	0.63	1.13	0.45	0.10	0.00	0.00	0.58	2	O	S	R
<i>Sasakia charonda</i>	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	1	O	S	R
Satyridae														
<i>Ypthima argus</i>	1.06	1.29	3.75	3.25	1.03	0.91	0.41	0.53	0.04	1.36	M	P	G	
<i>Minois dryas</i>	0.62	1.82	0.28	0.18	0.16	0.30	0.00	0.33	0.04	0.47	1	P	I	R
<i>Lethe sicelis</i>	0.85	0.68	0.14	0.45	0.65	0.15	0.30	0.48	0.08	0.42	2	P	I	
<i>Neope(g. or n.) sp.</i>	0.57	1.33	0.73	2.23	0.59	1.21	2.01	0.56	0.04	1.03	2	P	I	
<i>Mycalesis gotama</i>	0.47	0.30	2.39	1.43	0.19	0.30	0.43	0.13	0.08	0.64	M	P	G	
<i>Mycalesis francisca</i>	0.19	0.56	0.00	0.30	0.81	0.20	0.00	0.00	0.00	0.41	2	O	S	

¹⁾ Number of generations per year. M(multivoltine): more than bivoltine.

²⁾ Range of acceptable larval host plants. O(oligophagy): species whose larvae had been reported feeding on 10 or less plant species belonging to one taxonomic family; P(polyphagy): species the larvae of which had been reported feeding on more than 10 plant species belonging to one taxonomic family, or on a variety of hostplants belonging to two or more taxonomic families; C :carnivorous.

³⁾ Adaptive strategy. G: generalist species; I: intermediate species; S: specialist species.

⁴⁾ Status in the Red Data list of butterflies in Ibaraki Prefecture (Yata and Ueda 1993). V: vulnerable species, R: rare species.

Appendix 2. List of the butterfly species observed in the present study (chapter 2), their monthly mean density, and their characteristics.

Species	Mean annual density (no. adults/km)					Average abundance	CV of densities	Number of routes observed	Characteristics		
	Route A	Route B	Route C	Route D	Route E				voltinism ^a	Host plant ^b	Strategy ^c
Hesperiidae											
<i>Erynnis montanus</i>	0.00	0.00	1.00	0.00	0.00	1.00		1	1	O	S
<i>Daimio tethys</i>	0.00	1.00	1.00	0.00	0.00	1.00	0.00	2	M	O	
<i>Leptalina unicolor</i>	11.00	3.00	0.00	0.00	0.00	7.00	57.14	2	1	O	S
<i>Aeromachus inachus</i>	0.00	0.00	1.00	0.00	0.00	1.00		1	1	O	S
<i>Thymelicus sylvaticus</i>	3.00	0.00	0.00	0.00	0.00	3.00		1	1	P	
<i>Ochlodes venata</i>	7.50	6.00	0.00	0.00	0.00	6.75	11.11	2	1	P	
<i>Ochlodes ochracea</i>	6.00	1.00	0.00	0.00	0.00	3.50	71.43	2	2	P	
<i>Potanthus flavum</i>	1.50	0.00	1.00	0.00	0.00	1.25	20.00	2	2	P	
<i>Pelopidas jansonis</i>	0.00	1.00	0.00	0.00	0.00	1.00		1	2	O	S
<i>Pelopidas mathias</i>	1.00	1.00	1.00	0.00	0.00	1.00	0.00	3	M	P	G
<i>Parnara guttata</i>	7.78	5.50	11.00	4.00	2.67	6.19	47.57	5	M	P	G
Papilionidae											
<i>Papilio machaon</i>	1.00	1.00	0.00	0.00	1.00	1.00	0.00	3	M	P	G
Pieridae											
<i>Leptidea amurensis</i>	2.33	3.00	2.00	1.00	0.00	2.08	34.64	4	M	O	
<i>Eurema hecabe</i>	1.50	1.00	1.00	1.00	2.00	1.30	30.77	5	M	P	G
<i>Colias erate</i>	2.14	3.17	3.78	8.25	1.50	3.77	63.08	5	M	P	G
<i>Pieris rapae</i>	1.00	1.50	5.93	1.75	1.00	2.24	83.60	5	M	P	G
<i>Pieris melete</i>	1.00	1.00	1.70	1.00	1.00	1.14	24.56	5	M	P	G
<i>Pieris napi</i>	0.00	1.00	1.50	0.00	0.00	1.25	20.00	2	M	P	G
Lycaenidae											
<i>Lycaena phlaeas</i>	1.50	3.14	2.00	13.00	1.67	4.26	103.39	5	M	O	
<i>Lampides boeticus</i>	3.00	3.33	2.00	1.00	0.00	2.33	39.12	4	M	P	G
<i>Maculinea teleius</i>	1.00	0.00	0.00	0.00	0.00	1.00		1	1	O	S
<i>Everes argiades</i>	1.00	0.00	1.00	0.00	0.00	1.00	0.00	2	M	P	G
<i>Plebejus argus</i>	3.33	0.00	0.00	0.00	0.00	3.33		1	1	P	
<i>Curetis acuta</i>	0.00	0.00	0.00	1.00	0.00	1.00		1	M	P	G
Libytheidae											
<i>Libythea celtis</i>	0.00	0.00	0.00	1.00	0.00	1.00		1	1	O	S
Nymphalidae											
<i>Brenthis daphne</i>	1.00	0.00	0.00	0.00	0.00	1.00		1	1	O	S
<i>Argyronome laodice</i>	5.20	3.50	0.00	0.00	0.00	4.35	19.54	2	1	O	S
<i>Argynnis paphia</i>	1.00	0.00	1.00	0.00	0.00	1.00	0.00	2	1	O	S
<i>Fabriciana adippe</i>	4.50	2.50	0.00	0.00	0.00	3.50	28.57	2	1	O	S
<i>Limnitis camilla</i>	1.00	1.00	0.00	0.00	1.00	1.00	0.00	3	M	O	
<i>Limnitis glorifica</i>	1.50	0.00	0.00	0.00	0.00	1.50		1	2	O	S
<i>Neptis sappho</i>	1.00	0.00	1.00	0.00	0.00	1.00	0.00	2	M	P	G
<i>Neptis pryri</i>	2.33	0.00	2.67	0.00	1.00	2.00	36.00	3	1	O	S
<i>Polygonia c-aureum</i>	13.33	7.33	8.67	10.43	2.00	8.35	44.99	5	M	O	
<i>Nymphalis xanthomelas</i>	1.00	1.00	0.00	0.00	0.00	1.00	0.00	2	1	P	
<i>Inachis io</i>	0.00	0.00	1.00	0.00	0.00	1.00		1	1	P	
<i>Cynthia cardui</i>	0.00	1.00	0.00	2.00	1.00	1.33	35.36	3	M	P	G
Satyridae											
<i>Ypthima argus</i>	2.50	2.60	3.33	2.00	1.00	2.29	33.74	5	M	P	G
<i>Minois dryas</i>	36.00	12.00	4.00	2.00	1.50	11.10	117.20	5	1	P	
Total	126.95	67.58	58.57	49.43	18.33	99.82					
Total no. of species	30	24	22	14	13						
No. of generalist species	11	11	11	9	8						
No. of specialist species	8	4	4	1	1						
Species diversity (H')	2.733	2.849	2.730	2.163	2.502						
Species evenness (J')	0.804	0.896	0.883	0.820	0.975						
Dominance index (DI)	0.389	0.286	0.336	0.474	0.255						

^a Number of generations per year; M (multivoltine), more than bivoltine

^b Range of acceptable larval host plants; O (oligophagy), species whose larvae had been reported to feed on 10 or fewer plant species belonging to one taxonomic family; P (polyphagy), species the larvae of which feed on more than 10 plant species belonging to one taxonomic family, or on a variety of host plants belonging to two or more taxonomic families

^c Adaptive strategy; G, generalist species; S, specialist species

Appendix 3. List of the butterfly species observed in the present study (chapter 4), their (overall) monthly mean density at each area and section, and their characteristics.

Species	Overall monthly mean density ^a			Mean	C.V.	Section	Monthly mean density ^b			Characteristics			
	Area	A	B				C	C-1	C-2	C-3	Voitininism ^c	Host plant ^d	Strategy ^e
<i>Polytremis pellucida</i>		1.06	2.16	1.15	1.457	34.18		2.06	0.97	0.44	2	P	ToG
<i>Ypthima argus</i>		1.17	2.24	0.33	1.245	62.64		0.41	0.53	0.04	M	P	TG
<i>Eurema hecabe</i>		1.62	1.15	0.60	1.122	37.36		0.72	0.68	0.39	M	P	TG
<i>Parnara guttata</i>		1.32	1.14	0.60	1.019	29.95		1.14	0.24	0.42	M	P	TG
<i>Neope</i> sp.		0.95	1.19	0.87	1.001	13.70		2.01	0.56	0.04	2	P	ToG
<i>Eurema laeta</i>		1.62	0.70	0.26	0.858	66.03		0.17	0.25	0.36	M	O	RS
<i>Pseudozizeeria maha</i>		0.50	1.26	0.73	0.830	38.65		1.86	0.17	0.15	M	O	RS
<i>Lycaena phlaeas</i>		0.86	1.39	0.12	0.791	65.58		0.20	0.06	0.12	M	O	RS
<i>Celastrina argiolus</i>		0.60	0.57	1.00	0.726	26.73		2.13	0.76	0.11	M	P	TG
<i>Taraka hamada</i>		0.90	1.13	0.11	0.713	61.14			0.11		M	C ^f	RS
<i>Everes argiades</i>		0.95	0.85	0.11	0.639	58.57		0.10		0.13	M	P	TG
<i>Mycalasis gotama</i>		0.39	1.08	0.21	0.559	66.95		0.43	0.13	0.08	M	P	TG
<i>Minois dryas</i>		1.22	0.23	0.19	0.545	87.32			0.33	0.04	1	P	ToG
<i>Papilio xuthus</i>		0.67	0.55	0.31	0.508	29.56		0.52	0.31	0.11	M	P	TG
<i>Thoressa varia</i>		0.18	1.00	0.27	0.482	75.61			0.50	0.04	2	P	ToG
<i>Hestina japonica</i>		0.58	0.74	0.10	0.472	57.31		0.10			2	O	TS
<i>Lethe sicilis</i>		0.77	0.35	0.29	0.466	45.96		0.30	0.48	0.08	2	P	ToG
<i>Neptis sappho</i>		0.73	0.53	0.11	0.459	55.85		0.22	0.07	0.06	M	P	TG
<i>Antigius attilia</i>		0.50	0.69	0.10	0.430	57.19		0.10			1	P	ToG
<i>Pelopidas mathias</i>		0.27	0.92	0.11	0.429	81.92		0.15		0.07	M	P	TG
<i>Curetis acuta</i>		0.40	0.61	0.22	0.410	38.82		0.30	0.14		M	P	TG
<i>Polygona c-aureum</i>		0.51	0.58	0.09	0.393	54.47		0.10	0.09		M	O	RS
<i>Erynnis montanus</i>		0.77	0.15	0.11	0.342	87.74			0.11		1	O	TS
<i>Papilio machaon</i>		0.33	0.42	0.10	0.284	46.43		0.17	0.06	0.09	M	P	TG
<i>Papilio protenor</i>		0.24	0.42	0.18	0.278	36.68		0.29	0.06		M	P	TG
<i>Limnitis camilla</i>		0.32	0.39	0.12	0.277	40.20		0.16	0.09		M	O	RS
<i>Colias erate</i>		0.14	0.56	0.12	0.271	74.87			0.13	0.11	M	P	TG
<i>Papilio bianor</i>		0.29	0.24	0.25	0.260	8.52		0.39	0.11		2	O	TS
<i>Apatura metis</i>		0.19	0.42	0.10	0.237	56.93		0.10			2	P	ToG
<i>Narathura japonica</i>		0.16	0.39	0.11	0.218	55.18			0.11		2	P	ToG
<i>Anthocharis scolymus</i>		0.09	0.32	0.20	0.203	45.87		0.20			1	P	ToG
<i>Favonius orientalis</i>		0.19	0.26	0.13	0.192	26.63		0.20	0.06		1	O	TS
<i>Limnitis glorifica</i>		0.15	0.34	0.08	0.189	58.51		0.10	0.06		2	O	TS
<i>Daimio tethys</i>		0.23	0.18	0.11	0.174	27.63		0.16	0.06		M	O	RS
<i>Graphium sarpedon</i>		0.14	0.22	0.15	0.167	20.54		0.15			M	P	TG
<i>Kaniska canace</i>		0.21	0.21	0.08	0.164	36.20		0.10	0.06		M	P	TG
<i>Nymphalis xanthomelas</i>		0.09	0.28	0.10	0.157	55.73		0.10			1	P	ToG
<i>Vanessa indica</i>		0.10	0.16	0.20	0.151	28.62		0.20			M	P	TG
<i>Potanthus flavum</i>		0.12	0.17	0.06	0.115	37.40			0.06		2	P	ToG
<i>Isoteinon lamprospilus</i>		0.75	0.18		0.464	61.19					1	O	TS
<i>Pieris (m. or n.) sp.</i>		0.29	0.53		0.407	29.02					M	P	TG
<i>Atrophaneura alcinous</i>		0.41	0.40		0.404	1.44					M	O	RS
<i>Mycalasis francisca</i>		0.37	0.44		0.404	7.86					2	O	TS
<i>Pieris rapae</i>			0.60	0.11	0.358	68.20		0.12		0.11	M	P	TG
<i>Lampides boeticus</i>		0.38	0.28		0.328	15.74					M	P	TG
<i>Papilio macilentus</i>		0.31	0.20		0.254	20.33					2	O	TS
<i>Damora sagana</i>		0.20	0.15		0.174	13.67					1	O	TS
<i>Nepharlynnis anadyomene</i>		0.12	0.16		0.143	14.29					1	O	TS
<i>Rapala arata</i>		0.09		0.18	0.133	32.08		0.29	0.06		2	P	ToG
<i>Cynthia cardui</i>			0.16	0.10	0.130	23.08		0.10			M	P	TG
<i>Neozephyrus taxila</i>			0.65		0.647						1	O	TS
<i>Dichorragia nesimachus</i>		0.30			0.300						2	O	TS
<i>Argynnis paphia</i>		0.29			0.290						1	O	TS
<i>Polygona c-album</i>		0.28			0.280						2	P	ToG
<i>Japonica lutea</i>		0.19			0.190						1	O	TS
<i>Japonica saepestrata</i>			0.14		0.140						1	O	TS
<i>Papilio helenus</i>				0.10	0.100			0.10			2	P	ToG
<i>Neptis philyra</i>		0.09			0.090						1	P	ToG
<i>Sasakia charonda</i>		0.09			0.090						1	O	TS
<i>Callophrys ferrea</i>		0.09			0.090						1	P	ToG
<i>Ochlodes ochracea</i>		0.09			0.090						2	P	ToG
<i>Argyronome ruslana</i>		0.09			0.090						1	O	TS

^a No. of adults/ 100 m /month. Sections where no butterflies were observed are excluded in the calculation of this value. See text for the method of exact calculation.

^b No. of adults/ 100 m /month.

^c Number of generations per year. M (multivoltine); more than bivoltine.

^d Range of acceptable larval hostplants. O (oligophagy), species whose larvae had been reported feeding on 10 or less plant species belonging to one taxonomic family; P (polyphagy), species the larvae of which had been reported feeding on more than 10 plant species belonging to one taxonomic family, or on a variety of hostplants belonging to two or more taxonomic families; C, carnivorous.

^e Adaptive strategy. TG, typical generalist species; ToG, tolerant generalist species; TS, typical specialist species; RS, rebound specialist species.

^f Carnivorous was treated as oligophagous in this study.

