# Habitat Preferences, Distribution and Seasonality of the Butterflies (Lepidoptera, Papilionoidea) in a Montane Tropical Rain Forest, Vietnam

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**Abstract.** In this paper, the butterfly community of the Tam Dao montane rain forest in northern Vietnam is described ecologically and biogeographically. A negative correlation between the size of species geographic range and maturity of the successional stage of its preferred habitat was found. This means that butterflies confined to the climax forest tend to have a small range of distribution of endemitic type, whereas species associated with disturbed ruderal and similar habitats are much more widely distributed. Within the forest, understorey species are most habitat specific and endemitic, with the most important conservation value. Canopy fauna is much more heterogeneous and diverse, containing also non-forest components. The pronounced temporal change in the forest community is determined by the relatively higher seasonality of species with biogeographical affinities to the seasonal 'East Himalayan' region.

Apart from this historical component, the irregular migratory behaviour and response to the seasonal change in local environmental factors seem to be important. In the ruderal habitat, butterflies with large geographic range tend to have the highest population sizes; the reverse is true for the forest community. Differences in current and historical habitat commonness and disturbance intensity are proposed to explain this pattern. The present investigations of the butterfly community indicate the great importance of the Tam Dao rain forest for preservation of the biodiversity on frontiers between the Oriental and Palaearctic Regions.

**Key words.** Butterflies, montane rain forest, Vietnam, habitat preferences, disturbance, seasonality, geographic range, ordination, conservation.

## INTRODUCTION

Disturbance is generally considered to be one of the most important determinants of ecological community composition (Pianka, 1974; Grime, 1979; Southwood, 1988). The habitat preferences are closely related to the life history strategies of respective species; as the geographical range is also influenced by the species strategy, the correlations of species geographical range and its habitat preferences are expected and indeed they were documented (Spitzer & Lepš, 1988, Lepš & Spitzer, 1990, Novotný, 1991). At present, many data sets demonstrating the influence of disturbance are available for plant communities in temperate regions. On the contrary, data from tropical regions are rare and quantitative data on insect communities are rare as well.

The insect seasonality was demonstrated in all parts of the world, including equatorial tropics (Wolda, 1978a, b, 1988; Denlinger, 1986). Nevertheless, data, enabling the comparison of seasonality in various habitats and degree of

seasonal change in the activity of particular species are relatively rare. The mountain forest on the border of a tropical zone is particularly interesting from the seasonality point of view, as it includes species without pronounced seasonality, species with seasonality induced by environmental variation and species with seasonal behaviour as a consequence of their evolutionary history (i.e. species penetrating from the temperate monsoon environment).

Butterflies perform a suitable group for ecological studies. Their taxonomy is known (in comparison with other tropical insect groups) and there are some data available on their geographic distribution and for some species also on their life history. This is in contrast with other insect groups in the tropics, where one is often limited to working with morphospecies only.

The Tam Dao mountains is a small ridge in northern Vietnam (Fig. 1), covered by montane rain forest, surrounded by deforested areas. The butterfly communities in the Tam Dao mountains (Fig. 2) are a suitable object for a test of ecological hypotheses about the relation between a
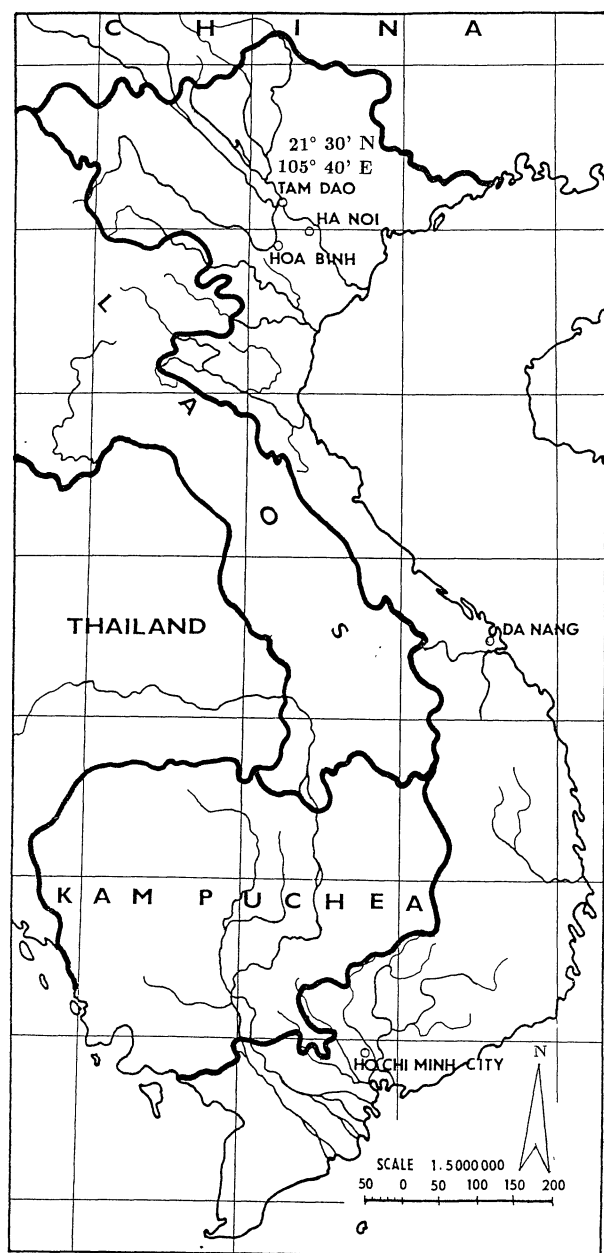
FIG. 1. Location of the Tam Dao Mountains in Vietnam.

successional status) and to obtain information about the habitat preference and seasonal behaviour of particular species of butterflies, some of which are of very restricted distribution or/and new for the area; (2) to test the hypothesis that there is a correlation between species habitat preference and its geographic range; supposedly, species with a large geographic area will prefer the most disturbed habitats; (3) to test differences between seasonal aspects in various habitat types; and (4) to provide data for the conservation of tropical Indochinese butterfly communities, based on a complete list of species and statistics of their ecological and biogeographical determinants.

## STUDY AREA

The study was carried out in the Tam Dao Mountains, a small ridge in northern Vietnam (75 km north of Hanoi, 21°30'N, 105°40'E, Fig. 1), reaching over 1200 m a.s.l., covered by 19,000 ha of evergreen montane rain forest that has been protected as a nature reserve since 1977. The area constitutes one of the very few last remnants of relatively undisturbed forest in this part of SE Asia. It is also important from the biogeography point of view, as it lies in mountains near the border of the tropics—'a zone in which tropical and northern temperate species mingle in great diversity' (Stott, 1991). The weather has a pronounced yearly periodicity, with one wet season (from May to September) and a relatively cold winter (see Fig. 3). There are some elements of temperate origin also in the composition of the forest (e.g. several species of maples—*Acer*, which are loosing their leaves towards the end of the wet season). From this point of view, the seasonality and its relation to actual environmental change and to the evolutionary history of a taxon is of interest. The human inference is more and more visible in the Tam Dao Mts; it is possible to find here ecosystems under various degree of disturbance— ranging from ruderals and agroecosystems in proximity of the village of Tam Dao to relatively undisturbed montane forest.

With respect to the degree of disturbance, we distinguished three zones: ruderal zone, transitional zone and forest zone. Their characteristics are as follows. (The nomenclature of plants chiefly follows Pham Hoang Ho (1970–72) with some corrections based on suggestions of J. E. Vidal-pers. comm.).

## Ruderal zone

The ruderal zone consists of cultivated and abandoned terraced fields on relatively steep slopes. The most common crops are batatas, other crops are ginger, manihot, bananas, citruses, peanuts and forms of *Raphanus sativus* L. The abandoned fields are overgrown by tall grasses such as *Miscanthus floridulus* (Labill.) Warb. and *Thysanolaena maxima* (Roxb.) O.Ktze and the short grass *Panicum lusonense* Presl. The most common scattered shrubs are *Saurauja roxburghii* Wall., *Duranta repens* L., *Debregeasia velutina* Gaud., *Rhus* cf. *chinensis* Muller and planted and feral citruses. The shrubs are accompanied by vines, particularly *Ipomoea* (e.g. *I. cairica* (L.) Sw.). Ruderal forbs are

species geographical distribution, its habitat preferences and seasonal behaviour; there are reasonably distinct habitats on a gradient of disturbance intensity, the communities are species rich (more than 100 species, excl. Lycaenidae), and individuals are sufficiently abundant. In general, very few data sets on butterfly communities are available from the Australasian region (Bowman *et al.*, 1990; Spitzer, *et al.*, 1987, Lepš & Spitzer, 1990). Nevertheless, in the Tam Dao Mountains, we could continue our previous investigations (Lepš & Spitzer, 1990).

The aim of this study is: (1) to compare species composition of butterfly communities in habitat types differing in the degree of disturbance (and supposedly in their

FIG. 2. Junglequeen (*Stichophthalma louisa*)—a characteristic forest butterfly in Tam Dao.
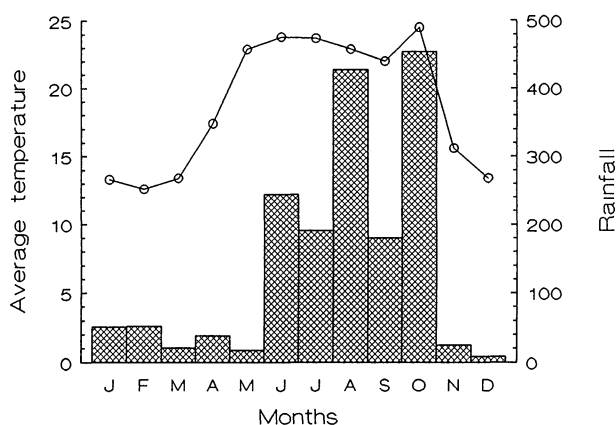


FIG. 3. Rainfall (bars, in mm) and average temperature (dots, in °C) in Tam Dao village (800 m a.s.l.) in 1988.

common such as *Synedrella nodiflora* (L.) Gaertn., *Ageratum conyzoides* L., *Bidens pilosa* L., *Solanum torvum* Swartz, *S. virginianum* L. The zone is a typical example of vegetation created by traditional agricultural activities in Indochina ('shifting agriculture', multiple cropping, and frequent disturbance). Such a long history of traditional

agriculture, distribution dynamics of opportunistic plant species and successional changes in SE Asia were discussed recently by Rambo & Sajise (1984), Chin (1985), and by Stott (1991). The degree of disturbance is high in this zone and the plant communities could be considered to be 'early successional'.

## Transitional zone

The transitional zone consists mainly of clearings with scattered shrubs (e.g. *Saurauja roxburghii* Wall., *Ficus* spp.) and clumps of trees (e.g. *Pasania fissa* Oersted var. *tonkinensis* Hickel et A.Camus) and shrubs. Both trees and shrubs support vines (e.g. *Hodgsonia* cf. *macrocarpa* Cognx.) and epiphytes (including hemiparazitic Loranthaceae and Santalaceae). The treeless parts are covered with tall grasses *Thysanolaena maxima* (Roxb.) O.Ktze and *Miscanthus floridulus* (Labill.) Warb., and patches of *Rubus alceaefolius* Poiret and *R. sorbifolius* Maxim. Local landslides (about 20%) and open land are characterized by fern *Dicranopteris linearis* (Burm.) Underw. and orchid *Arundina graminifolia* (Don) Hochr. Wild bananas and citruses are also present. The zone is very heterogeneous, containing patches of forest tree clumps as well as open areas with many species found also in the ruderal zone (e.g. *Rhopalephora scaberrima* (Bl.) Faden. and other Commelinaceae, *Polygonum chinense* L.,

*P. hydropiper* L., *Aeginetia* sp., *Aralia armata* Seem., *Urena lobata* L., *Houttuynia cordata* Thunb.). In this zone, disturbance is of medium intensity (between that of ruderal and forest zones). The vegetation is, in fact, a mosaic of patches of varying successional age; nevertheless, in majority, the successional age is higher than in the ruderal zone and obviously lower than in the forest zone.

## Forest zone

The closed forest (climax formation) is disturbed only by illegal selective logging by native people. It is rich in plant species—we estimated that there were at least 200 woody species along the two transects investigated in 1988. Emergent trees (incl. Dipterocarpaceae) were nearly eliminated in all accessible places. There were no apparent dominant trees there. In the tree layer, there are commonly found Fagaceae (mainly *Pasania fissa* Oersted var. *tonkinensis* Hickel et A. Camus, some oaks—*Quercus* spp.), Juglandaceae (e.g. *Engelhardtia roxburghiana* Lindl. ex Wall.), Annonaceae (e.g. *Polyathia* sp.), Magnoliaceae (*Michelia* sp.), Aceraceae (*Acer* spp.), and many species from various families (e.g. *Syzygium imitans* Merr. et Perry, *Eberhardtia* cf. *tonkinensis* H. Lec., *Dillenia* sp.). An especially species rich group of small trees and shrubs includes e.g. *Ardisia* cf. *sauraujaefolia* Pit., several species of *Ficus* (e.g. *F. hirta* Vahl), *Mallotus paniculatus* (Lamk.) Muell. Arg., *Tupidantus* sp., *Macaranga auriculata* (Merr.) A. Shaw, *M. denticulata* (Bl.) Muell. Arg., *Breynia indosinensis* Beille, *Symplocos* sp., *Maesa* sp., various Theaceae (*Eurya* sp., *Schima* sp.), Rubiaceae (*Gartnera* sp., *Chasalia curviflora* Thwaites, *Psychotria* sp., *Lasianthus* sp.), Melastomataceae (*Melastoma* spp., *Blastus borneensis* Cogn. var. *eberhardtii* (Guill.) C. Hans.), Polygalaceae (*Polygala* sp.), Verbenaceae (*Clerodendrum cyrtophyllum* Turcz), Rutaceae (*Atalantia* sp.), Caprifoliaceae (*Viburnum* sp.), Euphorbiaceae (*Alchornia* sp.), Urticaceae (*Villebrunea* sp.)., Apocynaceae (*Tabernaemontana* cf. *bovina* Lour.), tree ferns (*Cyathea*) and many others. The trees support many epiphytes, mainly orchids and ferns, hemiparasitic epiphytes from Loranthaceae (e.g. *Taxillus sinensis* (DC.) Danser) and Santalaceae (e.g. *Henslowia* cf. *umbelata* Bl.) and numerous climbers, e.g. *Epipremnum pinnatum* (L.) Engl. (the most common one), *Pothos* spp., *Smilax* spp., *Acacia pennata* (L.) Willd., *Bauhinia* sp., *Gnetum* cf. *montanum* Mgf., various species of Vitaceae (e.g. *Tetrastigma erubescens* Planch.), ferns, bamboos and palms (*Calamus* sp.). The gaps (natural or more often after illegal logging) are quickly overgrown by bamboos and various shrubs.

The forest understory is scattered (with cover of less than 50%) with sedges, grasses, ferns (incl. *Selaginella delicatula* (Desv.) Alston), many Zingiberaceae (*Zingiber* sp., *Alpinia* sp., *Amomum* sp.), small palms (*Caryota* sp., *Licuala* sp.) and other species: e.g. *Pandanus* sp., *Begonia* spp., *Amorphophallus paeoniifolius* (Dennst.) Nicols. var. *campanulatus* (Dene) Sivad., *Piper* spp., *Rhopalephora scaberrima* (Bl.) Faden, *Belamcanda chinensis* (L.) DC., *Curculigo* sp., *Anoectochilus* sp., *Balanophora fungosa* J.R. & G. Forster.

We are not aware of any detailed description of this forest type. In general, the formation of Tam Dao forest conforms with outlines and characteristics of the Indochinese montane forest described by Vidal (1979).

## METHODS

### Data collection

Intensive regular sampling was carried out between 2 and 22 September 1988, in late wet season, and between 5 June and 7 July 1991, in early wet season (Fig. 3). A few short term visits in other parts of the year also provided complementary information.

The data were collected using the transect method described by Pollard et al. (1975) and Pollard (1977) and applied in our previous studies (Spitzer et al., 1987, Lepš & Spitzer, 1990). Two observers walking together along each transect at the speed of approximately 100 m per 10 min recorded all butterflies seen (except Lycaenidae and Hesperiidae) in a belt approximately 20–40 m wide. Each transect was checked usually twice a day, in the morning and about midday. A few late afternoon samples were also taken.

Transects were located along a path tracking a contour at 800 m a.s.l., intersecting habitats of the three zones representing the gradient of a successional maturity: ruderal communities, transition zone, and closed forest. In 1988, four 200 m transect were demarcated: one in the ruderal zone, one in the transitional zone, and two in the natural forest. The exact same transects were used in 1991, but the ruderal and transition ones were extended and the two forest transect united, so that one 500 m transect was established in each of the three habitats.

Whereas ruderal and transition transect could be sampled adequately by the transect method, the forest canopy was only poorly amenable to the study. This is why the forest data refer mainly to the understorey. To overcome this drawback, supplementary point observations of canopy fauna were repeatedly performed in suitable places where the forest transect intersected an extremely steep slope so that the canopies of the trees growing down-hill could be seen. In this way, data on species-specific preferences of forest butterflies with respect to understorey, canopy, and flowering canopy trees were gained. In addition to transect counts, another four locations in the forest were visited and a 2 h lasting quantitative observation of their butterfly fauna was completed. Plot 1 was a 100 × 150 m enclave with small fields and ruderal communities, surrounding the Tay Tien Pagoda, situated 6 km into the forest. Plot 2 was a small clearing (< 100 m²) within the forest, about 1 km away from its edge, overgrown mainly with *Thysanolaena maxima*. Plots 3 and 4 were summits of two prominent hills within the forest. They both were completely forested, but trees on the very top of them were not tall, so that their canopy could be sampled. However, we are aware that the butterfly counts obtained by this method are not directly comparable to counts from classical Pollard's (1977) method; they were used mainly to illustrate the relative preferences of species. Obviously, the transect method is

less efficient for canopy fliers. Data from plots 1–4 were not included in diversity calculations.

## Geographic distribution

The taxonomic characteristics of the butterflies and their geographic ranges are derived from literature (Fruhstorfer, 1927; Kirchberg, 1942; Eliot, 1969; Holloway, 1973, 1984; Lewis, 1973; Fleming, 1975; Lekagul *et al.*, 1977; Corbet *et al.*, 1978; Arora & Mondal, 1981; Collins & Morris, 1985; Koiwaya, 1989; Yata, 1989) and our unpublished data.

The geographical distribution was categorized on the scale of 1–6 (smallest to largest) as follows:

1. East Himalayas, Yunnan and northern Indochina.
2. India and Indochina.
3. Oriental (Indo-Malayan) region.
4. Indo-Australian (Australasian) tropics.
5. Palaeotropics.
6. Larger than Palaeotropics—Cosmopolitan.

Distribution limits of some endemitic taxa of category 1 are not clear in subtropical China.

## Data analysis

Community data were analysed by means of CCA ordination to determine the relative importance of spatial and temporal variability in their composition (Ter Braak, 1986, 1987).

Canonical correspondence analysis (CCA) is a direct ordination method which relates the composition of samples to external (environmental) variables. It orders sampling units in such a way to obtain the best correlation between a linear combination of these variables and species abundance data. The CCA also allows for the filtering out of the influence of particular external variables (so called covariables) from the data. With covariables, CCA works only with the residual variation that remains after fitting the effect of covariables. The proportion of data variability which can be accounted for by environmental variables can be estimated by the hybrid CCA as the ratio of eigenvalues of constrained versus unconstrained axes. Constrained axes are constructed to maximize the fit with linear combinations of environmental variables, and remaining (unconstrained) axes represent a residual variation in the species data after extracting the constrained axes. The significance of the relationships between selected external variables and data structure can be tested by the Monte Carlo test. Values of external variables are randomly assigned to the samples and eigenvalues of the CCA analysis with new data compared with that of original data. With covariables, the Monte Carlo test, with permutations only within classes determined by environmental variables, can be performed. The method allows for the use of 'passive samples'—i.e. samples that do not influence the axes, but they are, after the extraction of axes, placed into the system according to their species composition (see Ter Braak, 1986, 1987 for detailed information on the CCA method).

The successional status of a habitat and season were used as external variables to explain the community structure of butterflies. The particular habitat types were selected to reflect the gradient of disturbance intensity (or successional maturity). Correspondingly, the value of 'successional status' was assigned 1 for the ruderal transect, 2 for the transitional transect and 3 for the forest transects. The optimum of species on the successional gradient is expressed by its score on the first (i.e. constrained) axis—low values are typical for ruderal species, high for species of undisturbed forest. The scaling of the axis is in the 'SD-units'; it roughly means that samples which are distant by 4 SD-units in ordination should have no common species and species 4 SD-units apart should not be found together (see Ter Braak, 1986, 1987 for a more technical explanation). Analogously, the species' seasonality was assessed by means of the CCA analysis with 'season' as an external variable with the value of 0 assigned to early wet season and the value of 1 to late wet season. To disentangle the effects of habitat and seasonal preferences of a species, the CCA analyses with successional status as an external variable and season as a covariable, and vice versa, were carried out.

An analysis of fine scale distribution of butterflies within the closed forest among 'understorey', 'canopy', and 'flowering trees' as habitat units was completed by means of the CCA ordination with each of these habitats used as a nominal external variable. The CCA score obtained by hybrid CCA ordination with one axis constrained was used as an indication of a species' optimum on the understorey - canopy gradient.

## RESULTS

### Habitat preference

The degree of habitat disturbance (or the successional maturity of present plant communities) is an important determinant of species composition; the first (constrained) ordination axis of CCA in highly significant. A list of all species of Tam Dao and their habitat preferences are given in Table 1. The most specific fauna is characteristic for the forest community: most of *Lethe* spp., *Neorina westwoodi* (= *N. patria* subsp. *westwoodi*), *Mandarinia regalis*, *Ragadia crisilda*, *Stichophthalma louisa* (incl. forms *sparta*, *mathilda*, and '*tonkiniana*'; their taxonomic status is not clear). Species like *Euploea mulciber*, *Argyreus hyperbius*, *Eurema hecabe*, *Papilio memnon* and *P. demoleus* are characteristic for ruderal transect with open vegetation formations. The most typical migratory species are temporarily associated with the same habitat as well.

The relationship between the size of geographic range and the species' position on the ruderal–forest gradient (expressed by means of the CCA score) is significant (Table 2). This means that species of the climax forest tend to have, on average, more restricted geographic distribution than species occurring in disturbed ruderal areas (Fig. 4).

### Distribution within forest

The forest butterfly community can be divided into two clear-cut strata (Fig. 5). There is a group of crepuscular un-

TABLE 1. Distribution of butterflies among habitats, their seasonality, and geographic distribution.

| Species | Distribution Habitat | | | Season | | CCA score Habitat | Season | Range |
|---|---|---|---|---|---|---|---|---|
| **Papilionidae** | | | | | | | | |
| *Atrophaneura crassipes* (Ober.) | | | (f) | (e) | | | | 2 |
| *Atrophaneura varuna* (Wh.) | | t | f | e | l | 1.45 | 1.53 | 2 |
| *Chilasa clytia* (L.) | (r) | | | | (l) | | | 3 |
| *Graphium agamemnon* (L.) | r | | f | e | | 0.14 | −1.75 | 4 |
| *Graphium sarpedon* (L.) | r | t | f | E | L | −1.24 | 0.49 | 4 |
| *Lamproptera curius* (F.) | r | t | f | e | l | 0.19 | 0.83 | 3 |
| *Meandrusa gyas* (Westw.) | r | t | (f) | e | | −0.81 | −1.77 | 1 |
| *Meandrusa payeni* (Bsd.) | | t | | | l | 0.22 | 2.38 | 2 |
| *Pachliopta aristolochiae* (F.) | (r) | | | | (l) | | | 3 |
| *Papilio chaon* Westw. | r | t | | e | | −0.84 | −1.77 | 2 |
| *Papilio demoleus* L. | R | | | e | l | −2.17 | 2.20 | 4 |
| *Papilio helenus* L. | R | T | F | E | L | −0.57 | −0.73 | 4 |
| *Papilio memnon* L. | R | T | f | E | L | −1.17 | 0.37 | 3 |
| *Papilio paris* L. | R | T | f | E | L | −0.98 | −0.09 | 3 |
| *Papilio polytes* L. | r | t | (f) | e | l | −1.23 | 1.17 | 3 |
| *Papilio protenor* Cr. | | (t) | (f) | | (l) | | | 2 |
| *Pathysa antiphates* Cr. | (r) | t | f | e | (l) | 0.44 | −1.75 | 3 |
| *Troides aeacus* (Feld.) | r | T | f | e | l | 0.40 | 2.06 | 2 |
| *Troides helena* (L.) | r | T | f | e | l | 0.40 | 2.06 | 3 |
| **Pieridae** | | | | | | | | |
| *Appias albina* (Bsd.) | R | t | | e | l | −1.54 | −0.44 | 3 |
| *Appias indra* (Moore) | | (t) | | (e) | | | | 2 |
| *Appias lalage* (Dbld.) | r | t | | e | (l) | −1.05 | −1.77 | 3 |
| *Appias lyncida* (Cr.) | r | t | | e | | −0.34 | −1.76 | 3 |
| *Appias nero* (F.) | | t | | | l | 0.22 | 2.38 | 3 |
| *Catopsilia pomona* (F.) | (r) | | | | (l) | | | 5 |
| *Cepora nadina* (Lucas) | r | t | f | e | l | −1.25 | −0.76 | 3 |
| *Delias acalis* (Godart) | | | f | e | | 2.52 | −1.71 | 2 |
| *Delias aglaja* (L.) | r | t | f | e | | −0.98 | −1.77 | 3 |
| *Delias agostina* (Hew.) | r | t | f | e | l | 1.16 | −0.01 | 2 |
| *Dercas verhuelli* (V.D.Hv.) | | t | f | e | (l) | 0.73 | −1.74 | 2 |
| *Eurema blanda* (Bsd.) | (r) | | | (e) | | | | 3 |
| *Eurema hecabe* (L.) | R | T | (f) | E | (l) | −1.40 | −0.76 | 4 |
| *Hebomoia glaucippe* (L.) | R | T | f | e | L | −0.58 | 1.34 | 3 |
| *Ixias pyrene* (L.) | r | | f | e | | −1.29 | −1.78 | 3 |
| *Pieris canidia* (L.) | R | t | | E | l | −2.19 | −1.19 | 3 |
| *Prioneris philonome* (Bsd.) | | (t) | | | (l) | | | 2 |
| *Prioneris thestylis* (Dbld.) | R | T | F | E | L | 0.33 | −0.64 | 2 |
| **Danaidae** | | | | | | | | |
| *Danaus genutia* (Cr.) | r | (t) | | e | l | −2.22 | −0.58 | 4 |
| *Euploea doubledayi* (Feld.) | | | (f) | | (l) | | | 2 |
| *Euploea midamus* (L.) | R | t | f | E | l | −0.86 | −1.56 | 2 |
| *Euploea mulciber* (Cr.) | R | T | F | E | L | −0.87 | −0.11 | 3 |
| *Parantica aglea* (Stoll) | r | t | f | e | l | −1.39 | 1.35 | 2 |
| *Parantica melaneus* (Cr.) | r | t | f | e | (l) | −0.73 | −1.77 | 3 |
| *Parantica sita* (Koll.) | r | t | F | E | l | 1.31 | −1.28 | 3 |
| *Radena similis* (L.) | r | | | | l | −2.16 | 2.33 | 3 |
| *Tirumala limniace* (Cr.) | r | t | f | e | l | −0.06 | −0.47 | 3 |
| *Tirumala septentrionis* (Butl.) | r | t | f | e | l | −1.29 | −0.73 | 4 |
| **Satyridae** | | | | | | | | |
| *Lethe confusa* Auriv. | | (t) | (f) | | (l) | | | 3 |
| *Lethe gemina* (Leech) | | t | f | e | (l) | 2.53 | 1.97 | 1 |
| *Lethe kansa* (Moore) | r | t | f | E | (l) | 1.33 | −1.73 | 2 |
| *Lethe mekara* (Moore) | | (t) | F | e | l | | | 3 |
| *Lethe philemon* Fruhst. | | t | f | e | | 1.93 | −1.72 | 1 |

TABLE 1. (Cont.)

| Species | Distribution | | | | | CCA score | | Range |
|---|---|---|---|---|---|---|---|---|
| | Habitat | | | Season | | Habitat | Season | |
| *Lethe syrcis* (Hew.) | | | f | e | | 2.52 | −1.71 | 1 |
| *Lethe verma* (Koll.) | R | t | f | e | L | −1.03 | 2.04 | 3 |
| *Lethe vindhya* (Feld.) | | t | f | e | | 1.73 | −1.72 | 2 |
| *Mandarinia regalis* Leech | | (t) | f | e | (l) | 2.52 | −1.71 | 1 |
| *Melanitis leda* (L.) | r | t | f | e | (l) | −1.65 | −1.78 | 5 |
| *Melanitis zitenius* (Herbst) | (r) | (t) | | | (l) | | | 3 |
| *Mycalesis gotama* (Moore) | (r) | t | f | e | (l) | 1.57 | −1.72 | 3 |
| *Mycalesis lepcha* (Moore) | | t | f | | l | 2.60 | 2.42 | 3 |
| *Mycalesis mineus* (L.) | | t | f | e | | 1.73 | −1.72 | 3 |
| *Mycalesis perseus* (F.) | | t | f | e | (l) | 1.73 | −1.72 | 4 |
| *Mycalesis unica* (Leech) | | t | f | e | | 1.73 | −1.72 | 1 |
| *Neope bhadra* (Moore) | | (t) | | | (l) | | | 1 |
| *Neorina westwoodi* (Moore) | | | f | | l | 2.60 | 2.42 | 1 |
| *Ragadia crisilda* Hew. | r | T | F | E | L | 2.41 | 2.05 | 2 |
| *Ypthima baldus* (F.) | R | t | f | E | L | −1.37 | 0.37 | 3 |
| *Ypthima motschulskyi* (Brem.) | r | t | f | e | | 0.83 | −1.74 | 2 |

Amathusiidae

| Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Aemona amathusia* Hew.* | | | (f) | | (l) | | | 2 |
| *Enispe euthymius* (Dbld.) | | t | | e | | 0.14 | −1.75 | 2 |
| *Faunis aerope* (Leech) | | t | F | e | (l) | 2.06 | −1.71 | 1 |
| *Faunis canens* (Hb.) | | | (f) | (e) | | | | 2 |
| *Faunis eumeus* (Drury) | r | | | e | | −2.24 | −1.80 | 2 |
| *Stichophthalma louisa* Wood-Mason | r | T | F | E | L | 1.98 | −1.34 | 1 |
| *Thaumantis diores* Dbld. | | | (f) | | (l) | | | 1 |

Nymphalidae

| Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Argyreus hyperbius* (Joh.) | R | t | (f) | E | L | −2.09 | 0.74 | 5 |
| *Ariadne ariadne* (L.) | R | t | | e | L | −2.13 | 2.27 | 3 |
| *Athyma cama* (Moore) | | (t) | | | (l) | | | 3 |
| *Athyma perius* (L.) | r | t | | | l | −1.69 | 2.34 | 3 |
| *Athyma selenophora* (Koll.) | r | (t) | f | | l | −1.48 | 2.34 | 3 |
| *Auzakia danava* Moore | | | (f) | (e) | | | | 1 |
| *Bhagadatta austenia* Moore | | | (f) | (e) | | | | 1 |
| *Cethosia biblis* (Drury) | r | t | f | e | (l) | −1.41 | −1.78 | 3 |
| *Cethosia cyane* (Drury) | r | t | | | l | −1.37 | 2.35 | 2 |
| *Chersonesia risa* (Dbld.) | r | | | e | | −2.24 | −1.80 | 3 |
| *Cirrochroa tyche* (Feld.) | R | t | f | E | l | −1.55 | −0.30 | 3 |
| *Cupha erymanthis* (Drury) | r | t | f | e | | −0.81 | −1.77 | 4 |
| *Cynthia cardui* (L.) | r | | (f) | e | l | −2.20 | 0.50 | 6 |
| *Cynthia indica* (Herbst)* | (r) | | | | | | | 5 |
| *Cyrestis thyodamas* (Bsd.) | R | t | f | E | (l) | −1.39 | −1.78 | 3 |
| *Dichorragia nesimachus* (Doy.) | | | (f) | (e) | | | | 2 |
| *Euripus nyctelius* (Dbld.) | | t | | | l | 0.22 | 2.38 | 3 |
| *Hestina nama* (Dbld.) | r | t | | e | l | −1.51 | 1.16 | 3 |
| *Kaniska canace* (L.) | (r) | | | (e) | | | | 3 |
| *Neptis hylas* (L.) | r | t | f | e | (l) | −1.45 | −1.78 | 4 |
| *Neptis miah* Moore | | (t) | (f) | (e) | (l) | | | 2 |
| *Neptis nata* (Moore) | r | t | | | l | −0.38 | 2.36 | 3 |
| *Neurosigma doubledayi* (Westw.) | | | f | | l | 2.60 | 2.42 | 1 |
| *Parthenos sylvia* (Cr.) | R | t | f | | L | −1.62 | 2.34 | 4 |
| *Penthema lisarda* Dbld. | | (t) | (f) | | (l) | | | 1 |
| *Phalanta phalanta* (Drury) | r | | | e | | −2.24 | −1.80 | 5 |
| *Polygonia c-aureum* (L.) | r | | f | e | | 0.14 | −1.75 | 3 |
| *Polyura nepenthes* (Grose Smith) | | (t) | | | (l) | | | 1 |
| *Precis atlites* (L.) | r | | | e | | −2.24 | −1.80 | 3 |
| *Precis almana* (L.) | r | | | e | | −2.24 | −1.80 | 3 |
| *Pseudergolis wedah* (Koll.) | | t | | | l | 0.22 | 2.38 | 2 |
| *Rohana parisatis* Westw. | | (t) | | | (l) | | | 3 |
| *Stibochiona nicea* (Gray) | r | T | F | E | L | 0.99 | 0.49 | 2 |
| *Sumalia daraxa* (Dbld.) | r | t | (f) | e | (l) | −1.05 | −1.77 | 3 |

TABLE 1. (Cont.)

| Species | Distribution | | | | | CCA score | | Range |
|---|---|---|---|---|---|---|---|---|
| | Habitat | | | Season | | Habitat | Season | |
| *Symbrenthia hippoclus* (Cr.) | r | t | (f) | e | (l) | −1.16 | −1.78 | 3 |
| *Vagrans egista* (Cr.) | R | T | f | E | l | −1.51 | −1.22 | 4 |
| *Vindula erota* (F.) | R | T | f | E | L | −0.28 | 0.69 | 3 |
| Riodinidae | | | | | | | | |
| *Abisara fylla* (Dbld.) | | t | f | e | l | 2.07 | 1.81 | 2 |
| *Abisara neophron* (Hew) | | (t) | | | (l) | | | 2 |
| *Dodona egeon* (Westw.) | | (t) | (f) | (e) | | | | 3 |
| *Zemeros flegyas* (Cr.) | r | t | | e | l | −0.49 | 1.18 | 3 |
| Libytheidae | | | | | | | | |
| *Libythea myrrha* Godart | r | | | e | | −2.24 | −1.80 | 3 |

Abbreviations: r, ruderal; t, transition; f, forest; e, early wet season; l, late wet season. A small letter denotes the presence, a capital letter the mean density over 0.6 specimens per 1 km of a transect within corresponding habitat or season. Abbreviations in parentheses denote occurrences recorded only outside of the transect. CCA scores and geographic range are explained in the text. *, Species not found in our sampling programme. *Troides aeacus* and *T. helena* were checked often flying and not always safely distinguished—for computation are pooled together. *Bhagadatta* Moore and *Auzakia* Moore seem to be congeneric with *Limenitis* Fabricius.

TABLE 2. Relationships between habitat preference, seasonality, abundance, and geographic range of butterfly species.

| Variable 1 | Variable 2 | r | P | | N |
|---|---|---|---|---|---|
| CCA habitat | Geographic range | −0.52 | 0.00 | *** | 92 |
| CCA habitat | ICCA seasonI | 0.03 | 0.79 | n.s. | 92 |
| CCA forest layer | CCA habitat | 0.72 | 0.00 | *** | 21 |
| CCA forest layer | Geographic range | −0.64 | 0.00 | *** | 21 |
| Ruderal abundance | Geographic range | 0.30 | 0.01 | * | 66 |
| Forest abundance | Geographic range | −0.29 | 0.03 | * | 59 |

*r*, Spearman correlation coefficient; *P*, the significance of correlation; *N* number of species tested. CCA habitat, CCA season = the species' CCA scores on the gradient ruderal–forest zone and early–late wet season, respectively (see Table 1); absolute values of CCA season were used for calculation. CCA forest layer = the species' CCA score on the gradient understorey–canopy within the forest. Abundance = number of specimens of a species per unit of transect length in the ruderal zone, and the forest zone, respectively. Geographic range scaling is given in Methods. CCA score increases from ruderal to forest, from early wet to late wet season, and from forest canopy to understorey, respectively. See text for further explanation.
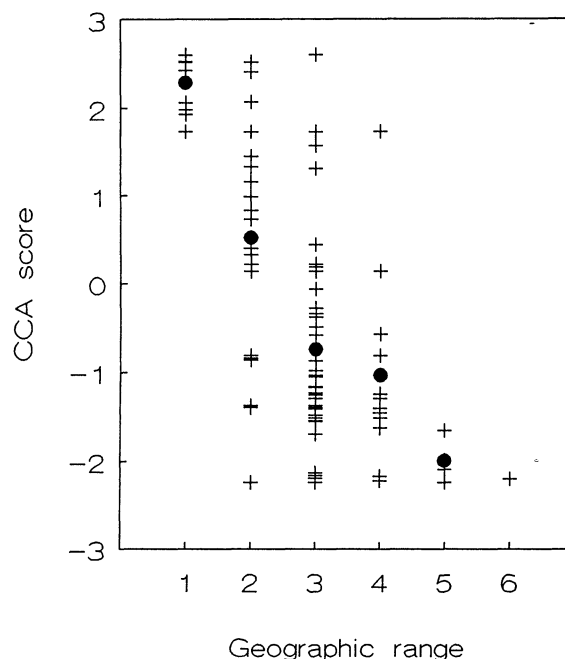


FIG. 4. The relationships between species' size of geographic range and successional maturity of preferred habitat. The species' optimum on the ruderal–forest gradient is expressed by the CCA score. Solid circles denote an arithmetical average of CCA scores within each range size category.

derstorey species, and a completely different canopy fauna, concentrated mainly, but not exclusively, around flowering trees. The canopy fauna significantly overlaps in the species composition with the ruderal butterfly community. There is a positive correlation between the species' CCA scores indicating its optimum on the ruderal–forest gradient (Table 1), and on the understorey–canopy vertical gradient within the forest (Fig. 5)–see Table 2. With respect to their habitat preference, butterfly species found in the forest form several groups. There are species confined exclusively to the forest understorey (*Faunis aerope, Stichophthalma louisa,*

*Ragadia crisilda,* and most of *Lethe* spp.), species confined to the forest canopy (*Delias aglaja* and *D. agostina*), eurytopic wide-ranging species visiting flowers both in ruderal and in forest canopy and migratory species flying over fo-
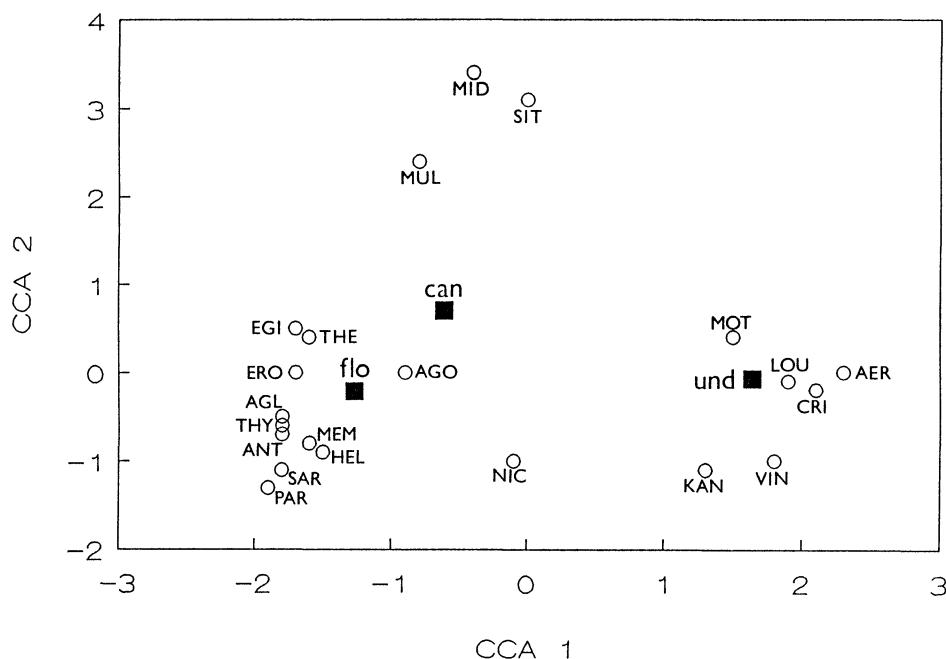
FIG. 5. CCA ordination of species with canopy (can), flowering canopy trees (flo) and understorey (und) habitats as explanatory variables. Solid marks denote centroids of variables, open marks species: AER, *Faunis aerope*; AGL, *Delias aglaja*; AGO, *Delias agostina*; ANT, *Pathysa antiphates*; CRI, *Ragadia crisilda*; EGI, *Vagrans egista*; ERO, *Vindula erota*; HEL, *Papilio helenus*; KAN, *Lethe kansa*; LOU, *Stichophthalma louisa*; MEM, *Papilio memnon*, MID, *Euploea midamus*; MOT, *Ypthima motschulskyi*; MUL, *Euploea mulciber*; PAR, *Papilio paris*; SAR, *Graphium sarpedon*. SIT, *Parantica sita*; THE, *Prioneris thestylis*; THY, *Cyrestis thyodamas*; VIN, *Lethe vindhya*.

rested areas (e.g. *Papilio* spp., *Graphium sarpedon, Vagrans egista, Euploea mulciber*). In other words, the overall degree of habitat specificity is much higher within the forest understorey than in the canopy. This is why understorey species tend to have more restricted geographic ranges than those of the forest canopy (Table 2). Samples from plots 1–4 corroborate these conclusions. They were assigned to the ruderal–forest gradient as passive samples. This gradient is characterized by centroids of habitat types used as external variables. Their CCA scores are as follows: ruderal: −1.07, transition: −0.04, and forest: 1.3. CCA scores of plots 1–4 are: plot 1:−1.21, plot 2: −0.83, plot 3 −0.65, plot 4: −0.32. Clearly, small-scale disturbance within the forest results in the establishment of butterfly fauna similar to that of man-influenced landscape outside the forest (plots 1 and 2). Canopy samples taken on the hill tops (plots 3 and 4) show an affinity to the ruderal part of the gradient as well. This is due to the presence of migrants (e.g. *Euploea mulciber, Cynthia cardui*) and eurytopic canopy species (e.g. *Papilio paris, P. helenus*). Certain species were found only on hill tops (*Dichorragia nesimachus*), but more data on hill-topping are needed.

## Seasonality

An amount of temporal change (early *v.* late wet season) within habitats is proportional to the eigenvalue ratio of constrained to unconstrained axes (Table 3). Early and late wet season aspects differ in all three habitats, but the change in the forest was by far more pronounced than in the ruderal and transition zone.

TABLE 3. Seasonal change of butterfly communities in various habitats between early and late wet season.

|  | Eig. 1 | Eig. 2 | Eig. 1/2 | P |
|---|---|---|---|---|
| Ruderal | 0.349 | 0.310 | 1.126 | 0.01 |
| Transition | 0.303 | 0.339 | 0.894 | 0.02 |
| Forest | 0.701 | 0.477 | 1.470 | 0.01 |

Eig. 1,2, eigenvalues of a constrained axis 1 and unconstrained axis 2; *P*, Significance of the constrained axis (Monte Carlo test, 99 permutations). Proportion of data variability attributable to temporal change corresponds to the axis 1/axis 2 eigenvalue ratio (Eig. 1/2).

In the forest community, replacement of community dominant *Stichophthalma louisa* by *Ragadia crisilda* accounts for a substantial portion of temporal change. Although *Stichophthalma louisa* and *Ragadia crisilda* were found in both study periods, the density of *Stichophthalma louisa* decreased seven times and that of *Ragadia crisilda* increased fourteen times between the early wet (1991) and late wet (1988) seasons. No *Stichophthalma louisa* specimens were seen during visits in May and December. If the same weight is given to each species, between-habitat differences in seasonality almost disappear. There was a diversity of patterns of temporal change among species within both ruderal and forest, so that no relationship between the species' CCA scores indicating its preferred habitat and the absolute value of its CCA score of 'seasonal' preference was found (Tables 1 and 2).

There is a difficulty with our data as they come from two relatively short periods from different years. Whereas data on habitat preferences obtained in both years were coherent (see Lepš & Spitzer, 1990 for comparison), data on species seasonality is difficult to interpret as differences between years are confused with seasonality. Even in seasonal species, their dynamics in various years may be dependent on a slight variation in patterns of rain (Owen, 1971; Wolda, 1978a). This is why differences in species' abundances between early wet season in 1991 and late wet season in 1988 must be evaluated with caution. Nevertheless, some differences are so striking that conclusions on the seasonality of respective species can be suggested. The respective CCA score cannot be a sole guide here, as many species with a particularly high (or low) score were represented by a limited number of specimens, which precluded any conclusions. In addition to *Stichophthalma louisa* and *Ragadia crisilda* with enormous changes in population density (see above), there are ten species where the evaluation of their seasonality has a merit: they were either common in the early wet season, and completely absent in the late wet season (*Delias aglaja, Lethe lanaris, Ypthima motschulskyi, Papilio chaon, Cupha erymanthis*), or vice versa (*Parthenos sylvia, Neorina westwoodi, Athyma selenophora, A. perius*).

## Community diversity and dominance structure

As seen from Table 4, the number of species, species diversity, and abundance of butterflies were higher in the ruderal area than in the closed forest; the transition area occupied an intermediate position. In addition to a lower number of species in the forest, diversity was low due to low evenness of butterfly population sizes. The forest community was strongly dominated by *Ragadia crisilda* in 1988 (65%) and by *Stichophthalma louisa* in 1991 (53%), whereas in the ruderal and transition zone no species represented more than 20% of the community (in the ruderal zone, maximum dominance was 19% in 1988—*Argyreus hyperbius*, 13% in 1991—*Pieris canidia*; in the transition zone it was 19% in 1988 and 17% in 1991—*Prioneris thestylis*). However, owing to the higher structural diversity of the forest, the efficiency of transect method is lower there, particularly for canopy fliers. Consequently, the canopy fliers component of the total forest species diversity is underestimated.

TABLE 4. Abundance and diversity of butterfly communities.

| Wet season | No. of species | | Density | | exp(H') | |
|---|---|---|---|---|---|---|
| | Early | Late | Early | Late | Early | Late |
| Ruderal | 59 | 33 | 59 | 50 | 24 | 17 |
| Transition | 62 | 38 | 45 | 29 | 23 | 18 |
| Forest | 54 | 23 | 37 | 25 | 8 | 5 |

Total number of species, butterfly density (number of specimens per 1 km of the transect), and species diversity calculated from pooled transect samples is summarized for the early and late wet seasons.

Species' population density (expressed as the number of specimens observed per unit transect length) was correlated with its geographic range; a positive correlation was found in the ruderal zone and a negative correlation in the forest zone (Table 2). In other words, species able to attain large population size (and dominance) in the ruderal zone are those with a geographic range larger than that of rare species in the community, but the reverse is true in the forest.

## DISCUSSION AND CONCLUSIONS

Our results support the hypothesis that the most characteristic climax forest species have the smallest geographic range of endemitic distribution. The opportunist butterflies with wide geographic distribution, most of them migrants, are associated with disturbed habitats (e.g. ruderals). Similar conclusions about habitat specialists and their distribution were reached also in other temperate, subtropical and tropical regions (Thomas & Mallorie, 1985; Spitzer & Lepš, 1988; Lepš & Spitzer, 1990; Bowman *et al.*, 1990; Thomas, 1991). The case of the Tam Dao Indochinese fauna seems to be the best documented through the checklist of species with quantitative analysis. The statistical evaluation is partially limited by the knowledge of the real geographic range of species. Gaston (1991) pointed out some of such limitations, but his suggestions seem to be unrealistic with regard to the records available.

The habitat conservation priority of endemitic butterflies associated with the unique climax rain forests is evident. Many resident species are endangered in almost all their (restricted) geographic range (e.g. *Meandrusa gyas* and *Atrophaneura crassipes*—see Collins & Morris, 1985; *Mandarinia regalis*, some endemitic *Lethe* spp.). Several species are recorded from Vietnam for the first time: *Meandrusa gyas, Ypthima motschulskyi, Lethe syrcis, Auzakia* (= *Limenitis*) *danava*, and *Bhagadatta* (= *Limenitis*) *austenia*.

Butterflies of ruderal habitats are able to fly over the canopy of large forests and establish themselves also in small open places in the forest. On the contrary, the species of forest understorey are found nearly exclusively there. For example, *Stichophthalma louisa*, although it comprised 53% of all individuals seen in the forest in the early wet season, was only exceptionally seen outside the forest; it avoided even small-scale clearings within the forest (Novotný *et al.*, 1992). Similarly, *Ragadia crisilda*, the most common forest understorey species in the late wet season, was only exceptionally seen in the transition zone. Clearly, isolated forest clumps separated by clearings are not able to support the populations of forest understorey butterflies. Those species are very probably not able to migrate over the non-forested areas.

The seasonality of selected groups of tropical insects is well established and the diversity of inducing factors known (see Wolda 1978b, 1989; Denlinger, 1986). Wolda (1978b, 1988, 1989) recorded remarkable insect seasonality in Neotropical rain forests in Panama. Some Lepidoptera of Sulawesi rain forests are similarly seasonal (Barlow & Woiwod, 1990).

In Vietnam the most characteristic seasonal patterns in

abundance fluctuations are closely associated with the monsoon climate. As to the butterfly seasonality, the best example seems to be seasonal occurrence and habitat preferences during the dry and wet season in the Vietnamese savanna (Spitzer, 1983; Spitzer *et al.*, 1987). In the Tam Dao montane forest, the seasonality is probably more complex, compared with the savanna. Reasons for the Tam Dao forest butterflies seasonal occurrence might be partially different and modified by the local biogeography and habitat history. The observed seasonality of the forest butterflies seems to be determined not only by plant phenology and the climate generally, but the butterfly biogeography and fauna history evolution are also involved in the seasonality phenomenon.

The relatively higher seasonality of the Tam Dao forest butterflies is mainly caused by the presence of endemitic taxa with strong affinities to the seasonal 'East Palaearctic' biota of the East Himalaya and subtropical China. Closed forest species *Lethe* spp., *Ypthima motschulskyi*, and *Mycalesis unica* belong to this biogeographical element. They are characteristic species of the June–July 'summer' period only. In contrast, strictly seasonal (September) occurrence of a forest species *Neorina westwoodi* is difficult to explain.

The ruderal fauna of the Tam Dao butterflies is composed mainly of widely distributed Oriental species which have less pronounced and irregular seasonality. The seasonal migratory behaviour seems to be very erratic and most of the migratory butterflies of the Tam Dao are opportunist widely distributed species—e.g. *Papilio demoleus*, *Eurema hecabe*, *Euploea mulciber*, *Cupha erymanthis*, *Cynthia cardui*, *Parthenos sylvia*, *Radena similis* and perhaps also *Vagrans egista*. Such species are forest canopy visitors during some migrations only and they are temporarily attracted by canopy flowers.

The low species diversity of the forest butterfly community in comparison to the ruderal area is striking. This pattern with a climax community less diverse than a disturbed one is opposite to what might be expected. This contrasts to studies on other insect taxa, where communities in climax tropical forests are as a rule the richest in species (e.g. Barlow & Woiwod, 1989; Morse *et al.*, 1988), and with population sizes of constituent species rather evenly distributed (e.g. no species exceeded the 5% dominance in Auchenorrhyncha samples taken along the forest transect in Tam Dao—Novotný, 1992). The diversity of the Tam Dao rain forest moths (Macroheterocera) is also high (Spitzer, unpubl. records). A tentative explanation may be that for generally heliophilous and flower-visiting Papilionoidea, the forest understorey is a rather marginal habitat occupied by 'specialized', i.e. crepuscular, species, many of them feeding on food sources other than flowers (e.g. *Stichophthalma louisa* feeds on sap exuding from wounded trees, not on flowers). Larvae of some understorey species are associated with specific plants, e.g. larvae of *Ragadia crisilda* feed on *Selaginella* ferns.

There has been much debate on the relationship between species' abundance in communities and the species geographical range size. According to Brown (1984), generalist species should be simultaneously locally abundant and widely distributed, as a consequence of their ability to exploit a wide range of resources on both local and regional scales. Gaston & Lawton (1990) extend this hypothesis by suggestion, that in rare and distinct habitats largely different from 'average' environmental conditions prevailing in the area, specialists (with small geographic range) are more efficient, which permits them to attain higher population sizes than generalists. Consequently, the abundance/distribution correlation should be negative in rare habitats, and positive in common ones. According to Novotný (1991), a high disturbance level favours generalists irrespective of habitat distinctiveness, which causes a positive correlation of local abundance and distribution.

A positive abundance/distribution correlation in the ruderal zone could correspond either to high habitat commonness or to intense disturbance. According to Holloway (1982), present-day Oriental butterfly fauna of ruderal habitats might recruit from non-forest seasonal climax formations widespread in interpluvials (glacial periods). Nevertheless, in the course of postglacial periods, forests became climatic climax ecosystems over a majority of the area. In that time, these butterflies persisted only in small-scale and ephemeral enclaves of successionally young vegetation originated due to disturbance. The subsequent spreading of ruderal ecosystems caused by human impact was extremely rapid. These expanding ruderals accumulated butterfly fauna of heterogeneous origin. Hypothetically, such communities might be composed of residents from non-forested enclaves and some relatively opportunistic species associated with the forest canopy. Both categories are characterized by good dispersal ability, which could account for their wide geographic distribution. The capability of ruderal butterflies to cope with disturbance was convincingly demonstrated, e.g. by a rapid recolonization of the Krakatau Islands (Yukawa, 1984; New *et al.*, 1988; Bush & Whittaker, 1991; New & Thornton, 1992). It is interesting to note that of twenty-six Krakatau butterfly species (excl. Lycaenidae), thirteen were found in the Tam Dao ruderal zone.

According to the above hypotheses, a negative abundance/distribution correlation in the Tam Dao climax rain forest should indicate that this habitat is distinct and rare. Naturally, the present situation has no merit for the explanation of this correlation as it is a result of recent human impact. Nevertheless, the forest actually might have been very distinct and limited in size even before man-induced disturbance, as montane ecosystems generally can be viewed as a 'habitat island' effectively isolated by lowlands. Moreover, such habitats are quite distinct due to specific climate. These factors could result in the evolution of efficient specialists which are able to establish abundant populations, but not disperse over a large area. A decrease in the area of such forest ecosystems leads inevitably to the irreversible loss of biodiversity.

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