Ecological determinants of butterfly communities (Lepidoptera, Papilionoidea) in the Tam Dao Mountains, Vietnam

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Ecology, diversity, abundance, succession, environmental relationships, biogeography, montane tropical forest, Oriental region

Abstract. Composition and environmental relationships of butterflies of the Tam Dao Mountains (northern Vietnam) were examined in the forest climax, transitional and ruderal communities as characterized by vegetation survey. A transect method was used for assessing butterfly presence and abundance. The results show high diversity and low constancy of a heterogeneous fauna of butterflies associated with the ruderal transect. The diversity of forest butterflies is lower, but their constancy is higher. More pronounced diurnal activity is exhibited by butterfly arrays in ruderal habitats. Large scale size of geographic range correlates negatively with the degree of association of a species with mature (near climax) forest. Species of endemic distribution in East Himalayas, Yunnan and northern Indochina, are associated with the forest climax of the Tam Dao Mountains. Several new faunistic records from Vietnam and a list of Tam Dao species are given.

The Tam Dao Mountains in northern Vietnam (75 km north of Hanoi, 21°30′N, 105°40′E) is an area of by 19 000 ha of montane forest that has been protected as a nature reserve since 1977 (Thai Van Trung 1985). Unfortunately, no detailed ecological characteristics are available. The area is entomologically little investigated and the flora and vegetation are also little known (collection of Petelot is in Paris herbarium; J. E. Vidal, pers. comm.). Our present paper is a continuation of synecological studies of Vietnamese butterflies (Papilionoidea; Spitzer et al. 1987). The present paper on the ecological determinants of butterfly communities of the montane zone has three aims: (1) to describe the relationship between diversity and abundance of S. E. Asian butterflies that are associated with particular successional stages; (2) to test the hypothesis that a species affinity to early successional stages is correlated with the size of its geographic range; and (3) to provide new faunistic and synecological data from Vietnam for the conservation of an isolated montane range covered with tropical monsoon forest.

MATERIAL AND METHODS

Data collection

Our studies were carried out during three weeks between 2 and 22 September, 1988 at the end of the wet season in the Tam Dao Mountains. Heavy rains lasted until about 15 September. The daily minimum and maximum temperatures were 22 °C and 35 °C, respectively.

We applied the same transect method as in our previous paper (Spitzer et al., 1987); the method is described by Pollard et al. (1975) and Pollard (1977). The transect checking was started approximately at 8.30 and was usually completed before 1 p.m. Each transect was checked usually twice a day, in the morning and about midday. A few late afternoon samples were also taken. Two observers walking together for 15–20 minutes along each 200 m transect recorded all butterflies seen (except Lycaenidae and Hesperiidae) in a belt about 40 m wide.

The transects were located along a horizontal path northwest of the village Tam Dao (about 950 m a.s.l.). Three habitats (Plates I, II)* representing the gradient of a successional maturity of the communities were selected: ruderal and agricultural communities close to the village, the transitional zone and the natural forest. One transect was in the ruderal zone, one in the transitional zone and two in the natural forest. The nomenclature of plants chiefly follows Pham Hoang Ho (1970–72) with some corrections based on suggestions of Vidal (pers. comm.).

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

The geographical distribution was arbitrarily categorized on the scale of 1 to 6 (smallest to largest range) 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

Description of study area

The ruderal transect: 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 Iusonense Presl. The most common scattered shrubs are Saurauja roxburghii Wall., Duranta repens L., Debregeasia velutina Gaud., Rhus cf. chinensis Muller and planted and feral citrus. The shrubs are accompanied by vines, particularly Ipomaea (e.g. I. cairica (L.) Sw.). Relatively common species are Rubus alceaefolius Poiret and Melastoma saigonensis (Ktze) Merr. Ruderal forbs are common such as Synedrella nodiflora (L.) Gaertn., Ageratum conyzoides L., Bidens pilosa L., Solanum torvum Swartz, S. virginianum L. The transect is a characteristic example of a 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 S. E. Asia are discussed recently by Rambo & Sajise (1984) and by Chin (1985).

The transitional transect: The transitional zone consists mainly of clearings with scattered shrubs

^{*} Plates I, II will be found at the and of this issue.

(e.g. Saurauja roxburghii Wall., Ficus spp.) and clumps of trees (e.g. Pasania fissa Oersted var. tonkinensis Hickel et A. Camus) and shrubs with vines (e.g. Hodgsonia cf. macrocarpa Cognx.) and epiphytes (including hemiparazitic Loranthaceae and Santalaceae). The treeless parts are covered with growths of Thysanolaena maxima (Roxb.) O. Ktze and Miscanthus floridulus (Labill.) Warb., and patches of Rubus alceaefolius Poiret and R. sorbifoilius Maxim. Local landslides (about 20%), containing a sharp division between forest and open land are characterized by Dicranopteris linearis (Burm.) Underw. and Arundina graminifolia (Don) Hochr. Wild bananas and citrus are also present. The zone is floristically very heterogeneous, with many species (e.g. Rhopalephora scaberrima (Bl.) Faden. and other Commelinaceae, Polygonum chinense L., P. hydropiper L., Aeginetia sp., Aralia armata Seem., Urena obata L., Houttuynia cordata Thunb.), which are also associated with the ruderal zone.

Forest transects: The closed forest (climax formation) is disturbed only by illegal selective logging by native people. It is floristically rich for this area – we estimated that there were at least 200 woody species along our two transects. Emergent trees (incl. Dipterocarpaceae) were nearly eliminated in all accessible places. There are no apparent dominant trees here. 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.), and many species from various families (e.g. Syzygium imitans Merr. et Perry, Eberhardtia cf. tonkinensis H. Lec., Dillenia sp.). Small trees and shrubs are the extremely species rich group, including 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., Blastus borneensis Cogn. var. eberhardtii (Guill.) C. Hans., Brevnia indosinensis Beille, Symplocos sp., Maesa sp., various Theaceae (Eurya sp. Schima sp.), numerous Euphorbiaceae, Apocyanaceae (e.g. Tabernaemontana cf. bovina Lour.), Rubiaceae, Urticaceae, tree ferns (Cyathea) and many others. The trees support many epiphytes, mainly orchids and ferns, hemiparasitic epiphytes from the 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 (cover 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: Pandanus sp., Begonia spp., Amorphophallus paeoniifolius (Dennst.) Nicols. var. campanulatus (Dcne) Sivad., Piper spp., Rhopalephora scaberrima (Bl.) Faden, Belamcanda chinensis (L.) DC., Curculigo sp., Anoectochilus sp., Balanophora fungosa J. r. & G. Forster, and others.

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).

Data analysis

By checking transects usually twice daily we obtained a set of 149 samples. Several methods of data analysis were applied: (1) Particular habitat types were characterized by "very characteristic species", i.e. by species seen more often in the habitat under consideration than in the rest of samples in the data set. The very characteristic species were selected in a similar way as in our previous paper (Spitzer et al., 1987). A species is considered to be characteristic if the value of the common t-statistics was greater than 2 when comparing the mean number of specimens in samples from the habitat with the mean number in the rest of the samples. It should be noted that the t-statistics is used as a descriptive tool, not as a rigid statistical test.

(2) The set of all samples was subjected to the divisive hierarchical classification by TWINSPAN -

two-way species indicator analysis (Hill, 1979); only the presence-absence data were used. In this procedure, the set is successively divided and each division has indicator species characteristic for each side of dichotomy.

- (3) The optimum of species on the successional gradient was assessed by the canonical correspondence analysis CCA, using the program CANOCO (Ter Braak, 1987). CCA is a method of constrained ordination; its aim is to relate the species composition of a community to external (environmental) variables. The successional status of a habitat type was used as a single environmental variable. 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 species score on the first (i.e. constrained) axis corresponds to the species optimum on the disturbance gradient (or to the "successional status" of the species) 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 distant 4 SD-units in ordination should have no common species and species distant 4 SD-units should not be found together (see Ter Braak, 1987, for more technical explanation).
- (4) The CCA was used to investigate temporal changes in composition of species assemblages during the day and during the period of observations. The entire set was divided into three parts according to the habitat type. Two environmental variables were used: the daytime and ordinal number of the day. The intensity of dependence of observed species assemblages on the two variables was evaluated by the ratio of the first two eigenvalues (i.e. those corresponding to contrained axes) and the second two eigenvalues, and by the correlations between species and environmental axes. (The higher value of the ratio or of the correlation, the more pronounced temporal dynamics.) The significance of the relationship was tested using the Monte Carlo permutation test (Ter Braak, 1987).

RESULTS

The list of all species of butteflies found and their habitat preferences are listed in Table 1. All the mean number of species, mean diversity, and mean number of individuals per sample were the highest in the ruderal transect and the lowest in forest (Table 2). The total number of species recorded was highest in the transitional transect (Table 2).

The TWINSPAN classification of the entire data set (Fig. 1) reflects the basic differences between butterfly communities of different habitats. The most distinct fauna with typical Ragadia crisilda characterizes the forest communities; no differences were found between the two closed forest transects. The division of open habitat samples separates well the ruderal samples from the transitional habitat samples, Ariadne ariadne, Euploea mulciber, Argyreus hyperbius and Papilio memnon being characteristic for ruderal transect and Troides helena and Prioneris thestylis for transitional samples. In the Tam Dao Mountains, T. helena is more frequent than the lowland species T. aeacus. Within the ruderal habitat samples, the further division separates samples from "optimum" (i.e. between 9.30 a.m. to 0.30 p.m.) from the rest. The samples from the "optimum" are more species rich – particularly species Parthenos sylvia, Argyreus hyperbius, Hebomoia glaucippe and Vindula erota restrict their activity before 9.30 a.m. and in the afternoon. In the other two groups, the ecological meaning of further divisions remains unclear.

TABLE 1. Transects, presence of butterflies, their score on the first CCA axis multiplied by 10 and geographic range.

Geographic range	<i>พศนพพ</i> ศพฺ	: 4466666666664
CCA	21 21 21 113 113 114 123 123 133	31 - 26 - 17 - 26 - 26 - 6 - 6
Closed	+++ + & &	++ +24
Habitat Forest clearings	++ +++ ++++++	+ + + + + + + +
Ruderals and agroecosystems	++ &&++++ + +	+ ++ ++ ++ ++
Species	Papilionidae Troides helena (L.) Troides aeacus (Feld.) Arrophaneura varuna (Wh.) Pachliopta aristolochiae (F.) Chilasa clytia (L.) Papilio demoleus L. Papilio helenus L. Papilio memnon L. Papilio protenor Cr. Papilio protenor Cr. Papilio paris L. Papilio paris Cr. Meandrusa payeni (Bsd.) Graphium sarpendon (L.) Lamproptera curius (F.)	Delias agostina (Hew.) Prioneris thestylis (Dbld.) Prioneris philonome (Bsd.) Pieris canidia (L.) Cepora nadina (Lucas) Appias nero (F.) Appias allaige (Dbld.) Appias allaina (Bsd.) Hebomoia glaucippe (L.) Dercas verhuelli (V.D.Hv.) Catopsilia pomona (F.) Eurema hecabe (L.)

Danaidae

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Danaus genutia (Cr.) Tirumala septentrionis (Butl.) Tirumala liminace (Cr.) Parantica aglea (Stoll) Parantica melaneus (Cr.) Parantica sita (Koll.) Radena similis (L.) Euploea doubledayi (Feld.) Euploea mulcither (Cr.) Euploea midamus (L.)	Ypthima baldus (F.) Melanitis leda (L.) Melanitis zitenius (Herbst) Lethe mekara (Moore) Lethe kansa (Moore) Lethe verma (Koll.) Lethe confusa Auriv. Lethe gemina (Lecth) Neope bhadra (Moore) Neorina westwoodi (Moore) Nycalesis perseus (F.) Mycalesis gofama (Moore) Mandarinia regalis Leech Ragadia crisilda Hew.	Faunis aerope (Leech) Sticopthalma louisa Wood-Mason Thaumantis diores Dbld.

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+ - occurrence in transects, ++ very characteristic occurrence in transects (t > 2 - see methods), P - occurrence in habitats, but not checked in transects Troides aeacus and T. helena were checked often flying and so not always safely distinguished - for computation are pooled together.

TABLE 2. Sample size and diversity characteristics of butterfly communities

Transect	Total number of species	Mean number of species	Mean diversity (H')	Mean number of individuals
Ruderal Transition	33	6.3	2.32	9.9
Forest	38 23	4.2 2.4	1.68 0.87	5.7 4.9

Further, three subsets from particular habitats were subjected to CCA with daytime and ordinal number of day ("date") as environmental variables (Table 3). The relationship was found significant in the open habitats and insignificant in the forest. Even in the open habitats, the relationship is weak; the eigenvalues corresponding to unconstrained axes are more than two times higher than eigenvalues corresponding to constrained axes. However, both the daytime and day play its role. The changes in the activity during a day are not striking, but obvious; the changes were detected by the TWINSPAN classification for the ruderal habitats,

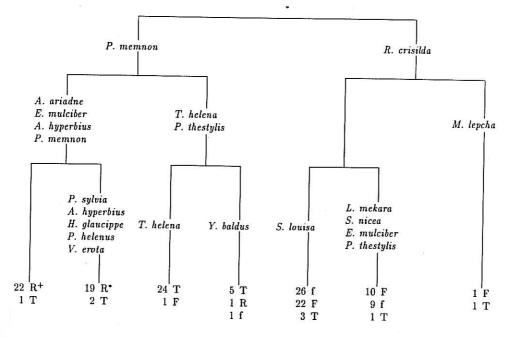


Fig. 1. Results of the TWINSPAN classification of all samples. Each dichotomy is labelled by indicator species. Composition of resulting groups is given at the ends of branches as numbers of samples from particular habitats. R – ruderal transect: + the majority of samples (19 out of 22) taken before 9.30 a.m. or after 0.30 p.m.; α the majority of samples (16 out of 19) taken from 9.30 a.m. to 0.30 p.m. T – transitional transect; T, T the two forest transects.

too. The dependence on the date need not be unequivocally interpreted as directional changes at the end of the wet season, but may be simply caused by migrations, causing an increase of particular species in certain part of observed period. As an example, Danaus genutia, Cirrochroa tyche, Cynthia cardui and Vagrans egista, increased their numbers in the ruderal habitat in the second half of the observed period, probably as a result of migration. It seems that the forest communities are the most constant ones and are less susceptible to migrations from outside than the open habitats.

TABLE 3. Indices derived from results of CCA of the three separate data sets (ruderal, transition, forest), characterizing the relationship species composition and date and daytime as "environmental variables".

	Ruderal	Transition	Forest
0	0.01	0.01	0.09
eigenvalue ratio	0.443	0.403	0.193
R (spec1, env1)	0.828	0.885	0.604
R (spec2, env2)	0.704	0.762	0.359
(spec1, date)	0.487	-0.882	-0.602
R (spec1, daytime)	0.614	0.317	0.125
R (spec2, date)	-0.569	0.063	-0.029
R (spec2, daytime)	0.472	0.712	0.352

P is the significance of relationship between the species composition and environmental variables, obtained by the Monte Carlo permutation test (99 random permutations).

Eigenvalue ratio is ratio of eigenvalues corresponding to first and second (i.e. constrained) and third and forth (i.e. unconstrained) axes.

R are correlation coefficients between species and environmental axes and species axes date and daytime.

The relationship between the size of geographic range and the score on the first CCA axis (Fig. 2, Table 1) is highly significant. The correlation coefficient is -0.68 and the Sperman rank correlation is -0.61. It means that species with small geographic range are typical for closed climax forest and species with large geographic range are characteristic for open ruderal communities. Typically, butterflies with small geographic range (see Table 1) - e.g. Lethe gemina, Neorina westwoodi, Mandarinia regalis, Panthema lisarda, Neurosigma doubledayi and all Amathusiidae species found, represent characteristic forest Lepidoptera, and belong to the East Himalayan biogeographic component. Most widely distributed species e.g. Papilio demoleus, Catopsilia pomona, Eurema hecabe, Neptis hylas, Cynthia cardui are closely associated with ruderal habitat. The same seems to be true for the vegetation, but unfortunately, our data do not allow for quantitative evaluation.

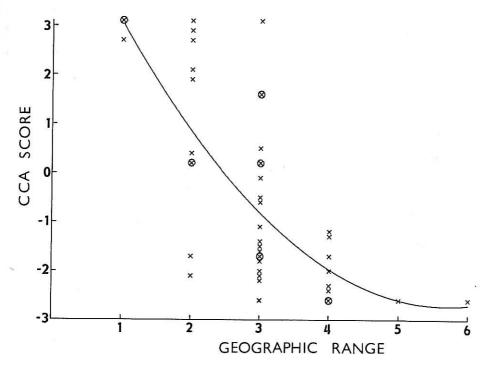


Fig. 2. The relationship between the geographic range and species affinity to climax habitat expressed by the species score on the first CCA axis. Spearman rank correlation coefficient $r_s = 0.61$. Points corresponding to more than one species are encircled. The line was estimated by means of quadratical regression.

DISCUSSION AND CONCLUSIONS

Our results show high diversity and low constancy of the heterogeneous fauna of butterflies associated with the ruderal transect: the diversity of stenotopic forest butterflies is lower, but their constancy is higher (Tables 1, 2, 3). Some species of the transitional transect and forest clearings might be canopy fliers (e.g. some papilionids) and were not checked sufficiently in forest transects (cf. Holloway, 1984). Similar results based on transect studies of the butterfly fauna were obtained in Cuba (Fontenla Rizo, 1987), but no other similar comparative tropical studies are available except our previous paper dealing with the Vietnamese savanna biome (Spitzer et al., 1987). The importance of the forest and forest margins for constant butterfly diversity was demonstrated from the Mediterranean forest environment (Thomas & Mallorie, 1985; Viejo Montesinos, 1986). The variable diversity and very heterogeneous fauna of Papilionoidea of tropical gardens in Africa, which is similar to the ecological situation of our ruderal transect, was found by Owen (1971) and Owen et al. (1972), but no comparative data from more mature communities are available. Many species of the ruderal transect are very good colonists of extreme

early successional habitats and are listed even from the Krakatau Islands (Yukawa, 1984; Bush, 1986). Not only the species composition, but also the spatial structure and microclimate of diverse forest and transitional ecotone vegetation provide the most important complex of ecological determinants for constant and diverse butterfly communities (see also Lawton, 1983; Janzen, 1985, and Spitzer et al., 1987). A good simple example of obligatory and ancient association with the tropical forest environment seems to be the common Tam Dao forest satyrid Ragadia crisilda, the larvae of which feed on Selaginella ferns of the dense forest floor only (Fukuda 1983).

The size of geographic range correlates negatively with the degree of association of a species with mature (near climax) communities. The most stenotopic species of the forest biome have the smallest geographic range (Table 1). Such taxons seem to be of endemic distribution in northern Indochina (East Himalaya). Most opportunistic species associated with the ruderal habitats (close to the r-selection strategy) tend to have a large geographic range and are widely distributed in the Australasian tropics. Similar relationship between size of geographic range and some attributes of bionomic strategies of rodents and noctuid moths were observed in the temperate zone recently (Glazier, 1986; Spitzer & Lepš, 1988). Geographically restricted species of Mediterranean butterflies were found to be biotope specialists (Thomas & Mallorie, 1985).

There are no published data on the Tam Dao Mountains butterflies and most of the species are little known synecologically (Spitzer et al., 1987). Most of the publications dealing with faunistics of Vietnamese Papilionoidea are old and some records need a modern revision (e.g. Dubois & De Salvaza, 1921, 1924; Fruhstorfer, 1927; Lemee & Tams, 1950; Tran Thi Bich Lan, 1981). Our new records from Vietnam represent several very characteristic species from the Tam Dao Mountains associated with the climax montane forest of northern Indochina (Neorina westwoodi, Lethe gemina and Neurosigma doubledayi). All the species of Table 1 with the category of small geographical range (1, and partly 2) are important faunistic records and the most valuable subjects from the nature conservation point of view. The Tam Dao populations of Sticophtalma louisa seem to be a local geographical race (see also Fruhstorfer, 1927, and Kirchberg, 1942) associated obligatorily with the montane forest (Plate II), but further studies of the Sticophtalma species (and other Amathusiidae) in northern Indochina are badly needed. The Tam Dao populations of Lethe gemina seem to differ on a geographic race (subspecies) level, too. The diverse local moth fauna, e.g. Tortricidae (Kuznetzov, 1988) and Noctuidae (Spitzer, unpublished data, about 350-400 species) indicate the great importance of the Tam Dao montane forest for nature conservation, and for preservation of the biodiversity on frontiers between Oriental and Palaearctic Regions.

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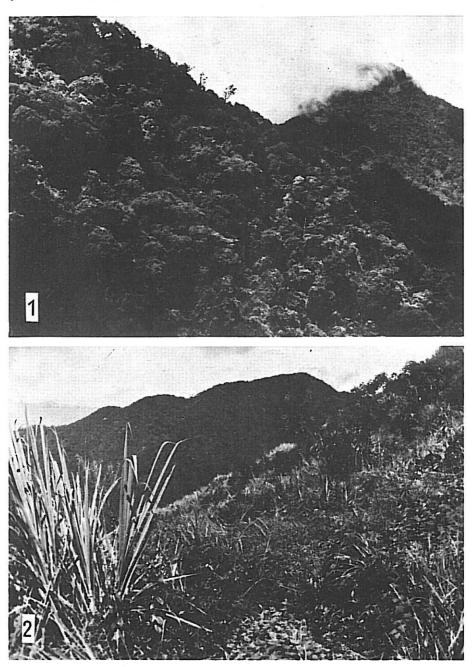


PLATE I. Figs 1-2:1 — The Tam Dao montane forest. 2 — Ruderals and agroecosystems in the Tam Dao Mts.

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PLATE II. Figs 1-2: 1 – Marginal (transitional) habitats of the Tam Dao forest. 2 – A female of Sticopthalma louisa Wood-Mason on the forest floor.