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EFFECT OF SMALL-SCALE DISTURBANCE ON BUTTERFLY COMMUNITIES OF AN INDOCHINESE MONTANE RAINFOREST

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Abstract
The differences between the composition of butterfly communities in gaps created by illegal logging and in closed canopy habitat were studied in montane forest in the Tam Dao Mountains, northern Vietnam. Methods of constrained ordination (canonical correspondence analysis, redundancy analysis) were used for data analysis. The species composition in the two habitats differs significantly: stenotopic species confined to the closed canopy habitat usually have a smaller geographic range. Although the species richness and diversity was higher in gaps, the conservation value of closed canopy habitat lies in the presence of species with restricted range. The creation of gaps by local people changes the natural disturbance regime and causes a threat to biota confined to the closed canopy forest. Bioindicator importance of the local butterfly fauna (Papilionoidea) was evaluated and a list of species is presented. © *1997 Elsevier Science Ltd. All rights reserved*

Keywords: rainforest, gaps, disturbance, butterflies, geographic range, conservation, constrained ordination, Tam Dao, Vietnam.

INTRODUCTION

The understorey of closed tropical rainforest is characterized by the presence of highly specialized biota. The environment of such habitats with closed canopy is very constant in most ecological features, forming a 'core space' of ecological stability within the formation of undisturbed rainforest (Whitmore, 1975; Jacobs, 1988; Brokaw & Scheiner, 1989; Blanc, 1992). Butterflies (Papilionoidea) of the understorey of rainforest are highly stenotopic, habitat-specific, and their geographic range of distribution is relatively small, often nearly endemic in a particular biogeographic forest type (Lepš & Spitzer, 1990; Spitzer *et al.*, 1993). Gap dynamics are considered to be an important factor for maintenance of

plant species diversity in such a forest. Nevertheless, some rate of gap formation and distribution of gap sizes is typical for natural conditions (e.g. Jacobs, 1988; Brokaw & Scheiner, 1989). In many tropical forests, the gaps formed by wood cutting are larger and formed at a much higher rate than under natural conditions. This is particularly true for the forest in Tam Dao Mts, Vietnam, where most gaps are formed by selective logging by local tree poachers (Collins *et al.*, 1991; Spitzer *et al.*, 1993). Each gap, natural or artificial, brings dramatic changes in environmental conditions of closed tropical rainforest not only for plants, but also for other biota. The response of butterfly communities to those changes is probably one of the most conspicuous; moreover, the butterflies are observed easily and the species are better known than other taxonomic groups of insects. Consequently, the butterfly communities are suitable subjects for the study of community response to disturbance, and butterflies may also be used as suitable bioindicators. Some recent detailed studies deal with changes in Lepidoptera communities caused by various types of disturbance in tropical rainforests (Bowman *et al.*, 1990; Lepš & Spitzer, 1990; Thomas, 1991; Holloway *et al.*, 1992; Spitzer *et al.*, 1993; Kremen, 1994; Kremen *et al.*, 1994). However, those disturbances were usually on a large scale. We aimed to study the butterfly community response to much smaller-scale disturbance, caused by gaps up to c.150–200 m^2.

Several studies have shown that disturbance is an important mechanism maintaining species diversity (e.g. Jacobs, 1988; Huston, 1994). Indeed, we have shown that both the diversity and species richness of butterfly communities were higher in ruderal communities near a village and in large clearings on the forest edge than in the closed forest (Lepš & Spitzer, 1990). However, the species differ in their conservation value: species with restricted area of distribution (endemic taxa) are of the highest conservation priority (Collins & Morris, 1985; New, 1991; Spitzer & Lepš, 1992; Spitzer *et al.*, 1993) because they are vulnerable and prone to global extinction; their

habitats are usually rare and endangered. Consequently, it is not just the species diversity, but mainly the presence of species with small areas of geographic distribution, which makes a community important for conservation purposes. Usually, the species with small geographic range are confined to a closed rainforest (Lepš & Spitzer, 1990; Thomas, 1991; Spitzer *et al.*, 1993). The goal of our study was to find differences between butterfly community composition in closed forest and in gaps, and to evaluate the importance of each for conservation purposes. In particular, we aimed to answer the following questions:

1. Are there any differences between butterfly species composition found in gaps and in the closed forest? Which species are associated with each habitat type?
2. Within any temporal changes in the community composition observable within the period of study, is there any difference in the magnitude of the changes in gaps vs forest?
3. Is the species composition in the closed forest influenced by the size and frequency of gaps in the neighbourhood? Is the species composition in gaps influenced by their size and abundance?
4. Is there any relationship between the forest:gap preference of species and their geographical range?

METHODS

Study area and sampling
The investigations were carried out in the Tam Dao Mountains Nature Reserve, a small ridge in northern Vietnam (75 km north of Hanoi, 21°30'N, 105°40'E). The mountains are covered by 19,000 ha of evergreen montane cloud rainforest. The outlines of vegetation and local environmental conditions are given by Lepš & Spitzer (1990) and Spitzer *et al.* (1993). In general, the formation of the Tam Dao montane cloud forest conforms with outlines and characteristics of the Indochinese montane forest described by Vidal (1979) and its conservation importance is given by Hamilton *et al.* (1995).

Three transects were established in the closed forest, each of 200 m but differing in the numbers and size of gaps through or by which they passed (Table 1). They were located along a contour path at about 950 m asl. Intensive regular sampling was carried out between 18 May and 12 June 1995 in the early wet season. The data were collected using the transect method described by Pollard *et al.* (1975) and Pollard (1977) and applied in our previous studies (Lepš & Spitzer, 1990; Spitzer *et al.*, 1993). Two observers, walking together along each transect at a speed of *c*. 100 m per 10 min, recorded all butterflies seen (except Lycaenidae and Hesperiidae) in a belt *c*. 20–40 m wide. Each transect was checked usually twice a day, in the morning and about midday.

Table 1. Lengths of closed forest and number and lengths of gaps in three 200 m transects

Transect	Forest (m)	Gaps One side	Gaps Both sides	Gaps Total	%	No.
1	138	52	10	62	31	7
2	163	7	30	37	18·5	4
3	170	18	12	30	15	6

Within each transect, butterflies were recorded either in the closed canopy, or in gaps, thus providing two types of community samples. The gaps were artifical openings in the canopy, formed by removal of trees and large shrubs during the past 1–5 years, and *c*. 4–15 m in size on average.

Geographic distribution of butterflies
The identification of butterflies and knowledge of their geographic ranges was based on a reference collection built up from repeated earlier visits made between 1984 and 1993 (Lepš & Spitzer, 1990; Spitzer *et al.*, 1993 and references therein). Their geographical distribution was categorized on a scale of 1–5 (smallest to largest): (1) East Himalayas, Yunnan and northern Indochina; (2) Northeastern India and all Indochina; (3) Oriental (Indo-Malayan) region; (4) Indo-Australian (Australasian) tropics; (5) Palaeotropics.

No species with a geographic range larger than the Palaeotropics was recorded in the forest. Distribution limits of some endemic taxa of category 1 are not clear in subtropical China.

Data analysis
Differences in species composition were evaluated using methods of constrained ordination: (partial) canonical correspondence analysis (CCA, Ter Braak, 1986, Ter Braak, 1987) and (partial) redundancy analysis (RDA), all using the program CANOCO, ver. 3·12. Both CCA and RDA are multivariate methods for relating the community species composition to underlying environmental variables. The CCA is a method based on the assumption of unimodal response of species abundance to environmental gradient and uses weighted averaging for calculation of ordination scores (sometimes called weighted averaging methods). The RDA is a method expecting linear relationship (see Jongman *et al.*, 1987, for more technical explanation of differences between the two groups of methods). Constrained ordinations roughly correspond to regressions, where both the explanatory and response variables are multivariate (although weighted averaging is used instead of the least squares in CCA). Traditionally, the explanatory variables are called environmental variables in constrained ordinations. Partial constrained ordinations correspond to partial regression, where the influence of covariables is first partialled out and the explanatory power of environmental variables (i.e. those in which we are

interested) is tested. The distribution-free Monte Carlo test provides significance values independent of any assumptions about the statistical properties of variables studied (restricted permutations were used in all partial analyses, see Ter Braak, 1987).

Carrying out several analyses with different combinations of environmental variables and covariables enables us to separate effects of particular variables. Both continuous and categorial variables were used. The ordination diagram provides information about ecological preferences of particular species. In CCA, species scores on particular axes could be used as a characteristic of species optimum on a particular gradient, whereas in RDA species scores correspond to strength and direction of correlation of the species with a particular factor. Because of the character of our data (many zeroes in the species × samples matrix), we used CCA in most cases. In one case, where we wanted to obtain a 'bioindication value' of a species for a particular gradient, we used RDA. It is well known (e.g. Jongman *et al.*, 1987) that infrequent species usually have the most extreme scores in weighted averaging methods. It is expected that their optimum will be outside the range of samples. On the other hand, bioindication values of species are given by the strength of their relationship with given environmental factors, which is better reflected by linear methods.

Each sample was characterized by the following variables (which were subsequently used either as environmental variables or covariables): GAP/FOREST—categorial variable, distinguishing the two sets of individuals seen at a single date in a transect; TRANSECT—categorial variable, giving the locality of the sample; TIME—continuous variable, the serial number of a day when the sample was taken; GAPSIZE—continuous variable, percentage of gaps within a particular transect. The analyses were carried out either with the complete set of samples, or with forest subset or gap subset.

For pooled samples from particular habitats in particular transects, we calculated the total number of species and diversity, expressed as antilogarithm of the Shannon diversity index:

$$H' = - \sum P.\log(P),\qquad(1)$$

where P is the proportion of individuals of a particular species.

RESULTS

A list of all butterfly species (Papilionoidea) recorded in the transects, their flight period, occurrence in transects, their habitat preference (CCA, RDA) and geographic range are given in Table 2. The numbers of individuals were slightly higher in closed forest, but the number of species, and particularly the diversity, was considerably higher in the gaps.

The multivariate analyses were numbered consecutively and their basic characteristics are listed in Table 3. Analysis 1 provided the information about the general pattern of species variability and preferences of particular species. The results of the first two ordination axes reveal that the gap/forest dichotomy and temporal trend were the two most important explanatory variables (Fig. 1). Generally, the species on the left-hand side of the diagram are typical of closed forest (e.g. *Ragadia crisilda*, *Faunis aerope*, *Lethe syrcis*) and species on the right side for the gaps (e.g. *Cethosia biblis*, *Vagrans egista*, *Hebomoia glaucippe*). The species increasing during the period are found on the top, species decreasing on the bottom, of the diagram (Fig. 1). The other analyses provided answers to the questions listed in the introduction.

Differences between closed forest and gaps (analyses 2 and 3)

The preferences for gap or closed forest are very strong and highly significant (note that for 499 random permutations, 0·002 is the lowest significance value obtainable). Species preferences are characterized by the score of particular species on the first CCA axis and first RDA axis (Table 2): species with high value prefer gaps, species with low value prefer closed forest.

Directional temporal changes (analyses 4 and 5)

Both in the forest and in gaps, significant changes were observed over the 26 days of the study; however, the changes were more pronounced in the closed forest.

Differences between transects, caused by different proportions of gaps (analyses 6 and 7)

Significant correlations between the area of gaps in a particular transect and species composition were found both in gaps and in the closed forest but more pronounced in gaps.

Relationship between habitat preference and geographical range

The species preferences, characterized by their position on the first CCA axis of analysis 2, are significantly correlated with their range ($r = 0·516$, $p < 0·01$, Fig. 2). A similar relationship was found for the RDA scores ($r = 0·509$, $p < 0·01$). Species with small geographical range tend to be confined to closed canopy habitat, whereas species with larger range are more often found in the gaps.

DISCUSSION AND CONCLUSIONS

Our results support the hypothesis that the most characteristic closed canopy (climax forest) species have the smallest geographic range. Their ecological characteristics conform to ideas about specialized understorey

Table 2. Presence of butterflies in closed forest (F) and gaps (G) in three transects in the study area with their CCA- and RDA-scores and geographic range

Family Genus Species[a]	Date	1 F	1 G	2 F	2 G	3 F	3 G	CCA	RDA	Range
Papilionidae										
Atrophaneura aidoneus (Dbld.)	19 May	0	0	0	0	2	0	−0·60	−0·10	1
Graphium agamemnon (L.)	18–29 May	0	0	0	1	0	3	1·34	0·20	4
Graphium sarpedon (L.)	18 May–12 June	0	2	0	4	1	5	0·96	0·26	4
Lamproptera curius (F.)	18 May–8 June	1	6	0	2	0	0	0·87	0·18	3
Papilio chaon Westw.	18 May	1	0	0	0	0	0	−0·84	−0·10	2
Papilio helenus L.	18 May–8 June	0	5	0	3	0	4	1·20	0·33	4
Papilio memnon L.	20 May–12 June	0	3	0	3	0	1	1·14	0·27	3
Papilio paris L.	19 May–4 June	0	3	0	1	0	0	1·09	0·20	3
Pathysa antiphates Cr.	20 May	0	1	0	0	0	0	1·17	0·10	3
Troides aeacus (Feld.)	18–25 May	1	2	0	1	0	3	1·01	0·15	2
Troides helena (L.)	18–31 May	0	1	0	1	0	0	1·17	0·14	3
Pieridae										
Appias albina (Bsd.)	21 May–10 June	0	0	0	1	0	1	1·21	0·14	3
Appias indra (Moore)	18 May–1 June	0	1	0	1	0	0	1·16	0·14	2
Appias nero (F.)	25 May	0	1	0	0	0	0	1·10	0·10	3
Appias pandione (Geyer)	22 May	0	1	0	0	0	0	1·14	0·10	3
Cepora nadina (Lucas)	19–29 May	1	2	0	0	0	0	0·44	0·06	3
Delias aglaia (L.)	18–31 May	0	1	1	0	0	1	0·58	0·06	3
Dercas verhuelli (V.D.Hv.)	24 May–9 June	0	2	0	0	0	0	1·00	0·14	2
Eurema hecabe (L.)	18–31 May	0	2	0	0	0	1	1·17	0·17	4
Hebomoia glaucippe (L.)	18 May–12 June	0	5	0	4	0	0	1·11	0·22	3
Ixias pyrene (L.)	8 June	0	0	0	0	0	1	1·16	0·10	3
Pieris canidia (L.)	1 June	0	0	0	1	0	0	1·13	0·10	3
Prioneris thestylis (Dbld.)	18 May–12 June	5	22	0	6	1	6	0·79	0·38	2
Danaidae										
Euploea eunice (Godart)	19–20 May	0	0	4	1	0	0	−0·33	−0·09	2
Euploea mulciber (Cr.)	18 May–12 June	2	24	4	7	5	7	0·73	0·24	3
Parantica melaneus (Cr.)	22–30 May	0	2	0	0	0	0	1·09	0·14	3
Parantica sita (Koll.)	18 May–12 June	2	5	0	2	4	1	0·34	0·05	3
Tirumala limniace (Cr.)	19 May	0	0	0	1	0	0	1·31	0·10	3
Tirumala septentrionis (Butl.)	18 May–8 June	0	4	0	2	0	0	1·09	0·25	4
Satyridae										
Lethe gemina (Leech)	18 May–2 June	2	0	5	0	2	1	−0·57	-0·21	1
Lethe kansa (Moore)	22 May	0	1	0	0	0	0	1·14	0·10	2
Lethe naga Doh.[b]	22 May–12 June	3	4	2	1	2	2	0·03	0·01	1
Lethe syrcis (Hew.)	18 May–12 June	7	1	6	2	5	2	−0·40	-0·28	1
Lethe verma (Koll.)	12 June	0	1	0	0	0	0	0·85	0·10	3
Lethe vindhya (Feld.)	19 May–12 June	6	1	2	0	1	3	−0·26	−0·12	2
Melanitis leda (L.)	20 May–9 June	0	0	1	1	1	0	−0·11	−0·05	5
Mycalesis malsarida Butl.	19 May–1 June	2	0	1	0	3	0	−0·77	−0·21	2
Mycalesis nicotia (Dbld.)	20 May–8 June	2	2	0	0	2	0	−0·26	−0·08	2
Neope muirheadi (Feld.)	21 May–7 June	5	1	0	0	0	0	−0·65	−0·16	2
Penthema lisarda Dbld.	18–19 May	1	0	1	0	0	0	−0·79	−0·14	1
Ragadia crisilda Hew.	18 May–12 June	79	0	59	0	78	0	−0·81	−0·66	2
Ypthima baldus (F.)	24 May–4 June	0	5	1	1	0	0	0·77	0·17	3
Amathusiidae										
Aemona amathusia Hew.	19–27 May	0	0	2	0	1	0	−0·74	−0·17	2
Faunis aerope (Leech)	20 May–8 June	1	0	1	0	8	0	−0·74	−0·24	1
Stichophthalma louisa W.–M.	18 May–19 May	0	0	0	1	1	0	0·36	0·01	1
Stichophthalma suffusa Leech[c]	25 May–12 June	52	30	18	6	21	8	−0·38	−0·23	1
Nymphalidae										
Argyreus hyperbius (L.)	31 May	0	1	0	0	0	0	1·02	0·10	5
Athyma cama (Moore)	25 May	0	1	0	0	0	0	1·10	0·10	3
Bhagadatta austenia Moore	18–22 May	0	0	0	0	2	2	0·41	0·01	1
Cethosia biblis (Drury)	27 May–12 June	0	1	0	3	0	5	1·08	0·21	3
Cirrochroa tyche (Feld.)	18–25 May	0	6	1	1	0	1	0·99	0·20	3
Cyrestis thyodamas (Bsd.)	18 May–12 June	0	4	0	2	0	5	1·12	0·31	3
Charaxes aristogiton (Feld.)	22 May	0	1	0	0	0	0	1·14	0·10	1
Chersonesia risa (Dbld.)	1–8 June	2	0	0	0	0	0	−1·09	−0·14	3
Kallima inachus (Doy.)	20–22 May	2	0	0	0	0	0	−0·89	−0·14	2
Neptis hylas (L.)	27–30 May	0	1	0	1	0	0	1·11	0·14	4

Table 2—*continued*

Family Genus Species[a]	Date	Transects 1 F	1 G	2 F	2 G	3 F	3 G	CCA	RDA	Range
Neptis miah Moore	20 May–7 June	0	2	0	1	0	2	1·20	0·23	2
Polyura nepenthes (Gr.- Sm.)	19–31 May	0	0	1	4	0	1	0·91	0·15	1
Precis almana (L.)	1 June	0	0	0	1	0	0	1·13	0·10	3
Stibochiona nicea (Gray)	22 May–12 June	5	3	1	1	0	0	−0·25	−0·06	2
Vagrans egista (Cr.)	20 May–12 June	0	6	0	3	0	0	1·01	0·23	4
Vindula erota (F.)	19 May–12 June	3	11	0	11	0	10	1·02	0·39	3
Riodinidae										
Abisara fylla (Dbld.)	19 May	1	0	0	0	0	0	−0·86	−0·10	2
Zemeros flegyas (Cr.)	21 May–1 June	1	2	0	0	0	0	0·40	0·06	3
No. of individuals		187	180	111	82	140	76			
No. of species		24	42	18	34	18	24			
Diversity (Antilog H′)		6·95	22·27	5·85	24·74	5·53	18·07			

[a]Species not recorded in the transects, but found in closed forest only (near TR 2, 3): *Coelites nothis* Westw. and *Parasarpa dudu* (Westw.). [b]*Lethe naga* Doh. = f. *typica* and f. *philemon* Fruhst. [c]*Stichophthalma suffusa* Leech is *S. howqua* (Westw.) ssp. *suffusa* Leech (= *tonkiniana* Fruhst.). This taxon was recorded together with *S. louisa* Wood-Mason in our previous studies (Spitzer *et al.*, 1993).

Table 3. Summary of multivariate analyses

Analysis	Analysed set	Environmental variables	Co-variables	Sp.–env.[a]	F[b]	p[c]
1 (CCA)	All	GAP/FOR, GSIZE, TIME	None	0·93	6·57	0·002
2 (CCA)	All	GAP/FOR	TIME, TRANSECT	0·93	6·58	0·002
3 (RDA)	All	GAP/FOR	TIME, TRANSECT	0·76	45·76	0·002
4 (CCA)	Forest	TIME	TRANSECT	0·95	7·53	0·002
5 (CCA)	Gap	TIME	TRANSECT	0·89	2·23	0·002
6 (CCA)	Forest	GAPSIZE	TIME	0·77	1·78	0·008
7 (CCA)	Gap	GAPSIZE	TIME	0·82	1·50	0·002

[a]Correlation of the first species with the first environmental axis (measure of the strength of the species–environment relationship).
[b]Test criterion for the significance of the first ordination axis.
[c]Significance value obtained from the Monte-Carlo test with 499 random permutations.

biota (e.g. Blanc, 1992). The forest gap species are mostly more opportunistic butterflies with wider geographic distribution than the closed canopy species (Table 2). The temporal changes in species composition and abundance conform to the pronounced seasonality of the Tam Dao biota. The late dry ('winter') season and early wet monsoon season are characteristic periods usually from early May to early June, with several very typical butterfly species (e.g. *Euploea eunice, Neope muirheadi*), which were not discovered in our previous surveys (see Spitzer *et al.*, 1993).

It should be noted that the transect sampling method has certain limitations. The species representation reflects not only its abundance, but also its activity. However, we are not aware of any other method readily usable in the field which provides better insight into butterfly species composition. Moreover, unless the activity differs considerably among habitats, the preferences are estimated correctly by all the statistical methods used.

This is the first attempt to evaluate bioindicator values of butterflies for small-scale disturbance in the tropical rainforest (but compare some larger-scale results: Bowman *et al.*, 1990; Lepš & Spitzer, 1990;

Thomas, 1991; Spitzer *et al.*, 1993; Kremen, 1994). The bioindicator value of each species is taxonomically highly specific (Table 2) and would provide a quick estimate of the degree of disturbance of a tropical rainforest. It seems that the RDA score is more reliable than the CCA score for characterizing the bioindicator value of particular species. The species with the lowest RDA score, *Ragadia crisilda*, was very abundant in closed forest, but never found outside the closed canopy. The CCA score provides the best estimate of species optimum on a particular gradient. However, the reliability of the estimate differs, and is very low in species found with low frequency. When a species is found as, say, two specimens in closed forest, no statistical methods can decide whether it concerns an erratic flight of a species which is abundant in some distant habitat, or a rare species confined to the forest. Consequently, the CCA tells us that the most probable optimum of the species is in the closed forest, whereas RDA shows that the reliability of association with closed forest is not very high (because the species is absent in many forest samples). Although statistical information is a useful guide, decisions about the conservation value of each species has to be made using other available information also.
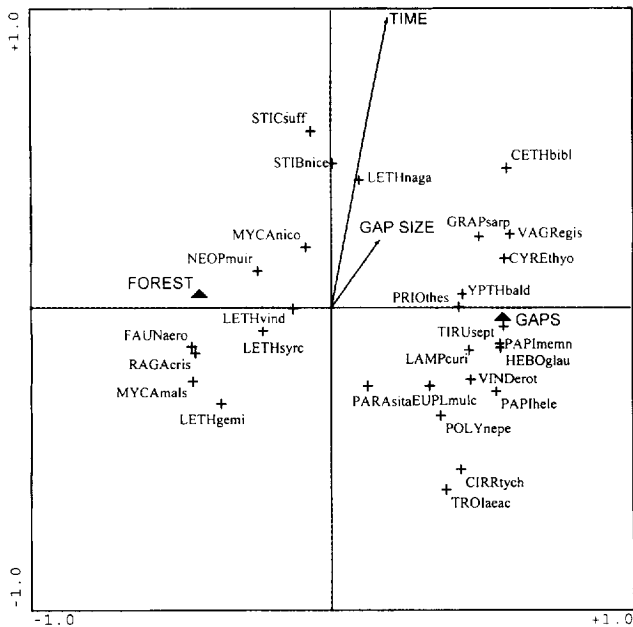
Fig. 1. Ordination diagram of the CCA analysis (analysis 1). The horizontal axis and the vertical axis are the first and the second CCA axes, respectively. Arrows show the direction of influence of continuous variables, circles are centroids of categorial variables. Species are labelled by eight-letter acronyms (genus in upper case, species in lower case, see Table 2).

Fig. 2. Relationship between the size of geographic range and species score on the first CCA axis. Species with a high CCA score prefer gaps, species with a low CCA score prefer closed canopy.

The conservation priorities are represented first of all by specialized stenotopic closed-canopy species with small geographic range (Table 2, Figs 1 and 2) (Spitzer *et al.*, 1993). The high proportion of this group of butterflies in closed forest indicates its high conservation value, regardless of the fact that both the number of species and diversity are relatively low; our results clearly show that integrated characteristics, such as diversity or number of species, are interesting but species identity is cardinal for stating conservation priorities. Nevertheless, the high degree of dominance of a single species, *Ragadia crisilda*, which accounted for about one-half of all individuals seen in closed forest, contradicts the traditional view that environmental stability brings about high species diversity in the tropics.

Each community type has its typical disturbance regime, characterized by the size–frequency distribution of gaps and rate of gap creation (Denslow, 1980). The change in disturbance regime usually has detrimental consequences for the ecosystem. Illegal logging (tree poaching) observed in Tam Dao differs from the natural disturbance regime in a much higher rate and size of gap creation, and probably also in selectivity: certain tree species are preferred by tree poachers. In our data, the trend in closed forest community composition is correlated with the frequency of gaps in a particular transect. However, as the abundance of gaps decreases with distance from forest edge and village (and also from large clearings), this result can hardly be taken as a proof of the influence of the proportion of the gaps. Several typical gap species (*Troides aeacus, Lamproptera*
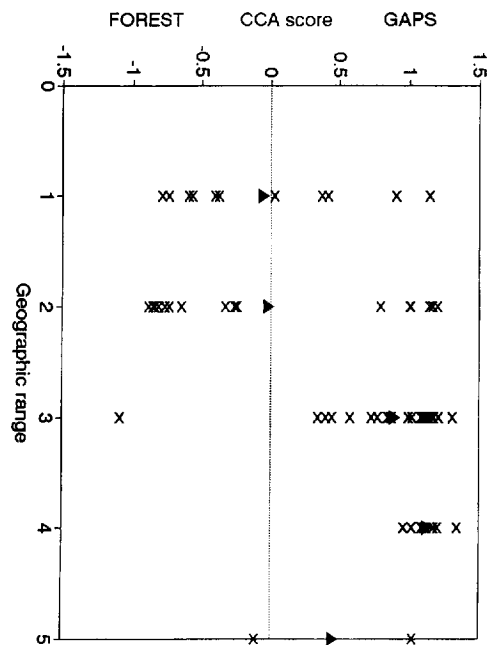
curius, Vindula erota, Prioneris thestylis) were found within the closed forest canopy of transect 1 which had the highest proportions of gaps. Many gap species are characteristic canopy flyers (Spitzer *et al.*, 1993).

The consequences of small-scale disturbance for survival of stenotopic closed canopy rainforest insects is generally poorly known (Whitmore, 1975; Sayer & Whitmore, 1991; Whitmore & Sayer, 1992; Frumhoff, 1995). The results of our study suggest that the butterfly communities in the Tam Dao closed rainforest are highly sensitive to even very small local damage by an increasing number of small man-made gaps along the transects (Table 1). In the Tam Dao Mts Nature Reserve, such small-scale but increasing destruction by local wood collectors seems to be one of the most serious conservation problems (Lepš & Spitzer, 1990; Collins *et al.*, 1991; Spitzer *et al.*, 1993). 'Destruction of tropical rainforests in southeast Asia, for example, seems inevitably to be leading to the extinction of many invertebrate species, and most of these events will never be specifically documented' (New, 1991). The endemic specialized closed canopy forest taxa are the most endangered groups.

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REFERENCES

Blanc, P. (1992). Les formes globales des plantes de sous-bois tropicaux et leur signification écologique. *Rev. Ecol. (Terre Vie)*, **47**, 3–49.

Bowman, D. M. J. S., Woinarski, J. C. Z., Sands, D. P. A., Wells, A. & McShane, V. J. (1990). Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. *J. Biogeogr.*, **17**, 227–239.

Brokaw, N. V. L. & Scheiner, S. M. (1989). Species composition in gaps and structure of a tropical forest. *Ecology*, **70**, 538–541.

Collins, N. M. & Morris, M. G. (1985). *Threatened swallowtail butterflies of the world. The IUCN Red Data Book.* IUCN, Gland and Cambridge.

Collins, N. M., Sayer, J. A. & Whitmore T. C. (1991). *The conservation atlas of tropical forests. Asia and the Pacific.* IUCN, Simon & Schuster, New York.

Denslow, J. S. (1980). Pattern of plant species diversity during succession under different disturbance regimes. *Oecologia, Berl.*, **46**, 18–21.

Frumhoff, P. C. (1995). Conserving wildlife in tropical forests managed for timber. To provide a more viable complement to protected areas. *BioScience*, **45**, 456–464.

Hamilton, L. S., Juvik J. O. & Scatena F. N. (1995). *Tropical montane cloud forests.* Springer-Verlag, New York.

Holloway, J. D., Kirk-Spriggs, A. H. & Chey, V. K. (1992). The response of some rain forest insect groups to logging and conversion to plantation. *Phil. Trans. R. Soc. Lond. B*, **335**, 425–436.

Huston, M. A. (1994). *Biological diversity. The coexistence of species on changing landscapes.* Cambridge University Press, Cambridge.

Jacobs, M. (1988). *The tropical rain forest. A first encounter.* Springer-Verlag, Berlin.

Jongman, R. H., Ter Braak, C. J. F. & van Tongeren, O. F. R. (1987). *Data analysis in community and landscape ecology.* Pudoc, Wageningen.

Kremen, C. (1994). Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecol. Appl.*, **4**, 407–422.

Kremen, C., Merenlender, A. M. & Murphy, D. D. (1994). Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conserv. Biol.*, **8**, 388–397.

Lepš, J. & Spitzer, K. (1990). Ecological determinants of butterfly communities (Lepidoptera, Papilionoidea) in the Tam Dao Mountains, Vietnam. *Acta Entomol. Bohemoslov.*, **87**, 182–194.

New, T. R. (1991). *Butterfly conservation.* Oxford University Press, Oxford.

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biol. Conserv.*, **12**, 116–134.

Pollard, E., Elias, D. O., Skelton, M. J. & Thomas, J. A. (1975). A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve in 1973. *Entomol. Gaz.*, **26**, 79–88.

Sayer, J. A. & Whitmore, T. C. (1991). Tropical moist forest: destruction and species extinction. *Biol. Conserv.*, **55**, 199–214.

Spitzer, K. & Lepš, J. (1992). Bionomic strategies in Lepidoptera, risk of extinction and nature conservation projects. *Nota Lepid. Suppl.*, **4**, 81–85.

Spitzer, K., Novotný, V., Tonner, M. & Lepš, J. (1993). Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *J. Biogeogr.*, **20**, 109–121.

Ter Braak, C. J. F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.

Ter Braak, C. J. F. (1987). *CANOCO—a FORTRAN Program for Canonical Community Ordination.* TNO Institute of Applied Computer Science, Wageningen.

Thomas, C. D. (1991). Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biol. Conserv.*, **55**, 269–281.

Vidal, J. E. (1979). Outline of ecology and vegetation of the Indochinese peninsula. In *Tropical botany*, ed. K. Larsen & L. B. Holm-Nielsen. Academic Press, London, pp. 109–123.

Whitmore, T. C. (1975). *Tropical rain-forests of the Far East.* Oxford University Press, Oxford.

Whitmore T. C. & Sayer J. A. (1992). *Tropical deforestation and species extinction.* Chapman & Hall, London.