

VERTICAL AND HORIZONTAL HABITATS OF FRUIT-FEEDING BUTTERFLIES (LEPIDOPTERA) ON SIBERUT, MENTAWAI ISLANDS, INDONESIA

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Abstract. Continental islands harbor only fractions of mainland biota, which has potentially important consequences for the ecological processes affecting community structure. We assessed for the first time abundance, species richness, and vertical and horizontal niches of fruit-feeding butterflies of the Mentawai islands chain, which has been separated from Sumatra for more than 500 000 years. The study was carried out on Siberut, the Mentawai's largest and least disturbed island, using standard banana-baiting at three vertical (1m, 15m, and 30m) and two horizontal levels (natural and disturbed forest), expending an effort of 544 trap-days. Overall capture rates were similar to other SE Asian trapping studies but with only 20 observed (28 estimated) species, fruit-feeding butterfly species richness was only half of that of similar studies on the larger islands of Borneo or Sulawesi. Abundance and species richness did not significantly differ between natural and disturbed forest, however the four most abundant species (*Dichorragia nesimachus*, *Mycalesis maianeas*, *Mycalesis oresis* and *Neorina lowii*) had significantly different capture rates between forest types and vertical levels. Multidimensional scaling revealed distinct vertically and horizontally structured butterfly communities. In an interspecific comparison, there was a moderate correlation between geographic range size and habitat specificity in Satyrinae: species with wider geographic ranges had a lower proportion of individuals in natural forest compared with narrow-ranging species, as found in various similar studies. Overall, details of community organization on Siberut appeared to be relatively similar to that of better-known and more species-rich communities (Borneo or Sulawesi), with no evidence for larger vertical or horizontal niches on the island and similar abundances of common species.

Key words: density compensation, diversity, island ecology, land use, *Nymphalidae*, tropical rainforest.

INTRODUCTION

Geographical history and stochastic occurrences play a critical role in the species composition of islands (Diamond 1975, Thornton 1996). Islands usually support fewer species than mainlands (MacArthur & Wilson 1967; e.g., butterflies: Dapporto & Dennis 2009). Intrinsic dispersal and competitive ability of species, and the environmental characteristics of islands (e.g. climate, geography, humidity) determine the probability that species colonize and persist. It has often been postulated that lower species richness on islands goes along with broader niches (niche expansion) and increased density (density compensation, e.g. MacArthur *et al.* 1972). "Density compensation" describes the constant overall abundance of

ecologically comparable species (ecospecies) on islands, despite lower species richness (Gonzalez & Loreau 2009). It has been documented for birds by comparing abundances of individual species in mainland versus island populations (e.g. MacArthur *et al.* 1972, Blondel *et al.* 1988) or in habitat fragments (Cody 1983, Aleixo & Vielliard 1995, Dos & Boçon 1999). Density compensation and niche expansion have been interpreted as evidence for interspecific competition and ecological release in closely related species (Newton 1998, Sørensen 1998).

The vertical structure of tropical rain forests can be described as a complex of distinct vegetation layers (Pomeroy & Service 1986, Whitmore 1993, Schulze *et al.* 2001). Vertical "strata" differ in abiotic (temperature, humidity) conditions as well as in resource availability and predation levels, and thus

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provide a microhabitat gradient within a given locality. Studies on vertical stratification of butterflies have been previously conducted in various tropical regions (Asia: Schulze *et al.* 2001, Tangah *et al.* 2004, Fermon *et al.* 2005; South America: DeVries *et al.* 1997; Africa: Hill *et al.* 2001, Molleman *et al.* 2006).

Many authors have described differences in butterfly communities between disturbed and undisturbed sites at understory level (e.g., for Asia: Hill *et al.* 1995, Hamer *et al.* 1997, Beck & Schulze 2000, Hamer & Hill 2000, Willott *et al.* 2000, Dumbrell & Hill 2005; for Africa: Kremen 1992, 1994, Lawton *et al.* 1998; for the Neotropics: Barlow *et al.* 2007; for a useful review see Bonebrake *et al.* 2010). However, as butterflies are aerial organisms, a three-dimensionally-designed research approach would be more appropriate, especially when examining differences in community structure between habitat types.

In this study we recorded fruit-feeding butterflies three-dimensionally to investigate differences in butterfly communities between disturbed and undisturbed forest in a Southeast Asian tropical island, Siberut. The study is the first one of its kind from the Sumatran region. From biogeographical theory and earlier studies conducted in Borneo and Sulawesi, we expected to find 1) vertically and horizontally structured butterfly communities, 2) disruptions of the vertical organisation through disturbance, and we hypothesized that 3) these patterns would be influenced by broader vertical and horizontal niches compared with those on mainlands. We expected the latter to result in community patterns different from those of more speciose communities, such as those from the better studied Borneo and Sulawesi. Since several Siberut butterflies are endemic at species level, we were also interested in relationships between geographic range size and habitat specificity, as have been studied in several studies on speciose butterfly communities (e.g. Fermon *et al.* 2001, Hamer *et al.* 2003, Bobo *et al.* 2006, Waltert *et al.* 2011).

METHODS

Study area. Siberut lies at the northern end of the Mentawai island group, approximately 130 km off the west coast of Sumatra. The Mentawai Islands were separated from Sumatra as long as 0.5–1 mya (Whitten *et al.* 2000), or as recently as 18 000–29 000 years ago during the last glacial maximum in the Pleistocene (Meijaard 2003). Siberut has a total surface area of 4030 km² and an estimated population of 25 000. The natural vegetation of the island

is primarily composed of tropical moist broadleaf forest of the Dipterocarpaceae family (Hadi *et al.* 2009). However the environment is now facing the impact of extensive logging and intensifying agricultural activity (Fuentes 1996/7). Apart from work on primates (e.g. Waltert *et al.* 2008), there have been no extensive studies so far on the ecology of plant or animal communities on Siberut and the Mentawai Islands. As far as we know, there has been until now no ecological study of butterflies or arthropods and the only scientific literature on butterflies are on faunistics and taxonomy (Aoki *et al.* 1982, Tsukada *et al.* 1985, Tsukada 1991).

Our research was based on work carried out at the field station of the Siberut Conservation Project (SCP). SCP is run in collaboration by the German Primate Center (DPZ) and Bogor Agricultural University (IPB). The field station is located in the northern part of the island, in the Peleonan forest (1°01'34"S, 98°50'16"E). The Peleonan forest is the subject of a long-term international research and conservation program and consists of approximately 5000 hectares of mostly primary, lowland forest, but includes also coastal and peat-swamp forest and tiny local farms (Quinten *et al.* 2010). Most of the study area is hilly, with elevations ranging from 2 to 182 m above sea level. The forest area is drained by numerous small to medium-sized creeks and rivers (Hadi *et al.* 2009). A total of 93 tree species has been recorded in the region. The tallest tree measured was 56 m in height, while 73% of trees were in the height class of 6–20 m. Euphorbiaceae, Myrtaceae, Lauraceae, and Moraceae are the commonest tree families found on the site. At species level, species of the genera *Mallotus* and *Knema*, as well as *Baccaurea sumatrana*, were most dominant in all dbh (diameter at breast height) classes (Hadi *et al.* 2009).

Our trapping sites were situated along a transect within 2 km to the north-east of the field station (Fig. 1). The main human disturbance at the research site was small-scale logging and farming activities by local people, who grew bananas and cocoa near the study sites.

Vegetation structure. At each of the fourteen trapping sites, 10 x 10-m vegetation plots were used to sample and characterize the vegetation structure. Plots were centred on each site. In each square, the dbh of all trees equal to and greater than 5 cm were recorded. Trees with a dbh of 5–10 cm were defined as understory trees, and trees >10 cm dbh as canopy (over-

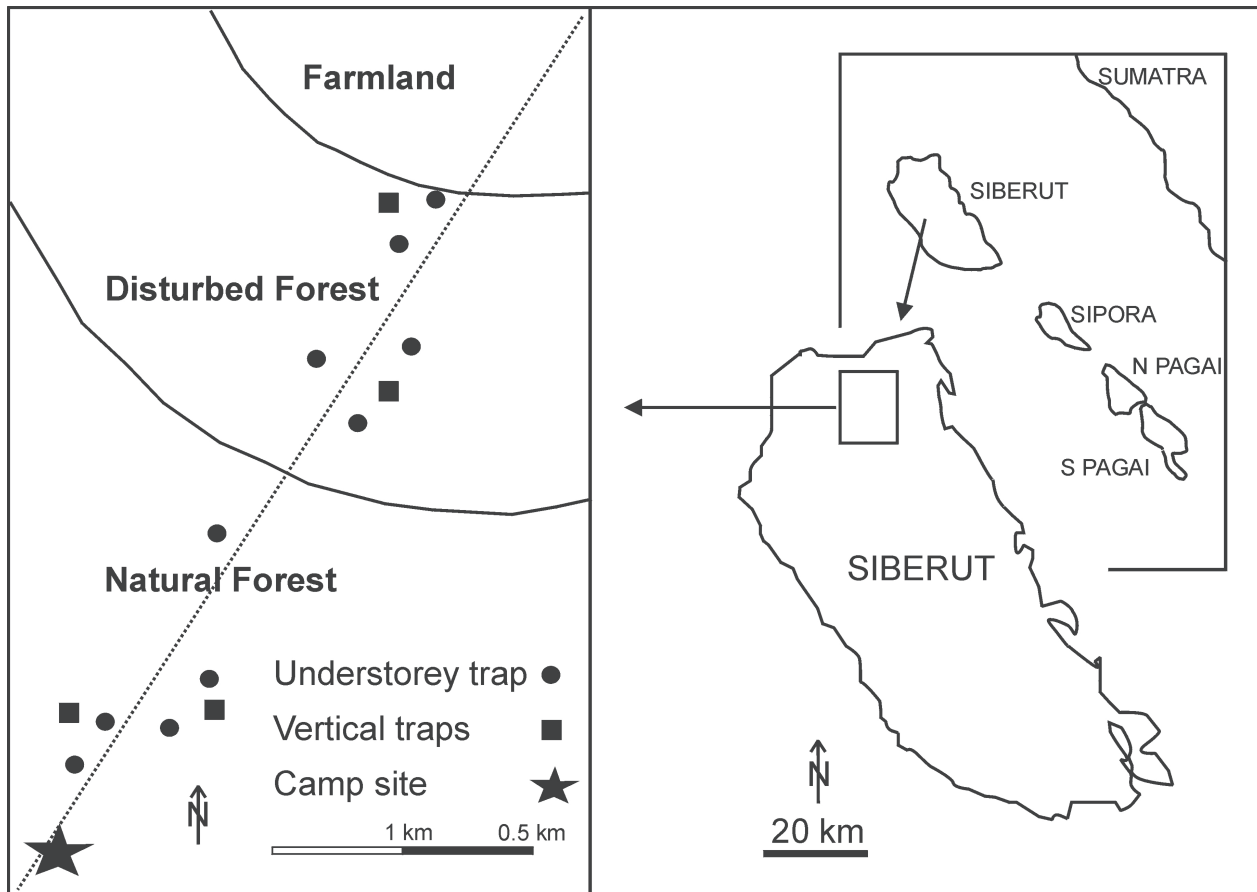


FIG. 1. Location of study area in Siberut (extracted from Hadi *et al.* 2009), and of the 14 trap locations (of single understory traps and of sets of 3 vertical traps) in natural and disturbed forest.

story) trees. Dbh was converted to basal area [m^2/ha] and calculated separately for understory and overstory trees.

Butterfly trapping. All trapping activities were conducted between 6 June and 17 July, 2009. Cylindrical gauze-traps (Rydon 1964) were used, in which a standard portion of mashed, fermenting banana was placed inside the trap to bait butterflies.

All traps were hand-made. Each trap was 30 cm in diameter and 60 cm long, and comprised a 30 x 30 cm plastified cardboard base. Each trap was stabilized by 2 rings (30 cm diameter), with 60-cm long white tissue connecting the rings to produce the cylindrical shape with the bottom open. Nylon strings were used to connect the bottom of the cylinder and the plastic cardboard, producing a 3-cm gap to allow the butterflies to enter. The bait was placed in the middle of the cardboard on a small plate.

Fourteen trapping sites were selected, of which seven were in primary forest and seven in disturbed forest, where there is currently farming and recently logging had been carried out. At four of these sites

(two primary forest and two disturbed forest sites) traps were established at different vertical heights. At each of these four trapping sites, a tree taller than 30 m was chosen in order to suspend traps at different heights. Traps were installed at ground level (1 m), in the midstory (15 m), and in the canopy (30 m), resulting in a total of $2 \times 2 \times 3 = 12$ traps at the four vertical trapping sites. Traps were placed for 32 non-rainy days and were checked for butterflies and rebaited every 24 hours, resulting in a total of 384 trap-days (12 traps x 32 days) at vertical trapping sites.

Of the other 10 trapping sites, five were in natural forest and five in disturbed forest. At these 10 sites, no traps were placed in the midstory or canopy, but only at understory level (1 m). These were left for 16 non-rainy days and were checked, sampled and rebaited every 24 hours, resulting in a total of 160 trap-days spent at the 10 understory sampling sites ($5 \times 2 \times 16$).

Butterfly identification. For field identification, most specimens trapped were preserved and given a

“specimen ID”, and if possible at least three individuals of each species were preserved for later identification. The preserved specimens were identified later in the laboratory of the Indonesian Institute of Sciences (LIPI). Trapped butterflies of known species identity were marked (to prevent recounting), and released. Species identification and geographic information was mainly based on the publications of Aoki *et al.* (1982), Tsukada *et al.* (1985), and Tsukada (1991). Taxonomic classification follows Wahlberg *et al.* (2009).

Statistical analysis. Differences in capture frequencies between natural and disturbed forest, and between the three vertical levels (1 m, 15 m, 30 m), were tested using the Chi-square test, based on the hypothesis that they are evenly distributed between habitats and vertical levels. Capture rates were tested for the whole nymphalid community, at subfamily as well as at species level.

The species richness of the butterfly community in each forest type was analyzed using EstimateS 7.52. Second-order Jackknife richness estimator (JACK2; Smith & van Belle 1984) was calculated to estimate the size of local species pools.

We also analyzed the species similarity of the butterfly communities in the understory traps and in the vertical trapping sites. Nonmetric multidimensional scaling was used to create a dissimilarity matrix among the different species types using the Bray-Curtis dissimilarity coefficient. Significant differences in community composition between vertical levels and forest types were obtained using ANOSIM.

RESULTS

Vegetation. Compared with the natural forest plots, those in disturbed forest had an overstory tree density that was reduced by an average of about 43%, and a total tree density reduced by *ca.* 42% (Table 1). Despite the average basal area being *ca.* 30% lower in disturbed compared with natural forest, there was no significant difference in basal area between habitat types, due to large variation between plots (Table 1).

The fruit-feeding butterfly fauna. A total of 244 fruit-feeding butterfly individuals belonging to 4 sub-families (Charaxinae, Limenitidinae, Pseudergolinae and Satyrinae, based on the taxonomy of Wahlberg *et al.* 2009), 14 genera, and 20 species were trapped (Table 2). Based on species richness estimators, JACK2, the local species pool was estimated to be 27.7 ± 1.73 species

All except one (morpho-)species were identified to species level. Most (eight) species had an Indomalayan distribution pattern, ranging from India to the Greater Sunda islands. The ranges of two species were even larger, extending northwards to Japan (*Melanitis phedima*) or southwards to Australia (*Dichorragia nesimachus*). The ranges of six species can be regarded as predominantly Southeast Asian, and two are found exclusively on the Mentawai Islands. For at least nine of these taxa, distinct subspecies have been described for the Mentawai Islands (Hanafusa 1993). The unidentified species belongs to the genus *Elymnias*. Its taxonomy is currently being investigated.

TABLE 1. Total number of trees (overstory and understory) enumerated, tree density, and mean basal area in 10 m x 10 m plots in natural and disturbed forest. Numbers in brackets are standard deviations. Statistics from Mann-Whitney U-test.

	Natural Forest (n = 7 plots)	Disturbed Forest (n = 7 plots)	Z	P
Overstory trees enumerated	44	32	-	-
Understory trees enumerated	25	19	-	-
Overstory tree density [ind/ha]	628.6 (75.6)	357.1 (190.2)	-2.47	0.013
Understory tree density [ind/ha]	457.1 (207.0)	271.4 (197.6)	-1.55	0.122
Total tree density [ind/ha]	1085.7 (177.3)	628.6 (111.3)	-3.09	0.002
Overstory basal area [m ² /ha]	49.1 (18.1)	34.5 (20.7)	-1.087	0.277
Understory basal area [m ² /ha]	1.82 (0.99)	1.12 (0.64)	-1.22	0.224
Total basal area [m ² /ha]	51.0 (18.5)	35.6 (20.8)	-1.087	0.277

TABLE 2: Individual numbers of fruit-feeding Nymphalidae species trapped at vertical trapping sites (three different heights), as well as in understory traps, in two forest types on Siberut, Indonesia. Also given is ranked geographic range size, based on our own classification (geographic information based on Aoki *et al.* (1982), Tsukada *et al.* (1985), and Tsukada (1991); 1 – endemic to Mentawai, 2 –Mentawai, Sumatra, Borneo, W Malay, 3 – Mentawai, Sumatra, Borneo, Palawan, 4 – Mentawai, Sumatra and eastward to Java, 5 – Mentawai, Sumatra and eastward to Wallacea) and that by Hamer *et al.* (2003). Lower rank indicates more widespread species.

	Rank (own classifica- tion)	Rank (Hamer <i>et al.</i> 2003)	Vertical Trap Sites						Understory Trap Sites		Total
			NF			DF			NF	DF	
			1 m	15 m	30 m	1 m	15 m	30 m			
Charaxinae (3 spp.)											
<i>Charaxes bernardus</i>	4	45	0	0	0	0	1	1	0	0	2
<i>Charaxes durnfordi</i>			0	1	0	0	0	0	0	0	1
<i>Prothoe franck</i>	3	45	5	0	0	1	0	0	3	1	10
Limenitidinae (5 spp.)											
<i>Lexias dirtea</i>	4	45	2	0	0	0	0	0	3	0	5
<i>Bassarona dunya</i>	3	27	2	0	0	0	0	0	2	0	4
<i>Bassarona teuta</i>	4	53	0	2	1	0	0	0	0	0	3
<i>Tanaecia visandra</i>	1		0	0	0	0	0	1	0	0	1
<i>Lebadea martha</i>	4	51	0	0	0	0	0	0	0	1	1
Pseudergolinae (1 sp.)											
<i>Dichorragia nesimachus</i>	4	56	3	12	5	2	5	0	5	2	34
Satyrinae (11 spp.)											
<i>Amathuxidia amythaon</i>	2	45	0	2	1	5	1	0	2	1	12
<i>Discophora necho</i>			0	0	0	1	0	0	0	0	1
<i>Zeuxidia amethystus</i>	2	38	0	0	0	0	0	0	2	0	2
<i>Elymnias nelsoni</i>	1		0	0	1	2	1	0	1	2	7
<i>Elymnias panthera</i>	4	18	0	0	2	1	1	4	0	2	10
<i>Elymnias spp.</i>			0	0	0	1	0	2	1	0	4
<i>Melanitis phedima</i>	5		0	0	0	8	0	1	1	1	11
<i>Melanitis zitenius</i>	5	55	0	0	0	1	0	0	0	0	1
<i>Mycalesis maianeas</i>	2	5	16	0	0	9	0	0	12	4	41
<i>Mycalesis orseis</i>	2	33	2	0	1	12	0	0	1	16	32
<i>Neorina lowii</i>	3	18	27	1	0	6	4	0	13	11	62
Total			57	18	11	49	13	9	46	41	244

Most individuals and species belonged to the Satyrinae subfamily, which contributed 183 (or 75% of total) individuals and eleven (or 55% of total) species. Second in abundance (but not species richness) was the Pseudergolinae subfamily with 34 (14%) individuals but only one species: *Dichorragia nesimachus*, followed by Limenitidinae (6% of indi-

viduals and 30% of species). The Charaxinae subfamily was least abundant with only 13 individuals recorded (5%), but was nevertheless represented by three (15% of total) species.

The commonest species was *Neorina lowii* (n = 62), representing about a quarter of all individuals, followed by *Mycalesis maianeas* (n = 41, 17%), *Dich-*

orrugia nesimachus (n = 34, 14%). and *Mycalesis orseis* (n = 32, 13%).

Differences between habitats. Overall numbers of trapped individuals were similar between natural forest (n = 132) and disturbed forest (n = 112) (Table 3; Chi-square test, $\chi^2 = 1.639$, df = 1, $P = 0.200$).

Total observed fruit-feeding butterfly species richness was identical in natural and disturbed forest (15 species). The species richness estimator, JACK2, showed a similar trend, indicating 20.81 ± 1.28 and 19.9 ± 1.41 species respectively.

Four of the 20 species had significantly different capture rates between forest types (Chi-square statistics for the nine species with at least seven individuals): *Dichorragia nesimachus*, *Mycalesis maianeas* and *Neorina lowii* showed significantly higher capture rates in natural forest than in disturbed forest, whereas *Mycalesis orseis* showed the opposite pattern.

In order to avoid potential bias in this analysis from possible shifts in vertical stratification between habitats (e.g. Fermon *et al.* 2005), an analysis was done exclusively using data from the vertical trapping sites. Frequency differences were identical and significant for *Dichorragia nesimachus* ($\chi^2 = 6.259$, df = 1, $P = 0.01$), *Mycalesis orseis* ($\chi^2 = 5.400$, df = 1, $P = 0.020$), and *Neorina lowii* ($\chi^2 = 8.526$, df = 1, $P = 0.004$). The distribution of *Mycalesis maianeas* was also similar but not significant at the 5% level ($\chi^2 = 1.960$, df = 1, $P = 0.162$).

At subfamily level, Limenitidinae and Pseudergolinae were found to have significantly different capture rates between natural and disturbed forest ($\chi^2 = 7.14$ and 7.53 , df = 1, $P = 0.008$ and 0.006 respectively, Table 3). Members of Satyrinae had either higher (*M. orseis*) or lower (*M. maianeas*, *N. lowii*) abundances in disturbed compared with natural forest, and no clear pattern was visible at subfamily level (Table 3). Furthermore, Charaxinae tended to be more common in natural forest, but this was not statistically significant.

With 65.2% (n = 86) or 86.6% (n = 97) of the butterflies found in natural and disturbed forest respectively, the proportion of Satyrinae was about equally high in both habitats. In contrast, with 18.9% (n = 25) of the natural forest butterflies, but only 6.8% (n = 9) of those in disturbed forest, the proportion of Pseudergolinae (through *Dichorragia*) differed considerably. The other two (less abundant) subfamilies Charaxinae and Limenitidinae, represented the remaining individuals (totaling 12.9% in natural forest and 5.4% in disturbed forest) in the count.

Based on nonmetric multidimensional scaling (NMDS) of fruit-feeding butterfly communities found in understory traps, there was a clearly visible distinction in community composition between natural and disturbed forest. We found significant differences in fruit-feeding butterfly community composition between natural and disturbed forest (ANOSIM; $R = 0.352$, n = 10, $P = 0.028$; see Fig. 2a)

TABLE 3. Total numbers of fruit-feeding-butterfly species and individuals trapped (only the four most abundant species were listed and statistically tested), in different habitats on Siberut island, Indonesia. Also given are abundances of subfamilies.

	Total	Habitat		χ^2	P
		Natural Forest	Disturbed Forest		
Total	244	132	112	1.64	0.2
All Charaxinae (3 spp.)	13	9	4	1.92	0.167 (N.S.)
All Limenitidinae (5 spp.)	14	12	2	7.14	0.008
All Pseudergolinae (1 sp.)	34	25	9	7.53	0.006
<i>Dichorragia nesimachus</i>	34	25	9	7.53	0.006
All Satyrinae (11 spp.)	183	86	97	0.661	0.416 (N.S.)
<i>Mycalesis maianeas</i>	41	28	13	5.49	0.019
<i>Mycalesis orseis</i>	32	4	28	18	<0.001
<i>Neorina lowii</i>	62	41	21	6.42	0.011

Vertical stratification. Abundance was generally highest at a trap height of 1 m, where 106 (68% of 157) individuals were trapped (only data from vertical trapping sites). At 15 m and 30 m, 31 (20%) and 20 (13%) individuals were found respectively. The distribution of numbers of individuals at different height levels did not differ between habitat types ($\chi^2 = 0.352$, $df = 2$, $P = 0.839$).

Of the 20 species sampled in the study, 70% or 14 species (species richness estimation based on JACK2: 18.9) were found at the lowest level. At midstory level, only 8 species (JACK2: 14.7) were found, while 10 species (JACK2: 16.8) were recorded at the canopy level (Table 2).

Based on NMDS scaling of Bray-Curtis dissimilarity coefficients from traps at different vertical heights, a distinction was visible between vertical levels but with some overlap due to a few exceptional traps. The species composition was significantly different between vertical strata (ANOSIM; $R = 0.3819$, $n = 12$ $P < 0.001$; see Fig. 2b).

At subfamily level, the capture rates of Pseudergolinae and Satyrinae were different between vertical levels ($\chi^2 = 7.53$ and 113.3 , $df = 1$, $P = 0.0048$ and $P < 0.001$ respectively). The trapping rates of Satyrinae decreased from 85 (1 m) to seven (15 m) and 11 (30 m) individuals. However, Pseudergolinae trapping rates were highest at 15 m (17 individuals) and lower at 1 m (5 individuals) and 30 m (5 individuals).

Three species had significantly different capture rates between vertical levels. *Dichorragia nesimachus* had a higher abundance at 15 m ($n = 17$) and 30 m ($n = 5$) than at 1 m ($n = 5$). *Neorina lowii* had a higher capture rate at 1 m than at 15 m ($n = 33$ and $n = 5$ respectively) and was absent at 30m. All 25 individuals of *Mycalesis maianeas* collected were found at the 1-m level.

Geographic range and habitat specificity. In an inter-specific comparison, there was no correlation between geographic range size and the proportion of individuals trapped in natural vs. disturbed forest (Spearman rank correlation coefficient $R = -0.096$, $P = 0.372$, $n = 14$ spp.), for which geographic range data was available through Hamer *et al.* (2003). The same analysis based on our own classification (Table 2) of geographic range sizes (including three more species) led to very similar results ($R = -0.142$, $P = 0.293$, $n = 17$ spp.).

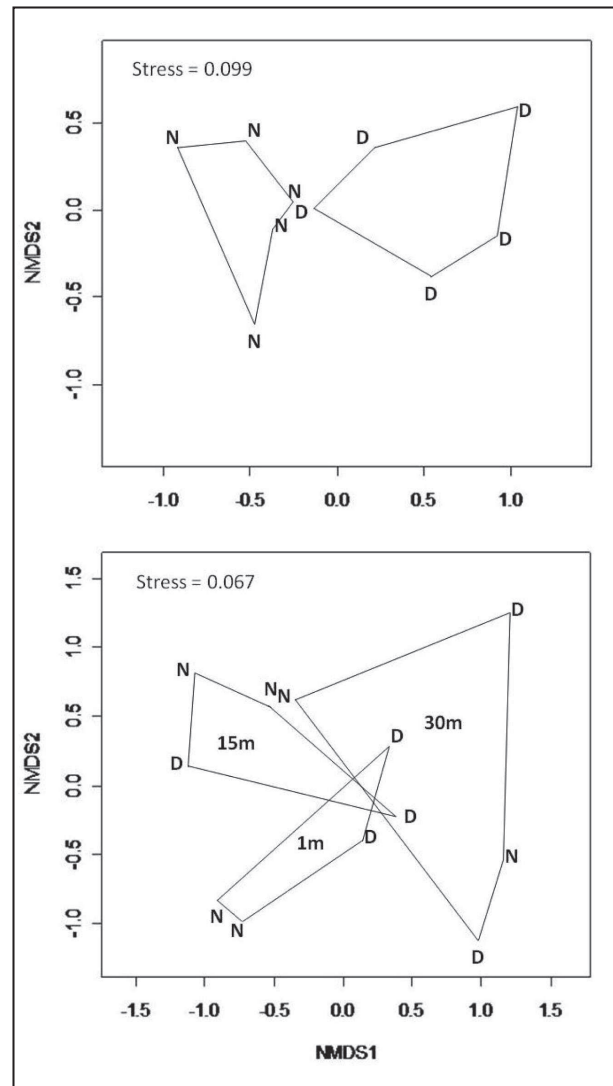


FIG. 2. Nonmetric multidimensional scaling (NMDS) of fruit-feeding butterfly communities of five natural forest (N) and five disturbed forest (D) understory trapping sites (a), and at three different trap heights (1 m, 15 m and 30 m) along the vertical strata of two natural forest (N) and two disturbed forest (D) sites (b). Compositional dissimilarity was based on the presence or absence of 20 species of fruit-feeding butterflies. Sites of the same habitat type (a) or vertical level (b) are connected by lines.

However, when analyzing Satyrinae separately, such a correlation was visible using our classification ($R = -0.586$, $P = 0.049$, $n = 9$ spp.), but not when using Hamer's ($R = -0.4320$, $P = 0.166$, $n = 7$ spp.); A similar analysis for the remaining species (Charaxinae/Limenitinae) did not show such a relationship ($R = -0.164$, $P = 0.378$, $n = 6$ spp., or $R = 0.129$, $P = 0.391$, $n = 7$ spp. respectively).

DISCUSSION

Overall abundance and species richness. The baseline trapping rate from natural forest understory reported in this study (0.67 ± 0.34 individuals per trap-day), was very similar to that from Sulawesi (0.71; Fermon *et al.* 2005), from the upper Amazon Basin (eastern Ecuador: 0.66; DeVries & Walla 2001), and within the range of those from Borneo (e.g. Schulze *et al.* 2001: 1.9; Hill *et al.* 2001 and Tangah *et al.* 2004: 1.1 – 1.7; Dumbrell & Hill 2005: 0.45; all from understory traps at 1 m at natural forest sites). However, trapping rates are influenced by trap design, frequency of visits, efficiency of the bait, and weather conditions during the sampling period. The relatively higher trapping rate of Schulze *et al.* (2001) compared with other studies may partly be due to more efficient sampling (more effective bait, visits twice per day). Compared with the other studies, the trapping rate on Siberut may be regarded as relatively similar, suggesting that overall abundance of fruit-feeding butterflies (across species) may also be similar to that of more species-rich communities of the Greater Sunda Islands and Sulawesi.

Abundances of the commonest species were also comparable to those of the very similar study conducted on Sulawesi (Fermon *et al.* 2005). On Sulawesi, the commonest species trapped in natural forest understory were *Lohora transiens*, *Lexias aetes*, and *Melantis velutina* (0.26, 0.11, and 0.09 individuals per trap-day respectively), constituting 64% of all trapped individuals in this (micro-)habitat. In our study, the commonest natural forest understory species were *Neorina lowii*, *Mycalesis maianeas*, *Prothoe franck*, and *Dichorragia nesimachus* (0.26, 0.19, 0.06, 0.06 individuals per trap-day respectively), representing 80% of all trapped individuals. Given this similar abundance distribution of common species, an overall comparable total abundance but a difference in species richness, on Siberut species of either medium and/or low abundance especially should have on average higher abundances than on Sulawesi. However, given the low sample size of the infrequent species this is difficult to substantiate. In addition, another thoroughly conducted trapping study on Sumatra would be necessary to be able to test such questions thoroughly.

As in most other studies on tropical forest arthropods, our study obviously failed to record all species potentially occurring at the study site. When accounting for survey effort and incomplete sampling, with 20 observed and up to 28 estimated species

(JACK2), the fruit-feeding butterfly fauna in our study area is certainly less diverse than those of local assemblages on Borneo and Sulawesi, (e.g. Hill *et al.* 2001, Schulze *et al.* 2001, and Fermon *et al.* 2005 report 54, 53 and 43 species respectively). Yet given that Siberut is only 0.5% of the size of Borneo and 1.3% of that of Sulawesi, fruit-feeding butterfly species richness is still remarkable, and indicates an overall very rich fruit-feeding community in the Sumatran (sub-)region.

Taxonomy and biogeography of Siberut fruit-feeding butterflies. Stochastic and historical factors (i.e. past climates, sea level changes) play a significant role in determining which species occupy islands and subsequently persist and whether biotic communities show characteristics of harmony/disharmony (Diamond 1975, Thornton 1996, Whittaker 1998). Of the 19 identified species of Nymphalidae, two are recognised Mentawaiian endemics, *Tanaecia visandra* and *Elymnias nelsoni*. All other species are known from the main island of Sumatra but at least seven represent distinct subspecies, endemic to the Mentawais (Aoki *et al.* 1982, Tsukada *et al.* 1985, Tsukada 1991, Hanafusa 1993). This degree of endemism is relatively lower than that of mammals (65% of mammal species are endemic) but similar to birds, which are also represented on the archipelago by at least one endemic species and twelve endemic subspecies (WWF 1982).

Vertical stratification. Similar to other vertical stratification studies, the trapping rate decreased considerably from 1m to the canopy (15 or 30 m) by about 63 and 76% respectively (decreases in Fermon *et al.* 2005: 56 and 52%; Schulze *et al.* 2001: 51 and 79%; Hill *et al.* 2001: 72% at 20 m). Also consistent with other studies, trapping rates between 15 and 30 m remained roughly similar but with a tendency to decrease with increasing height (e.g. Ecuadorian rainforest: DeVries *et al.* 1999, North Borneo: Dumbrell & Hill 2005, Sulawesi: Fermon *et al.* 2005). In accordance with abundance, species richness also decreased towards the canopy.

In contrast to our study, on Sulawesi and Borneo species richness was reportedly highest at midstory level, suggesting that at this level distinct vertical communities overlap (Schulze *et al.* 2001, Fermon *et al.* 2005). However comparisons are complicated since the relevant canopy heights in this study were lower than in Fermon *et al.* (2005) and Schulze *et al.* (2001), where sampling was done up to 50 m. The

higher upper canopy level of these two studies compared with this one also results in a larger spatial extent of what is considered “midstory”.

Of the subfamilies found in our study, only Satyrinae showed the clearest distinct preference for the lowest stratum, while no such clear relationship was found in Charaxinae and Limenitidinae. Pseudergolinae, represented by one species only (*Dichorragia nesimachus*), showed the highest abundance in the midstory level. Schulze *et al.* (2001) and Fermon *et al.* (2005) report a decrease in Satyrinae abundance from understory to canopy.

In species-rich butterfly communities, Charaxinae as a group, and especially the genus *Charaxes*, seem to prefer midstory (10-20) and/or canopy (30-50 m) levels (e.g. Schulze *et al.* 2001, Fermon 2002, Fermon *et al.* 2005). In our study, however, this subfamily had their highest abundance at the 1-m level, but this pattern was produced mainly by six individuals of the genus *Prothoe*, which differs from the colorful strong-bodied *Charaxes* by more drab coloration and a slender body, typical of more lower forest strata. There are two *Charaxes* species in our study, *C. bernardus* and *C. durnfordi*, which were captured at higher strata only (*c.f.* Schulze *et al.* 2001, Fermon 2002, Fermon *et al.* 2005).

At species level, only two species showed significant differences in abundance between vertical levels: *Dichorragia nesimachus* was generally found at mid-story to canopy level, the selection of the vertical strata by the species being very similar to that found by Fermon (2005). The second species, *Mycalesis maianeas*, was sampled only in the understory level, again similar to Fermon *et al.* (2005).

Disturbance is known to modify or influence vertical stratification of butterfly communities in tropical forests (e.g. DeVries 1988, Schulze *et al.* 2001, Fermon *et al.* 2005). Previous studies have shown that species which in natural forest appear to be confined to the canopy may be trapped in disturbed forest also at lower levels, suggesting that canopy species treat light gaps and forest edges as canopy (DeVries 1988).

Apart from the above mentioned patterns at subfamily and species level, at the community level clear distinct vertical strata were observed (ANOSIM; Figure 2b). This was in agreement with Fermon *et al.* (2005) who also found a clearly distinct community composition between strata in natural forest and a disruption of this pattern in disturbed forest.

Differences between forest types. Our vegetation analysis showed that tree densities in natural forest were significantly higher than in disturbed forest. Overall, figures of basal area in natural forest were consistent with previous vegetation surveys in Siberut (Hadi *et al.* 2009: 58.2 m²/ha for dbh class ≥10 cm, also from Peleonan forest; Whitten 1982b, from the Paitan forest: 47 m²/ha, dbh ≥15 cm; for peat swamp, Whitten 1982b reports average basal areas of 23 m²/ha, dbh ≥15 cm). This might indicate that our study sites were largely representative for natural and disturbed forests on Siberut.

Our study indicated that Limenitidinae and Pseudergolinae showed significantly higher abundances in natural forest than in disturbed forest (Table 3), while there were no such differences in the other two subfamilies, Charaxinae and Satyrinae. Four out of nine species analyzed were found to have significantly different capture rates between habitat types. These results are consistent with those of Fermon *et al.* (2005), whose study on Sulawesi can be considered as a template for our study, where the two different *Mycalesis* spp. (*M. horsfieldi* & *M. itys*) also showed higher abundances in natural compared with disturbed forest. *Dichorragia nesimachus* (also recorded by Fermon *et al.* 2005) showed a similar trend.

In our study, species richness was similar between habitats (Table 3). Studies on the effect of tropical forest disturbance on butterfly species richness have shown mixed results, from no differences in species diversity and/or richness between natural and disturbed forest (Hill *et al.* 2001, Borneo), to higher (Hill *et al.* 1995, Buru island, Indonesia; Beck & Schulze 2000, Borneo), or even lower species diversity and/or richness (Hamer *et al.* 1997, Sumba island, Indonesia; Willott *et al.* 2000, Borneo; Fermon *et al.* 2005, Sulawesi) in natural than in disturbed forest. Koh (2007) reviewed 20 studies on the effects of land use (with different gradients and types of human disturbance) on butterfly communities, concluding that there has been no consensus among researchers, and suggesting that spatial scale was the major factor influencing the inconsistent results. Some other surveys also suggested that research at a smaller spatial scale tends to result in higher species richness at disturbed sites, while at larger spatial scales the opposite trend is observed (Hamer & Hill 2000, Hill & Hamer 2004). Another reason for such inconsistencies could of course also be the descriptions of what is “secondary” or “disturbed” being inconsistent across studies.

Conclusion. We studied the ecology of fruit-feeding butterflies at one field site on Siberut island, where we sampled different forest types (natural vs. disturbed forest) and vertical habitats. The response of Siberut's butterfly community to human disturbance and vertical habitat patterns were very similar to that found in other studies (e.g. DeVries *et al.* 1997, Schulze *et al.* 2001, Fermon *et al.* 2005, Molleman *et al.* 2006). The fruit-feeding butterfly fauna of these forests may be regarded as a representative subset of that of the Greater Sunda Islands. While we cannot claim to have an overview on the island's overall butterfly community, the analysis of our local data set suggests that fruit-feeding butterfly species diversity on Siberut may be much lower than on some larger Indonesian islands (Greater Sunda/Wallacea), but also that the composition of the community as well as niche differentiation may be very similar. In addition, abundance rank patterns also seem to be similar to those of more species-rich communities (Table 2). Although the current data do not allow us to draw clear inferences, some density compensation may still occur, manifested in the slightly higher abundances of species of medium or low abundance rank compared with communities richer in species. It is still unclear whether such characteristics in community structure result in a higher "robustness" of Siberut's butterfly fauna towards anthropogenic disturbance. At species level, Siberut butterflies reacted to disturbance in a very similar fashion to those in other studies, suggesting that habitat niches of fruit-feeding butterflies are a fairly deterministic trait across the Greater Sunda Islands.

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