The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age

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Abstract. Concomitant with the rapid loss of tropical mature forests, the relative abundance of secondary forests is increasing steadily and the latter are therefore of growing interest for conservation. We analysed species richness of fruit-feeding nymphalid butterflies in secondary forest fragments of different age and isolation and in mature forest at the eastern margin of the Lore Lindu National Park in Central Sulawesi, Indonesia. From April to August 2001 we collected 2322 individuals of fruit-feeding butterflies, belonging to 33 species. Butterfly species richness increased with succession, but was significantly higher in mature forests than in all types of secondary forest. Isolation of the forest fragments did not have a significant effect on butterfly species richness in the range of distances (up to 1700 m) studied. Rather it appeared to affect only a few species. Species richness of endemic species was higher than of non-endemic species. Although endemic species were most diverse in mature forests, many species captured were restricted to secondary forests. Our results show that mature forest is essential for the conservation of nymphalid butterflies and for the endemic species in this area. However, considering the relatively large number of species found in these rather small habitat islands, secondary forest fragments, especially older successional stages, can be taken into account in conservation efforts and thus contribute to the preservation of tropical biodiversity on a landscape scale.

Introduction

The rapid destruction of tropical primary forests is one of the driving factors for the global loss of biodiversity (Sala et al. 2000) and is particularly devastating in areas characterized by a high degree of endemism (Hill et al. 1995). Moreover, remaining areas of tropical rainforest are threatened by the expansion of agricultural land-use resulting from human population growth (Ocana et al. 1992; Pimentel et al. 1992). As a consequence, human-managed

habitats presently dominate tropical landscapes (Pimentel et al. 1992; Schelhas and Greenberg 1996).

Recently, ecological studies in the tropics have focused on agricultural landscapes (e.g., Perfecto and Snelling 1995; Perfecto and Vandermeer 2002, Klein et al. 2002), or on gradients from native forest to highly modified habitats (Pinheiro and Ortiz 1992; Lawton et al. 1998; Beck et al. 2002). In particular secondary forests, which constitute an increasing part of tropical landscapes (see Brown and Lugo 1990), appear to bear a high potential for maintaining at least a certain part of tropical diversity (Lawton et al. 1998; Intachat et al. 1999; Raman 2001). This potential may be of particular importance in southeast Asian rainforest regions, where secondary forests arise as a result of shifting cultivation (Brown and Lugo 1990). Created by the cycles of cultivation, they build up a gradient of different successional stages. The importance of dynamic changes in habitat structure for forest inhabitants and endemics is little known. Many forest inhabitants, including many endemic species, are specialists, depending on particular abiotic and biotic habitat characteristics, such as low light-intensity, special food plants etc. (Janzen 1988; Singer and Ehrlich 1991). Therefore they respond very sensitively to environmental perturbations (Spitzer et al. 1993; Hamer et al. 1997). Habitat characteristics, such as vegetation and plant community structure, change during succession (Southwood et al. 1979; Brown and Southwood 1987), thereby influencing insect communities (Southwood et al. 1979). Although not arising from fragmentation, secondary forests often appear like small habitat fragments, surrounded by a matrix of agricultural land-use systems. Taking into account the equilibrium theory of island biogeography (Mac Arthur and Wilson 1967), the colonization of these habitat islands should depend on the distance to the nearest source habitat. Therefore, proximity to mature forest should be an important factor influencing the fragments' biodiversity.

The present study examines biodiversity of secondary forest fragments using butterflies, which are suited for biodiversity investigations for several reasons: They are a well-studied insect group and relatively easy to record and to identify. Accordingly, butterflies have often been used as indicators of habitat quality (Steffan-Dewenter and Tscharntke 1997; Schulze et al. 2002, 2004). The guild of fruit-feeding butterflies, belonging to the family Nymphalidae, is especially suited as an indicator for tropical rainforest diversity (Daily and Ehrlich 1995). We investigated the diversity of fruit-feeding butterflies in secondary forests fragments in the vicinity of the Lore Lindu National Park in Central Sulawesi, Indonesia. We addressed the following questions: (1) Does butterfly species richness differ among different successional stages of forests? (2) Does butterfly species richness decrease with increasing distance of the fragments to mature forest? (3) Do secondary forests contribute to the conservation of butterflies, in particular endemic species?

Methods

The study area

The Indonesian island Sulawesi is situated in the northern part of the Malayan archipelago, east of the Wallacea line. Due to its former geographical history, the island is characterized by a high percentage of endemic species (Whitten et al. 1988). The study area was located at the south-eastern border of the Lore Lindu National Park in Central Sulawesi, ca. 75 km southeast of the province capital Palu. The park covers an area of 229,000 ha of lowland and montane rainforest. It is a local biodiversity hotspot (e.g. 83% of Sulawesi's endemic avifauna can be found here (World Wildlife Fund 1981), and was declared as World Heritage Site by UNESCO. We conducted this study in the Napu Valley, which is situated at an altitude of 1100 m above sea level in the lower montane zone. Shifting cultivation in the Napu Valley caused a mosaic of different land-use systems, largely comprising coffee and cacao plantations, annual crops (e.g. maize), and rice fields. Secondary forest fragments of different successional stages were embedded in this agricultural landscape.

Study design

We sampled butterflies belonging to the guild of fruit-feeding Nymphalidae at altogether 28 sites. Twenty-four of these sites were secondary forest fragments of three different successional stages (each with eight replicates) and with different distances to the margin of the continuous mature forest of the National Park. Additionally four plots in the mature forest inside the park were surveyed. We used the term mature forest instead of primary forest, because this area presumably had already faced some anthropogenic influence before our study was conducted. We used a GPS to quantify distances of the forest fragments from the park. Study sites covered a distance gradient from 100 to 1700 m. All sites were located at an altitude of 1100–1200 m.

Secondary forests fragments were classified as follows: (1) Young secondary forests: approximately 5 years old, with vegetation consisting of one tree layer, predominantly pioneer trees (such as *Macaranga*), and perennial herbs (Musaceae, Zingiberaceae) with a height of about 5 m. (2) Intermediate secondary forests: about 15 years old, with no clear differentiation between understorey and canopy-layer, a shrub-layer was well developed. (3) Old secondary forests: about 30 years old, with vertical stratification into canopy (with a height of between 15 and 20 m) and ground vegetation. All secondary forest fragments had a size of approximately 1–2 ha to exclude area effects on butterfly diversity. (4) Mature forest sites: Situated about 300–700 m from the margin in the interior of the park. Numerous medium-sized and several emergent trees formed a multi-layered canopy with a maximum height of between 30 and 40 m.

Butterfly sampling

Butterflies were captured live, in traps baited with rotten mashed bananas. A detailed description of the trap design can be found at Daily and Ehrlich (1995). Traps were suspended from tree branches with string about 1.5 m above the ground. To prevent ants from entering the traps, branches touching the traps were removed and the string was prepared with some sticky glue. At each location five traps were set up along a 100 m trail. The traps were placed at a distance of 5 m from the trail. At all study sites traps were checked and baited daily. Trapping was conducted from the end of April until the end of August 2001. Butterflies were sampled until species accumulation curves for single forest sites approximately reached saturation. Due to damaged traps, and bait being removed by monkeys or squirrels, some sites required more trapping days than others. Therefore the number of trapping days ranged between 10 and 40 days per study site. Number of samples per site was not associated with habitat type (one-way ANOVA: $F_{3,24} = 2.07$, $n = 28$, $p = 0.1305$).

In the beginning, butterflies were killed for identification, but later all individuals could be identified in the field and released immediately afterwards. To avoid pseudoreplicates all butterflies were marked with a unique number on their forewing. Identification of the butterflies was carried out with the use of photographs of reference specimens from the Natural History Museum (London) and by using color plates of d'Abrera (1985).

Habitat parameters

To quantify habitat characteristics of the different forest types four parameters were measured at all study sites:

Vascular plants up to a height of 1.3 m were collected in 10 plots of 1 m^2, located alternately along the trails. Plant individuals were sorted to morphospecies (Beattie and Oliver 1994) and their abundance was recorded. In four plots of 25 m^2, situated along the trail, all woody plants higher than 1.5 m were counted and their circumference was measured at breast height. Because one of the mature forests sites had been cut before the stem diameter was measured, the number of repetitions for this habitat parameter is only 27. By using these data we calculated for all study sites the mean tree density as well as the mean stem diameter and the coefficient of variation (standard deviation/arithmetic mean) of the stem diameter as an indicator of structural habitat diversity.

Furthermore the percentage of shaded ground vegetation in 10 plots of 1 m^2 was estimated at midday. The mean percentage of shade was assumed to reflect the canopy density of single sites.

Statistical analyses

We estimated total species richness of butterflies using the estimator ACE (abundance-based coverage estimator of species richness) of the program

EstimateS v.5.0.1 (Colwell 1997) and EstimateS v.6.0b1 (Colwell 2000). This programm extrapolates to the absolute number of species which could be expected in the respective site . The abundance-based estimator ACE is especially suited for data in which some species are very common and others very rare (Colwell 1997), resembling our samples.

Percentages of saturation values were calculated, using the proportion of the number of captured species and estimated species for each site. To analyse differences in butterfly species richness, endemic species richness, and the habitat parameters between the four types of forest we used one-way analyses of variance (ANOVA).

Multiple regressions were used to test for a relationship between butterfly species richness and the habitat parameters age and isolation. We removed parameters from the analysis by backward selection until only significant ones remained. We used logistic regressions, to analyse the likelihood of forest fragment colonization by single species in relation to isolation and shading of the forests.

Percentages were arcsine-square-root-transformed, and distances to the forest were square-root-transformed (Sokal and Rohlf 1995). Statistical analyses were performed using the software Statgraphic Plus 3.0 for Windows (Manugistics 1997) and Statistica 5.5 (StatSoft 1999).

Results

Habitat parameters

Species richness of vascular plants in the understorey layer was highest in old secondary forests and significantly lower in young secondary forests and mature forest (Figure 1a). The structural diversity of the forests, quantified by the coefficient of variation (CV) of the stem diameter, was highest in old secondary forests and significantly lower in the young secondary forests and in mature forest (Figure 1b). A similar pattern appeared with the mean stem diameter: it was significantly higher in old than in young secondary forests, and intermediate in medium-aged and mature forest sites ($F_{3,23} = 6.96$, $n = 27$, $p < 0.01$). The four forest types did not differ significantly in their tree density ($F_{3,23} = 3.50$, $n = 27$, $p < 0.03$). The percentage of shaded ground vegetation increased steadily with the age of forest types Figure 1c), thus we were able to use this parameter as a measurement for the successional stage of the forests. Because most of the habitat parameters were highly intercorrelated (Table 1) we used only the degree of shaded ground vegetation and the distances between secondary forests and mature forest for analysing effects of age and isolation on butterfly diversity by multiple regressions.
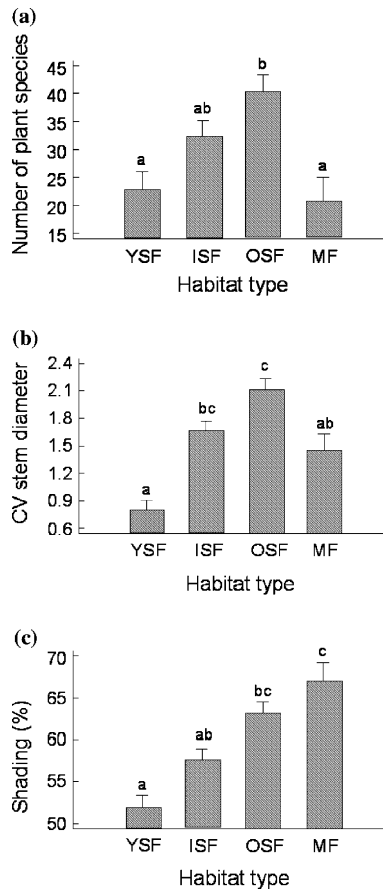
Figure 1. Habitat parameters for the four different forest types: (a) Species richness ($=$ number of species) of vascular plants in the understorey layer ($F_{3,24} = 6.77$, $n = 28$, $p < 0.01$). (b) Coefficient of variation (CV) of the stem diameter ($F_{3,23} = 24.0$, $n = 27$, $p < 0.0001$). (c) Mean percentage of shaded ground vegetation ($F_{3,24} = 14.20$, $n = 28$, $p < 0.0001$). Arithmetic means and standard deviation are given. All illustrated graphics are the results of a one-way ANOVA. Different letters indicate significant differences. Abbreviations: YSF, young secondary forest; ISF, intermediate secondary forest; OSF, old secondary forest; MF, mature forest. The abbreviations apply for all following graphs.

Butterfly species richness

We captured 2322 individuals of fruit-feeding nymphalid butterflies, belonging to 33 species. These species were subdivided into six subfamilies (Satyrinae, Morphinae, Limenitinae, Charaxinae, Nymphalinae and one individual belonging to the Apaturinae; Table 2). Many of the species were only captured once per site. One Satyrinae, *Melanitis leda*, was found at all study sites and constituted in single sites up to 80% of all individuals.

Table 1. Correlation matrix[a] of the different habitat parameters[b].

	Species number of ground vegetation	CV[c] of stem diameter	Tree density[d]	Mean stem diameter (cm)[d]	Distance (m) to mature forest[e]
CV[d] of stem diameter	0.49**				
Tree density[c]	−0.20	−0.33			
Mean stem diameter (cm)[c]	0.61***	0.46*	−0.59**		
Distance (m) to mature forest	0.5**	0.31	0.07	0.97	
Shading (%)	0.21	0.67***	−0.43*	0.37	−0.11

[a](r_p) Pearson correlation coefficient.
[b] Significance levels *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, $n = 28$.
[c]CV, coefficient of variation.
[d] $n = 27$.
[e] $n = 24$.

Species richness of Nymphalidae differed significantly between the different forest types, and was highest in mature forest. Intermediate secondary forest had significantly higher species richness than young, but not than old secondary forests (Figure 2).

Of the 33 recorded species 21 were endemic to Sulawesi. Altogether 18 endemic species were recorded in secondary forests, and nine of them were restricted to this habitat type, whereas three of altogether 13 endemic species were only found in mature forest. Of the non-endemic species three were restricted to mature forest and four were only found in secondary forest. In general, species richness of endemic species was higher than species richness of non-endemics ($F_{3,24} = 4.3$, $n = 28$, $p < 0.05$). Mature forests contained a significantly higher species richness of endemic butterflies than all types of secondary forest (Figure 3a). Richness of non-endemic species was significantly higher in mature forests than in young secondary forests, but not higher than in intermediate or old secondary forests (Figure 3b).

The number of recorded butterfly species and the estimated total number of butterflies species were significantly correlated ($r = 0.58$, $n = 28$, $p < 0.001$). Mean species saturation of all study sites was $73.3 \pm 16.34\%$. In a simple linear regression model there was no correlation neither between saturation values and the degree of shading ($r = 0.29$, $n = 28$, $p = 0.138$) nor saturation values and isolation ($r = 0.02$, $n = 28$, $p = 0.94$).

Habitat parameters and butterfly diversity

The results of the multiple regression analysis showed, that butterfly species richness was significantly related to age of forests (quantified by the percentage of shading) (Figure 4a), whereas the distance to the mature forest did not have

Table 2. Butterfly species recorded in the different forest types.

Subfamily	Genus	Species	Young secondary forests 5–9		Intermediate secondary forests 7–13		Old secondary forests 7–12		Mature forests 12–18		Probability of colonization
		Range of species number:	Individuals	Sites	Individuals	Sites	Individuals	Sites	Individuals	Sites	
Apaturinae	Helcyra	celebensis*	–	–	1	1	–	–	–	–	
Charaxinae	Charaxes	affinis*	23	6	25	8	17	6	11	4	
		mars*	–	–	–	–	–	–	2	2	
		nitebis*	1	1	2	2	2	2	8	2	
	Polyura	cognata*	–	–	–	–	–	–	1	1	
Limenitinae	Athyma	libnites*	–	–	3	3	1	1	–	–	
	Cyrestis	strigata*	–	–	1	1	2	2	2	1	
	Dichorragia	nesimachus	–	–	–	–	–	–	6	3	
	Dophla	evelina	–	–	–	–	–	–	1	1	
	Euthalia	amanda*	–	–	1	1	1	1	–	–	
	Lexias	aeetes*	7	2	2	2	6	2	43	4	↑ I
	Pseudergolis	avesta*	–	–	5	1	2	2	5	4	↑ SH, ↓ I
Morphinae	Amathusia	phidippus	5	5	8	7	14	6	7	4	
	Amathuxidia	plateni*	–	–	–	–	–	–	3	1	
	Discophora	bambusae*	1	1	2	2	8	3	2	2	↑SH
	Faunis	menado*	7	3	5	3	4	2	–	–	
Nymphalinae	Hypolimnas	anomala	–	–	1	1	–	–	–	–	
		diomea*	4	4	1	1	5	2	–	–	
	Rinopalpa	polynice	–	–	–	–	–	–	1	1	
	Symbrenthia	hippalus*	–	–	–	–	1	1	–	–	

Satyrinae

		Specimens	Sites	Specimens	Sites	Specimens	Sites	Specimens	Sites	Colonization
Elymnias	hicetus*	4	4	9	3	38	5	19	4	↓ I
Lethe	europa	38	8	33	7	38	5	–	–	↑ I
Lohora	sp.*	3	2	30	5	48	6	77	4	↑ SH
Melanitis	leda	318	8	510	8	379	8	19	4	
	phedima	62	7	65	8	84	8	13	4	
	pyrrha	1	1	3	2	61	3	–	–	↓ I
	velutina	1	1	5	4	6	3	20	4	↑ I
Mycalesis	janardina	16	5	25	6	51	8	4	4	↑ SH
	perseus	2	1	3	3	2	2	–	–	↑ SH
Ypthima	gavalisi*	–	–	1	1	2	2	–	–	
	nynias*	1	1	–	–	–	–	–	–	
	risompae*	2	1	4	3	3	2	–	–	↓ SH
Zethera	incerta*	–	–	1	1	–	–	2	2	

The total number of butterfly specimens and the total number of sites with records for each forest type are given. Based on significant results of logistic regressions, for each species the probability of forest colonization in relation to shading and isolation is given.
*Endemic species: I, Isolation; SH, Shading; ↑, increases with; ↓, decreases with.
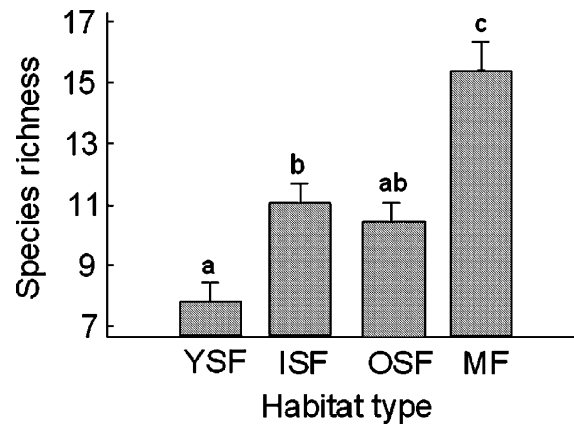
Figure 2. Butterfly species richness (= number of species) of the four different forest types: (One-way ANOVA: $F_{3,24} = 14.05$, $n = 28$, $p < 0.0001$). Arithmetic means and standard deviation are given. Different letters indicate significant differences. For abbreviations see Figure 1.
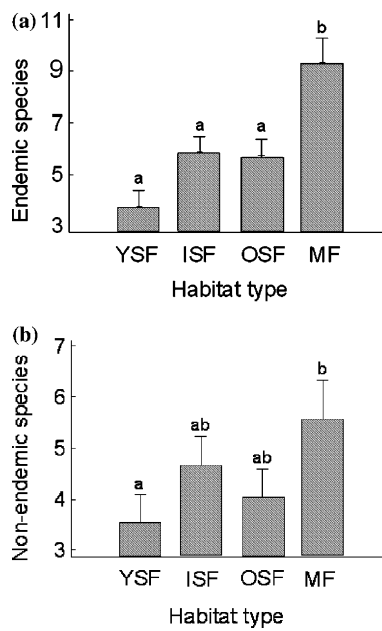

Figure 3. Species richness (= number of species) of endemic butterflies (a) and non-endemics (b) of the four different forest types. (One-way ANOVA: (a) $F_{3,24} = 8.26$, $n = 28$, $p < 0.005$, (b) $F_{3,24} = 3.72$, $n = 28$, $p < 0.05$.) Arithmetic means and standard deviation are given. Different letters indicate significant differences. For abbreviations see Figure 1.

any effect on species richness (Figure 4b). No significant relationship was found between species richness of ground vegetation and butterfly diversity.
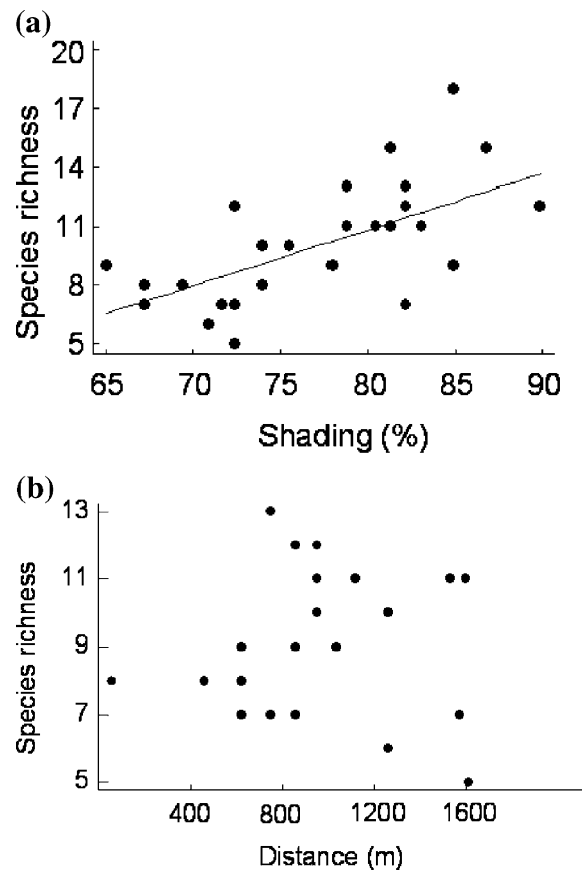
Figure 4. Butterfly species richness (= number of species) (a) in relation to shading (percentage of shaded ground vegetation) of secondary forest fragments. (Simple regression: $F_{1,22}$ = 5.94, r_2 = 0.46, n = 24, p < 0.05, y = 1.82 + 0.08* arcsin$\sqrt{}$ x) and (b) in relation to distance of secondary forest fragments to mature forests. (Simple regression: $F_{1,22}$ = 0.0, r^2 = 0.00, n = 24, p = 0.97, y = 9,37 – 0.0017*$\sqrt{}$ x).

In species-specific analyses with logistic regressions five species showed an increasing probability of occurence with increasing shading of ground vegetation. For three species a decreasing probability of occurence in forest fragments was found with increasing isolation. In contrast, one species seemed to prefer sunny sites and three species even preferred isolated forest fragments (Table 2).

Discussion

Our results suggest that secondary forest fragments harboured a lower species richness of fruit-feeding butterflies than mature forests. Furthermore we found that butterfly species richness increased during succession. In contrast to

expectations, distance to the mature forest did not affect species richness of nymphalid butterflies within the range of distances (100–1700 m) studied.

We found the species richness of fruit-feeding Nymphalidae to be related to the percentage of shading in forests, thereby supporting the suggestions by Lewis (2001) that light regime can influence diversity. Butterflies in particular react very sensitively to changes in light level. Insect diversity is known to depend on the microclimate (Perfecto and Vandermeer 1996), which itself is determined by the density of the canopy (Beer 1987). A higher degree of insolation leads to a higher temperature and lower humidity (Perfecto and Snelling 1995), which is expected often to have a negative effect on insect diversity in the tropics. Since the shading of ground vegetation, regulated by the canopy density, appeared to be a reliable measure for age of succession (Kennard 2002) these results support the hypothesis that diversity increases during succession (Brown and Southwood 1987).

Compared with mature forest, secondary forest exhibited lower butterfly species richness. Certainly the difference in habitat area between mature forest and secondary forest fragments contributed to the difference in species number. The investigated plots of the mature forest belonged to a continuous large area, whereas the secondary forests were fragments of a rather small size. The effects of habitat size on diversity have often been shown (Daily and Ehrlich 1995; Steffan-Dewenter and Tscharntke 2000). Additionally edge effects may have affected species numbers in small fragments.

A further explanation for the reduced species richness in secondary forests may be human impact. Anthropogenic habitats are usually less complex and contain fewer species than natural ones (Hill et al. 1995; Beck and Schulze 2000; Ricketts et al. 2000). A high structural variability, which is character-istic for late successional stages, may support a more diverse community (Brown and Hutchings 1997). In our study, the structural heterogeneity (quantified by the coefficient of variation of the stem diameter of trees) similarly increased with age of the secondary forests, whereas in mature forest it was relatively low. As a climax community mature forests seem likely to show low structural variability, due to their vegetational composition dominated by mature trees.

In this study, distances of up to 1700 m from fragments to mature forests (as is characteristic for the study area) had no effect on butterfly species richness. Shahabuddin and Terborgh (1999) suggested that fragments with a distance of up to 1 km from the source habitat may not experience a reduction of butterfly colonization. The majority of our studied fragments had a distance of less than 1 km to the mature forest, which might explain the missing effect of isolation on butterfly species richness in this study. Additionally, the effect of isolation can be influenced by the quality of the matrix in which the fragments are embedded (Ricketts 2001). The sur-rounding landscape can act as an additional habitat for forest inhabitants, and thus minimize the effect of isolation and associated extinctions. In our study we observed migration of butterflies to adjacent shaded coffee and

cacao plantations. These land-use systems may provide additional habitats for some Nymphalidae. In contrast, open areas or agricultural fields with little shadow may not provide adequate microclimatic conditions for species adapted to extremely shady environments and therefore may act as a barrier (Saunders et al. 1991). As colonization probability of three species decreased or increased with distance to mature forest respectively, community structure of butterflies may still change with increasing isolation (Lovejoy et al. 1986; Shahabuddin and Terborgh 1999). Moreover, larger distances to mature forest than those studied here can be expected to greatly affect butterfly communities (e.g. Ricketts 2001).

Conclusion

Biodiversity hot spots, such as the Indonesian island Sulawesi, which contain a high number of endemic species, often experience a rapid rate of destruction and should be of priority for conservation (Myers et al. 2000).

Although our results affirm the high value of natural habitats, such as mature forest, for biodiversity, the number of species found in the rather small secondary forest fragments was unexpectedly high. Moreover, although endemic species were most diverse in mature forest, the high number of endemic species only found in secondary forests allows the conclusion that these habitats are of great importance as additional habitats. Thus, the conservation value of secondary forest fragments should be taken into account, at least for the guild of fruit-feeding Nymphalidae. We conclude that in addition to the undisputable need for conservation of primary forests, even small fragments of secondary forests may contribute to the conservation of tropical biodiversity on a landscape scale.

Acknowledgements

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